Sustained attention to spontaneous thumb sensations activates brain somatosensory and other proprioceptive areas

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ABSTRACT

The present experiment was designed to test if sustained attention directed to the spontaneous sensations of the right or left thumb in the absence of any external stimuli is able to activate corresponding somatosensory brain areas. After verifying in 34 healthy volunteers that external touch stimuli to either thumb effectively activate brain contralateral somatosensory areas, and after subtracting attention mechanisms employed in both touch and spontaneous-sensation conditions, fMRI evidence was obtained that the primary somatosensory cortex (specifically left BA 3a/3b) becomes active when an individual is required to attend to the spontaneous sensations of either thumb in the absence of external stimuli. In addition, the left superior parietal cortex, anterior cingulate gyrus, insula, motor and premotor cortex, left dorsolateral prefrontal cortex, Broca's area, and occipital cortices were activated. Moreover, attention to spontaneous-sensations revealed an increased connectivity between BA 3a/3b, superior frontal gyrus (BA 9) and anterior cingulate cortex (BA 32), probably allowing top-down activations of primary somatosensory cortex. We conclude that specific primary somatosensory areas in conjunction with other left parieto-frontal areas are involved in processing proprioceptive and interoceptive bodily information that underlies own body-representations and that these networks and cognitive functions can be modulated by top-down attentional processes.

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1. Introduction

Humans have the ability to direct and concentrate their attention to focus and enhance bottom-up processes of either a somatosensory/external or proprioceptive/internal nature (Buschman & Miller, 2007; Petersen & Posner, 2012; Sarter, Givens, & Bruno, 2001; Treisman & Gelade, 1980). Attention towards particular somatic stimuli selectively enhances domain-specific cortical representations that probably are determinant for their conscious representation (Farb, Segal, & Anderson, 2013; Jones et al., 2010). For example, a form of insight meditation practice requiring sustained awareness of subtle somatic sensations spontaneously arising from different body parts produces an increased parieto-occipital gamma activity, a marker for enhanced sensory awareness, and an increased top-down attentional control over such increased perceptivity (Cahn, Delorme, & Polich, 2010). Similarly, somatic focusing of attention during mindfulness practice optimizes the modulation of alpha rhythms that play a key role in filtering inputs to primary sensory cortex before the arrival of a stimulus (Kerr et al., 2011).

Tactile attention biases the processing of selected stimuli relevant features by amplifying somatosensory cortex responses (Romo, Brody, Hernández, & Lemus, 1999). Moreover, compared to unattended loci, sustained attention to a body part results in enhanced processing of tactile stimuli at that location, suggesting that the activity within modality-specific somatosensory areas (SI and SII) is modulated by tactile-spatial attention (Sambo & Forster, 2011). Likewise, visual (Ishai, Haxby, & Ungerleider, 2002; Kosslyn et al., 1993; Lee, Kravitz, & Baker, 2012) and auditory cortex activation (Zatorre & Halpern, 2005) during mental imagery requires overlapping top-down mechanisms involved in attention and memory (Ishai et al., 2002).

Even though attention to externally driven bottom-up stimuli processing and multisensory integration has been amply explored (Héroux, Walsh, Butler, & Gandevia, 2013; Johansen-Berg & Lloyd, 2000; Koelewijn, Bronkhorst, & Theeuwes, 2010; Maravita, Spence, & Driver, 2003; Ruff, 2013; Sambo & Forster, 2011), somatosensory processing has not been studied in absence of external stimulation, motion, or retrieval of encoded percepts. Thus, most studies refer either to external bottom-up (i.e. somatosensory) input stimuli

or to memory related (i.e. visual or auditory recall of percepts) enhancement by top-down attentional mechanisms and do not directly address proprioceptive bottom-up stimuli underlying the knowledge of one's own body; a fundamental self-awareness feature that relies on both somatosensory and proprioceptive inputs that are actively and continuously mapped on tacit or implicit body representations (Bermúdez, 1998).

Body representation notions as brain features were first introduced by Head and Holmes (1911) a century ago and evolved over the years to distinguish a *body image* (a cognitive representation of the body based on stored knowledge and sensory experience underlying perceptual judgments) from a *body schema*, (a largely unconscious proprioceptive sketch intimately related to body movements) (De Vignemont, 2010; Gallagher, 2005). The role of bottom-up somatosensory mechanisms arising from skin receptors and resulting in primary somatosensory brain activations are relatively well established (for reviews see Mountcastle, 2005; Romo & Salinas, 2001). Moreover, the relation between such sensory processing to subsequent body representations has been shown to be distorted by tactile (Longo & Haggard, 2011) and visual information (Bruno & Bertamini, 2010; Héroux et al., 2013; Longo & Sadibolova, 2013; Taylor-Clarke, Jacobsen, & Haggard, 2004). Likewise, the proprioceptive sense of position of body parts relative to each other and to the body as a whole is initiated by receptor activity in the muscles, tendons, joints and skin, and is centrally processed by multimodal neurons in the posterior parietal cortex (Adrian & Umrath, 1929; Grigg, 1994; Kammers, van der Ham, & Dijkerman, 2006; Proske & Gandevia, 2012). It seems that both somatosensory inputs and proprioceptive information are integrated into body representations that are rather distorted in normal individuals and highly susceptible to experimental manipulations (Blanke & Metzinger, 2009; Ehrsson, 2007; Héroux et al., 2013; Lackner, 1988; Longo & Haggard, 2011; Stock, Wascher, & Beste, 2013). In this sense, body representations arise by the integration of multisensory inputs (Blanke, 2012; Longo, Azañón, & Haggard, 2010; Tsakiris, 2010) contributing to embodiment and self-consciousness features (Arzy, Thut, Mohr, Michel, & Blanke, 2006; Lou et al., 2004).

Here we hypothesize that tactile attention directed to focus upon a single target among stronger stimuli, can enhance sub-threshold information at the attended location and reveal, in the absence of external stimuli, movement or recall, brain areas required in the representation of onés own-body. In order to prove this hypothesis we will show that somatosensory and other proprioceptive brain areas can be activated solely by directing and sustaining attention to punctual body-parts in absence of external stimuli and thereby demonstrate that top-down attentional mechanisms can enhance the perceptivity of subtle and otherwise sub-threshold (i.e. unconscious) proprioceptive/internal bottom-up stimuli associated to specific body parts.

2. Materials and methods

2.1. Subjects

After standard exclusion criteria for functional magnetic resonance imaging (fMRI) research were applied, 37 healthy volunteers participated in the study (16 female and 21 male, mean age 35.58 years, SD 7.97, 14 left handed and 23 right handed). Subjects were evaluated with digital versions of the Symptom Checklist 90 and Edinburgh Inventory to exclude psychological and/or psychopathological symptoms, and to evaluate handedness (Derogatis, 1994; González-Santos, Mercadillo, Graff, & Barrios, 2007; Oldfield, 1971). Subjects were considered a "case" when scoring higher than the norm population on the Global Severity Index (GSI), or,

alternatively, when the subscale cutoff is exceeded in scores on by two or more subscales (Derogatis, 1983). According to this criteria as adapted to Mexican gender-specific norms (de la Rubia & Bravo, 2011) target symptom caseness was defined by a T-score at or above 63. Subjects with an Edinburgh Inventory score >24 were considered as right-handed (Oldfield, 1971). All subjects gave informed consent for the experimental procedure, and the protocol had IRB approval.

2.2. Experimental protocol

Brain activation was examined during covert focused attention directed towards the right or left thumb under two experimental conditions: (a) *External-Stimulus Condition* (manual caressing of either thumb with a 2-cm sponge brush at 1–2 Hz and stimulation aftereffect) and (b) *Spontaneous-Sensation Condition* in absence of any external stimulation (Fig. 1). Resting periods without attention tasks separated both experimental conditions. Subjects were instructed to focus their attention on either thumb during the two experimental conditions and to abstain from moving it during the whole experiment. The instructions emphasized that, in the absence of touch stimuli, the subjects should focus their attention on the spontaneous sensations arising from either thumb rather than visualizing or imagining this body part. The protocol consisted of a block design paradigm alternating between focusing of attention towards the *External-Stimulus* of either thumb (60 s blue block in Fig. 1) or focusing of attention towards *Spontaneous-Sensation* of the same body part in the absence of external stimuli (60 s yellow block in Fig. 1). The length of the blocks was decided after a pilot study where the response indicated that the subjects started to feel clear and distinct sensations 20–40 s after the instruction. The *External-Stimulus* block was further divided into a 30 s *Touch-Stimulus Condition* (shown as a dark-block in Fig. 1) and a 30 s *Stimulation Aftereffect Condition* (shown as a light-blue block in Fig. 1). *External-Stimulus* and *Spontaneous-Sensation* conditions were separated by 30 s resting intervals to ensure no overlapping brain activity. Each run lasted 540 s and consisted of three epochs. One epoch was a 180 s sequence of Touch-Stimulus, Stimulation Aftereffect, Resting, *Spontaneous-Sensation*, and Resting. While in the scanner, the subjects received a previously agreed one-word instruction ("attention" or "rest") via MRI compatible audio equipment (NordicNeuroLab, Bergen, Norway) directing them to focus their attention on the target thumb, or to rest. Subjects had their eyes closed during the whole experiment. Right and left thumbs were run in separate procedures. The order of right or left initial target thumb was random. All runs occurred in a single visit.

Additionally we acquired 12 min of resting state fMRI (i.e. 6 min before and 6 min after the attentional task runs), ~5 min of high-resolution structural 3D-T1-weighted images, and 36 directions diffusion tensor imaging. The total scanning time was less that 60 min. During the scanning an examiner closely monitored the subject's thumb to ensure there was no motion. If there was any perceptible movement the run was discarded. Only six runs from 3 subjects (all right handed) were discarded due to involuntary thumb movement, and the results presented were obtained from the remaining 34 subjects.

2.3. Magnetic resonance imaging

fMRI imaging was performed on a 3.0T GE MR750 instrument (General Electric, Waukesha, WI) using a 32-channel head coil. Functional imaging included 35 slices, acquired using a T2*-weighted EPI sequence with TR/TE 3000/40 ms, a 64×64 matrix and 4-mm slice thickness, resulting in a $4 \times 4 \times 4$ mm^3 isometric
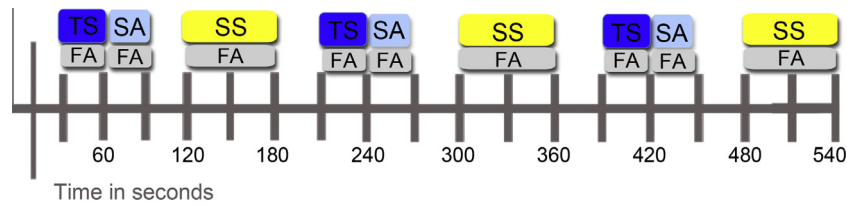
Fig. 1. Single run experimental paradigm for either thumb. *Touch-Stimulus* (TS, in dark-blue), Stimulation-Aftereffect (SA, in light-blue) and *Spontaneous-Sensation* (SS, in yellow). Focusing attention (FA, in gray) was required during every condition. No attentional task was required during resting periods between conditions (gaps). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

voxel. High-resolution structural 3D-T1-weighted images were acquired for anatomical localization (resolution of $1 \times 1 \times 1$ mm^3, TR = 2.3 s, TE = 3 ms) covering the whole brain. The images were acquired with an acceleration factor = 2.

2.4. Image processing and statistical analyses

2.4.1. Preprocessing

Functional image datasets were processed and analyzed with FSL 4.1.5 (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl) (Smith et al., 2004). The following preprocessing steps were applied: The skull and other non-brain areas were extracted from the anatomical and functional scans using the script brain extraction tool (BET) of FSL, motion correction using MCFLIRT (Jenkinson & Smith, 2001) with 6 degrees of freedom, spatial smoothing using a Gaussian kernel of FWHM 6 mm, mean-based intensity normalization, and non-linear highpass temporal filtering. Extracted brains of all participants were linearly registered into the brain-extracted MNI152 template using a linear spatial transformation function.

Statistical analysis was performed with FMRI Expert Analysis Tool using FMRIB's Improved Linear Model (FEAT FILM) Version 5.98 with local autocorrelation correction contrasts with a significance threshold criterion of $Z > 2.3$ with a cluster significance threshold of $p < 0.05$ corrected for multiple comparisons (Woolrich, Ripley, Brady, & Smith, 2001) and using the canonical hemodynamic response function (HRF) convolved with a function longer in duration (e.g., a longer boxcar function that is 60 s in the case of spontaneous sensation) to model the entire duration of the block and its time derivative as basic functions. The model included the following regressors with their corresponding HRF and their temporal derivatives: *Touch-Stimulus* and *Spontaneous-Sensation* as well as stimulation-aftereffect per thumb, with motion parameters controlled for in the model. The *Touch-Stimulus* regressor was modeled to fit a transient response curve in accord with previous somatosensory habituation reports (Klingner, Nenadic, Hasler, Brodoehl, & Witte, 2011; Moulton, Keaser, Gullapalli, & Greenspan, 2005) where somatosensory cortex activation peaked around 6 s after the onset of the stimulation and then exponentially returned to baseline for the rest of the block. In this manner it was ensured that only the touch-related processes were identified and measured. Only the responses obtained for *Touch-Stimulus* and *Spontaneous-Sensation* of each thumb were assessed. Unless otherwise specified, all activations, correlations, and contrasts had a significance threshold criterion of $Z > 2.3$ with a cluster significance threshold of $p < 0.05$ corrected for multiple comparisons (Friston & et al., 1994).

2.4.2. First-level fMRI analysis

First-level fMRI analysis of single subject data was performed with FMRI Expert Analysis Tool using FMRIB's Improved Linear Model (FEAT FILM) Version 5.98 with local autocorrelation correction (Woolrich et al., 2001) to identify those regions that increased

blood oxygen level dependent (BOLD) signal intensity for each of the two conditions relative to baseline.

2.4.3. Mid and higher-level analysis

To find out which brain regions are specifically involved during the process of attending to either thumb in each subject, a mid-level analysis was carried out using a fixed-effects model, which ignores cross-session/subject variance. Finally, to identify activations at the group-level related to these attention processes we conducted the analysis using FLAME (FMRIB's Local Analysis of Mixed Effects) and a voxel threshold of $p < 0.05$ and one-tailed t-testing (Worsley, 2002).

2.4.4. PPI connectivity analysis of BA 1/2 and BA 3a/3b

After having identified the involvement of the specific primary somatosensory cortices, (i.e. BA 1/2 and BA 3a/3b, see results), during sustained attention to either *Touch-Stimulus* or *Spontaneous-Sensation*, we performed a psychophysiological interaction (PPI) analysis (Friston et al., 1997; O'Reilly et al., 2012) to distinguish brain regions that showed significantly stronger covariation with BA 1/2 and BA 3a/3b during sustained and focused attention to *Touch-Stimulus* or *Spontaneous-Sensation*. The coordinates of the peak voxels from the random effect analysis comparing focusing to *Touch-Stimulus* vs. *Spontaneous-Sensation* (see results) were used to serve a landmark for the individual seed voxels. A region of interest (ROI) covering a sphere with a diameter of three voxels was searched around the peak voxel in BA 1/2 (−56, −24, −34) or BA3a/3b (−42, −12, 32). The time series of each ROI were then extracted, and a PPI regressor was calculated as the element-by-element product of the mean corrected activity of this ROI and a vector coding for the differential task effect of focusing to *Touch-Stimulus* versus focusing to *Spontaneous-Sensation*. The PPI regressors reflected the interaction between the psychological variable (focusing to *Touch-Stimulus* versus focusing to *Spontaneous-Sensation*) and the activation time course of BA1/2 or BA3a/3b. The individual contrast images reflecting the effects of the PPI on other brain areas were subsequently subject to a one-sample t-test. The results of the group analysis identified brain regions that showed increased activity during focusing to *Touch-Stimulus* versus focusing to *Spontaneous-Sensation* when the activity in BA1/2 or BA3a/3b was high. Statistic images were thresholded using clusters determined by $Z > 2.3$ and a cluster significance threshold (corrected for multiple comparisons) of $P < 0.05$ for the identification of brain areas that showed significant functional connectivity with the selected ROI.

Cortical reconstruction was performed with Freesurfer suite (http://surfer.nmr.mgh.harvard.edu/) (Dale, Fischl, & Sereno, 1999). The names of the brain regions reported were derived from the Jülich histological atlas (Eickhoff et al., 2007; Geyer, Schormann, Mohlberg, & Zilles, 2000) and the corresponding coordinates from the MNI152 template. In a separate analysis the subject's individual activations for each condition were correlated with the Edinburgh Handedness scores.

3. Results

3.1. First-level analysis

Sixty-eight runs (34 right thumb and 34 left thumb) from 34 subjects were included in the analysis. Fig. 2 shows that, compared with the resting task-free condition (neither external touch-stimuli nor spontaneous sensations), focusing of attention on *Touch-Stimulus* on each thumb produced a robust contralateral cortical activation where the peak MNI coordinates for the right thumb (Fig. 2B) were found in the left primary somatosensory cortex (BA2: $X = -56$ mm, $Y = -26$ mm, $Z = 34$ mm) and for the left thumb (Fig. 2A) in the right primary somatosensory cortex (BA1: 58, −18, 48). In addition, there was activation of the contralateral secondary somatosensory cortex (SII: −48, −30, 20) and right inferior parietal lobule (BA40: 68, −28, 30) for the right thumb stimulation, and secondary somatosensory cortex (SII: −56, −20, 18), right inferior parietal lobule (BA39: 58, −60, 20), and of the left secondary somatosensory cortex (SII: −56, −20, 18) for the left thumb (Fig. 2A and B). Coordinates of peak activation for this and all subsequent contrasts are shown in Table 1.

Compared with the resting task-free condition, focusing attention on *Spontaneous-Sensation* of the right thumb (Fig. 2D) showed a group activation of left parietal lobe (PL: −26, −48, 26), bilateral secondary somatosensory cortices (SII: 34, 2, 20 and −42, −2, 12), anterior cingulate cortex (BA32: −18, 14, 28) and right insula (BA13: 38, 10, 2). Focusing attention on *Spontaneous-Sensation* of the left thumb (Fig. 2C), showed activations in the left primary somatosensory cortex (BA3a: −46, 4, 16), left premotor cortex (BA6: −56, 10, 42), and left Broca's area (BA44: −50, 6, 8).

Since a left parieto-frontal activation common to all conditions was observed in the first-level analysis of the right handed subjects, we included a statistically suitable sample of the 14 left handed individuals to test if this group would presented a right lateralized parieto-frontal activation. After comparing all conditions between right- and left-handed groups only one significant difference was found, namely a positive correlation between right-handed individuals (Edinburgh scores >24) and *Z*-mean scores of left primary somatosensory cortex (BA1/2: −56, −18, 36) and left inferior parietal cortex (BA39: −54, −56, 20) area when the left thumb was externally stimulated ($r = 0.62$ and $p = 9.4e-05$, for peak coordinates see Supplementary Material and Fig. S1). In view of this result, we considered both groups as statistically not different regarding the *Spontaneous-Sensation* Condition.

Next, to eliminate the attention mechanisms common to both conditions and to distinguish the brain regions involved solely during *Touch-Stimulus* or *Spontaneous-Sensation* for either thumb, we contrasted them (i.e. *Touch-Stimulus > Spontaneous-Sensation*) using a voxel threshold at $p < 0.05$. Fig. 3 shows inflated left and right hemisphere brain images with activations for the respective contrasts. For the right thumb, contralateral posterior primary somatosensory cortex (BA2: −56, −24, 34) and right inferior parietal lobule (BA40: 70, −36, 22) were more active during *Touch-Stimulus* (blue clusters in Fig. 3B) while bilateral anterior primary somatosensory cortex (BA3a: 34, −14, 32 and −38, −14, 30), right premotor cortex (BA6: 16, −20, 52), left Broca's area (BA44: −42, 12, 10), right superior parietal cortex (BA7a: 24, −54, 52) and bilateral visual cortex (BA18: 36, −88, 8 and −22, −78, 22) were more active during *Spontaneous-Sensation* (yellow clusters in Fig. 3B). For the left thumb contralateral posterior primary somatosensory cortex (BA1: 58, −16, 48), bilateral inferior parietal cortex (BA40: 68, −42, 22 and −60, −26, 32) and right insula (BA13: 40, −8, 2) were more active during *Touch-Stimulus* (blue cluster in Fig. 3A) while only left anterior primary somatosensory cortex (BA3b: −44, −18, 42), left premotor cortex (BA6: −22, −28, 60) and left visual cortex (BA18: −24, −82, −4) were more active during *Spontaneous-Sensation* (yellow clusters in Fig. 3A).

3.2. Mid and higher-level analysis

A mid-level analysis for each subject was performed in order to further identify the brain regions involved during both *Touch-Stimulus* and *Spontaneous-Sensation* regardless of thumb laterality. This analysis was carried out at an individual level in order to average the right and left thumb contrasts and eliminate the particular thumb laterality mechanisms and attention processes involved. It was performed using a fixed-effects model, which ignores cross-session/subject variance. The data obtained from each subject was then used in the higher-level contrasts.

Using the data obtained from the mid-level analysis a higher-level analysis was performed at the group level. The higher-level contrast *Touch-Stimulus > Spontaneous-Sensation* (blue clusters in Fig. 4A) resulted in differential activations in left primary somatosensory cortex (BA1/2: −56, −24, 34) and the right temporoparietal junction (BA40: 52, −20, 16). The reverse contrast *Spontaneous-Sensation > Touch-Stimulus* (yellow clusters in Fig. 4A) showed differential activations in left primary somatosensory cortex (BA 3a/3b: −42, −12, 32), left motor (BA4: −16, −28, 56)
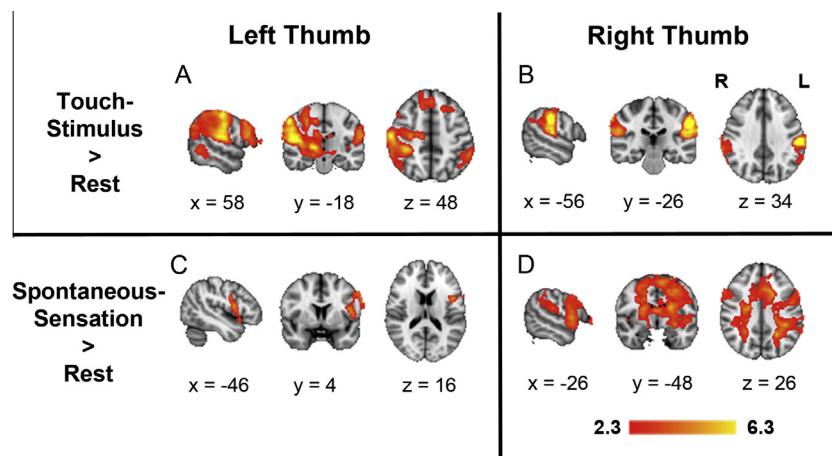

Fig. 2. Lower-level analysis: overall activations associated with focusing of attention during the different phases of the paradigm. (A) Focusing attention on *Touch-Stimulus* to the left thumb. (B) Focusing attention on *Touch-Stimulus* to the right thumb. (C) Focusing attention on *Spontaneous-Sensation* of the left thumb. (D) Focusing of attention on *Spontaneous-Sensation* of the right thumb. All activations, correlations, and contrasts had a significance threshold of $Z > 2.3$, with a cluster significance threshold of $p < 0.05$ (corrected for multiple comparisons). Images are presented in radiological convention and mapped to the MNI-152 template.

Table 1
Significant activation for all experiments.

Contrast	Anatomical location	Peak		
		x	y	z
Lower level				
Right thumb				
TS > rest[A]	Ba2 L, SI L	−56	−26	34
	Ba2 L, SII L, IPL L	−48	−30	20
	Ba40, IPL R	68	−28	30
SS > rest[A]	PL L	−26	−48	26
	SII R	34	2	20
	SII L	−42	−2	12
	Ba32, ACC	−18	14	28
	Ba13 R	38	10	2
SS > TS[B]	Ba2 L, SI	−56	−24	34
	Ba40 R, IPL R	70	−36	22
SS > TS[B]	Ba3a R, SI R	34	−14	32
	Ba3a L, SI L	−38	−14	30
	Ba6 R	16	−20	52
	Ba44 L	−42	12	10
	Ba7a R, SPL R	24	−54	52
	Ba18 R	36	−88	−8
Left thumb				
TS > rest[A]	Ba1 R, SI R	58	−18	48
	SII	−56	−20	18
	Ba39 R, IPL R	58	−60	20
	SII L	−56	−20	18
SS > rest[A]	Ba3b L, SI L	−46	4	16
	Ba6 L	−56	10	42
	Ba44 L	−50	6	8
TS > SS[B]	Ba1 R, SI L	58	−16	48
	Ba40 R, IPL R	68	−42	22
	Ba40 L, IPL L	−60	−26	32
	Ba13 R	40	−8	2
SS > TS[B]	Ba3b L, SI L	−44	−18	42
	Ba6 L	−22	−28	60
	Ba18 L	−24	−82	−4
Higher level				
TS > SS[B]	Ba1/2 L, IPL L, OP1 L	−56	−24	34
	Ba40 R, IPL R	52	−20	16
SS > TS[B]	Ba3a/3b L, SI L	−42	−12	32
	Ba4 L	−16	−28	56
	Ba6 L	0	12	44
	Ba7a L, SPL L, Precuneus	−22	−66	40
	Ba9 L, DLPC L	−42	8	22
	Ba13 L	−34	16	10
	Ba18	−24	−78	22
	Ba32, ACC	−4	12	46
	Ba44 L	−40	8	26

Peak activations for the lower- and higher-level analysis conditions. TS: *Touch-Stimulus*, SS: *Spontaneous-Sensation*, R: right, L: left, Ba: Brodmann area, PL: parietal lobe, IPL: inferior parietal lobule, SPL: superior parietal lobule, SI: primary somatosensory cortex, SII: secondary somatosensory cortex, OP: operculum, ACC: anterior cingulate cortex, DLPC: dorsolateral prefrontal cortex.

[A] Cluster threshold $z > 2.3$, $p < 0.05$.
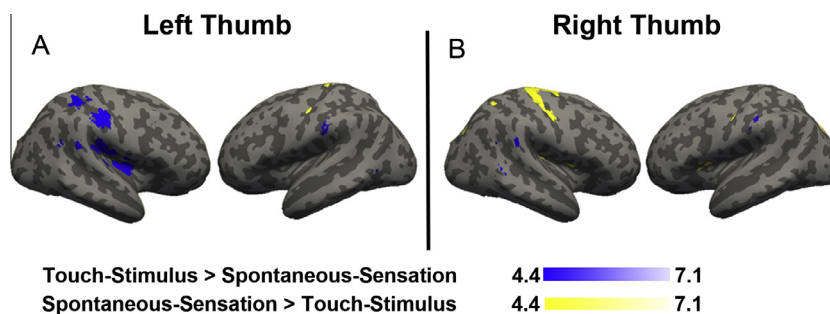[B] Voxel threshold at $p < 0.05$.

Fig. 3. Significant activations for the contrasts between *Touch-Stimulus* and *Spontaneous-Sensation* for left and right thumbs. (A) Inflated left and right hemispheres showing significant activations for the left thumb. (B) Inflated left and right hemispheres showing significant activations for the right thumb. Blue clusters: significant activation for the contrast *Touch-Stimulus > Spontaneous-Sensation*. Yellow clusters: significant activation for the contrast *Spontaneous-Sensation > Touch-Stimulus*. All contrasts are using voxel thresholding at $p < 0.05$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
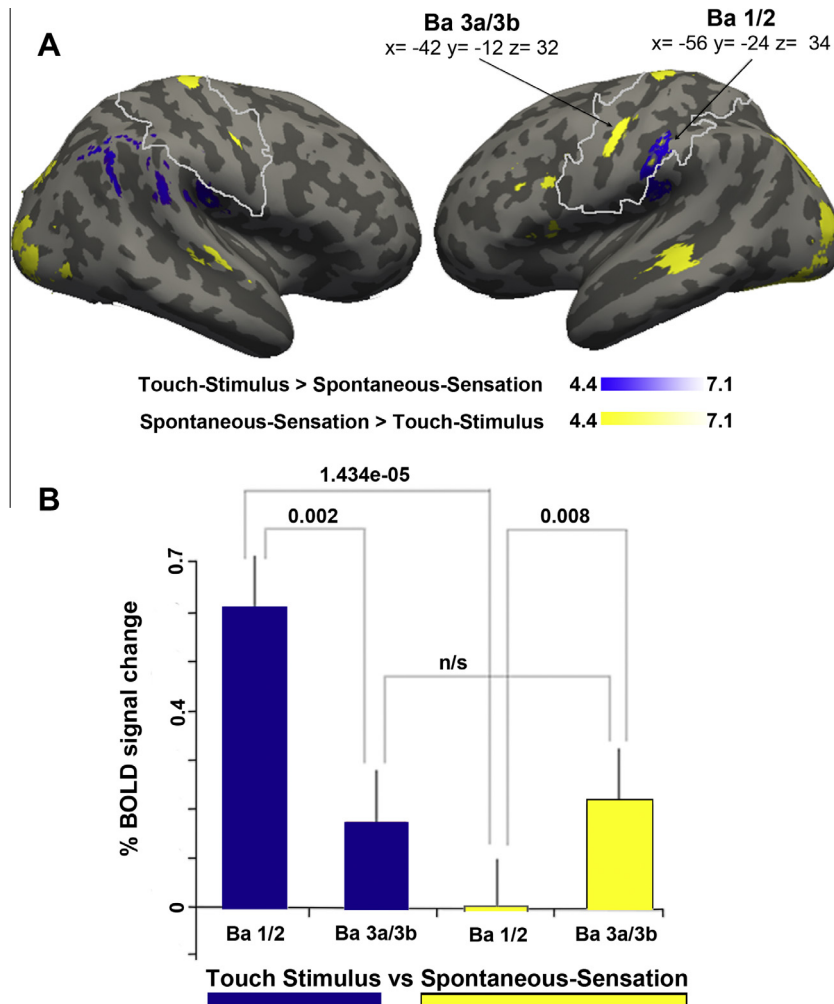
Fig. 4. Higher-level analysis: significant activations for the contrasts between *Touch-Stimulus* and *Spontaneous-Sensation* irrespective of laterality variables. (A) Inflated left and right hemispheres showing significant clusters of activation for contrast *Touch-Stimulus > Spontaneous-Sensation* (in blue) and for contrast *Spontaneous-Sensation > Touch-Stimulus* (in yellow). Arrows point to the respective peak voxel for each contrast, specifically BA 1/2 and BA 3a/3b (left hemisphere), after masking using the primary somatosensory regions (BA 3a/3b, 2 and 1 shown as a gray contour). All contrasts are using voxel thresholding at $p < 0.05$. (B) % BOLD signal change for peak voxels BA 1/2 and BA 3a/3b (shown in A) during focusing of attention to *Touch-Stimulus* (blue bars) and focusing of attention to *Spontaneous-Sensation* (yellow bars) after SI masking. Numbers shown are P values, N/S = not significant, ±sign is a standard error (SEM).

and premotor cortices (BA6: 0, 12, 44), left superior parietal cortex (BA7: −22, −66, 40), left dorsolateral prefrontal cortex (BA9: −42, 8, 22), left insula (BA13: −34, 16, 10), occipital cortex (BA18: −24, −78, 22), anterior cingulate gyrus (BA32: −4, 12, 46), and left Broca's area (BA44: −40, 8, 26).

3.3. Differential topographic activations in the primary somatosensory cortex

To further distinguish between the topographic activations and their signal intensity within the primary somatosensory cortex during the different conditions, we masked the previously described contrast Z-stat images using the primary somatosensory regions (BA 3a/3b, 2 and 1 shown as a gray contour in Fig. 4A) projected in the Jülich histological atlas (Eickhoff et al., 2007; Geyer et al., 2000) and we calculated the% BOLD signal change from the resulting peak activation voxel of the specific Brodmann areas. The peak voxel within BA 1/2 (−56, −24, 34; left hemisphere in Fig. 4A) was located in a more posterior portion of the anterior parietal cortex and the upper bank (operculum) of the lateral sulcus, and it responded significantly more than the peak voxel within BA 3a/3b (−42, −12, 32; left hemisphere in Fig. 4A) while attention was focused on *Touch-Stimulus* (left blue bar in Fig. 4B, $p = 0.002$).

Indeed, the voxel at BA 1/2 was only active while attention was focused on *Touch-Stimulus* (left blue bar in Fig. 4B, $p = 1.434e−05$). In contrast, the voxel at BA 3a/3b, located in a more anterior and deeper Rolandic sulcus portion of the same region, was equally active during both conditions (right yellow and blue bars in Fig. 4B, $p = 0.63$). This voxel at BA 3a/3b was significantly more active than the voxel at BA 1/2 while attention was focused on *Spontaneous-Sensation* (right yellow bar in Fig. 4B, $p = 0.008$). In fact, there was no activity in the voxel corresponding to BA 1/2 when attention was focused on *Spontaneous-Sensation* of either thumbs.

3.4. PPI analysis for BA 1/2

PPI analysis was performed to examine the functional connectivity of the respective primary somatosensory ROI's and other brain areas during focusing to *Touch-Stimulus* versus focusing to *Spontaneous-Sensation*. The PPI analysis for BA1/2 during focusing attention to *Touch-Stimulus* identified brain regions (light blue clusters in Fig. 5A) in a large portion of the posterior parietal cortex (BA40, centered at 46, −42, 48, Z = 5.4, $p < 0.05$ corrected), and the precuneus (BA7, centered at 4, −52, 42, Z = 5.1, $p < 0.05$ corrected). Active foci were also found in a rostral focus covering portions of the inferior and superior frontal gyrus (BA8, 50, 12, 32, Z = 4.5;

Table 2
Summary of psychophysiological interactions (PPI) between attention conditions (TS vs SS) and seed region.

Seed region and attention condition	Anatomical location	Peak		
		x	y	z
Ba 1/2				
TS	Ba7 R, Precuneus	4	−52	42
	Ba8 R, IFG	50	12	32
	Ba10 R, SFG	26	52	18
	Ba13 L, Insula	−34	14	0
	Ba32, ACC	0	50	−2
	Ba40 R,L PPC	46	−42	48
	Thalamus	12	−12	6
SS	–			
Ba 3a/3b				
TS	Ba4 R, PM	10	−28	68
	Ba19 R, FG	40	−68	−10
	Ba45 L, Broca's	−44	34	−2
SS	Ba9 R, SFG	12	50	34
	Ba32 ACC	0	44	0

TS: *Touch-Stimulus*, SS: *Spontaneous-Sensation*, R: right, L: left, Ba: Brodmann area, IFG: inferior frontal gyrus, SFG: superior frontal gyrus, ACC: anterior cingulate cortex, PPC: posterior parietal cortex, PM: primary motor cortex, FG: fusiform gyrus. All presented coordinates had a cluster threshold of $z > 2.3$, $p < 0.05$ and represent positive PPI, suggesting more positive correlation during TS or SS respectively.

BA10, centered at 26, 52, 18, $Z = 5.0$, $p < 0.05$ corrected) as well as the anterior cingulate (BA32, centered at 0, 50, −2, $Z = 4.5$, $p < 0.05$ corrected). Further covariations were found in the insula (BA13, centered at −34, 14, 0, $Z = 43.7$, $p < 0.05$ corrected) and thalamus (12, −12, 6, $Z = 4.7$). PPI analysis during focusing attention to *Spontaneous-Sensation* did not find reliable functional connectivity between BA1/2 and other brain areas. Coordinates of all psychophysiological interactions are shown in Table 2.

3.5. PPI analysis for BA 3a/3b

PPI analysis for BA3a/3b identified during focusing attention to *Touch-Stimulus* (light blue clusters in Fig. 5B) the fusiform gyrus (BA19, centered at 40, −68, −10, $Z = 4.93$, $p < 0.05$ corrected), primary motor cortex (BA4, centered at 10, −28, 68, $Z = 4.89$, $p < 0.05$ corrected) and left Broca's area (BA45, centered at −44, 34, −2, $Z = 3.38$, $p < 0.05$ corrected). During focusing of attention to *Spontaneous-Sensations* (yellow clusters in Fig. 5B), the superior

frontal gyrus (BA9, centered at 12, 50, 34, $Z = 3.78$, $p < 0.05$ corrected) and the anterior cingulate cortex (BA32, centered at 0, 44, 0, $Z = 3.57$, $p < 0.05$ corrected) were identified.

4. Discussion

After verifying in 34 healthy young volunteers that external touch stimuli to either thumb effectively activate brain contralateral somatosensory areas, and after subtracting the attention mechanisms employed in both the *Touch-Stimulus Condition* and the *Spontaneous-Sensation Condition,* the results show that when an individual is required to attend to the spontaneous sensations of either thumb in the absence of any external stimuli, the primary somatosensory cortex is also activated. Therefore, the main hypothesis of this work was largely corroborated with the finding that the focusing of attention on localized, spontaneous sensations of either thumb would activate the somatosensory cortex corresponding to the hand area. While top-down activation of primary-sensory areas has been found during visual (Ishai et al., 2002; Kosslyn et al., 1993; Lee et al., 2012) and auditory imagery (Zatorre & Halpern, 2005), this is the first time that an attention task directed to subtle spontaneous somatosensory sensations has been shown to be capable of activating primary somatosensory areas. Since the task instructions exclusively involved a top-down attentional gating that allowed for this subtle and otherwise elusive stimuli to reach a conscious perception, we verified that tactile attention shares the ability to focus upon a single elusive target among stronger stimuli, hence enhancing otherwise sub-threshold tactile processing at the attended location.

In accord with classical sensory physiology, and the recent results of Martuzzi, Van der Zwaag, Farthouat, Gruetter, and Blanke (2012) using touch-stimuli to the fingers, the control *Touch-Stimulus Condition* to either thumb activated the contralateral primary somatosensory parietal areas 1, 2, and 3b. Additionally, we found that, in contrast to the right thumb stimulus, touch-stimulation to the left thumb recruited a considerably larger contralateral somatosensory area as well as fronto-parietal regions. It is possible that such asymmetric activation results from a hemispheric dominance (including left-handed subjects) present in the general population (Wada, Clarke, & Hamm, 1975) whereby the right hemi-body is more sensitive to external stimuli than the non-dominant left hemi-body, which would require more neural resources
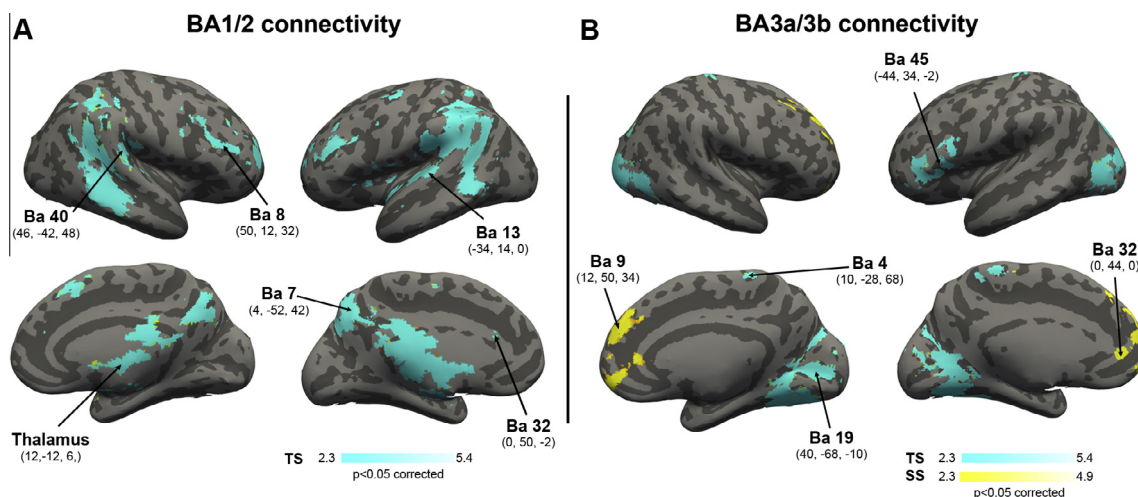

Fig. 5. Psychophysical interaction analysis. Inflated left and right hemispheres showing significant connectivity with (A) BA 1/2 or (B) BA 3a/3b either during focusing attention to *Touch-Stimulus* (TS, light blue) or *Spontaneous-Sensation* (SS, in yellow). All activations, correlations, and contrasts had a significance threshold of $Z > 2.3$, with a cluster significance threshold of $p < 0.05$ (corrected for multiple comparisons).

to process and interpret external stimuli (Lautenbacher, Roscher, Strian, Pirke, & Krieg, 1993). But in contrast to the wider contralateral activation for the left thumb compared to the right thumb in the *Touch-Stimulus Condition*, in the *Spontaneous-Sensation Condition* the left hemispheric activation not only was more significant for both thumbs, but actually there was no right hemisphere activity for the left thumb. The left hemisphere activation observed while attention was directed to the spontaneous sensations of either thumb was unexpected, especially the ipsilateral activation of BA3a/3b in the case of the left thumb, because the crossover disposition of the ascending somatosensory tracts would predict a contralateral activation. Nevertheless, in 1966 Sperry and Eccles reported that left hand writing was controlled by the left hemisphere and suggested that conscious representation of proprioceptive features of somatosensory and motor information may involve the dominant left hemisphere. Likewise, Turk et al. (2002) found in a split-brain patient who was asked to recognize morphed facial stimuli presented to each hemisphere as either himself or a familiar other, that there was a left hemisphere bias for self-recognition and Gazzaniga suggests that the left-hemisphere is the "interpreter" enabling the conscious representation of a unified self (Gazzaniga & Miller, 2009; Gazzaniga, 2000). In contrast to these reports, some studies in brain-damaged and healthy subjects point to right hemisphere dominance in bodily self-awareness. For example, hemi-neglect (Cabeza, Ciaramelli, & Moscovitch, 2012), anosognosia and hemi-asomatogonosia (Heilman, Barrett, & Adair, 1998) are likely to occur after right hemisphere brain damage and self-recognition is said to rely on the right hemisphere (Keenan, Nelson, O'Connor, & Pascual-Leone, 2001). This hemispheric discrepancy may depend in the type of information processed, so that right hemisphere structures relate to visuospatial information resulting in a *body image*, whereas the left hemisphere would be more involved in the interoceptive-prorpioceptive *body schema* processing (De Vignemont, 2010). This hypothesis requires to be experimentally tested.

Our results reveal that the proprioceptive/somatosensory dichotomy discovered in monkeys (Kaas, Nelson, Sur, Lin, & Merzenich, 1979; Prevosto, Graf, & Ugolini, 2011) is also present in the anterior parietal cortex of the human brain. Thus, attention brings into focus either bottom-up somatosensory sensations through the activation of BA 1/2 during *Touch-Stimulus,* or proprioceptive information through the activation of BA 3a/3b during *Spontaneous-Sensation*. In humans, Brodmann 3a and 3b roughly correspond to the posterior bank of the central sulcus and receive proprioceptive information from muscle spindle receptors (Craig, 2006; Prevosto et al., 2011). BA 2 receives inputs from BA 3 and BA 1 and constitutes a third level of cortical processing of tactile and proprioceptive information (Martuzzi et al., 2012; Pons & Kaas, 2004) so that, when tactile information is integrated with proprioceptive inputs in BA 2, tactile and proprioceptive information is combined in a haptic process (Lederman & Klatzky, 2009). The present findings support the idea that each one of the four areas constitutes a module with different connections and cognitive functions.

In addition to the activations found in the primary somatosensory cortex, our results show that when an individual actively attends to the spontaneous sensations of either thumb in absence of any external stimuli, other brain areas are activated. Thus, after subtracting the attention mechanisms employed in both the *Touch-Stimulus Condition* and *Spontaneous-Sensation Condition*, the left superior parietal cortex, anterior cingulate gyrus, insula, motor and premotor cortex, dorsolateral prefrontal cortex, Broca's area, and occipital cortices are activated. During the *Spontaneous-Sensation Condition* the left parietal cortex (Corradi-Dell'Acqua et al., 2008; Corradi-Dell'Acqua et al., 2009; Felician et al., 2004; Longo & Haggard, 2010; Longo et al., 2010; Shomstein, Kravitz, & Behrmann, 2012) probably participates in the spatial localization of

either thumb, while cingulate cortex activation (Bechara & Naqvi, 2004; Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004) in the interoceptive task. The insular activation (Menon & Uddin, 2010) may be associated with cognitive control (Craig, 2002; Simmons & et al., 2012) and the interoceptive attention to salient spontaneous thumb sensations. The dorsolateral prefrontal cortex (BA9) and Broca's area (BA44) are active during the required working-memory tasks, directing attention to internal representations of sensory stimuli (Curtis & D'Esposito, 2003; Kaas, Van Mier, Visser, & Goebel, 2012; Paulesu, Frith, & Frackowiak, 1993), body-part semantics (Braitenberg & Pulvermüller, 1992), and visuo-spatial body representation (Hauk & Pulvermüller, 2011; van Elk & Blanke, 2011). The activation found in the occipital cortex (Hagura, Hirose, Matsumura, & Naito, 2012) could be part of the long-term representation of the body involving its pictorial appearance and visualization. These matrix of activated brain areas during attention directed to focal spontaneous sensations is consistent with the growing evidence of an "interoceptive neural network" (Herbert & Pollatos, 2012) underlying body representation (Blanke, 2012; Longo et al., 2010; Lou et al., 2004; Tsakiris, 2010).

Finally, a psychophysiological interaction (PPI) analysis (Friston et al., 1997; O'Reilly et al., 2012) to distinguish brain regions that showed significantly stronger covariation with BA1/2 and BA3a/3b during sustained and focused attention to *Touch-Stimulus* showed increased connectivity of brain areas that have been identified in previous studies during similar simple non-noxious mechanical stimulation. Thus, the complexity of bottom-up stimulus processing involving different cortical networks during tactile attention is consistent with identified foci in parietal somatosensory, posterior parietal, and superior frontal locations (Burton & Sinclair, 2000; Lui et al., 2008; Porro, Lui, Facchin, Maieron, & Baraldi, 2004). However, for BA 3a/3b, we discovered stronger covariation with the fusiform gyrus (BA19), primary motor cortex (BA4) and left Broca's area probably related to multisensory experience integration since the fusiform gyrus participates in uni- and multisensory visual/tactile integration (James et al., 2002; Stevenson, Kim, & James, 2009) and object encoding processes (Kassuba et al., 2011). Similarly, the motor cortex has been found to display synchronous, context-dependent network dynamics during sensory processing so that complex stimuli representations may be achieved (Zagha, Casale, Sachdev, McGinley, & McCormick, 2013). Additionally, it has been shown that although there is predominantly cortical activation of specific motor or sensory cortices during either movement or touch, there is coactivation of these highly-interconnected brain areas (Trampel et al., 2011). Finally, Broca's area has been implicated during attention to sensory stimuli (Curtis & D'Esposito, 2003; Kaas et al., 2012; Paulesu et al., 1993) probably related to body-part semantics (Braitenberg & Pulvermüller, 1992), and visuo-spatial body representation (Hauk & Pulvermüller, 2011; Van Elk & Blanke, 2011) as previously discussed.

Conversely, PPI analysis for BA 3a/3b when attending to *Spontaneous-Sensations* in absence of external stimuli revealed increased connectivity with the superior frontal gyrus (BA9) and the anterior cingulate cortex (BA32). This further supports the notion that the frontal cortex together with the anterior cingulate cortex play a key role in top–down modulation to direct and focus attention to the unforced sensations of a target body part. Such top-down direction of attention is crucial for the enhancement of sub-threshold bottom-up information, the subsequent primary somatosensory cortex activation, and the heightened perceptivity. Thus, the ability to voluntarily direct, concentrate and sustain attention can bring into focus otherwise sub-threshold bottom-up information of either somatosenory/external or proprioceptive/internal nature. Tactile attention can therefore bias the processing of selected stimuli relevant features.

Attention towards particular somatic stimuli selectively enhances domain-specific cortical areas that probably are determinant for their conscious representation (Farb, Segal, & Anderson, 2013; Jones et al., 2010; Kerr et al., 2011) by amplifying somatosensory cortex responses (Romo et al., 1999). A voluntarily-controlled interoception by means of focused and sustained attention may provide an empirical research tool to investigate embodiment and self-awareness (Bekinschtein et al., 2009; Lutz et al., 2004; Singer, 2012), to disentangle external stimuli from interoceptive bodily sensations that are probably involved in their processing (Farb et al., 2013b), and eventually aid in the understanding of somatosensory and body representation disorders.

5. Conclusions

The present report demonstrates that by directing and sustaining attention to the spontaneous sensations of a body part in absence of external stimuli, the corresponding primary somatosensory cortex is activated. This implies that sustained attention enhances the tactile processing of otherwise sub-threshold and pre-reflective bottom-up information arising at the focused location. Consequently, since there is no ordinary external supra-threshold bottom-up information needed to activate primary somatosensory cortices; only by voluntarily attending to this quintessential sub-threshold bottom-up somatosensory information the primary somatosensory cortex is activated and the bottom-up perceptivity enhanced. Furthermore, other parieto-frontal brain structures involved in processing proprioceptive and interoceptive bodily states may constitute an "interoceptive neural network" underlying body representations. Therefore, directing and sustaining attention to a body part can be accomplished only if the target can be selected from a suitable body representation. There are probably several relatively independent mental representations of the body, each generated from distinctive sensory information and endowed with specific cognitive functions that impinge on different kinds of interactions between the individual and the environment. The human cognitive ability to direct attention may serve as a mechanism to select, enhance, and bring to consciousness a specific mental representation of the body (e.g. *body image* or *body schema*) through the activation of the neural substrates involved in its foundation.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.bandc.2014.03.009.

References

Adrian, E. D., & Umrath, K. (1929). The impulse discharge from the Pacinian corpuscle. *Journal of Physiology, 68*, 139–154.

Arzy Thut, G., Mohr, C., Michel, C. M., & Blanke, O. (2006). Neural basis of embodiment: Distinct contributions of temporoparietal junction and extrastriate body area. *Journal of Neuroscience, 26*, 8074–8081.

Bechara, A., & Naqvi, N. (2004). Listening to your heart: Interoceptive awareness as a gateway to feeling. *Nature Neuroscience, 7*(2), 102–103. http://dx.doi.org/10.1038/nn0204-102.

Bekinschtein, T. A., Dehaene, S., Rohaut, B., Tadel, F., Cohen, L., & Naccache, L. (2009). Neural signature of the conscious processing of auditory regularities. *Proceedings of the National Academy of Sciences of the United States of America, 106*(5), 1672–1677.

Bermúdez, J. L. (1998). Ecological perceptionin and the notion of a nonconceptual point of view. In J. L. Bermúdez, A. Marcel, & N. Eilan (Eds.), *The body and the self* (pp. 153–174). MIT Press.

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nature Reviews Neuroscience, 13*, 556–571.

Blanke, O., & Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. *Trends in Cognitive Sciences, 13*, 7–13.

Braitenberg, V., & Pulvermüller, F. (1992). Model of a neurological theory of speech. *Die Naturwissenschaften, 79*(3), 103–117.

Bruno, N., & Bertamini, M. (2010). Haptic perception after a change in hand size. *Neuropsychologia, 48*, 1853–1856.

Burton, H., & Sinclair, R. J. (2000). Attending to and remembering tactile stimuli: A review of brain imaging data and single-neuron responses. *Journal of Clinical Neurophysiology, 17*, 575–591.

Buschman, T. J., & Miller, E. K. (2007). Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science, 315*, 1860.

Cabeza, R., Ciaramelli, E., & Moscovitch, M. (2012). Cognitive contributions of the ventral parietal cortex: An integrative theoretical account. *Trends in Cognitive Sciences, 16*, 338–352.

Cahn, B., Delorme, A., & Polich, J. (2010). Occipital gamma activation during Vipassana meditation. *Cognitive Processing, 11*, 39–56.

Corradi-Dell'Acqua, C., Hesse, M. D., Rumiati, R. I., & Fink, G. R. (2008). Where is a nose with respect to a foot? The left posterior parietal cortex processes spatial relationships among body parts. *Cerebral Cortex, 18*, 2879.

Corradi-Dell'Acqua, C., Tomasino, B., & Fink, G. R. (2009). What is the position of an arm relative to the body? Neural correlates of body schema and body structural description. *Journal of Neuroscience, 29*, 4162.

Craig, A. D. (2002). How do you feel? Interoception: The sense of the physiological condition of the body. *Nature Reviews Neuroscience, 3*, 655–666.

Craig, A. D. (2006). Retrograde analyses of spinothalamic projections in the macaque monkey: Input to ventral posterior nuclei. *Journal of Comparative Neurology, 499*, 965–978.

Critchley, H. D., Wiens, S., Rotshtein, P., Ohman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. *Nature Neuroscience, 7*(2), 189–195. http://dx.doi.org/10.1038/nn1176.

Curtis, C. E., & D'Esposito, M. (2003). Persistent activity in the prefrontal cortex during working memory. *Trends in Cognitive Sciences, 7*, 415–423.

Dale, A. M., Fischl, B., & Sereno, M. I. (1999). Cortical surface-based analysis: I. Segmentation and surface reconstruction. *Neuroimage, 9*(2), 179–194.

De la Rubia, J. M., & Bravo, B. G. A. (2011). Validez Y Confiabilidad de la Escala de Síntomas Somáticos Revisada en Adultos Mexicanos. *Revista Electrónica de Psicología Iztacala, 14*, 206.

De Vignemont, F. (2010). Body schema and body image-pros and cons. *Neuropsychologia, 48*, 669–680.

Derogatis, L. (1983). The SCL-90-R Manual II: Administration, scoring, and procedures. *Baltimore: Clinical Psychometric Research*.

Derogatis, L. R. (1994). Symptom Checklist-90-R: Administration, scoring, and procedures manual. *Minneapolis, MN: National Computer Systems*, 9–11.

Ehrsson, H. H. (2007). The experimental induction of out-of-body experiences. *Science, 317*, 1048.

Eickhoff, S. B., Paus, T., Caspers, S., Grosbras, M. H., Evans, A. C., Zilles, K., et al. (2007). Assignment of functional activations to probabilistic cytoarchitectonic areas revisited. *Neuroimage, 36*(3), 511–521.

Farb, N. A. S., Segal, Z. V., & Anderson, A. K. (2013). Attentional modulation of primary interoceptive and exteroceptive cortices. *Cerebral Cortex, 23*(1), 114–126. http://dx.doi.org/10.1093/cercor/bhr385.

Farb, N. A. S., Segal, Z. V., & Anderson, A. K. (2013). Mindfulness meditation training alters cortical representations of interoceptive attention. *Social Cognitive and Affective Neuroscience, 8*(1), 15–26. http://dx.doi.org/10.1093/scan/nss066.

Felician et al. (2004). The role of human left superior parietal lobule in body part localization. *Annals of Neurology, 55*, 749–751.

Friston, K. J. et al. (1994). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping, 2*, 189–210.

Friston, K. J., Buechel, C., Fink, G. R., Morris, J., Rolls, E., & Dolan, R. J. (1997). Psychophysiological and modulatory interactions in neuroimaging. *Neuroimage, 6*, 218–229.

Gallagher, S. (2005). *How the body shapes the mind*. Oxford University Press.

Gazzaniga, M. S. (2000). Cerebral specialization and interhemispheric communication. *Brain, 123*(7), 1293.

Gazzaniga, M. S., & Miller, M. B. (2009). Chapter 20 – The left hemisphere does not miss the right hemisphere. In S. Laureys & G. Tononi (Eds.), *The neurology of consciousness* (pp. 261–270). San Diego: Academic Press.

Geyer, S., Schormann, T., Mohlberg, H., & Zilles, K. (2000). Areas 3a, 3b, and 1 of human primary somatosensory cortex. Part 2. Spatial normalization to standard anatomical space. *Neuroimage, 11*, 684–696.

González-Santos, L., Mercadillo, R. E., Graff, A., & Barrios, F. A. (2007). Del Listado de Síntomas 90 (SCL 90) y del Inventario de Temperamento y Carácter (ITC). *Salud Mental (Mex), 30*, 31.

Grigg, P. (1994). Peripheral neural mechanisms in proprioception. *Journal of Sport Rehabilitation, 3*, 2–17.

Hagura, N., Hirose, S., Matsumura, M., & Naito, E. (2012). Am I seeing my hand? Visual appearance and knowledge of controllability both contribute to the visual capture of a person's own body. *Proceedings of the Royal Society B: Biological Sciences, 279*, 3476–3481.

Hauk, O., & Pulvermüller, F. (2011). The lateralization of motor cortex activation to action-words. *Frontiers in Human Neuroscience, 5*, 149. http://dx.doi.org/10.3389/fnhum.2011.00149.

Head, H., & Holmes, G. (1911). Sensory disturbances from cerebral lesions. *Brain, 34*, 102.

Heilman, K. M., Barrett, A. M., & Adair, J. C. (1998). Possible mechanisms of anosognosia: A defect in self-awareness. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 353*, 1903–1909.

Herbert, B. M., & Pollatos, O. (2012). The body in the mind: On the relationship between interoception and embodiment. *Topics in Cognitive Science, 4*, 692–704.

Héroux, M. E., Walsh, L. D., Butler, A. A., & Gandevia, S. C. (2013). Is this my finger? Proprioceptive illusions of body ownership and representation. *Journal of Physiology*.

Ishai, A., Haxby, J. V., & Ungerleider, L. G. (2002). Visual imagery of famous faces: Effects of memory and attention revealed by fMRI. *Neuroimage, 17*, 1729–1741.

James, T. W., Humphrey, G. K., Gati, J. S., Servos, P., Menon, R. S., & Goodale, M. A. (2002). Haptic study of three-dimensional objects activates extrastriate visual areas. *Neuropsychologia, 40*, 1706–1714.

Jenkinson, M., & Smith, S. (2001). A global optimisation method for robust affine registration of brain images. *Medical Image Analysis, 5*, 143–156.

Johansen-Berg, H., & Lloyd, D. M. (2000). The physiology and psychology of selective attention to touch. *Frontiers in Bioscience, 5*, D894–904.

Jones, S. R., Kerr, C. E., Wan, Q., Pritchett, D. L., Hämäläinen, M., & Moore, C. I. (2010). Cued spatial attention drives functionally relevant modulation of the mu rhythm in primary somatosensory cortex. *Journal of Neuroscience, 30*, 13760–13765.

Kaas, J. H., Nelson, R. J., Sur, M., Lin, C. S., & Merzenich, M. M. (1979). Multiple representations of the body within the primary somatosensory cortex of primates. *Science, 204*(4392), 521.

Kaas, A. L., Van Mier, H., Visser, M., & Goebel, R. (2012). The neural substrate for working memory of tactile surface texture. *Human Brain Mapping*. http://dx.doi.org/10.1002/hbm.21500.

Kammers, M. P. M., van der Ham, I. J. M., & Dijkerman, H. C. (2006). Dissociating body representations in healthy individuals: Differential effects of a kinaesthetic illusion on perception and action. *Neuropsychologia, 44*, 2430–2436.

Kassuba, T., Klinge, C., Hölig, C., Menz, M. M., Ptito, M., Röder, B., et al. (2011). The left fusiform gyrus hosts trisensory representations of manipulable objects. *Neuroimage, 56*, 1566–1577.

Keenan, J. P., Nelson, A., O'Connor, M., & Pascual-Leone, A. (2001). Neurology: Self-recognition and the right hemisphere. *Nature, 409*, 305.

Kerr, C. E., Jones, S. R., Wan, Q., Pritchett, D. L., Wasserman, R. H., Wexler, A., et al. (2011). Effects of mindfulness meditation training on anticipatory alpha modulation in primary somatosensory cortex. *Brain Research Bulletin, 85*, 96–103.

Klingner, C. M., Nenadic, I., Hasler, C., Brodoehl, S., & Witte, O. W. (2011). Habituation within the somatosensory processing hierarchy. *Behavioural Brain Research, 225*, 432–436.

Koelewijn, T., Bronkhorst, A., & Theeuwes, J. (2010). Attention and the multiple stages of multisensory integration: A review of audiovisual studies. *Acta Psychologica (Amst.), 134*, 372–384.

Kosslyn, S. M., Alpert, N. M., Thompson, W. L., Maljkovic, V., Weise, S. B., Chabris, C. F., et al. (1993). Visual mental imagery activates topographically organized visual cortex: PET investigations. *Journal of Cognitive Neuroscience, 5*, 263–287.

Lackner, J. R. (1988). Some proprioceptive influences on the perceptual representation of body shape and orientation. *Brain, 111*, 281.

Lautenbacher, S., Roscher, S., Strian, F., Pirke, K. M., & Krieg, J. C. (1993). Theoretical and empirical considerations on the relation between "body image", body scheme and somatosensation. *Journal of Psychosomatic Research, 37*, 447–454.

Lederman, S. J., & Klatzky, R. L. (2009). Haptic perception: A tutorial. *Attention, Perception, & Psychophysics, 71*, 1439–1459.

Lee, S. H., Kravitz, D. J., & Baker, C. I. (2012). Disentangling visual imagery and perception of real-world objects. *NeuroImage, 59*(4), 4064–4073. http://dx.doi.org/10.1016/j.neuroimage.2011.10.055.

Longo, M. R., Azañón, E., & Haggard, P. (2010). More than skin deep: Body representation beyond primary somatosensory cortex. *Neuropsychologia, 48*(3), 655–668.

Longo, M. R., & Haggard, P. (2010). An implicit body representation underlying human position sense. *Proceedings of the National Academy of Sciences of the United States of America, 107*, 11727.

Longo, M. R., & Haggard, P. (2011). Weber's illusion and body shape: Anisotropy of tactile size perception on the hand. *Journal of Experimental Psychology: Human Perception and Performance, 37*, 720–726.

Longo, M. R., & Sadibolova, R. (2013). Seeing the body distorts tactile size perception. *Cognition, 126*, 475–481.

Lou, H. C., Luber, B., Crupain, M., Keenan, J. P., Nowak, M., Kjaer, T. W., et al. (2004). Parietal cortex and representation of the mental self. *Proceedings of the National Academy of Sciences of the United States of America, 101*, 6827–6832.

Lui, F., Duzzi, D., Corradini, M., Serafini, M., Baraldi, P., & Porro, C. A. (2008). Touch or pain? Spatio-temporal patterns of cortical fMRI activity following brief mechanical stimuli. *Pain, 138*, 362–374.

Lutz, A., Greischar, L. L., Rawlings, N. B., Ricard, M., & Davidson, R. J. (2004). Long-term meditators self-induce high-amplitude gamma synchrony during mental practice. *Proceedings of the National Academy of Sciences of the United States of America, 101*(46), 16369–16373.

Maravita, A., Spence, C., & Driver, J. (2003). Multisensory integration and the body schema: Close to hand and within reach. *Current Biology, 13*, R531–R539.

Martuzzi, R., Van der Zwaag, W., Farthouat, J., Gruetter, R., & Blanke, O. (2012). Human finger somatotopy in areas 3b, 1, and 2: A 7T fMRI study using a natural stimulus. *Human Brain Mapping*. http://dx.doi.org/10.1002/hbm.22172.

Menon, V., & Uddin, L. Q. (2010). Saliency, switching, attention and control: A network model of insula function. *Brain Structure and Function, 214*, 655–667.

Moulton, E. A., Keaser, M. L., Gullapalli, R. P., & Greenspan, J. D. (2005). Regional intensive and temporal patterns of functional MRI activation distinguishing noxious and innocuous contact heat. *Journal of Neurophysiology, 93*, 2183.

Mountcastle, V. B. (2005). *The sensory hand: Neural mechanisms of somatic sensation*. Harvard Univ Pr..

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*(1), 97–113.

O'Reilly, J. X., Woolrich, M. W., Behrens, T. E. J., Smith, S. M., & Johansen-Berg, H. (2012). Tools of the trade: Psychophysiological interactions and functional connectivity. *Social Cognitive and Affective Neuroscience, 7*, 604–609.

Paulesu, E., Frith, C. D., & Frackowiak, R. S. J. (1993). The neural correlates of the verbal component of working memory. *Nature, 362*, 342–345. doi:101038/362342a0.

Petersen, S. E., & Posner, M. I. (2012). The attention system of the human brain: 20 years after. *Annual Review of Neuroscience, 35*, 73–89. http://dx.doi.org/10.1146/annurev-neuro-062111-150525.

Pons, T. P., & Kaas, J. H. (2004). Corticocortical connections of area 2 of somatosensory cortex in macaque monkeys: A correlative anatomical and electrophysiological study. *Journal of Comparative Neurology, 248*, 313–335.

Porro, C. A., Lui, F., Facchin, P., Maieron, M., & Baraldi, P. (2004). Percept-related activity in the human somatosensory system: Functional magnetic resonance imaging studies. *Magnetic Resonance Imaging, 22*, 1539–1548.

Prevosto, V., Graf, W., & Ugolini, G. (2011). Proprioceptive pathways to posterior parietal areas MIP and LIPv from the dorsal column nuclei and the postcentral somatosensory cortex. *European Journal of Neuroscience, 33*(3), 444–460. http://dx.doi.org/10.1111/j.1460-9568.2010.07541.x.

Proske, U., & Gandevia, S. C. (2012). The proprioceptive senses: Their roles in signaling body shape, body position and movement, and muscle force. *Physiological Reviews, 92*, 1651–1697.

Romo, R., Brody, C. D., Hernández, A., & Lemus, L. (1999). Neuronal correlates of parametric working memory in the prefrontal cortex. *Nature, 399*(6735), 470–473. http://dx.doi.org/10.1038/20939.

Romo, R., & Salinas, E. (2001). Touch and go: Decision-making mechanisms in somatosensation. *Annual Review of Neuroscience, 24*, 107–137.

Ruff, C. C. (2013). Sensory processing: Who's in (top-down) control? *Annals of the New York Academy of Sciences, 1296*, 88–107.

Sambo, C. F., & Forster, B. (2011). Sustained spatial attention in touch: Modality-specific and multimodal mechanisms. *TheScientificWorldJournal, 11*, 199–213. http://dx.doi.org/10.1100/tsw.2011.34.

Sarter, M., Givens, B., & Bruno, J. P. (2001). The cognitive neuroscience of sustained attention: Where top-down meets bottom-up. *Brain Research Reviews, 35*, 146–160.

Shomstein, S., Kravitz, D. J., & Behrmann, M. (2012). Attentional control: Temporal relationships within the fronto-parietal network. *Neuropsychologia, 50*(6), 1202–1210. http://dx.doi.org/10.1016/j.neuropsychologia.2012.02.009.

Simmons, W. K. et al. (2012). Keeping the body in mind: Insula functional organization and functional connectivity integrate interoceptive, exteroceptive, and emotional awareness. *Human Brain Mapping*. http://dx.doi.org/10.1002/hbm.22113.

Singer, W. (2012). What binds it all together? Synchronized oscillatory activity in normal and pathological cognition. In F. G. Barth, P. Giampieri-Deutsch, & H. D. Klein (Eds.), *Sensory Perception* (pp. 57–70). Vienna: Springer.

Smith, S. M., Jenkinson, M., Woolrich, M. W., Beckmann, C. F., Behrens, T. E. J., Johansen-Berg, H., et al. (2004). Advances in functional and structural MR image analysis and implementation as FSL. *Neuroimage, 23*, S208–S219.

Sperry, R. W. (1966). Brain bisection and mechanisms of consciousness. In J. C. Eccles (Ed.), *Brain and Conscious Experience* (pp. 298–313). New York: Springer-Verlag.

Stevenson, R. A., Kim, S., & James, T. W. (2009). An additive-factors design to disambiguate neuronal and areal convergence: Measuring multisensory interactions between audio, visual, and haptic sensory streams using fMRI. *Experimental Brain Research Experimentelle Hirnforschung Expérimentation Cérébrale, 198*, 183–194.

Stock, A.-K., Wascher, E., & Beste, C. (2013). Differential effects of motor efference copies and proprioceptive information on response evaluation processes. *PLoS One, 8*, e62335.

Taylor-Clarke, M., Jacobsen, P., & Haggard, P. (2004). Keeping the world a constant size: Object constancy in human touch. *Nature Neuroscience, 7*, 219–220.

Trampel, R., Schafer, A., Heidemann, R. M., Ivanov, D., Lohmann, G., Geyer, S., et al. (2011). High resolution functional mapping of primary motor cortex and primary somatosensory cortex in humans at 7T. *Proceedings of the International Society for Magnetic Resonance in Medicine, 2011 Annual Meeting Proceedings*, 3586.

Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology, 12*, 97–136.

Tsakiris, M. (2010). My body in the brain: A neurocognitive model of body-ownership. *Neuropsychologia, 48*, 703–712.

Turk, D. J., Heatherton, T. F., Kelley, W. M., Funnell, M. G., Gazzaniga, M. S., & Macrae, C. N. (2002). Mike or me? Self-recognition in a split-brain patient. *Nature Neuroscience, 5*(9), 841–842. http://dx.doi.org/10.1038/nn907

Van Elk, M., & Blanke, O. (2011). The relation between body semantics and spatial body representations. *Acta Psychologica, 138*(3), 347–358. http://dx.doi.org/10.1016/j.actpsy.2011.09.001

Wada, J. A., Clarke, R., & Hamm, A. (1975). Cerebral hemispheric asymmetry in humans: Cortical speech zones in 100 adult and 100 infant brains. *Archives of Neurology, 32*, 239.

Woolrich, M. W., Ripley, B. D., Brady, M., & Smith, S. M. (2001). Temporal autocorrelation in univariate linear modeling of FMRI data. *Neuroimage, 14*(6), 1370–1386.

Worsley, K. (2002). Statistical analysis of activation images. In P. Jezzard, P. Matthews, & S. Smith (Eds.), *Functional Magnetic Resonance Imaging: An Introduction to Methods* (pp. 251–270). New York: Oxford Univ. Press.

Zagha, E., Casale, A. E., Sachdev, R. N. S., McGinley, M. J., & McCormick, D. A. (2013). Motor cortex feedback influences sensory processing by modulating network state. *Neuron, 79*, 567–578.

Zatorre, R. J., & Halpern, A. R. (2005). Mental concerts: Musical imagery and auditory cortex. *Neuron, 47*(1), 9–12. doi:16/j.neuron.2005.06.013.