Interacting effects of vision and attention in perceiving spontaneous sensations arising on the hands

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Abstract Visual input and attention enhance tactile perception. But do they influence the perception of spontaneous sensations (SPS) arising in the absence of any external stimulus? We have investigated this by requiring subject to focus attention on each hand while orienting overtly toward it (convergent focusing) or away (divergent focusing) and to subsequently describe the properties of the SPS they felt. Subjects performed this task under free viewing conditions or while blindfolded. Enhanced perception of SPS was found under convergent focusing and also under free viewing conditions. However, the effects of focusing were different whether visual input was available or not. When visual input was available, SPS were enhanced in the fingers but suppressed in the palm, suggesting that enhancement and suppression operated to refine perception of SPS. When visual input was unavailable, only enhancement was observed, even in areas of the hand where suppressing effects were found under free viewing conditions. These interacting effects between vision and attention were observed exclusively in the left hand. A control experiment failed to evidence whether looking at different parts of the hand modulates SPS. We suggest that vision facilitates perception and, when interacting with attention, it enables better perception by promoting suppression of SPS arising in areas of lower sensitivity that may interfere with processing in more sensitive zones. The results are discussed with respect to mechanisms lateralized in the right cerebral hemisphere, and a role of SPS in the maintenance of a conscious image of the body is suggested.

Keywords Spontaneous sensations · Attention · Vision · Touch · Multisensory · Somatosensory awareness · Hemispheric lateralization

Introduction

Those tickly, tingling, itching and other sensations usually perceived during periods of rest and without external triggers (i.e., spontaneous sensations or SPS) may provide information about the spatial frontiers of the body and contribute, thereafter, to the construction and maintenance of the conscious image of the body. Yet, despite the frequency and familiarity of these sensations, they have been the subject of only one preliminary (Naveteur et al. 2005; control experiment) and one targeted (Michael and Naveteur 2011) study. The protocol was based on psychophysical (Naveteur et al. 2005) and physiological research
(Ochoa and Torebjörk 1983; Macefield et al. 1990) and required subjects to focus their attention briefly on one hand and then to map the location and extent of their SPS on a model of the hand and describe their characteristics. The hand was chosen for sake of simplicity, for the critical role hands play in everyday activity, and the role they might play in defining the frontiers of the body.

In the Michael and Naveteur study (2011), three main features were observed, shedding some light on the primary processes involved in SPS. Firstly, although SPS were reported over the entire surface of the hand, they were unevenly distributed. They were most frequent over the fingertips, and frequency gradually diminished toward the palm. This graded pattern is obtained when the hand is placed motionless palm-down in slight contact with a smooth surface but, impressively, also palm-up and without contact with any object. This might be the signature of receptors and the trace they leave on the cortical representation of the hand, the proximo-distal sensitivity gradient of which has not yet been found (Iwamura et al. 1983; Hashimoto et al. 1999a, b). Secondly, most of the variables analyzed revealed a dominance of the left hand, with all subjects being right-handed. Processes associated with the right cerebral hemisphere may be responsible for these lateralized effects. Such processes include tactual pros- cessing (e.g., Fontenot and Benton 1971), spatial perception (e.g., Semmes 1965; Milner and Taylor 1972; Dodds 1978), spatial attention (e.g., Mesulam 1999), and interoceptive awareness (e.g., Vaitl 1996; Craig 2004). Thirdly, the manipulation of overt attention, which consisted in participants directing their head and gaze toward (convergent focusing) or away from (divergent focusing) the hand being tested (Honorable et al. 1989; Naveteur et al. 2005), yielded one of the most interesting results. Under convergent focusing, SPS over the sensitive zones (i.e., fingertips) were described as occupying larger areas, and the extent of some of the SPS on less sensitive zones (i.e., palm) was described as being reduced. We have suggested that these findings reflect the two complementary processes of attention, namely enhancement and suppression (Chelazzi et al. 1993), which have been described in all sensory modalities. This specific topography fits in well with research work that showed that how the body is represented in the somatosensory cortex is modulated by attention (Hyvärinen et al. 1980; Hsiao et al. 1993; Mima et al. 1998; Noppeney et al. 1999; Iguchi et al. 2002) and, in particular, the discovery that attention enlarges the cortical representation of the fingers (Hämäläinen et al. 2002). If SPS were instrumental in the construction and maintenance of the conscious image of the body, then this is a finding that supports that awareness of one’s own body is rather attentional in nature (Kinsbourne 1998). The effect of attention on SPS is consistent with reports of an enhancement of tactile processing in the direction of head and gaze (Honorable et al. 1989).

One of the limitations of our previous study, however, was that directing the head and gaze toward the tested body part (i.e., overt focusing) was not dissociated from viewing that body part (i.e., visual input). Yet, behavioral and electrophysiological studies (Tipper et al. 1998; Kennett et al. 2001; Taylor-Clarke et al. 2002; Press et al. 2004; Forster and Eimer 2005; Serino et al. 2007) clearly distinguished the effects of each factor on tactual performance, and visual enhancement of touch was observed even with non-informative visual input. This is backed up by neurophysiological studies, which have suggested that sight-induced changes in the cortical somatosensory representation of the body can account for such effects and that the sight of the stimulated part of the body may influence early stages of somatosensory processing (Forster and Eimer 2005; Fiorio and Haggard 2005; Schaef er et al. 2005, 2006, 2008). Several theories assign a major role to vision in constructing and maintaining the conscious image of the body (Price 2006; Longo and Haggard 2010; Kinsbourne 1998), and there are empirical findings to support them. For instance, models of human figures made by blind children out of plasticine (Kinsbourne and Lempert 1980) indicate that they have a mental representation of human form in which body parts such as the hands are exaggerated in size. Wolpert et al. (1998) also reported the case of a patient with parietal damage whose right leg and arm would fade from consciousness when the patient looked away, to return only when she looked at them. These observations suggest visual feedback plays an important role in calibrating the conscious image of the body (Price 2006), but also that it allows body image to arise and be held in consciousness. Since the coherence of the internal representation that gives rise to our perception of our body is seemingly based on multiple integrated signals (Longo and Haggard 2010), each of these factors might be expected to have different effects on SPS. But do they interact? Tipper et al. (1998) reported that adding visual information produced no further facilitation than orienting alone, thus aligning themselves with earlier findings by Driver and Grossenbacher (1996). However, these negative findings may be attributed to an inability to detect contributions made by sight to a substantial effect of orienting. A recent event-related potential study (Sambo et al. 2009) showed that tactile-spatial attention was modulated by visual input and in particular the sight of the stimulated body part, which, in that case, was the hand. Furthermore, neuroimaging data (Macaluso et al. 2000) suggest that when the stimulated part of the body is visible, activities within the somatosensory cortex are enhanced. This last point is quite exciting since it suggests that although visual input and focusing alone may have specific effects, they...
also interact in such a way that the precise information provided by sight may facilitate attentional selection and the processing of tactile signals (Eimer 2004; Macaluso 2006). Accordingly, SPS are expected to vary as a function of visual input and focusing, both separately and in combination. Indeed, it has been suggested that the sight of a body part can also raise awareness of internal bodily sensations (Lloyd et al. 2008; Mirams et al. 2010), and this fits in well with the idea that interoception may play a part in the perception of SPS (Michael and Navetuer 2011).

The aim of the present study is thus to unravel the effects of vision and attention, alone and in combination, on the occurrence and characteristics of SPS on hands. Based on the aforementioned studies, it was expected that (a) visual input would enhance the perception of SPS, (b) focusing would mainly enhance the perception of SPS, and (c) focusing with and without visual input would have different effects due to interactions between vision and attention. This hypothesis is difficult to develop further because the directly linked literature does not allow doing so (e.g., Tipper et al. 1998; Sambo et al. 2009). Furthermore, based on our previous study, it was also expected that (d) the frequency of SPS would follow a proximo-distal gradient, and (e) the left hand would be more sensitive than the right in right-handers. We examined this by asking subjects to focus on one hand for a short time, either while directing their eyes and their head toward it or while directing them in the opposite direction. Half of the subjects were tested under free viewing conditions whereas the other half were tested while blindfolded. They were then asked to map the intensity, location, and extent of any SPS they felt.

Main experiment

Methods

Subjects

The study was conducted in accordance with the Helsinki Declaration. Subjects were excluded if they were not right-handers (i.e., if the Edinburgh laterality inventory score was smaller than 0.50; Oldfield 1971), had a history of neurologic or psychiatric disease, and had taken psychoactive substances (e.g., marijuana, antidepressants, anxiolytics, etc.) in the month leading up to the testing session. After having applied these exclusion criteria, 91 volunteer undergraduates from the University of Lyon 2 were included, and they received course credits. However, 11 subjects (12.1%) reported no SPS in more than half of the tested conditions and were excluded from the data analysis. The mean age of the remaining 80 subjects (65 women and 15 men) was 20.9 ± 4.2 (age range: 17–44), their mean body mass index was 20.3 ± 2 kg/m² (range: 16.3–26), they were all right-handers according to the laterality inventory (0.84 ± 0.15), and all gave their written informed consent.

Protocol and procedure

Subjects were tested in groups of 4–5 in a quiet room with an ambient temperature of 19°C. They sited at a desk, in line, each was facing the back of another, rendering impossible to see the responses of the others. They first read and signed the consent text, supplied information such as gender, age, height and weight, and then completed the Edinburgh laterality inventory (Oldfield 1971). The next step consisted in the main investigation of SPS, and for that subjects were asked to remove any jewels worn on their hands and wrists. For the sake of homogeneity, all subjects were required to spend 15-s cleaning their hands with an antiseptic gel used for medical purposes (Aniosgel® 85 NPC, ≈3 ml per participant). A minimum latency of 15 s was respected between the cleansing operation and the start of the test (Navetuer et al. 2005; Michael and Navetuer 2011). The experimenter distributed a sheet of smooth paper (everRey, white, 120 g, 21 × 29.7 cm), a wooden red disk (5 cm diameter), and announced the beginning of the testing session. All subjects were asked to put the disk on one side as referred to their body midline and the sheet of paper on the other side. The tested hand was placed palm-down on the paper, without any pressure and with the fingers slightly apart. The other hand was placed on their knee. Two variables were manipulated: the tested hand and the focusing condition. Convergent focusing refers to the condition where subjects were looking at their hand and focusing their attention on it, while divergent focusing refers to the condition where they were looking at the red disk while focusing their attention on the tested hand. Thus, four separate conditions were tested: (a) convergent focusing left hand, (b) convergent focusing right hand, (c) divergent focusing left hand, and (d) divergent focusing right hand. All of the subjects completed each condition once, balanced in a latin-square order. Half of the subjects (N = 40) were assigned to the free viewing group (FV) and the remainder to the blindfolded group (BF). Due to the total duration of the test (i.e., 45 min), it was impossible to carry out this experiment with the viewing condition as a within-subject factor (which would have given testing sessions of more than 11/2 h). The two groups did not differ in respect to their age, laterality coefficient, or body mass index (Table 1).

All subjects received a blindfold. It was a relaxation mask, which was chosen to be in transparent flexible plastic and filled with colorless gel for allowing ambient light to be perceived by subjects the eyes shut without other visual input to be perceived. At the beginning of each trial, they were required to put on the mask without covering their
Table 1 Characteristics of the two groups that participated in the main experiment of the present study

<table>
<thead>
<tr>
<th></th>
<th>Free view</th>
<th>Blindfolded</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>20.5 (2.5)</td>
<td>21.3 (5.3)</td>
<td>0.39</td>
</tr>
<tr>
<td>Laterality</td>
<td>0.85 (0.15)</td>
<td>0.85 (0.16)</td>
<td>0.43</td>
</tr>
<tr>
<td>BMI</td>
<td>27.05 (7.5)</td>
<td>26.15 (6.4)</td>
<td>0.56</td>
</tr>
<tr>
<td>F/M</td>
<td>35/05</td>
<td>30/10</td>
<td></td>
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</tbody>
</table>

Bicaudal P values were derived from an independent samples t test.

Shaded areas on each printed hand were projected onto a 140 × 140 grid with 1 mm² resolution and then converted into binary codes (0 = not shaded cell; 1 = shaded cell). The result, for each subject and each tested condition, was individual maps of spatially distributed binary codes. Superimposition of the 80 individual binary maps produced four frequency maps (one per condition), with the value in each cell representing the percentage of subjects having shaded it. This meant it was possible to carry out statistical analyses of the spatial extent and topography of the reported sensations. Significant differences found for cells located over the extreme contours of the hands were considered artifacts produced during the binary conversion.

Statistical methods

The data were subjected to a number of analyses: (a) total spatial extent (percent shaded surface as compared to the whole hand map), intensities, and confidence ratings were rank-transformed and entered separated non-parametric analyses of covariance with the focusing condition (convergent vs. divergent) and tested hand (left vs. right) as within-subject factors, and the viewing condition (FV vs. BF) and the order of test as between-group factor; age, body mass index, and laterality index were used as covariates; (b) The surface of the glabrous skin of the hand was divided into anatomical segments (phalanges and palm; 15 segments) on the basis of pilot measures; (c) realized on 10 subjects. This size of segments did not differ (\(\chi^2(14) = 4.75; \text{NS}\)) from those reported by Johansson and Vallbo (1979). Based on the logic of the relative receptor density (Johansson and Vallbo 1979), we computed the

\[1\] Johansson and Vallbo (1979) used the Length x Width product to estimate the overall surface of the hand. The total glabrous skin surface was then separated into eighteen regions (4 palm segments and 14 phalanges; the thumb was divided in 2 phalanges, contrary to the other fingers) defined by the natural flexure lines. In our pilot investigation, we followed those guidelines but, for the purposes of our investigation, we retained the 14 phalanges plus 1 palm area. The mean area occupied by each segment (percent as reported to the surface of the whole hand) of the 10 participants was then compared to the areas reported by Johansson and Vallbo (1979; p. 287) with a goodness-of-fit test.
relative spatial extent of sensations, that is, percent shaded surface within a segment (distal phalange, intermediate phalange, etc.) as compared to the surface of the whole segment. Relative surfaces were entered a non-parametric analysis of covariance with the focusing condition (convergent vs. divergent), tested hand (left vs. right), and anatomical segment (distal, intermediate, proximal, and palm) as within-subject factors, and the viewing condition (FV vs. BF) and the order of test as between-group factor; age, body mass index, and laterality index were used as covariates; (c) Spearman correlation analyses were conducted between age, body mass index and laterality index and the percentage of shaded surfaces, overall reported intensities, and overall confidence ratings; (d) the topography was investigated through cell-by-cell comparisons between the conditions of interest yielding significance maps representing the cells where reliable changes were found. Between-subject factors were assessed with the exact test for binary independent measures (Barnard 1945), while within-subject factors were assessed with the exact test for the significance of change (Liddell 1983). For the cell-by-cell comparison, the alpha level was set to 0.05 bicaudal. In order to reject random patterns of significant cells, we carried out spatial analyses that detect and localize significant clusters. The significance maps resulting from the above-mentioned comparisons were subjected to binary conversion (0 = non-significant; 1 = significant), and a spatial scan procedure for binary data (Kullendorff 1997) was subsequently used. This test consists in a circular window that scans the maps for clusters. On the basis of previous simulations, the maximal radius was set at 6 cells (representing a maximal scanned surface of 113 cells). Spatial analyses were carried out using home-made software; (e) the variety of the reported sensations was analyzed with a Chi-square goodness-of-fit test to assess whether sensations were all reported equally frequently; finally, (f) the variety of SPS (i.e., number of different sensations) was rank-transformed and entered a non-parametric analysis of covariance with the focusing condition (convergent vs. divergent) and tested hand (left vs. right) as

2 Several observations were made on the basis of the spatial scan: (1) within the scan window, only groups of 6 cells or more were found to be significant, which corresponds to a skin surface equal or larger than 1 cm² on a real hand. This leads us to accept a group of at least 6 cells as a significant cluster; (2) groups of aligned cells were never classified as being clusters; (3) in some cases, isolated cells that were in spatial proximity were detected as significant clusters at high P-levels, suggesting that the whole area they occupied was classified as distinct from others and as being a whole group; (4) spatially separated groups were sometimes identified as belonging to a single one; (5) isolated cells that were in spatial proximity to groups of cells were sometimes considered by the test as being part of that group; (6) finally, cell groups that visually seemed related were determined as belonging to two distinct clusters.

within-subject factors, and the viewing condition (FV vs. BF) and the order of test as between-group factor; age, body mass index, and laterality index were used as covariates.

Results

Total spatial extent

Only the viewing condition X focusing interaction reached significance \( F(1,72) = 6.06; P < 0.05; \) Fig. 1a). Newman-Keuls post hoc comparisons revealed that there was no difference between the FV and BF groups under convergent focusing (10.2% and 10.9% of the whole hand, respectively; NS), while SPS were perceived as occupying larger areas under divergent focusing in the FV than the BF group (10.8 and 8.3%, respectively; \( P < 0.001 \)). Besides, the difference between convergent and divergent focusing was significant only in the BF group (\( P < 0.01 \)).

Relative spatial extent

The viewing condition X focusing interaction reached significant \( F(1,78) = 5.03; P < 0.05 \) due to a difference between convergent and divergent focusing under BF conditions (convergent: 12.6%; divergent: 9.4%; \( P < 0.05 \)) but not free viewing conditions (convergent: 10.3%; divergent: 10.1%; NS). This pattern backs up the results of spatial extent analyses. The main effect of anatomical segment was significant \( F(3,234) = 29.2; P < 0.001 \); distal: 17.9%; intermediate: 6.8%; proximal: 6.3%; palm: 10.7%). The viewing condition X anatomical segment interaction was also significant \( F(3,234) = 2.74; P < 0.05 \). Post hoc Newman-Keuls comparisons revealed that this interaction came exclusively from a reliable difference in the palm where relative surfaces were reported as larger by the FV group (12.3%) than the BF group (9.2%; \( P < 0.005 \)). Finally, the main effect of tested hand reached marginal significance \( F(1,78) = 3.7; P < 0.058 \) with relative surfaces being larger in the left (10.9%) than the right (9.9%) hand.

Intensity

The main effect of focusing condition reached significance \( F(1,72) = 4.46; P < 0.05 \), with SPS being perceived as more intense under convergent focusing (convergent: 3.3; divergent: 2.9). The main effect of hand also reached significance \( F(1,72) = 4.04; P < 0.05 \), with stronger intensities reported for the left hand (left: 3.3; right: 2.9). No other reliable differences were found.
Confidence ratings

As far as confidence in locating SPS, the only significant finding was the main effect of the tested hand ($F(1,72) = 6.4; P < 0.05$), with subjects reporting being more confident as for localizing SPS in the left hand (left: 6.0; right: 5.0). The analysis of confidence in the reported spatial extent revealed no reliable effects.

Correlations

Intensity correlated positively with spatial extent ($\rho(78) = 0.69; P < 0.001$), confidence in localization ($\rho(78) = 0.43; P < 0.001$) and confidence in spatial extent ($\rho(78) = 0.43; P < 0.001$). Spatial extent correlated positively with confidence in localization ($\rho(78) = 0.37; P < 0.001$) and confidence in spatial extent ($\rho(78) = 0.33; P < 0.005$). The two confidence ratings correlated positively with each other ($\rho(78) = 0.73; P < 0.001$). When considered independently for each hand, confidence in localization correlated positively with both spatial extent ($\rho(78) = 0.47; P < 0.001$) and perceived intensity ($\rho(78) = 0.32; P < 0.01$), as did confidence in spatial extent (with spatial extent: $\rho(78) = 0.38; P < 0.001$; with intensity: $\rho(78) = 0.48; P < 0.001$). No other correlations were found.

Topography

Figure 2a shows that sensations were reported over the whole hand but were not distributed in a uniform manner. For the comparisons between conditions, only significant clusters are taken into account. A large dominance of the left hand was evidenced when considered independently of focusing and viewing condition (Fig. 2b). SPS were more frequent in the left palm (in the frontier with the wrist). Taken independently from the tested hand and viewing condition, focusing produced reliable increase in the frequency at which SPS were reported, mostly over the distal phalanx of the major and the ring fingers (Fig. 2c). The viewing condition also changed the perception of SPS. They were more frequent in the FV group than the BF group (Fig. 2d) and they were mostly located in the palm. This last finding supports the aforementioned interaction between viewing condition and anatomical segment in which the FV group reported SPS of larger relative spatial extent in the palm.

Focusing interacted with the viewing condition for producing changes exclusively in the left hand. The analysis consisted in comparing convergent and divergent focusing for each hand and viewing condition (Fig. 3). In the FV condition, convergence led subjects to report sensations more frequently (i.e., enhancement) in the tip of the ring finger, the surface of which was covering 0.6% of the whole hand. Sensations were less frequently reported (i.e., suppressed) under convergent focusing in the palm, and such effects occupied a surface of 1.3%. This pattern is quite close to what was reported by Michael and Naveteur (2011). A rather different pattern was observed in the BF condition, where effects of enhancement were observed over a 2.2% of the surface of the hand, showing that subjects perceived more SPS under convergent focusing. No significant clusters of suppression were observed. These differences in the effects of focusing observed between the FV and BF conditions reveal that attentional enhancement operates whether visual input is available or not but attentional suppression requires visual input to operate correctly. Hence, SPS are not suppressed whenever visual input is not available. Overall, this suggests that, when interacting with orienting, visual input reduces enhancement and increases suppression, a finding that is entirely new since it intimates that modulation of tactile perception by vision as reported in previous studies comes from a combined effect of attentional enhancement and suppression.
Types of sensations

All eleven proposed sensations were reported at least once, and some subjects reported one additional sensation. There were no noticeable differences between the tested conditions for each sensation. However, the percentage of subjects reporting each sensation was not the same, as revealed by the Chi-square goodness-of-fit test ($\chi^2(13) = 79.8; P < 0.001$). Tingling was the most frequent sensation (18.1%), followed by beat/pulse (14.9%),...
cooling (13.3%), warming (12.7%), flutter (8.3%), tickle (7.3%), muscle stiffness (7%), vibration (6.4%) and numbness (5.7%). The least frequent sensations were skin stretch (2.3%), itch (1.8%), movement (0.5%), electric flux (0.1%) and skin stiffness (0.1%).

Variety of sensations

The viewing condition X focusing X tested hand interaction reached significance ($F(1,72) = 4.74; \ P < 0.05$). In order to better understand this interaction, the results of the two groups were submitted to separate ANOVAs with the focusing condition and the tested hand as within-subject factors. A significant focusing X tested hand interaction was found in the results of the FV group ($F(1,36) = 5.02; \ P < 0.05$; Fig. 1b). Post hoc Newman-Keuls tests showed that, in the left hand, the variety of SPS was bigger under convergent focusing (mean number of different SPS: 1.95) than under divergent focusing (1.60; $P < 0.05$), while no such difference was found in the right hand (convergent: 1.53; divergent: 1.60; NS). Furthermore, the left convergent condition yielded a larger variety of SPS than the right convergent condition ($P < 0.05$). No significant effects were found for the BF group.

Control experiments

The main experiment revealed that focusing modified the characteristics of SPS either alone or in combination with other factors. Participants were asked to focus their attention on the tested hand without further instructions and to look either toward it or away. It is possible that that some of them oriented toward a specific part rather than the whole hand. Besides, even though our previous investigation (Michael and Naveteur 2011) showed that a proximo-distal gradient can be obtained without contact between the hand and a stimulus, additional arguments could advantageously strengthen the idea that the gradient found in the main experiment is not due to such a contact. Two control
experiments were therefore designed in order to investigate (a) whether the characteristics of SPS vary as a function of the hand part at which gaze is directed and (b) whether a proximo-distal gradient can be obtained without any contact between the glabrous skin of the hand and a stimulus.

Gaze target experiment

The sample of the first control experiment was made of 24 female volunteers (mean age: 20.1 ± 1.6; mean body mass index: 22 ± 3 kg/m²) among which two left-handers and two ambidextrous (Oldfield 1971). The experiment was conducted under free viewing, and the target of gaze (fingers or the center of the palm) was manipulated at a within-subject level while the focus of attention was held constant, that is, on the whole hand. Other details of the procedure were the same as in the main experiment except that confidence ratings were not collected. All participants reported SPS in at least two conditions out of four. The main effect of gaze target failed to reach significance in the analysis of intensities ($F(1,20)=0.1$; NS), total spatial extent ($F(1,20)=1.49$; NS), and relative spatial extent ($F(1,20)=0.39$; NS). In the analysis of relative spatial extent, the main effect of anatomical segment reached significance ($F(3,60)=6.36$; $P<0.001$; distal: 24.7%; intermediate: 14.5%; proximal: 10.8%; palm: 11.7%). Topographical analyses revealed no significant differences between the two gaze targets. The results of all analyses suggest that gaze target does not exert a particular influence on the characteristics of SPS as far as attention is focused on the whole hand. The analysis of the variety of SPS did not yield any reliable effect.

Gradient in vividness experiment

The sample of the second control experiment was made of 80 right-handers (71 women and 9 men; mean age: 20.6 ± 2.1; mean body mass index: 21.1 ± 2.8 kg/m²). The experiment was conducted under free viewing. Subjects were required to gaze their hand turned palm-up without contact with any stimulus (i.e., hand in the air) and to note the intensity with which they felt each of 19 hand segments (5 of which were in the palm) on a reduced model of the hand (1 = just perceptible; 10 = very intense). Each hand was tested separately. The main effect of anatomical segment reached significance ($F(3,237)=66.04$; $P<0.001$; distal: 5.95; intermediate: 3.7%; proximal: 3.23%; palm: 3.99%). This result completes our previous observations (Michael and Navetuer 2011) that proximo-distal gradients can be obtained without the hand being in contact with any stimulus and even extends those findings by suggesting that the vividness with which subject perceive their hands also follows this gradient.

Discussion

The present study aimed at investigating the effects of visual input and attention on the perception of SPS arising on the hands. Subjects were asked to focus on one hand while they oriented toward or away from it, both conditions being completed either under free viewing or while blindfolded. It was found that attention and vision, both alone or in combination, modulated the reported SPS. In addition, SPS were unevenly distributed and a lateral dominance was found.

Effects of attention and vision

In agreement with the existing literature about exteroception (Honoré et al. 1989; Pierson et al. 1991; Navetuer and Honoré 1995; Rorden et al. 2002), focusing alone increased not only the perceived intensity of SPS, but also their frequency and topography. Visual input also enhanced the frequency and relative spatial extent of SPS, while no effect on the perceived intensity and total spatial extent was found. More frequent SPS and larger zones of SPS were reported in a large lateral area of the palm in the free viewing condition, suggesting that visual input overall increased perception of SPS. This tallies with reports on visual enhancement of exteroceptive tactile perception (Tipper et al. 1998; Kennett et al. 2001; Taylor-Clarke et al. 2002; Press et al. 2004; Macaluso et al. 2000; Serino et al. 2007; Fiorio and Haggard 2005; Forster and Eimer 2005), and changes in the functional activity of the somatosensory cortices with visual input (Schaefer et al. 2005, 2006, 2008), but it is also consistent with studies that have suggested that perception of bodily signals may be enhanced by vision (Weisz et al. 1988). Interestingly, contrary to the effects of attention, concentrated over the fingertips, that is, the highly sensitive zones of the glabrous area, the effects of vision were concentrated over the least sensitive zones, that is, the palm. The fact that no main effect of either factor was found in the analysis of the total spatial extent (i.e., percentage of shaded surface) of SPS is intriguing. It suggests that, even though intensity and surface are highly correlated, they are seemingly differentially sensitive to such factors.

In line with Macaluso et al. (2000) and Sambo et al. (2009), we found that visual input and focusing interacted. Such interactions were evidenced in the analysis of total and relative spatial extent of SPS, their topography and variety, but not intensity. However, our findings go way beyond the existing literature (Tipper et al. 1998; Forster and Eimer 2005; Sambo et al. 2009) by discovering some fundamental differences between the effects of attention under free viewing and under blindfolded conditions. Under free viewing conditions, no difference was found in the spatial extent of SPS between convergent and divergent focusing. In the
blindsight, however, a clear effect of focusing was observed, with total spatial extent being greater under convergent focusing. The topographical analyses showed that these differential effects of focusing as a function of viewing condition were a matter not of degree, but rather of changes in the attention mechanisms involved. In fact, the existence of two complementary but opposite effects was observed in the free viewing condition, and this may explain why no focusing effect was evidenced in the analysis of total and relative spatial extent: more SPS were observed in some areas of the hand and less in others, both under convergent focusing. This is reminiscent of the enhancement-suppression mechanisms of attention (Chelazzi et al. 1993; LaBerge 1995) observed in all sensory modalities and is quite similar to the results reported by Michael and Naveteur (2011), who suggested that attention enhances perception on areas of high sensitivity (such as the distal phalanges) which become natural processing targets. According to them, attention also suppresses SPS projected away from these most sensitive hand segments, yet having the propensity to interfere with the processing taking place near the most sensitive segments. This intimates that different hand segments may be somewhat independent as sites of attention-modulated sensations, a suggestion that is backed up by indirect findings on exteroceptive sensations (Galvez-Garcia et al. 2011). An overall coarse division of the hand in “more” (i.e., fingers) or “less” (i.e., palm) sensitive zones, as suggested by several physiological and psychophysical studies, probably makes more sense than a partition in smaller segments. According to this more global view, the exact location of enhancing and suppressing effects within a segment is of low relevance. At the present stage of knowledge, the distinction between more or less sensitive zones is revealed when subjects gaze toward or away from the tested hand (main experiment; see also Michael and Naveteur 2011), and not when they gaze the tested hand but toward each one of these zones separately (control experiment).

A different pattern was found in the blindfold condition. SPS were more frequent under convergent focusing and mostly located near the distal phalanx, corresponding therefore to the expected enhancing effect in sensitive areas. However, enhancing effects were also observed in areas where suppressive effects were found in the free viewing condition, and there is no suppressive effect in the blindfold condition. These entirely new results allow insight to be gained into the role of visual input as regards the perception of SPS. The attentional suppression of noisy SPS suggested by Michael and Naveteur (2011) is not operational without visual input, whereas the enhancing effect, observed both in the free viewing and in blindfold conditions, can operate without visual input. The occurrence of suppressing effects in the free viewing condition is only of interest because it elegantly supports the hypothesis that vision facilitates attentional selection of tactile locations due to the highly accurate spatial information it provides (Eimer 2004; Macaluso et al. 2000; Sambo et al. 2009). Two findings confirm this: the fact that the areas where suppression was observed in the free viewing condition showed enhancing effects in the blindfold condition, and the fact that the overall area of the enhancing effects was larger in the blindfold condition, which suggested that probably those SPS that could interfere were processed as relevant, but also that the difficulty to suppress caused enhancement to increase. This is reminiscent of the balance between enhancing and suppressive mechanisms suggested by models of attention (Michael et al. 2006). What is new is that SPS are modulated by visual input. Even though some previous behavioral studies failed to evidence any interactions between vision and orienting (Driver and Grossenbacher 1996; Tipper et al. 1998), the question of whether the source of effects of vision is facilitatory or inhibitory had already been asked (Tipper et al. 1998). Investigation of SPS may constitute the starting point toward an answer. Based mainly on the topographical analyses, we may assume that vision facilitates perception, as suggested through its main effect, but when interacting with orienting, vision enables better perception by promoting inhibition. To our knowledge, these are the very first results to suggest that vision promotes inhibition. A recent electrophysiological investigation (Cardini et al. 2011) put forward a similar interpretation of the effects of vision. The authors recorded somatosensory evoked potentials (SEPs) elicited by electrical stimulation of two adjacent fingers, either individually or simultaneously, while participants viewed either their own hand or an object. The observed suppression of SEPs produced by simultaneous stimulation increased when participants looked at the tested hand, suggesting that vision enhanced the spatial sensitivity of touch by increasing inhibition in the somatosensory cortex. Even though the level of analysis is not the same between the study of Cardini et al. (2011) and ours, we believe that their conclusions are in agreement with ours.

Other effects

Gradients

In agreement with our previous investigation (Michael and Naveteur 2011), the present study evidenced that SPS were reported all over the hand. However, their uneven distribution evoked a proximo-distal gradient despite a slight exception for the palm in the main experiment, which might tentatively be attributed to its functional importance for manipulatory activity. This seems to be a general distribution of SPS, which can also arise without the contact between the hand and any stimulus (Michael and Naveteur 2011 and control experiment in this paper). Even though the origin of
such a graded pattern is not yet firmly established, the suggestion is that it may originate from both peripheral and central factors (Vallbo and Johansson 1984). The involvement of receptors may confer a precise representation of what is felt and where, and yet it is still plausible that they are not always involved in the perception of SPS (for a review see Gallace and Spence 2008 and Longo et al. 2010). This is in line with the suggestion made by Duncan and Boynton (2007) that the divergence and convergence between the thalamus and cortex may account for variations in sensitivity better than variations in receptor density alone.

**Lateralized patterns**

In the main experiment, subjects reported more intense and larger SPS in their left hand were more confident about their location in the left hand, and topographical frequency was greater over the lower part of the palm of the left hand. Interacting effects of viewing condition and focusing were exclusively found in the left hand, as reflected through the analyses of topography and the variety of SPS. In keeping with neuroimaging studies (Tecchio et al. 1997; Sörös et al. 1999; Jung et al. 2003), we have already argued (Michael and Naveteur 2011) that this dominance is not attributable to differences in the cortical representation of the hands. Right hemispheric processes, however, such as tactual processing, spatial perception, spatial attention and interoception, could contribute separately or in combination to the rise of left hand dominance (e.g., Weinstein and Sersen 1961; Semmes 1965; Milner and Taylor 1972; Varney and Benton 1975; Benton et al. 1978; Dodds 1978; Vaitl 1996; Cameron and Minoshima 2002; Craig 2004). Another interpretation of the lateralized pattern is that the left hand of right-handers is probably actually less sensitive. In other words, subjects detect and localize SPS less accurately but, insofar as they are less confident about their location and extent, they tend to overestimate their intensity and surface in order to comply with the experimental procedure. The results of the confidence ratings, which were not collected in our previous study, rule out such a hypothesis. Subjects localized SPS in the left hand more confidently than in the right hand, which is the exact opposite of what would be expected. Furthermore, contrary to what might be expected if less confidence led subjects to overestimate the characteristics of SPS, confidence ratings correlated positively with intensity ratings and the proportion of shaded surfaces. Consequently, these findings do not support the confidence-overestimation interpretation.

What are the functions of spontaneous sensations?

The term “conscious image of the body” encompasses perceptions and sense impressions about the organization of one’s own body and, in some instances, how the body relates to that of others (Longo et al. 2010). Apart from the impact somatosensory (Gandevia and Phegan 1999), proprioceptive (de Vignemont et al. 2005), thermal, and nociceptive (Paqueron et al. 2003) modulations have on the conscious image of the body, vision certainly plays an essential role in shaping and calibrating it (Tipper et al. 1998; Press et al. 2004; Taylor-Clarke et al. 2002; Price 2006; Longo et al. 2010). Intriguing cases in neuropsychology show that the conscious body image can be selectively lost or affected in such a way that part of the body feels as if it has disappeared (Critchley 1953). This is known as asomatagnosia. Vision is seemingly also critical in maintaining the internal representation of the body, as attested by the report by Wolpert et al. (1998) of the case of an asomatagnostic patient whose right arm and leg used to fade gradually from consciousness, returning only when she looked at them. This surprising observation suggests that seeing the body allows its image to arise and be held in consciousness.

Do SPS contribute toward the creation and/or maintenance of a conscious body image? They are very common phenomena that can be experienced by anyone at any time. Our data support the view that their perception is modulated by factors such as attention and the availability of visual input, but also that they depend mainly on processes lateralized to the right cerebral hemisphere in right-handers. That these phenomena are so robust and can be easily perceived and described tells us very little about their function. Some of their characteristics, however, lead us to believe they might have some part to play in the conscious body image, or at least our image of our own hands. SPS are detected and described over the whole surface of the hand and are perceived as being sufficiently precise for there to be high levels of confidence as to their location and extent. Their qualities are also perceived as being so specific that subjects are able to identify them as tickles or tingling, etc. In the absence of any stimulus, the percept depends on the representation of the body part under investigation. Be the perception and the subjective report of SPS based on distorted body representations (Longo et al. 2010) are not disturbing at all—this is what we define as the conscious image of the body. In that way, SPS provide information about the spatial frontiers of the hands and thus about the perceived shape of that part of the body, but also what can be felt there, in a manner that could help the subject remain conscious of functionally important extremities (Naveteur et al. 2005). Interestingly, in our previous (Michael and Naveteur 2011) and present studies, orienting attention toward the hands changed how these SPS were perceived, but such a finding is hardly surprising if we assume that the body image is the representation over which attention is shifted (Wolpert et al. 1998) and is attentional in nature.
From our results, we can also assert that visual input determines at least in part the quality and quantity of the effects of attention on SPS, as is the case with exteroception (Macaluso et al. 2000; Macaluso 2006; Sambo et al. 2009). The findings also suggest that seeing other objects while trying to attend to the source of SPS produces interference, which ties in nicely with Wolpert et al. (1998) who asserted that attention and vision enable the image of the body to be consciously maintained and that attending to somewhere else and looking elsewhere may cause this image to fade from consciousness.

Another point that might signal an active functional role for SPS in the conscious body image is their lateralization. They are more frequent over the left hand than the right hand in right-handers, which could reflect activity in the posterior parietal cortex (PPC) mostly of the right cerebral hemisphere (Critchley 1953), and probably the right insula, which plays an important role in interoceptive awareness (Craig 2004). Deficits of body image (i.e., asomatognosia) and self-awareness (i.e., anosognosia) are most frequent following right hemisphere lesions. If SPS have any role to play at all in the conscious body image, the fact that their distribution follows the proximo-distal sensitivity gradient may be a sign that the conscious image of the body possesses certain properties similar to those of the real body (Ramachandran and Hirstein 1998).

Alternatives

Michael and Navetuer (2011) argued that the inherent methodological limits of the investigation of SPS leave room to doubt that what subjects reported were really SPS. In fact, the possibility that some of the reported sensations were actually exteroceptive cannot be ruled out, especially since natural oscillations of the body (i.e., sway) could allow actual input from the environment and therefore produce sensations (Jeka 1997). There are several arguments that run counter such an alternative. First, postural sway may probably explain SPS that feel like vibrations, movement and skin stretch, but, for instance, in the main experiment, the sum of these SPS did not exceed 10% of the reported SPS. SPS that were most frequent (tingling, warming, cooling) cannot really be attributed to postural sway. Second, it was shown that closing the eyes increases sway (Jeka 1997), whereas we found that SPS were reduced in the absence of visual input.

We are confident therefore that the most important findings cannot be attributed to contact between the hands and the table, nor to spontaneous postural sway.

Conclusions

The aim of the present study was to investigate the role of visual input and attention, alone and in combination, in the perception of SPS. First, our findings replicate those reported recently, in that (1) SPS occurring on the hands are distributed according a proximo-distal gradient, despite being reported over the whole surface of the hand, (2) they are more frequent in the left hand, and (3) attentive vision enhances some of them while suppressing others. From these three characteristics, it is clearly established that SPS are relatively stable phenomena. The present results also build considerably on those of our previous study by showing that visual input enhances the perception of SPS but also allows for the attentional suppression of noisy SPS. Even though the function of SPS is not clear, it is not unreasonable to suspect that they are involved in the construction and maintenance of a conscious image of the body. To date, several questions still remain unanswered as far as the nature and specificity of SPS are concerned. Rising the question of the unity of the interoceptive system, SPS the participants had to report were quite different between them. Should different sensations be analyzed separately? Further detailed investigations should be dedicated for better understanding. Another outstanding question is whether it is really the vision of the hand itself, which is monitored for SPS, or if the vision of a configuration depicting a human hand (cf. Gallace and Spence 2008) would be sufficient for effects to arise. These issues open the way to new investigations of these phenomena.

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