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The tickly homunculus and the origins of spontaneous sensations arising on the hands

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ABSTRACT

Everyone has felt those tingling, tickly sensations occurring spontaneously all over the body in the absence of stimuli. But does anyone know where they come from? Here, right-handed subjects were asked to focus on one hand while looking at it (convergent focusing) and while looking away (divergent focusing) and subsequently to map and describe the spatial and qualitative attributes of sensations arising spontaneously. The spatial distribution of spontaneous sensations followed a proximo-distal gradient, similar to the one previously described for the density of receptive units. The intensity and spatial extent of the reported sensations were modulated by the focusing condition, especially in respect of the left hand. Convergent focusing acted upon the conscious perception of sensations by enhancing or suppressing them. To our knowledge, this is the first ever study of spontaneous sensations, and it offers considerable insight into their sources. The presence of the proximo-distal distributional gradient is a clear sign that receptive units are involved. The enhancement/suppression effects also confirm the involvement of attention. Finally, left-hand dominance suggests several right-hemisphere processes may be involved, such as spatial and tactile perception, and probably interoception.

1. Introduction

Everyone knows what it is like to feel spontaneous sensations (SPS), those tingling, tickly and other sensations usually perceived during periods of rest and without external triggers. But, does anybody know what causes them? To date, this question has never been investigated, even though there are good reasons to think they are the result of an interaction of several different factors. This study is a first step forward.

The fact that SPS occur all over the body and feel similar to sensations driven by external events and those received from inside the body suggests the skin and musculoskeletal apparatus (joints, tendons and muscles) as major sources. Mechanoreceptors (Johnson, 2001) and thermoreceptors (Green, 2004) are scattered over the surface of the body, producing an uneven distribution of tactile (Weinstein, 1968) and thermal (Stevens & Choo, 1998) sensitivities. The densities of cutaneous receptors also vary at local levels. As far as hands are concerned, there is considerable evidence that tactile (Johansson & Vallbo, 1979; Vallbo & Johansson, 1984) and thermal (Li, Petrini, Defrin, Madeleine, & Arendt-Nielsen, 2008) sensitivities are not the same all over, and yet combining the distribution of all the different types of receptors with that of joint

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receptors, muscle spindles and Golgi tendon organs (Burke, Gandevia, & Macefield, 1988) produces a proximo-distal gradient. There is an impressive accumulation of receptive units in the fingertips, but their density diminishes sharply over the rest of the fingers, and less sharply thereafter in the palm of the hand. Psychophysical studies have shown that, at least for tactile perception, sensitivity as assessed via various stimulus detection and discrimination procedures follows this gradient (Johansson & Vallbo, 1979; Vallbo & Johansson, 1976, 1978). Most of the aforementioned receptive units show spontaneous activity at rest and at room temperature (Hulliger, Nordh, Thelin, & Vallbo, 1979; Johansson & Vallbo, 1979; Knibestöl, 1975; Macefield, Gandevia, & Burke, 1990; Ochoa & Torebjörk, 1983). One study even evidenced spontaneous ongoing activity in itch fibers as paralleled to intense localized itching (Schmelz et al., 2003). Could it be that SPS stem from the spontaneous activity of receptors? If so, two patterns of results were to be expected: (a) like the receptors, spontaneous sensations would be distributed over the whole hand, and (b) like the receptors, the densities would follow a proximo-distal gradient.

Studies focusing on the perception of sensory events offer several lines of evidence showing that attention is a prerequisite for their conscious perception (Posner, 1994). For instance, given the close relationship between attention and eye movements (Rizzolatti, Riggio, Dascola, & Umiltà, 1987; Shepherd, Findlay, & Hockey, 1986), it not surprising that directing one's eyes towards the stimulated part of the body causes cutaneous perceptual thresholds to be lower (Naveteur & Honoré, 1995) than when they are directed away (see also Honoré, Bourdeaud'hui, & Sparrow, 1989; Kennett, Taylor-Clarke, & Haggard, 2001; Pierson, Bradshaw, Meyer, Howard, & Bradshaw, 1991; Press, Taylor-Clarke, Kennett, & Haggard, 2004; Rorden, Greene, Sasine, & Baylis, 2002; Serino, Farnè, Rinaldesi, Haggard, & Làdavas, 2007). This is in keeping with the suggestions by Dehaene and Changeux (2005) that activity in both the attention system and brain sensory areas exerts a facilitatory effect on conscious perception of sensory external stimuli, as well as with the point made by Schubert and colleagues (2006), according to whom attention processes are instrumental for conscious perception of tactile stimuli. These studies support the idea of strong links between attention and conscious perception, but deal with sensations driven by external events, not SPS. The fact that SPS are usually perceived during rest periods (i.e., when attention is free to explore any event or sensation) and less so when we are occupied with other activities (i.e., when attention is oriented elsewhere), leads to the hypothesis that orienting attention to the part of the body being explored would enhance conscious perception of those sensations, whilst directing it away would reduce it. Thus it would parallel the influence of attention on somatosensory perception.

Signals from the receptive organs are naturally processed in the corresponding areas of the somatosensory cortex, the interface between receptors and attention. The body representation in the somatosensory cortex is highly modulated by attention, as evidenced through single unit recordings in monkeys (Hsiao, O'Shaughnessy, & Johnson, 1993; Hyvärinen, Poranen, & Jokinen, 1980) and brain imaging techniques in humans (Hämäläinen, Hiltunen, & Titievskaja, 2002; Mima, Nagamine, Nakamura, & Shibasaki, 1998; Noppeney, Waberski, Gobbelé, & Buchner, 1999). For instance, directing attention to the stimulated area of the body induces reliable changes in the firing rates of single neurons (Hsiao, O'Shaughnessy, & Johnson, 1993), influences magnetic field strengths (Iguchi, Hoshi, Tanosaki, Taira, & Hashimoto, 2002; Mima et al., 1998), and enlarges activated areas (Hämäläinen et al., 2002). Furthermore, there is evidence that somatosensory representation of the digits shifts according to the direction of spatial attention (Noppeney et al., 1999). Another interesting observation, made with single unit recordings in animals (Hsiao et al., 1993) and brain imaging in humans (Hämäläinen et al., 2002; Iguchi et al., 2005), is that attention regulates the cortical representation of hands by enhancing task-relevant inputs and suppressing other noise inputs. This enhancement-suppression combination is a known attention-related phenomenon (Chelazzi, Miller, Duncan, & Desimone, 1993; LaBerge, 1995) and might also be expected to modulate the cortical coding of SPS; it is still unclear whether such coding takes place within the somatosensory cortex. Interestingly, there is evidence of large-scale, low frequency spontaneous neuronal fluctuations in the human somatosensory cortex during rest (Nir et al., 2008), although the functional significance of these neuronal events is not well understood.

To sum up, the putative presence of a proximo-distal gradient, and enhanced perception of spontaneous sensations arising in some locations and suppression of others when attending to the tested hand, would constitute behavioral evidence of attentional modulation of cortical somatosensory coding of signals spontaneously triggered by receptors. Furthermore, as exteroceptive tactile perception changes with age (Stevens & Patterson, 1995), it may be expected that the description of SPS change also with age. But as age influences body mass (Kuczmarski, Kuczmarski, & Najjar, 2001), it can be expected that the description of SPS changes also with body mass. We examined these issues by asking subjects to focus on one hand for a short time, either while looking at it or while looking at a salient item in the opposite direction, and then to map the intensity, location and extent of any spontaneous sensations they felt. The results back all of our hypotheses and even offer an additional argument about lateralized cortical processes.

2. Main experiment

2.1. Methods

2.1.1. 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 score was smaller than 0.50), had a history of neurologic or psychiatric disease, had taken psychoactive substances (e.g., marijuana, antidepressants, anxiolytics, etc.) in the 3 months leading up to the testing session, and if they reported no SPS in more than two of the four tested conditions. Of the 84 undergraduates from the University of Lyon