Cognition 166 (2017) 174–183

Contents lists available at ScienceDirect

Cognition

journal homepage: www.elsevier.com/locate/COGNIT

Original Articles

Unconscious integration of multisensory bodily inputs in the peripersonal space shapes bodily self-consciousness

Roy Salomon [a,b,c,1], Jean-Paul Noel [a,b,d,1], Marta Łukowska [e], Nathan Faivre [a,b,f], Thomas Metzinger [g,h], Andrea Serino [a,b,1,*], Olaf Blanke [a,b,i,1,*]

[a] Center for Neuroprosthetics, School of Life Sciences, Ecole Polytechnique Fédérale de Lausanne, Lausanne, Switzerland
[b] Laboratory of Cognitive Neuroscience, Brain Mind Institute, Ecole Polytechnique Fédérale de Lausanne, Lausanne, Switzerland
[c] Gonda Multidisciplinary Brain Research Center, Bar-Ilan University, Ramat-Gan, Israel
[d] Vanderbilt Brain Institute, Vanderbilt University, Nashville, USA
[e] Consciousness Lab, Institute of Psychology, Jagiellonian University, Cracow, Poland
[f] Centre d'Economie de la Sorbonne, CNRS UMR 8174, Paris, France
[g] Philosophisches Seminar/Gutenberg Research College, Johannes Gutenberg-Universität, Mainz, Germany
[h] Frankfurt Institute for Advanced Studies, Frankfurt, Germany
[i] Department of Neurology, University Hospital, Geneva 1211, Switzerland

ARTICLE INFO

Article history:
Received 14 April 2016
Revised 17 May 2017
Accepted 17 May 2017

Keywords:
Consciousness
Multisensory integration
Peripersonal space
Bodily self-consciousness
Continuous flash suppression
Visual awareness

ABSTRACT

Recent studies have highlighted the role of multisensory integration as a key mechanism of self-consciousness. In particular, integration of bodily signals within the peripersonal space (PPS) underlies the experience of the self in a body we own (self-identification) and that is experienced as occupying a specific location in space (self-location), two main components of bodily self-consciousness (BSC). Experiments investigating the effects of multisensory integration on BSC have typically employed supra-threshold sensory stimuli, neglecting the role of unconscious sensory signals in BSC, as tested in other consciousness research. Here, we used psychophysical techniques to test whether multisensory integration of bodily stimuli underlying BSC also occurs for multisensory inputs presented below the threshold of conscious perception. Our results indicate that visual stimuli rendered invisible through continuous flash suppression boost processing of tactile stimuli on the body (Exp. 1), and enhance the perception of near-threshold tactile stimuli (Exp. 2), only once they entered PPS. We then employed unconscious multisensory stimulation to manipulate BSC. Participants were presented with tactile stimulation on their body and with visual stimuli on a virtual body, seen at a distance, which were either visible or rendered invisible. We found that participants reported higher self-identification with the virtual body in the synchronous visuo-tactile stimulation (as compared to asynchronous stimulation; Exp. 3), and shifted their self-location toward the virtual body (Exp.4), even if stimuli were fully invisible. Our results indicate that multisensory inputs, even outside of awareness, are integrated and affect the phenomenological content of self-consciousness, grounding BSC firmly in the field of psychophysical consciousness studies.

1. Introduction

Based on clinical and experimental research in humans, it has been proposed that multisensory integration is a key mechanism for self-consciousness. In particular, bodily self-consciousness (BSC) has been shown to depend on the integration of multisensory bodily stimuli (Blanke, 2012; Blanke, Slater, & Serino, 2015; Ehrsson, 2012a; Tsakiris, 2010). Research has focused on two central aspects of BSC: people normally self-identify with a given body, which they perceive as their own (self-identification) and they experience their self at the location of their body (self-location) (Blanke, 2012; Blanke & Metzinger, 2009). The notion that BSC depends on multisensory integration of bodily inputs is evidenced by neurological patients who present deficits in multisensory integration together with an altered perception of their own body (Blanke, Landis, Spinelli, & Seeck, 2004; Blanke, Ortigue,

* Corresponding authors at: Laboratory of Cognitive Neuroscience, Ecole Polytechnique Fédérale de Lausanne (EPFL), Lausanne 1015, Switzerland.

E-mail addresses: andrea.serino@epfl.ch (A. Serino), olaf.blanke@epfl.ch (O. Blanke).

[1] These authors contributed equally to this work.

http://dx.doi.org/10.1016/j.cognition.2017.05.028
0010-0277/

Landis, & Seeck, 2002), and by experimental manipulations of BSC in healthy subjects using multisensory conflicts (Ionta et al., 2011; Lenggenhager, Tadi, Metzinger, & Blanke, 2007; Petkova & Ehrsson, 2008; Petkova, Khoshnevis, & Ehrsson, 2011; Salomon, Lim, Pfeiffer, Gassert, & Blanke, 2013). For example, in the full body illusion, viewing an avatar's body being stroked, while concurrently receiving the same tactile stimulation on one's own body, makes participants self-identify with the avatar (Ehrsson, 2007; Petkova & Ehrsson, 2008) and induces changes in self-location such that subjects perceive themselves closer to the avatar's position (Ionta et al., 2011; Lenggenhager et al., 2007).

Under normal conditions, multisensory body-related stimuli occur within a limited distance from the body, which defines the peripersonal space (PPS Serino et al., 2015). Accordingly, neuronal populations have been described both in monkeys and in humans integrating somatosensory stimulation on the body with visual and/or auditory stimuli specifically when presented close to the body (Graziano & Cooke, 2006; Ladavas & Serino, 2008; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997). PPS and BSC are thought to involve common neural structures in premotor, posterior parietal, and temporo-parietal cortex (Blanke et al., 2015; Grivaz, Blanke, & Serino, 2017; Makin, Holmes, & Ehrsson, 2008) and it has recently been shown that the full body illusion leads to a shift in PPS from the physical body toward the virtual body that participants identify with (Noel, Pfeiffer, Blanke, & Serino, 2015), compatible with an extension of the PPS boundary (Serino, Canzoneri, Marzolla, di Pellegrino, & Magosso, 2015). These data link processing and integration of multisensory stimuli within PPS to self-consciousness, and to BSC in particular (Blanke et al., 2015; Noel, Cascio, Wallace, & Park, 2016).

Conscious experience has also been related to the integration of sensory information in the brain by other authors (Dehaene & Naccache, 2001; Mudrik, Faivre, & Koch, 2014; Tononi, 2008). Indeed, consciousness is characterized by a unity of experience in which information from multiple sensory modalities is integrated and bound together (Bayne, 2002; James, Burkhardt, Bowers, & Skrupskelis, 1981). Recent experimental work has shown that non-visual stimuli that are consciously perceived may be integrated with stimuli rendered invisible through various masking paradigms (i.e. auditory (Alsius & Munhall, 2013; Lunghi, Morrone, & Alais, 2014), tactile (Lunghi & Alais, 2013; Lunghi, Binda, & Morrone, 2010; Salomon, Galli, et al., 2015), olfactory (Zhou, Jiang, He, & Chen, 2010), proprioceptive (Salomon, Lim, Herbelin, Hesselmann, & Blanke, 2013) and vestibular (Salomon, Kaliuzhna, Herbelin, & Blanke, 2015)). It was further shown that even a subliminal auditory and a subliminal visual stimulus can be integrated despite unawareness (Faivre, Mudrik, Schwartz, & Koch, 2014; Noel, Wallace, & Blake, 2015). It is unknown, however, whether integration of unconscious multisensory events affects self-consciousness, and BSC in particular, which is often considered a distinct and specific form of conscious content (Dehaene & Changeux, 2011; Faivre, Salomon, & Blanke, 2015; Gallagher, 2000).

Previous research on the multisensory basis of BSC focused on the integration of sensory inputs that are presented above the visual and tactile thresholds for conscious access. Yet as it has been argued that BSC is based on low-level and pre-reflexive brain mechanisms, it is possible that the sensory events shaping the experience of the self need not be consciously perceived. While there is no experimental evidence suggesting that the multisensory integration processes of BSC do not require conscious awareness of the multisensory stimuli, interactions between unconscious multimodal stimuli have been shown in humans (see above) (Faivre et al., 2014; Salomon, Kaliuzhna, et al., 2015; Salomon, Lim, Herbelin, et al., 2013) and at the neuronal level in anesthetized animals (Graziano, Hu, & Gross, 1997; Meredith & Stein, 1986; Stein & Stanford, 2008). Here, in a series of four experiments, we tested for the first time whether multisensory integration of bodily stimuli underlying BSC also occurs for signals presented below the threshold of conscious perception. We first asked whether tactile stimuli on the body are preferentially integrated with visual stimuli presented within; as compared to outside the PPS, when visual inputs were subliminal and tactile inputs supraliminal (Exp. 1) or when visual were subliminal and tactile inputs were near-threshold (Exp. 2). Next, we investigated whether it is possible to manipulate BSC by using visuo-tactile stimulation administered below the threshold for conscious access. To this aim, we coupled tactile stimulation on the body with invisible synchronous visual stimuli on a virtual body to induce the full body illusion (Lenggenhager et al., 2007) and tested whether this would affect self-identification, as assessed by questionnaires (Exp.3) and self-location, as assessed by the location of PPS boundaries (Exp. 4).

2. Methods

2.1. Participants

In total 98 participants (31 females, mean age = 23.0 ± 2.7) were included in this series of experiments. Thirty-two subjects took part in Exp. 1, 15 in Exp. 2, 25 in Experiment 3, and 26 in Exp. 4 (the first experiment being a between-subject experimental design, while the latter three being within-subjects). All participants were right-handed, had normal or corrected-to-normal visual acuity, reported normal hearing and touch, and had no history of psychiatric or neurological disorder. All volunteers provided written informed consent to participate in the study, which was approved by the Brain Mind Institute Ethics Committee for Human Behavioral Research of the EPFL, and conducted in accordance with the Declaration of Helsinki.

2.2. Materials and procedure

2.2.1. Experiment 1

Visual stimuli consisted of a three-dimensional virtual white wireframe ball either looming toward or receding from the participants' face (Fig. 1A). The ball, presented in stereoscopy, travelled approximately 2 m in virtual space at a velocity of 50 cm/s until making fictive contact with the participant's face, or in the opposite direction in the case of receding stimuli. Visual stimuli were presented on a head-mounted display (HMD, VR1280 Virtual Research Systems, Inc., Santa Clara, CA, USA) with a resolution of 1280 × 1024 pixels, representing a 60-degree diagonal field of view, at 60 Hz. Half the participants performed the task while the visual stimuli presented were visible (henceforth: Visible group), whereas for the other half of participants (henceforth: Invisible group) the dynamic visual stimulus was suppressed via Continuous Flash Suppression (CFS; Tsuchiya & Koch, 2005). CFS was achieved by presenting circular high-contrast dynamic noise patches suppressors (''Mondrians''), flashed rapidly (10 Hz) to the participants' dominant eye, as determined prior to the study with the Miles test (Miles, 1930). See Supplementary Information online for a full description of the continuous flash suppression procedure and control experiments.

In addition to the visual stimuli, participants' were outfitted with a vibrotactile device (Precision MicroDrives shaftless vibration motors), placed on the forehead. Vibrotactile stimulation was presented supra-threshold for 100 ms. Participants provided speeded responses to vibrotactile stimulation with a wireless gamepad (XBOX 360 controller, Microsoft), which they held in their right hand. In-house software ExpyVR (freely available at http://lnco.epfl.ch/expyvr) was used for the rendering and