



Original Articles

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



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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.

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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,

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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 suprathreshold (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://lnc.epfl.ch/expyvr>) was used for the rendering and

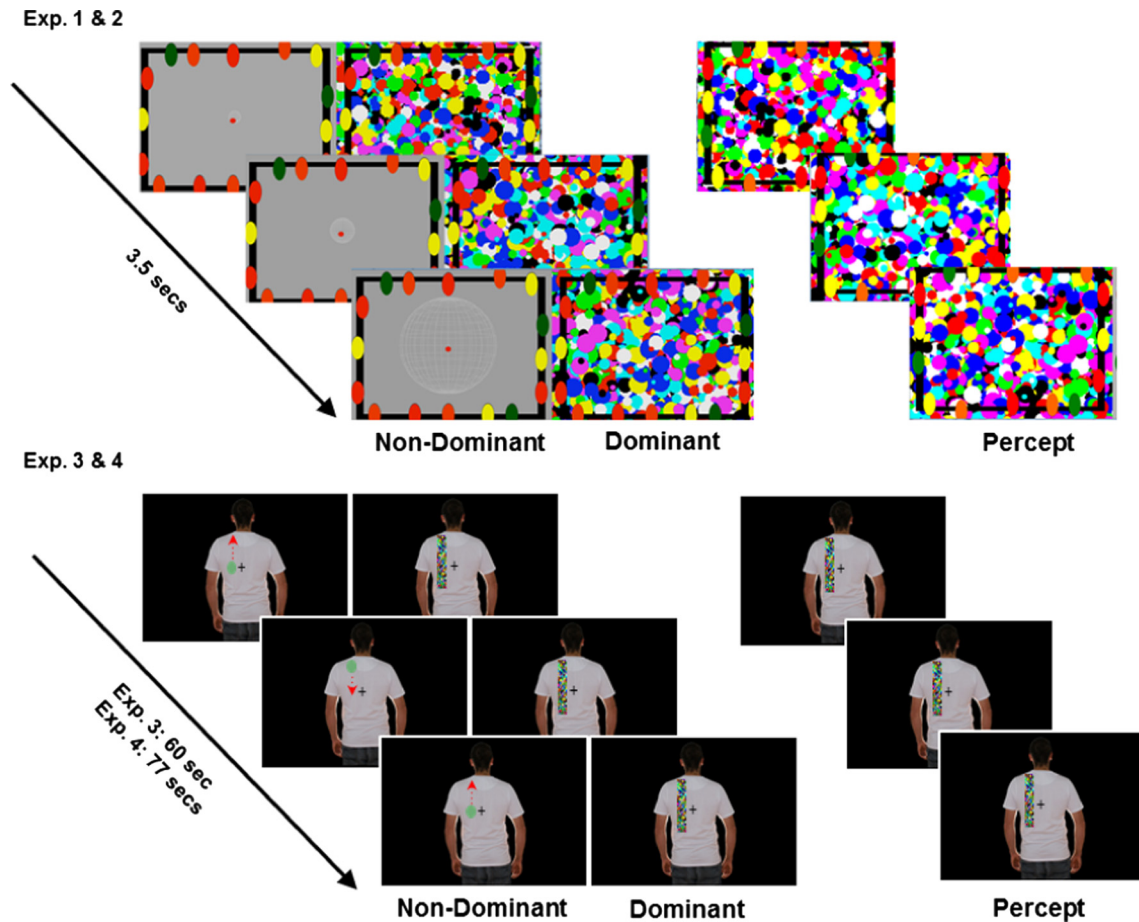


Fig. 1. Experimental design. Top. Experimental stimuli in the Invisible condition in Exp. 1 & 2. A wireframe ball approaching the participants' face was presented to the non-dominant eye while highly salient colored masks were rapidly (10 Hz) flashed to the dominant eye (CFS masking). Due to CFS, participants perceived the masks, while the approaching ball was invisible. Bottom. Experimental stimuli in the Invisible condition in Exp. 3 & 4. An image of a body with a moving dot on the back was presented to the non-dominant eye. The dot could be moving synchronously or asynchronously to the tactile stimulation on the participants' back. Critically, CFS masking of the region of the dot movement in the Invisible trials rendered the dot invisible, thus, both in the synchronous and asynchronous stimulation condition the percept was of a body image with rectangular flashing masks only.

presentation of visual and vibrotactile stimuli. Reaction times (RTs) were measured relative to the onset of tactile stimulation.

On experimental trials (70% of total trials) both tactile and visual stimulation were administered. The beginning of every trial was indicated by the presentation of a red fixation cross participants were to fixate upon. Then, on experimental trials, after a variable delay of 500–1000 ms (uniform distribution), a wireframe ball travelled toward (looming) or away from (receding) the participant's face. At one of seven possible visual stimulus onset asynchronies (vSOA; $T_1 = 0.5$, $T_2 = 1.0$, $T_3 = 1.5$, $T_4 = 2.0$, $T_5 = 2.5$, $T_6 = 3.0$, or $T_7 = 3.5$ s), a brief vibrotactile stimulation was delivered. We used the perceived distance from the visual stimulus at the moment of tactile stimulation as the independent variable. Since, for the looming stimuli this distance is inversely proportional to the elapsed looming time, we coded $T_1 = D_7$, $T_2 = D_6$, and so on. In the case of receding visual stimuli, spatial and temporal dimensions map onto each other linearly and positively such that $T_1 = D_1$, $T_2 = D_2$, and so on. Previous studies using the same protocol showed that RTs to tactile stimulation decrease once a stimulus enters the participant's PPS (Canzoneri, Magosso, & Serino, 2012; Serino, Noel et al., 2015; Teneggi, Canzoneri, di Pellegrino, & Serino, 2013). Here we investigated whether the distance-dependent modulation of tactile RT is present even when the approaching visual stimuli entering PPS are invisible, suggesting that multisensory integration within the PPS occurs also in the

absence of visual awareness. In order to control for a mere temporal effect (i.e., participants might become faster at later delays), we also included a control condition, whereby receding visual stimuli were administered, and for which we predicted no distance-dependent modulation of RT for face stimulation (see e.g., Serino, Noel et al., 2015). Additionally, in 20% of trials (baseline trials), no visual stimulation was given. Reaction times to unimodal tactile stimuli were recorded at T_1 and T_7 , and used as baseline to correct for a spurious temporal effect and in order to confirm that speeding in RTs as a consequence of visual stimuli within PPS reflected true multisensory facilitation. Finally, 10% of trials were catch trials, in which a visual stimulus was delivered (either approaching or receding) but no tactile stimulation was presented, and thus participants were to withhold from responding. These catch trials were employed in order to monitor task compliance and avoid an automatic association between visual stimulation and motoric response.

2.2.2. Experiment 2

Materials and procedure followed as for Experiment 1, with two exceptions. First, visible and invisible conditions of visual stimulation were administered within-subjects, in separate blocks, with a counter-balanced order between participants. Secondly, tactile target stimuli were presented with a miniature solenoid, (M & E Solve, Rochester, UK; <http://www.me-solve.co.uk>, ~1–2.5 V, 5 ms) and

was surrounded by 4 vibrotactile motors (see above and [Supplementary Information](#)) serving as tactile masks, which were active throughout the duration of a trial. The intensity of the tactile target stimulus on the face was titrated with a staircase procedure before each experimental block so to be detected in 60% of trials, without visual stimulation (see [Supplementary Information](#) for further details). The intensity of the tactile masks was kept constant.

2.2.3. Experiment 3

The procedure to induce the full body illusion consisted in applying tactile stimulation on the participants' back and visual stimulation on a virtual body (avatar; H: 20.5° W: 11.3°), seen through a HMD. Tactile stimulation was administered by using a haptic robotic system (Salomon, Lim, Pfeiffer, et al., 2013). Visual stimuli consisted of a colored visual dot (size: H: 0.7°, W: 0.7) that was moving up and down along the left side of the avatar's back (see Fig. 1B). In the critical condition inducing the illusion, the movement of the haptic robot was fully synchronized temporally and spatially with that of the dot on the avatar's back. In the control, asynchronous condition, the visual and tactile stimulation were uncorrelated by using different visual and tactile motion profiles. In order to make the pattern of visuo-tactile stimulation invisible to the participants, visual stimuli was administered in a CFS paradigm, whereby the visual dot was presented to the non-dominant eye, while Mondrians (8.9° × 1°) were presented to the dominant eye. In order to measure phenomenological experience associated with the full-body illusion, two experimental questions, adapted from previous designs (Ionta et al., 2011; Lenggenhager et al., 2007; Petkova & Ehrsson, 2008; Petkova et al., 2011; Salomon, Lim, Pfeiffer, et al., 2013) were administered after each 60 s of visuo-tactile stimulation: (i) self-identification (Q1: 'How strong was the feeling that the body you saw was you?') and (ii) illusory touch (Q2: 'How strong was the feeling that the touch you felt originated from the body you saw?'). Participants responded using a scale from 1 (Completely disagree) to 10 (Completely agree). Following these two questions, masking efficiency was assessed by asking participants to answer three additional questions: subjective target visibility (Q3: 'Did you see anything but the Mondrians?', possible responses; Nothing/Something/ Fully), explicit knowledge of the target's color (Q4: 'What color was the dot?', possible responses; Blue/Green), and its spatio-temporal relation to the tactile stimulation (Q5: 'Was movement of the dot synchronized with the touch you felt on your back?' possible responses; yes/no). No control questions regarding phenomenology associated with the FBI were employed, as on the critical unconscious trials participants were unaware of the visuo-tactile manipulation and thus immune to suggestibility or expectancy biases for which these questions control.

2.2.4. Experiment 4

The procedure to induce the full body illusion was identical to that of Experiment 3, with two differences: the omission of the non-masked (visible) condition and longer visuo-tactile stimulation lasting 77 s per trial, allowing intermingled testing of PPS. In order to assure that CFS was efficiently preventing visual awareness; participants were required on each trial to press a button in case they saw the visual dot. Intermingled with visuo-tactile stimulation, PPS was measured via an audio-tactile paradigm (Canzoneri et al., 2012; Galli, Noel, Canzoneri, Blanke, & Serino, 2015; Noel et al., 2014). The task was similar to that described for Experiment 1 and 2, with the exception that an auditory (broadband noise), and not a visual stimulus approached the participant's chest. Six different audio-tactile distances were probed (see [Supplementary Information online](#)). We used audio-tactile stimulation, instead of visuo-tactile stimulation (as in Exp. 1 & 2), in order to keep the experimental manipulation used to induce

the full body illusion (visuo-tactile stroking) and that used to measure its effect on peripersonal space (audio-tactile interaction) orthogonal with each other (as in Noel et al., 2015).

2.3. Data analyses

Trials in which participants reported seeing the visual stimuli, correctly identified the color or did not respond to the awareness questions were removed from the analysis (28% of trials in Exp. 1 and 21% in Exp.2; 4% in Exp. 3 and 12% in Exp. 4). We note that the high number of discarded trials is likely due to the challenge in masking dynamic stimuli as well as the meticulous care taken in identifying trials in which trials were not fully suppressed.

For PPS measurement (Exp. 1–2 & 4), we first calculated on a subject-per-subject basis the mean RT (Exp. 1 & 4) and detection rates (Exp. 2) for the baseline unimodal tactile conditions. Subsequently, the fastest mean baseline condition (i.e., T1) was subtracted from the participant mean in all the other conditions to provide a measure of facilitation induced on tactile processing by visual or auditory stimuli perceived at a different distance from the participant's body (See (Noel et al., 2014, 2015) for a similar approach). Subsequently, on a subject-per-subject basis, RT or detection rates relative to baseline were fitted to both linear and sigmoidal curves (see Canzoneri et al., 2012, for details). For each experiment we modelled the data with the best fit (linear for Exp. 1 & 2, and sigmoidal in Exp. 4 – See [Supplementary Information](#)) and then compared the values extracted from the fitting procedure across conditions. In Experiment 3, we analysed responses to BSC questions (Q1 & Q2) during the visible and invisible conditions using repeated measures ANOVA with synchronicity (Synchronous/Asynchronous) and visibility (Visible/Invisible) as within-subject factors. Normality of the data was assessed using the Shapiro-Wilk test, and non-parametric tests were used when the normality assumption was violated. When interactions were present, non-parametric one-tailed (based on previous findings showing the presence of the illusion in synchronous but not asynchronous condition) Wilcoxon rank order tests were used to explore modulation of BSC within each synchronicity level and corrected for multiple comparisons using the Holm-Bonferroni approach such that the family-wise error rates were controlled with $\alpha = 0.05$. We supplemented this analysis with a Bayesian analysis (Jasp 8.0.1, Love et al., 2015; Rouder, Speckman, Sun, Morey, & Iverson, 2009) using default priors (i.e., r scale = $\sqrt{2/2}$) and reported BF10 factors for null effects (for more details see [Supplementary materials](#)).

3. Results

3.1. Invisible looming stimuli within the PPS affect tactile perception (Exp. 1)

We analysed RT to the tactile stimulation as a function of the different distances of the virtual ball and its direction, in the visible and invisible conditions. As shown in Fig. 2A, there was a clear distance dependent modulation of RT, as a function of the location of the visual stimulus, both for the Visible and Invisible conditions. This was not the case for Receding visual stimuli, excluding the possibility that the present finding was a mere temporal effect (see [Supplementary material online, Fig. S2A](#)). Next, we fitted individual data to a linear function (which was the model to best fit the results; see [Supplementary analysis online](#)), comparing the slope of the function, as a measure of how strongly tactile processing was influenced by the location of the task-irrelevant visible and invisible approaching balls. The presence of a positive slope, steeper for looming visual stimuli, would indicate a stronger

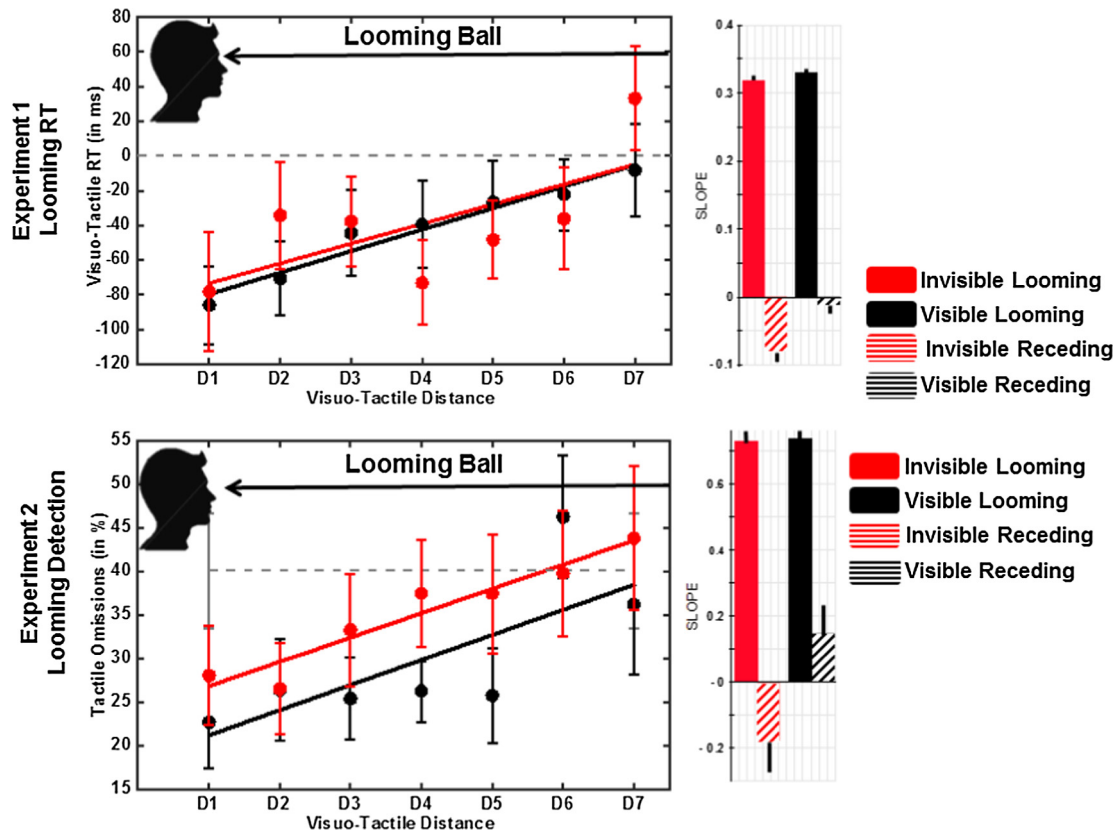


Fig. 2. PPS in absence of awareness. (A) Experiment 1. RTs to tactile targets as a function of the distance of the approaching visual stimulus. In order to show a truly multisensory visuo-tactile facilitation effect, RTs are reported as the difference between responses to tactile stimuli when they were coupled with visual stimulation and responses to tactile stimulation alone. Baseline unimodal tactile RTs (administered in 20% of trials) are thus by definition equal to zero (illustrated by the dashed line; (Noel et al., 2015)). Data for both the conditions in which the looming visual stimuli was visible (black) and invisible (red) were fitted to linear functions (see [Supplementary material online](#)). Error bars indicate ± 1 S.E.M. For both conditions, tactile processing speeded up as the visual stimulus approached the body. (B) Exp. 2. Omission to tactile targets as a function of the distance of the approaching visual stimulus (Convention follows as in A). Tactile stimulation was set to be detected on 60% of trials, (i.e., omitted on 40% of unimodal tactile trials). Perception increased as the ball approached the body, both in the visible (black) and invisible (red) conditions.

multisensory integration effect for visual stimuli entering the PPS. The slope values were submitted to a 2×2 mixed ANOVA with Ball Direction (Looming and Receding), as within-subjects factor, and Condition (Visible and Invisible), as between-subject factor. The main effect of Ball Direction was significant ($F(1,28) = 69.52$, $p < 0.0001$, partial $\eta^2 = 0.71$): the slope of the function was positive only for looming (mean slope = 0.33 ± 0.02) and not for receding (mean slope = 0.07 ± 0.02) stimuli. There was no main effect of Condition ($p = 0.64$), nor a Condition \times Ball Direction interaction ($p = 0.93$). A Bayesian analysis (see [Supplementary material](#)) indicated strong evidence ($BF_{10} = 8.61$) supporting the model with no interaction between Condition and Ball Direction. Thus, the modulation of tactile processing due to the distance of the task-irrelevant visual stimuli at the time of touch was found for both visible and invisible balls. Importantly, the positive value of the looming slope was significantly different from zero for both conditions (visible: $t(14) = 11.80$, $p < 0.001$; invisible: $t(16) = 11.60$, $p < 0.001$). Hence, a distance-dependent modulation of tactile processing was found when task-irrelevant looming stimuli, that were not consciously perceived, were presented, indicating that multisensory integration within the PPS occurs even in absence of awareness for the visual stimulus.

3.2. Invisible looming stimuli increase tactile awareness (Exp. 2)

In Experiment 2, we investigated whether invisible visual stimuli, occurring within the PPS, modulate not only the processing of

supra-threshold tactile stimuli, but also enhance the perception of near-threshold tactile stimulation. To this aim, we used a staircase procedure (see [Supplementary Information online](#)), so that tactile targets were perceived in 60% of trials, when presented alone. Then, near-threshold tactile target stimuli were coupled with looming (or receding, as a control condition) visual stimuli that were again either fully visible or rendered invisible through CFS (as in Exp. 1). We predicted that visible and invisible visual stimuli occurring within PPS would also boost the detection of near-threshold tactile stimuli (but only for looming stimuli), thus increasing subjects' accuracy in reporting tactile stimulation. [Fig. 2B](#) reports the percentage of missed tactile targets as a function of the distance of looming visual stimuli and shows that tactile detection increased as the virtual ball approached the subjects (see [Fig. 2B](#)). Data were fitted with a linear function (as the best model fitting the data, see [Supplementary analyses online](#)) and analysed as in Exp. 1. The main effect of Ball Direction was significant ($F(1,14) = 287.03$, $p < 0.001$, partial $\eta^2 = 0.95$), with steeper slopes for looming (mean slope = 0.73 ± 0.03) as compared to receding visual stimuli (mean slope = 0.07 ± 0.001) (see [Fig. S2B](#)). As in Exp. 1, there was no main effect of Condition ($p = 0.31$), nor a Condition \times Ball Direction interaction ($p = 0.18$), meaning that the same spatially dependent modulation of tactile perception was found both in the visible and in the invisible conditions. This was supported by Bayesian analysis (see [Supplementary material](#)) that showed evidence ($BF_{10} = 4.75$) supporting a model with no interaction between Condition and Ball Direction. To summarize, visual

stimuli within the PPS, enhance the perception of near-threshold tactile stimuli on the body, even when they are rendered fully invisible.

3.3. Invisible visuo-tactile conflicts modulate self-identification (Exp. 3)

Having demonstrated visuo-tactile integration for unconscious sensory inputs within PPS, we next asked whether we could modulate BSC by manipulating the spatio-temporal congruency of visuo-tactile stimuli (Blanke, 2012; Ehrsson, 2007; Lenggenhager et al., 2007), even when the multisensory conflict was not consciously perceived. To this aim, in Exp. 3, we used visuo-tactile stimulation to induce the full body illusion using either fully visible stimuli (as done in previous studies) or identical visual stimuli rendered invisible by means of CFS. Participants received above-threshold tactile stimulation on their back, administered by means of a robotic stroking set up (Ionta et al., 2011; Salomon, Lim, Pfeiffer, et al., 2013), while concurrently seeing an avatar from behind, presented binocularly through a head-mounted display. The avatar was shown on the HMD as receiving tactile stimulation on the back, represented by a colored dot moving at the same speed and to the same extent as the tactile stimulation participants received on their back (see Fig. 1B). In the synchronous condition, normally inducing the full body illusion (Ionta et al., 2011; Lenggenhager et al., 2007; Salomon, Lim, Pfeiffer, et al., 2013), the visual stimulation on the avatar's body and tactile stimulation on the participant's body were corresponding. An asynchronous visuo-tactile stimulation, in which the visual and tactile stimulations were unrelated, was administered as a control condition. The experiment was run in a 2×2 factorial design, in which we manipulated the synchrony of stimulation, as well as the visibility of the moving dot: it was either fully visible, as in the standard full body illusion, or rendered invisible by masking the region of visual stroking with Mondrian patterns flashed to the dominant eye (see [Supplementary Information online](#) and (Salomon, Galli, et al., 2015) for details). On each trial, participants were stroked for 1 min. Stimulus visibility was strictly controlled (see [Supplementary Information](#) for full details). Trials in which participants reported seeing a visual stimulus apart from the masks were removed from analysis (3% of trials). In the remaining fully suppressed trials participants were at chance for reporting the dot's color and visuo-tactile synchrony (mean accuracy 49% and 50% respectively see [Supplementary materials](#) for further analysis). The modulation of BSC was measured with two questions (modified from (Lenggenhager et al., 2007)) probing self-identification (Q1: 'How strong was the feeling that the body you saw was you?') and illusory touch (Q2: 'How strong was the feeling that the touch you felt originated from the body you saw?'), using a scale from 1 (Completely disagree) to 10 (Completely agree).

Participants' responses indicated that a change in BSC was obtained by means of synchronous stimulation both in the visible and in the invisible conditions. First, a repeated measures ANOVA on Q1 scores with synchrony (Synchronous/Asynchronous) and visibility (Visible/Invisible) as within-subject factors revealed a significant main effect of synchrony ($F(1, 19) = 24.47$, $p = 0.00009$, partial $\eta^2 = 0.56$), with higher self-identification in the synchronous ($M = 4.0$, $S.E.M. = 0.59$) than in the asynchronous ($M = 3.2$, $S.E.M. = 0.59$) condition. Moreover, the main effect of visibility was significant ($F(1, 19) = 8.08$, $p = 0.01$, partial $\eta^2 = 0.29$), with considerably higher self-identification ratings in the visible ($M = 4.1$, $S.E.M. = 0.55$) than in the Invisible ($M = 3.0$, $S.E.M. = 0.45$) condition. The interaction between synchrony and visibility was also significant ($F(1, 19) = 7.41$, $p = 0.014$, partial $\eta^2 = 0.28$), with larger differences in self-identification as a function of synchrony ratings in the visible (Visible-synchronous $M = 4.8$, $S.E.M.$

$= 0.56$, Visible-asynchronous $M = 3.5$, $S.E.M. = 0.51$) than the invisible (Invisible-synchronous $M = 3.2$, $S.E.M. = 0.44$, Invisible-asynchronous $M = 2.8$, $S.E.M. = 0.48$) condition. Importantly, non-parametric one tailed Wilcoxon paired samples tests (Holm-Bonferroni corrected) revealed significantly higher ratings for self-identification with the avatar after synchronous as compared to asynchronous visuo-tactile stroking both in the Invisible ($Z = 2.17$; $p = 0.014$, Cohen's $d = 0.51$) and the Visible ($Z = 3.39$; $p = 0.0003$, Cohen's $d = 0.96$; see Fig. 3) condition. Thus, albeit self-identification was generally low (i.e., ~ 4 within a 0–10 range), both the visible and invisible synchronous visuo-tactile stroking evoked a significantly higher degree of body ownership than their asynchronous counterparts. While the effect size was larger in the visible than invisible condition (conscious, Cohen's $d = 0.96$ vs. unconscious Cohen's $d = 0.51$), both conditions showed a medium to large effect size (Cohen, 1977). This result shows that visuo-tactile stimulation led to relatively higher explicit self-identification responses in a synchrony-dependent manner even when participants were not aware of the type of visual stimulation they were receiving.

Responses to the second question regarding illusory touch, revealed a significant main effect of synchrony, with higher misattribution of touch ($F(1, 19) = 23.89$, $p = 0.0001$, partial $\eta^2 = 0.55$) in the synchronous ($M = 3.3$, $S.E.M. = 0.45$) than in the asynchronous ($M = 2.5$, $S.E.M. = 0.41$) condition. The main effect of Visibility was not significant ($F(1, 19) = 0.2$, $p = 0.87$, partial $\eta^2 = 0.001$). The interaction between visibility and synchrony was significant ($F(1, 19) = 12.23$, $p = 0.002$, partial $\eta^2 = 0.39$), with larger differences in illusory touch as a function of synchrony in the visible (Visible-synchronous $M = 3.6$, $S.E.M. = 0.56$, Visible-asynchronous $M = 2.3$, $S.E.M. = 0.45$) than the invisible (Invisible-synchronous $M = 3$, $S.E.M. = 0.43$, Invisible-asynchronous $M = 2.8$, $S.E.M. = 0.45$) condition. Here, as for self-identification, non-parametric Wilcoxon paired samples tests (Holm-Bonferroni corrected) indicated that participants misattributed tactile stimulation to the virtual body significantly more strongly in the case of synchronous as compared to asynchronous stimulation not only in the visible ($Z = 3.66$; $p = 0.00013$, Cohen's $d = 1.03$), but even in the invisible ($Z = 1.89$; $p = 0.02$, Cohen's $d = 0.47$) condition, i.e. when they were not aware of the spatio-temporal pattern of visuo-tactile stimulation (see Fig. 3). Together, these findings show that modulations of BSC by visuo-tactile conflict occur even when the visual stimuli, and the resulting multisensory conflict, are not consciously experienced. This result is the first empirical evidence that explicit changes in the phenomenal content of BSC arise by manipulating multisensory cues in the absence of awareness.

3.4. Invisible visuo-tactile conflicts modulate perceived self-location (Exp. 4)

We finally investigated if an unconscious multisensory manipulation of BSC would also modulate self-location (Blanke, 2012; Lenggenhager, Mouthon, & Blanke, 2009; Lenggenhager et al., 2007). Previously, we showed that during the full body illusion (induced with fully perceived visual and tactile stroking), the boundaries of PPS representation, as assessed by means of an audio-tactile interaction task, shifted from being centred at the participants' body, toward the location of the avatar's body with whom the participants identified (Noel et al., 2015). Here, we applied the same paradigm, but tested whether a similar change in PPS, reflecting a change in self-location, can be achieved when visuo-tactile stimulation applied to induce the full body illusion is not visible to the participant. To this aim, epochs of masked visuo-tactile stimulation (as in Exp. 3) were intermingled with audio-tactile trials measuring PPS (see Methods and [Supplementary information](#) for details). Perceptual awareness for the visual

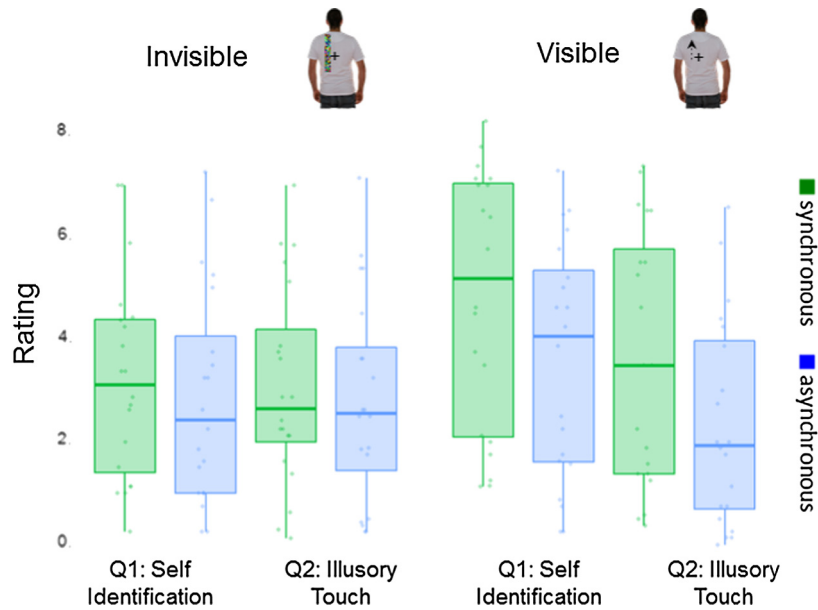


Fig. 3. Modulation of self-identification by an invisible multisensory conflict. Boxplots of responses to BSC questions relating to self-identification and illusory touch for synchronous and asynchronous visuo-tactile stimulation. Significant modulation was found for the full body illusion condition (synchronous vs. asynchronous visual tactile stimulation) for both invisible (left) and visible (right) conditions. Whiskers represent data range. Dots represent individual participants' scores.

stimuli was controlled as in Exp. 3 and only trials in which the participants were completely unaware were included in the analysis (12% of trials were excluded, see [Supplementary Information](#)). The PPS paradigm was similar to that used in Exp. 1, but we used auditory looming stimuli, instead of visual stimuli, in order to keep the form of multisensory stimulation used to induce the full body illusion (visuo-tactile) orthogonal to that used to test its effect on perceived self-location (auditory-tactile). Participants were requested to respond as quickly as possible to a tactile vibration administered on their trunk, while task-irrelevant sounds approached their body. [Fig. 4A](#) shows RT to tactile targets as a function of the distance of the sound at the time of tactile stimulation. In order to test whether the boundaries of PPS varied between the synchronous and the asynchronous stroking conditions, RTs were fitted with a sigmoidal function ([Canzoneri et al., 2012](#); [Serino et al., 2015](#); [Teneggi et al., 2013](#)). The sigmoidal's central point,

representing an index of the location of PPS boundary, and slope, representing an index of the gradient of PPS representation were compared (Synchronous vs. Asynchronous). The central point location was significantly different in the Synchronous ($M = 4.5$, $S.E.M. = 0.22$) as compared to the Asynchronous ($M = 3.3$, $S.E.M. = 0.25$) condition ($t(20) = 2.452$, $p = 0.024$, partial $\eta^2 = 0.198$), indicating that participants' PPS boundary was more distant from the participant's body, and thus closer to the avatar's body, in the Synchronous condition than in the Asynchronous control condition. No main effect of synchrony was found on the slope ($p = 0.34$), which was however different from 0 in both conditions (both p -values < 0.03), indicating a distance-dependent modulation of tactile processing. Thus, the manipulation of multisensory cues, of which participants were not aware of (yet inducing changes in the phenomenal content BSC, Exp. 3), caused a shift in self-location toward the virtual body participants identified with, as

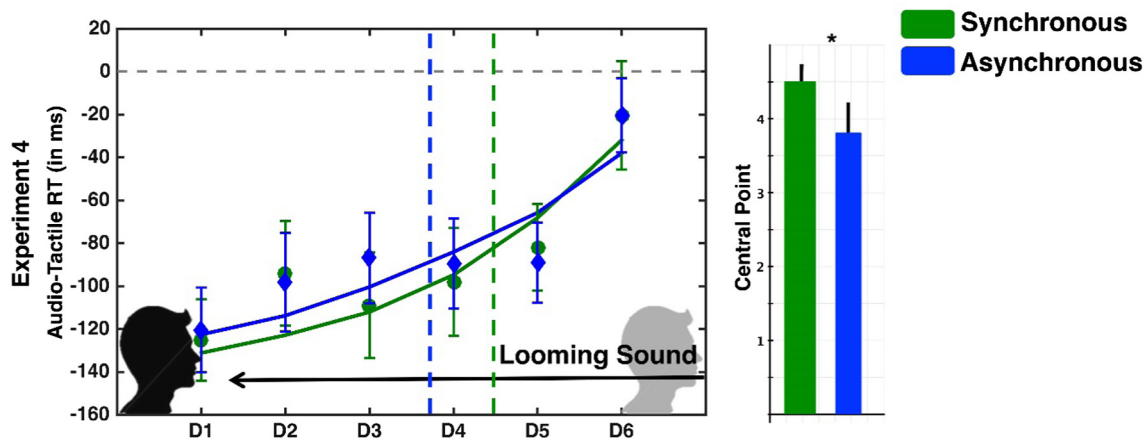


Fig. 4. Modulation of self-location by an invisible multisensory conflict. RTs to tactile targets as a function of the distance of the approaching auditory stimuli (D7-D1) and the visuo-tactile stroking condition (synchronous in green and asynchronous in blue). RTs are reported as the difference between responses to tactile stimuli when they were coupled with visual stimulation and response to tactile stimulation alone. Baseline unimodal tactile RTs (administered on 20% of trials) are thus by definition equal to zero (illustrated by the dashed line). Data was fitted to a sigmoidal function. Error bars indicate ± 1 S.E.M. The vertical dashed lines indicate the mean central point of the sigmoidal fitting, computed as a measure of the distance at which sounds start affecting RTs and analysed in order to quantify PPS boundaries. This value was located at a farther distance in the synchronous (green) as compared to the asynchronous (red) visuo-tactile stroking conditions, indicating a more extended PPS in the former case.

shown here based on the effect on the PPS boundary (Noel et al., 2015).

4. Discussion

4.1. Unconscious multisensory integration in PPS

The self is essential to our understanding of consciousness (Blanke & Metzinger, 2009; Damasio, 2012; Metzinger, 2004) and recent work has highlighted the role of multisensory integration and PPS in self-consciousness, especially in BSC (for reviews see Blanke, 2012; Blanke et al., 2015; Ehrsson, 2012b; Faivre, Arzi, Lunghi, & Salomon, 2017; Noel et al., 2016). The present study brings novel comprehensive evidence that multisensory integration in PPS does not require conscious awareness and, importantly, that these unconscious multisensory processes modulate the phenomenological content of BSC.

In the first two experiments we show that multisensory integration of bodily signals within the PPS occurs when visual stimuli are presented below the perceptual threshold. This was demonstrated by showing that visuo-tactile interaction in PPS occurs when visual stimuli are rendered invisible (Exp.1), and in the second experiment even when the tactile stimuli associated with invisible visual stimuli were presented near the tactile threshold (Exp.2). Thus, conscious perception of visual and tactile stimuli is not required for multisensory integration of bodily signals within the PPS. To the best of our knowledge, these findings represent one of the first accounts of increased tactile sensitivity in healthy subjects as a function of the distance of a stimulus in a different modality (e.g. Cléry, Guipponi, Wardak, & Hamed, 2015), and the first to demonstrate this effect unconsciously. In this manner, the current report represents an interesting link with neuropsychological observations (e.g. Farnè, Pavani, Meneghello, & Làdavas, 2000), reporting enhanced cross-modal interaction between contralesional tactile stimulation and ipsilesional visual (or auditory) stimulation in the near space (as opposed to the far space) in patients suffering from cross-modal extinction due to right-brain damage. In the patients, contralesional tactile stimulation is by definition below the threshold of conscious perception (under condition of bilateral stimulation). Thus, the present findings directly bridge classical neuropsychological research, which firstly demonstrated dedicated multisensory processing for stimuli within the PPS in humans, and studies on PPS in healthy subjects.

Previous behavioural findings showed that the processing of invisible stimuli is affected by concurrent non-visual stimuli above perceptual threshold (Alsius & Munhall, 2013; Lunghi et al., 2010, 2014; Maruya, Yang, & Blake, 2007; Salomon, Lim, Herbelin, et al., 2013; Zhou et al., 2010). Data from Experiment 1 demonstrate the complementary effect, in which invisible visual stimuli impact processing of supra-threshold tactile stimuli. Experiment 2 further extends this finding, by showing that an invisible visual stimulus even modulates awareness for tactile stimuli near the tactile threshold, thus extending recent work revealing interactions between two unconscious stimuli during sleep (Arzi et al., 2012) and wakefulness (Faivre et al., 2014). The present study is the first report, to the best of our knowledge, of a multisensory interaction between near-threshold tactile and visual stimuli and in revealing that this unconscious visuo-tactile effect depends on the distance from the body (PPS). The present results are compatible with neurophysiological studies showing that, on anesthetized animals, at a single neuron level, multisensory integration occurs in absence of awareness, and that this effect is modulated by the spatial alignment of multisensory inputs (Stein & Stanford, 2008). More specifically concerning the spatial modulation of these multisensory responses as a function of distance from the body, although most

studies on bimodal and trimodal neurons mapping PPS in monkeys have been performed on awake animals, there is also evidence of bimodal responses for stimuli within PPS in anesthetized monkeys (Graziano et al., 1997). However, a neural integrative response to multisensory inputs in the absence of awareness does not imply that those inputs can affect conscious perception. The present findings, therefore, extend those neurophysiological data by showing that an unperceived visual stimulus affects the processing of a fully perceived (Experiment 1) or even of a near-threshold (Experiment 2) tactile event in a distance dependent manner.

These effects might rely on the activation of PPS neurons in the premotor and posterior parietal cortex (Bremmer et al., 2001; Graziano, Cooke, & Taylor, 2000; Huang, Chen, Tran, Holstein, & Sereno, 2012), which are activated not only by above thresholds sensory inputs occurring close to the body (Macaluso & Maravita, 2010; Serino, Canzoneri, & Avenanti, 2011), but possibly also by below-threshold sensory events. Indeed, beyond classical feedforward mechanisms, recent imaging studies have shown representations of body related haptic and proprioceptive signals in visual regions (Astafiev, Stanley, Shulman, & Corbetta, 2004; David et al., 2007; Ionta et al., 2011; Limanowski & Blankenburg, 2016) allowing integration of these signals and their propagation to the posterior parietal cortex and the premotor cortex where bimodal and trimodal neurons mapping the PPS are located (Bremmer et al., 2001; Huang et al., 2012). Furthermore, a recent study employing MEG has revealed that unseen visual information is maintained and propagates from occipital visual regions to parietal and frontal regions (King, Pescetelli, & Dehaene, 2016). Thus, the visual receptive field of PPS neurons may be activated by invisible visual inputs, when these are presented within the PPS, thus interacting with tactile stimulation on the body, speeding up tactile RT or enhancing tactile perception as found in the current experiments.

4.2. Unconscious multisensory integration underlies BSC

Recent accounts suggest that modulation of BSC through manipulation of multisensory inputs, as during the full body illusion, depends on the extension of the visual receptive fields of bimodal PPS neurons (Blanke, 2012; Ehrsson, 2012b; Makin et al., 2008; Noel et al., 2015). Based on this and the findings of Experiments 1 and 2, we predicted that sub-threshold multisensory stimulation may also impact BSC and subjective responses about the self. This departs from previous studies using visuo-tactile stimulation to manipulate BSC, in which the applied stimuli were well above the perceptual thresholds (e.g. Ehrsson, 2007; Lenggenhager et al., 2007; Petkova & Ehrsson, 2008; Salomon, Lim, Pfeiffer, et al., 2013). While it is evident that we are not consciously aware of most multisensory processing (including those involved in BSC), to date it is not known whether unconscious multisensory stimuli can influence the content of BSC and how such effects with unconscious stimulation compare to effects obtained with conscious stimulation. Here we show that subjective and objective responses about the phenomenal content of BSC are modulated by unconscious multisensory stimuli and that this modulation, although weaker, is qualitatively comparable to modulations obtained with fully conscious stimuli. Experiment 3 indicated that for two patterns of stimulation, which were perceptually identical to the participants – i.e., seeing an avatar (without seeing the stroking) and feeling tactile stimulation – different explicit self-related experiences were induced that depended on an unperceived temporal relationship between visual and tactile stimulation (i.e., synchronous vs. asynchronous). At the subjective level – in Experiment 3 – while the response scores for the self-identification and illusory touch questions were relatively weak in both the visible and invisible conditions, they showed a consis-

tent synchrony dependent modulation, in line with previous studies showing a central role for multisensory integration in BSC (e.g. Ehrsson, 2007; Lenggenhager et al., 2007; Petkova & Ehrsson, 2008; Salomon, Lim, Pfeiffer, et al., 2013). At an implicit level – in Experiment 4 – we show that this unconscious multisensory integration not only alters explicit self-identification, but also impacts where participants implicitly perceived themselves to be (implicit self-location), as we observed a shift of the PPS boundary toward the virtual body, in the same direction as induced when multisensory stimuli are administered in fully conscious manner (Noel et al., 2015).

Consciousness is characterized by a unity of experience in which information from multiple sensory modalities is integrated and bound together (Bayne, 2002; James et al., 1981) and, accordingly, current theories of consciousness postulate that integration of information, including unconscious stimuli, is critical for perceptual awareness (Baars, 2002; Mudrik et al., 2014; Tononi, 2008). Recent work has shown that consciously perceived stimuli can be integrated with subliminal stimuli (Alsius & Munhall, 2013; Lunghi et al., 2010; e.g. Lunghi et al., 2014; Salomon, Galli, et al., 2015; Salomon, Kaliuzhna, et al., 2015; Salomon, Lim, Herbelin, et al., 2013; Zhou et al., 2010; for review see Deroy et al., 2016). The present data show that unconscious multisensory integration also extends to a distinct form of conscious content (Dehaene & Changeux, 2011; Faivre et al., 2015; Gallagher, 2000), i.e., self-consciousness targeted experimentally through multisensory stimulation affecting BSC. Thus, we provide the first experimental support to the idea that the multisensory integrative processes underlying BSC are enabled in the absence of stimulus awareness. Importantly, the present findings also show that the phenomenological content of self-consciousness may be manipulated by unconscious multisensory bodily signals. We consider this empirical observation to be particularly significant, as theoretical approaches influential in driving empirical efforts in BSC postulate the existence of a pre-reflective self. This pre-reflective self is the experience of oneself as the subject of experience, prior to any reflexive form of consciousness, whereby the subject takes himself as an object of consciousness (Legrand, 2006). This pre-reflective self is posited to emanate from multisensory and sensorimotor integration and to be the base for higher-order forms of self-representations (Blanke & Metzinger, 2009; Salomon, in press). However, the demonstration of the role of integrated sensory signals to modulate bodily self-consciousness without perceptual awareness was lacking. Thus, BSC is strongly grounded in the field of psychophysical consciousness studies, suggesting that comprehensive notions of self-consciousness may follow similar principles. It is, nonetheless, important to highlight that future work may further characterize the phenomenological experience associated with the full-body illusion under conscious and unconscious conditions. Using additional illusory paradigms, such as the body swapping illusion (e.g. Petkova & Ehrsson, 2008) or manipulations of ownership based on visuomotor correspondences (Banakou, Groten, & Slater, 2013; Banakou & Slater, 2014) as well as further neuroimaging (e.g., fMRI) and physiological (e.g., skin conductance) measurements and further phenomenological probing (e.g., expanded questionnaires) could increase our understanding of the mechanisms underlying unconscious modulations of BSC.

Author contributions

R.S., J.P.N., A.S., and O.B., conceived of the experiments, which were performed by R.S., J.P.N., M.L., and analysed by R.S., J.P.N., and A.S. N.F.; T.M. provided valuable analysis tools and conceptual contributions to the manuscript, which was written by R.S. and A.S. All authors edited and approved the final version of the manuscript.

Competing interests

We declare we have no competing interests.

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Appendix A. Supplementary material

Data from all experiments are available at osf.io/bnypm. Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.cognition.2017.05.028>.

References

- Alsius, A., & Munhall, K. G. (2013). Detection of audiovisual speech correspondences without visual awareness. *Psychological Science*, 24(4), 423–431.
- Arzi, A., Sheldesky, L., Ben-Shaul, M., Nasser, K., Oksenberg, A., Hairston, I. S., & Sobel, N. (2012). Humans can learn new information during sleep. *Nature Neuroscience*, 15(10), 1460–1465.
- Astafiev, S. V., Stanley, C. M., Shulman, G. L., & Corbetta, M. (2004). Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nature Neuroscience*, 7(5), 542–548.
- Baars, B. J. (2002). The conscious access hypothesis: Origins and recent evidence. *Trends in Cognitive Sciences*, 6(1), 47–52.
- Banakou, D., Groten, R., & Slater, M. (2013). Illusory ownership of a virtual child body causes overestimation of object sizes and implicit attitude changes. *Proceedings of the National Academy of Sciences*, 110(31), 12846–12851.
- Banakou, D., & Slater, M. (2014). Body ownership causes illusory self-attribution of speaking and influences subsequent real speaking. *Proceedings of the National Academy of Sciences*, 111(49), 17678–17683.
- Bayne, T. (2002). *The unity of consciousness*.
- Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nature Reviews Neuroscience*, 13(8), 556–571.
- Blanke, O., Landis, T., Spinelli, L., & Seeck, M. (2004). Out-of-body experience and autoscopic of neurological origin. *Brain*, 127(2), 243.
- Blanke, O., & Metzinger, T. (2009). Full-body illusions and minimal phenomenal selfhood. *Trends in Cognitive Sciences*, 13(1), 7–13.
- Blanke, O., Ortigue, S., Landis, T., & Seeck, M. (2002). Stimulating illusory own-body perceptions. *Nature*, 419(6904), 269–270.
- Blanke, O., Slater, M., & Serino, A. (2015). Behavioral, neural, and computational principles of bodily self-consciousness. *Neuron*, 88(1), 145–166.
- Bremmer, F., Schlack, A., Shah, N. J., Zafiris, O., Kubischik, M., Hoffmann, K.-P., ... Fink, G. R. (2001). Polymodal motion processing in posterior parietal and premotor cortex: A human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron*, 29(1), 287–296.
- Canzoneri, E., Magosso, E., & Serino, A. (2012). Dynamic sounds capture the boundaries of peripersonal space representation in humans. *PLoS ONE*, 7(9), e44306.
- Cléry, J., Guipponi, O., Wardak, C., & Hamed, S. B. (2015). Neuronal bases of peripersonal and extrapersonal spaces, their plasticity and their dynamics: Knowns and unknowns. *Neuropsychologia*, 70, 313–326.
- Cohen, J. (1977). *Statistical power analysis for the behavioral sciences*. New York: Academic Press.
- Damasio, A. (2012). *Self comes to mind: Constructing the conscious brain*. Random House Digital Inc.
- David, N., Cohen, M. X., Newen, A., Bewernick, B. H., Shah, N. J., Fink, G. R., & Vogeley, K. (2007). The extrastriate cortex distinguishes between the consequences of one's own and others' behavior. *Neuroimage*, 36(3), 1004–1014.
- Dehaene, S., & Changeux, J. P. (2011). Experimental and theoretical approaches to conscious processing. *Neuron*, 70(2), 200–227.

- Dehaene, S., & Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: Basic evidence and a workspace framework. *Cognition*, 79(1), 1–37.
- Deroy, O., Faivre, N., Lunghi, C., Spence, C., Aller, M., & Noppeney, U. (2016). The complex interplay between multisensory integration and perceptual awareness. *Multisensory Research*, 29, 585–606. <http://dx.doi.org/10.1163/22134808-00002529>.
- Ehrsson, H. H. (2007). The experimental induction of out-of-body experiences. *Science*, 317(5841), 1048.
- Ehrsson, H. H. (2012a). The concept of body ownership and its relation to multisensory integration. In: *The New Handbook of Multisensory Processes*, B. E. Stein (Ed.), *The New Handbook of Multisensory Processes* (pp. 775–792). MA: MIT Press (Cambridge).
- Ehrsson, H. H. (2012b). *The concept of body ownership and its relation to multisensory integration*.
- Faivre, N., Arzi, A., Lunghi, C., & Salomon, R. (2017). Consciousness is more than meets the eye: A call for a multisensory study of subjective experience. *Neuroscience of Consciousness*, 3(1).
- Faivre, N., Mudrik, L., Schwartz, N., & Koch, C. (2014). Multisensory integration in complete unawareness evidence from audiovisual congruency priming. *Psychological Science*, 25(11), 2006–2016.
- Faivre, N., Salomon, R., & Blanke, O. (2015). Visual consciousness and bodily self-consciousness. *Current Opinion in Neurology*, 28(1), 23–28.
- Farnè, E., Pavani, F., Meneghello, F., & Ládavas, E. (2000). Left tactile extinction following visual stimulation of a rubber hand. *Brain*, 123(11), 2350–2360.
- Gallagher, S. (2000). Philosophical conceptions of the self: Implications for cognitive science. *Trends in Cognitive Sciences*, 4(1), 14–21.
- Galli, G., Noel, J. P., Canzoneri, E., Blanke, O., & Serino, A. (2015). The wheelchair as a full-body tool extending the peripersonal space. *Frontiers in Psychology*, 6, 639. <http://dx.doi.org/10.3389/fpsyg.2015.00639>.
- Graziano, M. S., & Cooke, D. F. (2006). Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia*, 44(6), 845–859.
- Graziano, M. S. A., Cooke, D. F., & Taylor, C. S. R. (2000). Coding the location of the arm by sight. *Science*, 290(5497), 1782–1786.
- Graziano, M. S., Hu, X. T., & Gross, C. G. (1997). Visuospatial properties of ventral premotor cortex. *Journal of Neurophysiology*, 77(5), 2268–2292.
- Grivaz, P., Blanke, O., & Serino, A. (2017). Common and distinct brain regions processing multisensory bodily signals for peripersonal space and body ownership. *Neuroimage*, 147, 602–618.
- Huang, R. S., Chen, C. F., Tran, A. T., Holstein, K. L., & Sereno, M. I. (2012). Mapping multisensory parietal face and body areas in humans. *Proceedings of the National Academy of Sciences of the United States of America*, 109(44), 18114–18119.
- Ionta, S., Heydrich, L., Lenggenhager, B., Mouthon, M., Fornari, E., Chapuis, D., ... Blanke, O. (2011). Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective. *Neuron*, 70(2), 363–374.
- James, W., Burkhardt, F., Bowers, F., & Skrupskelis, I. (1981). *The principles of psychology*. Harvard Univ Press.
- King, J.-R., Pescetelli, N., & Dehaene, S. (2016). Brain mechanisms underlying the brief maintenance of seen and unseen sensory information. *Neuron*, 92(5), 1122–1134.
- Ladavas, E., & Serino, A. (2008). Action-dependent plasticity in peripersonal space representations. *Cognitive Neuropsychology*, 25(7–8), 1099–1113.
- Legrand, D. (2006). The bodily self: The sensori-motor roots of pre-reflective self-consciousness. *Phenomenology and the Cognitive Sciences*, 5(1), 89–118.
- Lenggenhager, B., Mouthon, M., & Blanke, O. (2009). Spatial aspects of bodily self-consciousness. *Consciousness and Cognition*, 18(1), 110–117.
- Lenggenhager, B., Tadi, T., Metzinger, T., & Blanke, O. (2007). Video ergo sum: Manipulating bodily self-consciousness. *Science*, 317(5841), 1096.
- Limanowski, J., & Blankenburg, F. (2016). Integration of visual and proprioceptive limb position information in human posterior parietal, premotor, and extrastriate cortex. *The Journal of Neuroscience*, 36(9), 2582–2589.
- Love, J., Selker, R., Marsman, M., Jamil, T., Dropmann, D., Verhagen, A. J., ... Wagenmakers, E.-J. (2015). *JASP (Version 0.8.1) [Computer software]*.
- Lunghi, C., & Alais, D. (2013). Touch interacts with vision during binocular rivalry with a tight orientation tuning. *PLoS ONE*, 8(3), e58754.
- Lunghi, C., Binda, P., & Morrone, M. C. (2010). Touch disambiguates rivalrous perception at early stages of visual analysis. *Current Biology*, 20(4), R143–R144.
- Lunghi, C., Morrone, M. C., & Alais, D. (2014). Auditory and tactile signals combine to influence vision during binocular rivalry. *The Journal of Neuroscience*, 34(3), 784–792.
- Macaluso, E., & Maravita, A. (2010). The representation of space near the body through touch and vision. *Neuropsychologia*, 48(3), 782–795.
- Makin, T. R., Holmes, N. P., & Ehrsson, H. H. (2008). On the other hand: Dummy hands and peripersonal space. *Behavioural Brain Research*, 191(1), 1–10.
- Maruya, K., Yang, E., & Blake, R. (2007). Voluntary action influences visual competition. *Psychological Science*, 18(12), 1090–1098.
- Meredith, M. A., & Stein, B. E. (1986). Visual, auditory, and somatosensory convergence on cells in superior colliculus results in multisensory integration. *Journal of Neurophysiology*, 56(3), 640–662.
- Metzinger, T. (2004). *Being no one: The self-model theory of subjectivity*. MIT Press.
- Miles, W. R. (1930). Ocular dominance in human adults. *The Journal of General Psychology*, 3(3), 412–430.
- Mudrik, L., Faivre, N., & Koch, C. (2014). Information integration without awareness. *Trends in Cognitive Sciences*.
- Noel, J.-P., Cascio, C., Wallace, M., & Park, S. (2016). The spatial self in schizophrenia and autism spectrum disorder. *Schizophrenia Research*. <http://dx.doi.org/10.1016/j.schres.2016.09.021>.
- Noel, J. P., Grivaz, P., Marmaroli, P., Lissek, H., Blanke, O., & Serino, A. (2014). Full body action remapping of peripersonal space: The case of walking. *Neuropsychologia*.
- Noel, J. P., Pfeiffer, C., Blanke, O., & Serino, A. (2015). Peripersonal space as the space of the bodily self. *Cognition*, 144, 49–57.
- Noel, J.-P., Wallace, M., & Blake, R. (2015). Cognitive neuroscience: Integration of sight and sound outside of awareness? *Current Biology*, 25(4), R157–R159.
- Petkova, V. I., & Ehrsson, H. H. (2008). If I were you: Perceptual illusion of body swapping. *PLoS ONE*, 3(12), e3832.
- Petkova, V. I., Khoshnevis, M., & Ehrsson, H. H. (2011). The perspective matters! Multisensory integration in ego-centric reference frames determines full-body ownership. *Frontiers in Psychology*, 2.
- Rizzolatti, G., Fadiga, L., Fogassi, L., & Gallese, V. (1997). NEUROSCIENCE: Enhanced: The space around us. *Science*, 277(5323), 190–191. <http://dx.doi.org/10.1126/science.277.5323.190>.
- Rouder, J. N., Speckman, P. L., Sun, D., Morey, R. D., & Iverson, G. (2009). Bayesian t tests for accepting and rejecting the null hypothesis. *Psychonomic Bulletin & Review*, 16(2), 225–237.
- Salomon, R. (in press). The assembly of the self from sensory and motor foundations. *Social Cognition* (in press).
- Salomon, R., Galli, G., Łukowska, M., Faivre, N., Ruiz, J. B., & Blanke, O. (2015). An invisible touch: Body-related multisensory conflicts modulate visual consciousness. *Neuropsychologia*.
- Salomon, R., Kaliuzhna, M., Herbelin, B., & Blanke, O. (2015). Balancing awareness: Vestibular signals modulate visual consciousness in the absence of awareness. *Consciousness and Cognition*, 36, 289–297.
- Salomon, R., Lim, M., Herbelin, B., Hesselmann, G., & Blanke, O. (2013). Posing for awareness: Proprioception modulates access to visual consciousness in a continuous flash suppression task. *Journal of Vision*, 13(7).
- Salomon, R., Lim, M., Pfeiffer, C., Gassert, R., & Blanke, O. (2013). Full body illusion is associated with widespread skin temperature reduction. *Frontiers in Behavioral Neuroscience*.
- Serino, A., Canzoneri, E., & Avenanti, A. (2011). Fronto-parietal areas necessary for a multisensory representation of peripersonal space in humans: An rTMS study. *Journal of Cognitive Neuroscience*.
- Serino, A., Canzoneri, E., Marzolla, M., di Pellegrino, G., & Magosso, E. (2015). Extending peripersonal space representation without tool-use: Evidence from a combined behavioral-computational approach. *Frontiers in Behavioral Neuroscience*, 9, 4.
- Serino, A., Noel, J. P., Galli, G., Marmaroli, P., Lissek, H., & Blanke, O. (2015). Body parts-centered versus and full body-centered peripersonal space representations. *Scientific Reports*.
- Stein, B. E., & Stanford, T. R. (2008). Multisensory integration: Current issues from the perspective of the single neuron. *Nature Reviews Neuroscience*, 9(4), 255–266.
- Teneggi, C., Canzoneri, E., di Pellegrino, G., & Serino, A. (2013). Social modulation of peripersonal space boundaries. *Current Biology*, 23(5), 406–411.
- Tononi, G. (2008). Consciousness as integrated information: A provisional manifesto. *The Biological Bulletin*, 215(3), 216–242.
- Tsakiris, M. (2010). My body in the brain: A neurocognitive model of body-ownership. *Neuropsychologia*, 48(3), 703–712.
- Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, 8(8), 1096–1101.
- Zhou, W., Jiang, Y., He, S., & Chen, D. (2010). Olfaction modulates visual perception in binocular rivalry. *Current Biology*, 20(15), 1356–1358.