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Peripersonal space as the space of the bodily self

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ABSTRACT

Bodily self-consciousness (BSC) refers to experience of one's self as located within an owned body (self-identification) and as occupying a specific location in space (self-location). BSC can be altered through multisensory stimulation, as in the Full Body Illusion (FBI). If participants view a virtual body from a distance being stroked, while receiving synchronous tactile stroking on their physical body, they feel as if the virtual body were their own and they experience, subjectively, to drift toward the virtual body. Here we hypothesized that – while normally the experience of the body in space depends on the integration of multisensory body-related signals within a limited space surrounding the body (i.e. peripersonal space, PPS) – during the FBI the boundaries of PPS would shift toward the virtual body, that is, toward the position of experienced self-location. To test this hypothesis, we used synchronous visuo-tactile stroking to induce the FBI, as contrasted with a control condition of asynchronous stroking. Concurrently, we applied an audio–tactile interaction paradigm to estimate the boundaries of PPS. PPS was measured in front of and behind the participants' body as the distance where tactile information interacted with auditory stimuli looming in space toward the participant's physical body. We found that during synchronous stroking, i.e. when participants experienced the FBI, PPS boundaries extended in the front-space, toward the avatar, and concurrently shrunk in the back-space, as compared to the asynchronous stroking control condition, when FBI was induced. These findings support the view that during the FBI, PPS boundaries translate toward the virtual body, such that the PPS representation shifts from being centered at the location of the physical body to being now centered at the subjectively experienced location of the self.

1. Introduction

A fundamental aspect of our sense of self as subject of conscious experience is the experience of the bodily self, that is, the feeling of being located within a body we own and control (Blanke & Metzinger, 2009; Gallagher, 2005; Jeannerod, 2006). Empirical data demonstrate that the feeling of owning a body (self-identification), as well as the sense of being located within the boundaries of that body (self-location), are fundamentally rooted in the congruent and cohesive integration of multiple sensory modalities within the spatio-temporal dimensions of the physical body (Blanke, 2012). In fact, manipulating the spatio-temporal congruency of different sensory modalities can induce different bodily illusions, such as the Rubber Hand Illusion (RHI: Botvinick & Cohen, 1998), the Full Body Illusion (FBI: Lenggenhager, Tadi, Metzinger, & Blanke, 2007) and Out-of-Body illusions (Ehrsson, 2007). During the FBI subjects see a virtual body (avatar), placed 2 m in front them, being stroked, while synchronously receiving a congruent tactile stimulation on their physical body. Under such circumstances participants report to identify with the virtual body (change in self-identification), and feel displaced toward the virtual body (change in self-location). These effects are absent, or reduced, when tactile and visual stimulation are asynchronously administered. Bodily illusions such as the RHI and the FBI reveal that both body-part and full-body representations are malleable in that a sense of ownership can be induced for physical or virtual replacements of our body and that the spatial limits of self-experience can go beyond those of our physical body.

While similar findings have been repetitively reported for different multisensory manipulations (see Blanke, 2012; Ehrsson, 2012; Serino et al., 2013 for reviews), the brain mechanisms underlying these effects are not yet known. It has been proposed that, during the FBI, synchronous tactile stimulation on the participants'

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body and visual stimulation from the avatar seen at an extracorporeal location might enlarge the visual and receptive fields of neurons coding for peripersonal space (PPS) (Blanke, 2012). Multisensory PPS neurons integrate tactile, visual, and auditory stimuli when presented at a limited distance from the body (Bremmer, Duhamel, Ben Hamed, & Graf, 2002; Gentile, Petkova, & Ehrsson, 2011; Graziano & Cooke, 2006; Makin, Holmes, & Ehrsson, 2008; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997), but not when further away. This limit defines the boundary of PPS, that have also been reported to be plastic in that the space where multisensory stimuli are integrated extends when individuals interact with far locations, for instance, by using tools (Làdavas & Serino, 2008; Maravita & Iriki, 2004; Serino, Canzoneri, Marzolla, di Pellegrino, & Magosso, 2015). It is possible that feeling touch on one's own body, while viewing tactile stimulation administered on a virtual body at a distance may also alter the boundaries of the PPS representation. Accordingly, previous studies have shown that the spatial constraints of multisensory integration between vision and touch vary during the FBI (Aspell, Lenggenhager, & Blanke, 2009) or the RHI (Pavani, Spence, & Driver, 2000; Zopf, Savage, & Williams, 2010). Here we describe how the boundaries of PPS shape during the FBI. In particular, we test the hypothesis that, while normally the PPS representation is bound to the physical body, during the FBI PPS becomes referenced at the illusory self-location.

To test that hypothesis, we induced the FBI (Lenggenhager et al., 2007), while we concurrently measured the spatial extent of PPS representation by means of a dynamic audio–tactile interaction task (Canzoneri, Magosso, & Serino, 2012; Noel et al., 2014; Galli, Noel, Canzoneri, Blanke, & Serino, 2015). In order to experimentally induce a change in BSC, we administered tactile stimulation on the participant's physical body, while synchronously showing (visual stimuli) spatially conflicting tactile stimulation on a virtual body. In the control condition, tactile and visual stimulation were administered asynchronously. Change in BSC was reported through a questionnaire. Concurrently, in order to define the boundary of PPS representation, participants were asked to respond as fast as possible to vibro-tactile stimuli administered on their trunk, while task-irrelevant sounds loomed toward their trunk. Based on previous findings (Canzoneri, Marzolla, Amoresano, Verni, & Serino, 2013; Canzoneri et al., 2012; Canzoneri et al., 2013; Teneggi, Canzoneri, di Pellegrino, & Serino, 2013), we predicted that reaction times to tactile stimuli would decrease once the sound overcame a particular distance from the body, which can be taken as a proxy for the boundary of PPS. In Experiment 1, dynamic sounds were presented in the participants' front-space. In this way, we tested whether during synchronous visuo-tactile stroking inducing the FBI, the PPS boundary extends in the front, toward the virtual body, as compared to the asynchronous control condition. In Experiment 2, moving sounds were presented in the participants' back-space, to test whether the extension of PPS toward the virtual body in the front-space (as predicted in Experiment 1) was associated with a concurrent shrinkage of PPS in the back-space (or whether it was rather associated with no change). Such findings would indicate a shift of PPS representation from the physical body to the illusory perceived location of the self. We predicted no changes in PPS boundaries (either in the front or in the back) during the asynchronous stroking condition, where no FBI was induced.

2. Material and methods

2.1. Participants

Nineteen and fifteen students from the Ecole Polytechnique Federale de Lausanne participated in Experiment 1 (9 females, mean age = 23.0 years, range 18–29) and in Experiment 2 (4 females, mean age 24.2 years, range 19–31), respectively. Sample size for Experiment 1 was derived from power analysis of prior studies (Leggenhager et al., 2007, 2009) and for Experiment 2 based on the effect size in Experiment 1. All participants were right-handed, had normal or corrected-to-normal eyesight, normal hearing, and no history of neurological or psychiatric disease. The study was approved by Brain Mind Institute Ethics Committee for Human Behavioral Research of the EPFL and conducted in line with the Declaration of Helsinki. All participants gave informed consent prior to participation and were remunerated with 20 Swiss Francs for their time.

2.2. Stimuli and apparatus

Fig. 1A shows the experimental setup. In order to measure the boundaries of PPS representation, participants stood in the middle of two arrays of 8 speakers each, placed besides their chest, one on the right and one on the left, at 50 cm distance from their midline. Four speakers on each side were placed in the participant's front-space, and were utilized in Experiment 1 to map the front PPS, and 4 speakers on each side were placed in the participant's back-space and were utilized in Experiment 2 to map their back-space PPS. The loudspeakers extended from 100 cm in front of the subjects to 100 cm in the back. The sounds were perceived as if coming from the center (in between the two arrays). A control experiment (i.e., sound localization, $n = 7$) validated the paradigm demonstrating that participants perceived the sounds as dynamically approaching their body (see further detail in Supplementary Material).

In addition, participants were outfitted with a vibro-tactile device (Precision MicroDrives shaftless vibration motors, model 312-101), which was placed on the participant's chest in Experiment 1 and on his/her back in Experiment 2, at stern level. Participants were handed a wireless gamepad (XBOX 360 controller, Microsoft, Redmond, WA), which they held in their right hand and used to respond to vibro-tactile stimulation.

In order to induce the FBI, two video cameras (Logitech HD Webcam C270, 1280×720 pixels, Logitech Fluid Crystal Technology) recorded the participant from a distance of 200 cm (in the back), and this signal was relayed stereoscopically to a Head Mounted Display (HMD, Oculus Rift SDK, Oculus VR, 100° field of view, 60 Hz) worn by the subject. Synchronous visuo-tactile stroking was achieved by direct real-time (<50 ms delay) display of visual signals from the cameras to the HMD. During asynchronous visuo-tactile stimulation the camera signal was delayed by 500 ms before feeding it to the HMD.

2.3. Experimental manipulations and outcome measures

2.3.1. Full Body Illusion manipulations

For each experiment, synchronous and asynchronous visuo-tactile stroking were presented in separate blocks, whose order was counterbalanced between participants. These conditions differed in the temporal synchrony between felt and seen touch (synchronous: <50 ms delay; asynchronous: 500 ms delay, where tactile stimulus preceded the visual stimulus). Participants stood straight and, through a video feed relayed to the HMD, passively watched a virtual body, i.e. a video recording of their own body from 200 cm behind their actual location. The experimenter randomly stroked the participants' upper back at approximately 2 Hz. At the end of each condition, the FBI questionnaire (adapted from Lenggenhager et al., 2007) was administered to quantify the subjective experience associated with the FBI. Questions were: Q1. How strong was the feeling that the rod you saw was directly touching you? Q2. How strong was the feeling that the touch you felt was where you saw the stroking? Q3. How strong was the

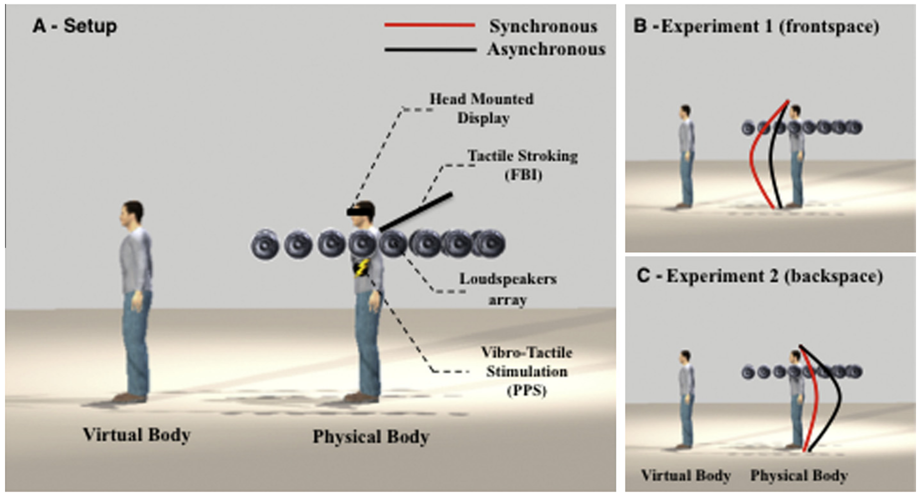

Fig. 1. *Experimental Setup and hypothesis.* (A). In order to induce the Full Body Illusion (FBI), the participant viewed on a head-mounted display a virtual body in front. Tactile stroking was administered to the participant's back while synchronous or asynchronous visual stroking was seen on the back of the virtual body. Peripersonal Space (PPS) representation was measured by recording response times to vibrotactile stimuli applied to the participant's chest, while concurrent task-irrelevant looming sounds were administered from a loudspeaker array placed beside the participant. We hypothesized that during synchronous stroking, i.e., when the FBI is induced, PPS representation extends toward the virtual body in the front-space (B, red line), and concurrently shrinks in the back-space (C, red line), as compared to the asynchronous stroking control condition (B and C, black lines). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

feeling that you were drifting forward? Q4. How strong was the feeling that you were drifting backward? Q5. How strong did you feel the touch simultaneously at two locations in space? Q6. How strong was the feeling that the visual image you saw was really you? Q7. How strong was the feeling that you had more than one body? Q8. How strong was the feeling that you were floating in the air? Q9. How strong was the feeling that you were dissociated from your body (as if yourself and your body were in different locations)? Q10. How strong was the feeling that you were located at some distance behind the visual image of the body you saw? And Q11. How strong was the feeling that you were looking at someone else? Questions were computerized and presented in random order. Participants responded on a visual horizontal 11-point scale ranging from 0 (lowest) to 10 (highest)".

We did not include in our design a proper concurrent behavioral measure of changes in self-location to show a drift toward the avatar induced by the FBI, as employed by other studies (e.g., Lenggenhager et al., 2007). Thus, we assessed only subjective changes in BSC by means of questionnaires.

2.3.2. Peripersonal space measurement

In order to measure changes in PPS during the FBI, visuo-tactile stimulation was intermingled with audio–tactile trials. In those PPS trials, a looming sound approached the participant (in the front, for Experiment 1, and in the back, for Experiment 2) at a velocity of 75 cm/s. On each trial, after one out of six possible delays from sound onset (SOA; T1 = 190 ms to T6 = 1.14 s in increments of 190 ms), a tactile vibration (100 ms duration) was delivered. SOAs correspond in the spatial dimension to audio–tactile distances of 15 (.190 × 75), 30, 45, 60, 75, and 90 cm. Participants were instructed to respond by button press as fast as possible upon perceiving the vibro-tactile stimulus on their chest (for Experiment 1) or back (for Experiment 2) and their reaction times (RT) were measured. As sounds loomed from far to close, the sooner a tactile vibration was given (e.g. at T1), the further away was the sound located in space (e.g. D6) when participants received tactile stimulation. We define, hence, T1 through T6 as corresponding in the spatial dimension to D6 (far from the participant) through D1 (close to the participant). In addition to experimental trials, baseline and catch trials were included. Baseline trials were unimodal tactile trials in which participants responded to touch (at the temporal equivalent to either D1 or D6), but no auditory stimulus was delivered. Catch trials were unimodal auditory trials in which participants had to withhold response (as there was no tactile stimuli).

2.4. Procedure

After an initial 60 s visuo-tactile stroking induction-phase to the FBI, three trials of the PPS task were administered. Interstimulus interval between these consecutive PPS trials was set to 0.5 s. Then, 10 s of merely FBI inducement followed, before the next round of three PPS trials. The FBI stroking continued throughout the experiment, and this pattern (three PPS trials followed by 10 s of solely FBI stroking) was repeated until the end of the block. Each block (and therefore, each stroking condition) consisted of 72 PPS experimental trials (12 repetitions × 6 Sound Distances), 24 baseline trials (12 repetitions × 2 baseline Temporal delays T1 and T6), and 12 catch trials.

3. Results

3.1. Experiment 1 (front-space)

3.1.1. Full Body Illusion: Questionnaire

We analyzed whether Synchronous, as contrasted with the Asynchronous, visuo-tactile stimulation was effective in inducing the FBI. To this aim, for each question, we run a series of paired-sample *t*-test between the two conditions. Results are reported in Fig. 2 (left panel) and demonstrated that participants scored higher in Question 1 (how strong was the feeling that the rod you saw was directly touching you?; $t(18) = 3.45$, $p < 0.01$), Question 2 (how strong was the feeling that the touch you felt was where you saw the stroking?; $t(18) = 13.54$, $p < 0.001$), and Question 3 (how strong was the feeling that you were drifting forward?; $t(18) = 2.75$, $p < 0.05$) during the Synchronous visuo-tactile condition than during the Asynchronous condition. These findings suggest that our set-up allowed for inducing the FBI illusion in the Synchronous condition, at least inasmuch as to provoke participants to more strongly agree with the statement that they felt as

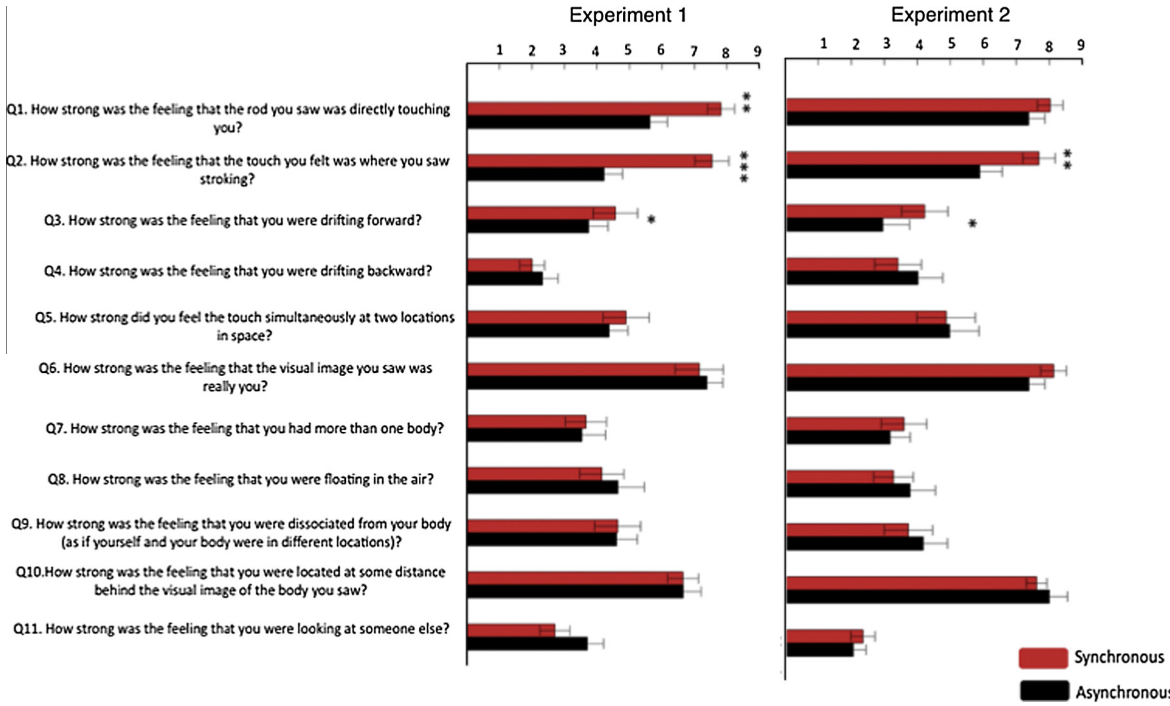

Fig. 2. Body Illusion questionnaire results from Experiment 1 (Left Panel) and Experiment 2 (Right Panel). Average responses (Error bars represent S.E.M.) are plotted as a function of visuo-tactile stroking condition (synchronous in red; asynchronous in black). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

if drifting toward the virtual body. The significant difference between Synchronous and Asynchronous conditions with regard to the self-location question, and the lack thereof in the self-identification one, contrasts with prior findings (see Lenggenhager et al., 2007) and may emanate from a number of methodological differences between these studies (e.g., particular setup of the FBI, the addition of the PPS testing, and/or the wording of the questions).

3.1.2. Peripersonal space: audio–tactile interaction task

Subsequently we analyzed whether the visuo-tactile synchrony manipulation, inducing the FBI, also altered audio–tactile interaction in PPS. A Paired-Samples *t*-test ran on the catch trials showed Synchronous ($M = 98.2\%$, S.E.M = 3%) and Asynchronous ($M = 97.2\%$, S.E.M = 4%) stroking conditions did not differ ($t(18) = .741$, $p > 0.05$) and participants were very accurate at the task.

Mean reaction times (RT) to tactile stimuli at the different sound distances were computed, after trimming responses exceeding 2.5 the RT standard deviation (<3% of total trials). A 2 (Synchrony: Synchronous vs. Asynchronous) × 6 (Sound Distance: D1 through D6) within-subjects ANOVA was performed on participants' RT to vibro-tactile stimulation. Results, shown in Fig. 3, highlighted a significant main effect both for Synchrony ($F(1,18) = 12.24$, $p < 0.01$, $\eta^2 = 0.40$) and for Sound Distance ($F(5,90) = 22.88$, $p < 0.001$, $\eta^2 = .56$). The main effect of Synchrony suggests a general boost of multisensory processing after synchronous stimulation in the front-space, i.e. in the space where the virtual body was presented. More importantly for the purpose of the present study, the two-way Synchrony × Sound Distance interaction was also significant ($F(5,90) = 2.51$, $p < 0.05$, $\eta^2 = 0.12$), implying that such multisensory boosting effect was not homogenous in the front-space, but it was stronger at some specific distances from the body. Thus, to study the source of the significant two-way interaction, we ran two separate ANOVAs, one per Synchrony condition, with Sound Distance as main factor. The aim of these analyses was to identify, for the Synchronous and the Asynchronous conditions, the critical distance at which looming sounds speeded up tactile RT, which can be considered as a proxy of the boundary of PPS, and to test whether this distance varied between the two conditions. The main effect of distance in the Synchronous condition was significant ($F(5,90) = 21.65$, $p < 0.001$, $\eta^2 = .54$) and post hoc comparisons (paired *t*-test) showed that RT at D1 through D5 were equivalent to each other, and significantly faster than RT at D6 ($p < 0.05$, Bonferroni-corrected – alpha set at 0.05/6 – number of comparisons, all Cohen's $d > 0.32$). In the case of the Asynchronous condition the main effect of Sound Distance ($F(5,90) = 12.68$, $p < 0.001$, $\eta^2 = .41$) was also significant; however as expected and differently to the Synchronous condition, results revealed that now only D1 through D4 exhibited similar reaction times, while these were significantly different from D5 and D6 ($p < 0.05$, Bonferroni-corrected, all Cohen's $d > 0.24$). These results imply that the PPS boundary under Asynchronous visuo-tactile stimulation was placed between D4 and D5, whereas it enlarged to be placed between D5 and D6, i.e. at a farther location of space, toward the virtual body, under Synchronous visuo-tactile stimulation. Indeed, multiple comparisons at each sound distance between Synchronous and Asynchronous conditions showed that RT was statistically significant only at D5 ($t(18) = -3.64$, $p < 0.01$, Bonferroni-corrected, Cohen's $d = 0.61$), with faster RTs in the Synchronous ($M = 343$ ms; S.E.M = 12 ms) than in the Asynchronous condition ($M = 387$ ms; S.E.M = 16 ms).

Finally, in order to assure that the aforementioned results were due to a facilitation of tactile processing due to multisensory integration of audio–tactile signals, we compared tactile RT when the looming sound was perceived at the different distances with RT in unimodal tactile baseline trials, when no sounds were administered. Faster RT in audio–tactile conditions as compared to unimodal tactile conditions can be considered a facilitation effect due to multisensory integration within the PPS. To this aim we compared RT to audio–tactile trials for each Sound Distance with

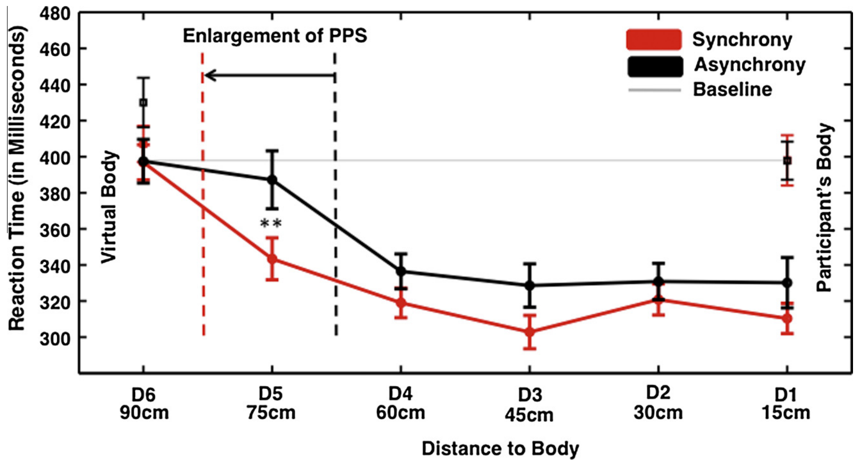

Fig. 3. PPS representation in the front-space (Experiment 1) for the synchronous and the asynchronous Stroking condition. Reaction times (RT) to the tactile stimulus on the chest are plotted as a function of Stroking condition and the distance of the auditory stimuli at the time of tactile stimulation. Error bars represent S.E.M. and ** indicate difference between Synchronous and Asynchronous condition, $p < 0.01$ (Bonferroni-corrected): The grey horizontal line indicates RT in baseline, unimodal tactile trials.

the average (across synchrony conditions) of the fastest baseline condition (T1 or T6), that is, the fastest unimodal tactile RT condition calculated for each participant individually. In this way we adopted the most conservative approach to detect facilitation of tactile processing due to sound presentation as compared to unimodal tactile processing. This analysis allows for correcting for potential expectancy effects and to compare across experiments with different participants, however, it must be noted that it also tends to underestimate the expansion of PPS representation, as the comparison is always to the fastest unimodal condition. In Experiment 1, 12 out of the 19 participants showed numerically faster RTs for unimodal tactile stimulation at T6 than T1.

Comparison to baseline demonstrated that in the case of the Synchronous stroking stimulation, RT at D1 through D5 were significantly faster from baseline ($p < 0.05$, corrected, all Cohen's $d > 0.34$), but not RT at D6 ($p = 0.63$). For the Asynchronous condition, only RT at D1 through D4 were significantly faster from baseline ($p < 0.05$, Bonferroni corrected, all Cohen's $d > 0.27$), but not RT and D5 and D6 (both p-values > 0.41). These comparisons confirm that the limit of audio–tactile interaction, i.e. the PPS boundary, was located between D4 and D5 in the Asynchronous stroking condition, and between D5 and D6, i.e. further away from the physical body and closer to the avatar, during the Synchronous condition.

3.2. Experiment 2 (back-space)

3.2.1. Full Body Illusion: Questionnaire

As for Experiment 1, we examined whether Synchronous, as contrasted with the Asynchronous, visuo-tactile stimulation was effective in inducing the FBI by comparing, for each question, participants' responses between the two conditions by means of paired-sample t-tests. Results are reported in Fig. 2 (right panel) and demonstrated that participants scored higher in Question 2 (how strong was the feeling that the touch you felt was where you saw the stroking?; $t(14) = 2.88$, $p < 0.01$), and critically, on Question 3 (how strong was the feeling that you were drifting forward?; $t(14) = 1.99$, $p < 0.05$) during the Synchronous visuo-tactile condition than during the Asynchronous condition. A similar trend was found for Question 1 (how strong was the feeling that the rod you saw was directly touching you?; $t(14) = 1.37$, $p = 0.04$, one-tailed), which exhibited a significant difference between Synchronous and Asynchronous stroking conditions in Experiment 1.

3.2.2. Peripersonal space: audio–tactile interaction task

A paired-samples t-test ran on the auditory unimodal trials revealed that, as for Experiment 1, participants were generally very accurate at withholding response when it was demanded from them (Synchronous condition: $M = 96.4\%$, S.E.M = 1.5%; Asynchronous condition: $M = 93.5\%$, S.E.M = 2.6%), and this did not differ between stroking conditions ($t(14) < 1$, ns).

Mean RT to vibro-tactile stimulation (trimmed for 2.5 standard deviations, <2% total trials) was entered into a 2 (Synchrony) × 6 (Sound Distance) within-subjects ANOVA. Results, shown in Fig. 3, demonstrated a significant main effect of Sound Distance ($F(5,70) = 12.54$, $p < 0.001$, $\eta^2 = 0.47$), as well as a Sound Distance × Synchrony interaction ($F(5,70) = 5.97$, $p < 0.001$, $\eta^2 = 0.29$). In order to interpret the source of the two-way interaction, we ran two separate ANOVAs, one per Synchrony condition. The main effect of Sound Distance in the Synchronous condition was significant ($F(5,70) = 9.57$, $p < 0.001$, $\eta^2 = .40$) and post hoc comparisons showed that RT at D1 through D4 were equivalent to each other, and significantly faster than RT at D5 and D6 ($p < 0.05$, Bonferroni-corrected, all Cohen's $d > 0.19$). In the case of the Asynchronous condition the main effect of Sound Distance ($F(5,70) = 11.82$, $p < 0.001$, $\eta^2 = .45$) was again significant; however, post hoc comparisons revealed that D1 through D5 exhibited similar reaction times, while these were significantly different from D6 ($p < 0.05$, Bonferroni-corrected, all Cohen's $d > 0.25$). These results imply that the PPS boundary under Asynchronous visuo-tactile stimulation was placed between D5 and D6, whereas it shrank to be placed between D4 and D5, i.e. at a closer location of space, under Synchronous visuo-tactile stimulation.

Multiple comparisons at each sound distance revealed that only the comparison between Synchronous and Asynchronous conditions at D5 was statistically significant ($t(14) = 4.12$, $p < 0.01$, Bonferroni-corrected, Cohen's $d = 0.70$), with slower RTs in the Synchronous condition (Mean RT = 352 ms; S.E.M = 15 ms) than in the Asynchronous condition (Mean RT = 310 ms; S.E.M = 17 ms). Note that the location at which audio–tactile RT differed in space (namely, D5) was the same as in Experiment 1, however, the direction of the effect is inversed here. While in Experiment 1, at D5 participants were faster in the Synchronous condition, now they are faster in the Asynchronous condition.

Lastly, we compared tactile RT when the looming sounds were perceived at the different distances with RT in unimodal tactile baseline trials in order to assure that the above-mentioned distance effects were in fact a space-dependent multisensory facilitation effect. To this aim, as in experiment 1, we compared RT to audio–tactile trials for each Sound Distance with the average of the fastest RT at the baseline (In Experiment 2, 10 out of 15 participants showed numerically faster unimodal tactile RTs at T6 than T1). Comparison to baseline demonstrated that in the case of the Synchronous stroking stimulation, RT at D1 through D4 were significantly faster from baseline ($p < 0.05$, corrected, all Cohen's $d > 0.21$), but not RT at D5 and D6. For the Asynchronous condition RT at D1 through D5 were significantly faster from baseline ($p < 0.05$, Bonferroni corrected, Cohen's $d > 0.27$). These comparisons confirm that the limits of audio–tactile interaction, i.e. the PPS boundary, was located between D5 and D6 in the Asynchronous stroking condition, and between D4 and D5 in the Synchronous one.

3.3. Comparison between front-space and back-space PPS during synchronous and asynchronous visuo-tactile stroking

In order to compare the effect of synchronous visuo-tactile stimulation, inducing the FBI, on PPS representation in the front and back-space, we ran a final analysis using a mixed-model ANOVA with Synchrony (Synchronous or Asynchronous) and Sound Distance (D1 through D6) as within-subjects variables, and with Experiment (Exp 1, front-space; Exp 2, back-space) as the between-subjects variable. Results demonstrated a main effect of Sound Distance ($F(5,160) = 30.173$, $p < 0.001$, $\eta^2 = .485$), yet no main effect of Synchrony ($F(1,32) = 3.609$, $p = .076$), nor Experiment ($F(1,32) = 0.095$, $p = 0.760$). Findings did show a Sound Distance × Experiment interaction ($F(5,160) = 3.996$, $p = .007$) – steeper decrease in the front-space than in the back-space – yet did not reveal a Synchrony × Experiment interaction ($F(1,32) = 2.198$, $p = .092$). Most importantly, however, and as expected from the aforementioned results, findings did revealed a significant three way interaction ($F(5,160) = 6.97$, $p < 0.001$, $\eta^2 = 17$). This results is explained by the significant enlargement of PPS in the front-space in the Synchronous condition as opposed to the Asynchronous condition (Section 3.1.2), and to a significant reduction of PPS in the back-space in the Synchronous condition as opposed to the Asynchronous one (Section 3.2.2). For illustration purposes, this result is displayed in Fig. 4 as the absolute value of the difference between multimodal audio–tactile trials at each spatial distance (B6 corresponding to the furthest distance in the back, and F6 corresponding to the furthest distance in the front) and the fastest unimodal tactile baseline condition. Thus, positive values represent a multisensory facilitation effect induced by sounds within the PPS on tactile processing (see Fig. 5).

4. Discussion

In the present study we induced the Full-Body Illusion (FBI) in order to manipulate the experience of one's own bodily self in space. When participants received a tactile stimulation on their physical body while viewing a synchronous stimulation administered to a virtual body seen at a distance, they reported a greater feeling of being directly touched by the stimulus touching the virtual body, of feeling touch at the location of the virtual body (Q1 and Q2), and of feeling to drift forward toward the virtual body (Q3), indicating a shift in the experienced location of the self from their physical body toward a virtual replacement of it. In line with previous findings, these effects were more weakly induced during asynchronous visuo-tactile stimulation (see Blanke, 2012; Lenggenhager et al., 2007; Serino et al., 2013). The focus and main new finding from the present study is that the FBI was associated with a shift in the representation of the PPS. We used an audio–tactile interaction task to identify the point in space where a looming sound speeded up tactile processing as a proxy of the boundaries of multisensory PPS (see Canzoneri, Marzolla et al., 2013; Canzoneri, Ubaldi et al., 2013; Canzoneri et al., 2012; Noel et al., 2014; Teneggi et al., 2013).

In Experiment 1, when we measured the extension of PPS in the front-space, between the participant's physical body and the avatar, we found, as predicted, that the PPS boundary enlarged toward the location of the avatar in the synchronous visuo-tactile stroking condition inducing the FBI, as compared to the asynchronous control condition (boundary of PPS initially between 60 and 75 cm, and then enlarged to be located between 75 and 90 cm). In Experiment 2, mapping PPS on the participant's back, we found that the PPS boundary shrunk in the synchronous as compared to the asynchronous condition (initially located 75–90 cm away, and then shrunk to be placed 60–75 cm away). Taken together, these two new findings support the view that during the FBI, PPS boundaries translate toward the virtual body, such that the PPS representation shifts from being centered at the location of the physical body to being now centered at the subjectively experienced location of the self.

Previous studies suggest that multisensory receptive fields of PPS neurons can react to artificial copies of the body. In patients with cross-modal extinction, Farnè, Pavani, Meneghello, and Làdavas (2000) showed that visual stimuli presented close to a prosthetic hand interacted with tactile stimuli at the patient's contralesional hand as much as visual stimuli presented close to the patient's real hand did. In close analogy, in monkeys, stimuli applied to a fake arm triggered responses from PPS neurons, suggesting that PPS receptive fields can incorporate a fake limb (Graziano, Cooke, & Taylor, 2000). More recently, Brozzoli, Gentile, and Ehrsson (2012) showed in humans that brain areas likely representing PPS around the hand, such as the ventral premotor cortex and the posterior parietal cortex, which normally process visual stimuli presented in a limited peri-hand space, responded to visual stimuli presented close to a rubber hand after synchronous visuo-tactile stimulation of the participants' and of the rubber hand. These findings generally show that some response properties, which normally apply to one's own real hand, transfer to an artificial replacement of the hand. Similar effects have also been shown after individuals use a tool to extend the physical limits of their own body (see e.g., Canzoneri, Marzolla et al., 2013; Farne & Ladavas, 2000; Iriki et al., 1996), and those findings have been advocated to suggest that tools can be included into one's own body representation (Iriki and Maravita, 2004; Maravita, Spence, Kennett, & Driver, 2002). Results from our study are different from those previous ones at least in one critical respect. Contrarily to the cases of rubber hand and tool-use, during the FBI, we did not find only an extension of PPS in the direction of the avatar's location, but also a concurrent contraction of the back PPS. The combination of these effects suggest a genuine spatial shift of PPS representation, centered on the location of the physical body prior to the FBI, toward the subjectively perceived location of the self during the FBI (as assessed by responses to questionnaire). While normally integration of tactile stimuli at the body and of external stimuli in the environment (in this case sounds) is maximal around the location of the physical body, when participants experienced a forward drift of their perceived self location (see Question 3), due to the FBI, the spatial gradient of multisensory integration congruently shifted in the direction of self-location as induced by the FBI. These findings show that not only arm-related PPS representations are malleable. More importantly, we show that the center of the PPS representation is not bound to the physical body, but it is centered at the experienced location of the self. Normally self-location and body location coincide, and so does PPS. However, if body location and self-location are dissociated, for instance by means of conflicting multisensory

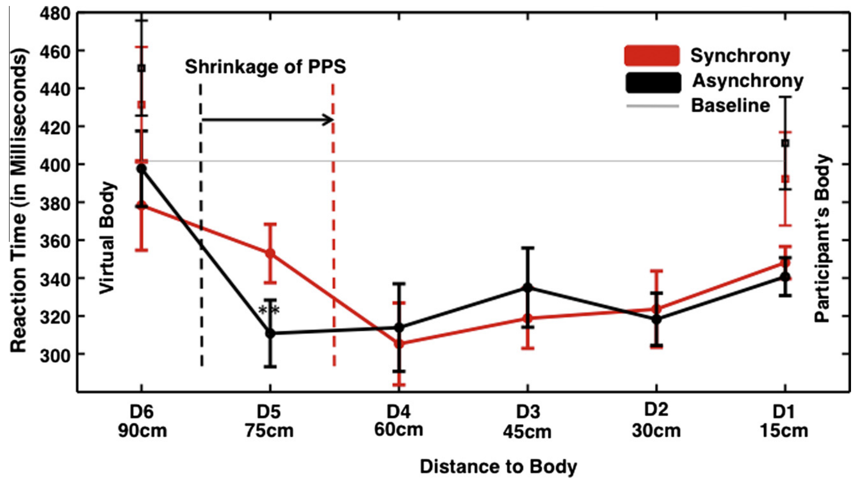

Fig. 4. PPS representation in the back-space (Experiment 2) during Synchronous and Asynchronous stroking. RT to the tactile stimulus on the back is plotted as a function of Synchrony during the Full Body Illusion and the distance of the auditory stimuli at the time of tactile stimulation. Error bars represent S.E.M. and ** indicate difference between Synchronous and Asynchronous condition, $p < 0.01$ (Bonferroni-corrected): The grey horizontal line indicates RT in baseline, unimodal tactile trials.

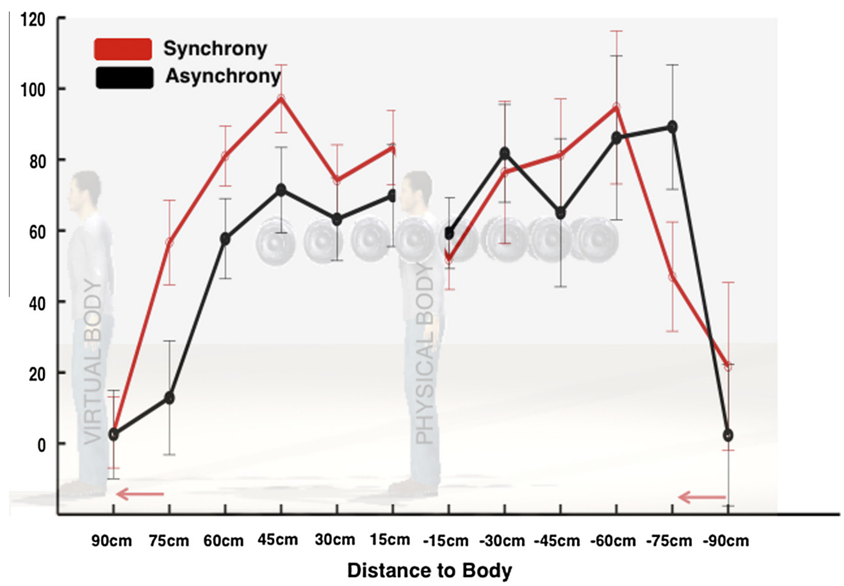

Fig. 5. PPS representation in the front- and back-space during Synchronous and Asynchronous stroking. RT difference between unimodal tactile stimulus on the trunk and multimodal audio–tactile stimuli is plotted as a function of Synchrony of visuo-tactile stimulation during the Full Body Illusion and the distance between the auditory stimuli and the body. Error bars represent S.E.M. Higher values imply higher facilitation on tactile processing due to audio–tactile interaction.

stimulation, PPS representation shapes congruently with the change in self-experience. More generally, the present findings suggest that PPS can be considered as a representation of the self in space, which may mediate interactions between the individual and the environment. This proposal fits with previous results showing that the size of PPS varies across individuals not only depending on the dimension of their bodies (Longo & Lourenco, 2007), but also, more interestingly, depending on individual personality traits (e.g., claustrophobia and anxiety; Lourenco, Longo, & Pathman, 2011; Sambo & Iannetti, 2013). Our data also corroborate recent reports showing that PPS shapes not only during physical body-objects interactions, such as those mediated by tool-use, but also during virtual interactions with far objects, mediated by a computer mouse (Bassolino, Serino, Ubaldi, & Ladavas, 2010) or surgical robots (Rognini et al., 2013; Sengül et al., 2012), and even after social interactions with other persons, depending on the positive or negative value of those interactions (Teneggi et al., 2013).

An interesting question arising from the present results and from other previous studies is whether there is a spatial limit in extending PPS representation and altering bodily processing. Moreover, where would this spatial limit be for shifting one's self-location? For instance, Aspell, Lavanchy, Lenggenhager, and Blanke (2009), demonstrated that synchronous stroking inducing the FBI modulated multisensory interactions between visual and tactile stimuli in the so-called crossmodal congruency effect (CCE) using a spatial disparity (between visual and tactile stimuli) of 2 m (between virtual and physical body), thus suggesting that multisensory effects, and thus PPS changes, induced by the FBI might extend well beyond the modulation shown in the present study within 1 m (see also Palluel, Aspell, & Blanke, 2011). The present results cannot answer this question because in this study the avatar was presented at a distance of 2 m, and PPS was only mapped for up to 1 m. Future studies may test changes in PPS along a continuous range between the physical body and the virtual body, and even beyond it, to identify a spatial limit in potential PPS extension. Other studies might also measure the effectiveness of the FBI illusion and the related changes in multisensory integration with the virtual body being placed at variable distances from the participant's body to identify a spatial limit, or gradient, in the possibility of incorporating a virtual body (as done for the related rubber hand illusion; i.e. Lloyd, 2007). Such research might have important application in the study of embodiment and presence in virtual reality and tele-presence (see Sanchez-Vives & Slater, 2005).

Two other issues need clarification before concluding. First, it is important to mention an alternative explanation for the present results, namely that synchronous visuo-tactile stimulation may have also resulted in a reallocation of spatial attention, rather than in shifting PPS representation (see Holmes, Sanabria, Calvert, & Spence, 2007, for relevant discussion). In order to exclude that a shift in attention per se explains the present findings, we conducted a control experiment, which is fully described as Supplementary Material online. We ran the same experimental protocol, as in Experiment 1, with the exception that receding, instead than looming sounds were used. Previous data show that receding sounds do not induce a spatial dependent modulation of tactile processing for trunk and face stimulation (Noel et al., 2014; Teneggi et al., 2013), and therefore they cannot capture any change in PPS representation due to the FBI illusion. On the contrary, any effect due to a shift of spatial attention should equally affect the interaction of tactile stimuli with both looming (as in Experiment 1) and receding (as in the supplemental experiment) sounds. In fact, results from the supplemental experiment showed that audio–tactile interaction with receding sounds did not vary depending on visuo-tactile stimulation in the synchronous vs. the asynchronous condition. The comparison between the significant results in Experiment 1 and the null results from the supplemental experiment suggests that the effects of the FBI on audio–tactile interaction found in the present study should be interpreted as a genuine change in PPS representation, rather than as a shift in spatial attention. This conclusion is related to the second issue. We used an audio–tactile interaction paradigm to assess the enlargement of PPS representation due to the FBI despite the fact that most data about PPS representation and its plasticity come from experiments where visuo-tactile stimulation was used in monkeys and humans (for reviews Graziano & Cooke, 2006; Makin et al., 2008). Thus, although existing hypotheses about the effects of bodily illusions (such as the rubber hand illusion or the FBI (Blanke, 2012; Ehrsson, 2012)) predict an extension of visual receptive fields of multisensory neurons, no direct predictions have been posited for the auditory receptive fields of multimodal neurons as their spatial properties have been less frequently investigated (Graziano, Reiss, & Gross, 1999; Schlack, Sterbing-D'Angelo, Hartung, Hoffmann, & Bremmer, 2005; see Occelli, Spence, & Zampini, 2011). However, our methodological choice came from the need of separating the type of multisensory interaction used to measure the effect of the FBI on PPS (audio–tactile) from the type of multisensory interaction used to induce the illusion (visuo-tactile). Showing an effect of visuo-tactile stimulation on the spatial boundaries of audio–tactile integration, actually, strengthens the finding of a purely multisensory change in spatial representation due to the FBI. We suggest that this effect depends on a shift of multisensory receptive fields of PPS neurons (Blanke, 2012; Ehrsson, 2012; Serino et al., 2013), although we acknowledge that the present data cannot provide neurophysiological evidence to such a proposal.

In conclusion, the present study supports a neurophysiological explanation for the effects of conflicting multisensory stimulation on BSC during the FBI: viewing a tactile simulation on a another body at a distance, while receiving synchronous tactile stimulation on one's own body, changes PPS boundaries. Such change is characterized not simply by an extension of PPS representation towards the location of seen touch, but rather by a shift or translation of PPS from the location of the physical body to the experienced location of the self.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.cognition.2015.07.012.

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