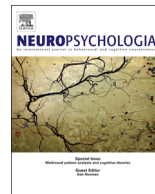




Contents lists available at ScienceDirect

Neuropsychologia

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

Full body action remapping of peripersonal space: The case of walking

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ARTICLE INFO

Article history:

Received 2 May 2014

Received in revised form

4 July 2014

Accepted 24 August 2014

Keywords:

Peripersonal Space

Audio-Tactile

Action

Locomotion

ABSTRACT

The space immediately surrounding the body, i.e. peripersonal space (PPS), is represented by populations of multisensory neurons, from a network of premotor and parietal areas, which integrate tactile stimuli from the body's surface with visual or auditory stimuli presented within a limited distance from the body. Here we show that PPS boundaries extend while walking. We used an audio-tactile interaction task to identify the location in space where looming sounds affect reaction time to tactile stimuli on the chest, taken as a proxy of the PPS boundary. The task was administered while participants either stood still or walked on a treadmill. In addition, in two separate experiments, subjects either received or not additional visual inputs, i.e. optic flow, implying a translation congruent with the direction of their walking. Results revealed that when participants were standing still, sounds boosted tactile processing when located within 65–100 cm from the participants' body, but not at farther distances. Instead, when participants were walking PPS expands as reflected in boosted tactile processing at ~1.66 m. This was found despite the fact the spatial relationship between the participant's body and the sound's source did not vary between the Standing and the Walking condition. This expansion effect on PPS boundaries due to walking was the same with or without optic flow, suggesting that kinematics and proprioceptive cues, rather than visual cues, are critical in triggering the effect. These results are the first to demonstrate an adaptation of the chest's PPS representation due to whole body motion and are compatible with the view that PPS constitutes a dynamic sensory-motor interface between the individual and the environment.

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1. Introduction

Most human interactions, be it sensorimotor or be it social, are carried out by our body and are performed in our peripersonal space (PPS), that is, the space immediately surrounding our body (Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981; Di Pellegrino, Ladavas, & Farne, 1997; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997). Landmark electrophysiological studies in monkeys claimed the existence of multimodal neurons in the posterior parietal cortex, in particular in the ventral intraparietal sulcus (VIP, Hyvärinen & Poranen, 1974; Schlack, Sterbing-D'Angelo, Hartung, Hoffmann,

& Bremmer, 2005), in the premotor cortex (PMc, Fogassi et al., 1996; Duhamel, Colby, & Goldberg, 1998; Bremmer, Duhamel, Ben Hamed, & Graf, 2002) and in the putamen (Graziano & Gross, 1994), devoted to the representation of PPS. These neurons respond to tactile stimuli administered to specific body parts, most commonly the arm, the head, and the chest (Duhamel et al., 1998), and also to visual or auditory stimuli presented within a limited space surrounding these body parts. The fact that the response properties of these neurons are independent from eye position, whereas they depend on the position of the different body parts in space, suggests that they do not encode an eye-centered, but a body-part centered, multisensory representation of PPS (Avillac, Denève, Olivier, Pouget, & Duhamel, 2005; Graziano, Cooke, & Taylor, 2000; Graziano & Cooke, 2006).

Notably, electrical stimulation of premotor and parietal brain areas containing PPS neurons elicits complex motor responses of the arm and head (Graziano, Taylor, & Moore, 2002), suggesting

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that PPS representation, which is constructed based on multisensory integration mechanisms, also supports motor functions. In particular, PPS can be conceived as a multisensory-motor system interfacing the body and the environment. Two main non-mutually exclusive hypotheses have been advanced as to the functional relevance of PPS. On the one hand it is proposed that PPS, serving as a rapid, putatively coarse-grain, sensorimotor interface (Makin, Holmes, Brozzoli, & Farnè, 2012) could act as a personal safety boundary allowing for timely responses to approaching threats (Graziano & Cooke, 2006). This view is primarily supported by the observation that electrical stimulation to VIP and PMc areas in monkeys provokes defensive-like motor outputs, such as squinting, blocking, and ducking (Cooke & Graziano, 2004; Cooke, Taylor, Moore, & Graziano, 2003). Furthermore, evidence indicates that looming stimuli elicit a greater response in the aforementioned neural areas than receding stimuli do (Graziano, Hu, & Gross, 1997). In turn, defensive reactions to looming stimuli have been documented across a wide range of animals (Schiff, Caviness, & Gibson, 1962).

On the other hand, it has been proposed that PPS might represent a sensorimotor interface subserving goal-oriented actions and the rapid online update and correction between motor outputs and their concomitant sensory consequences (Rizzolatti et al., 1981, 1997; Brozzoli, Ehrsson, & Farnè, 2014). This latter view is most prominently supported by the fact that visual responses of bimodal neurons increase during the execution of reaching movements (Godschalk, Lemon, Kuypers, & van der Steen, 1985). In addition, VIP neurons appear to be a fundamental nexus in spatial coordinate system transformation (Avillac et al., 2005) aiding in converting sensory input from its native reference frames (eye-centered, head-centered, and chest-centered) to a spatiotopic and egocentric coordinate system allowing for motor output. Lastly it has been proposed that PPS might not only be germane to action execution, but also to action observation, as some mirror neurons seem to show selectivity between actions performed inside and outside PPS (Caggiano, Fogassi, Rizzolatti, Thier, & Casile, 2009; Bonini, Maranesi, Livi, Fogassi, & Rizzolatti, 2014).

Although extensive, the literature reviewed above refers exclusively to single-cell data on monkeys. Yet it is indeed conceivable that PPS may play a different functional role as we move across animal models and from single cell recordings, to systems neuroscience, to behavior. Extensive literature from neuropsychology (Di Pellegrino et al., 1997; Farnè, Demattè & Lådavas, 2005), experimental psychology (Spence, Pavani, & Driver, 2000; Holmes, Sanabria, Calvert, & Spence, 2007; Zampini, Torresan, Spence, & Murray, 2007; Tajadura-Jimenez, Kitagawa, Valjamae, Zampini, & Murray, 2009) and neuroimaging (Bremmer, Schlack, Shah, Zafiris, & Kubischik, 2001; Makin, Holmes, & Zohary, 2007; Gentile, Petkova, & Ehrsson, 2011; Brozzoli, Gentile, Petkova, & Ehrsson, 2011; Huang, Chen, Tran, Holstein, & Sereno, 2012; Sereno & Huang, 2014) supports the existence of a similar system integrating multisensory information within the PPS in the human brain (see Makin et al. (2007), Lådavas and Serino (2008), Macaluso and Maravita (2010), and Brozzoli et al. (2014) for reviews).

Recent studies have focused on elucidating the interaction between PPS representation and the motor system in humans. Makin, Holmes, Brozzoli, Rossetti, and Farnè (2009), as well as Serino, Annella, and Avenanti (2009), have shown that the excitability of the hand representation along the corticospinal tract is modulated as a function of the location of visual (Makin et al., 2009) or auditory (Serino et al., 2009) stimuli presented near or far from the hand. It was found that the direction (facilitation vs. inhibition) and the timing (from 50 to 300 ms) of the modulation of the motor hand representation depends on the current state of the motor system itself (i.e., whether participants were preparing

an action or were at rest) and originates from areas within the parieto-frontal PPS network. Indeed, Avenanti, Annella, and Serino (2012) have shown that virtual lesions to the PMc (provoked by means of transcutaneous direct current stimulation) abolished the modulation of the hand motor representation in the cortico-spinal tract due to the presence of near or far sounds (Avenanti et al., 2012, see also Serino, Canzoneri, and Avenanti (2011), for similar effects on reaction time data). Taken together these findings reveal a direct connection between the processing of sensory stimuli near the hand and on-going motor outputs, supporting the claim that PPS representation might act as multisensory-motor interface between the body and the environment also in humans.

Other lines of evidence further suggest that it is not only the case that PPS representation modulates the motor system, but also that actions conversely define PPS representation, i.e. actions determine what is coded as far and near space. For instance, both in monkeys (Iriki, Tanaka, & Iwamura, 1996) and in humans (Farnè & Lådavas, 2000; Berti & Frassinetti, 2000; Maravita, Husain, Clarke, & Driver, 2001; Serino, Bassolino, Farnè, & Lådavas, 2007; Canzoneri, Ubaldi, Rastelli, Finisguerra, Bassolino, & Serino, 2013) using a tool to act upon the far space extends PPS representation, so that far stimuli in the space where the tool is used are subsequently coded as being within the PPS (see Maravita and Iriki (2004) for a review). More recently, Brozzoli, Pavani, Urquizar, Cardinali, and Farnè (2009) showed that visuo-tactile interaction between tactile stimuli applied to the hand and visual stimuli shown on a far object, that participants were asked to reach-to-grasp, was stronger during the execution and even during the initiation of the reach-to-grasp movement, as compared to when the hand was static (see also Brozzoli, Cardinali, Pavani, and Farnè (2010)).

In summary, data from monkeys and humans support the view that the fronto-parietal PPS system integrates multisensory stimuli in the space around the body and is involved in the translation of such multisensory representations into potential motor acts. However, most evidence supporting this view comes from studies investigating the representation of PPS around the hand, mainly focusing on visuo-tactile interactions and involving hand movements, while head or full body movements have been relatively neglected. Our movements, however, are not limited to upper limb actions, but frequently involve movements of the whole body in space; as during locomotion. In the present study, we asked whether and how the PPS representation varies during the most common full body action, i.e., walking.

Our group has developed a behavioral measure to quantify the extension of PPS around different body parts, i.e. the upper limb (Canzoneri, Magosso, & Serino, 2012; Canzoneri et al., 2013; Canzoneri, Amoresano, Marzolla, Verni, & Serino, 2013), and the face (Teneggi, Canzoneri, di Pellegrino, & Serino, 2013). In this task, participants are requested to respond as fast as possible to a tactile stimulus administered on their chest, while task-irrelevant sounds are presented, giving the impression of a sound source looming toward or receding from their bodies. The tactile stimulus is given at five different temporal delays from sound onset, implying that tactile information is processed when the sound is perceived at five different distances from the subject. Because we have repeatedly shown that a sound boosts tactile reaction times when presented close to, but not far from, the stimulated body part, that is, within and not outside the PPS (Serino et al., 2007, 2011; Bassolino, Serino, Ubaldi, & Lådavas, 2010), we use that task to capture the critical distance from the participant's bodies where sounds affect tactile reaction time as a proxy for the boundary of PPS representation.

In **Experiment 1**, the aforementioned paradigm was applied while participants either stood immobile or walked on a treadmill. In such a manner we measured the extension of peri-chest space,

and how it varied during locomotion, while the body part onto which we applied touch was neither moving in tridimensional space, nor performing the motor execution itself (as it is mainly the legs and also arms, but not the chest, that move during locomotion). In this way we minimized any confounding effect on tactile processing due to movement of the stimulated body part and we kept constant the relative distance between the sound source and the stimulated body part for the walking and the immobile condition. If whole-body actions shape PPS representation, we predicted that PPS would be extended while participants walked, as compared to they were immobile, implying that the distance where sounds affect tactile processing should be farther away from the participants in the former as compared to the latter condition.

In **Experiment 2** we tested the role of concurrent visual information conveying optic flow cues in shaping PPS representation. To this aim, while walking or standing immobile on the treadmill, participants were also exposed to an optic flow projected onto a 10 m² screen in front of them. Optic flow is a powerful visual cue implying forward translations (Royden & Moore, 2012), especially during walking (Gibson, 1950). Thus, results from **Experiment 2**, i.e., with optic flow, have been compared to the no-optic flow conditions run in **Experiment 1**, in order to determine whether kinematic information related to body motion or visual information related to the environment is critical in shaping PPS representation.

2. Methods

2.1. Participants

Eighteen (7 female, mean age 23 years old, ± 3) participants took part in **Experiment 1** and another 18 in **Experiment 2** (9 female, mean age 25 years old, ± 4). None of the subjects participated in both experiments. Participants had normal or corrected-to-normal visual acuity and reported normal tactile and auditory sensitivity. All participants gave their informed consent to take part in this study, which was approved by the local ethics committee – La Commission d’Ethique de la Recherche Clinique de la Faculté et de Médecine de l’Université de Lausanne, and were paid for their participation.

2.2. Materials and apparatus

As schematized in **Fig. 1**, participants either walked (in the Walking Condition) or stood (in the Standing Condition) on a treadmill (U.N.O. X-Trail 2.0, Beny Sports, Nürnberg, Germany) that was 0.5 m wide and 1.3 m long (as in Kannape & Blanke, 2013). The console and the handlebars of the treadmill were detached in order to permit participants an unimpeded view of a 4.0 × 2.5 m² back-projection screen (width × height, 1280 × 1024 pixels, 60 Hz) onto which a fixation cross (10 × 10 cm² cross) was displayed at each individual participant’s eye-level height and on his or her body midline. During the Walking conditions participants walked on the treadmill at a constant speed of 0.70 m/s. For participants involved in **Experiment 2**, in addition to the fixation cross, a moving dot pattern (40 dots/m², simulating ~78 cm/second) was generated in OpenGL simulating depth linear forward vection (Ohmi, Howard, & Landolt, 1987; Ohmi & Howard, 1988). Participants were placed 2 m away from the back-projection screen, which itself formed the back wall for a tracking arena (JVC DLA-SX21 projector, JVC U.S.A., Wayne, NJ).

In order to map PPS representation, an audio rendering system composed of two uniform linear arrays of eight loudspeakers each (JBL Control 1 Pro WH Pair, M-Audio FastTrack Ultra 8R) were placed alongside the participant. The speakers were placed horizontally starting at the participant’s chest level, and extending for 2 m, maintaining altitude, until the back-projection screen. Participants were placed at the exact center between the two arrays, 50 cm along the coronal plane from each array of speakers (see **Fig. 1**). This system simulated a white noise sound source either approaching from 2 m away until the position of the participant, or receding from the subject until it was 2 m away. Dynamic sounds were utilized because PPS neurons have been shown to be particularly sensitive to looming stimuli (Rizzolati et al., 1981; see also Graziano and Cooke (2006)). The sound traveled at a constant velocity of 75 cm/second and loudness of 50 dB. The algorithm governing the movement of sound has been extensively explained elsewhere (Serino et al., 2014). Lastly, a vibrotactile device (Precision MicroDrives shaftless vibration motors, model 312-101, 3 V, 60 mA, 9000 rpm, 150 Hz, 5 g) was placed on the participant’s chest. The exact location of the vibrotactile device varied slightly depending on the

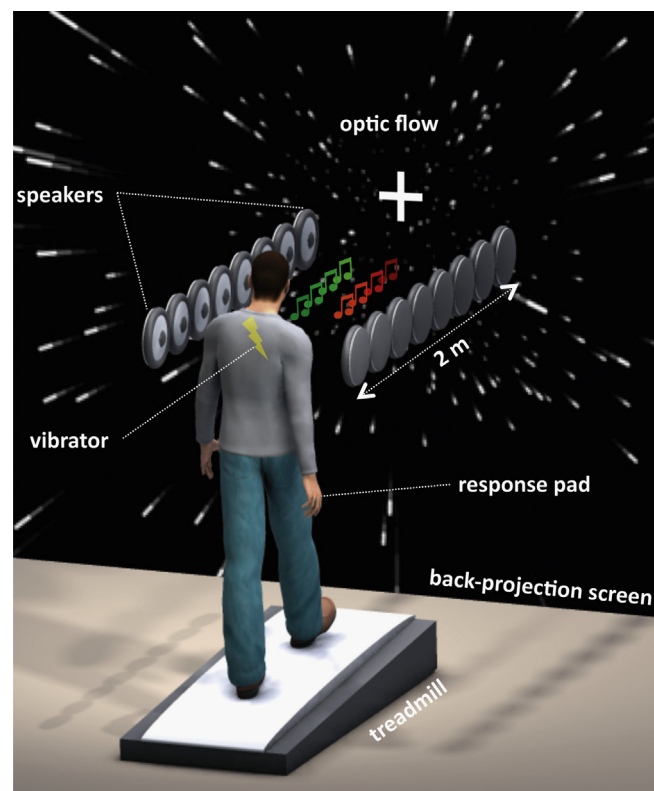


Fig. 1. General setup for Experiments 1 and 2. Participants either walked or stood immobile on a treadmill while fixating a cross situated at their eye-level at a distance of 2 m in front of them on a back-projection screen which either remained black (**Experiment 1**) or onto which a starfield moving toward the participant was shown (**Experiment 2**). The task consisted of responding as quickly as possible by pressing a button on a response pad with the thumb of the right hand whenever a vibrator delivered a tactile stimulus to the participant’s chest (in yellow). Task-irrelevant looming (in red) or receding (in green) sounds were presented by an array of speakers. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

participant’s height, in order to assure a congruent height between the array of speakers and the location of vibrotactile stimulation. On target trial, the vibrotactile device was activated so to produce a 100 ms tactile stimulation. Participants were handed a wireless gamepad (XBOX 360 controller, Microsoft, Redmond, WA, 215 Hz sampling rate), which they held in the right hand and used to respond to vibrotactile stimulation. RTs were measured relative to the onset of tactile stimulation.

2.3. Protocol and experimental design

For both experiments, the design comprised three within-subjects variables, i) Sound Direction (Looming or Receding), ii) Sound Distance (D_1 through D_5), and iii) Locomotion condition (Standing or Walking). Sound Direction and Sound Distance were randomized in a trial-per-trial fashion. At the onset of a trial either a looming or a receding sound was presented and started to move either toward (looming) or away (receding) from the participant. Then, at a certain temporal interval from sound onset ($T_1=0.44$ s, $T_2=0.88$ s, $T_3=1.33$ s, $T_4=1.77$ s, or $T_5=2.22$ s), the vibrotactile stimulation on the chest was given. Thus, for different temporal intervals, tactile stimulation was given when the white noise was perceived at a given distance from the body. That is – say for the case of a looming sound – as by definition the looming sound is approaching the participant’s body as a function of time, the longer the temporal interval between sound onset and tactile onset, the shorter the distance between auditory and tactile stimulation (which by definition always happens on the body). The correspondence between the temporal interval from sound onset and the spatial distance between sound and touch location was coded so that for a receding sound the temporal dimension matched linearly and positively with the spatial dimension (T_1 through T_5 is equivalent to D_1 through D_5), while for the approaching sound, the temporal and spatial dimensions match linearly and negatively (T_1 through T_5 corresponds to D_5 , D_4 , D_3 , D_2 and D_1 , respectively). Note that D_1 corresponds to a distance between audio and touch of 33 cm (which is 0.75 (velocity of sound, in m/s) × 0.44 (T_1 , in s) in the case of receding sounds, or $2 - 0.75 \times 2.22$ (T_5), in the case of looming sounds), $D_2=0.66$ cm, $D_3=100$ cm, $D_4=133$ cm, and $D_5=1.66$ cm.

In addition to these experimental trials, we inserted baseline and catch trials within the randomization. Baseline trials were unimodal tactile trials in which no auditory stimuli were given. Tactile stimulation was administered at 2 time intervals from the trial onset corresponding to T1 and T5 in audio-tactile trials. Baseline trials were compared to audio-tactile trials to show a facilitation effect on tactile processing due to auditory stimulation, in particular when sounds were presented close to the body. They were also used to eventually correct off-line for a possible anticipation effect on RT due to the fact that at increasing temporal interval the probability of receiving a tactile stimulation also increased, and therefore participants might be more ready to respond to tactile targets happening at the end of the trial. For each subject, his/her unimodal tactile fastest RT condition (T1 Walking, T5 Walking, T1 Standing, or T5 Standing) was subtracted from mean RTs in experimental trials. Hence, during analysis we adopt the most conservative approach possible by comparing experimental RTs to multimodal stimulation to the most rapid mean unimodal response. By definition, unimodal baseline is equal to zero and negative values indicate a facilitation in reaction time to the multimodal condition as compared to the mentioned unimodal baseline.

Catch trials were trials in which we presented a sound (either looming or receding) yet no vibrotactile stimulation was given, and therefore participants were to withhold response. This last condition was included in order to avoid automatic association between the sounds and a motor response. Lastly, the order of the Locomotion condition was blocked and counterbalanced between subjects. All conditions were repeated 16 times, giving a total of 512 trials per subject (2 Locomotion conditions \times 2 Sound Direction conditions \times (5 Distances + 2 Baselines + 1 Catch) \times 16 repetitions). Inter-stimulus interval was randomized between 1 and 1.5 s. The total experimental time was about 50 min (for each experiment).

Upon arrival to the laboratory, participants were instructed to either stand still or walk on the treadmill (according to the condition), to maintain fixation on the back-projection screen (which could be composed by either solely the fixation cross for participants involved in [Experiment 1](#) or the fixation cross and the optic flow for participants involved in [Experiment 2](#)), and to respond by button-press to the vibrotactile stimulation as fast as possible. They were told that in most trials they would hear sounds, but that these were irrelevant for the task, and therefore they were invited to ignore them.

2.4. Control measures

In order to control that participants' absolute position in space did not vary between the Walking and the Standing immobile conditions, in a subset of our sample (2 participants in [Experiment 1](#), and 3 participants in the [Experiment 2](#)), subjects' movements were tracked and recorded by an active optical motion capture system (2 infrared markers, ReActor2, Ascension Technology, Burlington, VT) at a sampling frequency of 15 Hz. The two infrared markers were placed on the subject's head (one above each ear), and their tridimensional location in space was analyzed off-line. Lateral ([Fig. 2](#): x-axis) and sagittal ([Fig. 2](#): y-axis) translation was tracked. As the depth dimension is of particular interest here, we performed a Paired Samples *t*-test on the y-axis, comparing the amount of translation between the Standing and Walking conditions. Results revealed no significant difference between Locomotion conditions ($t < 1$, C.I. = [-1.03, 1.06]). Moreover, as illustrated in [Fig. 2](#), in the case of translation, participants were more prone to drifting backward (e.g., participants #1, and #4) than forward (e.g., participant #5). Finally, it must be noted that the range of translation was relatively small, never exceeding 10 cm.

In addition, in order to demonstrate that the pattern of moving dots administered as optic flow in [Experiment 2](#) was effective in inducing translational cues, we recorded postural changes provoked by optic flow stimulation in 12 subjects (1 female, mean age = 24.2 ± 3.4). Effective optic flow usually induces body oscillations to maintain postural sway ([Bardy, Warren, & Kay, 1996, 1999; Warren, Kay, & Yilmaz, 1996](#)). In order to check that administration of optic flow was effective in [Experiment 2](#), in the present control experiment participants were placed standing at the center of a force plate (Wii Balance Board; Nintendo, Kyoto, Japan) 2 m away from the back-projection screen (as in [Experiments 1 and 2](#)) and gazed at a fixation point while the optic flow stimulus was present, or not. Participants completed 10 trials of 2 min (5 with optic flow, and 5 without) in a randomized order. Center of gravity data in the anterior-posterior axis was streamed at 60 Hz and subsequently filtered to 10 Hz (as in [Wei, Stevenson, & Kording, 2010](#)). As a measure of postural sway, the variance within in a time-series was extracted for each trial, averaged within a participant and compared across conditions (optic flow or no optic flow). Paired-Samples *t*-test revealed that while participants were submitted to the optic flow, they swayed significantly more ($M = 0.97$, S.E. = 0.12) than during the no optic flow condition ($M = 0.69$, S.E. = 0.18; $t(11) = 1.78$, $p < 0.05$), thus confirming the soundness of our optic flow manipulation.

3. Results

Experiment 1. There were no detection omissions, and a Paired-Samples *t*-test on the number of false alarms revealed no difference

between Standing still (2.0%, S.E.M. = 1.1%) and Walking ($M = 1.8\%$, S.E.M. = 1.4) ($t < 1$).

Baseline-corrected audio-tactile RT were submitted to a repeated-measures ANOVA (Locomotion condition \times Sound Direction \times Sound Distance), and findings presented a significant Locomotion condition \times Sound Direction ($F(1,17) = 8.93$, $p < 0.001$, $\eta^2 = 0.34$), Locomotion condition \times Sound Distance ($F(4,68) = 3.71$, $p = 0.009$, $\eta^2 = 0.17$), Sound Direction \times Sound Distance ($F(4,68) = 12.59$, $p < 0.001$, $\eta^2 = 0.42$), and Sound Direction \times Sound Distance \times Locomotion condition ($F(4, 68) = 8.70$, $p < 0.001$, $\eta^2 = 0.33$) interactions.

In order to elucidate the root of these interactions, separate ANOVAs were conducted for each Sound Direction condition. The repeated-measures ANOVA conducted on the looming sounds, shown in [Fig. 3](#), revealed a Sound Distance main effect ($F(4, 68) = 17.66$, $p < 0.001$, $\eta^2 = 0.51$), in addition to a Locomotion condition main effect ($F(1,17) = 36.58$, $p < 0.001$, $\eta^2 = 0.68$). Most interestingly, results also revealed a significant Locomotion condition \times Sound Distance interaction ($F(4, 68) = 5.27$, $p < 0.001$, $\eta^2 = 0.23$). In order to explain such interaction, separate One-way ANOVAs were conducted on the Standing and Walking locomotion conditions. Analysis performed on the Standing condition showed a significant main effect for Sound Distance ($F(4,68) = 19.15$, $p < 0.001$, $\eta^2 = 0.53$). In order to identify the position in space where sounds significantly boosted tactile processing, as a proxy of PPS boundaries, we ran subsequent Bonferroni-corrected One-Sample *t*-tests between RT at different audio-tactile distances and baseline. Those analyses demonstrated that RT at D1 and D2 (all $t > 3.8$, all $p < 0.05$), but not at D3, D4, and D5, were significantly different from the unimodal tactile baseline. Considering the sound administration device used in the present paper, these results mean that while standing and immobile, auditory stimulus came to interact and modify significantly tactile perception when sounds where at a distance from the body of approximately 65–100 cm (respective distance of D2 and D3).

The same analysis (One-Way ANOVA) was carried out on the Walking condition and revealed a significant main effect for Sound Distance ($F(4,68) = 4.13$, $p < 0.05$, $\eta^2 = 0.159$). Crucially, and differently than for the Standing condition, Bonferroni-corrected One-Sample *t*-test showed that, compared to the fastest unimodal tactile condition, RT to audio-tactile trials were faster at all distances probed (D1–D5; all $t > 3.6$, all $p < 0.05$), implying that, even at a distance of 1.66 m from the participant's body (the distance of D5), auditory stimuli significantly speeded up the processing of touch being applied to the chest. Thus, the spatial position where sounds affected tactile processing was significantly different between the Standing and Walking conditions. In particular, Paired-Samples *t*-tests (Bonferroni corrected) performed between the two Locomotion conditions showed that RT were faster in Walking than in the Standing condition at D3–D5 (all $t > 3.60$, all $p < 0.05$), i.e. when sounds were located in the far space. Taken together, results from [Experiment 1](#) suggest that the PPS representation enlarged between the Standing condition (in which RT solely at D1 and D2 were faster than unimodal tactile baseline) and the Walking condition (in which RT at D1 through D5 were faster than unimodal tactile baseline).

The 2(Locomotion condition) \times 5(Sound Distance) repeated-measures ANOVA conducted solely on the receding sounds demonstrated no Sound Distance main effect ($F(4, 68) = 1.57$, $p > 0.05$, $1 - \beta = 0.46$), no Locomotion main effect ($F(1,17) = 0.38$, $p > 0.05$, $1 - \beta = 0.30$), and no interaction ($F(4,68) = 2.83$, $p > 0.05$, $1 - \beta = 0.80$). Hence analyses on the receding sounds were discontinued, as there was no evidence for a space-dependent modulation of multisensory processing. Mean RTs difference between multimodal audio-tactile trials and the fastest unimodal tactile trials (in milliseconds) for receding sounds are reported in [Table 1](#).

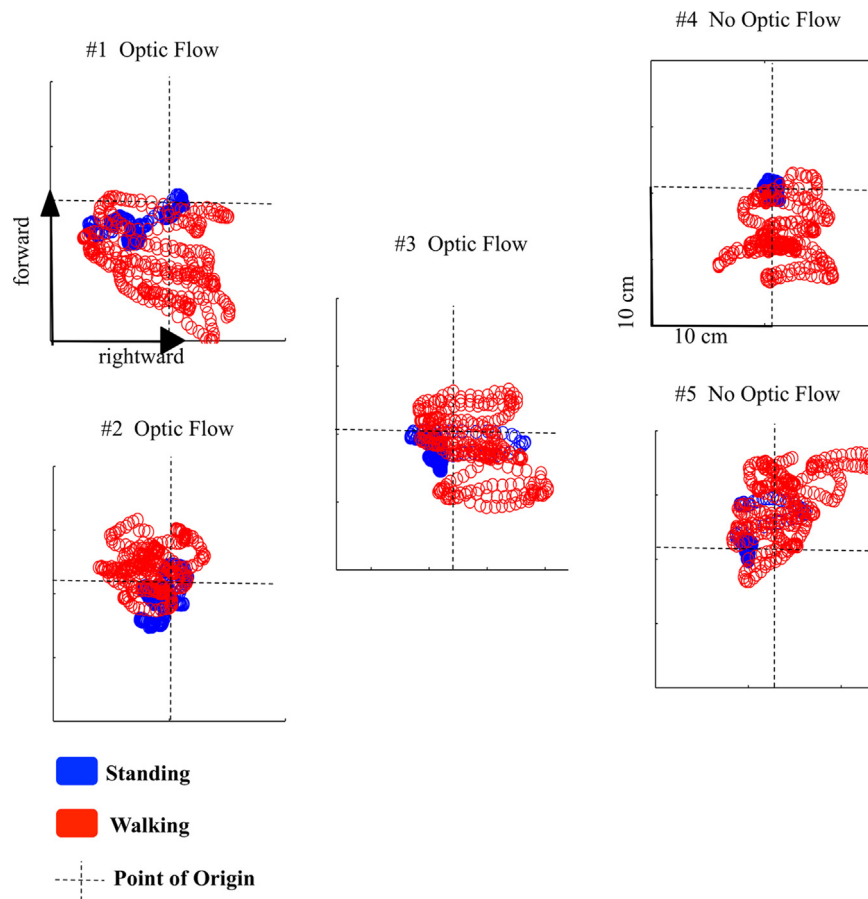


Fig. 2. Bird's-eye view (upward indicates forward motion) of active optical motion tracking data for 5 participants (3 from Experiment 1, “no optic flow”; 2 from Experiment 2, “optic flow”). Intersection of dashed lines indicates the location where participants were placed at the beginning of the experiment (point of origin). Red points indicate locations occupied by the participant during the walking condition, while blue ones indicate placements occupied by the participant during the standing condition. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

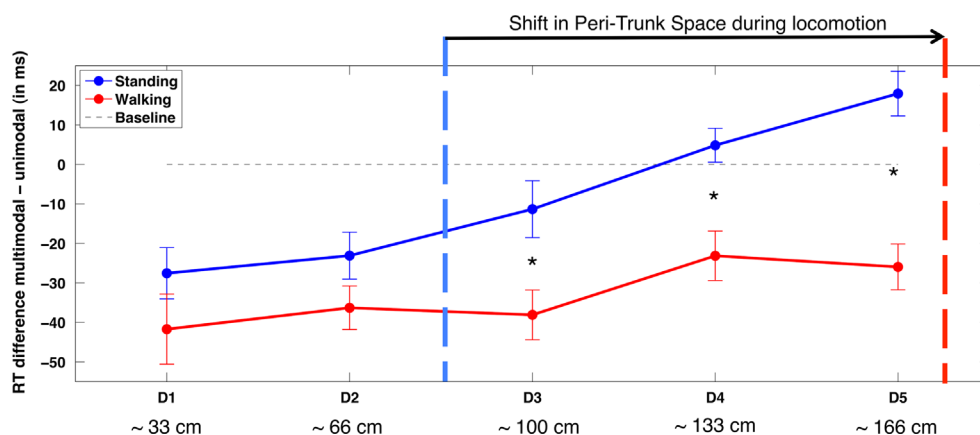


Fig. 3. Experiment 1 Results. Mean RT difference between fastest tactile unimodal (by definition, therefore, unimodal RT=0, gray shaded area indicates S.E. for unimodal condition) and audio-tactile multimodal conditions as a function of sound distance from the participant (D1=closest, D5=farthest). Negative values on the y-axis indicate a multimodal facilitation. Red=Walking condition, Blue=Standing condition, Dashed line= unimodal tactile baseline condition. Error bars indicate ± 1 S.E. and * $p < 0.05$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Experiment 2. Experiment 2 was the same as Experiment 1, but now optic flow information was added to the Standing immobile and the Walking conditions in order to test the role of visual inputs, conveying translational cues, in shaping PPS representation. As for Experiment 1, there were no detection omissions, and a paired t -test on the number of false alarms revealed no

difference between Standing still ($M=0.9\%$, $S.E.M=0.7\%$) and Walking ($M=2.7\%$, $S.E.M=2.1\%$) ($t < 1$).

A 2(Locomotion condition) \times 2(Sound Direction) \times 5(Sound Distance) repeated-measures ANOVA was performed on baseline-corrected RT in the audio-tactile condition. Results revealed a main

effect for Sound Distance ($F(4, 68)=6.58, p < 0.001, \eta^2=0.27$), as well as for Sound Direction ($F(1, 17)=54.13, p < 0.001, \eta^2=0.76$). Most importantly, analysis also demonstrated significant Locomotion condition \times Sound Direction ($F(1,17)=43.97, p < 0.001, \eta^2=0.72$), Locomotion condition \times Sound Distance ($F(4,68)=7.92, p < 0.001, \eta^2=0.31$), Sound Direction \times Sound Distance ($F(4,68)=7.32, p < 0.001, \eta^2=0.30$), and Sound Direction \times Sound Distance \times Locomotion condition ($F(4, 68)=10.33, p < 0.001, \eta^2=0.37$) interactions.

As for [Experiment 1](#), in order to study the source of the significant interactions, we conducted two separated ANOVAs, one for each sound direction. The repeated-measures ANOVA conducted on the looming sounds with the factors Sound Distance and Locomotion condition showed a Sound Distance main effect ($F(4, 68)=10.56, p=0.003, \eta^2=0.38$), in addition to a Locomotion condition main effect ($F(1,17)=9.94, p=0.006, \eta^2=0.36$). Most interestingly, results also revealed a significant Locomotion condition \times Sound Distance interaction ($F(4, 68)=6.82, p < 0.001, \eta^2=0.28$).

In order to exploit this interaction, which is shown in [Fig. 4](#), separate One-way ANOVAs were conducted on the Standing and Walking locomotion conditions. Analysis performed on the Standing condition showed a significant main effect for Sound Distance ($F(4,68)=18.81, p < 0.001, \eta^2=0.52$). Subsequent Bonferroni-corrected One-Sample *t*-test, ran in order to identify the location of the PPS boundaries, demonstrated that RT at D1 and D2 (all $t > 5.0$, all $p < 0.05$), but not at D3, D4, and D5, were significantly different from the unimodal tactile baseline. These results confirm those of [Experiment 1](#), and suggest that while standing still, looming sounds boost the processing of a stimulus on the chest when they occur at a distance from the body smaller than ~ 65 to 100 cm (respective distance of D2 and D3). The One-Way ANOVA carried out on the Walking locomotion condition also revealed

a significant main effect for Sound Distance ($F(4,68)=3.17, p < 0.05, \eta^2=0.157$). Differently than for the Standing condition, Bonferroni-corrected One-Sample *t*-test showed that D1–D5 were significantly faster than the baseline unimodal tactile condition (all $t > 3.9$, all $p < 0.05$). This implies that even at a distance of 1.66 m (the distance of D5), sounds significantly speeded up tactile processing on the chest, as it was found in [Experiment 1](#). The direct comparisons between the two Locomotion conditions at each Sound Distance showed Bonferroni-corrected significant differences at D2, D3, and D5 (all $t > 3.20$, all $p < 0.05$). Taken together, results from [Experiment 2](#), as those from [Experiment 1](#), suggest that the PPS representation expands when participants walk as compared to when they stand still.

The $2(\text{Locomotion condition}) \times 5(\text{Sound Distance})$ repeated-measures ANOVA conducted solely on the receding sounds demonstrated no Sound Distance main effect ($F(4, 68)=1.78, p > 0.05, 1-\beta=0.61$), nor a significant Locomotion main effect ($F(1,17)=0.95, p > 0.05, 1-\beta=0.31$), nor a significant interaction ($F(4, 68)=2.91, p > 0.05, 1-\beta=0.65$). Hence, analyses on the receding sounds were discontinued, as there was no evidence for a space-dependent modulation of multisensory processing. Data are reported in [Table 1](#).

Thus, results from [Experiment 1](#), when participants were standing or walking with no additional visual information, and those from [Experiment 2](#), where optic flow was added as a visual cue suggesting a translation in space, revealed a similar expansion in depth of PPS, with no apparent change due to optic flow presence or absence. To confirm, we ran a final analysis directly comparing the results from the two experiment. A $2(\text{Locomotion condition: Standing vs. Walking}) \times 2(\text{Sound Direction: Looming vs. Receding}) \times 5(\text{Sound Distance}) \times 2(\text{Experiment: no-optic flow vs. optic flow})$ mixed ANOVA was carried out on baseline corrected

Table 1
Mean difference between the fastest unimodal tactile RT and multimodal (audio–tactile) RT as a function of the distance between the auditory and tactile stimuli (D1=closest, D5=furthest), for both [Experiment 1](#) (upper panel) and [Experiment 2](#) (lower panel), for receding sounds. Values are in milliseconds. Negative values indicate facilitation from unimodal to multimodal condition. Values in parentheses indicate S.E. Note that all values are negative indicating that as general rule, audio–tactile receding RTs were faster than tactile RTs. However, this difference was not significant and was independent from the position of sounds in space, i.e. not related to PPS.

Distance	D1	D2	D3	D4	D5
Experiment 1					
Standing	–23 (29)	–23 (28)	–25 (19)	–25 (23)	–25 (24)
Walking	25 (32)	–26 (29)	–23 (33)	–24 (33)	–25 (22)
Experiment 2					
Standing	–24 (21)	–25 (23)	–24 (22)	–23 (18)	–23 (27)
Walking	–22 (22)	–25 (24)	–25 (15)	–24 (29)	–23 (23)

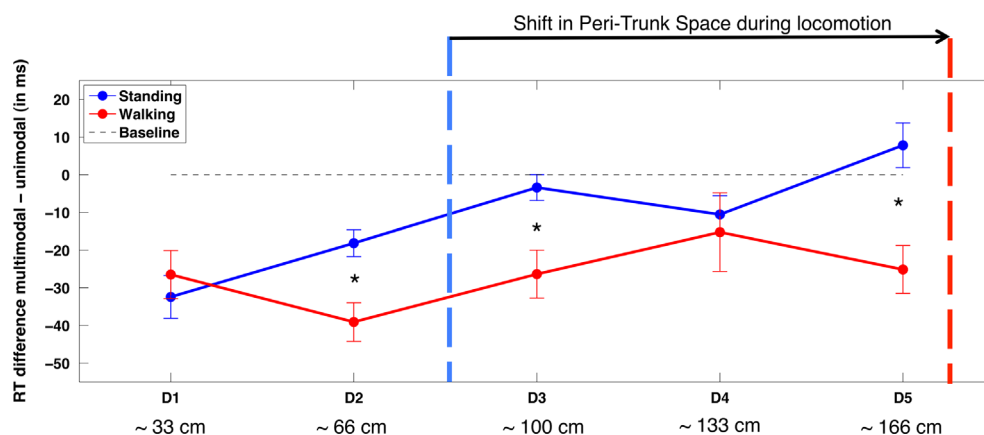


Fig. 4. [Experiment 2](#) Results. Mean RT difference between fastest tactile unimodal trials and audio–tactile multimodal trials as a function of sound distance from the participant (D1=closest, D5=furthest). Negative values on the y-axis indicate a multimodal facilitation. Red=Walking condition, Blue=Standing condition, Dashed line= unimodal tactile baseline condition. Error bars indicate ± 1 S.E. and * $p < 0.05$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

RT. No main effect of Experiment (optic flow vs. no optic flow; $F < 1$), or any interaction with Experiment was found (all $p > 0.50$).

4. Discussion

In the present study we show that during a full body action, as is the case of walking, the PPS representation of the chest expands in the direction of walking. We found that, while our participants were walking, looming sounds interacted with processing of tactile information on the body when they were located at farther distances than compared to when participants were standing. Two related findings support this conclusion. First, we found that while participants were standing and immobile, their RTs to tactile stimuli at the chest, processed simultaneously with dynamic sounds, were faster than RT to unimodal tactile stimuli when sounds were closer than approximately 65 cm from their body. In contrast, if participants were walking, sounds located even at 165 cm from their body still boosted tactile processing. Thus, the boundaries of PPS representation expanded forward in the direction of walking. Importantly, this effect did not depend on a change in the relative actual distance between the sound source and body, as in the walking condition participants were walking on a treadmill, and therefore did not move in tridimensional space. Motion capture data of head position showed that participant's averaged position in space was comparable between the walking and the standing immobile conditions. Thus, motor command and kinesthetic inputs related to walking were sufficient to change the PPS boundaries, although no significant changes in the relative positions of the body and external stimuli occurred. In addition, we found the same difference in PPS representation both in [Experiment 1](#), when participants were standing or walking without additional visual information, and in [Experiment 2](#), when participant's were facing a screen onto which optic flow stimuli were projected in order to add visual cues suggesting a forward translation compatible with their walking. Thus, motor and kinesthetic cues during locomotion are sufficient to expand PPS, without necessarily requiring additional visual and environmental inputs, as those tested here.

These results are, to the best of our knowledge, the first demonstration of an action modulation of PPS representation due to movements of the whole body. Indeed, [Berti, Smania, Rabuffetti, Ferrarin, Spinazzola, D'Amico, Ongaro and Allport \(2002\)](#) concluded that patients exhibiting extrapersonal neglect did not remap PPS representation (far space as near space) during locomotion. However, they equally stated that perhaps a more extended walking event (their patients at maximum walked for 3 m before testing PPS representation) would be able to capture a locomotion-dependent remapping of PPS. Our results, in which we test healthy participants who walk for an extended period of time, and in which we utilized a different measure, represent the first report of such locomotion-dependent remapping of PPS.

Previous studies suggest that PPS representation remaps as a function of hand actions. [Brozzoli et al. \(2009, 2010\)](#), for instance, showed that the amount of visuo-tactile interaction between tactile stimuli at the hand and visual stimuli placed on an object to be grasped, increased at the beginning and during the reaching phase of the grasping movement, suggesting that hand movements extend the space of multisensory integration. Although in line with that conclusion, the present results are new in several respects.

First, differently from previous studies, in the present study the body part receiving tactile stimulation in order to measure the PPS representation, i.e. the chest, did not translate forward in space and was also not directly involved in the action, i.e. walking. In contrast, [Brozzoli et al. \(2009, 2010\)](#) tested the hand

representation while the hand was also the body-part that received tactile stimulation and moved during the experiment. Such movement might represent a possible confounding effect for the change in visuo-tactile interaction found during the reaching movements by [Brozzoli et al. \(2009, 2010\)](#) (although these concerns do not apply for the weaker effects found before the movement). Indeed, the execution of a hand movement physically reduces the space between the hand and the object to be grasped and accordingly the stronger changes in visuo-tactile interaction found during the reaching phase of the movement by [Brozzoli et al. \(2009, 2010\)](#) might be partially due to an increased physical proximity between the hand and the object. Similarly, movement in space necessarily implies a velocity; yet [Fogassi et al. \(1996\)](#) demonstrated that PPS neurons in the inferior premotor cortex are sensitive to such feature of movement kinematics and showed that receptive fields extend proportionally as the velocity of the incoming stimuli increases. Thus, the change of peri-hand space representation during hand reaching might be partially due to comparisons between a static condition, lacking velocity or other movement kinematics, and movement conditions with different combinations of such features. Additionally, moving one's hand toward a visual target inevitably alters the visual input into the system (e.g., by occluding the target, by the hand entering the visual field, etc.), and therefore cannot discriminate between an experimental effect produced solely by the motor command to move, from a visual effect produced by the sensory consequences of such movement. In the present study we exclude possible confounding effects due to the movement of the tested body part, by having participants walk on the treadmill, and therefore not translating in space, and also by stimulating and testing a body part, i.e. the chest, not directly involved in performing the walking movement.

Secondly, and more interesting from a conceptual point of view, most previous evidence about the features and plastic properties of PPS representation focuses on multisensory, mostly visuo-tactile, interactions around the hand. As a consequence, the concept of PPS is frequently described as a form of hand-centered visual processing of near objects (see e.g. [Makin, Holmes, and Ehrsson \(2008\)](#), [Makin et al. \(2012\)](#), [Brozzoli, Gentile, and Ehrsson \(2012\)](#), and [Brozzoli, Ehrsson, & Farne, 2014](#)). Although it is true that the most commonly studied populations of PPS neurons are devoted to integrate visuo-tactile information in the peri-hand space, neural populations within the same fronto-parietal network also underlie other forms of multisensory interaction, e.g. audio-tactile and trimodal audio-visuo-tactile and vestibular inputs, within the space surrounding not only the hand, but also the head ([Duhamel et al., 1998](#); [Graziano, Reiss & Gross, 1999](#); [Schlack, Hoffmann, and Bremmer \(2002\)](#); [Sereno & Huang, 2006](#)) and the chest ([Graziano & Gross, 1994](#); [Duhamel, Bremmer, Ben Hamed, & Graf, 1997](#); [Huang et al., 2012](#), [Sereno & Huang, 2014](#); [Serino et al., 2014](#)).

Considering the proposed role of PPS representation as a multisensory-motor interface between the body and the environment ([Rizzolatti et al., 1997](#); [Graziano & Cooke, 2006](#)), it is reasonably conceived that a specialized populations of PPS neurons map specific sectors of space around individual body parts (see e.g. [Farnè et al. \(2005\)](#)) and concur to body parts movements ([Makin et al., 2009](#); [Serino et al., 2009](#)). However, the body also moves as a whole leading to displacements of the individual in the environment (i.e. [Kannape, Schwabe, Tadi, & Blanke, 2010](#); [Kannape & Blanke, 2013](#)). Moreover, phenomenologically, the experience of our body and self in space is not limited to that of single body parts, mostly the hand, but concerns the body as a whole (see e.g. [Blanke and Metzinger \(2009\)](#), for a discussion about the distinction between partial, body-part ownership, and global, full-body, identification). Recent data from our lab suggest

that peri-chest PPS might be particularly important to ground a more global, unified representation of the PPS around the whole body within the environment (Serino et al., 2014). Coherently with this view and extending earlier data about expansions of PPS during movement to full-body movement, the present study shows that during whole body movements the peri-chest PPS expands in the direction of the body movement.

The fact that PPS representation is extraordinarily plastic as a function of the interaction between the individual and the environment is well established as extensive literature ascertains that PPS boundary re-shape as a consequence of tool-use (Farnè & Làdavas, 2000; Maravita & Iriki, 2004; Farnè, Iriki, & Làdavas, 2005; Serino et al., 2007; Bassolino et al., 2010; Canzoneri, Ubaldi, et al., 2013), social interaction or the aversion of thereof (Ferri, Ardizzi, Ambrosecchia, & Gallese, 2013; Teneggi et al., 2013; Sambo & Iannetti, 2013), and illusory body-part ownership (Graziano et al., 2000; see also Brozzoli et al. (2012)). Here we show that an online form of plasticity in PPS representation occurs also during one of the most common and simple everyday activity, walking. In order to explain the effects of tool-use (Iriki et al., 1996; Maravita & Iriki, 2004; Magosso, Ursino, di Pellegrino, Làdavas, & Serino, 2010; Canzoneri et al., 2013) for instance, it has been proposed that the visual (or auditory) receptive field of PPS neurons might enlarge toward the space where the tool has been used to extend the action possibilities of the body (see e.g. Macaluso and Maravita (2010) and Gallese and Sinigaglia (2009)). A similar extension effect of receptive fields of PPS neurons to incorporate artificial replacements of the body has also been proposed to account for illusory ownership of fake hands during the rubber hand illusion (Makin et al., 2008), or of virtual bodies, during the full body illusion (Blanke, 2012).

Results from the present study, i.e. the forward shift of the spatial limits of audio-tactile integration in the direction of walking, and thus toward the far space, may behaviorally capture the extension of auditory receptive fields of multisensory neurons mapping the chest PPS during walking. As mentioned above, Fogassi et al. (1996) found that in most PPS neurons in the PMc, the size of visual receptive field varies as a function of the velocity of looming stimuli, increasing the velocity of visual stimuli approaching the animal's body produced an expansion in depth of the neuron's receptive field. The functionality of such extension might be to predict and anticipate possible contacts between external objects and the body. A stimulus moving faster toward the body have higher chances of colliding with the body earlier than a slow stimulus, and therefore should be detected and processed earlier, i.e. when it is farther in space, as integrated with tactile processing on the body. Walking implies that static stimuli become looming stimuli, and also increases the velocity of already looming stimuli. We propose that the extension effect of PPS boundaries found in the present study during locomotion reflect a short-term, putatively fast, modulation of PPS receptive fields to anticipate possible collision during walking. Furthermore, we predict that the faster the translation, the larger should one's representation of PPS become. This remains, however, a speculation and a question that will merit further empirical work in the future.

It is interesting to note that there might be potential differences between plasticity of the peri-hand and peri-chest PPS representations during movements. First of all, the two body parts move with different velocities, i.e., hands movements are faster than whole-body movements, and therefore peri-hand neurons and peri-chest neurons might be tuned to capture changes in the relative position between the body and external objects occurring at different speeds. In addition, in case of whole body translation, the position of external stimuli changes with respect to all body parts, while in the case of merely hand movements, the distance

between the external stimuli and the chest and/or the face does not change. Thus, body part movements or whole body movements might differently affect peri-hand, peri-chest or periface PPS representations (similarly, see Brain (1941), for a classic distinction between "grasping space" and "walking space").

In any case, the aforementioned interpretation of the findings from the present study concords with the definition of PPS neurons as "looming detectors". According to Graziano and Cooke (2006), the main function of PPS representation would be in protecting the body from possible threats. Looming is a fundamental signal for threat to the body, and indeed neurons responding selectively to looming stimuli have been identified in a number of species along the evolutionary axis. Looming detectors found in the fly brain, locust brain, and pigeon brain, have been hypothesized to play a role in obstacle avoidance during flight (Sun & Frost, 1998; Rind, 2002; Schuster, Strauss, & Gotz, 2002). In the present study, we actually found that looming, and not receding, sounds boost the processing of tactile information and that the distance from the body where such effect occurs is farther in space during walking, compatible with the interpretation of PPS as a looming detector.

More in general, we believe that the main function of PPS is in interfacing the body and the environment by integrating tactile information on the body with visual or auditory information related to external stimuli in space, potentially interacting with the body, in order to support appropriate motor behaviors, being those of defense, but also those of approach. If external stimuli or the body move faster with respect to each other, such integration effect has to be anticipated, and the extension of the visual or auditory receptive field of PPS neurons represents such anticipation. Extensive experimental data and a number of computational models show how motor commands are transferred to sensory systems, even before motor execution, so to predict and anticipate the consequences of behavior (see e.g. von Helmholtz (1860/1962), Wolpert, Ghahramani, and Jordan (1995), Friston (2010), and Clark (2013)). The present findings might be rooted in a similar predictive mechanism in the domain of multisensory integration in space.

A final point concerns the inputs that drive plasticity in the PPS system. In Experiment 1, the difference between the walking and the standing condition was signaled by motor, kinesthetic, and proprioceptive cues, whereas visual and auditory inputs were the same for both conditions. In Experiment 2, instead, participants were also exposed to optic flow to add visual cues implying a translation in the direction of walking. Optic flow information is indeed a powerful cue to perceive the spatial relationship between moving objects and moving observers (Royden & Moore, 2012), especially during walking (Gibson, 1950). Thus, in the walking condition, the direction of visual information was coherent with motor and kinesthetic inputs, and therefore we could test whether additional visual inputs boosted the plasticity effect of walking on PPS. On the other hand, in the standing condition, visual and motor/kinesthetic information were not coherent with each other, and therefore, we could test whether visual cues (alone) about translation were able to modulate plasticity in PPS representation and potentially induce similar effects as those observed during walking. Although a control experiment confirmed that the optic flow stimulation used in Experiment 2 was sufficient to induce translational visual cues affecting participants' postural sway, results from Experiment 2 showed that optic flow did not induce any additional effect on PPS representation, at least as measured by the present audio-tactile task. Rather, the close homology between the results obtained in Experiment 1 and Experiment 2 suggests that movement and kinesthetic cues play a stronger role in shaping PPS representation than visual cues do; at least within the limits tested here. Thus, it seems that the interaction between motor commands

and bodily-related feedback, e.g. proprioception, is necessary for the remapping of PPS observed. In order to disentangle the role of motor commands and sensory re-afferent signals in modulating PPS representation, more studies will have to be carried out. Such future studies could examine, for instance, the implications of different walking speeds, carefully matched optic flow and gait speeds, but also motor and gait imagery on spatial PPS modulations. Or alternatively, by means of brain-computer interfaces, we could envision a scenario in which motor commands are executed by one system (the participant) while the output of such commands is effectuated by another (the computer, or robot).

To conclude, here we show that a global representation of PPS centered on the chest is shaped “on-line” by walking, i.e. the most common and ecologically relevant full-body action. These results add new evidence about the role of PPS as a multisensory-motor interface between the body and the environment.

5. Acknowledgments and funding

Authors would like to acknowledge Javier Bello Ruiz and Henrique De Barba for technical assistance. AS is supported by the Volkswagen Foundation (the Un(bound) Body project, Ref. 87 336) and OB is supported by the Swiss National Science Foundation (CRSII1_125135/1) and the Bertarelli foundation.

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