



Review article

Peripersonal space (PPS) as a multisensory interface between the individual and the environment, defining the space of the self

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ABSTRACT

Our brain has developed a specific system to represent the space closely surrounding the body, termed peripersonal space (PPS). This space has a key functional role as it is where all physical interactions with objects in the environment occur. Here I describe how multisensory neurons in a specific fronto-parietal network map the PPS by integrating tactile stimuli on the body with visual or auditory information related to external objects specifically when they are close to the body. I show how PPS representation is not only multisensory, but actually multisensory-motor, as the PPS system interacts with motor areas to trigger appropriate responses. The extent of PPS is not fixed, but it is shaped by experience, as PPS may encompass farther portions of space, once the individual has interacted with them, (e.g., with tools), or it contracts, if interactions are limited because of external constraints, body, or brain injury. Interactions between the individual and the environment are not only physical but may also be “abstract”. Recent data show that PPS adapts as a consequence of technology-mediated or social interactions. Finally, I propose that besides low-level sensory-motor representations of the space around the different parts of the body, mediating body-objects interactions, the multisensory PPS system also underlies a general representation of the self as distinct from the environment and the others. PPS thus supports self-location, contributes to bodily self-consciousness and mediates higher-level cognitive functions.

1. Body-centered space representations

The brain represents space to perceive and interact with external stimuli in the environment. Space representation implies a reference frame, i.e. a fixed origin and a series of coordinate axes relative to which spatial locations and stimuli are expressed. More than 30 years of research in neuroscience, ranging from neurophysiology and neuropsychology to psychophysics and neuroimaging, have established that the brain constructs multiple representations of space, each with a given reference frame, depending on the source of sensory stimulation and the nature of interaction between the individual and the environment (Andersen et al., 1997; Soechting and Flanders, 1992). With the exception of abstract or geographical spatial maps, the body, or to given body part, constitutes the origin of most of spatial representations. To this aim, information from different sensory systems signaling the position of external stimuli in the environment is combined with information about the body part to which the specific set of reference frames is referred. For example, imagine a bee is approaching your right hand. The location of the bee in space will (initially) be processed in an

eye-centred reference frame, as you see the bee, and in a head-centred reference frames, as you hear the bee's noise. However, your brain also needs to process the bee's location in relation to your hand, if you want to avoid being stung. Thus, the location of the bee is simultaneously processed in multiple coexisting spatial representations, with different reference frames and under different sensory codes. Nonetheless, our experience of space is not fragmented, as usually we do not have explicit access to each of these spatial representations individually, but likely to their integration. This appears to be referred to a more global reference frame constituting the egocenter, i.e., the center of awareness, which, under normal conditions, is centred to a global representation of our body (Alsmith and Longo, 2014; Bertossa et al., 2008; Blanke and Metzinger, 2009).

Thus, one main feature of space representation is the reference to the body and its parts. The brain does not represent space homogeneously, but different neuronal populations represent different sectors of space, as defined in terms of distance from the body, such that it is commonly assumed that at least three “spaces” exist. Namely, the personal space, coinciding with the body surface, the peripersonal

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space, the space close to body (most commonly defined as the space within reach), and the extrapersonal space, the space far from the body. Such distinction is supported by the description of different neuropsychological patients suffering unilateral neglect (i.e. a deficit in perceiving, representing, and orienting toward stimuli in the contralateral side of space), which selectively affect one of these sectors of space, leaving relatively spared the other sectors (Beschlin and Robertson, 1997; Bisiach et al., 1986; Halligan and Marshall, 1991; Menneer et al., 1992; Vuilleumier et al., 1998). In close analogy, experimental lesions to different cortical areas in monkeys induce neglect-like symptoms which are selective for peripersonal (following lesions to Brodmann area 6) or extrapersonal (following lesions to area 8) space (Rizzolatti et al., 1983).

In this paper, I will focus on the representation of the space near the body; the peripersonal space (PPS). PPS represents a particularly relevant sector of space, as it is where all physical interactions between the individual and the environment take place. Hence, it makes sense that a neural system specifically dedicated to representing PPS has been selected through evolution. I will describe how PPS is represented through the integration of different sensory inputs, which are all coded in reference to specific body parts, or even to the body as whole, through somatosensory processing. I will argue that PPS representation is not only multisensory in nature, but actually multisensory-motor, by showing how neural systems representing the PPS interact with the motor system. I will review evidence and propose a neural mechanism to explain how the PPS can plastically extend to incorporate farther portions of space, once the individual has interacted with it, through tools or more abstract forms of interaction. I will conclude by proposing that the multisensory mechanism underlying PPS represents a general interface between the individual and the environment. I will argue that beside multiple body-part centred PPS representations, also a global PPS surrounding the whole body exists, underlying a general representation of the self as distinct from the environment and from others, thereby supporting self-location and mediating higher-level cognitive functions.

It is important to note that other interesting review papers about PPS are already available (see e.g. (Brozzoli et al., 2012a; Clery et al., 2015a; de Vignemont and Iannetti, 2014; di Pellegrino and Ladavas, 2015; Graziano and Cooke, 2006; Ladavas, 2002; Ladavas and Serino, 2008; Macaluso and Maravita, 2010; Makin et al., 2012; Rizzolatti et al., 1997a; Spence et al., 2004a)). However, these previous papers focus on data from a single species (e.g., monkeys, see (Graziano and Cooke, 2006; Rizzolatti et al., 1997a) from a single form of multisensory interaction (mainly visuo-tactile interaction, see (Macaluso and Maravita, 2010; Spence et al., 2004a)), on a single sector of space (usually the peri-hand space; see Brozzoli et al., 2012a; Makin et al., 2012), on the neural bases of PPS (Clery et al., 2015a; di Pellegrino and Ladavas, 2015), or finally on the different functions of PPS (see de (de Vignemont and Iannetti, 2014; Graziano and Cooke, 2006; Rizzolatti et al., 1997a)). By taking into account also the contributions of these previous reviews, my aim here is to treat all these issues together and coherently, in order to describe a comprehensive account of what PPS is and to propose a rather novel view of the role PPS plays for our cognitive system.

2. Multisensory representation of PPS in the primate brain

2.1. Multisensory receptive fields and the boundaries of PPS in the macaque brain

There is no PPS in the real world, as there is no physical distinction between near and far space; rather physical distance from the body can be more correctly described as a continuum along one coordinate, with a reference frame originating at the body. Yet, the primate brain represents PPS as separated from the far space, as if there were a boundary between what might interact with the body and what cannot.

The spatial extent of multisensory receptive fields of particular neurons described in specific fronto-parietal areas of the primate brain captures this notion. Neurophysiology data from the early 1980s described multisensory neurons, with a tactile receptive field centred on a body part, and with a visual and/or an auditory receptive field anchored to the same body part, and extending in space for a given distance, variable among the different neurons and depending on environmental contexts. Thus, these neurons respond to (Clery et al., 2015a; Graziano and Cooke, 2006) and integrate (Avillac et al., 2007) tactile stimulation on the body and visual or auditory information related to an external stimulus, but only when this is located within a spatial range from the body, defined by the size of their multisensory receptive fields, which in turn defines the extent of the PPS. Neurons with such features have been described in: 1) the posterior parietal cortex, between the superior parietal and the inferior parietal lobules to more posterior regions along the intraparietal sulcus (IPS), in particular in the ventral intraparietal area (VIP; (Avillac et al., 2007; Duhamel et al., 1998), and in area 7b (Leinonen, 1980); 2) the frontal cortex, in particular in the ventral premotor cortex (vPMC, in area 6, and F4; (Rizzolatti et al., 1981a, b); and 3) in the putamen (Graziano and Gross, 1993). Most neurophysiological evidence demonstrates multimodal responses from these neurons - i.e., activity generated by stimulation in more than a single sensory modality - whereas one particular study (Avillac et al., 2007) has shown proper multisensory integration - i.e., significantly different activity in the condition of multisensory (visuo-tactile) stimulation as compared both to the individual conditions of unisensory (visual or tactile) stimulation and to the sum of individual unimodal responses. Evoked multisensory responses could be weaker (sub-additive) or stronger (super-additive) than the sum of unimodal responses, but in either cases they were indicative of a neural computation which synthesizes inputs from different modalities, rather than simply responding to them (see Stein and Stanford, 2008 for a discussion). This evidence shows proper multisensory integration properties for PPS-sensitive neurons (see Bernasconi et al., 2018 and 2.4 for recent data in humans).

These fronto-parietal areas are strongly interconnected with each other, directly or indirectly project to the cortico-spinal tracts (see paragraph 4), and together are considered to form one of the multiple fronto-parietal multisensory-motor networks underlying a number of sensory-motor functions (Andersen et al., 1997; Colby, 1998; Greffes and Fink, 2005; Rizzolatti et al., 1997b, 2002). It is possible to highlight some regularity in the size and the distribution of the neurons' receptive fields in the different regions. In general, compared to tactile receptive fields in lower-tier parietal regions such as S1, the size of the tactile receptive field of such multisensory neurons is large and may cover an entire hand/arm, the head, or trunk (Fogassi et al., 1996; Graziano and Gross, 1995; Graziano et al., 1997). Some may cover an entire body half or even bilateral body regions (Leinonen et al., 1979). The size of the visual or auditory receptive fields typically matches that of the tactile receptive field and the different receptive fields overlap spatially and extend from the body for varying distances. More specifically, in vPMC, most neurons have tactile receptive fields covering the arm, but they can also cover the shoulder, upper trunk, or face region. The visual receptive fields (Fogassi et al., 1996; Graziano et al., 1997) of vPMC neurons have variable dimensions ranging from a limited portion of space of just 5 cm up to 1 m. Auditory receptive fields have been estimated as extending into space by approximately 30 cm (Graziano et al., 1999). In most VIP neurons, the tactile receptive fields are usually centred on the head (Avillac et al., 2005; Duhamel et al., 1998), but have also been reported for the upper trunk, shoulder, or arm (Iriki et al., 1996). Visual (Bremmer et al., 2001a; Duhamel et al., 1997) and auditory (Schlack et al., 2005) receptive fields in area VIP are usually limited to the upper part of space and cover a distance of 10–60 cm from the body surface, almost always on the same side of space as the tactile receptive field. Most bimodal neurons in area 7b have even larger tactile receptive fields and may cover the arm, the head, the trunk, and sometimes even the whole body bilaterally. Again, the size

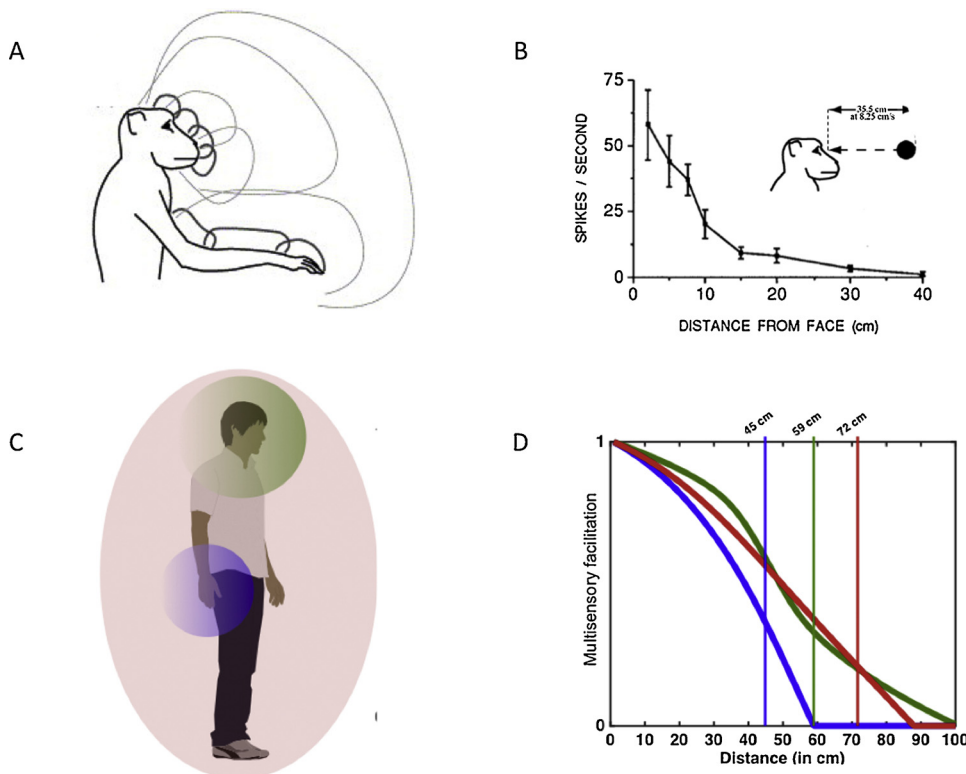


Fig. 1. PPS representation in primates. A: Dimension of visual receptive fields of PPS neurons as described in fronto-parietal areas of the macaque. Different neurons map different sectors of space around different body part (adapted from [Graziano and Cooke, 2006](#)). B: Example of a typical response of a PPS neuron to visual stimulation as a function of the distance of an approaching stimulus. C: Ideal representation of the extent of the PPS around the trunk (red), hand (blue) and face (green) in humans as identified by the degree of multi-sensory interactions from behavioral tasks (see [A. Serino et al., 2015a](#)). D: Degree of multi-sensory facilitation induced on tactile processing by an external object, as a function of its distance from the different parts of the body, namely, trunk (red), hand (blue) and face (green).

and location of their visual (or auditory) receptive fields are congruent with the dimensions of the tactile receptive field and also extend bilaterally over large regions of the visual field, sometimes covering more than 1 m ([Graziano and Gross, 1995](#); [Hyvarinen, 1981](#); [Jiang et al., 2013](#); [Leinonen, 1980](#); [Leinonen et al., 1979, 1980](#); [Leinonen and Nyman, 1979](#)). Thus, within these fronto-parietal regions, the receptive fields of bi- and tri-modal neurons cover specific parts of the body and extend proportionally over the surrounding space, with neurons in the premotor cortex representing predominantly the upper limb, in VIP the head and the face, and in area 7 the trunk ([Clery et al., 2015a](#); [Graziano and Cooke, 2006](#); [Graziano and Gross, 1995](#)) see [Fig. 1A](#)). These data point to the existence of specific multisensory representations of the space around different parts of the body, i.e. of multiple peripersonal spaces.

2.2. Human PPS

The existence of a similar system in humans, processing and integrating tactile stimuli on the body together with visual or auditory stimuli specifically occurring close to the body, is supported by converging evidence from neuropsychology, experimental psychology and neuroimaging studies.

Data from brain damaged patients suffering from extinction first demonstrated preferential multisensory interaction in the space near the body. Extinction patients typically fail reporting stimuli presented on the side of space contralateral to their brain lesions when concurrently presented with ipsilesional stimuli ([Bender and Feldman, 1951](#)), due to competition for awareness between a damaged and an intact spatial representation (see [Jacobs et al., 2011](#)). Extinction also occurs when stimuli of different sensory modalities, e.g. touch and vision, are administered to both sides of space i.e., crossmodal extinction ([Mattingley et al., 1997](#)). Critically, the degree of crossmodal extinction is modulated as a function of the distance of stimuli from the patient's body: tactile stimulation to the patients left hand, for instance, is significantly more affected by concurrent visual stimulation administered close, as compared to far from, the patient's right hand ([di Pellegrino](#)

[et al., 1997](#); [Ladavas et al., 1998a](#)). The same distance dependent modulation of crossmodal extinction has been reported for visuo-tactile ([Farne et al., 2005a](#); [Ladavas et al., 1998b](#)) and for audio-tactile ([Farne and Ladavas, 2002](#)) stimulation on and around the face. Together, these findings suggest that competition between the sides of space occurs preferentially between tactile stimulation on a part of the body, and visual or auditory stimulation close to the homologous body part in the other side of space. Less or no competition occurs for stimuli far from the homologous body part. This evidence has been advocated to demonstrate the existence of different multisensory representations of the space around different body parts, as separated from the representations of further positions of space in humans ([di Pellegrino and Ladavas, 2015](#); [Ladavas, 2002](#); [Ladavas and Farne, 2004](#)).

Behavioral data in healthy human participants confirm that the processing of tactile information on the body is more effectively influenced by visual ([Macaluso and Maravita, 2010](#)) or auditory ([Occeci et al., 2011](#)) stimuli occurring near, as compared to far from, the body, as shown by using the crossmodal congruency task ([Spence et al., 2004b](#)). In this task participants are asked to discriminate the elevation of vibro-tactile targets administered either to the thumb (held in a lower position) or the index finger (upper position), while ignoring visual cues presented either at the same or a different elevation. Participants' responses are faster and more accurate when the tactile target and the visual cue are presented at the same elevation (congruent conditions): an effect termed crossmodal congruency effect (CCE; [Spence et al., 2000](#)). Importantly, the strength of the CCE depends on the relative distance between tactile targets and visual cues, as the CCE is stronger when visual cues are presented close to the hand, as compared to when they are administered at a far location ([Pavani et al., 2000](#); [Maravita et al., 2003](#)). Spatial-dependent CCE effects have been also shown by administering tactile targets and auditory cue ([Tajadura-Jiménez et al., 2009](#); [Zampini et al., 2007](#)), or by stimulating other body regions such as the head, the back ([Aspell et al., 2010](#)) and the lower limbs ([Schicke et al., 2009](#); [Pozeg et al., 2015](#)). Together these findings show that tactile processing is more strongly affected by visual or auditory stimuli presented in the space near to rather than far from the

body.

Similar results have been obtained by using simpler multisensory interaction tasks. Participants were required to reply as fast as possible to tactile stimulation at their hand, while concurrently task-irrelevant sounds were presented either near or far from the stimulated hand. Responses to the tactile target were further sped up by the close sound, as compared to the far sound (Serino et al., 2007, 2011), suggesting that stimuli inside the PPS influenced tactile processing more strongly than stimuli outside the PPS (see (Ladavas and Serino, 2008) for a review). Based on this concept, over the last years my group developed a behavioral task not only to prove the existence, but also to quantify the extent of PPS in humans. In its original version, tactile targets on the hand were coupled with dynamic sounds, that were to be ignored, originating from a far location and approaching the participant's stimulated hand (Canzoneri et al., 2012). By presenting tactile target stimuli at different temporal delays from sound onset, we probed audio-tactile interaction when sounds were perceived at different distances from the body. As expected, we found that sounds accelerated up tactile processing (as compared to a condition of unimodal tactile stimulation). However, this effect was not linearly proportional to the spatial distance between the hand and the sound at the time of tactile processing, but occurred specifically when sounds overcame a limited distance (i.e. 40–50 cm for the hand) from the body (see Fig. 1D; Bassolino et al., 2014; Canzoneri et al., 2013a, 2013b; Serino et al., 2015b). In this way, it was possible to identify a spatial limit within which external stimuli interacted with tactile processing, delineating the boundary of PPS. Corresponding results were found not only for audio-tactile stimulation around the hand, but also around the face (Teneggi et al., 2013) and the trunk (Galli et al., 2015; Noel et al., 2014, 2015). Furthermore, similar effects have been shown also in case of visuo-tactile stimulation (Serino et al., 2015a,b) or even trimodal, visuo-audio-tactile stimulation, with the combination of modalities resulting in an improved characterization of PPS at the single-subject level (Serino et al., 2018). Several other groups have used this task to study different properties of PPS (Ferri et al., 2015a,b; Kandula et al., 2015, 2017; Maister et al., 2015a; Taffou and Viaud-Delmon, 2014). A relevant finding emerging from this task is that the distance at which multisensory interaction occurred varies as a function of the stimulated body part, being closest to the body for hand stimulation (i.e. around 30–45 cm), at an intermediate distance for face stimulation (i.e., 50–60 cm) and farthest (i.e., 70–80 cm) for trunk stimulation (Serino et al., 2015a); see Fig. 1C). These data support the existence of multiple representations of the PPS around different body parts, whose size may vary, in agreement with the neurophysiology data in monkeys reviewed above (see also Clery et al., 2017, 2015b; Farne et al., 2005b).

Finally, the task has been implemented by collecting reaction times via manual, vocal or foot responses, and the spatial modulation of tactile processing as a function of the distance of the external stimuli has been confirmed with multiple response effectors. Interesting differences might emerge by comparing the congruency between the tested PPS representation and the responding body part, as, when the two differ, additional reference frames transformations might be required. At the best of my knowledge, no empirical study has directly tested this hypothesis. However, the spatial-dependent modulation of reaction times collected by vocal (e.g., Canzoneri et al., 2012; Serino et al., 2015b) or manual (e.g., Serino et al., 2015a) responses for hand stimulation, for instance, does not appear qualitatively different from different studies, although raw reaction times clearly differ. Finally, Bernasconi et al. (2018) adapted the same task during electrocorticography (ECOG) in epileptic patients, without collecting any behavioral response. The results allowed identifying an electrophysiological marker of PPS processing, by showing a space-dependent modulation of somatosensory-evoked potentials as a function of the distance of an external sound from the patient's body (see 2.4). This method can be adapted to non-invasive scalp electroencephalography to provide a measure of PPS not involving a voluntary response from

the participant, thus allowing to extend the assessment to pathological conditions (or to infants testing), whereby the execution of an overt behavioral task is impossible (see e.g., Noel et al., Multisensory Integration in the Peri-Personal Space of Patients with Disorders of Consciousness and Cognitive-Motor Dissociation submitted for publication).

2.3. Different PPS tasks or different systems?

Other behavioral tasks have been used to study PPS in humans, such as explicit (Delevoye-Turrell et al., 2010) or implicit (Cardellicchio et al., 2011; Costantini et al., 2010) reachability judgments, or more indirect measures, such as a line bisection task. For instance, it is known that neurologically-healthy participants show a leftward bias in bisecting horizontal lines when presented in near space, an effect known as pseudoneglect (Jewell and McCourt, 2000). Laurencio and Longo demonstrated, however, that such deviation shifts to a rightward bias when lines are presented in the far space, and they measured the location where this left-to-right bias occurs as a proxy of the extent of an individuals' PPS (Longo and Lourenco, 2006, 2007a,b). Recently, Iannetti and his group developed a physiological measure to assess the dimension of human PPS around the face. They demonstrated that the strength of the hand-blink reflex (HBR), elicited by stimulation of the median nerve at the wrist, varies as a function of the distance between the stimulated hand and the face of the participants (Sambo et al., 2012; Sambo and Iannetti, 2013). Interestingly, by systematically varying the arm posture with respect to the head, Bufacchi et al. (2016) designed a model of the shape of the peri-head space as captured by the modulation of the hand-blink reflex and suggested that it is approximated by a half-ellipsoid, whose center is on the face and that extends as a bubble elongated along the vertical axis (Bufacchi et al., 2016; Sambo et al., 2012; Sambo and Iannetti, 2013), in a gravity depending way (Bufacchi and Iannetti, 2016).

All the above tasks capture a distinction between processing of near and far stimuli, which is arguably the hallmark of PPS (but see Bufacchi and Iannetti, 2018 for a discussion). However, while they might be related to the multisensory PPS system as described by monkey neurophysiological studies, they seem to rely on rather different neurophysiological processes. For instance, it has been proposed that reaching is coded by a fronto-parietal network including area F2 and the medial part of the intraparietal sulcus (MIP) (Colby, 1998; Rizzolatti et al., 1997b, 1998), and connected with areas of the dorsal visual stream, such as area V6 and V6a, also known as parietal reaching areas. This network is close to, but anatomically and functionally distinguished from the F4-VIP network where multisensory PPS neurons have been described (Matelli and Luppino, 2001) (see (Clery et al., 2015a) for a more extensive model including reaching and grasping function). The hand-blink reflex is a subcortical response, likely mediated by facilitatory and inhibitory projections within the brainstem (Miwa et al., 1998). The fact that the HBR is mediated by the location of the hand in space, and further by other more complex factors, such as the expectation of receiving a near-face stimulation (Sambo et al., 2012), individual personality factors (Sambo and Iannetti, 2013) or the presence of other people (Fossataro et al., 2016), implies that its underlying brain stem circuit receives projections from other somatosensory, vestibular, or cognitive areas. However, it has not yet been established whether the latter correspond to the multisensory PPS system described in the vPMC-PPC network in monkeys. Accordingly, de Vignemont and Iannetti propose that there may be at least two PPS systems, one dedicated to protecting the body from harmful stimuli, whose behavioral counterpart is captured by the hand-blink reflex, and the other underlying goal directed movements, as captured by multisensory-motor tasks (de Vignemont and Iannetti, 2014).

In the present paper, although I will discuss results from studies using different methods to study the PPS, I will mostly focus on a concept of PPS as an area of multisensory integration near the body,

implemented by the multisensory receptive fields of vPMc and PPC neurons described in the monkey's brain and their possible behavioral and neural counterpart in the human brain.

2.4. Neural correlates of the human PPS

Neuroimaging studies have highlighted multisensory representations of the PPS in humans, which largely correspond anatomically and functionally with the populations of PPS neurons described in the macaque brain (Bremmer et al., 2001b; Makin et al., 2008).

Most studies have focused on the processing of multisensory signals in the space around the hand. Makin et al. (2007) showed that regions along the intraparietal sulcus, in the lateral occipital complex (LOC), and the ventral premotor cortex were activated more strongly when a stimulus approached the participant's hand (near condition), as compared to the same visual stimulation presented at a distance of 70 cm from the hand (far condition) (Makin et al., 2007). Gentile et al. (2011) further showed that these areas do not only process signals that are on or close to the arm, but also integrate multisensory stimuli (i.e., showing super-additive or sub additive response; (Stein and Stanford, 2008)), when occurring within the arm-centered PPS. Brozzoli et al. (2011) developed an fMRI adaption paradigm to identify multisensory arm-related neuronal activations responding to stimulation within the PPS. They found that IPS, the inferior parietal lobe (supramarginal gyrus), the dorsal and ventral PMC, the cerebellum, and the putamen show reduced activation (adaptation) to consecutive visual stimulation near the hand, but not for consecutive far stimuli, compatible with their role in processing multisensory cues within the PPS. Taken together these neuroimaging studies highlight a network of premotor and parietal areas (also involving the putamen and the cerebellum) associated

to the processing of visual stimuli occurring within the hand PPS (See Fig. 2).

To provide causal evidence that these areas are necessarily involved in PPS representation, we used low-frequency repeated transcranial magnetic stimulation (TMS) to interfere with neural activity in vPMc and IPS (as identified by Makin et al., 2007), while participants were involved in the same audio-tactile interaction task described in 2.2 (Serino et al., 2007). We found that inhibitory TMS over both vPMc and IPS, but not at a control site over the visual cortex, abolished the facilitation effect on reaction times for tactile stimuli at the hand induced by auditory stimuli within the hand PPS. These findings suggest that vPMc and IPS represent two necessary nodes of a fronto-parietal network processing and integrating multisensory stimuli within the hand-PPS, in analogy with the brain regions of the monkey brain where multisensory neurons with hand-centred receptive fields have been described (see 2.1).

Similar, although not identical areas, were identified by neuroimaging studies assessing multisensory stimulation of the space around the face. Bremmer et al. (2001a) showed that neural activity associated with tactile stimulation on one's face overlapped with activity evoked by visual or auditory stimuli approaching (as contrasted to receding) the face in three cortical regions: IPS, ventral PMC, and lateral inferior parts of the postcentral gyrus. Based on this response profile, Bremmer et al. proposed that the IPS region was the human homologue of monkey area VIP, a proposal further corroborated by (Sereno and Huang, 2006), who found that the IPS region contained aligned maps of tactile and visual stimuli in the peri-face region, and that this activity encoded stimuli in a face-centred reference frame. This face-related IPS/VIP region partially overlaps with the PPS hand-related areas described above (see Fig. 2). A more recent study investigated

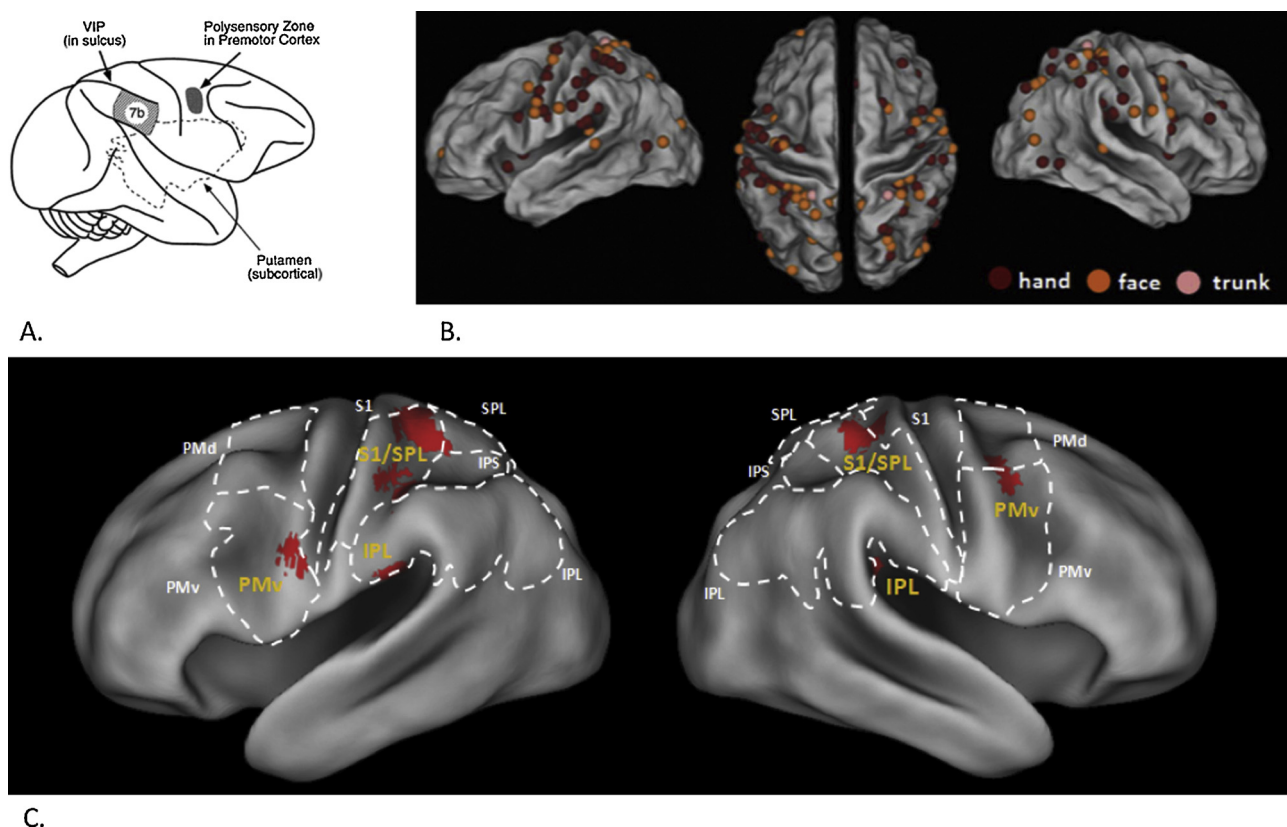


Fig. 2. Brain regions representing the PPS in the primate brain. A. Regions of the macaque brain where PPS neurons have been described (adapted from (Graziano and Cooke, 2006)). B. Peak-activation voxels in MNI space reported by different neuroimaging studies mapping the PPS in humans, decomposed by body part (as included in (Grivaz et al., 2017)). C. Brain areas showing consistent activation across the different fMRI studies on PPS representation in humans from the meta-analysis conducted by Grivaz et al. (2017) (SPL superior parietal lobule, S1 primary somatosensory cortex, IPL inferior parietal lobule, IPS intraparietal sulcus, PMv/d ventral/dorsal premotor cortex).

multisensory interaction in the space around other body parts. Huang et al. (2012) administered tactile stimulation on the face, shoulder, hand, legs and toes, while concurrently stimulating different sectors of the visual field, in order to highlight overlapping topographical representations of the tactile and visual space around different body parts. The authors found an overlap of activity induced by tactile stimulation of each body part and the visual stimulation of spatially congruent sectors of the visual field (i.e., head tactile stimulation with upper visual field; leg tactile stimulation with lower visual field). Visuo-tactile maps of different body parts were identified in the superior posterior parietal cortex: the face representation was located within the IPS/VIP region, as described above, whereas the representation of the lower body parts was located more medially and posteriorly, while the finger and hand representations more laterally and anteriorly.

In a recent paper (Bernasconi et al., 2018), we also asked whether PPS-related processing in humans reflects truly multisensory integration, or it is simply based on a proximity-dependent modulation of the response in one or more sensory modalities. To this aim, we used intracranial electroencephalography in patients implanted with intracranial electrodes for epilepsy monitoring in order to measure neuronal response to tactile (trunk) stimulation and/or auditory stimulation occurring at three consecutive distances from the patient's body. Response to multisensory audio-tactile stimulation was compared to that to unimodal tactile, unimodal auditory stimulation and the sum of the two, to highlight super-additive or sub-additive processing, indicative of truly multisensory integration. This way, we firstly identified a pool of electrodes (19% of the responsive electrodes) showing evidence of super- or sub-additive responses. Among those, 30% of the electrodes also showed a spatially-dependent modulation of their multisensory responses when the auditory stimuli were at different distances from the body. Thus, these electrodes, which were located in the post-central gyrus, in the insula and in the para-hippocampal gyrus, demonstrated PPS-dependent multisensory integration (see Avillac et al., 2007 for same evidence in non-human primates).

Thus, converging neuroimaging findings support the view that in humans, the space around different parts of the body is represented in a multisensory way by a network of specific neuronal populations, mainly located in the premotor cortex and in the posterior parietal cortex. In a recent meta-analysis, we used an activation likelihood estimation (ALE) algorithm to identify consistent activations between the different neuroimaging studies on PPS in humans (Grivaz et al., 2017). The results of these analyses are summarized in Fig. 2, where statistical maps highlighted 7 consistently activated clusters processing unisensory and multisensory events within PPS, bilaterally in the superior parietal cortex, in the temporo-parietal cortex and in the premotor cortex. Interestingly, meta-analytic coactivation mapping techniques showed that these clusters were extensively interconnected with each other, with two main patterns of functional connectivity, one involving IPL and IPS regions with primary somatosensory regions, and the other one limited to the SPL and premotor regions. Finally, we used automated regional behavioral analysis to assess which brain functions these PPS regions were more frequently associated with. We found that across 5 general domains (Action, Perception, Cognition, Interoception and Emotion), PPS premotor and parietal regions were significantly associated to Action/Execution tasks. These findings suggest that in humans, as in monkeys, PPS frontal and parietal regions constitute one of the several fronto-parietal networks, involved in sensory-motor processes, mediating individual-environment interactions (Rizzolatti et al., 1997b, 1998).

2.5. A possible neural architecture for the human PPS

In order to synthesize how PPS representation might be implemented in the primate brain, we proposed a neural network model describing computationally how tactile stimuli on the hand and visual or auditory stimuli presented close, but not far from the hand, are

integrated (Magosso et al., 2010b,c; Serino et al., 2015b). The model includes a series of unisensory layers (representing tactile, auditory or visual areas) connected to a multisensory layer. The strength of the synapses from unisensory to multisensory neurons is set to reproduce the response tuning that has been observed for near-body stimuli of the PPS system. In particular, strong synapses project to the multisensory neurons from the unisensory neurons with tactile, visual, or auditory receptive fields on the body or at short distances from the body. In contrast, the synaptic weights from unisensory visual and auditory neurons with receptive fields covering the far space are weak. This way, tactile stimulation on the hand and/or visual or auditory stimulation close to the hand is sufficient to activate the multisensory neurons. Conversely, visual or auditory stimulation far from the hand is not strong enough to induce a multisensory activity.

In series of in-silico experiments, participants' tactile perception has been modeled as the result of activation of multisensory neurons when exceeding a given perceptual threshold. Simulations have successfully reproduced behavioral data showing faster and more accurate perception when tactile stimulation is coupled with visual (Magosso, 2010; Magosso et al., 2010c) or auditory (Serino et al., 2015b) stimuli close to the body, and they were able to reproduce the graded and space-dependent modulation of tactile processing depending of the position of looming sounds in space as shown behaviorally by Canzoneri et al. (2012). When the activity of both hemispheres was simulated, the model also explained data from brain-damaged patients suffering from crossmodal extinction, by implementing inhibitory feedback projections from multisensory to unisensory neurons and inhibitory projections between the two hemispheres (Magosso et al., 2010b). Finally, by implementing neural adaptation to persistent stimulation as a mechanism sensitive to stimulus velocity, the model can also explain how PPS is more extended in depth when probed with faster as compared to slower stimuli (Noel et al., 2018a; Fogassi et al., 1996). Thus, the model proposed by Magosso and Serino was able to simulate a large set of behavioral data in healthy and brain damaged participants.

A model based on the size of tactile and visual receptive fields has been used by Roncone et al. (Roncone et al., 2016) to implement PPS representation into a humanoid robot, iCub (Metta et al., 2010). By running simulation and real experiments with iCub, the authors showed that the model architecture was able to learn and predict the trajectory of different stimuli in the environment as colliding or not the robot's body, and to implement appropriate reactions.

3. Reference frames and PPS representation

3.1. Body-part centred reference frames

Up to now, I have described PPS representation as if the body and its parts were static. In such conditions, the relative position of external stimuli with respect to the body is easily computed in terms of a series of coordinate systems that are centred to a fixed point of origin, coinciding with the body part to which each specific PPS representation refers. This is obviously an artificial condition, which occurs rarely in real life. Rather, one of the main properties of PPS representation is that it implies a series of neuronal computations allowing to keep aligned the coding of multisensory stimuli, each originally computed by a specific sensory-modality dependent system of reference, into a unique frame of reference centered to a specific body part. For instance, Graziano et al. (1997) showed that the visual receptive fields of PPS neurons in vPMC are anchored to the tactile receptive field on the arm, so that if the monkey's arm is moved, the neuron's responsiveness to visual stimuli coherently shifts (see Graziano and Cooke, 2006). At the same time, the response of such neurons is independent from eye and head direction (Fogassi et al., 1996). These response properties indicate that these neurons underlie an upper-limb centred multisensory representation of space.

Conversely, multisensory neurons with tactile receptive fields on the

face, mainly described in area VIP, the head direction is critical to modulate their response to visual stimuli, whereas the location of the arm is irrelevant (Avillac et al., 2007, 2005; Duhamel et al., 1997, 1998; Graziano and Gross, 1995). Thus, their multisensory receptive fields are kept aligned in head-centred reference frame. Finally, neurons in area 7 with large receptive fields centered on the trunk and covering one side or even the whole body, show visual responses that are mostly independent from eye, head, and upper limb position (Hyvarinen, 1981; Jiang et al., 2013; Leinonen, 1980; Leinonen et al., 1979, 1980; Leinonen and Nyman, 1979). Such body-part independent multisensory receptive fields are necessary to build a more global multisensory representation of the space around the whole body, centred to the trunk.

3.2. Reference frames transformation

Several studies have investigated the computational mechanisms necessary to transform different signals from specific sensory modalities, originally coded in receptor-specific reference frames (i.e., eye-centered or retinal for visual inputs, head-centered for auditory inputs, body-part centered for tactile inputs) into common reference frames. I will not address this issue here, as other authors have extensively done it before (for reviews, see (Andersen, 1997; Colby, 1998; Pouget et al., 2002)), but I will briefly mention the different mechanisms that have been proposed, which are relevant for PPS representation.

Early studies focused on visuo-motor transformations necessary to re-map visual inputs originally coded in eye-centered reference frames into body-part centered reference frames (Andersen et al., 1985; Cohen and Andersen, 2002; Salinas and Thier, 2000). These reference frame transformations have been proposed to be implemented at the level of individual neurons, so that a single cell's response to a visual stimulus occurring within their receptive field is rescaled as a function of eye or head direction (a mechanism known as gain fields). Neurons with gain fields properties have been extensively described in parietal cortex and fronto-parietal networks supporting body-object interactions (for reviews see (Colby, 1998; Grefkes and Fink, 2005)), including the areas hosting PPS neurons. Other authors extended these reference frame transformation models to the population level and implicated not only visuo-motor neurons, but also auditory, somatosensory, as well as vestibular and proprioceptive neurons in multisensory integration processes. In particular, Pouget et al. (Deneve and Pouget, 2004; Ma et al., 2006; Pouget et al., 2002) proposed an influential computational framework based on neural networks dynamics, consisting of multiple layers ranging from layers coding unisensory inputs in native reference frames to multisensory layers with common reference frames. Following this approach, unisensory layers are interconnected with different multisensory layers, containing so-called basic function units, which, via attractor dynamics, code multisensory stimuli in mixed reference frames, including partially shifting receptive fields. Such models are supported by neurophysiological data showing that multisensory neurons in VIP present not only eye-centered or head-centered receptive fields, but also mixed or combined receptive fields (e.g., combining eye-centred and head-centered reference frames (Duhamel et al., 1997)). Thus, such models have been applied to account for reference frames transformation necessary for the multisensory representation of the space around the face (Avillac et al., 2005). Computationally this problem is much more challenging for the upper limb (which has many more degrees of freedom, independently from eyes and head position), and thus less neurophysiological and computational data on reference frames transformation necessary for hand-centred representations are available.

Reference frames transformation, and its computational counterpart, is a necessary, but not a sufficient condition to explain PPS representation, which in addition requires a mechanism underlying multisensory integration of bodily cues and external cues occurring close to the body. This mechanism might rely on the computational and spatial properties of multisensory receptive fields of PPS neurons, as

proposed for instance by Magosso and Serino (Magosso et al., 2010b; Serino et al., 2015b) and described in Section 2.5. The neural mechanism allowing reference frame transformation system and the PPS multisensory integration system might interact, for instance, via intermediate neuronal layers between the unimodal and the multisensory layers, which re-code unisensory inputs into a common, body-part centered reference frame, necessary for PPS representation (see (Makin et al., 2013) for a possible neural model).

3.3. Proprioceptive and visual cues involved in reference frames transformation necessary for PPS

Empirical studies from different fields provide evidence about the source of information necessary to keep reference frames aligned and centered to specific body parts. First, the fact that visual receptive fields of arm-centred vPM neurons move depending by arm position in space suggests that proprioceptive information about the arm is critical for arm-centred PPS representation. Indeed, in some vPM neurons, the position of the arm modulated the response of PPS neurons to visual stimuli, even when the monkey's arm was hidden from view, and thus only proprioceptive inputs signaled whether a visual stimulus was actually approaching the arm (Graziano, 1999). Neuropsychological data from patients with crossmodal extinction shows the same proprioceptive-depending coding of PPS in humans: a visual stimulus presented in the right side of space induced less extinction for left hand tactile stimulation when the patients held their hand behind their back, or when the right visual stimulus was presented at the same eccentricity, but at an elevated location, i.e. when right visual stimulation actually occurred farther from the patient's hand as signaled by proprioceptive cues (Ladavas et al., 1998a). Analogous posture dependent modulations of visuo-tactile or audio-tactile interaction was found by using respectively the CCE (Spence et al., 2004b) or an audio-tactile interaction task (Serino et al., 2011). Correspondingly, the difference in neural activity induced by near-hand as compared to far stimulation in IPS (Makin et al., 2007) and vPMC (Brozzoli et al., 2011) is reduced, or even vanishes, if participants place their hand far from the location of the near visual stimulation, by retracting or by crossing their hands. Thus, converging evidence from multiple experimental approaches shows that hand-centered PPS representations are coded depending on proprioceptive inputs.

Proprioception, however, is not the unique source of information to code the location of the different body parts in space. In fact, evidence suggests that vision of the body contributes to arm-centered coding of PPS. Graziano et al. (1999) showed that some vPMC neurons modulated their response to a visual stimulation presented to the right or to the left visual field not only according to the posture of the monkey's real arm, but also depending on the location of an artificial reproduction of a monkey arm. Thus, top-down visual information related to the location of a fake arm, in addition to proprioception of the real arm, modulates the location of multisensory receptive fields of PPS neurons. Coherent effects were shown in extinction patients: a visual stimulus presented on the right visual field, far from the patient's real hand (held on the patient's back and occluded from view), but close to a fake hand, induced the same level of extinction for left tactile stimulation as when visual stimulation was applied close to the patient's real hand (Farne et al., 2000). In the same vein, Pavani et al. (2000) showed that visual cues induced a stronger CCE over tactile targets (administered to the participants' hidden hands), when the cues were presented on fake hands, as compared to when they were presented exactly at the same spatial location, but without fake hands. Interestingly, also visual cues, occurring at a distance from the participants' hand, but seen through mirror reflection of the hand (Maravita et al., 2002a), or on a hand shadow (Pavani and Castiello, 2004), induced strong CCE effects for tactile hand stimulation, as if they were presented close to the hand. These behavioral findings suggest that visual information about the hand location in space strongly contributes to the recoding of external

stimuli as occurring within or outside the participants' hand-PPS. Finally, neuroimaging studies confirmed that such top-down visual-dependent coding of the hand space is implemented within the same brain areas putatively hosting PPS neurons in the human brain. Visual stimuli presented close to a fake hand, but farther apart to the subject's real hand (that was held in a retracted posture) induced stronger activation in IPS as compared to far visual stimuli (Lloyd et al., 2006; Makin et al., 2007; see Brozzoli et al., 2012b for similar results in vPMC). Thus, converging data show that visual information about the body, in addition to proprioceptive inputs, contributes to body-part centered multisensory representation of PPS. Importantly, proprioceptive and visual cues are not fully independent from each other, as two constraints have been systematically reported for these effects to occur. First, visually-dependent modulation of multisensory responses does not occur if visual information about the body does not match a configuration compatible with the structural constraints of the body, as the above described effects are not reproduced if the fake hand is placed in an impossible body posture (e.g., rotated by 180°). In addition, recoding effects of multisensory signals depending on an artificial visual stimulus occur only if the latter visually resembles a part of the body, as the previous effects are not reproduced if a wooden or a plastic 3D object is placed at the location of the fake hand.

To summarize, PPS representation implies a coding of multisensory signals in body-parts centered reference frames, to which proprioceptive and visual signals about body parts location in space strongly contribute. Most of the data reviewed in this section refer to arm-centred PPS representations, while less data is available for head-centred or trunk-centred representations. This might be because the representation of the different parts of the body actually relies on different anatomical and functional constraints. Direct visual signals from our own face, for instance, are absent (or available only with a mirror or technology), whereas the arm and hand are often in our visual fields. Moreover, proprioceptive input is also different, given the axial head system involved in neck proprioception for head and face, or the axial trunk system, compared to the strongly lateralized proprioception system for arm and hand position, and the different degrees of freedom in movements of the different body parts. Thus, it is possible, that while for arm-centred PPS representation, proprioceptive and visual cues are critical, vestibular inputs are more important for head-centered PPS representation. This hypothesis fits with the finding that monkey VIP regions process not only visual, tactile or auditory stimuli within the space around the head, but also vestibular inputs signaling head direction and head motion (Bremner et al., 2002, 2001a; Pfeiffer et al., 2014). Few empirical data are available in humans concerning the role of vestibular inputs to PPS processing. Some studies showed vestibular-dependent modulation of tactile, visual or cross-modal (Ferrè et al., 2014; 2015; Kaliuzhna et al., 2018) processing. Recently, Pfeiffer et al. (2018) showed that whole body rotation, tapping into the activity of semicircular channels, affects, in a direction-specific manner, how external sounds in space modulate tactile perception as a function of their distance from the body, thus showing a vestibular-dependent modulation of PPS processing. Vestibular inputs importantly contribute to determine the orientation of the whole body with respect to the external environment and therefore they are relevant for determining space-dependent modulation of multisensory processing in combined trunk- and head-centered reference frames, thus contributing to the representation of the whole body PPS (Pfeiffer et al., 2014).

4. Multisensory-to-motor PPS representation

Reference frame transformations have been traditionally studied in the context of sensory-motor integration necessary for goal-oriented behavior. The VIP and vPMC (F4) regions, where PPS neurons have been described, form one of the several fronto-parietal networks bridging the posterior parietal and the premotor cortex and supporting specific sensory-motor functions in the primate brain (see Colby, 1998;

Grefkes and Fink, 2005; Rizzolatti et al., 1997b, 2002)). Thus, since its discovery, the multisensory features of PPS representation have been interpreted in light of its role in the motor system. In this section, I will review the main findings linking multisensory and motor features of the PPS system and discuss them in relation to the different proposed functions of PPS.

Neurophysiological evidence suggests a strong link between PPS representation and the motor system. vPM is actually a motor region, and area F4, in particular, directly projects to the spinal cord and to M1 (He et al., 1995; Rizzolatti and Luppino, 2001). Multisensory neurons in F4 are also active during movements of the body part where their sensory receptive fields are anchored (Rizzolatti et al., 1981a, 1981b). In addition, electrical stimulation of both F4 (Cooke and Graziano, 2004a,b) and VIP (Cooke et al., 2003; Thier and Andersen, 1996; Cooke et al., 2003; Stepniewska et al., 2005, 2014) regions, containing PPS neurons, induce involuntary arm, eye or head movements, with very short latency (up to 10 ms; Cooke and Graziano, 2004a,b).

In humans, auditory (Finisguerra et al., 2014; Serino et al., 2009) or visual (Makin et al., 2009) stimuli presented near the hand have been shown to modulate the excitability of the hand representation in the primary motor cortex differently than far stimuli. These studies recorded motor-evoked potentials from hand muscles induced by delivering single-pulse transcranial magnetic stimulation (TMS) over the hand-motor representation, in order to measure the excitability of the hand cortico-spinal tract. Such measure was compared when a visual (Makin et al., 2009) or an auditory (Serino et al., 2009) stimulus was presented either near or far from the hand, while the TMS pulse was delivered at different delays from the visual or auditory stimulation. This enabled studying the temporal dynamics of cortico-spinal modulation due to spatial location of the external stimuli. Results showed that, at very short latencies (i.e. between 50–75 ms), the hand motor representation was more excited for near as compared to far-hand stimulation, as activation of the hand-PPS resulted in automatic and implicit motor preparation. No space-dependent modulation of the motor system was found if the hand was placed far from the source of near and far stimulation, showing that such effects occur in hand-centred reference frames. If participants were concurrently involved in another motor task, motor excitability was lower for near-hand stimulation, as if they implicitly inhibited the automatic motor response evoked by PPS stimulation in order to select another response relevant for the task (Makin et al., 2009). After few milliseconds, the facilitation induced by near stimulation in passive conditions disappeared: Serino et al. (2009) found that 300 ms post stimulation the space-dependent modulation of the hand cortico-spinal motor representation actually reversed, with higher excitability associated with far sounds. This result was interpreted as a consequence of a time-dependent modulation of cortico-spinal excitability associated with near vs. far stimulation. Serino et al. (2009) proposed that 300 ms after onset, a near sound is irrelevant for motor responses, whereas a far stimulus might potentially require a motor response and thus may be associated with higher corticospinal excitability as compared to near stimulation at the same time delay. Providing support for this proposal, Finisguerra et al. (2014) measured hand muscles motor evoked potentials after single-pulse TMS when dynamic sounds approached or receded from the hand. Hand cortico-spinal excitability progressively increased at closer distances of the sounds from the hand, with a significant effect occurring when the sound was closer than 60 cm. These results, on the one hand, mirror the spatial boundary of PPS representation, as described by the modulation of tactile reaction time due to dynamic sounds reported by Canzoneri et al. (2012) (as described in 2.2). On the other hand, they capture the relationship between the spatial and temporal coding of PPS, which is critical for processing and reacting dynamically to multisensory stimuli in ecological contexts, when stimuli in the environment move with respect to the body. Accordingly, further studies revealed interesting dynamic properties of PPS neurons, which allow them to code the spatial relationship between external stimuli and the body in ecological

dynamic contexts. For instance, both the response profiles of PPS neurons (Graziano et al., 1997) and reaction times to tactile stimuli in humans (Canzoneri et al., 2012; Serino et al., 2015a) are modulated by the direction of incoming sensory cues, with stronger response for looming, as compared to receding stimulation, and larger receptive fields when probed with faster as compared to slower stimuli (Fogassi et al., 1996; Noel et al., 2018a). Together, these findings show that multisensory neurons mapping the PPS are tuned to the dynamics of external events, and this information is directly transferred to the motor system to prompt appropriate motor responses with respect to the location of external stimuli in space.

In every-day life, the location of external objects as inside or outside the PPS depends not only on objects dynamics, but also on the movements of the body and its parts. Recent behavioral data suggest that PPS representation is mapped dynamically as a function of voluntary body movements, in an anticipatory way. Brozzoli et al. measured the CCE induced by visual cues embedded on an object placed at 47 cm from the participant's hand and that participants were instructed to reach and grasp. Visuo-tactile cues were administered at different time points, so that multisensory interaction was probed at different phases of hand movements. Results show that, as compared to static conditions, CCE was higher during, and even immediately before, the hand movement, showing that a far visual stimulus affects tactile processing at the hand, if a hand movement approaching towards it is executed or planned. In other words, the spatial constraints of multisensory interactions are re-coded in a dynamic and even an anticipatory manner (Brozzoli et al., 2009, 2010, 2012a; Makin et al., 2012). Results from Noel et al. (2014) provided evidence that this is the case not only for hand movements, but also for whole body movements. We measured the boundary of the peri-trunk PPS, by means of the dynamic audio-tactile interaction task described above (Canzoneri et al., 2012), while participants either stood or were walking on a treadmill. In the latter condition, despite no physical displacement of the relative distance between the participants' body and the auditory stimuli occurred, tactile processing was modulated by sounds presented at much farther location (around 165 cm) than in the static condition (around 80–90 cm), suggesting that walking extends the PPS boundaries. Taken together, these studies suggest that the multisensory receptive fields of PPS neurons dynamically shape to include the target position of body movements, in addition to the actual location of the body. Although there is no direct neurophysiological evidence that this is the case, these effect resemble the well-described shifts of the visual receptive fields of parietal neurons toward the target location of an eye movement, before the saccade starts (Colby and Goldberg, 1992). Within the visual system, this property is considered a key mechanism for updating the retino-centric coordinates as a function of changes in eye position, and thus generating a stable and accurate representation of the visual space (Andersen and Buneo, 2002; Colby and Goldberg, 1999). I propose that a similar mechanism might act for PPS neurons, whose multisensory receptive fields may dynamically vary in size and location, depending not only on the actual, but also the predicted, location of the body and its parts during interaction with the environment.

5. Plastic properties of PPS representation

Normally, physical interactions between the body and external objects occur within the PPS. However, primates can use tools, or technology, to reach targets outside the physical limits of their body. A seminal paper by Iriki et al. (1996), showed that, after an extensive period of tool-use to reach food pellets placed out of reach, the visual receptive fields of IPS neurons in macaques extended toward the space where the tool was operated (Iriki et al., 1996). Farne and Ladavas (2000) provided the first demonstration of an analogous effect in humans by showing that the extent of crossmodal extinction induced on left tactile perception by visual stimuli in the right far space increased if these stimuli were presented close to a tool that the patient had actively

operated (see also Maravita et al., 2001, 2002b). Further behavioral studies in neurologically-healthy participants proved increased multi-sensory interactions between stimuli on the body and external stimuli presented at the location where a tool was functionally used (Canzoneri et al., 2013b; Maravita et al., 2001), suggesting an extension of the participant's PPS toward the space where the individual interacted with an external object via the tool; (see (Ladavas and Serino, 2008; Maravita and Iriki, 2004; Martel et al., 2016) for reviews, but see Holmes, 2012 and Holmes et al., 2007 for a different account).

5.1. Principles of PPS extension due to tool-use

Several studies highlighted a series of principles ruling the PPS extension mediated by tool-use. First, the tool has to be actively used to reach far objects, since just holding a tool (Farne and Ladavas, 2000; Iriki et al., 1996; Maravita et al., 2001; Serino et al., 2007), or pointing toward far objects (Canzoneri et al., 2013b; Serino et al., 2015b), or operating a short tool within the PPS (Bourgeois et al., 2014) is insufficient to alter PPS representation. Second, the location of space undergoing changes in multisensory processing (interpreted as an extension of PPS representation) is determined by where and how the tool is functionally used, not by its physical length or structure. Farne et al. (2005a) showed that two tools of the same length, whose functional part was located either at the end of the tool or at a middle position along the tool axis, induced an extension of PPS that reached the tip of the tool in the first case, whereas was limited to the middle of the tool in the second case. Finally, changes in multisensory processing due to brief tool-use experiences are fast to occur (even after few seconds of use; Holmes et al., 2007), and are reversible in the short term, as different studies reported that while PPS extension is observed immediately after tool-use, such effect disappears after a few minutes of no tool-use (Farne et al., 2007). The exact temporal dynamics of tool-use effects on PPS are not clear, since, at the best of my knowledge, no study tested the relationship between the duration of tool-use experience and that of the effects on PPS. The reversibility of these effects, however, is again compatible with the idea that PPS shapes depending on experience: it elongates when multisensory cues are processed from a far location due to tool-use, and it contracts back to its standard dimension, once this extended multisensory processing is over.

Interestingly, there are cases where a tool is used everyday and for long time periods. We investigated how PPS representation reshapes under these circumstances by studying blind cane users, as a special case of extensive and functionally highly relevant tool-use (Serino et al., 2007). Blind cane users and sighted individuals were asked to respond as soon as possible to tactile stimuli on their hand, while ignoring concurrent sounds that were presented either close to the stimulated hand, or approximately 120 cm from the hand. Participants were while holding either a blind cane (at whose tip the source of far sounds were placed), or a short handle (control condition). Results showed that in the handle-condition, both groups of participants were faster to respond to tactile stimuli associated with near as compared to far sounds. However, in blind-cane users, and not in sighted controls, holding the cane resulted in faster reactions to touches coupled with sounds occurring at the far space, i.e. at the tip of the cane, suggesting an extension, or more properly, a remapping of PPS to the location where a new functional boundary for body-object interactions emerges. Such effect was specifically triggered by holding the cane in expert blind cane users, whereas multisensory interaction was limited in the space close to the body when they did not hold the cane. We interpreted these findings as if long-term tool use experience results in a permanently extended PPS representation, which, however is selectively activated depending on the presence of the tool (see Longo and Serino, 2012 for comments).

5.2. Mechanisms of plasticity in PPS representation

Under normal conditions, external cues are associated with tactile stimulation when occurring near the body, i.e. within the PPS. Tool-use, however, allows physical interaction with external stimuli placed at farther spatial locations, and this may extend PPS representation. The studies reviewed above suggest that the spatial (where the tool is used), the temporal (for how long the tool is used) and the functional (how the tool is used) features of tool-use experience determine the way PPS extends. We adopted a neural network model to propose a possible neural mechanism underlying such experience-dependent plasticity in PPS.

In the model described in Section 2.5, PPS representation was implemented by a network of unimodal areas (tactile, visual and auditory) connected to a multisensory layer. The strength of the synapses from unisensory to multisensory areas determined stronger multisensory responses for stimuli within the PPS, as the multisensory neurons received strong projections from neurons in unisensory visual or auditory areas with receptive fields close to the hand, and weak projections from unisensory neurons with receptive fields far from the hand. To account for the plasticity of PPS, this model was expanded so that the strength of these synapses is not fixed, but is continuously defined through experience, according to a Hebbian learning rule aimed at simulating everyday life hand-objects integration. Hand stimulation activates the tactile unisensory layers, which in turn activates the multisensory layer. Under normal conditions, tactile stimulation is coupled with visual or auditory stimulation occurring close to hand (activating visual or auditory unisensory neurons with close receptive fields). Instead, neurons with receptive fields covering far space are not, or much more rarely and randomly associated to tactile stimulation. This way, the synaptic connections between unimodal visual or auditory neurons with receptive fields close to the body continuously strengthen due to the concurrent firing of the post-synaptic multisensory neurons (activated by tactile stimulation), while those with unimodal visual or auditory neurons with far receptive fields decay. However, such stimulation patterns vary if people use tools to reach far objects. During tool-use, people receive a tactile stimulation on their hand from the tool and a temporally coherent visual and/or auditory stimulation from the far space, where the tool exerts its function. As a consequence, such synchronous tool-use mediated near-far multisensory stimulation may result in a strengthening of the synapses between unisensory neurons with far receptive fields and multisensory neurons. Under this condition, indeed, the multisensory neurons are activated by the unisensory tactile neurons due to hand stimulation and the unisensory visual/auditory neurons with far receptive fields are activated by tool-related far sensory information. Thus, accordingly to a Hebbian learning principle, the synapses between the two sets of neurons are reinforced. A series of simulation experiments (Serino et al., 2015b) validated this hypothesis, and showed that the neural network model was able to reproduce the extension of PPS induced by tool-use as measured by behavioral results in healthy participants (Canzoneri et al., 2013b). Importantly, the model also suggested a novel hypothesis: tool-use per se may not be necessary to extend PPS, but it may be sufficient to reproduce the pattern of multisensory stimulation associated with tool-use - i.e. synchronous tactile stimulation at the hand and visual or auditory stimulation at the far space. Serino et al. (2015b) provided experimental findings confirming this hypothesis. PPS extended after that participants were exposed to a multisensory stimulation training consisting in receiving tactile stimulation on their hand coupled with a synchronous sound occurring at 1 m distance. Importantly, as predicted by the model accordingly to Hebbian learning, no change in PPS was obtained after a stimulation regiment that was identical to the previous one except that tactile and auditory stimuli were separated by 500 ms (see Fig. 3).

These findings show how the shape of PPS might be predicted depending of the nature of multisensory experience individuals receive, thanks to the architecture of the multisensory network. Accordingly,

the same neural network model, and the proposed Hebbian-based plasticity mechanism, was able to reproduce the differential effects on PPS extension found by different tool-use activities. In particular, some studies showed that the area of enhanced multisensory interaction extends continuously from the hand to the functional part of the tool in a tool-use training consisting in collecting far objects and retrieving them back (Bonifazi et al., 2007; Farne et al., 2007). Other studies showed that multisensory interactions during tool-use increased selectively for stimuli presented at the sector of space where the tool was used, e.g. near the hand or at the tips of the tool, but not in the middle of the tool, if the tool handles or tips were used to press a button (Holmes et al., 2004). Because of the different nature of the tasks, between the two conditions of tool-use, relevant multisensory information occurs from different sectors of space (i.e., continuous range between near and far space in the first case, and from distinct and segregated spatial locations in the second case). The neural network model proposed explains how changes in multisensory integration may manifest as a continuous PPS extension along the whole space (as in Farne et al., 2007) or as a distinct spot of increased multisensory processing at segregated location where the tool is functionally operated (as in Holmes et al., 2004). Indeed, in the former case, during tool-use, multisensory information is processed at each spatial location, thus strengthening the synapses to the multisensory neurons from all the unisensory neurons whose visual/auditory receptive fields are stimulated by the training. Conversely, in the second case, only the unisensory neurons with receptive fields at the location where the tool is used are activated, and therefore only their synapses to the multisensory neurons reinforces, whereas the synapses from unisensory neurons with receptive fields at other spatial locations, receiving no stimulation, do not change (Ursino et al., 2007).

Finally, the model also suggested a rather counterintuitive hypothesis: once PPS is extended due to tool-use-related multisensory stimulation, an extended PPS representation should be temporarily found even if the participants do not hold the tool during testing. An experiment with a patient suffering crossmodal extinction directly confirmed such prediction from the model (Maggioso et al., 2010a).

Note that in order to reproduce the reversibility of the tool-use effects, a decay factor is implemented in the unisensory-multisensory synapses, so that if tactile stimulation is repetitively associated with no concurrent visual/auditory stimulation, the related synapses weaken. As a consequence, this model predicts that PPS may also shrink beyond its normal range, if no multisensory stimulation is provided. This prediction was confirmed by a study showing that impeding arm movements via upper limb immobilization for 10 h, thus depriving the coupling of somatosensory stimulation with normal visual and auditory cues from the space close to the hand, actually reduced the extent of the hand PPS (Bassolino et al., 2014).

To conclude, the case of tool-use represents an intriguing model not only to study the mechanisms underlying changes in PPS, but also to suggest important insight into the mechanisms normally shaping its representation, and potentially ruling its development. I propose that the extent of PPS, as defined by the size of multisensory receptive fields of PPS neurons, is constantly shaped by experience, depending on the temporal coupling of somatosensory stimulation at the body and visual and/or auditory external cues. Under normal conditions, such coupling occurs in a limited sector of space, where the body can physically interact with external objects, which normally defines the PPS boundaries. However, under special conditions, bodily stimulation can be systematically coupled with multisensory cues from other sectors of space. As a consequence, and due to their neural architecture and learning principles, the receptive fields of PPS neurons can reshape as to include the specific location from where multisensory stimuli were coupled with body stimulation. This form of experience-dependent plasticity in the receptive fields of multisensory neurons has been shown for other multisensory neurons, in the anterior ectosylvian sulcus of the cat, underlying audio-visual interaction. Wallace and Stein (2007) showed that when newborn cats were raised in an environment

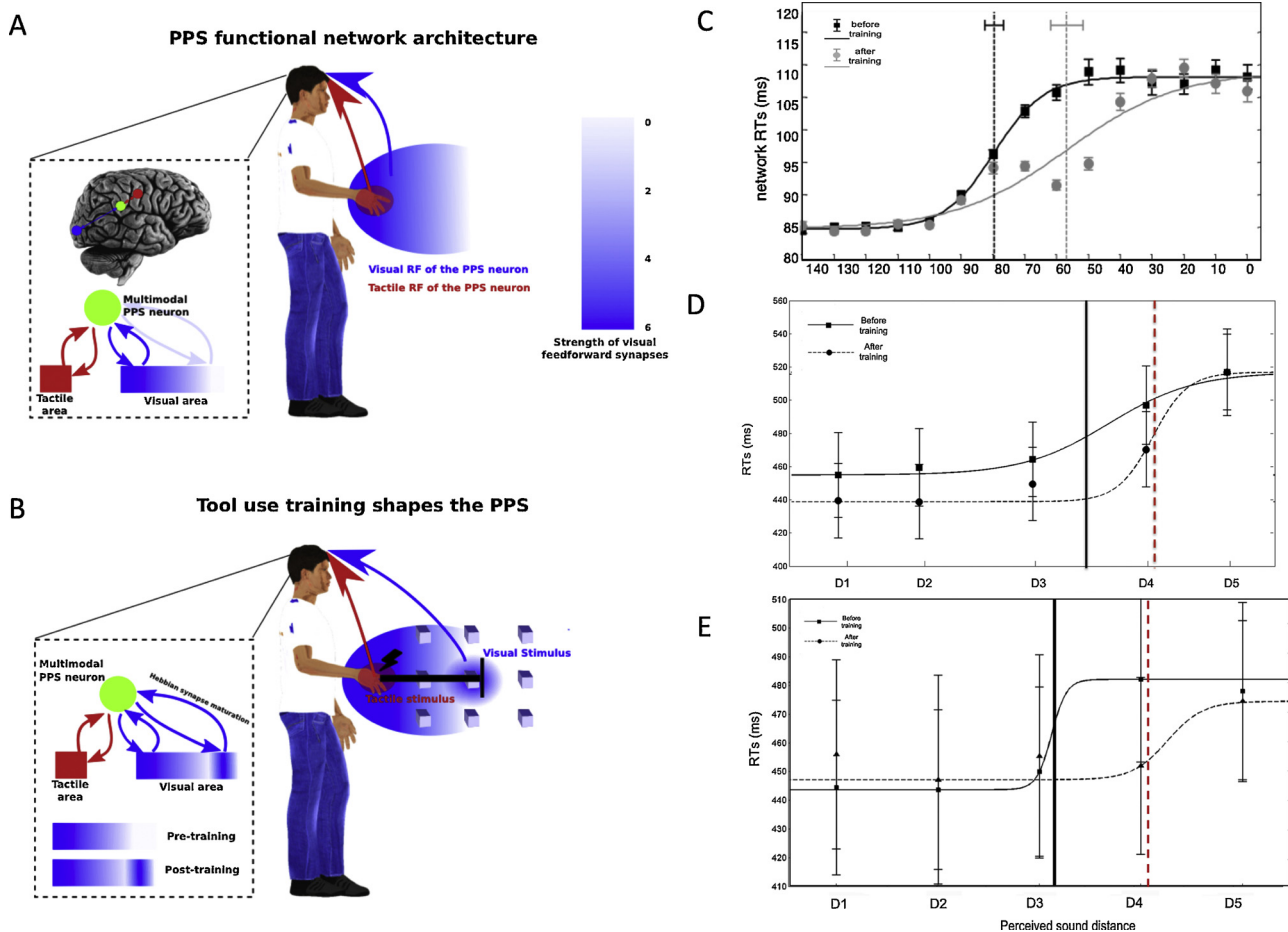


Fig. 3. A neural network model of PPS representation and its plasticity. A. *Structure of the model:* example of peri-hand space representation via visuo-tactile interaction. PPS is represented as a series of unisensory areas - in this case a tactile area (red) and a visual area (blue), with receptive fields on the hand (tactile) and beyond (visual), connected to a multisensory region via feedforward and feedback synapses. In order to reproduce the main characteristic of PPS representation, i.e. stronger interaction for multisensory stimuli close to the body, the strength of the synapses from the unisensory to the multisensory neurons are set so to be stronger from visual neurons with receptive fields close to the hand and weaker from neurons with far receptive fields (see (Magosso et al., 2010a)). B. *Effect of tool-use training on the PPS hand network.* During tool-use, tactile stimulation on the hand are coupled to visual stimulation from a far location, thus strengthening, via a hebbian-like mechanism, the synapses from neurons with visual receptive fields in the far space to the multisensory regions. As a consequence, multisensory stimuli from the space where the tool has been used increases, thus extending the PPS. C. *In-silico demonstration of PPS extension after stimulation.* A neural network model trained with synchronous tactile stimulation at the hand and far (auditory or visual) stimulation shows enhanced multisensory integration for far stimuli and PPS extension after the training (from (Serino et al., 2015b)). D. *In-vivo demonstration.* Human participants exposed to synchronous tactile hand stimulation and auditory far stimulation (without any tool) show similar PPS extension after the training. E. *Effect of proper tool-use.* The PPS extension effect is similar to what obtained after tool-use (From (Canzoneri et al., 2013b), see 5.1).

where visual stimuli from a given location were systematically coupled with auditory cues in a contralateral location, the multisensory neurons in this area developed bilateral audio-visual receptive fields. What characterizes PPS neurons with respect to other multisensory neurons is their body-centered reference frames: the spatial constraints of their multisensory responses are determined by the distance of visual or auditory stimuli from the somatosensory receptive fields of PPS neurons, which are anchored to a specific body part.

5.3. Technology to push beyond the boundaries of PPS

Besides the experimental cases reviewed above, humans use everyday a variety of tools allowing them to interact with objects or other people outside the boundaries of their PPS (see Section 6). This has exponentially increased in the last few decades with the introduction of digital technologies allowing not only physical, but also virtual interactions. In order to test technology-mediated interactions impact on PPS, Bassolino et al. (2010) studied the computer mouse as a special case of tool, which is used with the body, thus inside the PPS, but whose

effects may manifest far away and are visible through the computer screen. By using the audio-tactile interaction task described in 2.2, Bassolino et al. (2010) found that when participants held a computer mouse in their right hand (the hand they normally used to operate the mouse), sounds far from their hand, but close to a computer screen, speeded up their tactile reaction times. The effect was evident not only when they were directly operating the mouse, but also when they were holding it, while a cursor moved on the screen. However, a sound placed close to the screen (where a cursor moved) minimally affected reaction time to tactile stimulation on the right hand if participants were simply placing their hand on a desk, as predicted according to the null effects of passive tool exposure shown by previous studies (e.g., Bassolino et al., 2010; Farne and Ladavas, 2000). These findings suggest that long-term experience of using the mouse developed an extended representation of the hand-PPS, which was immediately activated by just holding the mouse. Interestingly, when the experiment was repeated by stimulating the left hand (that participants normally did not use to operate the mouse), far sounds affected tactile processing only during active mouse-use, and not while passively holding the mouse,

suggesting that PPS representation around different body effectors specifically shapes and are selectively activated depending on the level of experience.

Another interesting line of research concerns the control and use of robotic devices. For instance, [Sengul et al. \(2012\)](#) tested the case of using a surgical robot to operate at a remote location during simulated surgeries. Participants used a bimanual interface to control two virtual surgical devices presented in a virtual environment. By measuring CCE, the authors showed that tactile responses to finger stimulation were strongly influenced by the visual cues presented at the tip of the surgical devices, showing a remapping of crossmodal interaction between the hand PPS and the virtual space where the tools were operated (see also [Rognini et al., 2013](#)). [Romano et al. \(2015\)](#) tested the effects of a training consisting in using a robotic hand (to grasp objects), controlled via electromyographic signals from the participant's arm and equipped with pressure sensors able to provide sensory feedback. They found that after a 4-weeks training with such robotic hand, but not before the training, visual cues placed on the robotic hand affected responses to tactile stimuli administered to the participant's real hand, suggesting that the artificial hand was included into the participant's hand-PPS.

The device tested by Romano et al. was actually a robotic limb developed as a prosthesis for upper limb amputees. [Canzoneri et al. \(2013a\)](#) directly investigated the consequence of limb loss and prosthesis implantation on PPS representation in a group of chronic upper limb amputees, normally using a functional myoelectric or kinesthetic prosthesis. Tactile stimuli were applied to their residual limb, while task-irrelevant sounds approached their limb, and the critical distance at which sound affects tactile processing was measured as a proxy of the extent of upper limb PPS (as in [Canzoneri et al., 2012](#), see 2.2). Data showed that, when patients were tested without their prosthesis, the PPS around the amputated limb shrunk, as compared to their healthy limb and to healthy controls. However, wearing their functional prosthesis speeded up their reaction times to tactile stimuli on their residual limb, as if these were recoded as occurring to the prosthetic hand.

Together, these data show that technologies, used to push our action possibilities beyond the standard limits of our physical body, plastically reshape PPS representations. The possibilities offered by current digital technology in expanding our everyday interactions are massively growing. Thanks to its plasticity properties and the underlying neural mechanisms exposed in this section, I propose that PPS represents an ideal interface to support such expanded interaction. The cases exposed here focus on relatively simple forms of interaction, mainly mediated by hand movements. Future work should investigate the consequence of progressively more abstract and virtual forms of interactions mediated by new technologies, so that the extended PPS might represent a model to study technology-mediated case of extended cognition (see the Extended Mind concept, [Clark and Chalmers, 1998](#); See [Herbelin et al., 2016](#)).

6. Social PPS

Multisensory mechanisms underlying PPS representation might be involved not only in physical, body-object interactions, but also in more abstract contexts. This is supported by an emerging body of evidence showing that PPS representation is affected by the presence of other individuals, as well as by the nature of interactions with others.

Converging single-cell recordings in monkeys and fMRI data in humans show that some PPS neurons respond to visuo-tactile stimulation not only within one's own PPS, but also related to the PPS of others. [Ishida et al. \(2010\)](#) recorded visuo-tactile neurons in the macaque VIP, and identified some neurons responding to tactile stimulation on a part of the animal's body, and to visual stimuli approaching not only the same part of the animal's body, but also the body of an experimenter facing the animal. In a closely related fashion, [Brozzoli et al. \(2013\)](#) demonstrated in humans that activity in PPS-related vPMC regions was modulated not only accordingly to the distance of an object

from the participant's hand (as described in 2.4), but also by the distance of the same object from another person's hand. In a series of studies, we showed that viewing a face being touched affected tactile perception on one's own face – an effect called visual remapping of touch ([Serino et al., 2008](#); [Làdavas and Serino, 2010](#)). fMRI results linked this effect to the activity of VIP and vPMC, which were shown to be more strongly activated when participants viewed two fingers approaching a face presented on a screen as compared to a control condition whereby the fingers were not directed towards the face ([Cardini et al., 2011](#)). Together, these findings show that one's own PPS system also implements a mechanism to map the PPS of others (see also [Fossataro et al., 2016](#) for compatible evidence for the case of the defensive PPS, as assessed by the spatial modulation of the hand-blink reflex).

The possibility of processing stimuli in other people's PPS in turn affects the representation of one's own PPS. [Heed et al. \(2010\)](#) showed that the strength of visuo-tactile interaction (as assessed via CCE) for stimuli within one's own PPS reduces if another person is present within the participant's PPS and performs a similar task. By using the dynamic audio-tactile interaction task (described in 2.2), we also found that the size of participants' PPS was affected by the presence of another individual: looming sounds affected tactile processing at a significantly closer distance from the participant's body, when the task was performed while participants faced a stranger, sitting at 1 m distance, as compared to when facing a non-human body, i.e. a mannequin, used as a control ([Teneggi et al., 2013](#)). This finding suggests that one's own PPS shrinks in presence of an unknown individual. Interestingly, follow-up experiments showed that the nature of social relationship with others further shapes PPS representation. PPS extended up to include the space around the other person, after that the participant had interacted with the other person in a fairly manner, and not after an unfair interaction. Interestingly, the nature of the interaction was manipulated via a modified version of the mutual advantage game, thus implying no physical exchange between the participant and the other person. Together these findings suggest that in presence of an unknown individual, our PPS shrinks, as to leave space to the other, whereas after a positive exchange, even if abstract, PPS expands as to create a common space of interaction.

Such regulation of PPS in social context is reminiscent of an influential notion in social sciences, i.e., the personal space. By introducing the concept of interpersonal distance, namely the relative distance people keep between each other, Hall defined personal space as the zone around the body that people feel like “their private space” and cannot be intruded by others without causing discomfort ([Hall, 1966](#)) (see also [Hayduk, 1983](#)). An interesting question is whether and to what degree the multisensory mechanisms underlying PPS representation described in the present paper is involved in defining the personal space. Few recent papers addressed this issue by testing in the same participants both the extent of their PPS and interpersonal distance. [Iachini et al. \(2014\)](#) presented participants in a virtual reality environment with a visual stimulus, depicting a virtual human character, a robot or a body-size cylinder. They asked them to indicate at which distance they could either reach the stimulus with their arm – i.e., reachability judgment in order to measure PPS – or they felt discomfort with respect to it – i.e. interpersonal distance judgment in order to measure personal space. Results showed similar distances in the different experimental conditions between the reaching and comfort judgments, suggesting a high degree of overlap between PPS and personal space. In a follow-up study, the same group tested how these two space measures were affected by the perceived morality of the other person. The results showed that morality judgments similarly affected the two spatial representations, with larger reachability and interpersonal distances with immoral than moral others ([Iachini et al., 2015](#)). However, the fact that both representations were affected by the same manipulations does not imply that they underlie the same function, or even that they overlap. [Pellencin et al. \(2017\)](#) directly tested

the effects of the social perception of other on interpersonal distance and on the multisensory representation of PPS. They applied a visuo-tactile interaction task (see 2.2 and Serino et al., 2015a), implemented into a virtual reality social context. Virtual objects moved in the space between the participant and another person, that in different experimental conditions was perceived as either a moral or an immoral other via a social impression manipulation. The results showed an extension of the multisensory PPS when participants faced a moral other (as compared to an immoral other), which was also associated with a reduction of their interpersonal distance, as measured by a comfort distance task. Thus, the perceived morality of another person affected participants' PPS representation, such that people were faster in processing tactile stimuli on their body when visual stimuli occurred close to another person, if this person was perceived as moral. Concurrently, this moral other was perceived as less intrusive when approaching (Pellencin et al., 2017). However, the two measures, neither in Pellencin et al. (2017), nor in Iachini et al. (2014) did correlate between each other. Thus, currently available results show that PPS and personal space are sensitive to common factors, including the social perception of the others and the possibility and willingness to interact with them. However, this evidence is not sufficient to determine the degree of overlap or separation between the two spatial representations. Results from a study by Patane et al. (2017) provides evidence for a possible dissociation. Participants' PPS was extended when they used a tool to reach far objects (as reviewed in 5.1), without any social interaction. This effect, however, was associated to no change in interpersonal distance, excluding the possibility of a full overlap between PPS and personal space. In sum, it is fair to propose that the ability of the PPS system in detecting potential physical interactions between one's own body, another person's body, and external events is important in regulating spatial processing within social contexts, thus suggesting a possible effect of PPS on interpersonal distance. At the same time, it is also possible that emotional and social factors emerging from face-to-face interaction with others in turn modulate PPS neurons' ability to map the space around the others into one's own PPS (Cardini et al., 2012). Further studies are necessary to deeply understand the direction and the strength of the relationship between PPS representation and interpersonal distance.

7. PPS and self-consciousness

In the previous sections, I described PPS as the results of the activity of neuronal populations which integrate somatosensory stimulation on one's own body with visual or auditory cues related to external objects when they can touch the body. Such multisensory bodily processing results in a representation of the space where the individual potentially interacts with the environment. Influential accounts have proposed that the continuous and coherent integration of multisensory bodily signals is a key element underlying subjective bodily experience, such as the feeling that different parts of our body are our own, or body ownership (Gallagher, 2000; Jeannerod, 2003) (Blanke, 2012; Ehrsson, 2012; Makin et al., 2008; Tsakiris, 2010). Blanke and Metzinger (2009) further proposed that at the global level, when ownership generalizes to the unity of the body, this feeling coincides with self-identification, i.e. the experience of the self as linked to a body that is owned. This constitutes one key component of Bodily Self Consciousness, i.e., the experience of the self as a subject of the experience grounded into a body that is felt as one's own (self-identification), which occupies a specific location in space (self-location) and which faces the world from a specific perspective (first-person perspective). It has been proposed that the multisensory mechanism underlying PPS representation, by integrating multisensory cues related to the body, is a key mechanism underlying the sense of body ownership (Ehrsson, 2012; Makin et al., 2008; Tsakiris, 2010) and other components of bodily self-consciousness (Blanke, 2012; Serino et al., 2013), thus suggesting that the PPS system is directly involved in underlying subjective experience

(Legrand et al., 2007; Legrand and Ruby, 2009). Together with Olaf Blanke, we extensively presented the arguments linking PPS processing and bodily self-consciousness elsewhere (Blanke et al., 2015). Here I will summarize the key points and link them to the model of PPS I am proposing in the present paper.

7.1. PPS and hand ownership

The experimental, neuroscientific study of bodily self-consciousness has exponentially increased since the introduction of one experimental paradigm allowing us to manipulate body ownership, i.e. the rubber hand illusion (Botvinick and Cohen, 1998). Viewing an artificial hand being stroked in synchrony with strokes applied to one's own corresponding non-visible hand induces an illusory feeling that the artificial hand is one's own, as proved by subjective (assessed via questionnaires), perceptual (e.g., proprioceptive drift, i.e., a shift in the perceived position of the real hand towards the artificial hand), and physiological (e.g., enhanced skin conductance in response to a threat administered to the rubber hand or a reduction in the real hand temperature) measures (see (Ehrsson, 2012; Tsakiris, 2010) for reviews). Importantly, minimal or no effects are obtained if the real and the artificial hand are stimulated with an asynchronous pattern.

Thus, in terms of sensory stimulation, the rubber hand illusion consists of tactile stimuli felt on the participant's real hand synchronously coupled with visual stimuli seen on an artificial object, visually resembling the participant's hand, but occupying a spatial location other than the natural hand. In everyday life, tactile hand stimulation is normally associated with synchronous visual stimulation within the hand's PPS. This spatio-temporal congruency between multisensory inputs activates simultaneously the tactile and visual receptive fields of fronto-parietal PPS neurons whose receptive fields are centered on the hand. During the rubber hand illusion, the activation of the tactile receptive field of these neurons is systematically associated, due to synchronicity of stimulation, with the activation of a visual receptive field not perfectly overlapping the hand location. However, from the plastic properties of the PPS system as described in Section 5, a (relatively) prolonged stimulation on the hand coupled with visual (or auditory) stimulation from a farther location, is able to re-tune the multisensory receptive fields of PPS neurons toward the location of the visual inputs, i.e. where the rubber hand is placed during the stimulation paradigm. As a consequence, multisensory integration in the space of the rubber hand might assume the same multisensory properties as the hand PPS (see Blanke, 2012; Blanke et al., 2015; Ehrsson, 2007; Makin et al., 2008; Serino et al., 2013 for reviews). This hypothesis has been directly validated by behavioral, neurophysiological and neuroimaging data. For instance, Zopf et al. (2010) showed that the amount of CCE induced by visual stimuli presented on a rubber hand increased as a function of illusory ownership induced over the rubber hand. In monkeys, Graziano et al. (2000) showed that prolonged visuo-tactile stroking (as that used to induce the rubber hand illusion in humans) affected the tuning properties of PPC neurons. In a key study, these authors describe some neurons in area 5, that normally respond to the position of the arm in space based only on proprioceptive information about the position of the animal's real arm, and are insensitive to visual information about the location of a seen fake arm. They then applied synchronous visuo-tactile stroking repeatedly to the monkey's hidden real arm and to the visible fake arm. Re-evaluating the visual tuning of the same neurons immediately afterward demonstrated that these neurons were now tuned to the visual location of the fake arm. As in the rubber hand illusion in healthy humans, such neuronal tuning changes were absent after asynchronous visuo-tactile stroking. Similar effects in humans were demonstrated in a neuroimaging study by Brozzoli et al. (2012). These authors first showed that repetitively presenting a visual stimulus close to the participants' real hand induced an adaptation effect in the bilateral PPC and PMC, sign of PPS processing within those areas (see Section 2.4; Brozzoli et al., 2011). The same adaptation effect was not

obtained if the same stimuli were presented close to a fake hand that was positioned in the contralateral space. However, if that prolonged visuo-tactile stroking was used to induce illusory hand ownership for the contralateral fake hand, adaptation effects in PPC and PMC regions were also evoked also by the repeated visual stimuli presented near the fake hand (Brozzoli et al., 2012b). These findings suggest that these areas, which normally code for the space around the real hand, after synchronous visuo-tactile stroking also coded the space surrounding the fake hand.

Further corroborating the link between PPS processing and changes in hand ownership as induced by the rubber hand illusion, recent findings show that illusory hand ownership can be induced by coupling tactile real hand stimulation with visual stroking presented close to the rubber hand, even without touching it (Ferri et al., 2013; Guterstam et al., 2013). These effects can be explained by the concurrent activation of the hand tactile receptive fields of PPS neurons and their visual receptive fields, evoked by visual stimuli approaching, even if not touching, the rubber hand. A direct prediction of this hypothesis is that if visual stimulation from the rubber hand occurs beyond the external boundary of the visual receptive fields of PPS neurons, the illusion should not be induced. This prediction has been confirmed by experimental (Lloyd, 2007) and computational (Samad et al., 2015) data showing that the strength of the rubber hand illusion decays significantly when the fake hand is placed farther than 30–40 cm from the real hand, i.e. a distance resembling the size of PPS neurons as shown by data in monkeys and humans (reviewed in Section 2).

Thus, changes in hand ownership can be induced by manipulating the spatio-temporal coherence of multisensory bodily inputs processed by the PPS system. As a consequence, it has been argued that normal ownership for real body parts does actually depend on the coherent multisensory integration of bodily cues, and that multisensory fronto-parietal PPS areas, due to their integrative and plastic properties, are a key neural substrate for this form of multisensory integration involved in bodily self-consciousness (Blanke, 2012; Blanke et al., 2015; Makin et al., 2008; Serino, 2016; Serino et al., 2013). Supporting this account, it has been highlighted that regions of the vPM and PPC, overlapping or close to the ones putatively hosting hand-centred PPS neurons, are activated during visuo-tactile stroking inducing the rubber hand illusion, and the strength of these activations also correlated with subjective changes in hand ownership (Brozzoli et al., 2012b; Ehrsson et al., 2004; Makin et al., 2007). In addition, regions in similar fronto-parietal areas are also sensitive to the degree of the spatio-temporal coherence between visual and tactile stimulation on the hand (Gentile et al., 2013), thus being able to discriminate between patterns of synchronous vs. asynchronous stimulation and spatial disparity determining the occurrence of the rubber hand illusion (Costantini and Haggard, 2007). To test the hypothesis that neural mechanisms involved in PPS representation and body ownership overlap, we directly compared regions of interest highlighted by available neuroimaging studies assessing PPS representation, on the one hand, and body ownership, on the other hand (Grivaz et al., 2017). Two individual meta-analyses were conducted on studies assessing PPS representation around the hand, face, and trunk and changes in hand, face and full body ownership, as induced multisensory illusions. PPS related regions included superior parietal, temporo-parietal and ventral premotor regions, whereas areas involved in body ownership included the posterior parietal cortex (right and left IPS and SPL), right ventral premotor cortex, and the left anterior insula (see 2.3 and Fig. 2). We then searched for common activity between the two networks. The conjunction analysis showed two clusters of overlap, located in the left parietal cortex - dorsally at the intersection between the SPL, the IPS and area 2, and ventrally between areas 2 and IPS. On the other hand, specific and distinct activations were located at the temporo-parietal junction in IPL for PPS and in the anterior insula for body ownership (see Fig. 4). Thus, PPS and body ownership showed some degree of overlap, but also dissociation, with PPS areas being located closer to sensorimotor

regions across the central sulcus, and body ownership areas being located more anteriorly or posteriorly. Accordingly, co-activation maps of the regions of interests associated with both PPS and body ownership encompassed largely overlapping fronto-parietal networks, involving regions whose functions have been previously associated with sensorimotor tasks for the PPS regions and with attention and awareness tasks for body ownership regions. Finally and most interestingly, these analyses also showed that the PPS and body ownership regions, besides being anatomically overlapping in SPL/IPS/area 2, were largely connected with each other. Grivaz et al.'s (2017) findings suggest that multisensory integration processes in PPS, as implied in subjective bodily experience, rely on the functional interaction between multisensory-motor regions and awareness-related fronto-parietal regions, anatomically overlapping in a specific location of the posterior parietal cortex and being extensively interconnected.

The previous conclusion arises from studies mostly focusing on hand ownership, but the meta-analyses also included PPS and body ownership studies focusing on face and whole-body processing. In the next two paragraphs, I will review more specifically findings concerning these body parts, and their implication for other aspects of bodily-self-consciousness beyond body parts ownership (see (Serino et al., 2013)).

7.2. PPS, face ownership and self-identity

It has been shown that synchronous visuo-tactile stimulation of one's own face and of another person's face (usually seen in a computer screen) results in illusory ownership for the other's face (Cardini et al., 2013; Sforza et al., 2010; Tsakiris, 2008); the so-called enfacement illusion (see (Apps and Tsakiris, 2014) for a review). fMRI data show the pattern of visuo-tactile stimulation on the participant's and the other's face used to induce the enfacement effect was reflected in a modulation of neural activity in a portion of the right IPS (Apps et al., 2013). This region largely corresponds to the VIP area, which has been shown both in humans and monkeys to respond to tactile stimulation on one's own face, to visual stimulation within one's own peri-face space, but also to visual stimuli approaching another face (see paragraph 6). Therefore, prolonged synchronous visuo-tactile stimulation between one's own and another person's face, tapping into the properties of VIP neurons, might make the space around the other person's face to be re-coded as one's own PPS (Bufalari et al., 2015). Accordingly, Maister et al. (2015b) showed that after synchronous visuo-tactile stimulation inducing the enfacement illusion, auditory stimuli presented close to the other person's body more strongly affected tactile processing on one's own body, suggesting that the space of the other was re-coded as part of one's own PPS (see Fig. 4B and C).

What is particularly relevant in the case of the enfacement illusion is that this effect is associated with important consequences in self-recognition and self-other distinction. Indeed, it has been shown that after synchronous visuo-tactile self-other face stimulation, participants are more prone to recognize as their own a morphed face containing a higher proportion of the other person's face (mixed with their own) ((Serino et al., 2013; Sforza et al., 2010; Tsakiris, 2008) see (Serino et al., 2013) for a possible electrophysiological mechanism of this effect). This change in self-recognition is also associated with a reduction between self-other distinction, as shown by implicit multisensory indices, such as an increase in the visual remapping of touch effect when touch was seen on the other person's face (Cardini et al., 2013), and more explicit social measures, such as a tendency in feeling the other to be closer and more similar to oneself (Maister et al., 2015b; Paladino et al., 2010; Fini et al., 2013).

The possibility of inducing experimental changes in self-recognition by means of the enfacement illusion is particularly intriguing for linking PPS processes to self-consciousness. Indeed, the ability of recognizing one's own face, for instance in the mirror, is considered a hallmark of self-awareness (Gallup, 1968; Rochat and Zahavi, 2011). Accordingly, the mirror-mark test has been extensively used to study self-awareness.

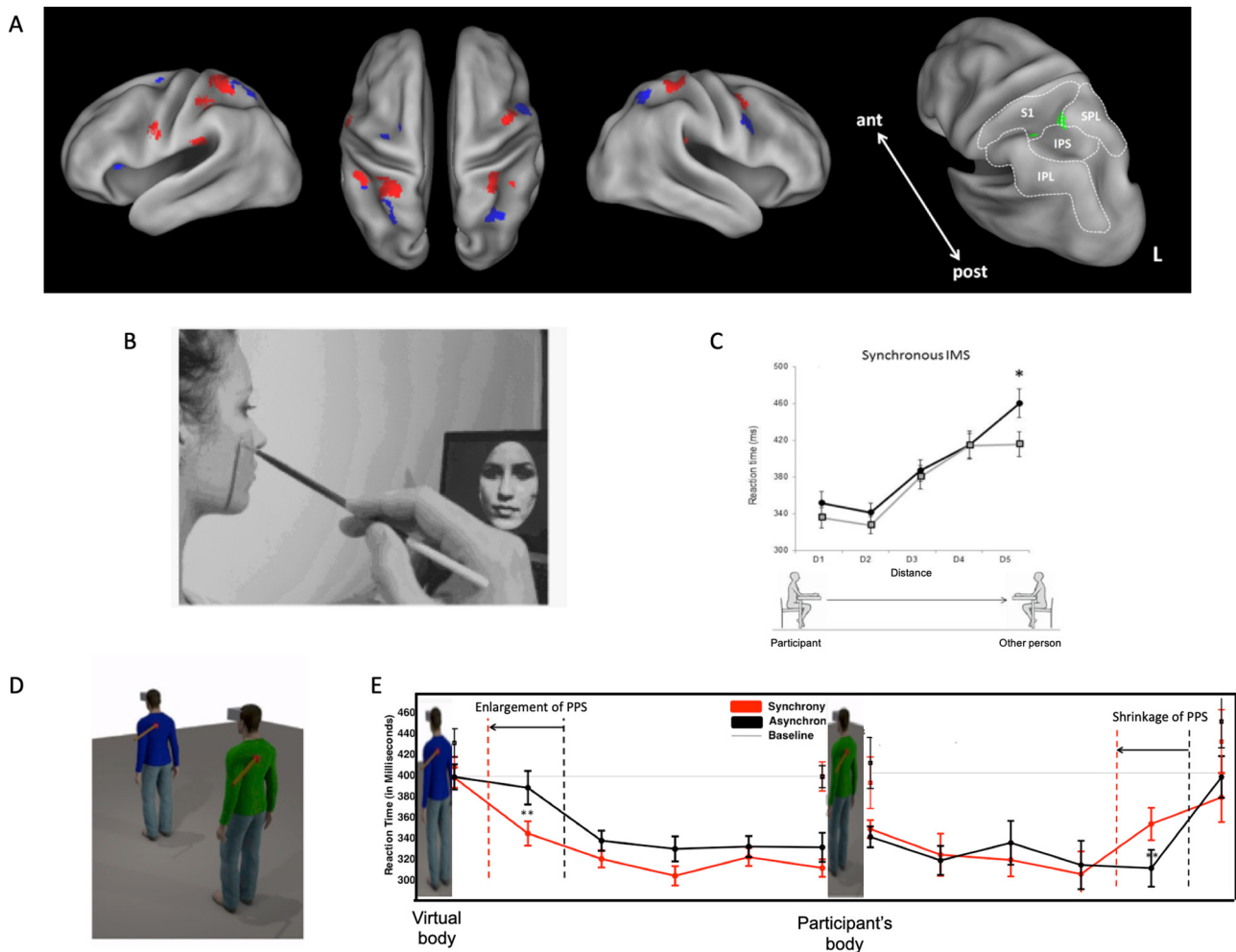


Fig. 4. Role of PPS multisensory mechanisms in bodily self-consciousness. A. Brain regions underlying PPS representation (red) and bodily self-consciousness (blue) and their anatomical overlap (see (Grivaz et al., 2017)). B, C Multisensory interpersonal stimulation delivered to the participant's face and another person's face induces feeling of ownership for the other's face (enfacement) and a remapping of the space around the other as one's own PPS (Maister et al., 2015b). C, D Multisensory stimulation on one's trunk and on avatar's trunk seen at a distance induces a shift of the perceived self-location towards the avatar, an extension of the participant's PPS towards the front and shrinkage on the back, compatible with a shift of the PPS center towards the perceived location of the self.

In this test, a spot is attached on the subject's head, while she is unaware of it. When placed in front of a mirror, if the subject shows spontaneous behaviors toward one's own face as to remove the mark, instead of toward its mirror reflection, she passes the test, suggesting she is able to recognize herself. While humans and great apes normally pass the mirror mark test, smaller primates, like rhesus monkeys, usually fail (Suddendorf and Butler, 2013). A paper by Chang et al. (2015) shows that Rhesus monkeys might be trained to pass the mirror mark test by means of a visuo-tactile stimulation training. The training, lasting 12–35 days, consisted in projecting a laser red light, inducing irritant sensations, to random locations of the monkeys' face, while they were placed in front of a mirror. This way, somatosensory stimulation on the monkeys' face was systematically coupled with visual stimulation of the face seen in the mirror. After such a training, monkeys systematically explored their own face when presented with non-irritant light spots projected to their face seen in the mirror, and such behavior generalized to more ecological tests in their home cage. These findings suggest that, after prolonged synchronous visuo-tactile stimulation, the macaques have learned to remap visual information seen into the mirror to their own PPS, and this was associated to an improved performance in the mirror mark test. The training implemented by Chang et al. in the macaque closely resembles the pattern of stimulation used to induce the enfacement illusion in humans, which also results in changes in self-recognition. It is too speculative to state that

the acquired ability to pass the mirror mark test can be considered a hallmark of acquired self-awareness in the macaque. However, the ability of processing at the same time one's own and the other's PPS, and to remap multisensory stimuli between self and others, might be a key underpinning of self-awareness and be of relevance for social cognition. This account may be of particularly intriguing consequences for developmental psychology, in order to understand the neural mechanisms underlying self-representation and social competencies (Rochat and Morgan, 1995; Rochat and Zahavi, 2011).

7.3. Full body PPS as the space of the self

When synchronous multisensory stimulation is applied to the trunk, it induces global changes in whole body experience, such as illusory self-identification with an artificial body, as during the body swap illusion (Petkova and Ehrsson, 2008), or changes in the perceived location of the self, as during the full body illusion ((Lenggenhager et al., 2007); see (Serino et al., 2013) for a review). In the body swap illusion, participants receive tactile stimulation on their chest, while looking down at their body, but seeing a mannequin body through a head-mounted display. Again, if visuo-tactile stimulation is applied synchronously to the participant's and the virtual body, people self-identify with the mannequin, as shown by means of questionnaires or increased physiological reactions to threats administered to the mannequin

(Ehrsson, 2007). Such effects have been linked to the processing of multisensory cues in premotor and intraparietal areas, putatively containing PPS neurons (Gentile et al., 2015; Petkova et al., 2011). Interestingly, those global changes in bodily self-experience might be evoked by stimulating the chest, the leg and the hand; however, limbs must be attached to the trunk for these effects to occur, pointing to the existence of a full body representation, centred to the trunk, to which body part specific representations refer to. Accordingly, Gentile et al. (2015) by using multi-voxel pattern analyses during the administration of the body swap illusion while stimulating different body parts, identified a pattern of neuronal response, which was common to any location of synchronous visuo-tactile stimulation, independently from the stimulated body parts. These findings point to a mechanism integrating multisensory inputs across different body parts, according to a trunk-centred reference frame. This is compatible with the existence of a global representation of the body in space, a whole-body PPS, to which body-part specific PPSs refer to, as suggested by the neurophysiological, neuroimaging and behavioral data reviewed in Section 2.

Data from the full body illusion suggest that this trunk-centered whole body PPS might be the space where we perceived our self to be. Usually, self-location coincides with the location of one's physical body. Synchronous multisensory stimulation applied to one's own trunk and to the trunk of a virtual body seen at a distance makes participants feel the virtual body as their own, and critically, perceive themselves to be at a location closer to that of the virtual body, during and after synchronous stimulation (Lenggenhager et al., 2007). We used the audio-tactile PPS task described in 2.2 to measure participants' PPS while they were exposed to synchronous visuo-tactile stroking to induce the full-body illusion (Noel et al., 2015). As compared to the asynchronous control condition, the PPS was found to extend in the front-space - toward the virtual body, for which illusory self-identification was experienced and toward which experienced self-location shifted - and to concurrently shrink in the back-space (see Fig. 4D and E). These findings suggest that during the full-body illusion, the boundaries of PPS reshape according to the experimentally induced changes in self-perception, so that the trunk-centered, whole-body, PPS is referenced to the experienced location of the self, rather to the location of the physical body. We might picture the whole-body PPS as a volume, whose center is represented where multisensory stimuli related to the body are normally referenced. Usually, this location coincides with a part of the physical body, most likely the trunk, as it represents the more global body reference. However, if a systematic pattern of multisensory stimulation from the environment, as during the full body illusion, triggers a plastic re-coding of multisensory bodily cues at a location external from the physical body, the center of the whole body PPS, and consequently its volume, shifts accordingly, together with a change in the subjective self-location. At the moment, it is not possible to establish a causal direction in the relationship between these effects, i.e. whether the changes in self-location occur because of the PPS shift, or vice-versa. However, a bottom-up model, whereby multisensory stimulation induces a shift of the PPS center and this results in a recalibration of self-location as a perceptual counter part of such PPS shift, is seemingly a more parsimonious explanation than the alternative account. This proposal is supported by recent data from Salomon et al., (Salomon et al., 2017) showing that a pattern of synchronous visuo-tactile stimulation, which was made invisible to the participants, by means a continuous flash suppression paradigm, selectively induced the full body illusion (as compared to invisible asynchronous stimulation) and coherently extended PPS representation toward the virtual body. Thus, multisensory processing of bodily inputs responsible for PPS representation and implied in BSC does not require awareness, and act in a bottom-up fashion to modulate subjective experience.

Such whole-body PPS representation, grounding self-location, might interact with other systems to locate oneself in the external environment. First, vestibular inputs can be integrated with other multisensory inputs – e.g., vision (Fetsch et al., 2010), audition, somatosensation

(Lopez et al., 2008) and even interoception (zu Eulenburg et al., 2013) to orient self-perception with respect the environmental gravitational field, thus also contributing to the orientation and direction of the first-person perspective (Vogeley and Fink, 2003). The temporo-parietal junction, in particular at the intersection of the posterior superior temporal gyrus and the angular gyrus (Ionta et al., 2011; Pfeiffer et al., 2014), might be a key area where such integration occurs. Such ego-centric representation of the self in space might then interact with more allocentric maps of the environment, processed mainly in the hippocampus and in the retrosplenial cortices to place oneself in the external environment (see Guterstam et al., 2015).

7.4. The space of the self and its role in cognitive functioning

The possibility of changing global aspects of bodily self-consciousness, and self-location in particular, by modifying the spatial determinants of PPS representation via multisensory stimulation, might have consequence on different levels of cognitive processing. Indeed, a large body of theoretical and empirical studies, under the general framework of “embodied cognition”, (Barsalou, 2008; Gallagher, 2005; Gibbs, 2005) propose that our mental processes, even high-level cognitive processes, are situated in and depend on the status and the experience of our physical body. Accordingly, in a recent study we showed that by altering the perceived location of oneself in space through the full body illusion, it is possible to modify the way participants process words conveying spatial or even social concepts. Accordingly to the Construal Level Theory by Liberman and Trope (2014), different aspects of semantic information (spatial, temporal, social and probabilistic reasoning) are processed as referenced to the body, so that these concepts are represented on a common dimension in terms of psychological distance from one's own physical body. An implicit association task (Trope and Liberman, 2010) is typically used to probe this effect: participants see a landscape and are requested to classify as fast as possible whether a visual cue (e.g. an arrow) is presented in a location either proximal or distal to them. The visual cue is associated with a word, conveying in different studies spatial (“Near”, “Far”), social (“Us”, “Them”), temporal (“Now”, “Tomorrow”), or probability (“Sure”, “Maybe”) semantic distance. In different trials, the association between the word's “semantic” distance and its location of the scene (on the proximal or distal visual cue) is manipulated so that psychological and physical distance can be congruent or incongruent. Typically, participants are faster to respond to the location of the visual cue associated to a word of congruent semantic distance (e.g., the proximal visual cue with the word “near”). In Canzoneri et al. (2016), we reproduced this paradigm, while presenting a virtual body at the location of the distal visual cue. We then used visuo-tactile stimulation on the back of the participants and on that of the virtual body to experimentally manipulate the perceived self-location. In the control condition of asynchronous visuo-tactile stimulation, we replicated the well-established congruency effect between psychological and physical distance. Critically, when visuo-tactile stimulation between the participant's and the virtual body was applied synchronously, as to induce the full body and a shift of the individual's PPS toward the distal location in the scene, we abolished this congruency effect up to even reverse it for the distal visual cues. In that case, the word “near” had to be coupled to the distal visual cue, where participants perceived themselves to be in the scene, to evoke faster reactions. The same effect was obtained not only for spatial concepts, but also for more abstract concepts, such as social distances (e.g., “us” and “them”). Thus, psychological distance was re-coded as a function of the perceived location of the self in space, beyond the boundaries of the physical body. In another study, Bergouignan et al. (2014) used another form of whole body illusion to manipulate the perceived point of view of participants during the encoding of an event - i.e., by using cameras and head-mounted displays participants were “immersed” in a social interaction from a point of view either coinciding with their physical body or with a disembodied location.

When tested about their memory for that event one week later, participants had worse recollection for the event experienced from a disembodied point of view, and this effect was associated with a difference of activation in the posterior hippocampus. These findings suggest that since memory encoding and retrieval are normally linked to an embodied point of view, altering the unity between the experience of the external world and that of the physical body affects episodic memory and its neural processing.

Together, these two studies suggest that since bodily self-consciousness grounds different levels of cognitive processes (e.g., semantic processing or episodic memory), multisensory manipulations affecting bodily self-consciousness may impact high-level mental functions. Critically for the purposes of the present paper, such high-level effects are obtained by using very simple and low-level manipulations, tapping into the spatio-temporal coherence of multisensory bodily cues. The PPS system is responsible for the processing and integration of these cues, thus gathering a deep knowledge about the underlying computational and neural mechanisms of PPS may open new insights into our understanding of the human mind, and potentially suggest novel way to improve or rehabilitate its functions. Accordingly, recent lines of work are currently testing the link between multisensory integration, PPS representation, altered mental states and psychopathology (see Noel et al., 2017). A recent study on healthy participants showed that audio-visual sensory deprivation on the one hand alters the definition of the boundary between the PPS and the far space and, on other hand, induces altered mental states and strange experiences, such as higher tendency to hallucination; importantly the two effects are related to each other (Noel et al., 2018b). Few reports claim that PPS is altered in patients with schizophrenia. Delevoeye-Turrell et al. (2011) used both a stop-distance task, to measure interpersonal distance, and reachability judgments, to measure the extent of the reaching space in schizophrenic patients. Results were not conclusive, showing higher variability in patients than in controls, but no specific pattern of alteration. More recently, Di Cosmo et al. (2017) used our audio-tactile interaction task to measure the size of PPS in schizophrenia patients and in healthy participants with high vs. low schizotypal traits. Both patients and high-schizotypal individuals showed a narrower PPS as compared to healthy controls and low-schizotypal individuals, suggesting that the quality of PPS representation might be altered in psychosis. This conclusion is of interest, given the strong link proposed in the review between multisensory integration in PPS and bodily self-consciousness, and the interpretation of Schizophrenia as a disorder of the self (Sass and Parnas, 2003). However, proper empirical examinations of bodily self-consciousness in schizophrenia patients, by testing their response to multisensory bodily illusions, gave conflicting results. Some studies showed enhanced sensitivity to the rubber hand illusion (i.e., higher ratings to illusion questionnaires), which has been interpreted as a consequence of a disorder in self-other distinction (e.g., Thakkar et al., 2011). Other studies, implementing more objective measures (e.g., proprioceptive drift) or proper control conditions (e.g., the comparison between synchronous and asynchronous stimulation or suggestibility questions) showed higher scores in patients with respect to controls, but no synchronous-specific (see e.g., Kaplan et al., 2014) nor question-specific differences. This was confirmed by a recent study by Shaqiri et al. (2017), which included a meta-analysis of the previous rubber hand illusion papers, and an experiment comparing sensitivity to the full body illusion in 59 schizophrenia patients and 30 controls; a general tendency to higher ratings in patients was found, which however was similar for synchronous and asynchronous stimulation. These results can be interpreted as a lack of specific deficits in multisensory bodily processing leading to bodily illusions in schizophrenia. However, it is possible that the absence of a difference in synchronous vs. asynchronous stimulation in generating bodily illusions depends on a higher tendency in schizophrenia patients to integrate multisensory cues even when temporally unmatched, as recent data demonstrate (see Hornix et al., 2018; Zhou et al., 2018). Thus, it is possible that multisensory

integration in space and time is altered in schizophrenia, and these deficits are linked to disturbances in self-related processing. However, this proposal needs further careful empirical investigation given the complexity of the syndrome, the variability of the patients' symptoms and the consequent challenges of running proper experimental protocols. Interestingly, a similar debate, with similarly inconclusive current findings, is ongoing for patients with autism spectrum disorder (see e.g., Cascio et al., 2012; Stevenson et al., 2014; Asada et al., 2016; Candini et al., 2016; Noel et al., 2017). I will not enter in this debate here for matter of space, but the current research both on schizophrenia and autism shows an interest in exploring complex neuro-psychiatric diseases, characterized by a disturbance in self-related processes and/or in self-other interactions, by looking at deficits in lower-level multisensory integration processes, and in particular those underlying PPS representation as an interface between the individual and the environment, including the others.

8. Conclusion and outlook: PPS as the body beyond the body, from multisensory integration for sensory motor behavior to self-environment interface for cognition

In this paper, I reviewed evidence about determinants, mechanisms, properties, and functions of PPS. I started from seminal evidence in monkeys, linking PPS representation to the multisensory receptive fields of fronto-parietal neurons, integrating tactile information on the body with visual or auditory information about an external stimulus in the proximal space. This basic form of multisensory integration, centred on the body and extending few centimeters beyond it - which has been further highlighted by several cross-disciplinary studies in humans - allows the brain to detect and anticipate potential interactions between the body and an external event, and eventually trigger appropriate responses, via direct connections to the motor system. The boundaries of the PPS are plastic, so that PPS shapes depending on where the body interacts with external stimuli in the environment, likely via a hebbian-like mechanism. These proprieties capture most of the definitions and functions of the PPS system previously proposed, such as “a margin of safety” (Graziano and Cooke, 2006), implied in defensive behavior (de Vignemont and Iannetti, 2014), or a sensory-motor system necessary for hand-object interaction, not only for defensive, but also for approaching purposes (Brozzoli et al., 2014; Makin et al., 2012), likely acting in a predictive manner (Clery et al., 2017; Clery et al., 2015a,b; Kandula et al., 2017; Djikerman, personal communication). Some models, reviewed here, exist to explain how these multisensory-motor spatial maps might be computationally implemented in unisensory and multisensory networks (see e.g., Magosso et al., 2010b), also taking into account required reference frames transformations (see e.g., Pouget et al., 2002). The field still misses models – and solid empirical data (see e.g., Orioli et al., 2018) – explaining on how PPS representations develop, i.e., how the multisensory receptive fields of PPS neurons emerge (see e.g., Wallace and Stein, 2007), how they remain in spatial register (Bremner et al., 2008), how PPS development interacts, supports or depends on the development of motor capabilities. Novel computational approaches, based on machine learning and features extraction for regular statistics in the environment (e.g., Makin et al., 2013; Noel et al., 2018c) have been proposed to account for multisensory integration and coordinate transformation. Whether and how they could apply to explain the development of PPS representation, and what could be their neural implementation is still unknown.

In addition, I propose that the basic form of multisensory integration underlying PPS, originally developed for interactions between body parts and objects (and that we probably share with several other species), further developed in humans to support more abstract and complex cognitive functions. At the more general level, PPS determines where the individual potentially interact with the external world, thus constituting a primary boundary between the self and the environment, including the others. I have presented evidence showing who PPS is

sensitive to a number of sensory-motor as well cognitive, social and psychological factors. Accordingly, in a recent opinion piece, [Bufacchi and Iannetti \(2018\)](#) propose that PPS should be conceived as a series of actions fields, i.e., a value maps of possible responses aiming at creating or avoiding contacts between the body and stimuli in the environment. Under this acceptance, the PPS system would include a number of other brain areas, beyond the PPS multisensory network described here, spanning from subcortical structures (mediating reflexes) pre-frontal regions (underlying action selection and inhibition), limbic areas (processing emotions). Personally, I believe that the contact-prediction function specifically defining the PPS system is mediated by the multisensory PPS neurons in the sensory-motor fronto-parietal network described here. This system interacts with (i.e. affects and is modulated by) other brain regions to support goal-oriented or defensive behaviors. How such interactions take place is probably the key current open question in the field of PPS research. Tailored neuroimaging studies, focusing on functional connectivity between different neural structures, linked to biologically plausible computational models will support this endeavor.

Finally, the PPS around the whole body, centered to the trunk, also defines the location of our body, where we perceive our self to be and from which we perceive the external world, thus being involved in global aspects of bodily self-consciousness. Accordingly, experimental alterations of bodily self-consciousness, as those induced by bodily illusions, rely on the manipulation of the spatio-temporal constraints of multisensory integration determined by the PPS system. Those manipulations, which shape PPS representation accordingly to rather simple and precise neural mechanisms, induce a temporary alteration in the unity between the physical body and the experienced self, whereby the experienced self is linked to the location of the PPS rather than to that of the physical body, thus suggesting that PPS defines the space of the self.

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