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11 Peripersonal Space

Its Functions, Plasticity, and Neural Basis

Eleonora Vagnoni and Matthew R. Longo

1. Introduction

There is agreement on the notion that the brain codes the space immediately around our body differently from the space farther away. This idea of separate representation was proposed by Brain (1941), who distinguished between what he called "grasping space" and "walking space." Brain introduced this idea while investigating the selective impairment that right brain-damaged patients may show for one of the two sections of space. Since then, the study of patients with damage to the right hemisphere has played an important role in developing understanding of the characteristics of multisensory spatial representation in humans (Làdavas, 2002; Làdavas & Farnè, 2004; Legrand, Brozzoli, Rossetti, & Farnè, 2007). Research across several disciplines has investigated these different representations, yielding interesting insights that have subsequently been applied and followed up in cognitive neuroscience and experimental psychology. For example, Hediger (1955), a zoo biologist, systematically observed animal behavior and noted that the sight of a predator is not enough to cause an animal to flee. Instead, the animal creates a precise margin of safety and escape is triggered only when a threatening object intrudes into this "flight zone." Hall (1966), an anthropologist, identified four different sections of space around humans' bodies: the intimate, personal, social, and public spaces or distances. Interestingly, he was among the first to describe this space representation as dynamic, highlighting the link between space representation and action, two crucial aspects of peripersonal space that have subsequently been widely investigated in the neuroscience tradition. The first empirical studies on the concept of "personal space" were conducted by the environmental psychologist Robert Sommer (1969), who investigated how interactions in small groups are influenced by the spatial arrangements of individuals and the personal space of schizophrenic patients. With both observational and experimental manipulations, Sommer showed that schizophrenic patients preferred a greater distance between themselves and another person (a confederate) and avoided any social interactions (Sommer, 1969). Sommer did not directly refer to the work of Hall in his studies; however, he cited the definition of personal distance given by Hediger (1955) as the normal spacing that non-contact animals maintain between themselves and their fellows, also used by Hall (1966). Therefore, we might infer that these authors referred to the same portion of space when using the term "personal space."

In cognitive neuroscience, the space close to the body has been referred to as peripersonal space (PPS) (Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981a). It is debated whether the personal space (also called interpersonal space; Evans & Howard, 1973; Gifford & Sacilotto, 1993; Previc, 1998) and peripersonal space are just different terms used by various disciplines to indicate the same portion of space, or if there are two functionally different and independent spatial representations (de Vignemont & Iannetti, 2015; Iachini, Coello, Frassinetti, & Ruggiero, 2014; Lloyd, 2009; Patané, Farnè, & Frassinetti, 2017; Patané, Iachini, Farnè, & Frassinetti, 2016; Vagnoni, Lewis, Tajadura-Jiménez, & Cardini, 2018).

In this chapter, we will focus on the PPS as defined in the cognitive neuroscience tradition and we will explore three different conceptions of PPS. Specifically, we will examine the idea of PPS as related to the defense of the body against threat, as a space for goal-directed action, and as a space for social interaction. After reviewing the existing literature on the defensive, space for action, social PPSs, and their plasticity, we will discuss how these representations relate to each other and examine some of the models already theorized.

2. The Defensive Function of Peripersonal Space

In this section, we will describe studies on the defensive aspect of PPS in monkeys, some of the paradigms used in human studies, and the predictive mechanisms at the basis of the defensive PPS investigated in both humans and monkeys. Neurophysiological studies on monkeys have shown that single neurons, belonging to a set of interconnected multisensory cortical (fronto-parietal) and subcortical (putamen) areas, code information coming from different sensory modalities. These neurons respond to tactile stimuli applied to the skin and visual or auditory stimuli approaching (or close to) the body. For example, neurons with peripersonal receptive fields have been described in the ventral intraparietal area (VIP) and a polysensory zone in the precentral gyrus (PZ) of the monkey (Graziano & Cooke, 2006). These two interconnected cortical areas are activated by visual, tactile, and auditory stimuli (Colby, Duhamel, & Goldberg, 1993; Graziano, Hu, & Gross, 1997a, 1997b; Graziano, Reiss, & Gross, 1999; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981a, 1981b; Schlack, Hoffmann, & Bremmer, 2002). Neurons within these areas are bimodal or trimodal, with a tactile receptive field on a body surface and a visual (or auditory) receptive field located in the space surrounding the body part. Interestingly, Graziano and colleagues (Cooke, Taylor, Moore, & Graziano, 2003; Graziano, Taylor, & Moore, 2002) showed that electrical stimulation of VIP and PZ evokes defensive-like movements aimed at protecting the body part where the sensory receptive fields of the neurons are located. In the light of this finding, Graziano and Cooke (2006) described PPS as a bubble around our body that creates a margin of safety relative to approaching dangers.

In humans, PPS has been investigated with several multisensory interaction paradigms, such as the visuo-tactile crossmodal congruency task (Holmes, Sanabria, Calvert, & Spence, 2007; Spence, Pavani, & Driver, 2000; Spence, Pavani, Maravita, & Holmes, 2004, 2008), the audio-tactile crossmodal congruency task (Aspell, Lavanchy, Lenggenhager, & Blanke, 2010; Occelli, Spence, & Zampini, 2011), and audio-tactile interaction paradigms, such as the temporal order judgment task (Zampini, Torresan, Spence, & Murray, 2007). In general, these paradigms show response facilitation to multisensory stimuli presented close to the body, compared to more distant stimuli. In all these paradigms the stimuli are static while, as Canzoneri and colleagues (Canzoneri, Magosso, & Serino, 2012) noted, in the animal literature neurons in the PPS system show a preference for moving objects (Fogassi et al., 1996). The preference for moving stimuli is so strong that the neurons in the PPS network have been described as looming detectors (Colby et al., 1993; Graziano & Cooke, 2006). Therefore, Canzoneri and colleagues (2012) created a paradigm with looming stimuli to be used with humans. Specifically, they presented tactile stimuli to the participant's hand and auditory stimuli looming towards, or receding away from, the participant's body. Participants were required to respond to the tactile stimuli as fast as possible while ignoring the sound. This paradigm reveals that the sound approaching the participant's body modulates reaction times to the tactile stimuli so that participants become quicker in responding to the tactile stimuli as the sound approaches their body. Specifically, the facilitation of reaction time occurs when the sound is perceived at a critical spatial range so that after that point in space reaction times are significantly shorter. According to the authors, this facilitation in reaction times can be considered as a proxy of the boundaries of PPS. Intriguingly, recent results suggest that the effect of such looming sounds may vary depending on the direction from which they are coming, suggesting interesting anisotropies in the shape of PPS (Spence, Lee, & van der Stoep, in press).

Serino and colleagues (Serino, Canzoneri, & Avenanti, 2011) investigated the neural basis of PPS by applying low-frequency repetitive transcranial magnetic stimulation (rTMS; 1 Hz). Specifically, they tested whether virtual lesions of the left ventral premotor cortex (vPMc), posterior parietal cortex (PPc), relative to the visual cortex (V1, used as a control site) affected audio-tactile interaction in the PPS around the hand.

The authors showed that virtual lesions to vPMc and PPc, but not to V1, eliminated the facilitation of reaction time due to near sounds, showing a disruption of audio-tactile interactions around the hand. This result suggests the necessity of the fronto-parietal network in the multisensory representation of PPS.

Several recent studies have focused explicitly on the defensive aspect of PPS, investigating its extension through the hand blink reflex (HBR). The HBR is provoked by intense electrical stimulation of the median nerve (Alvarez-Blanco, Leon, & Valls-Solé, 2009; Sambo, Liang, Cruccu, & Iannetti, 2012b). Sambo and colleagues showed that the HBR is modulated by the proximity of the stimulated hand to the face; indeed, the HBR is substantially increased when the hand is inside the PPS surrounding the face (Sambo et al., 2012b). The authors interpreted the effect as a result of a tonic, top-down modulation of the brainstem circuits mediating the HBR. They have proposed that such modulation is carried by associative cortical areas (e.g., the premotor cortex and the ventral intraparietal area) involved in representing the PPS and mapping the location of somatosensory stimuli into an external reference frame. Bufacchi and colleagues (Bufacchi, Liang, Griffin, & Iannetti, 2016) investigated the geometric shape of PPS by testing the goodness of fit of several models to HBR data. They showed that the best-fitting model suggested that the nervous system's representation of the body area "defended" by the HBR can be described as a half-ellipsoid centered on the face; moreover, the defensive PPS extending from this area has the shape of a bubble elongated along the vertical axis. Given that the HBR is modulated by the hand position in head-centered coordinates, the defensive PPS seems to be anchored to the face (Bufacchi et al., 2016). Using the HBR paradigm Bisio and colleagues (2017) and Wallwork and colleagues (2016) have argued that the defensive PPS is modulated by the predictive motor mechanisms. However, even if the authors interpreted the results in the same way, their data show an opposite pattern. Specifically, Bisio and colleagues (2017) showed that the HBR is enhanced when the hand approaches the face but it is reduced when it recedes from it. In this study, HBR magnitude was not dependent on movement direction when the hand was far from the face. In contrast, Wallwork and colleagues (2016) reported no difference between movement directions at the near position while the HBR increased at the far position when the hand was moving towards the face. While in both studies the effects were interpreted as a modulation of predictive motor mechanisms on PPS, Bufacchi (2017) reconciles these opposite findings with a different interpretation of the results. According to Bufacchi, another possibility is that these two studies show the flexibility of PPS.

In recent years there has been a growing interest in the predictive mechanisms at the basis of the defensive PPS. It is indeed crucial for a safety system to be able to predict successfully the arrival of approaching stimuli. Cléry and colleagues (Cléry, Guipponi, Odouard, Wardak, & Ben Hamed, 2015a) claim that the PPS network of areas is involved not only in the defense of the body towards dangers but also in the prediction of intrusive impact with the body. Indeed, they showed that when visual looming stimuli are presented approaching the face of human participants there is an enhancement of the tactile processing at the predicted time of impact, so that the observers seem to predict the tactile consequence of a visual stimulus approaching the face. In this way the PPS representation serves to alert the nervous system of a potentially dangerous impact (Cléry et al., 2015a). To investigate this hypothesis, the authors conducted an fMRI study in monkeys and showed that the cortical network subserving defensive PPS plays a crucial role in the prediction of an impact with the body.

The predictive mechanism described earlier has also been investigated through a reaction time task by Kandula and colleagues (Kandula, Hofman, & Dijkerman, 2015). The authors presented visual stimuli, specifically an arm moving towards the participant's face, while tactile stimuli were applied to the cheek of the observer at the time of, before, and after the expected collision. Kandula and colleagues (2015) showed that the reaction times to tactile stimuli delivered at the time of the expected collision were faster relative to the reaction times to tactile stimuli delivered before or after the impending collision. In accordance with Cléry and colleagues (Cléry et al., 2015a), the authors (Kandula et al., 2015) claim that this predictive mechanism subserves the construction of a safety zone around the body.

3. The Modulation of the Defensive Peripersonal Space

Looming stimuli have been extensively used to investigate the PPS in both monkeys and humans. In humans, stimuli on a direct collision course with an observer have also been used to investigate time-to-collision judgments. In this kind of paradigm, participants are asked to estimate when an approaching stimulus would collide with their body. Interestingly, when participants are asked to estimate the arrival time of looming stimuli they underestimate it (McLeod & Ross, 1983; Neuhoff, 2001; Schiff & Oldak, 1990). This underestimation has been interpreted as an adaptive response that allows more time to engage in a defensive behavior (Bach, Neuhoff, Perrig, & Seifritz, 2009; Neuhoff, 2001). Indeed, although this underestimation is a perceptual error it is much more dangerous to respond too late to something approaching our body than to respond to it too soon. Thus, an anticipatory bias, modulated by motor abilities, may increase the chances of survival in comparison to unbiased perception (Haselton & Nettle, 2006). Traditionally, looming has been viewed as a purely optical cue to object approach (cf. Gibson, 1979). Indeed, the rate of expansion on the retina should be sufficient to estimate the arrival time of looming stimuli (McLeod & Ross, 1983). However, given the clear ethological importance of looming objects, we hypothesized that if stimuli were intrinsically threatening that would affect perceived time-to-collision, compared to if the stimuli were non-threatening (Vagnoni, Lourenco, & Longo, 2012). Specifically, we predicted that perceived time-to-collision for threatening stimuli would be underestimated even more relative to non-threatening stimuli. In agreement with our prediction, the time-to-collision of threatening stimuli was underestimated more relative to non-threatening stimuli, an effect that has also been found in other studies both in our lab in several subsequent studies (Vagnoni, Andreanidou, Lourenco, & Longo, 2017; Vagnoni, Lourenco, & Longo, 2015) and in other labs (Brendel, DeLucia, Hecht, Stacy, & Larsen, 2012; Brendel, Hecht, DeLucia, & Gamer, 2014). Interestingly, the underestimation was stronger for those more fearful of the threatening stimuli presented in the task (Vagnoni et al., 2012) or, as in the study of Brendel and colleagues (2014), was present only for spider-fearful individuals, showing a clear relation between spatial perception and the specific fears of participants. Therefore, both the characteristics of the stimuli—for example, their semantic content—and the individual characteristics of the observers—for example, their level of fear—influence the estimation of the arrival time of looming stimuli. Perceiving a stimulus as arriving sooner, and therefore being within our PPS earlier, has an adaptive advantage especially when the stimulus approaching our body is represented by a dangerous object. Moreover, it seems that having a specific fear of the approaching stimulus prompts the use of a more conservative margin of safety (Taffou & Viaud-Delmon, 2014).

These results have been replicated not only by our research group (Vagnoni et al., 2012, 2015, 2017) but also by others with the same (Brendel et al., 2012, 2014) and different paradigms. For example, Taffou and Viaud-Delmon (2014) modified the bimodal paradigm of Canzoneri and colleagues (2012) described earlier to show how the PPS expands in the presence of a feared object. The authors presented threatening (dog growling) and non-threatening (sheep bleating) sounds looming towards the rear hemi-field while tactile stimuli were delivered to the participant's hand at several time delays. Specifically, the tactile stimulus was delivered when the sound was perceived at several distances from the body. The participants were asked to respond as quickly as possible to the tactile stimulus ignoring the approaching sound. The original version of this task (Canzoneri et al., 2012) shows that the reaction times to the tactile stimuli are modulated by the simultaneous presentation of the to-be-ignored looming sound so that the reaction times become progressively faster as the sound is perceived closer to the body. In their study, Taffou and Viaud-Delmon (2014) showed that this facilitation occurred farther in space for cynophobic (i.e., dog-phobic) participants when the approaching sound was the feared stimulus (dog growling) relative to the non-feared one (sheep bleating). Similar findings have been shown by de Haan and colleagues (de Haan, Smit, Van der Stigchel, & Dijkerman, 2016). The authors presented threatening and non-threatening stimuli (butterflies and spiders) approaching on a horizontal screen. The tactile reaction time task required the participants to respond as soon as possible to the tactile stimuli while looking at the screen. The authors showed that the reaction times were faster when the stimuli were closer to the hand. This facilitatory effect was stronger when the visual stimuli were spiders, relative to butterflies, but only if the participants were afraid of spiders (de Haan et al., 2016).

The studies cited demonstrate how it is not only the semantic content of the stimulus—for example, the threatening aspect—but also the individual characteristics of the observers—for example, the level of fear—that influence the extension and modulation of the PPS. However, fear is not the only emotion that is related to the PPS representation. For example, Lourenco, Longo, and Pathman (2011) showed that claustrophobic traits are related to the extension of PPS. The authors used a task widely used to investigate the PPS in neurological patients, the line bisection task. With this task, it has been shown that when participants bisect horizontal lines close to the body, they show a slight leftward bias that, however, shifts rightward when the line is presented in far space (Longo & Lourenco, 2006, 2007, 2010; Varnava, McCarthy, & Beaumont, 2002). The authors (Lourenco et al., 2011) found that subjects with a high level of claustrophobia showed a more gradual rightward shift over distance. The rate at which the shift in the line bisection occurs can be used to quantify the extent of the PPS space representation (Longo & Lourenco, 2006); therefore, the more gradual shift suggests a larger representation of the PPS space in subjects with a high level of claustrophobia traits. The influence of anxiety on the extension of PPS representation has also been investigated with another paradigm, the hand blink reflex (HBR). In this paradigm the boundaries of PPS are measured with the strength of the HBR in relation to the position of the stimulated hand from the face. Sambo and Iannetti (2013) reported an increased HBR in more anxious individuals when the stimulated hand was at the same distance from the face, relative to less anxious individuals, suggesting that the "safety margin" is larger in more anxious individuals.

4. Peripersonal Space as Reaching Space

The idea that our experience of space is deeply related to our ability to act has been influential, at least as far back as the work of Berkeley (1709). The PPS has been also called the "action space" by Maravita and colleagues (Maravita, Husain, Clarke, & Driver, 2001), indeed, it has been traditionally hypothesized that this network plays a role in guiding voluntary object-oriented actions (Bremmer, 2005; Fogassi & Luppino, 2005; Graziano, 1999; Maravita, Spence & Driver, 2003; Maravita, 2006; Rizzolatti et al., 1981a, 1981b; 1987; 1997). In this section, we will start by illustrating the early studies on "action PPS" in monkeys, and then describe studies providing evidence of a motor function of PPS through the investigation of PPS in amputees or during motor actions.

Objects close to the body are more relevant to behavior than distant objects given that we can act on them directly with our body (Rizzolatti et al., 1997, 1998). Many neurons within the inferior premotor cortex show motor properties, which is in accordance with the role of this brain area as a perception-to-action interface (Brozzoli, Makin, Cardinali, Holmes, & Farnè, 2012). Indeed, several authors have demonstrated the presence of many visuo-tactile neurons in inferior area 6, where areas F4 and F5 are located (Gentilucci et al., 1988; Rizzolatti et al., 1997), parietal areas 7b (Hyvärinen, 1981), and the putamen (Crutcher & DeLong, 1984) of the monkey that respond to visual and tactile stimulation as well as during motor activity. Moreover, the visual responses of some neurons in the inferior premotor cortex increase while reaching towards an object (Godschalk, Lemon, Kuypers, & van der Steen, 1985), as well as during reaching and grasping movements of the arm and hand (Godschalk, Lemon, Nijs, & Kuypers, 1981; Rizzolatti & Gentilucci, 1988), and mouth (Rizzolatti et al., 1981b). Apart from the premotor cortex, parietal area 7b also exhibits motor properties linked to approaching movements of a body part towards an object (Gardner et al., 2007; Lacquaniti & Caminiti, 1998; Rizzolatti et al., 1997).

Moreover, in agreement with the interpretation of a motor function of the PPS, several lesion studies on monkeys have shown that lesions to the anterior or posterior part of the PPS network result in motor impairments, mostly involving the execution of visually guided reaching actions (Battaglini et al., 2002; Ettlinger & Kalsbeck, 1962; Rizzolatti, Matelli, & Pavesi, 1983).

Another finding that strongly points towards the motor function of PPS is the fact that bimodal neurons with tactile receptive fields on the face are activated during reaching movements of the arm towards the part of the space corresponding to its receptive field (Gentilucci et al., 1988; Godschalk et al., 1981). This means that there is coordination between sensory and motor responses. According to several authors (Bartolo et al., 2014; Bourgeois & Coello, 2012; Bourgeois, Farnè, & Coello, 2014; Brozzoli et al., 2012; Coello et al., 2008; Costantini, Ambrosini, Tieri, Sinigaglia, & Committeri, 2010; Quinlan & Culham, 2007) this suggests that sensory inputs and motor responses are expressed in a common frame of reference to locate objects near to the body and to guide movements towards them.

In subregion F5 of inferior area 6 there are motor neurons with visual properties called "mirror neurons" (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). These neurons discharge when the monkey performs an action as well as when the monkey sees another monkey or human performing the same action (di Pellegrino et al., 1992; Gallese, Fadiga, Fogassi, & Rizzolatti 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Recently, it has been shown that some of these neurons are specifically tuned for actions executed within the PPS (Caggiano, Fogassi, Rizzolatti, Thier, & Casile, 2009). Moreover, a different subpopulation of mirror neurons showed the opposite preference (actions performed in the extrapersonal space). Interestingly, this study showed that space was coded not in a metric fashion but in an operational way so that actions executed within the PPS but not accessible (placing a screen between the actor and the monkey) were treated as actions being executed in the extrapersonal space. Indeed, in this case, the extrapersonal-tuned mirror neurons were activated. According to Caggiano et al. (2009), these neurons allow not only for an understanding of the other's actions but also for planning "the next move" that could be a possible interaction or withdrawal.

If the PPS codes "actions possibilities" it could be true that if we have less opportunity to act on a specific part of the space we code it in a different way. Makin and colleagues (Makin, Wilf, Schwartz, & Zohary, 2010) showed that hand amputation is associated with a mild visual "neglect" of the part of the space close to the missing hand. The authors asked amputees to perform a landmark position judgment task. In this task, the participants had to tell which of two stimuli presented (briefly and after a mask) was farther away from a central fixation point. The results showed that participants favored the intact side. Crucially, this bias disappeared if the targets were placed in far space. Therefore, the possibility of actions influences the space perception of the actor. Brozzoli and colleagues (Brozzoli, Pavani, Urquizar, Cardinali, & Farne, 2009) investigated the remapping of the PPS during action. One of the most used paradigms to investigate the PPS representation is the crossmodal congruency paradigm. In this task participants are asked to discriminate between two locations of a tactile stimulus, while an irrelevant visual distractor was delivered at a congruent or incongruent location. Brozzoli and colleagues (2009) showed that while initiating a grasping action the interaction between visual distractors and tactile stimuli on the hand performing the action was increased relative to the static condition. This effect disappeared if the tactile stimulation occurred on the other hand (the one that was not performing the action), showing that the effect was strictly hand centered. Moreover the same authors (Brozzoli, Cardinali, Pavani, & Farnè, 2010) showed that a continuous updating of the PPS varies according to the characteristics of the motor acts. Specifically the perceptual modulation seems to be further enhanced in cases of relatively complex object-oriented actions, like grasping, relative to simpler actions, like pointing.

5. The Modulation of Space for Action PPS

The plasticity of PPS has been investigated originally through the modulation of space for action PPS. In an influential study, Iriki and colleagues (Iriki, Tanaka, & Iwamura, 1996) analysed the responses of neurons in the caudal post-central gyrus of the monkey (which contains the anterior intraparietal AIP area, ventral intraparietal VIP area, medial intraparietal MIP area, lateral intraparietal LIP area, and caudal intraparietal CIP area) after training the monkey to reach food with a rake. Interestingly, after the training, neurons in the post-central gyrus responded to visual stimulation in the monkey's extrapersonal space. According to the authors, the visual receptive fields of neurons representing the PPS expanded following tool use (this interpretation has been severely criticized by Holmes and colleagues: Holmes, 2012; Holmes, Calvert, & Spence, 2004; Holmes & Spence, 2004). After this seminal work, the modulation of PPS by tool use has been investigated in humans, both healthy individuals and also neurological patients with conditions such as extinction and neglect. It is crucial to note that extinction occurs only for stimuli presented within the PPS of the patients (di Pellegrino, Basso, & Frassinetti, 1997; Làdavas et al., 1998a, 1998b) and therefore this deficit has been investigated extensively in relation to the PPS representation. Interestingly, it has been shown that after using a rake to retrieve distant objects, visual stimuli presented in extrapersonal space also induced crossmodal extinction (Berti & Frassinetti 2000; Bonifazi, Farnè, Rinaldesi, & Làdavas, 2007; Farnè et al., 2005, 2007; Maravita & Iriki, 2004).

The same effect of expansion of PPS after tool use was shown in neglect patients (Berti & Frassinetti, 2000). If extinction patients can detect unilateral stimuli on both sides of space, but ignore contralesional stimuli only when presented together with competing ipsilesional ones (Driver, Mattingley, Rorden, & Davis, 1997) neglect patients typically ignore stimuli contralateral to the side of their brain damage (contralesional stimuli) (Bisiach & Vallar, 2000). Intriguingly, some patients show neglect specifically for the space close to the body (Halligan & Marshall, 1991) or far from it (Cowey, Small, & Ellis, 1994, 1999), providing a clear double-dissociation between the representation of peripersonal and extrapersonal space. Berti and Frassinetti (2000) tested a patient who showed left neglect when bisecting lines (i.e., rightward bias) with a laser pointer presented within peripersonal space, but not when they were presented in extrapersonal space. Remarkably, however, when responding with a stick, neglect appeared in both locations, as if the space that was previously coded as extrapersonal space was now coded as peripersonal.

Many studies have also investigated the plasticity of PPS representation in healthy adults (for a review of this literature see Cardinali, Brozzoli, & Farne, 2009). According to some authors, the use of a tool demonstrates an extension of the limits of multisensory integration from the PPS to the tool's action space, showing therefore that PPS representation is dynamically shaped as a function of subjects' action space (Gallese & Sinigaglia, 2010). However, according to others (Holmes et al., 2004; Holmes & Spence, 2004) after tool use there is not an expansion of the PPS representation; instead, the tip of the tool becomes behaviorally relevant to visuo-tactile interactions associated with the hand that manipulates the tool. In other words, through the active manipulation of the tip of the tool the representation of the extrapersonal space is incorporated into the brain's visuo-tactile representations of the body and of PPS (Holmes et al., 2004).

Interestingly, the plasticity of PPS seems to be symmetrical, and indeed PPS can both expand and contract. For example, Longo and Lourenco (2006) adapted the paradigm used by Berti and Frassinetti (2000) in neglect patients to test healthy participants. As had been shown previously (Varnava et al., 2002), when participants used a laser pointer to bisect lines they showed a gradual left-to-right shift in bias with increasing viewing distance. Critically, however, when participants used a stick to respond, a consistent leftward bias was found at all distances, as if they were all coded as being within the PPS. In contrast, Lourenco and Longo (2009) conducted a study to investigate how motor effort influences PPS representation. Specifically, the authors asked participants to bisect lines (the same task used in neglect patients). The authors showed that participants, when unencumbered, showed the classic pattern of leftward bias when bisecting lines at the closest distances and a rightward shift in bias with increasingly farther distances. Interestingly, increasing the effort involved in the task—namely, putting weights on participants' wrists while bisecting lines—led to a contraction of PPS representation. This study showed how PPS contracts when the motor effort required to perform the task is increased (Lourenco & Longo, 2009).

The relation between motor ability and PPS representation was also recently investigated by Bassolino and colleagues (2015). In this study the authors showed how restraining the use of one arm for ten hours resulted in a contraction of PPS on the arm's side. Interestingly, while overusing the other arm did not result in an expansion of PPS, it did nevertheless modify body representation, with the "overused" arm being perceived as longer. The authors concluded that PPS representation seems to be shaped as a function of the dimension of the acting space, whereas more general body representations seem to be influenced by a complex interplay between visual and sensorimotor information.

The literature on the effect of tool use and in general motor ability on PPS focused mainly on the hand PPS given its crucial role during actions. However, recently several studies investigated the PPS representation related to other body parts (head and trunk by Serino et al., 2015; feet, Stone, Kandula, Keizer, & Dijkerman, 2018). Serino and colleagues showed body part (head, trunk, and hand)–specific PPS representations, differing in extension and directional tuning. According to the results of this study the distinct PPS representations are not fully independent from each other, but referenced to the common reference frame of the chest (Serino et al., 2015). Moreover, the chest PPS representation varies during locomotion (Noel et al., 2015). Specifically, it has been shown that during walking PPS boundaries are expanded compared with standing still. These results are in line with the view that PPS constitutes a dynamic sensory-motor interface between the individual and the environment (Brozzoli et al., 2012; Noel et al., 2015).

6. The Social Aspect of Peripersonal Space

The space around our body is not only the space that we act upon or where the presence of an object prompts defensive reactions but also the space where interactions with others occur. In this section we review a series of studies that investigate the neural basis of the "social" PPS in monkeys and humans.

In 2010, Ishida and colleagues (Ishida, Nakajima, Inase & Murata, 2010) examined the responses of "body-matching neurons" in parietal area VIP of the monkey. The authors investigated, through single cell recording, the responses of neurons when visual stimuli were presented close to the monkey's body or close to the body of an experimenter standing in front of the monkey. The authors showed that a population of neurons responded both when visual stimuli were presented within 30 cm from the monkey's body and when the visual stimuli were presented within 30 cm of the experimenter's body (therefore 120 cm from the monkey's body). Interestingly, some neurons showed strong responses only when the visual stimuli were presented within 30 cm from each body but not in between those two regions. It seems therefore that they code specifically the PPSs of the monkey and the experimenter, but not the space between them.

Another experiment, again on monkeys, investigated the responses of a subpopulation of neurons in F5. We have already mentioned that some F5 neurons exhibit mirror properties, responding both to an action performed by the monkey and during the observation of an action performed by someone else, while "canonical neurons" respond simply to the presentation of an object (Rizzolatti & Luppino, 2001). Caggiano and colleagues (2009) showed that a subpopulation of mirror neurons in F5 responded differently to actions performed within the monkey's PPS or outside it. These neurons seem to be sensitive to the section of space where the other performs the action. Interestingly, the authors showed that some of these neurons code the PPS/extrapersonal space not in a metric but in an operational way. Indeed, if a transparent panel was placed in front of the monkey, thereby restricting its working space, while the action was performed by the experimenter within the monkey's PPS some of the neurons that were responding to the actions performed within the PPS stopped responding. Moreover, some of the neurons that were active during the execution of actions in the extrapersonal space of the monkey started to respond. According to the authors, the functional meaning of these neurons is to encode the observed actions to plan subsequent behavioral responses—for example, approaching the other to initiate an interaction.

Neurons in area F5 of the monkey were further investigated in relation to action observation within and outside PPS by Bonini and colleagues (2014), who showed that canonical and mirror properties are often present in the same cortical sites. Interestingly, the authors found a new population of neurons showing both canonical and mirror properties. These neurons responded similarly to objects and actions within PPS; however, they showed a stronger response to action observation than object presentation when the visual stimuli were in extrapersonal space. Therefore it seems that while the coding of actions occurred in both PPS and extrapersonal space the coding of objects was limited to the PPS. As in the study of Caggiano and colleagues (Caggiano et al., 2009), some neurons coded the PPS in an operational (action possibility) rather than metric (absolute distance) way. Moreover, the orientation of the object was not related to the possibilities of action (affordance) of the monkey when the object was presented in its extrapersonal space but to the possibilities of action (affordance) of another agent. The authors interpreted these findings as evidence that the canonical-mirror neurons are not involved in the processing of the object's affordances, and they do not play a role in the visuo-motor transformations related to grasping. Instead, the fact that these neurons respond when the object is rotated during the observation of an action performed by someone else suggests that their activity is linked to the representation of the impending action of the observed agent (Bonini et al., 2014).

The social aspect of the PPS has also been investigated in humans. In an elegant study, Brozzoli and colleagues (Brozzoli, Gentile, Bergouignan, & Ehrsson, 2013) demonstrated that the same parietal areas respond to stimuli presented close to one's own hand and the hand of another person. The authors used an fMRI BOLD adaptation method to investigate a subpopulation of neurons that exhibit selectivity to specific stimulus characteristics. Specifically, they investigated brain areas coding the proximity of a physical visual stimulus to the hand, regardless of whether the hand was the participant's own or that of another person. The findings of this study showed that the left ventral premotor (PMv) area adapted to visual simulation near the participant's hand

and the other person's hand. According to the authors, the same neuronal populations within the PMv could represent the neural basis of the shared representation of our own PPS as well as the PPS of another person.

7. The Modulation of the "Social" Peripersonal Space

Interest in how the representation of the space around our body is modulated by the presence of other people is relatively new in the neuroscience field. However, in the last few years many studies have investigated it with different paradigms.

It has long been hypothesized that even in the absence of interaction or intention to interact with an object, the simple sight of an object automatically triggers the motor representation of the corresponding motor possibilities (affordance) (Gibson, 1979). For example, the orientation of a handle's mug may facilitate the execution of an action (grasping) if the handle is spatially aligned with the responding hand (Tucker & Ellis 1998, 2001). This effect has been called spatial alignment and refers to the decrease of reaction times when a subject performs a motor act which is congruent with that afforded by a seen object (Tucker & Ellis 1998, 2001). The description of the spatial alignment effect is of interest here given that it has been used to investigate the social aspect of the PPS. For example, Costantini and colleagues (Costantini, Committeri, & Sinigaglia, 2011) showed that the spatial alignment occurs not only when the object is presented within the PPS of the participant but also when the object (a mug) is outside the participant's PPS but within the PPS of an avatar. Moreover, in line with studies on monkeys, behavioral results in humans suggest that the PPS is coded in an operational (action possibility) rather than metric (absolute distance) way (Costantini et al., 2010, 2011).

Another paradigm widely used to investigate the PPS representation is the crossmodal congruency (CC) task (Holmes et al., 2007; Spence et al., 2000). In this task visual stimuli are used as distractors and participants are asked to respond only to the tactile stimuli which are spatially congruent or incongruent with the distractors. Several studies have shown that the visual distractors influence the reaction times to the tactile stimuli but only if they are presented within the PPS of the participants (Holmes et al., 2007; Spence et al., 2000). Heed and colleagues (Heed, Habets, Sebanz, & Knoblich, 2010) asked participants to complete the crossmodal congruency task with and without another person who responded to the visual distractors. The results of this study showed that performing the task together reduced the crossmodal interference effect on the tactile judgments but only if the other person was performing the task within the subject's PPS and when responding to all rather than a subset of visual distractors. Interestingly, these findings seem to suggest that when a task is performed with another person also the goal of the task is shared; moreover, the distractors seem to influence participant's reaction times less, given that there is someone else acting on them.

Teneggi and colleagues (Teneggi, Canzoneri, di Pellegrino, & Serino, 2013) showed that PPS boundaries shrink when participants sit in front of another person, as compared to a mannequin, placed in far space. The authors used the bimodal paradigm described previously (Canzoneri et al., 2012). They were asked to respond to tactile stimuli delivered to their hand while distractor sounds (looming sounds) were presented. Participants completed the bimodal task twice and in between the two sessions they played an economic game with the other person (a confederate). Interestingly, the results showed that after playing an economic game with another person, the PPS boundaries between self and the other merged but only if the other person acted cooperatively (Teneggi et al., 2013). Similarly, but with a visuo-tactile instead of an audio-tactile task, Pellencin and colleagues (Pellencin, Paladino, Herbelin, & Serino, 2018) showed that PPS expands when participants are facing a person whom they consider to be moral more so than when participants are facing a person whom they consider immoral.

Maister and colleagues (2015) used the same paradigm as Teneggi and colleagues (2013) to investigate whether shared sensory experiences modulate the PPS representation, using a body illusion called the "enfacement illusion." It has been demonstrated that the enfacement illusion can induce feelings of ownership over the other's body (Sforza, Bufalari, Haggard, & Aglioti, 2010; Tsakiris, 2008; Tajadura-Jiménez, Longo, Coleman, & Tsakiris, 2012), which has also been shown to increase the remapping of the other's sensory experiences onto our own bodies (Cardini, Tajadura-Jiménez, Serino, & Tsakiris, 2013). In the study of Maister and colleagues (2015), participants completed two sessions of the PPS bimodal task. In between the two sessions of the PPS task, they were touched on the face while watching another person being touched simultaneously. This interpersonal multisensory stimulation usually results in an increased perceived physical similarity between the two faces, the so-called enfacement illusion (Tajadura-Jiménez et al., 2012). Maister and colleagues (2015) found the typical facilitatory effect of the looming sounds on the reaction times to the tactile stimuli (Canzoneri et al., 2012). Moreover, they also showed that after participants experienced synchronous interpersonal stimulation shared with another person, reaction times to tactile stimuli delivered when the looming sound was perceived as close to the other's body were faster, demonstrating increased audio-tactile integration in the other's PPS. It is interesting to note that these results are different from the ones of Teneggi and colleagues (2013). Indeed, if in the former study (Maister et al., 2015) it seems that the interpersonal multisensory stimulation prompted a remapping of the other's PPS into the participants' PPS, in the latter (Teneggi et al., 2013) the results showed an expansion of the PPS, possibly to include the other person and form a common space of interaction.

It would be interesting to investigate in which cases PPS expands and in which instead we remap the other's PPS onto ours. It is possible that in the case of the economic game manipulation, when we face a cooperative person we are willing to create a common space for interaction, so that the manipulation acts at a motor level, while, instead, in the case of the interpersonal multisensory stimulation the mechanisms act at a sensory level. Interestingly, this difference mirrors the one between the work of Ishida and colleagues (2010) and the works of Caggiano et al. (2009) and Bonini et al. (2014). Specifically, in Ishida et al. (2010), the stimulation was just a visual stimulus presented close to either the monkey's or the experimenter's body. This stimulation activated part of the classic PPS network (VIP area). In their work, the authors showed that the monkey was remapping the other's PPS into its own PPS. However, when there is a motor manipulation (actions performed within or outside the PPS) it seems that the circuit activated is slightly different (the F5 area). Moreover, the results from Caggiano and colleagues (2009) show a gradient in the activity of the neurons tuned for the PPS or extrapersonal space. Specifically, it seems that the neurons also represent the space between the observer and the actor, something that is absent in the remapping of PPS where neurons responded only to stimuli close to one own PPS or the other's PPS and not for the space in between.

8. Models of the Relation Between Different Functions of PPS

Since the first studies on monkeys (Graziano & Cooke, 2006; Rizzolatti et al., 1997) two main interpretations have been given to the PPS. For some authors, PPS represents the space for action, and it is defined as the space that we can reach extending our arms (Maravita et al., 2001). According to others, the PPS is a safety zone around our body that subserves a defensive function (Graziano & Cooke, 2006). Despite the great number of studies investigating the PPS few attempts have been made to systematically organize them within a model. De Vignemont and Iannetti (2015) described two possible models that could define the PPS functions: the Swiss army knife and the specialist model. According to the Swiss army knife model, there is only one PPS representation where a stimulus that we want to reach or a dangerous stimulus that we want to avoid is represented on the same map. In this model, the location of the stimulus is mapped in the same representation, and the meaning of the stimulus triggers a different response (reaching versus avoidance). In the specialist model, instead, the stimulus is represented on a different map according to its meaning. The authors reviewed the motor and sensory signatures of the working and defensive space in the light of the specialist model. Moreover, they delineated a very interesting comparison of how the two PPS representations are differently influenced by emotion—specifically, anxiety.

According to de Vignemont and Iannetti (2015) some motor signatures differ between goal-oriented actions and defensive behaviors. For example, defensive actions are possibly a wider category that includes very different reactions, from freezing to navigational veering during locomotion to avoid obstacles, squinting, ducking, and withdrawing (Bracha, 2004; Dosey & Meisels, 1969; Graziano & Cooke, 2006). Usually it is easy to differentiate between goal-directed actions and defensive behaviors. There are cases, however, where it is more difficult to do so—for example, when we reach a tool to defend ourselves from an imminent attack (de Vignemont & Iannetti, 2015). According to de Vignemont and Iannetti (2015), another difference between the motor outcomes of these two putative PPS representations is the attention to specific body parts and the degree of automaticity of the actions. Indeed, whereas the hands may be especially critical for goal-directed action, during defensive responses, attention is spread across the whole body, and possibly focused more on the face. Moreover, in general, defensive reactions are automatic while goal-directed actions are voluntary (de Vignemont & Iannetti, 2015). However, even this differentiation can be difficult to make given that goal-directed actions are triggered by environmental affordances (Chao & Martin, 2000; Costantini et al., 2010; Gibson, 1979; Grafton, Fadiga, Arbib, & Rizzolatti, 1997; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995), an effect that can be described as automatic, and defensive reactions can be modulated by high-level cognitive factors (Sambo, Forster, Williams, & Iannetti, 2012a; Sambo & Iannetti, 2013; Sambo et al., 2012b).

If there are some controversies regarding the different motor signatures of the two PPSs the sensory signatures have not yet been systematically investigated. It is true that to defend our body we need a fast sensory process while to grasp and manipulate an object we need to code the fine sensory characteristics of an object. Therefore mapping the objects on two different maps could have advantages. Some parietal neurons show a preference for threatening visual stimuli (Dong, Chudler, Sugiyama, Roberts, & Hayashi, 1994); moreover, salient sensory information can be transmitted directly from the thalamus to the multisensory cortices without being processed in primary and secondary sensory-specific areas (Liang, Mouraux, & Iannetti, 2013). These could be the neural basis of a fast coding of dangerous stimuli. In the light of the specialist model, de Vignemont and Iannetti (2015) made a very interesting observation on the opposite effects that anxiety has on the PPS representation intended as working space or defensive space. Indeed, some studies have shown that anxiety reduces our working space (Graydon, Linkenauger, Teachman, & Proffitt, 2012; Nieuwenhuys, Pijpers, Oudejans, & Bakker, 2008), while others have shown how more anxious individuals show a larger defensive PPS (Lourenco et al., 2011; Sambo & Iannetti, 2013). It indeed seems that anxiety induces an underestimation of our reaching ability (Graydon et al., 2012) while it expands our protecting space (Brady & Walker, 1978; Evans & Howard, 1973).

Even if de Vignemont and Iannetti (2015) claim the existence of two distinct PPS maps, they specify that this doesn't preclude the possibility for an object to be represented on both or an interaction between the two. Moreover, the defensive function of PPS is likely the most ancestral while part of the sensorimotor processes could have been coopted for the "space for action" function (Brozzoli et al., 2012). This idea is in line with the "massive redeployment" principle proposed by Anderson (2007, 2010) and Dehaene and Cohen (2007). On this view, some brain regions that were originally shaped by natural selection for a specific cognitive function are recycled to support other cognitive functions. This putative recycling mechanism could be an adaptive strategy given that using a neural system for new aims is more parsimonious than developing a new one.

The specialist model has also been proposed to explain the relationship between defensive and action PPS by other authors (Cléry, Guipponi, Wardak, & Ben Hamed, 2015b). Cléry and colleagues (2015b) discussed the existence of two different PPS representations and delineated two different neural circuits subserving the working and defensive space, mostly based on monkey studies. According to these authors, the neural basis of the space for action PPS is represented by the 7b-AIP-F5 parieto-premotor network (and possibly other functionally coupled cortical and subcortical regions), while the VIP-F4 parieto-premotor network subserves the protective space. Moreover, in accordance with the model proposed by de Vignemont and Iannetti (2015), Cléry and colleagues (2015b) suggested the possibility of interactions between the two networks.

As we have already discussed in the previous section, in the last few years interest has grown regarding the social aspect of PPS. Both the review of de Vignemont and Iannetti (2015) and the review of Cléry and colleagues (2015b) took into consideration this aspect. However, neither of them suggested the presence of another, separate circuit for the "social" PPS. Indeed, even if it is now clear that social stimuli and interactions modulate the PPS representation, we can speculate that these effects are mapped on the defensive or working space circuits according to the specific situation (Cléry et al., 2015b). If we take, for example, the studies on monkeys (Bonini et al., 2014; Caggiano et al., 2009; Ishida et al., 2010), we can see that the presence and actions of another person modulate the classic defensive PPS network (Ishida et al., 2010) or the space for action PPS (Bonini et al., 2014; Caggiano et al., 2009). In Ishida et al.'s study, the visual stimulation presented close to either the monkey's body or the experimenter's body activated part of the classic defensive PPS network (VIP area). Instead, when there was an actor performing movements close or far from the monkey's body the space for action circuit (F5) was activated (Bonini et al., 2014; Caggiano et al., 2009). According to the situation, we represent the other person as someone with whom we want to interact or a dangerous stimulus that we want to avoid. This is a speculation and further studies should investigate systematically how the social aspect relates to the space for action and defensive aspects of the PPS representation.

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