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Peripersonal space in the brain

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Abstract

Research in neuroscience reveals that the brain constructs multiple representation of space. Here, we primarily focus on peripersonal space (PPS) representation, the region of space immediately surrounding our bodies and in which objects can be grasped and manipulated. We review convergent results from several generations of studies, including neurophysiological studies in animals, neuropsychological investigations in monkeys and brain-damaged patients with spatial cognition disorders, as well as recent neuroimaging experiments in neurologically normal individuals. Collectively, these studies show that the primate brain constructs multiple, rapidly modifiable representations of space, centered on different body parts (i.e., hand-centered, head-centered, and trunk-centered), which arise through extensive multisensory interactions within a set of interconnected parietal and frontal regions. PPS representations are pivotal in the sensory guidance of motor behavior, allowing us to interact with objects and, as demonstrated by recent studies, with other people in the space around us.

Contents

1. Introduction	126
2. Neurophysiological studies of peripersonal space in animals	127
3. Neuropsychological studies of peripersonal space in monkeys and humans	128
4. Neuroimaging studies of peripersonal space in humans	130
5. Social modulation of peripersonal space	131
6. The function of peripersonal space representation	131
7. Conclusions	132

Acknowledgments	132
References	132

1. Introduction

In everyday life, we experience the space around us as a unitary and seamless whole. Yet, a growing body of evidence in contemporary neuroscience reveals that the brain constructs not one but various functionally distinct representations of space. A key division is between near, peripersonal space and far, extrapersonal space representations. This was initially suggested by Brain (1941), who proposed the existence of a grasping distance and a walking distance to explain the selective impairment that right brain-damaged patients may show for one or the other region of space. The notion of a separate representation in the brain for the space immediately around the body was emphasized in subsequent neurophysiological studies (Hyvärinen and Poranen, 1974; Leinonen and Nyman, 1979; Mountcastle, 1976), and substantially elaborated and expanded by Rizzolatti et al. (1981a,b), who introduced the term peripersonal space to highlight the close links between somatosensory (i.e., bodily) and visual processing exclusively pertaining to this sector of space.

Peripersonal space defines the region of space immediately

surrounding our bodies in which objects can be grasped and manipulated. By contrast, extrapersonal space refers to the space

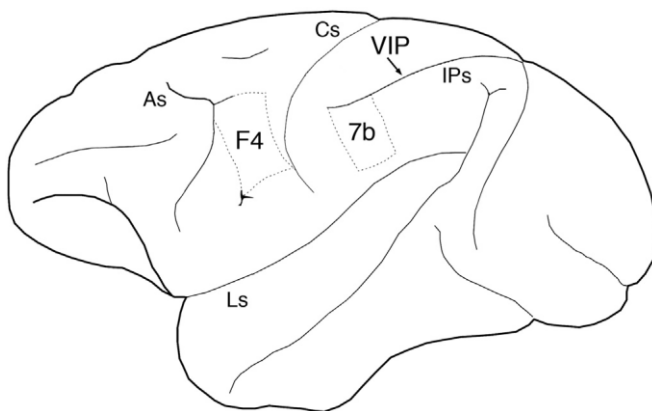


Fig. 1. Lateral view of the monkey cerebral cortex showing three regions containing neuronal populations that selectively encode peripersonal space: area F4 in the frontal lobe, area 7b and the Ventral Intraparietal Area (VIP), which is buried in the depth of the intraparietal sulcus (IPs), in the parietal lobe. As $\frac{1}{4}$ arcuate sulcus; Cs $\frac{1}{4}$ central sulcus; Ls $\frac{1}{4}$ lateral sulcus (see main text for more details).

beyond grasping distance, in which exploratory eye movements occur. The near vs. far space distinction has been utterly fecund in cognitive psychology and neuroscience, providing a theoretical frame of reference for several targeted studies, both in human and non-human primates, and thence an understanding of how the brain encodes the space around us.

Here, we primarily focus on peripersonal space (PPS), review-

ing convergent results from several generations of studies, including neurophysiological studies in animals, neuropsychological investigations in monkeys and brain-damaged patients with spatial cognition disorders, as well as recent neuroimaging experiments in neurologically normal individuals. Collectively, these studies reveal that the primate brain constructs multiple, rapidly modifiable representations of space, centered on different body parts (i.e., hand-centered, head-centered, and trunk-centered), which arise through extensive multisensory interactions within a set of interconnected areas in the parietal and frontal cortex. PPS representations are pivotal in the sensory guidance of motor behavior, allowing us to interact with objects and, as demonstrated by recent studies, with other people near us (Figs. 1 and 2).

2. Neurophysiological studies of peripersonal space in animals

Discrete processing of PPS was first revealed by single-cell recordings in monkeys, within a network of interconnected sensorimotor areas, such as the parietal and frontal premotor cortices,

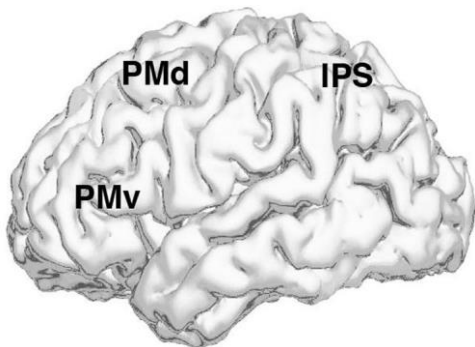


Fig. 2. Lateral view of the human cerebral cortex showing three regions revealing modulation of the BOLD signals specific to visual stimuli presented in peripersonal space: dorsal premotor (PMd) and ventral premotor (PMv) areas in the frontal lobe, and the anterior portion of the intraparietal sulcus (IPS) in the parietal lobe (see main text for more details).

which are crucial for the control of somatic, head and arm movements (Graziano et al., 1994; Hyvärinen and Poranen, 1974; Rizzolatti et al., 1981a,b; Gentilucci et al., 1983).

In the macaque monkey, the inferior aspect of the premotor cortex (area 6), particularly its caudal portion (i.e., the histochemical area F4 where proximal arm movements are represented; Matelli et al., 1985), contains neurons that reliably respond to tactile stimulation. These neurons are characterized by relatively large tactile receptive fields (RFs), located primarily on the monkey's face, neck, arm, hand (or both hands) and face (i.e., in the peribuccal region; Rizzolatti et al., 1981a), and

arranged to form a crude map of the body surface. A large proportion of neurons in area F4 are bimodal, discharging in response to both tactile and visual stimuli. Critically, unlike classical visual neurons, F4 neurons respond poorly to light stimuli far from the animal, but are effectively triggered mostly by real three-dimensional objects moving near the animal, in its peripersonal space (Gentilucci et al.,

1983, 1988; Rizzolatti et al., 1981a). Some F4 neurons respond only to stimuli very close to the body surface (less than 10 cm away; percutaneous neurons), while others can be triggered by stimuli located further away, but always within the animal's reaching distance (e.g., distant peripersonal neurons). The visual and tactile RFs of F4 neurons are in spatial register with one another, thus forming a single responsive region mapping the bodily surface and the space immediately adjacent to it. More recently, Graziano et al. (1999) showed that F4 neurons integrate not only tactile and visual but also auditory information about the location of objects within PPS, thereby indicating that premotor area F4 instantiates a multimodal representation of nearby space.

One relevant characteristic of these neurons is that the visual RF location is independent of eye movements, remaining in the same position in PPS regardless of gaze deviation (Fogassi et al.,

1992, 1996; Gentilucci et al., 1983; Graziano et al., 1994). Importantly, Graziano et al. (1994) reported that, for bimodal visual–tactile neurons with tactile RFs on the arm or hand, passive displacement of the monkey's limb causes a shift in the location of the visual RF, thus revealing that the visual RF is 'anchored' to the tactile RF on the limb, and moves with it. When neurons with tactile RFs on the face were tested, visual RFs were found to move when the head was turned, but not when visual fixation changed (Graziano et al., 1997a).

These results provide strong evidence that, unlike brain areas related to the control of eye movements, F4 neurons do not code space in a coordinate system centered on the retina (Andersen

1987; Goldberg et al., 1990). Rather, F4 neurons appear to code the location of a visual stimulus with respect to the face, arm, hand, or other body parts. This type of body part-centered reference frame appears to be extremely appropriate for organizing head and arm movements toward or away from visual objects, since head and arm movements are also programmed in body part-centered coordinates (Cohen and Andersen, 2002).

Two other findings are relevant here. First, F4 neurons that responded to visual stimuli presented in PPS continued to respond when the lights were extinguished and, unbeknownst to the animal, the previously presented object was silently removed (Graziano et al., 1997b). Thus, premotor neurons seem to encode space not only as a consequence of external (i.e., bottom-up) stimuli, but also in response to internally generated (i.e., top-down) signals, based on working memory. As such, they may play a role in the guidance of movement toward (or away from) objects that are no longer visible, such as objects that are occluded, behind the animal, or no longer fixated (see Moll and Kuypers, 1977).

Second, some bimodal, visual–tactile neurons were shown to respond to visual objects presented near a fake monkey arm prepared by a taxidermist and placed in a realistic posture (Graziano, 1999). In this study, a stuffed monkey arm was placed above a horizontal opaque barrier that occluded the monkey's real arm from view. The responses of the bimodal neurons were modulated by the seen

position of the fake arm. That is, the movement of the artificial arm caused a shift in the visual RF, even though the position of real arm did not change. Furthermore, when the monkey's real arm was moved out of view (i.e., when only proprioceptive signals were available), the shift in location of the visual RF was significantly reduced, although still present, relative to when the animal could see its own arm. Overall, these results suggest that premotor neurons generate a representation of PPS in arm-centered coordinates using both visual and proprioceptive information about the position of the arm.

Bimodal, visual–tactile neurons with properties similar to those of neurons in the ventral premotor area have also been recorded in the posterior parietal lobe, particularly in areas 7b and VIP, two areas heavily linked to the F4 region of premotor cortex (Matelli et al., 1986; Cavada and Goldman-Rakic, 1989). These visual–tactile neurons represent a high proportion of area 7b. Their tactile RFs are distributed over the face, arm and hand, and show a crude somatotopic organization with considerable overlap between the representations of different body parts. Most of these neurons respond to visual stimuli moving toward the monkey, within about 10 cm of the tactile RF (although in some cases, visual stimuli presented further away, but still within a reachable distance, were also effective). Importantly, the tactile and visual RFs are aligned in a spatially congruent manner. Graziano and Gross (1995) tested bimodal neurons with tactile RFs on the arm by moving the monkey's upper limb to different positions. Unlike in ventral premotor cortex, visual responses appeared to be independent of the position of the arm. Note, however, that some previous studies reported a change in the visual response in area 7b as the arm moves (Leinonen et al., 1979), indicating that bimodal cells with this property can be found in area 7b as well as in ventral premotor cortex, although in a smaller proportion.

The ventral intraparietal area (area VIP) contains two main classes of neurons responding to sensory stimulation: visual neurons and bimodal, visual–tactile neurons (Colby et al., 1993; Duhamel et al., 1998). VIP bimodal neurons share quite similar response properties to those of neurons in area 7b. One crucial difference concerns the distribution of somatosensory RF locations, which in area VIP selectively emphasizes head and face representations. It has been suggested that area VIP is involved in the construction of a multisensory, head-centered representation of near space.

Neural activity primarily devoted to represent the space near the body has also been found in the putamen (Graziano and Gross, 1993, 1995), a subcortical region of the primate brain that receives projections from both inferior area 6 and area 7b (Matelli et al., 1986; Cavada and Goldman-Rakic, 1989). Similarly to the bimodal neurons described above, the visual and tactile RFs in the putamen are spatially aligned, with the visual RFs being anchored to the tactile ones. Thus, bimodal cells with tactile RFs on the arm respond visually when the arm is within the monkey's field of view, but fail to respond when the arm is moved out of view (Graziano and Gross, 1995).

There is abundant evidence in animals as well as in humans that PPS processing operates in a very plastic and dynamic manner. In monkeys, the visual RFs of neurons in PPS-coding regions are not fixed or static, but rather are dynamic, readily modifiable and shaped by sensorimotor experience. Fogassi et al. (1996) showed that an increase in the velocity of approaching stimuli produced an online expansion of visual RF depth in most F4 neurons, such that fast-moving stimuli were signaled earlier than slow-moving ones. This property could be critical for facilitating the preparation and/or execution of actions in response to fast-moving objects. In a seminal study, Iriki et al.

(1996) trained monkeys to use a rake to retrieve food pellets dispensed beyond the reach of the animal's hand. Single-unit activity was recorded in the intraparietal region, where neurons respond to both tactile stimuli delivered to the hand and to visual stimuli near the hand. These neurons' visual RFs followed the hand when it was moved in space. Critically, the authors revealed an elongation of the cells' visual RFs along the axis of the rake immediately after it was used to retrieve the distant food pellets. This expansion incorporated the space now accessible with the rake into the visual RF. Moreover, the expanded visual RFs shrank back to their original size after a short rest in tool activity, even if the monkey was still passively holding the rake. Thus, the expansion of the visual RFs was strictly dependent upon the purposeful use of the rake to reach distant objects.

In monkeys, the brain areas involved in encoding PPS in the frontal and posterior parietal lobes are immediately adjacent to, or coextensive with, regions containing mirror neurons that selectively respond during both action execution and observation (di Pellegrino et al., 1992; Gallese et al., 1996). Interestingly, recent studies in monkeys have begun to explore the relationship between these two systems, particularly how a mirror neuron-like mechanism might reflect and encode the PPS of other individuals. In one intriguing study (Ishida et al., 2010), single neurons were recorded from monkey area VIP. The studied neurons were bi-modal and had tactile and visual RFs aligned in a spatially congruent manner. Objects presented near the tactile RF, approximately 30 cm from the monkey's skin, activated these bimodal neurons, similarly to the visual-tactile neurons described above. Critically, some bimodal neurons also exhibited responses to visual stimuli presented near the corresponding body parts of another individual (an experimenter) facing the monkey from approximately 120 cm away (i.e., well beyond the monkey's PPS). For example, a neuron with a tactile RF on the arm not only responded to a visual stimulus presented close to the monkey's own arm, but also to visual stimuli presented close to another individual's arm. Importantly, the neuron failed to respond when the same stimulus was presented close to other body parts of the experimenter, ruling out visual attention as an alternative interpretation of the findings. This study is of great interest, as it suggests that individuals might encode the body parts of others using a representation of their own body parts, a 'matching' mechanism that is functionally similar to how mirror neurons encode one's own actions and the actions of others.

3. Neuropsychological studies of peripersonal space in monkeys and humans

Studies of the behavioral effects of focal brain lesions have played a critical role in supporting the existence of a selective representation of the space near the body, often employing direct adaptations of animal paradigms, as well as seeking and exploiting homologies. One of the first pieces of empirical evidence for a double dissociation between peripersonal and extrapersonal space came from a study carried out on the frontal cortex of macaques (Rizzolatti et al., 1983). After unilateral ablation of postarcuate premotor cortex, monkeys exhibited a marked impairment in detecting and grasping objects (i.e. food) presented contralaterally to the ablated side, particularly with the mouth, in both the somatosensory and visual modalities. Critically, the deficit was selective for PPS, as the animals continued to react normally to objects placed in far space. In stark contrast, unilateral removal of the frontal eye field (Brodmann area 8) caused severe inattention and reduced exploratory eye movements toward stimuli displayed in far contralesional space, with no obvious deficits for the space near the body. These findings clearly support the existence of separate spatial maps for the control of different behaviors.

Evidence for discrete brain representations of the space near the body and its parts has also come from neuropsychological studies in humans, particularly in neurological patients with disorders of spatial attention. Patients with right hemisphere lesions, particularly those involving the frontal and parietal cortex, often exhibit a deficit known as contralesional extinction (Bender, 1952). In this condition, single stimuli presented to either side are detected with little difficulty, but, if the same stimuli are presented to both sides simultaneously, the stimulus on the contralesional side is typically missed (i.e., extinguished by the ipsilesional stimulus). Extinction is thought to reflect an unbalanced competition between concurrent targets for access to limited attentional resources (Ward et al., 1994; di Pellegrino et al., 1997a). Due to unilateral brain damage, stimuli presented in the contralateral space evoke a weak activation of that portion of space and, therefore, they are extinguished when competing with stimuli presented in the intact ipsilesional space.

Relevant to this discussion, contralesional extinction may be found not only between concurrent stimuli in the same sensory modalities (i.e., unimodal extinction), but also between stimuli in different modalities (i.e., crossmodal extinction), for instance, between concurrent tactile and visual events. Accordingly, several studies of patients with left, contralesional tactile extinction following right-hemisphere damage have revealed that tactile stimulation on the patient's affected left hand is extinguished by concurrent visual stimulation on the right. Critically, however, this crossmodal, visual–tactile extinction only arises if visual stimuli are presented in the space near the ipsilesional, right hand; visual stimuli far from the hand produce only mild tactile extinction at best (di Pellegrino et al., 1997b; Làdavas et al., 1998a,b). Moreover, in line with the single-unit findings in monkeys mentioned earlier, responses to visual stimuli presented near the patient's right hand remain anchored to the hand when it is moved to the opposite hemispace, revealing that crossmodal extinction between vision and touch operates in a hand-centered frame of reference (di Pellegrino et al., 1997b). This pattern of results is what would be expected if visual stimuli presented near the hand were processed by an integrated visual–tactile mechanism processing PPS. Specifically, due to this crossmodal interaction, visual events near the ipsilesional hand strongly activate a visual–tactile hand representation within bimodal neurons coding PPS, thereby leading to competition with the impaired tactile representation on the contralesional side.

Visual and tactile inputs are integrated in a similar way in other peripersonal space regions, namely around the face (Làdavas et al., 1998b; Farnè et al., 2005a). In these studies, visual–tactile extinction was found when presenting concurrent visual and tactile stimuli on the patient's face. As with the hand, crossmodal extinction was more evident when the visual stimulus was presented near the face rather than in a distant region, thus confirming and extending previous evidence of crossmodal links between vision and touch in human PPS.

Furthermore, a subsequent study (Farnè et al., 2005b) showed that the space near the body is separately encoded for distinct body parts, thus revealing that PPS is organized in a modular fashion. Extinction of touches delivered to the left hand was much stronger when visual stimuli were presented close to the homologous right hand, compared to when the same visual stimuli were presented close to the nonhomologous right cheek. Despite being close to the body, visual stimuli presented near nonhomologous body parts were treated as if they were far from the body, most likely because they were far from the relevant (homologous) body part. Importantly, this finding was observed only when visual stimuli were presented near the ipsilesional side of the patients'

body. In contrast, when visual stimuli were presented far from the ipsilesional side of the patients' body, the amount of visual–tactile extinction obtained in homologous and nonhomologous combinations was absolutely comparable.

Lesion studies have also documented crossmodal interactions between touch and audition in human PPS (Làdavas et al., 2001), thus paralleling the neurophysiological findings in monkeys that neurons in ventral premotor cortex encode the location of nearby objects through touch, vision, and audition (Graziano et al., 1997a,

1997b). In right brain-damaged patients, contralesional tactile extinction on the neck was stronger when acoustic stimuli were presented near to, as compared to far from, the ipsilesional side of the head, even though auditory stimulus intensity at the patient's ear remained constant. Interestingly, crossmodal audio-tactile extinction was more severe when assessed in the patients' back space (where vision is not available), relative to the front space (where vision is usually available), suggesting that different degrees of multisensory integration may occur depending upon the functional relevance of a given modality for that particular sector of space (Farnè and Làdavas, 2002).

Closely related to the experiments on animals reviewed earlier (see Graziano, 1999), neuropsychological research has addressed whether visual or proprioceptive information about the position of a body part (i.e., the hand) in space is critical for obtaining crossmodal, visual–tactile effects segregated in PPS. In patients with left tactile extinction, Farnè and colleagues (2000) showed that a visual stimulus displayed near a fake, rubber hand, but far from the patient's real hand, causes severe contralesional tactile extinction, comparable to that obtained when the same visual stimulus is presented near the patient's hand. However, this crossmodal effect was evident only when the rubber hand was placed in a plausible posture relative to the patient's body. When the fake hand was placed in an impossible spatial arrangement based on the patient's posture, visual stimuli around the fake hand failed to extinguish contralesional tactile stimuli. These findings suggest that in humans, as in monkeys (Graziano, 1999), viewing a fake hand can successfully ‘fool’ the system coding PPS, and that the brain mainly uses vision, rather than proprioception, to determine the location of the hand or any other body part in space (di Pellegrino and Frassinetti, 2000).

An intriguing characteristic of the multisensory representations of the region surrounding the body concerns their plasticity. Although a far visual stimulus typically undergoes only a weak interaction with tactile stimuli applied to the body, both neurophysiological and neuropsychological studies have documented that the use of different tools can change the way in which individuals interact with stimuli in far space. The general idea is that a visual stimulus in far space, when repeatedly reached with the tip of a tool, may start to be processed as if it is near to the body and, thus, have an increased influence over tactile processing. Through tool-use, for example, it is possible to functionally remap space so that “far becomes near” (Berti and Frassinetti, 2000). These authors asked patients with visual neglect to use a long stick to bisect distant horizontal lines, and showed that the patients' right hemispatial bias, which initially only affected lines in near space, was transferred to far space. Similar results have been described in extinction patients who, after tool-use, showed changes in cross-modal extinction that were compatible with a tool-use-dependent remapping of action space (see Farnè and Làdavas,

2000; Maravita et al., 2001).

By investigating left crossmodal extinction in right brain-damaged patients, Farnè and Làdavas, (2000) found that ipsilesional visual stimuli presented at the distal edge of a long rake induced more left tactile extinction immediately after tool-use (i.e., retrieving far objects with the rake for 5 min) than before tool-use. Moreover, when tool-use was impeded, the severity of cross-modal extinction decreased to pre-tool-use levels. Stronger crossmodal extinction at a location far from the hand after tool-use has been taken as evidence for an extension of the PPS surrounding the hand along the tool axis, whereas its reduction following tool inactivity provides behavioral evidence for a backward contraction of the formerly extended PPS of the hand. This finding has now been confirmed in humans by several other studies (see also Holmes and Spence, 2006; Ishibashi et al., 2004; Làdavas,

2002; Làdavas and Serino, 2008; Maravita et al., 2002; Maravita and Iriki, 2004).

PPS extension, however, requires actual use of the tool, for no extension is observed if the tool is passively held in the subjects' hands (Ishibashi et al., 2004; Làdavas and Farnè, 2006). In particular, Farnè et al. (2005b) investigated whether a prolonged passive experience with a rake was sufficient to elongate the PPS of the hand, or whether active tool-use was necessary. The results showed that the severity of visual-tactile extinction, assessed at the distal edge of the rake after a prolonged passive experience with the tool, did not differ from that obtained when the tool was absent. In contrast, crossmodal extinction at the distant location substantially increased following an equally long period of active use of the same tool. Therefore, in close agreement with both neurophysiological and neuropsychological findings (Iriki et al., 1996; Maravita et al., 2001), these results suggest that plastic modifications of PPS require the tool to be actively utilized in a task.

Interestingly, the extension of PPS after tool-use has been described by previous reports as lasting only briefly, because multi-sensory PPS contracts to the pre-tool-use level several minutes after the end of training. However, tool-use is quite a common experience in everyday life, and indeed there are some subjects who habitually and functionally use a tool to interact with objects in far space, such as blind persons who employ a cane to navigate in their daily environment. A study in our laboratory investigated audio-tactile interaction in the space around the hand and in extrapersonal space in order to measure an extension of the auditory PPS in blind cane users and in a control group of sighted, blind-folded subjects (Serino et al., 2007). The results showed that in sighted subjects the auditory PPS is normally limited to the area surrounding the hand, whereas in blind subjects it is immediately extended as soon as they hold their cane, even without any active temporary use of the tool. These findings suggest that long-term experience with a cane in blind people produces a special and durably extended representation of PPS, which can be dynamically and functionally engaged depending on contextual demands.

Overall, the findings that crossmodal links between touch, vision and audition may occur in a privileged manner in the space near the body, operate in body part-centered coordinate systems, and may rapidly change after tool-use, have been taken as evidence of the existence, in humans, of an integrated multimodal system coding PPS similar to that which has been found in monkeys (Làdavas, 2002).

4. Neuroimaging studies of peripersonal space in humans

A more recent generation of studies has used brain imaging to investigate the anatomical underpinnings and functional mechanisms of PPS in healthy humans. These studies further highlight the homologies between cortical areas explored with single-cell recordings in the monkey and cortical regions in the human brain that are selective for processing objects in the space near us. In their functional magnetic resonance imaging (fMRI) study, Makin et al. (2007) identified regions within the intraparietal sulcus, the lateral occipital complex, and the premotor cortex that showed significantly stronger activation in response to a ball

approaching the subject's hand, compared to the same stimulus moving away from the subject's hand. Critically, the greater activation for the near vs. far ball was lost when the hand was retracted, thereby indicating that these brain regions represent visual objects with respect to hand position, rather than simply responding to low-level visual differences in the near and far ball conditions. Moreover, in these areas, selective responses to objects in near space were abolished when the hand was occluded from view; however, a dummy hand placed in a natural position near the objects was sufficient to reactivate these brain areas, irrespective of the position of the subject's real hand. These results indicate that the response of these areas to visual stimuli located in the PPS of the hand is based primarily on visual information about hand position, regardless of information from proprioception, a conclusion that nicely accords with evidence obtained from neurophysiological studies in monkeys, as well as lesion experiments in neurological patients.

Both neurophysiological and neuropsychological works illustrate strong crossmodal links in the internal construction of PPS (see Driver and Spence, 1998; Holmes and Spence, 2004; Làdavas,

2002). In line with these findings, several fMRI studies have demonstrated that regions within the intraparietal and premotor cortices respond to multisensory stimuli in PPS (Bremmer et al.,

2001; Ehrsson et al., 2004; Lloyd et al., 2003; Makin et al., 2007; Macaluso and Driver, 2005; Sereno and Huang 2006). The study of Gentile et al. (2011) examined how these regions of the brain integrate visual and tactile stimuli delivered in the PPS space of the hand. While participants were in the scanner gazing at their hand, unisensory and multisensory stimuli (small spherical objects) were presented in the space immediately surrounding the hand. Superadditive, nonlinear BOLD responses during multisensory visual–tactile stimulation were observed in the cortex lining the intraparietal sulcus (IPS), the insula, the dorsal premotor cortex, and the putamen, thus nicely matching the neurophysiological findings on multisensory areas in both non-human primates and humans.

A subsequent study from the same laboratory (Gentile et al.,

2013) revealed that responses in the same parietal and premotor areas depended on spatial and temporal congruence of the visual and tactile signals. Furthermore, visual–tactile integration requires congruency between the seen and felt orientations of the hand, indicating that multisensory integration in the PPS of the hand requires congruent visual and proprioceptive information from the hand, again in close accord with results in animals (Graziano,

1999) and brain-damaged patients (Farnè et al., 2000).

In addition to the brain areas mentioned above, other imaging studies have showed the superior parietal occipital junction to be a critical neural region for representing the visual space near the hand and the face (Gallivan et al. 2009; Quinlan and Culham

2007), extending our current knowledge of the PPS neural network in humans.

In recent studies (Brozzoli et al., 2011, 2012), fMRI adaptation was used to directly investigate the neuronal populations with selective responses to visual events occurring within the space near the hand. The term “adaptation,” or “repetition suppression,” (Grill-Spector, 2006) refers to decreased neural responsiveness to repeated stimuli. Compared to the standard neuroimaging approach, fMRI adaptation has the capacity to reveal population of neurons selective to specific stimulus features within a single voxel and, therefore, is more closely related to electrophysiological recordings in animals than a traditional fMRI analysis (Grill-Spector, 2006). The first study by Brozzoli and colleagues (2011) revealed that areas in the IPS, the inferior parietal lobule, and the dorsal and ventral portions of the premotor cortex exhibit selective BOLD signal adaptation to an object moving near the subject's outstretched hand. Crucially, no significant reduction in the BOLD

signal was demonstrated when the hand was retracted, or when the stimulus was presented in a far location, regardless of whether the hand was outstretched or retracted.

A follow-up study (Brozzoli et al., 2012) exploited fMRI adaptation to investigate whether, similarly to findings in monkeys (Graziano and Gross, 1995), regions in the intraparietal and premotor cortices remap the PPS of the hand as it is moved in space, that is to say whether PPS is coded in hand-centered coordinates in the human brain. In line with the hypothesis and previous studies, cortices lining the IPS and premotor cortices showed adaptation effects when the stimulus was presented near the hand; critically, the effect followed the hand when it was moved across two positions in space. Moreover, the study examined whether construction of PPS centered on the hand is mediated by perceived ownership of the hand. To this aim, the participants' feelings of owning a prosthetic hand were manipulated by applying either synchronous or asynchronous brushstrokes on both the visible prosthetic hand and the participant's hand, which was hidden from view (i.e., rubber-hand illusion, Botvinick and Cohen,

1998). Results showed that PPS remapping in the premotor cortex is closely related to feelings of ownership of the fake hand, such that the stronger the participants rated the feeling of ownership over the prosthetic hand, the stronger the prosthetic hand-centered adaptation in premotor cortex.

5. Social modulation of peripersonal space

Typically, the study of the PPS, both in human and non-human primates, has involved the use of three-dimensional objects presented near the body and its parts. However, the space close around us is not only the privileged region of space for grasping and manipulating objects but also for interacting with other individuals. Accordingly, a number of recent studies begun to explore how selectively social information can modulate our internal representation of the PPS. In their behavioral study, Heed et al. (2010) instructed participants to respond to the elevation (up or down) of tactile stimuli applied on the hand, and ignore visual distractor presented concurrently near or far from the tactile stimulus, for instance near the nonstimulated hand. In line with several earlier studies (Driver and Spence, 1998), responses were faster and more accurate when the visual distractor occurred near the tactile stimulus than when it occurred farther away, indicating crossmodal integration

of spatially congruent visual and tactile events. Crucially, the crossmodal congruency effect was significantly reduced when the participant performed the task with a partner who sat in front to her and responded to visual stimuli. Note, however, that the social modulation of visual–tactile integration required the partner's presence within the participant's PPS. When the partner was outside of the participant's PPS, or she did not perform a task on visual stimuli, no modulation of visual–tactile interaction was observed. The social modulation of visual–tactile integration was interpreted as due to top-down modulation, so that knowing that the partner acts upon visual events near to one's body reduces the crossmodal links between vision and touch in the space around us. In other words, the possibility exists that the PPS may shrink when other agents act into our vicinity.

The study carried out by Teneggi et al. (2013) supports and extends this view. In several experiments, participants performed a tactile detection task on their face while concurrent task-irrelevant sounds were presented, giving the impression of a sound either approaching toward, or receding from, their face. Since sounds affect touch when occurring within PPS, it was possible to measure the critical distance where sounds speeded up tactile reaction time as a proxy of PPS boundaries. The first experiment showed that PPS representation shrinks (i.e., PPS boundary moves closer to the subject's body) when the far space is occupied by another person, as compared to when it is occupied by an artificial, body-like object of comparable size, suggesting that one's own PPS changes in the presence of others. In a second experiment, a separate group of participants performed the audio-tactile interaction task facing another subject, both before and after performing with her an economic game involving material gains. When the other subject behaved cooperatively, results revealed that there were no more detectable PPS boundaries between the self and other, thus suggesting that the participant's PPS had extended as far as to include the space around the other. By contrast, when the other subject failed to cooperate during the economic interaction, the PPS boundaries between self and the other did not change. Thus, the study showed that PPS representation not only responds to the presence of others, but is also shaped by interactions with others and, more specifically, by valuation of other people's behavior during social interaction.

By using fMRI adaptation, a more recent study (Brozzoli et al.,

2013) explored whether the human brain contains neuronal populations encoding the space near both one's own hand and another person's hand, analogous to “body-matching neurons” identified in monkey parietal cortex (see Ishida et al., 2010, see previous paragraph). Participants viewed a small ball moving either near to their hand, or to another person's hand, which was positioned with the same orientation of the participants' hand and located in far space. An artificial hand, also located far from the subject, served as a control condition. Regions within the ventral premotor cortex revealed stronger BOLD adaptation effects when the ball was near either the participant's hand or another person's hand, rather than close to the artificial hand. These findings suggest the existence of a shared representation of the space near oneself and other persons in the human premotor cortex. This mirror-like, embodied simulation mechanism for the space near us may provide the neural substrate for how the representation of one's own PPS accommodates in the presence of others during social interactions (Teneggi et al., 2013).

6. The function of peripersonal space representation

What is the function of the PPS representation? Why does the brain construct multiple, body part-centered representations of the space immediately around us? Neurophysiological studies in monkey have revealed that neurons in the putamen, area VIP, and inferior area 6 have motor functions as well as multisensory functions (Rizzolatti et al., 1997). In humans, studies using single-pulse TMS have shown that auditory (Serino et al., 2009; Avenanti et al., 2012) or visual (Makin et al., 2009) stimuli presented within PPS transiently modulate the excitability of the hand representation in the primary motor cortex as compared to stimuli presented in extrapersonal space. For this reason, PPS representations are probably best described as multisensory-motor interfaces, which serve to encode the location of nearby sensory stimuli to generate suitable motor acts. The types of action that are controlled by PPS representations consist of movements of the head, arm and hand directed both towards and away from nearby stimuli. The interesting point is that the same neuron that controls hand movements on the basis of cutaneous information can also do it on the basis of visual or auditory information. Importantly, the visual receptive fields of these neurons remain anchored to the observer's body or body parts, regardless of the position of the eyes and of the body parts. This is a fundamental function because, even for very simple actions, such as avoiding a stimulus coming towards the face or the hand (see Graziano and Cooke, 2006, for a review), or reaching to grasp an object, or getting food into the mouth (see Rizzolatti et al., 1997), the motor system needs to

compute the position of the visual stimulus relative to the head, hand, or both. Thus, the body part-centered PPS representations provide an effective mechanism to guide actions directed at objects within reaching distance using different effectors. It remains unclear whether PPS representations may primarily subserve goal-directed, approaching actions toward objects (Rizzolatti et al.,

1981a, 1997), or involuntary, defensive/avoidant reactions in response to close threats (Graziano et al., 2002), although the two hypotheses are clearly not mutually exclusive (see Brozzoli et al.,

2014). One fascinating aspect is the observation that PPS representation is not only pivotal for the sensory guidance of actions, but it is also dynamically modulated by voluntary actions themselves, so that performing a reach-and-grasp movement enhances crossmodal, visual–tactile interaction in the space around the acting hand, immediately before action execution (Brozzoli et al.,

2010). This result suggests a mechanism that allows voluntary actions to structure the visual space in which they unfold, indicating dynamic and bidirectional links between PPS representations and actions (Rizzolatti et al., 1997).

7. Conclusions

We have provided an inevitably limited review of the studies into the neural and functional mechanisms underlying the representation of PPS in the brain, both in humans and monkeys. Since its introduction, the concept of a segregated representation of the space near the body, i.e., the space within grasping distance, has been an important source of several ideas and experiments. We have reviewed converging evidence from several generations of studies, including neurophysiological research in animals, as well as neuropsychological and neuroimaging works in humans. These studies reveal how the brain links somatosensory information from our body to visual and auditory signals arising from objects in the space immediately around our body, using a body part-centered frame of reference, within a network of highly interconnected frontal and parietal regions that participate in the control of movements. While most studies on PPS have ignored social information

and typically used non-biological stimuli in a neutral environment, there is currently great interest in understanding the mechanisms and neural underpinnings of how the presence of others affect our representation of the space around us.

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