

Peripersonal space: a multisensory interface for body-object interactions

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Peripersonal Space:

A multisensory interface for body-object interactions

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Abstract

Research in the last four decades has brought a considerable advance in our understanding of how the brain synthesizes information arising from different sensory modalities. Indeed, many cortical and subcortical areas, beyond those traditionally considered to be 'associative,' have been shown to be involved in multisensory interaction and integration (Ghazanfar and Schroeder 2006). Visuo-tactile interaction is of particular interest, because of the prominent role played by vision in guiding our actions and anticipating their tactile consequences in everyday life. In this chapter, we focus on the functional role that visuo-tactile processing may play in driving two types of body-object interactions: avoidance and approach. We will first review some basic features of visuo-tactile interactions, as revealed by electrophysiological studies in monkeys. These will prove to be relevant for interpreting the subsequent evidence arising from human studies. A crucial point that will be stressed is that these visuo-tactile mechanisms have not only sensory, but also motor-related activity that qualifies them as multisensory-motor interfaces. Evidence will then be presented for the existence of functionally homologous processing in the human brain, both from neuropsychological research in brain-damaged patients and in healthy participants. The final part of the chapter will focus on some recent studies in humans showing that the human motor system is provided with a multisensory interface that allows for continuous monitoring of the space near the body (i.e., peripersonal space). We further demonstrate that multisensory processing can be modulated on-line as a consequence of interacting with objects. This indicates that, far from being passive, the monitoring of peripersonal space is an active process subserving actions between our body and objects located in the space around us.

1. Multisensory and motor representations of peripersonal space

1.1. *Multisensory features of peripersonal space: Visuo-tactile interaction around the body*

The binding of visual information available outside the body with tactile information arising, by definition, on the body, allows the representation of the space lying in-between, which is often the theatre of our interactions with objects. The representation of this intermediate space has become known as “peripersonal space” (Rizzolatti et al. 1981b, c). The definition of peripersonal space (PpS hereafter) originates from single-unit electrophysiological studies in macaque monkeys, based on a class of multisensory, predominantly visual-tactile neurons. Over the years, such neurons have been identified in several regions of the monkey brain, including premotor area 6, parietal areas (Brodmann's area 7b and the ventral intraparietal area, VIP), and the putamen (Fogassi et al. 1999; Graziano 2001; Rizzolatti et al. 1997). The most relevant characteristic of these neurons, for present purposes, is that, in addition to responding both to visual and tactile stimulation (referred to here as visuo-tactile), their visually evoked responses are modulated by the distance between the visual object and the tactile receptive field (RF). This allows for the coding of visual information that is dependent, or centred, on the body part that contains the tactile RF.

Premotor visuo-tactile interactions

The most detailed series of studies on the properties of visuo-tactile neurons have been performed in the premotor cortex. Neurons in the F4 sub-region of inferior area 6 in ventral premotor cortex (Matelli et al. 1985) are strongly responsive to tactile stimulation. They are characterized by relatively large tactile RFs located primarily on the monkey's face, neck, arm, hand, or both hands and face (e.g., in the peribuccal region, Gentilucci et al. 1988; Rizzolatti et al. 1981a). A large proportion (85%) of the tactile neurons in this area

discharges also in response to visual stimuli. According to the depth of the visual RFs extending out from the body, these bimodal neurons were originally subdivided into pericutaneous (54%) and distant peripersonal neurons (46%). The pericutaneous neurons responded best to stimuli presented a few centimeters from the skin (10 cm or less, Rizzolatti et al. 1981b), whereas the distant peripersonal neurons responded to stimuli within reach of the monkey's arms. We will refer to both as 'peripersonal' visuo-tactile neurons throughout the text. Therefore, an important property of these neurons (and neurons in other PpS-related areas, see below), is that their visual RFs are limited in depth from the tactile RFs (in most cases from ~5 to ~50 cm). The visual RFs are generally independent of gaze direction (Fogassi et al. 1992; Gentilucci et al. 1983), being spatially related instead to the body-parts on which the tactile RFs are located. Moreover, when the arm is moved under the monkey's view, the visual RF follows the body-part, being 'anchored' to the tactile RF thus keeping a rough spatial match between the locations of the visual RF and the arm with every displacement (Graziano et al. 1994; Graziano et al. 1997; Figure 1).

Although less numerous, visuo-tactile neurons are present also in the rostral sub-region F5 of area 6, and have smaller tactile RFs than F4 neurons. The tactile RFs are frequently located on the face, the hand, or both. However, the visual properties of these neurons were shown to be quite different: even though stimuli presented close to the body resulted in stronger responses, the size of the stimuli appeared to be a more critical factor in driving the activity of F5 neurons (Rizzolatti et al. 1988; Rizzolatti and Gentilucci 1988).

<Insert figure 1 about here>

Parietal visuo-tactile interactions

The posterior parietal lobe of the macaque brain contains two sub-regions with visuo-tactile properties: Area 7b of the inferior posterior parietal lobe, and the ventral section of the intraparietal sulcus (VIP). As in the premotor cortex, electrophysiological studies in awake monkeys revealed that visuo-tactile integration in these areas arises at the single unit level (Hyvärinen and Poranen 1974; Hyvärinen 1981; Leinonen et al. 1979; Leinonen and Nyman 1979; Mouncastle et al. 1975; Robinson et al. 1978; Robinson and Burton 1980a, b)¹. Within area 7b, most neurons were responsive to tactile stimuli, and presented a gross somatotopic organization, with separate face, arm, and hand representations (Hyvärinen and Shelepin 1979; Hyvärinen 1981; Robinson and Burton 1980a). Within the face and arm regions of this map, visuo-tactile cells (33%) have been reported (Hyvärinen and Poranen 1974; Hyvärinen and Shelepin 1979; Hyvärinen 1981; Leinonen et al. 1979; Leinonen and Nyman 1979). What is the function of these responses? Researchers initially interpreted these visual responses as an “anticipatory activation” that appeared before the neuron's tactile receptive field (RF) was touched (Hyvärinen and Poranen 1974, page 675). Importantly, a close correspondence between the tactile and visual RFs has been documented, especially for tactile RFs on the arm (Leinonen et al. 1979). That is, these neurons' activation was shown to be dependent upon the distance of the effective visual stimulus from the body-part. Most of these neurons responded to visual stimuli moving towards the monkey, within about 10 cm of the tactile RF (although in some cases, stimulation presented further away, but still within a reachable distance, was also effective).

Multisensory neurons have also been found in the monkey area VIP, in the fundus of the intraparietal sulcus (Avillac et al. 2005; Colby and Duhamel 1991; Colby et al. 1993; Duhamel et al. 1998). VIP neurons respond to tactile and visual stimulation presented

¹ A possibly earlier report can be attributed to Sakata and colleagues' report (Sakata et al, 1973, page 100). In this study about the functional organization of area 5, the authors stated: “Even the relatively rare neurons which we could activate visually were more powerfully driven by somatosensory stimuli”. However, no further detail or discussion was offered concerning the limitation in depth of the visual RF.

within a few centimeters of the tactile RF. Unlike area 7b neurons, tactile RFs in VIP are primarily located on the face and head, and visual RFs are anchored to a region of space around the face (Colby et al. 1993).

Subcortical visuo-tactile interaction

Pools of multisensory neurons have also been found in subcortical structures of the macaque brain. The multisensory encoding of events has been well established in the superior colliculus (Stein and Meredith 1993; Wallace and Stein 2007). Such collicular activity, however, seems not to be devoted primarily to representing the space near the body (for a full discussion of the properties and functional roles of multisensory neurons in the superior colliculus, see Wallace, this volume). The putamen, on the other hand, seems to be a relevant region for the visuo-tactile processing of events in the space around the body (Graziano and Gross 1993, 1994, 1995). Visuo-tactile neurons in the putamen with tactile RFs on the arm, hand, and face are somatotopically organized. Just as for the cortical visuo-tactile neurons, the visual and tactile RFs in the putamen show a rough spatial correspondence, with the visual RFs being anchored to the tactile ones. Most of the neurons also responsive to visual stimuli, as long as they are presented close to the tactile RF. A large portion (82%) of face neurons responds best to visual stimuli presented in a region of space within 10-20 cm from the tactile RF. Neurons with tactile RFs on the arm and hand present even more shallow visual RFs around the hand (up to 5 cm, Graziano and Gross 1993).

← *A visuo-tactile network*

The neurophysiological findings described in the previous sections define a set of at least four distinctive areas with similar visuo-tactile responses: premotor inferior area 6, parietal areas 7b and VIP, and the putamen. These areas are heavily interconnected, forming a

tight network (Matelli and Luppino 2001; Rizzolatti et al. 1997; Rizzolatti et al. 1998).

Neurons in this network share some common features: 1) The visual responses lie primarily within a head-face or arm-hand centered somatosensory representation of the body; 2) Visual stimuli moving near the monkey modulate the neurons' responses stronger than farther stimuli. This suggests that these neurons allow for body-part-centered coding of visual stimuli within sectors of space adjacent to the tactile surface. This network possesses all of the necessary properties to bind together external visual information around the body and tactile information on a specific body part (Fogassi et al. 1992; Graziano and Gross 1993; Rizzolatti et al. 1997).

Dynamic features of peripersonal space representation

An important characteristic of some visuo-tactile areas is the dynamic property of their visual receptive fields. Fogassi and colleagues (Fogassi et al. 1996) found that the depth of the visual RFs of F4 visuo-tactile neurons can increase with increases in the velocity (20-80 cm/s) of a visual stimulus approaching the cutaneous RF. This property could be crucial for preparing and/or executing actions towards nearby objects. Iriki and colleagues (Iriki et al. 1996) revealed that, after training monkeys to use a rake as a tool to reach food pellets placed outside their reaching space, some neurons in the post-central gyrus (somewhat extending into the intraparietal sulcus) began to display visual responses. In addition, although concerns have been raised in this respect (Holmes and Spence 2004), such visual responses appeared to be modulated by active, but not by passive, tool-use. The newly-acquired visual RFs seemed to have expanded towards the tool-tip. A few minutes after the active tool-use, the visual RFs apparently shrank back to their original size. In other words, the dynamic aspects of the visual RF may depend on the execution of specific motor actions (Rizzolatti et al. 1998).

An interesting recent finding showed that visuo-tactile neurons within area 7b and VIP also respond when another individual's body-part is approached by a visual stimulus (Ishida et al. 2009). Similarly to the visuo-tactile neurons described above, these "body-matching neurons" respond to visual stimuli presented near the tactile RF. Moreover, the neurons are responsive to a visual stimulus presented close to the corresponding body-part of another individual (a human experimenter) being observed by the monkey. For instance, a neuron displaying a tactile RF on the arm 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. For some of these neurons, this matching property seems to be independent of the position of the observed individual with respect to the observing monkey (up to 35 degrees of rotation).

1.2. Motor features of peripersonal space: Visuo-tactile interaction around the acting body

Why should the brain maintain a representation of the space around the body separate from a representation of far extrapersonal space? One possibility is that this dichotomy stems purely from perceptual aims, giving a "greater" perceptual salience to visual events occurring in the vicinity of the body. Following this idea, the parieto-frontal network, together with the putamen, would code visual space with individual body-parts as its reference. This is suggested by the sensory properties of this set of neurons, responding selectively for visual information close to the body. However, we believe that this interpretation does not fully describe the potential functional applications of this system, since it does not correspond with some of the evidence described above. First, it may be difficult to interpret the complex tactile RFs of some of these neurons (for instance, single neurons in area F4 that represent both the hand and face, as reported by Rizzolatti et al. 1981a, b). Second, it doesn't account for the dynamic changes of their visual RFs, as observed in cases of objects approaching the body (Fogassi et al. 1996). More critically, a

purely perceptual account does not fit with the presence of such bimodal neurons in a predominantly 'motor' area, such as the premotor cortex. Numerous visuo-tactile neurons in inferior area 6 (Gentilucci et al. 1988; Rizzolatti et al. 1981c; Rizzolatti et al. 1987; Rizzolatti et al. 1988; Rizzolatti and Gentilucci 1988; Rizzolatti et al. 1997), parietal areas 7b (Hyvärinen 1981; Hyvärinen and Poranen 1974; Hyvärinen and Shelepin 1979; Leinonen 1980; Leinonen et al. 1979; Leinonen and Nyman 1979; Robinson et al. 1978), and the putamen (Crutcher and DeLong 1984) respond not only to passive visual and tactile stimulation, but also during motor activity.

These findings raise the more compelling possibility that the multisensory representation of PpS serves some motor function. Objects in the vicinity of the body are indeed more relevant by virtue of the possible interactions our body can establish with them (Graziano et al. 1993; Rizzolatti et al. 1997, 1998). Therefore, hand-centered representation of PpS provides us with extremely valuable information regarding the spatial position of objects with respect to our hands. Here follows a description of the motor aspects associated with PpS brain areas, as revealed by electrophysiological studies in macaque monkeys.

The premotor cortex has both direct (Martino and Strick 1987) and indirect (Godschalk et al. 1984; Matsumura and Kubota 1979; Muakkassa and Strick 1979; Pandya and Vignolo 1971) access to the control of upper limbs movements, via projections to the spinal cord and the primary motor cortex, respectively. The motor properties of neurons in the inferior premotor cortex support a role for this structure in a perception-to-action interface. In particular, the visual responses of some neurons within this area are enhanced when a reaching movement is performed towards an object (Godschalk et al. 1985), as well as during reaching and grasping movements of the arm and hand (Godschalk et al. 1981; Godschalk et al. 1985; Kurata et al. 1985; Kurata and Tanji 1986; Rizzolatti and Gentilucci 1988), and mouth (Rizzolatti et al. 1981c). Moreover,

neurons in this area show a rather precise degree of motor representation. Proximal and distal movements are represented separately (in areas F4/F1 and area F5, respectively), with the proximal neurons mostly activated for arm and face movements. (Gentilucci et al. 1988; Kurata and Tanji 1986; Murata et al. 1997; Raos et al. 2006; Rizzolatti et al. 1987; Rizzolatti et al. 1988; Rizzolatti and Gentilucci 1988). Crucially, the passive RFs and the active movements appear to share related functional roles: neurons with visuo-tactile RFs on the face also discharged during arm reaching movements towards the upper part of space which corresponds to its visual RF. This suggests that the sensory and motor responses are expressed in a common reference frame for locating objects in the space close to the body and for guiding movements toward them. We believe that such a complex motor mechanism cannot subserve a purely perceptual function.

Parietal area 7b also has motor properties. As in the premotor cortex, parietal motor functions seem to be related to approaching movements of a body-part toward an object (Gardner et al. 2007; Lacquaniti and Caminiti 1998; Rizzolatti et al. 1997). Indeed, the posterior parietal cortex is part of the dorsal stream of action-oriented visual processing (Milner and Goodale 1995), and both inferior and superior parietal lobules are interconnected with the premotor cortex (see above).

Ablation and reversible inactivation studies in monkeys have shown a direct relationship between the PpS network and motor responses. These studies tested for the behavioural consequences of a lesion within premotor and posterior parietal areas, where visuo-tactile neurons have been found. Interestingly, lesions to both the anterior or posterior parts of this network seem to produce very similar patterns of motor impairments, most of which affect, in particular, the execution of visually-guided reaching actions (Battaglini et al. 2002; Deuel and Regan 1985; Ettlinger and Kalsbeck 1962; Faugier-Grimaud et al. 1978; Gallese et al. 1994; Halsban and Passingham 1982; Moll and Kuypers 1977; Rizzolatti et al. 1983). After premotor ablation, for instance, the monkeys

were unable to reach when the movement required the monkey to avoid an obstacle with the contralesional arm. Arm movements were executed without correctly taking into account visual information within PpS (Battaglini et al. 2002; Moll and Kuypers 1977). Similarly, removal of postarcuate regions in the premotor cortex where the mouth is represented (presumably in area F4), caused a severe impairment in grasping with the mouth (Rizzolatti et al. 1983). Attentional deficits have also been reported after selective damage to visuo-tactile parietal and premotor regions (Rizzolatti et al. 1983) in the form of spatial hemineglect and extinction. The monkeys appeared to be unaware of visual (or tactile) stimuli presented in the contralesional space. Crucially, this deficit was selective for the space around the body.

Sub-region F5 of the inferior area 6 is also characterized by the presence of 'mirror' neurons, a special class of motor neurons with visual properties. These neurons are selective for the execution of a specific motor act, such as precision grasping. They also discharge when the monkey observes another monkey or a human executing the same action (di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 1996)². Relevant for this chapter is a recent study which showed selectivity in certain mirror neurons for actions performed within the observer's PpS rather than in its extrapersonal space (peripersonal mirror neurons, Caggiano et al. 2009). A different sub-population of mirror neurons showed the opposite preference (i.e. selectivity for actions performed in extrapersonal space, rather than PpS). Moreover, peripersonal and extrapersonal space appeared to be defined according to a functional criterion: When accessibility to PpS was limited (e.g., by placing a screen in front of the monkey), the responses of several peripersonal mirror neurons were reduced during observation of actions performed in the inaccessible portion of the space. That is, when PpS was inaccessible for action, it has been represented as

² A first report of neurons responding while the monkey was watching an action performed by another individual is already present in an early electrophysiological study over the parietal area 7b (Leinonen 1980, page 305) : « [...] two cells discharged when the monkey grasped an object [...] or when the monkey saw an investigator grasp an object »

farther extrapersonal space. Indeed, in such circumstances, extrapersonal mirror neurons started to respond to observation of actions performed in the inaccessible PpS.

1.3 *A multisensory-motor network for body-object interactions in peripersonal space*

The above reviewed studies provide a large body of indirect evidence in favour of the proposal that this parieto-frontal network binds together visual and tactile information in order to generate an appropriate motor program towards objects in the world. We would like to suggest that the occurrence of multisensory and motor processing within the same area provides an interface between perception and action.

What kind of body-object interactions can body-centered PpS representation subserve? PpS has traditionally been suggested to play a role in guiding hand actions towards objects within reaching distance (Bremmer 2005; Fogassi and Luppino 2005; Graziano 1999; Maravita et al. 2003; Maravita 2006; Rizzolatti 1987). Indeed, the evidence described above seems to support the involvement of some PpS areas in reaching and grasping. Another intriguing possibility that has recently been investigated is the involvement of the PpS network in defensive (re)actions. By acting as an anticipatory sensory-motor interface, PpS may serve for the early detection of potential threats approaching the body (Fogassi et al. 1996) in order to drive involuntary defensive movements (Cooke and Graziano 2004; Graziano and Cooke 2006). The most direct evidence in favour of this hypothesis comes from cortical electrical stimulation studies (although concerns have been raised in this respect. see Strick 2002; Graziano et al. 2002). Electrical stimulation of the ventral premotor cortex and the VIP (Graziano and Cooke 2006) has been reported to elicit a pattern of movements that is compatible with defensive arm movements and the withdrawal of the arm or the head (Cooke and Graziano 2003). However, the same anticipatory features may also have evolved to serve voluntary object-oriented actions (Gardner et al. 2007; Rizzolatti et al. 1981a, b; Rizzolatti

et al. 1997). In support of this view are the results of the described electrophysiological recording studies, showing the motor properties of both parietal and periarculate visuo-tactile neurons, whose discharges are mostly correlated with reaching and grasping movements (see paragraph 1.2). The two hypotheses (involuntary and voluntary object-oriented actions) are not mutually exclusive and one could speculate that a fine-grained and sophisticated function could have developed from a more primordial defensive machinery, using the same visuo-tactile spatial coding of the PpS (see the “neuronal recycling hypothesis” as proposed by Dehaene 2005). This hypothetical evolutionary advancement could lead to the involvement of the PpS mechanisms in the control of the execution of voluntary actions *towards* objects. Some comparative data showed, for instance, that prosimian sensory areas corresponding to the monkeys' parietal areas already present some approximate motor activity. The most represented movements are very stereotyped limb retractions that are associated with avoidance movements (Fogassi et al. 1994).

2. Multisensory based peripersonal space representation in humans

Several studies support the existence of a similar body-part centered multisensory representation of the space around the body in the human brain. In this respect, the study of a neuropsychological condition called 'extinction' (Bender 1952; Brozzoli et al. 2006) has provided considerable insight into the behavioural characteristics of multisensory spatial representation in the human brain (Làdavas 2002; Làdavas and Farnè 2004; Legrand et al. 2007). Evidence for visuo-tactile interactions is also available in healthy people, in the form of distance-modulated interference exerted by visual over tactile stimuli (Brozzoli et al. 2009a, b; Spence et al. 2004, 2008). The crucial point of these studies is the presence, both in the brain-damaged and healthy populations, of stronger visuo-tactile interactions when visual stimuli are presented in near, as compared to far space. These studies thus support the idea that the human brain also represents PpS through an integrated visuo-tactile system (Figure 2).

<Insert Figure 2 about here>

2.1 Peripersonal space representation in humans

Peripersonal space representation in neuropsychological patients

Extinction is a pathological sign following brain damage, whereby patients fail to perceive contralesional stimuli only under conditions of double simultaneous stimulation, thus revealing the competitive nature of this phenomenon (di Pellegrino and De Renzi 1995; Driver 1998; Ward et al. 1994). A number of studies have shown that extinction can emerge when concurrent stimuli are presented in different sensory modalities: A visual stimulus presented near to the ipsilesional hand can extinguish a touch delivered on the contralesional hand (di Pellegrino et al. 1997; see also Costantini et al. 2007, for an example of crossmodal extinction within a hemi-space). Crucially, such cross-modal visuo-

tactile extinction appears to be stronger when visual stimuli are presented in near as compared to far space, thus providing neuropsychological support for the idea that the human brain represents PpS through an integrated visuo-tactile system. Moreover, in accordance with the findings from the electrophysiological studies described in the previous section, visual responses to stimuli presented near the patient's hand remain anchored to the hand when it is moved to the opposite hemi-space. This evidence suggests that PpS in humans is also coded in a hand-centered reference frame (di Pellegrino et al. 1997; Farnè et al. 2003). A converging line of evidence suggests that the space near the human face is also represented by a multisensory mechanism. We demonstrated that visuo-tactile extinction can occur by applying visual and tactile stimuli on the patient's face (Farnè et al. 2005a). Interestingly, the extinction was strongest when the homologous body part was being stimulated (i.e., left and right cheeks, rather than left hand and right cheek), suggesting that different spatial regions, adjacent to different body-parts, are represented separately (Farnè et al. 2005a). In a further study, we presented four extinction patients with visual stimuli near and far from the experimenter's right hand, as well as from their own right hands (Farnè et al., unpublished data). While the visual stimulus presented near the patients' hands successfully extinguished the touch on the patients' left hand, no cross-modal extinction effect was found to support a possible body-matching property of the human PpS system. This discrepancy with the evidence reported in the electrophysiological literature might stem from the fact that we used a more radical change in orientation between the observer's own and the observed hands (more than 35 degrees, see section 1.1). Finally, we have shown that the human PpS also features plastic properties, akin to those demonstrated in the monkey: Visual stimuli presented in far space induced stronger cross-modal extinction following the use of a 38 cm rake to retrieve (or act upon) distant objects (Farnè and Làdavas 2000; see also Berti and Frassinetti 2000; Bonifazi et al. 2007; Farnè et al. 2005b, 2007; Maravita and Iriki 2004).

The patients' performance was evaluated before tool-use, immediately after a 5 minute period of tool-use, and after a further 5 to 10 minute resting period. Far visual stimuli were found to induce more severe contralesional extinction immediately after tool-use, compared with before tool-use. These results demonstrate that, while near and far spaces are separately represented, this spatial division is not defined a priori. Instead, the definition of near and far space may be derived functionally, depending upon movements that allow the body to interact with objects in space.³

Peripersonal space representation in neurotypical participants

In healthy participants, most of the behavioural evidence for the hand-centred visuo-tactile representation of near space derives from a visuo-tactile interference (VTI) paradigm. In this series of studies, participants were asked to discriminate between two locations of a tactile stimulus, while an irrelevant visual distractor was delivered at a congruent or incongruent location. The overall effect was a slowing in response times for the incongruent trials, as compared with the congruent ones (Pavani and Castiello 2004; Spence et al. 2004, 2008). More relevant here is the fact that the interference exerted when the visual distractor was presented near to as compared to far from the tactile targets. In analogy with the cross-modal extinction studies, the VTI was stronger when the visual information occurred close to the tactually stimulated body-part rather than in far space (see Spence et al. 2004, 2008, for reviews). Using the same approach, the effect of tool-use on VTI in near and far space has been studied in healthy individuals (Holmes et al. 2004, 2007a, b, 2008), with some differences in results as compared to studies conducted in neurological patients, as described above (see also Maravita et al. 2002).

³ We have recently studied the effects of tool-use on the body schema (Cardinali et al. 2009c). We have found that the representation of the body has been dynamically updated with the use of the tool. This dynamic updating of the body schema during action execution may serve as a sort of skeleton for PpS representation (for a critical review of the relationship between human PpS and body schema representations See Cardinali et al. 2009a).

Evidence for the existence of multisensory PpS is now accumulating from neuroimaging studies in healthy humans. These new studies provide further support for the homologies between some of the electrophysiological evidence reviewed above and the PpS neural mechanisms in the human brain. Specifically, brain areas that represent visual and tactile information on and near to the hand and face in body-centered coordinates have been reported to be the anterior section of the intraparietal sulcus and the ventral premotor cortex (Bremmer et al. 2001; Makin et al. 2007; Sereno and Huang 2006). These findings correspond nicely with the anatomical locations of the monkey visuo-tactile network. Moreover, recent studies have identified the superior parietal occipital junction as a potential site for representing near-face and near-hand visual space (Gallivan et al. 2009; Quinlan et al. 2007). This new evidence extends our current knowledge of the PpS neural network, and may guide further electrophysiological studies to come.

While using functional brain imaging enabled us to demonstrate that multiple brain areas in both sensory and motor cortices modulate their responses to visual stimuli based on their distance from the hand and face, it did not allow us to determine the direct involvement of such representations in motor processing. In a series of experiments inspired by the macaque neurophysiological literature, we recently examined the reference frames underlying rapid motor responses to real, three-dimensional objects approaching the hand (Makin et al. 2009). We asked subjects to make a simple motor response to a visual 'Go' signal while they were simultaneously presented with a task-irrelevant distractor ball, rapidly approaching a location either near to or far from their responding hand. To assess the effects of these rapidly-approaching distractor stimuli on the excitability of the human motor system, we used single pulse transcranial magnetic stimulation (TMS), applied to the primary motor cortex, eliciting motor evoked potentials (MEPs) in the responding hand. As expected, and across several experiments, we found that motor

excitability was modulated as a function of the distance of approaching balls from the hand: MEP amplitude was selectively reduced when the ball approached near the hand, both when the hand was on the left and on the right of the midline. This suppression likely reflects the proactive inhibition of a possible avoidance responses that is elicited by the approaching ball (see Makin et al. 2009). Strikingly, this hand-centred suppression occurred as early as 70 ms after ball appearance, and was not modified by the location of visual fixation relative to the hand. Furthermore, it was selective for approaching balls, since static visual distractors did not modulate MEP amplitude. Together with additional behavioural measurements, this new series of experiments provides direct and converging evidence for automatic hand-centered coding of visual space in the human motor system. These results strengthen our interpretation of PpS as a mechanism for translating potentially relevant visual information into a rapid motor response.

Together, the behavioural and imaging studies reviewed above confirm the existence of brain mechanisms in humans that are specialized for representing visual information selectively when it arises from near the hand. As highlighted in the previous section on monkey research, a strong binding mechanism of visual and tactile inputs has repeatedly been shown also in humans. Importantly, these converging results have refined and extended our understanding of the neural processes underlying multisensory representation of PpS. Namely, by identifying various cortical areas that are involved in different sensory-motor aspects of PpS representation, and the time course of hand-centered processing.

The tight relationship between motor and visual representation of near space in the human brain led us most recently to an intriguing question: Would the loss of a hand through amputation (and therefore the inability of the brain to represent visual information with respect to it) lead to changes in visual perception? We recently discovered that hand-amputation is indeed associated with a mild visual 'neglect' of the amputated side:

Participants with an amputated hand favoured their intact side when comparing distances in a landmark position-judgment task (Makin et al. 2010). Importantly, this bias was absent when the exact same task was repeated with the targets placed in far space. These results thus suggest that the possibility for action within near space shapes the actor's spatial perception, and emphasize the unique role that PpS mechanisms may play as a medium for interactions between the hands and the world.

A multisensory interface for body-objects interactions

Until recently, the characteristics of visuo-tactile PpS in humans had been assessed exclusively while the relevant body parts were held statically. Even the most 'dynamic' properties of PpS, such as tool-use modulation of the visuo-tactile interaction, have been studied in the static phase preceding or following the active use of the tool (Farnè et al. 2005; Holmes et al. 2007b, Maravita et al. 2002). An exception could be found in those studies showing dynamic changes of PpS during tasks such as line bisection (e.g., Berti and Frassinetti 2000), although multisensory integration was not measured in these studies. However, if the PpS representation is indeed directly involved in body-object interactions, then modulations of visuo-tactile interaction should be found without needing the use of any tools. On the contrary, the visuo-tactile interaction, or the dynamic 'remapping' of near space should be a basic, primary property that only secondarily can be generalized to tool-use (see Brozzoli et al. 2009b). In this respect, the execution of a voluntary free-hand action, for instance reaching towards an object, should induce a rapid on-line remapping of visuo-tactile spatial interactions, *as the action unfolds*. To test this hypothesis in humans, we conceived a modified version of the visuo-tactile interference paradigm (VTI) described above, where multisensory interactions were assessed also during the dynamic phases of an action. We asked a group of healthy participants to perform two tasks within each trial: The first task was perceptual, whereby participants

discriminated the elevation (up or down) of a tactile target delivered to a digit on one hand (index finger or thumb) trying to ignore task-irrelevant visual distractor presented on a target object. The second motor task consisted of grasping the target object, which was presented in four different orientations, with the index finger and thumb in a precision grip. The visuo-tactile stimulation was presented at one of three different timings with respect to the execution of the action: Either in a static phase, when the grasping hand had not yet moved; At the onset of the movement (0 ms); Or, in the early execution phase (200 ms after movement onset). When participants performed the action with the tactually stimulated hand, the VTI was enhanced (i.e., there was more interference from the visual distractor on the tactile task) as compared to the static phase (Figure 3a). This effect was even more pronounced when the visuo-tactile interaction was assessed during the early execution phase of the grasping. Crucially, if the same action was performed with the non-stimulated hand, no multisensory modulation was observed, even though both hands displayed comparable kinematic profiles (Brozzoli et al. 2009b, see Figure 3b). This result provided the first evidence that, in humans, a motor-evoked remapping of PpS occurs, which is triggered by the execution of a grasping action: As in the monkey brain (see Section 1.1 of this manuscript), the human brain links sources of visual and tactile information that are spatially separated at the action onset, updating their interaction as a function of the phase of the action. Our brain updates the relationship between visual and tactile information well before the hand comes into contact with the object, since the perceptual re-weighting is already effective at the very early stage of the action (Figure 3a and b). The finding that such visuo-tactile re-weighting was observed selectively when both perceptual and grasping tasks concerned the same hand, not only confirms the hand-centered nature of the PpS, but critically extends this property to ecological and adaptive dynamic situations of voluntary manipulative actions. Furthermore, the kinematics analysis revealed possible parallels between the motor and perceptual performances, showing that

a difference in the kinematic pattern was reflected by a difference in the perceptual domain (see Brozzoli et al. 2009b, for details).

It is worth noting that the increase in VTI that was triggered by the action, even if already present at the very onset of the movement (Figure 3a and b), kept increasing during the early execution phase. That is, an even stronger interference of visual on tactile information was revealed, as the action unfolded in time and space. This suggests that performing a voluntary action triggers a continuous monitoring of action space, which keeps 'assisting' the motor execution of the action during its whole dynamic phase.

In order to investigate more deeply the relationship between PpS remapping and the motor characteristics of the action, we tested whether different multisensory interactions might arise as a function of the required sensory-motor transformations. We would expect that action-dependent multisensory remapping should be more important whenever action performance requires relatively more complex sensory-motor transformations.

In a more recent study (Brozzoli et al. 2009a), we asked a group of healthy participants to perform either grasping movements (as in Brozzoli et al. 2009b), or pointing movements. For both movements, the interaction between task-irrelevant visual information on the object and the tactile information delivered on the acting hand increased in the early component of the action (as reflected in a higher VTI), thus replicating our previous findings. However, a differential updating of the VTI took place during the execution phase of the two action types. While the VTI magnitude was further increased during the execution phase of the grasping action (with respect to movement onset), this was not the case in the pointing action. In other words, when the hand approached the object, the grasping movement triggered stronger visuo-tactile interaction than pointing. Thus, not only a continuous updating of PpS occurs during action execution, but this remapping varies with the characteristics of the given motor act. If (part of) the remapping

of PpS is already effective at the onset of the motor program, the perceptual modulation will be kept unchanged. But in the case of relatively complex object-oriented interactions like grasping, the remapping of PpS will be dynamically updated with respect to the motor command.

3. Conclusion

The studies reviewed in this chapter uncover the multisensory mechanisms our brain uses in order to directly link between visual information available outside our body and tactile information on our body. In particular, electrophysiological studies in monkeys revealed that the brain builds a body-parts centred representation of the space around the body, through a network of visuo-tactile areas. We also reviewed later evidence suggesting a functionally homologous representation of PpS in humans, which serves as a multisensory interface for interactions with objects in the external world. Moreover, the action-related properties of PpS representation feature a basic aspect which might be crucial for rapid and automatic avoidance reactions, i.e. a hand centred representation of objects in near space. We also showed that PpS representation is dynamically remapped during action execution, as a function of the sensory-motor transformations required by the action kinematics. We therefore suggested that PpS representation may also play a major role in voluntary action execution on nearby objects. These two hypotheses (involuntary and voluntary object-oriented actions) are not mutually exclusive and one could speculate that, from a more primordial defensive function of this machinery, a more fine-grained and sophisticated function could have developed using the same, relatively basic visuo-tactile spatial computational capabilities. This development could lead to its involvement in the control of the execution of voluntary actions towards objects.

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References

- Avillac, M., Denève, S., Olivier, E., Pouget, A. and Duhamel, J.R. 2005. Reference frames for representing visual and tactile locations in parietal cortex. *Nature Neuroscience*, 8: 941-49.
- Baizer, J.S., Ungerleider, L.G. and Desimone R. 1991. Organization of visual inputs to the inferior temporal and posterior parietal cortex in macaques. *Journal of Neuroscience* 11: 168-90.
- Battaglini, P.P., Muzur, A., Galletti, C., Skrap, M., Brovelli, A. and Fattori, P. 2002. Effects of lesions to area V6A in monkeys. *Experimental Brain Research*, 144: 419-22.
- Bender, M. 1952. *Disorders in perception*. Springfield: Thomas.
- Berti, A. and Frassinetti, F. 2000. When far becomes near: remapping of space by tool use. *Journal of Cognitive Neuroscience*, 12: 415-20.
- Blangero, A. et al. 2007. Optic ataxia is not only 'optic': impaired spatial integration of proprioceptive information. *Neuroimage*, 36: T61-8.
- Bremmer, F. 2005. Navigation in space - the role of the macaque ventral intraparietal area. *Journal of Physiology*, 566: 29-35.
- Bremmer, F. et al. 2001. Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron*, 29: 287-96.
- Brozzoli, C., Cardinali, L, Pavani, F. and Farnè, A. 2009a. Action specific remapping of peripersonal space. *Neuropsychologia*, *In Press*.
- Brozzoli, C., Demattè, M.L., Pavani, F., Frassinetti, F., and Farnè A. 2006. Neglect and extinction: within and between sensory modalities. *Restorative Neurology Neuroscience*, 24: 217-32.

Brozzoli, C., Pavani, F., Urquizar, C., Cardinali, L. and Farnè A. 2009b. Grasping actions remap peripersonal space. *NeuroReport*, 20: 913-917.

Bonifazi, S, Farnè, A., Rinaldesi, L. and Ladavas, E. 2007. Dynamic size-change of perihand space through tool-use: spatial extension or shift of the multi-sensory area. *Journal of Neuropsychology*, 1: 101-114.

Boussaoud, D., Ungerleider, L.G. and Desimone, R. 1990. Pathways for motion analysis: cortical connections of the medial superior temporal and fundus of the superior temporal visual areas in the macaque. *Journal of Comparative Neurology*, 296: 462-95.

Caggiano, V., Fogassi, L., Rizzolatti, G., Thier, P. and Casile, A. 2009. Mirror neurons differentially encode the peripersonal and extrapersonal space of monkeys. *Science*, 324: 403-6.

Cappe, C. and Barone, P. 2005. Heteromodal connections supporting multisensory integration at low levels of cortical processing in the monkey. *European Journal Neuroscience*, 22: 2886-902.

Cardinali, L., Brozzoli, C. and Farnè, A. 2009a. Peripersonal Space and Body Schema: Two Labels for the Same Concept? *Brain Topography*, In Press.

Cardinali, L., Brozzoli, C. and Farnè, A. 2009b. Peripersonal space and body schema. *Encyclopedia of Behavioral Neuroscience*, In Press.

Cardinali, L., Frassinetti, F., Brozzoli, C., Urquizar, C., Roy, A. and Farnè, A. 2009c. Tool-use induces morphological up-dating of the body schema. *Current Biology*, In Press.

Castiello, U. 2005. The neuroscience of grasping. *Nature Review Neuroscience*, 6: 726-36.

Cerri, G., Shimazu, H., Maier, M.A. and Lemon, R.N. 2003. Facilitation from ventral premotor cortex of primary motor cortex outputs to macaque hand muscles. *Journal of Neurophysiology*, 90: 832-42.

- Colby, C.L. and Duhamel, J.R. 1991. Heterogeneity of extrastriate visual areas and multiple parietal areas in the macaque monkey. *Neuropsychologia*, 29: 517-37.
- Colby, C.L., Duhamel, J.R. and Goldberg, M.E. 1993. Ventral intraparietal area of the macaque: anatomic location and visual response properties. *Journal of Neurophysiology*, 69: 902-14.
- Cooke, D.F. and Graziano, M.S. 2003. Defensive movements evoked by air puff in monkeys. *Journal of Neurophysiology*, 90: 3317-29.
- Cooke, D.F. and Graziano, M.S. 2004. Sensorimotor integration in the precentral gyrus: polysensory neurons and defensive movements. *Journal of Neurophysiology*, 91: 1648-60.
- Cooke, D.F., Taylor, C.S., Moore, T. and Graziano, M.S. 2003. Complex movements evoked by microstimulation of the ventral intraparietal area. *Proceedings of the National Academy of Science, USA*, 100: 6163-8.
- Costantini, M., Bueti, D., Pazzaglia, M. and Aglioti, S.M. 2007. Temporal dynamics of visuo-tactile extinction within and between hemispaces. *Neuropsychology*, 21: 242-50.
- Crutcher, M.D. and DeLong, M.R. 1984. Single cell studies of the primate putamen. II. Relations to direction of movement and pattern of muscular activity. *Experimental Brain Research*, 53: 244-58.
- Dehaene, S. 2005. Evolution of human cortical circuits for reading and arithmetic: The “neuronal recycling” hypothesis. In *From Monkey Brain to Human Brain*, S. Dehaene, J.R. Duhamel, M. Hauser, and G. Rizzolatti, eds. (Cambridge, MA: MIT Press), pp. 133–157.
- Deuel, R.K. and Regan, D.J. 1985. Parietal hemineglect and motor deficits in the monkey. *Neuropsychologia*, 23: 305-14.
- Desmurget, M., Epstein, C.M., Turner, R.S., Prablanc, C., Alexander, G.E., and Grafton S.T. 1999. Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nature Neuroscience*, 2: 563-67.

di Pellegrino, G. and De Renzi, E. 1995. An experimental investigation on the nature of extinction. *Neuropsychologia*, 33: 153-70.

di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V. and Rizzolatti, G. 1992. Understanding motor events: a neurophysiological study. *Experimental Brain Research*, 91: 176-80.

di Pellegrino, G., Ladavas, E., and Farné, A. 1997. Seeing where your hands are. *Nature*, 21: 730.

Driver, J. 1998. The neuropsychology of spatial attention. In *Attention*, ed. H. Pashler, 297-340. Hove: Psychology Press.

Duhamel, J.R., Colby, C.L., and Goldberg, M.E. 1998. Ventral Intraparietal area of the macaque: congruent visual and somatic response properties. *Journal of Neurophysiology*, 79: 126-36.

Duffy, F.H. and Burchfiel, J.L. 1971. Somatosensory system: organizational hierarchy from single units in monkey area 5. *Science*, 172: 273-5.

Ettlinger, G. and Kalsbeck, J.E. 1962. Changes in tactile discrimination and in visual reaching after successive and simultaneous bilateral posterior parietal ablations in the monkey. *Journal of Neurology, Neurosurgery and Psychiatry*, 25: 256-68.

Falchier, A., Clavagnier, S., Barone, P. and Kennedy, H. 2002. Anatomical evidence of multimodal integration in primate striate cortex. *Journal of Neuroscience*, 22: 5749-59.

Farné, A. et al. 2003. Visuo-motor control of the ipsilateral hand: evidence from right brain-damaged patients. *Neuropsychologia*, 41: 739-57.

Farné, A., Bonifazi, S., and Ladavas, E. 2005. The role played by tool-use and tool-length on the plastic elongation of peri-hand space: A single case study. *Cognitive Neuropsychology*, 22: 408-418.

- Farnè, A., Demattè, M., and Ladavas, E. 2003. Beyond the window: multisensory representation of peripersonal space across a transparent barrier. *Journal of Physiology Paris*, 50: 51-61.
- Farnè, A., Demattè, M.L. and Ladavas, E. 2005a. Neuropsychological evidence of modular organization of the near peripersonal space. *Neurology*, 13: 1754-58.
- Farnè, A., Iriki, A., and Ladavas, E. 2005b. Shaping multisensory action-space with tools: evidence from patients with cross-modal extinction. *Neuropsychologia*, 43: 238-48.
- Farnè, A. and Ladavas, E. 2000. Dynamic size-change of hand peripersonal space following tool use. *NeuroReport*, 11: 1645-9.
- Farnè, A., Serino, A. and Ladavas, E. 2007. Dynamic size-change of peri-hand space following tool-use: determinants and spatial characteristics revealed through cross-modal extinction. *Cortex*, 43: 436-43.
- Faugier-Grimaud, S., Frenois, C. and Stein, D.G. 1978. Effects of posterior parietal lesions on visually guided behavior in monkeys. *Neuropsychologia*, 16: 151-68.
- Fogassi, L. et al. 1992. Space coding by premotor cortex. *Experimental Brain Research*, 89: 686-90.
- Fogassi, L. et al. 1996. Coding of peripersonal space in inferior premotor cortex (area F4). *Journal of Neurophysiology*, 76: 141-57.
- Fogassi, L., Gallese, V., Gentilucci, M., Luppino, G., Matelli, M. and Rizzolatti, G. 1994. The fronto-parietal cortex of the prosimian Galago: patterns of cytochrome oxidase activity and motor maps. *Behavioral Brain Research*, 60: 91-113.
- Fogassi, L. and Luppino, G. 2005. Motor functions of the parietal lobe. *Current Opinion in Neurobiology*, 15: 626-31.
- Fogassi, L., Raos, V., Franchi, G., Gallese, V., Luppino, G. and Matelli, M. 1999. Visual responses in the dorsal premotor area F2 of the macaque monkey. *Experimental Brain Research*, 128: 194-9.

Gallese, V., Fadiga, L., Fogassi, L. and Rizzolatti G. 1996. Action recognition in the premotor cortex. *Brain*, 119: 593-609.

Gallese, V., Murata, A., Kaseda, M., Niki, N. and Sakata, H. 1994. Deficit of hand preshaping after muscimol injection in monkey parietal cortex. *NeuroReport*, 5: 1525-9.

Gallivan, J.P., Cavina-Pratesi, C. and Culham, J.C. 2009. Is that within reach? fMRI reveals that the human superior parieto-occipital cortex encodes objects reachable by the hand. *Journal of Neuroscience*, 29: 4381-91.

Gardner, E.P. et al. 2007. Neurophysiology of prehension. I. Posterior parietal cortex and object-oriented hand behaviors. *Journal of Neurophysiology*, 97: 387-406.

Gentilucci, M. et al. 1988. Somatotopic representation in inferior area 6 of the macaque monkey. *Experimental Brain Research*, 71: 475-90.

Gentilucci, M., Scandolara, C., Pigarev, I.N., and Rizzolatti, G. 1983. Visual responses in the postarcuate cortex (area 6) of the monkey that are independent of eye position. *Experimental Brain Research*, 50: 464-468.

Ghazanfar, A.A. and Schroeder, C.E. 2006. Is neocortex essentially multisensory? *Trends in Cognitive Science*, 10: 278-85.

Godschalk, M., Lemon, R.N., Nijs, H.G. and Kuypers, H.G. 1981. Behaviour of neurons in monkey peri-arcuate and precentral cortex before and during visually guided arm and hand movements. *Experimental Brain Research*, 44: 113-6.

Godschalk, M., Lemon, R.N., Kuypers, H.G. and Runday, H.K. 1984. Cortical afferents and efferents of monkey postarcuate area: an anatomical and electrophysiological study. *Experimental Brain Research*, 56: 410-24.

Godschalk, M., Lemon, R.N., Kuypers, H.G., and van der Steen, J. 1985. The involvement of monkey premotor cortex neurones in preparation of visually cued arm movements. *Behavioral Brain Research*, 18: 143-57.

- Graziano, M.S.A. 1999. Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. *Proceedings of the National Academy of Science, USA*, 96: 10418-21.
- Graziano, M.S.A. 2001. A system of multimodal areas in the primate brain. *Neuron*, 29: 4-6.
- Graziano, M.S.A. and Cooke, D.F. 2006. Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia*, 44: 2621-35.
- Graziano, M.S.A. and Gandhi, S. 2000. Location of the polysensory zone in the precentral gyrus of anesthetized monkeys. *Experimental Brain Research*, 135: 259-66.
- Graziano, M.S.A. and Gross, C.G. 1993. A bimodal map of space: somatosensory receptive fields in the macaque putamen with corresponding visual receptive fields. *Experimental Brain Research*, 97: 96-109.
- Graziano, M.S.A. and Carl G. Gross. 1994. Multiple pathways for processing visual space. In *Attention and Performance XV*, eds. C. Umiltà, and M. Moscovitch, 181-207. Oxford: Oxford University Press.
- Graziano, M.S.A. and Carl G. Gross. 1995. The representation of extrapersonal space: a possible role for bimodal, visuo-tactile neurons. In *The Cognitive Neurosciences*, ed. M. Gazzaniga, 1021-34. MIT Press.
- Graziano, M.S., Hu, X.T. and Gross, C.G. 1997. Visuospatial properties of ventral premotor cortex. *Journal of Neurophysiology*, 77: 2268-92.
- Graziano, M.S., Taylor, C.S., Moore, T. and Cooke, D.F. 2002. The cortical control of movement revisited. *Neuron*, 36: 349-62.
- Graziano, M.S., Yap, G.S. and Gross, C.G. 1994. Coding of visual space by premotor neurons. *Science*. 266: 1054-7.
- Halsband, U. and Passingham, R. 1982. The role of premotor and parietal cortex in the direction of action. *Brain Research*, 240: 368-72.

Holmes, N.P., Calvert, G.A. and Spence, C. 2004. Extending or projecting peripersonal space with tools? Multisensory interactions highlight only the distal and proximal ends of tools. *Neuroscience Letters*, 372: 62-7.

Holmes, N.P., Sanabria, D., Calvert, G.A. and Spence, C. 2007a. Tool-use: capturing multisensory spatial attention or extending multisensory peripersonal space?. *Cortex*, 43: 469-89. Erratum in: *Cortex*, 2007, 43: 575.

Holmes, N.P. and Spence, C. 2004. The body schema and multisensory representations of peripersonal space. *Cognitive Processing*, 5: 94-105.

Holmes, N.P., Calvert, G.A. and Spence, C. 2007b. Tool use changes multisensory interactions in seconds: evidence from the crossmodal congruency task. *Experimental Brain Research*, 183: 465-76.

Hyvärinen, J. 1981. Regional distribution of functions in parietal association area 7 of the monkey. *Brain Research*, 206: 287-303.

Hyvärinen, J. and Poranen, A. 1974. Function of the parietal associative area 7 as revealed from cellular discharges in alert monkeys. *Brain*, 97: 673-92.

Hyvärinen, J and Shelepin, Y. 1979. Distribution of visual and somatic functions in the parietal associative area 7 of the monkey. *Brain Research*, 169: 561-4.

Iriki, A., Tanaka, M. and Iwamura, Y. 1996. Coding of modified body schema during tool use by macaque postcentral neurons. *NeuroReport*, 7: 2325-30.

Ishida H., Nakajima, K., Inase, M. and Murata, A. 2009. Shared mapping of own and others' bodies in visuo-tactile bimodal area of monkey parietal cortex. *Journal of Cognitive Neuroscience*, In press: 1-14.

Jeannerod, Marc 1988. *Motor Control: concepts and issues*. New York: Wiley J.

Jones, E.G. and Powell, T.P. 1970. An anatomical study of converging sensory pathways within the cerebral cortex of the monkey. *Brain*. 93: 793-820.

- Kurata, K. and Tanji, J. 1986. Premotor cortex neurons in macaques: activity before distal and proximal forelimb movements. *Journal of Neuroscience*, 6: 403-11.
- Kurata, K., Okano, K. and Tanji, J. 1985. Distribution of neurons related to a hindlimb as opposed to forelimb movement in the monkey premotor cortex. *Experimental Brain Research*, 60: 188-91.
- Lacquaniti, F. and Caminiti, R. 1998. Visuo-motor transformations for arm reaching. *European Journal of Neuroscience*, 10: 195-203. Review. Erratum in: *European Journal of Neuroscience*, 1998, 10: 810.
- Ladavas, E. 2002. Functional and dynamic properties of visual peripersonal space. *Trends in Cognitive Sciences*, 6: 17–22.
- Ladavas, E. and Farnè, A. 2004. Visuo-tactile representation of near-the-body space. *Journal of Physiology Paris*, 98: 161-170.
- Legrand, D., Brozzoli, C., Rossetti, Y. and Farnè, A. 2007. Close to me: multisensory space representations for action and pre-reflexive consciousness of oneself-in-the-world. *Consciousness and Cognition*, 16: 687-99.
- Leinonen, L. 1980. Functional properties of neurones in the posterior part of area 7 in awake monkey. *Acta Physiologica Scandinava*, 108: 301-8.
- Leinonen, L., Hyvärinen, J., Nyman, G. and Linnankoski, I. 1979. I. Functional properties of neurons in lateral part of associative area 7 in awake monkeys. *Experimental Brain Research*, 34: 299-320.
- Leinonen, L. and Nyman, G. 1979. II. Functional properties of cells in anterolateral part of area 7 associative face area of awake monkeys. *Experimental Brain Research*, 34: 321-33.
- Luppino, G., Murata, A., Govoni, P. and Matelli, M. 1999. Largely segregated parietofrontal connections linking rostral intraparietal cortex (areas AIP and VIP) and the ventral premotor cortex (areas F5 and F4). *Experimental Brain Research*, 128: 181-7.

Lynch, J.C., Mountcastle, V.B., Talbot, W.H. and Yin, T. C.T. 1977. Parietal lobe mechanisms for directed visual attention. *Journal of Neurophysiology*, 140: 462-89.

Makin, T.R., Holmes, N.P., Brozzoli, C., Rossetti, Y., and Farnè, A. 2009. [Coding of visual space during motor preparation: Approaching objects rapidly modulate corticospinal excitability in hand-centered coordinates.](#) *Journal of Neuroscience*, 29: 11841-51.

Makin, T.R., Holmes, N.P, and Ehrsson, H.H. 2008. On the other hand: dummy hands and peripersonal space. *Behavioral Brain Research*, 191: 1-10.

Makin, T.R., Holmes, N.P. and Zohary, E. 2007. Is that near my hand? Multisensory representation of peripersonal space in human intraparietal sulcus. *Journal of Neuroscience*, 27: 731-40.

Makin, T.R., Wilf, M., Schwartz, I., and Zoary, E. 2010. Amputees “neglect” the space near their missing hand. *Psychological Science*, In press.

Maravita, A. 2006. From body in the brain, to body in space: Sensory and intentional aspects of body representation. In *The human body: Perception from the inside out*, eds.G. Knoblich, M. Shiffrar, and M. Grosjean, 65–88..Oxford University Press.

Maravita, A. and Iriki, A. 2004. Tools for the body (schema). *Trends In Cognitive Science*, 8: 79-86.

Maravita, A., Spence, C. and Driver, J. 2003. Multisensory integration and the body schema: close to hand and within reach. *Current Biology*, 13: R531-9.

Maravita, A., Spence, C., Kennett, S. and Driver, J. 2002. Tool-use changes multimodal spatial interactions between vision and touch in normal humans. *Cognition*, 83: B25-34.

Martino, A.M. and Strick, P.L. 1987. Corticospinal projections originate from the arcuate premotor area. *Brain Research*, 404: 307-12.

Matelli, M., Camarda, R., Glickstein, M. and Rizzolatti, G. 1984a. Interconnections within the postarcuate cortex (area 6) of the macaque monkey. *Brain Research*, 310: 388-92.

Matelli, M., Camarda, R., Glickstein, M. and Rizzolatti, G. 1984b. Afferent and efferent projections of the inferior area 6 in the macaque monkey. *Journal of Comparative Neurology* 251: 281-98.

Matelli, M. and Luppino, G. 2001. Parietofrontal circuits for action and space perception in the macaque monkey. *Neuroimage*, 14: S27-32.

Matelli, M., Luppino, G, and Rizzolatti, G. 1985. Patterns of cytochrome oxidase activity in the frontal agranular cortex of the macaque monkey. *Behavioral Brain Research*, 18: 125-36.

Matsumura, M. and Kubota, K. 1979. Cortical projection to hand-arm motor area from post-arcuate area in macaque monkeys: a histological study of retrograde transport of horseradish peroxidase. *Neuroscience Letters*, 11: 241-6.

Maunsell, J.H. and van Essen D.C. 1983. The connections of the middle temporal visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey. *Journal of Neuroscience*, 3: 2563-86.

Meredith, M.A. and Stein, B.E. 1986. Visual, auditory, and somatosensory convergence on cells in superior colliculus results in multisensory integration. *Journal of Neurophysiology*, 56: 640-62.

Mesulam, M.M., Van Hoesen, G.W., Pandya, D.N. and Geschwind, N. 1977. Limbic and sensory connections of the inferior parietal lobule (area PG) in the rhesus monkey: a study with a new method for horseradish peroxidase histochemistry. *Brain Research*, 136: 393-414.

Milner, A. D. and Melvin A. Goodale. 1995. *The visual brain in action*. Oxford: Oxford University Press.

Moll, L. and Kuypers, H.G. 1977. Premotor cortical ablations in monkeys: contralateral changes in visually guided reaching behavior. *Science*. 198: 317-9.

- Mountcastle, V.B., Lynch, J.C., Georgopoulos, A., Sakata, H. and Acuna, C. 1975. Posterior parietal association cortex of the monkey: command functions for operations within extrapersonal space. *Journal of Neurophysiology*, 38: 871-908.
- Muakkassa, K.F. and Strick, P.L. 1979. Frontal lobe inputs to primate motor cortex: evidence for four somatotopically organized 'premotor' areas. *Brain Research*, 177: 176-82.
- Murata, A., Fadiga, L., Fogassi, L., Gallese, V., Raos, V. and Rizzolatti, G. 1997. Object representation in the ventral premotor cortex (area F5) of the monkey. *Journal of Neurophysiology*, 78: 2226-30.
- Murray, M.M. et al. 2005. Grabbing your ear: rapid auditory-somatosensory multisensory interactions in low-level sensory cortices are not constrained by stimulus alignment. *Cerebral Cortex*, 15: 963-74.
- Pandya, D.N. and Vignolo, L.A. 1971. Intra- and interhemispheric projections of the precentral, premotor and arcuate areas in the rhesus monkey. *Brain Research*, 26: 217-33.
- Paulignan, Y., MacKenzie, C., Marteniuk, R. and Jeannerod, M. 1991. Selective perturbation of visual input during prehension movements. 1. The effects of changing object position. *Experimental Brain Research*, 83: 502-12.
- Pavani, F. and Castiello, U. 2004. Binding personal and extrapersonal space through body shadows. *Nature Neuroscience*, 7: 14-16.
- Pisella, L. et al. 2000. An 'automatic pilot' for the hand in human posterior parietal cortex: toward reinterpreting optic ataxia. *Nature Neuroscience*, 3: 729-36.
- Prabhu, G. et al. 2009. Modulation of primary motor cortex outputs from ventral premotor cortex during visually guided grasp in the macaque monkey. *Journal of Physiology*, 587: 1057-69.
- Quinlan, D.J. and Culham, J.C. 2007. fMRI reveals a preference for near viewing in the human parieto-occipital cortex. *Neuroimage*, 36: 167-87.

- Raos, V., Umiltá, M.A., Murata, A., Fogassi, L. and Gallese, V. 2006. Functional properties of grasping-related neurons in the ventral premotor area F5 of the macaque monkey. *Journal of Neurophysiology*, 95: 709-29.
- Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G. and Matelli, M. 1988. Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Experimental Brain Research*, 71: 491-507.
- Rizzolatti, G., Fadiga, L., Fogassi, L. and Gallese, V. 1997. The space around us. *Science*, 11: 190-91.
- Rizzolatti, G., Fadiga, L., Gallese, V. and Fogassi, L. 1996. Premotor cortex and the recognition of motor actions. *Brain Res Cogn Brain Research*, 3: 131-41.
- Rizzolatti, G., and Gentilucci, M. 1988. Motor and visual-motor functions of the premotor cortex. In *Neurobiology of Neocortex*, eds. P. Rakic, and W. Singer, 269-84. John Wiley and sons Ltd.
- Rizzolatti, G., Gentilucci, M., Fogassi, L., Luppino, G., Matelli, M. and Ponzoni-Maggi, S. 1987. Neurons related to goal-directed motor acts in inferior area 6 of the macaque monkey. *Experimental Brain Research*, 67: 220-4.
- Rizzolatti, G. and Luppino, G. 2001. The cortical motor system. *Neuron*, 31: 889-901.
- Rizzolatti, G., Luppino, G. and Matelli, M. 1998. The organization of the cortical motor system: new concepts. *Electroencephalography and Clinical Neurophysiology*, 106: 283-96.
- Rizzolatti, G. and Matelli, M. 2003. Two different streams form the dorsal visual system: anatomy and functions. *Experimental Brain Research*, 153: 146-57.
- Rizzolatti, G., Scandolara, C., Gentilucci, M. and Camarda, R. 1981a. Response properties and behavioral modulation of "mouth" neurons of the postarcuate cortex (area 6) in macaque monkeys. *Brain Research*, 225: 421-4.

- Rizzolatti, G., Scandolara, C., Matelli, M. and Gentilucci, M. 1981b. Afferent properties of periarculate neurons in macaque monkeys. I. Somatosensory responses. *Behavioral Brain Research*, 2: 125-46.
- Rizzolatti, G., Scandolara, C., Matelli, M. and Gentilucci, M. 1981c. Afferent properties of periarculate neurons in macaque monkeys. II. Visual responses. *Behavioral Brain Research*, 2, 147-163.
- Robinson, D.L., Goldberg, M.E. and Stanton, G.B. 1978. Parietal association cortex in the primate: sensory mechanisms and behavioral modulations. *Journal of Neurophysiology*, 41: 910-32.
- Robinson, C.J. and Burton, H. 1980a. Organization of somatosensory receptive fields in cortical areas 7b, retroinsula, postauditory and granular insula of M. fascicularis. *Journal of Comparative Neurology*, 192: 69-92.
- Robinson, C.J. and Burton, H. 1980b. Somatic submodality distribution within the second somatosensory (SII), 7b, retroinsular, postauditory, and granular insular cortical areas of M. fascicularis. *Journal of Comparative Neurology*, 192: 93-108.
- Sakata, H., Takaoka, Y., Kawarasaki, A. and Shibutani, H. 1973. Somatosensory properties of neurons in the superior parietal cortex (area 5) of the rhesus monkey. *Brain Research*, 64: 85-102.
- Seltzer, B. and Pandya, D.N. 1980. Converging visual and somatic sensory cortical input to the intraparietal sulcus of the rhesus monkey. *Brain Research*, 192: 339-51.
- Sereno, M.I. and Huang, R.S. 2006. A human parietal face area contains aligned head-centered visual and tactile maps. *Nature Neuroscience*, 9: 1337-43.
- Shimazu, H., Maier, M.A., Cerri, G., Kirkwood, P.A. and Lemon, R.N. 2004. Macaque ventral premotor cortex exerts powerful facilitation of motor cortex outputs to upper limb motoneurons. *Journal of Neuroscience*, 24: 1200-11.

- Spence, C., Pavani, F. and Driver, J. 2004. Spatial constraints on visual-tactile cross-modal distractor congruency effects. *Cognitive Affective and Behavioral Neuroscience*, 4: 148-69.
- Spence, C., Pavani, F., Maravita, A. and Holmes, N. 2004. Multisensory contributions to the 3-D representation of visuotactile peripersonal space in humans: evidence from the crossmodal congruency task. *Journal of Physiology Paris*, 98: 171-89.
- Spence, C., Pavani, F., Maravita, A. and Holmes, N. P. 2008. Multisensory interactions. In *Haptic Rendering: Foundations, Algorithms, and Applications*, eds M.C. Lin, and M.A. Otaduy, 21-52. A K Peters Ltd., Wellesley, MA.
- Stein, Berry. E. and M.Alex Meredith. 1993. *The merging of the Senses*, Cambridge, MA: MIT Press.
- Strick, P.L. and Kim, C.C. 1978. Input to primate motor cortex from posterior parietal cortex (area 5). I. Demonstration by retrograde transport. *Brain Research*, 157: 325-30.
- Strick, P.L. 2002. Stimulating research on motor cortex. *Nature Neuroscience*, 5: 714-5.
- Ungerleider, L.G. and Desimone, R. 1986. Cortical connections of visual area MT in the macaque. *Journal of Comparative Neurology*, 248: 190-222.
- Wallace, M.T. and Stein, B.E. 2007. Early experience determines how the senses will interact. *Journal of Neurophysiology*, 97: 921-6.
- Wang, Y., Celebrini, S., Trotter, Y. and Barone, P. 2008. Visuo-auditory interactions in the primary visual cortex of the behaving monkey: electrophysiological evidence. *BMC Neuroscience*, 9: 79.
- Ward, R., Goodrich, S. and Driver, J. 1994. Grouping reduces visual extinction: neuropsychological evidence for weight-linkage in visual selection. *Visual Cognition*, 1: 101-29.

Figures captions

Figure 1: Representation of visual stimuli in hand-based coordinates.

Visual responses of a typical premotor neuron with a tactile RF (hatched) on the forearm and hand, and a visual RF within 10cm of the tactile RF. On each trial, the arm contralateral to the neuron was fixed in one of two positions: **(A)** on the right (light grey symbols and lines), or **(B)** on the left (dark grey symbols and lines) and the visual stimulus was advanced along one of four trajectories (numbered 1-4). **C.** Responses of the neuron to the four stimulus trajectories when the arm was visible to the monkey were recorded for both positions. When the arm was fixed on the right, the response was maximal for trajectory 3, which was approaching the neuron's tactile RF. When the arm was fixed on the left, the maximal response shifted with the hand to trajectory 2, which was now approaching the tactile RF. This example shows that neurons in the monkey's premotor cortex represent visual information with respect to the tactile RF.

Modified from Graziano et al. 1999.

Figure 2: Peripersonal space representation.

Head- and hand-centred peripersonal space (green areas) with respect to the reaching space (red region).

Modified from Cardinali et al. 2009b.

Figure 3. Grasping actions remap peripersonal space

A. Action induces a re-weighting of multisensory processing as shown by a stronger VTI at the action Onset (55 ms) compared to the Static condition (22 ms). The increase is even more important (79 ms) when the stimulation occurs in the early Execution phase (200 ms after action starts). **B.** Dynamics of the free hand grasping; the figure shows as schematic of estimated the position of the hand in the instant when the stimulation occurred, for the static condition (blue panel), exactly at the onset of the movement (yellow panel) or during the early execution phase (light blue panel). Wrist displacement (green trajectory) and grip evolution (pink trajectories) are shown in each panel.

Modified from Brozzoli et al. 2009.