

# Neuronal bases of peripersonal and extrapersonal spaces, their plasticity and their dynamics: knowns and unknowns

Justine Cléry, Olivier Guipponi, Claire Wardak and Suliann Ben Hamed  
*Centre de Neuroscience Cognitive, UMR5229, CNRS-Université Claude Bernard Lyon I,  
67 Boulevard Pinel, 69675 Bron, France*

**Corresponding author:** Suliann Ben Hamed, [benhamed@isc.cnrs.fr](mailto:benhamed@isc.cnrs.fr)

**Keywords:** near space; far space; peripersonal space; extra-personal space; parietal cortex; intraparietal cortex; prefrontal cortex; premotor cortex; dynamic

DOI: 10.1016/j.neuropsychologia.2014.10.022

## Abstract:

While space is perceived as unitary, experimental evidence indicates that the brain actually contains a modular representation of space, specific cortical regions being involved in the processing of extra-personal space, that is the space that is far away from the subject and that cannot be directly acted upon by the body, while other cortical regions process peripersonal space, that is the space that directly surrounds us and which we can act upon. In the present review, we focus on non-human primate research and we review the single cells, areal and cortical functional network mechanisms that are proposed to underlie extrapersonal and peripersonal space representations. Importantly, the current dominant framework for the study of peripersonal space is centered on the key notion that actions and specifically arm and hand-related actions, shape cortical peripersonal space representations. In the present review, we propose to enlarge this framework to include other variables that have the potential to shape peripersonal space representations, namely emotional and social information. In the initial section of the manuscript, we thus first provide an extensive up-to-date review of the low level sensory and oculomotor signals that contribute to the construction of a core cortical far and near space representation, in key parietal, premotor and prefrontal periarculate cortical regions. We then highlight the key functional properties that are needed to encode peripersonal space and we narrow down our discussion to the specific parietal and periarculate areas that share these properties: the parieto-premotor peripersonal space network and the parieto-premotor network for grasping. Last, we review evidence for a changing peripersonal space representation. While plastic changes in peripersonal space representation have been described during tool use and their underlying neural bases have been well characterized, the description of dynamical changes in peripersonal space representation as a function of the emotional or social context is quite novel and relies on behavioral human studies. The neural bases of such a dynamic adjustments of peripersonal space coding are yet unknown. We thus review these novel observations and we discuss their putative underlying neural bases.

## 1 INTRODUCTION

While our surrounding environment is often perceived as a unitary construct onto which we act and with which we interact, an ever growing body of neuropsychological evidence demonstrates that the brain actually contains a modular representation of space, some cortical regions being involved in the processing of extra-personal space, that is the

space that is far away from the subject and that cannot be directly acted upon by the body, while other cortical regions appear to process peripersonal space, that is the space that directly surrounds us and which we can directly interact with (figure 1).

Early lesion studies in the non-human primate (Rizzolatti et al., 1983) show that the unilateral ablation of the pre-arcuate cortex to area 8, corresponding to the frontal eye-field or



**Figure 1 :** Spaces around the body. The *peripersonal space* is the space that directly surrounds us and with which we can directly interact whereas the *extrapersonal space* is the space that is far away from the subject and that cannot be directly acted upon by the body.

FEF, results in a decrease of contralateral eye movements and a neglect in the contralateral space, that is to say a deficit in the visual processing of objects in this part of the visual field (see also Wardak et al., 2006). Interestingly, this neglect is more pronounced in the far extra-personal space and is not associated with somatosensory deficits. In contrast, post-arcuate lesions to area 6 result in a severe contralateral visual neglect, limited to peripersonal space and associated with a somatosensory neglect. This bimodal neglect in peripersonal space is also associated with a deficit in the use of the contralateral hand.

In humans, cases of neglect restricted to the near peripersonal space have been described (Berti and Frassinetti, 2000; Beschin and Robertson, 1997; Bisiach et al., 1986; Guariglia and Antonucci, 1992; Halligan et al., 2003; Halligan and Marshall, 1991; Ortigue et al., 2006), as well as cases of neglect restricted to the far extrapersonal space (Coslett et al., 1993; Cowey et al., 1994, 1999; Vuilleumier et al., 1998; Ackroyd et al., 2002; Ortigue et al., 2006), though these deficits in near and far space processing appear to depend on the

ongoing task being performed by the subjects (Aimola et al., 2013; Keller et al., 2005).

The reversible perturbation of the right angular gyrus (ANG) using transcranial magnetic stimulation (TMS) alters near space perception while that of the right supramarginal gyrus (SMG) induces a more marked deficit in far as compared to near space (Bjoertomt et al., 2002, 2009). Functional and lesion studies confirm the involvement of a dorsal network in the coding of near space in humans including the left dorsal occipital cortex, the left intraparietal cortex and the left ventral premotor cortex, and the complementary involvement of a ventral network in far space processing, including the ventral occipital cortex bilaterally and the right medial temporal cortex (Aimola et al., 2013; Weiss et al., 2000). Interestingly, in normal subjects, neural perceptual processes (e.g. a bisection judgment task) and motor processes (e.g. a manual bisection task) remain unaffected by whether the task is being performed in the near or the far space (Weiss et al., 2003). This is in agreement with the report of similar far and near space dissociations in patients whether performing a perceptual or a motor task (Pitzalis et al., 2001).

In the face of this accumulated knowledge, the precise neural bases underlying near and far space processing, the construction of extrapersonal and peripersonal space representations and their relation with perception, action and body awareness are growing at a slower pace, since the seminal monkey studies issued some 15 years ago. These early studies highlight two distinct parieto-premotor networks (Jeannerod et al., 1995; Rizzolatti et al., 1998, 2014; Sakata et al., 1998; Luppino et al., 1999; Rizzolatti and Luppino, 2001; Rizzolatti and Matelli, 2003): a parieto-premotor peripersonal space network, composed of a parietal region (area VIP, see below) and a premotor region (area

F4, see below), and a parieto-premotor network for grasping with the hand, composed of two parietal region (areas AIP and 7b, see below) and a premotor region (area F5, see below). The theoretical framework developed by the majority of these studies, when discussing these two functional networks is an action-based perspective of space. In other words, it is centered on the key construction that actions and specifically arm and hand-related actions shape cortical peripersonal space representations. In the present review, we propose to enlarge this framework to include other variables that have the potential to shape peripersonal space representations. In the initial section of the manuscript, we thus first provide an extensive up-to-date review of the low level sensory (visual -including disparity, tactile, proprioceptive) and oculomotor (vergence) signals that contribute to the construction of a core far and near space cortical representation, in key parietal and premotor and prefrontal periarculate cortical regions. In the next section, we highlight the key functional properties that are needed to encode peripersonal space and we narrow down our discussion to the specific parietal and periarculate areas that share these properties. These areas coincide with the parieto-premotor peripersonal space network and the parieto-premotor network for grasping with the hand, mentioned above. Section 4 thus provides a review of seminal data on the contribution of the peripersonal space network to the definition of a defense space, as well as more recent evident evidence on its contribution to the prediction of impact to the body and to the coding of other's peripersonal space. Likewise, section 5 provides a review of the contribution of the grasping network to goal directed hand movements in peripersonal space and to the mirroring of other's bodily movements. In all these sections, we focus on non-human primate research and we review the single cells, areal and cortical functional network mechanisms that possibly underlie the processes of interest. In the last section, we

review evidence for a changing peripersonal space representation. While such changes and their underlying neural bases have been well characterized during tool use, the description of changes in peripersonal space representation as a function of the emotional or social context is quite novel, mostly relying on human studies, and their underlying neural correlates are yet unknown. We conclude with a discussion of the putative neural mechanisms that could subserve such changes.

## **2 NEURAL BASES OF FAR VERSUS NEAR SPACE REPRESENTATION**

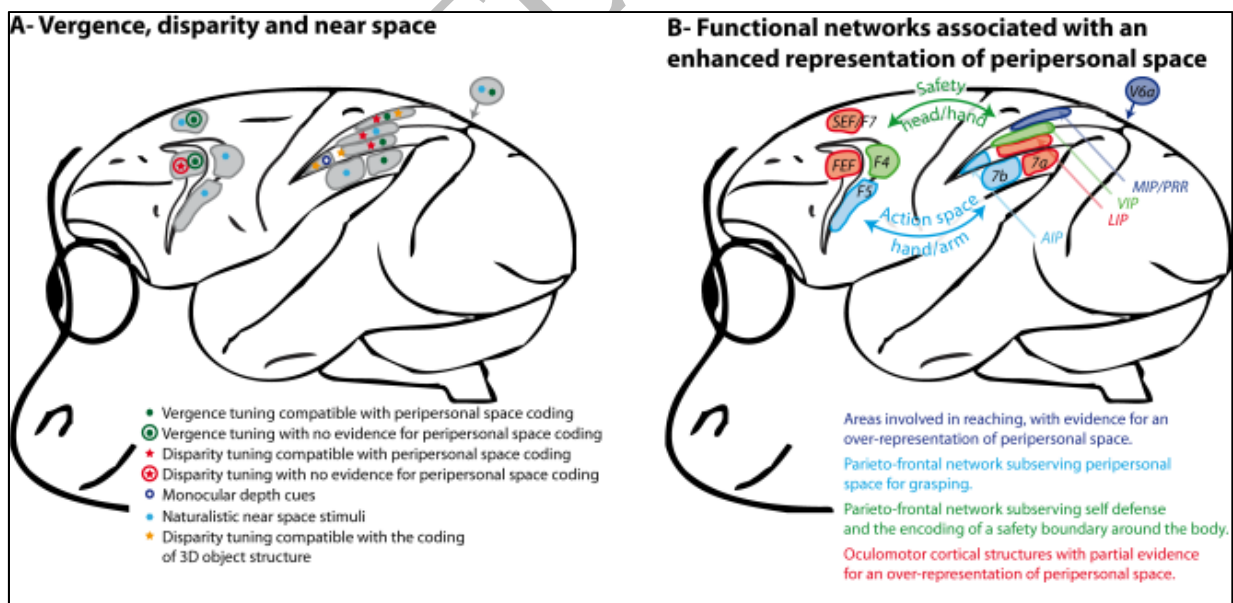
Locating a visual object with respect to our own body involves the combination of both low level and high level cues. The high level cues are based on the cognitive interpretation of what is being perceived. For example, we can infer the distance at which a lion stands from us based on its apparent size and on the prior knowledge we have of the size of an adult lion. Low level cues include both oculomotor information such as eye vergence and visual cues such as binocular disparity information. Vergence corresponds to the conjugate eye movements that allow both eyes to focus onto a given visual object. As a result, an image of this object is projected onto each fovea, at the center of each of the right and left retinas. Vergence signals, by providing the brain with information about where the eyes are fixating in space at the same time provide information about the location of the object that is being fixated. However, when we are actively fixating a specific object, we are also able to simultaneously estimate the location of a visual stimulus located in front or behind this fixated object. This estimate is constructed by combining eye vergence signals with binocular disparity information. Binocular disparity corresponds to the difference in where the image of a given object falls on the left and right retina. The binocular disparity of a fixated object is thus null. The disparity of an object that is located between

the eye convergence point and the face is negative, while that of an object located beyond the eye fixation point is positive. An early model suggests that the encoding of the spatial location of an object can be achieved through the modulation of the neuronal response of disparity selective neurons by eye vergence signals (Pouget and Sejnowski, 1994). And indeed, neuronal response modulation by vergence and disparity cues is documented in the several cortical regions which have been proposed to contribute to near and far space processing.

## 2.1 Contribution of the parietal cortex to the coding of near peripersonal and far extrapersonal space (figure 2a)

Several parietal areas contribute to an enhanced representation of near space, through diverse mechanisms. In the medial parietal area V6A (Luppino et al., 2005), a significant proportion of neurons are modulated by gaze position in 3D-space as well as by vergence signals, i.e., by the location in depth of the

visual object being foveated (Hadjidimitrakis et al., 2011, 2012; Breveglieri et al., 2012). Importantly, at the population level, the preferred fixation distances extend up to 30cm from the monkey's body, i.e. within the limits of the space that can be reached by the monkey's arm. Fixations beyond 50cm, i.e. beyond the monkey's reaching space, are also represented, but to a lesser extent. Interestingly, fixations around 45cm from the monkey's body, at the limit of the arm's reaching distance, are the least represented. The significance of this functional limit or 'gap zone' between a peripersonal reachable space and an extrapersonal unreachable space is not clear (Hadjidimitrakis et al., 2011, 2012; Breveglieri et al., 2012). A similar neuronal preference for eye fixation within the near peripersonal space is also described in other parietal areas. The majority of 7a neurons, on the cortical convexity of the inferior parietal cortex, are described to prefer fixations within 50 cm from the monkey's face (Sakata et al., 1980). The close by area 7b is dominated by the tactile modality. However, up to 30% of its



**Figure 2:** (a) Meta-analysis of evidence for low level depth cues in identified intraparietal and peri-arcuate functional areas, color coded as identified in the legend. (b) Functional networks associated with an enhanced representation of peripersonal space: areas involved in reaching (dark blue), parieto-frontal network subserving peripersonal space for action (cyan), parieto-frontal network subserving self defense and the encoding of a safety boundary around the body (green), oculomotor structures with partial evidence for an over-representation of peripersonal space (red).

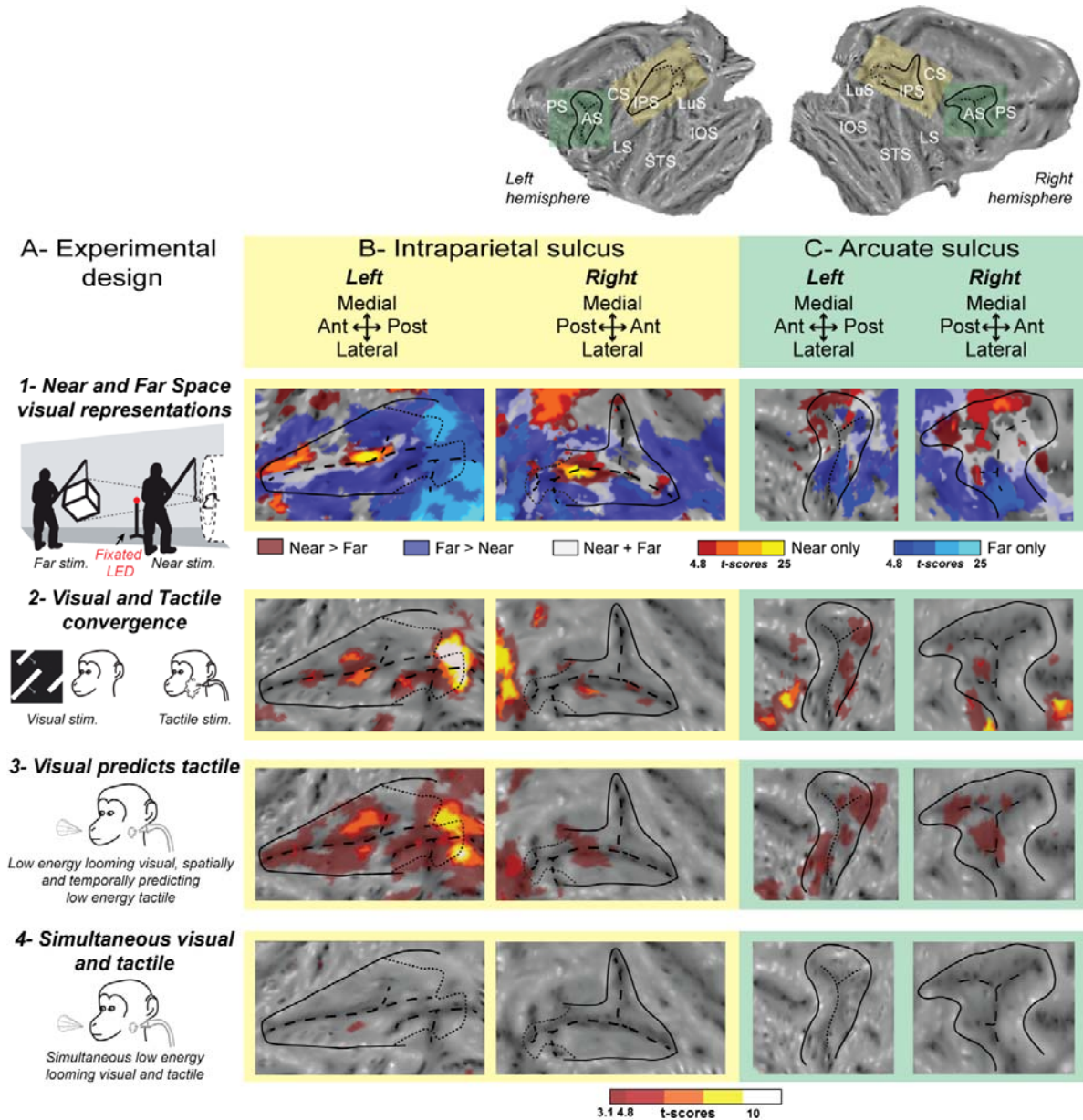
face and arm related tactile neurons also have a response to visual stimuli presented close to their tactile receptive field (Hyvärinen and Shelepin, 1979; Hyvärinen, 1981). A preference for peripersonal space is additionally described in lateral intraparietal area LIP, lying on the lateral bank of the intraparietal sulcus IPS and characterized by an enhanced central visual field representation (Ben Hamed et al., 2001). Indeed, 72.5% of LIP neurons have a higher discharge rate for fixations in the near peripersonal space (Genovesio and Ferraina, 2004; Gnadt and Mays, 1995). These neurons also have higher discharge rates for disparities corresponding to visual stimuli presented between the monkey and the fixated spatial location, i.e. presented in the near peripersonal space (Genovesio and Ferraina, 2004). A similar preferential coding of the portion of space closest to the monkey can also be found on the medial bank of the IPS, in medial intraparietal area MIP or parietal reach region PRR (Bhattacharyya et al., 2009). This correlates with an alignment of disparity tuning curves and gain modulation by vergence angle during the preparation of arm reaching movement can be seen. Last, a preferential coding for moving visual stimuli in near peripersonal space is described in the ventral intraparietal area VIP, using either natural object presentations (Colby et al., 1993) or stereoscopic visual presentations allowing for a quantification of binocular disparity information during a fixed-vergence design (Yang et al., 2011; Bremmer et al., 1997, 2013) (figure 2)

A recent fMRI study in the non-human primate, designed to investigate the coding of 3D visual shape, allows to capture how the intraparietal cortex encodes disparity information in the  $\pm 0.6^\circ$  range (Durand et al., 2007). The authors show a change in the hemodynamic signals as a function of the position of the presented visual stimuli in depth in the anterior part of lateral intraparietal area LIP, in caudal intraparietal area CIP, in

medial lateral area MIP/PRR, as well as in posterior parietal area PIP, matching observations from the same group in humans (Durand et al., 2009). In these parietal regions, this coding of position in depth is often associated with the coding of the 3D structure of complex objects. In contrast, in anterior parietal area AIP, the coding of 3D structure is present (Durand et al., 2007; Srivastava et al., 2009; Verhoef et al., 2010; Theys et al., 2012), in the absence of a coding of the position of visual stimuli in depth (Durand et al., 2007). Most interestingly, the majority of AIP neurons remained selective for 3D objects in the absence of disparity cues, indicating that 3D structure was partially extracted from monocular depth cues (Romero et al., 2013). A significant proportion of AIP neurons also express short latency, low visual selectivity responses to 2D object fragments containing a particular curvature (Romero et al., 2014). These responses are highly dependent upon the location of the visual stimuli within the neuron's receptive field (Romero et al., 2014). All this taken together suggests that AIP might be more interested in object fine structure rather than in its actual position in space, thus possibly challenging the contribution of this cortical region in extracting object affordances that can further be used to program and execute appropriate grip (Romero et al., 2014). Notably, in adjacent area VIP, Durand et al. (2007) do not describe any disparity-related fMRI activations, contrasting with Bremmer et al., 2013. This is most probably due to the fact that while Durand et al. (2007) manipulated disparities in the order of  $\pm 0.6^\circ$ , Bremmer et al. (2013) report that about 60% of VIP cells preferred near space disparities of  $-2^\circ$  or below (see next paragraph).

While most of the above cited studies highlight a preferential encoding of near peripersonal space, they nonetheless often describe a simultaneous though weaker encoding of far space. In a recent monkey fMRI study (Cléry et al, ongoing work), we





**Figure 3:** fMRI mapping of the contribution of the intraparietal and periaucate cortex to peripersonal and extrapersonal space coding, in a representative non-human primate individual. Top panel: flattened representation of the cortex, obtained with Caret (left and right hemispheres of individual monkey). The yellow inset corresponds to the IPS and the green inset corresponds to the AS, as represented in (B) and (C). Black solid lines indicates the limit between the convexity and the banks of the IPS and AS; black dashed lines indicate the bottom of the sulcus and black dotted line, the projection on the flat map of the most posterior coronal section of the IPS, just before the annectant gyrus. AS, Arcuate sulcus; CS, central sulcus; IOS, inferior occipital sulcus; IPS, intraparietal sulcus; LS, lateral sulcus; LuS, lunete sulcus; PS, principal sulcus; STS, superior temporal sulcus. (A) Experimental design for each study : 1) Neural bases of near and far space visual representations; 2) Neural bases of visual and tactile convergence; 3) Neural consequences of prediction of impact to the face by visual looming stimulus over tactile-related activation; 4) Neural consequences of simultaneous visual and tactile presentations. (B) Parietal cortical activations presented on the flattened IPS (yellow inset in the whole brain flat maps presented in the top panel). (C) Periaucate cortical activations presented on the flattened AS (green inset in the whole brain flat maps presented in the top panel). On all maps, colors represent t-score scales as indicated by the legends. In study 1, all t-scores are at FWE-corrected level ( $p < 0.05$ ). In studies 2 to 4, t-scores are color-coded from 3.1 uncorrected level ( $p < 0.001$ ) to above FWE-corrected level ( $p < 0.05$ ).

identify only few parietal loci representing near space to the exclusion of far space (figure

3, horizontal panel 1). Specifically, we use moving naturalistic cubes of identical angular

(apparent) size to stimulate either the far space (1.5 m away from the monkey's face) or the near space (15 cm from the monkey's face), while the monkeys are fixating an LED placed at an intermediate location (90 cm from their face, fixation being controlled with a video eye tracker, fixation window of 2°, figure 3a1). As a result, this study involved a larger disparity range than those manipulated in Durand et al., (2007). Posterior and medial to the intraparietal sulcus, the upper most medial portion of area V6A selectively encodes visual objects presented in the near peripersonal space (not shown). Within the intraparietal sulcus (IPS), a selective coding for near peripersonal space can be seen in ventral intraparietal area VIP (figure 3b1, red to yellow), matching Bremmer et al. (2013). Interestingly, this selective near space representation does not encompass the entire VIP, but nicely coincides with the VIP visuotactile convergence patches as identified with full strength tangential moving bars and full strength airpuff tactile stimulations to the perioral skin (figure 3b2, Guipponi et al., 2013a). Note that none of these two experimental contexts (figure 3b1, far vs. near space stimulation; figure 3b2, visual and tactile convergence as identified from full strength sensory stimulations) lead to lateral bank LIP activations, indicating that our observations are not confounded by microsaccades, nor to medial bank activations, indicating that our observations are not confounded by blinks (Guipponi et al., 2014). In comparison, the fundal cortex surrounding these patches appears to equally represent near and far spaces (figure 3b1, white) and the posterior medial intraparietal bank as well as a large extent of the lateral intraparietal bank preferentially represents far space (figure 3b1, blue). Overall, this fMRI study captures the extent of parietal cortex dedicated to near space and far space processing respectively. It highlights the fact that there is actually a strong overlap between the near and far space encoding networks. These overlapping

representations are possibly at the origin of the construction of a unitary perceived space representation. However, how this is precisely achieved is yet unclear. A precise analysis of how vergence signals interact with disparity signals for space representation can potentially shed light of this question as well as account for the apparent partial discrepancy between these fMRI observations in the lateral and medial banks and the above cited single cell recording studies.

In humans, Quinlan and Culham (2007) show a strong overrepresentation of peripersonal space in the dorsal parieto-occipital sulcus (dPOS), in a region possibly corresponding to the human homolog of area V6A (Pitzalis et al., 2013). In this study, subjects viewed looming and receding moving visual stimuli presented close to their face (moving in the range of 13 to 17 cm from the face), at an intermediate distance from their face (moving in the range of 33 to 43 cm from the face) or far away (moving in the range of 73 to 95 cm from the face). In dPOS, BOLD contrast increased for closer stimuli. Interestingly, this was not the case in the putative hVIP, which was activated by moving stimuli irrespectively of their distance from the face. This suggests that while near space representation in dPOS strongly relies onto vergence signals, the VIP neurons might actually rely on the combination of several depth cues, including disparity, as described by Bremmer et al. (1997, 2013) and in our fMRI study on near and far space representations.

Overall, while there is clearly a growing understanding of how near and far spaces are encoded in the parietal cortex, we are still missing a systematic fine grained parametric analysis of how oculomotor vergence and sensory disparity signals interact, in a spatial range encompassing extremely close visual stimuli and far away an reachable stimuli, applied to the entire parietal cortex at the same time. Likewise, it would be

interesting to further understand how higher level cues interact with vergence and disparity signals to construct a representation of space. Durand et al. (2007) have used such an approach to explore how objects are encoded in 3D. A similar approach could be extended to the analysis of space representation at large. Our ongoing Cléry et al. is an initial step in this direction. In particular, it would be of high interest to substantiate the notion of “gap zone” functionally delimiting far space from peripersonal space.

## 2.2 *Contribution of the premotor and prefrontal cortex to the coding of near peripersonal and far extrapersonal space (figure 2a)*

Similarly to what has been described in the parietal cortex, several premotor and prefrontal cortical regions demonstrate a preferential coding for near peripersonal space. As discussed previously, post-arcuate lesions to area 6, including areas F4 and F5, result in a severe contralateral visual neglect, limited to peripersonal space. Correlating with these observations, the neurons of area F4 essentially represent visual objects located in the peripersonal space (Rizzolatti et al., 1981; Gentilucci et al., 1988; Graziano et al., 1994; Gross and Graziano, 1995; Fogassi et al., 1996). Specifically, these neurons can be divided into pericutaneous neurons (54%), responding to visual stimuli presented in the close vicinity (a few centimeters) of the skin and distant peripersonal neurons (46%), responding to visual stimuli presented at a distance from the skin, within the animal's reaching distance (Rizzolatti et al., 1981). Interestingly, the visual receptive fields of these neurons are independent of the position of the eyes or the body and remain anchored to a specific body part. For example, a neuron responding to a visual object presented close to the right hand when the arm is stretched away from the body will continue to respond to a visual stimulus presented close to the right hand even if the arm is held close to the chest,

(Graziano et al., 1994; Fogassi et al., 1996; Gentilucci et al., 1983). These neurons essentially represent the near peripersonal space around the face and the arms (for review, Rizzolatti et al., 1997, 2002). Adjacent area F5, along the inferior branch of the arcuate sulcus, contains highly overlapping movement representations of the hand and mouth, as revealed by electric stimulation studies (Rizzolatti et al., 1988; Hepp-Reymond et al., 1994). Accordingly, the neurons of this premotor cortical region respond to hand-grasping both in the light and in the dark and 50% of these neurons additionally presentation 3D graspable visual objects (Murata et al., 1997; Rizzolatti et al., 1988; Raos et al., 2006). These F5 neurons, called ‘canonical’ neurons have a visual selectivity that matches their motor selectivity, responding best to the object that calls for their preferred hand-grasping configuration (Murata et al., 1997; Raos et al., 2006). Following the inactivation of F5, the hand shaping that relies on the visual properties of the object to be grasped is disrupted (Fogassi et al., 2001). In relation with the scope of the present review, the visual response of F5 neurons is selective of near peripersonal space though their response mostly relies on whether the viewed object is graspable or not (operational quality) rather than on their distance from the body (Bonini et al., 2014). In the peri-arcuate cortex facing area F4, across the arcuate sulcus, the neurons of the frontal eye field (FEF, area 8) are also modulated by the distance at which a visual object is presented. Specifically, a prefrontal cortical region just anterior to the saccadic FEF is modulated by eye vergence (Gamlin and Yoon, 2000; Akao et al., 2005; Alkan et al., 2011). In addition, the FEF neurons are modulated by binocular disparity (Ferraina et al., 2000). However, none of these studies on pre-arcuate cortex functions highlight a preferential encoding of near or far extrapersonal space, in contrast with the description of a more pronounced visual neglect in the far extra-personal space



following a lesion of this pre-arcuate cortex than in near peripersonal space (Rizzolatti et al., 1983).

The same monkey fMRI study as cited above (Cléry et al., ongoing work, figure 3, horizontal panel 1) provides additional information on near and far space representation around the arcuate sulcus (figure 3c1). Within the upper branch of the arcuate sulcus, we describe stronger activations for near visual stimuli than for far visual stimuli including the premotor convexity (dorsal premotor areas F2 and F7, figure 3c1, red), and the prefrontal dorsal convexity (the medial portion of the FEF and area 46p, figure 3c1, red). A clear bilateral activation selective to the near visual space stimulation at the exclusion of the far space stimulation can be seen in area F7, at a location compatible with the supplementary eye field SEF (not shown). The SEF is described to encode oculomotor information in a diversity of frames of references, ranging from eye- to head- to space/body (Martinez-Trujillo et al., 2004) to object-centered frame of reference (Olson and Gettner, 1995; Olson, 2003). Vergence-related activations have been described in the SEF (Alkan et al., 2011), these activation being stronger for predictive vergence than random vergence (Alvarez et al., 2010) behavior. But to our knowledge, the specific contribution of this area to near space processing has not been documented yet. A second bilateral activation specific to the disparity induced by near visual space stimulation can be seen on the posterior bank of the arcuate sulcus, across from the FEF, at a location compatible with F4 (figure 3c1, red). This postarcuate preferential near space representation is surrounded by cortex that equally represents near and far spaces (figure 3c1, white). In comparison, a preferential far space representation is observed at the tip of the lower branch of the arcuate sulcus, the inferior premotor convexity (lateral F5), as well as the prefrontal ventral convexity (figure

3c1, blue).

### 3 *MULTIMODAL PERIPERSONAL SPACE REPRESENTATIONS.*

As discussed in the introduction, peripersonal space corresponds to the space that surrounds our body at the frontier with our skin. Bimodal visuo-tactile neurons responding both to tactile stimulations to the skin and to visual stimulations in the near space are suggested to be at the origin of this peripersonal space representation, as reviewed by others (Brozzoli et al., 2012; Ladavas and Farn , 2004). A parieto-premotor network appears to play a crucial role in this peripersonal space representation. Indeed, amongst the several cortical areas discussed above as having an enhanced representation of peripersonal space, only few have neurons with these specific response properties underlined above. Peripersonal neurons firing both when a tactile stimulus is delivered to the animal’s skin and when a visual stimulus is presented in the space near the part of the body where the tactile field is located can be found in two key parietal cortical areas. First, in the ventral intraparietal area VIP, which is a site of audio-visuo-tactile convergence in both humans (Bremmer et al., 2001) and non-human primates (Colby et al., 1993; Duhamel et al., 1998; Guipponi et al., 2013a), as well as a site of multisensory integration (Avillac et al., 2004, 2005, 2007). VIP neurons encode visual information in a gradient of eye- to head- frame of reference (Duhamel et al., 1997; Avillac et al., 2005), while tactile stimuli are encoded in a stable, unique head-centered frame of reference (Avillac et al., 2005). As a result, in a fraction of VIP neurons, the visual and tactile receptive fields spatially match irrespectively of eye position. For the remaining neurons, the relationship between the visual and tactile receptive fields depended on gaze direction. Visuo-tactile neurons can also be found in parietal area 7b. This area presents a coarse somatotopic organization,

with a face representation on the upper inferior parietal convexity, at the border with area 7a. Lateral, along the inferior parietal convexity, and adjacent to this face representation comes an arm and hand followed by a foot representation (Hyvärinen and Shelepin, 1979; Hyvärinen, 1981; Robinson and Burton, 1980). In the face and arm region of 7b, about 33% of the cells are described as bimodal, their visual receptive fields spatially matching their tactile receptive fields (Hyvärinen and Poranen, 1974; Hyvärinen and Shelepin, 1979; Hyvärinen, 1981; Leinonen et al., 1979; Leinonen and Nyman, 1979). Peripersonal neurons can also be found in the premotor cortex, both in areas F4 and F5, in rostral area 6 (Gentilucci et al., 1988; Rizzolatti et al., 1988; Graziano et al., 1994; Gross and Graziano, 1995; Fogassi et al., 1996). This multisensory convergence in ventral premotor cortex is also observed in humans (Bremmer et al., 2001), corroborating the somatosensory neglect observed following premotor area 6 lesions (Rizzolatti et al., 1983).

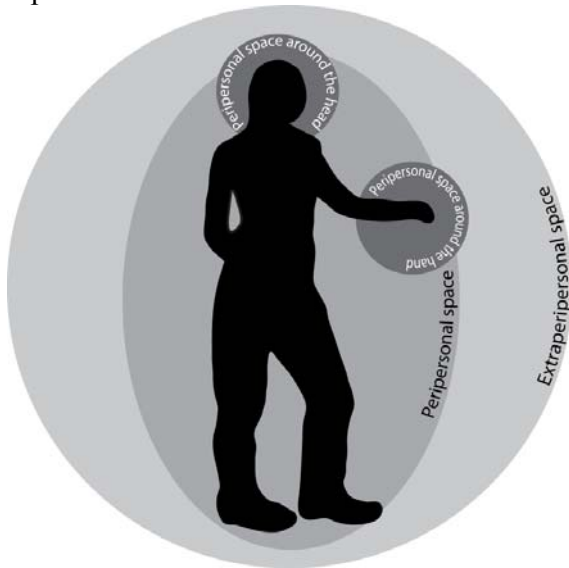
In addition to their bimodal visuo-tactile response selectivities, the ventral premotor cortex F4 and F5 and the parietal areas VIP and 7b share important functional characteristics in relation with space and self-motion processing. For example, both premotor areas F4 and F5 (in humans, Bremmer et al., 2001; in monkeys, figure 3c2 Guipponi et al., 2013b) and parietal area VIP (Bremmer et al., 2001, in monkeys, 1999, 2000, 2002a; Guipponi et al., 2013a) are activated by large field optic flow stimulations eliciting a percept of relative motion of the subject with respect to the surrounding environment. Area VIP is activated by vestibular stimulations, contributing to the representation of the subject's displacement in its environment (Chen et al., 2011a, 2011b, 2013; Bremmer et al., 2002b; Akbarian et al., 1993). Vestibular projections to premotor cortex are also described, though they appear to be restricted, to the monkey area 6pa,

coinciding with area F5 (Akbarian et al., 1993, 1994). Last, the tactile receptive fields of both cortical regions preferentially represent the face and more so the peri-oral region of the face or the arm and hand. Face representation is more marked in areas VIP (Colby et al., 1993; Duhamel et al., 1998) and F4 (Graziano et al., 1994, 1997; Fogassi et al., 1996; Gentilucci et al., 1983) while arm representation is more marked in areas 7b (Hyvärinen and Shelepin, 1979; Hyvärinen, 1981; Robinson and Burton, 1980) and F5 (Murata et al., 1997; Rizzolatti et al., 1988; Rizzolatti and Luppino, 2001; Raos et al., 2006). As a result, two distinct functional circuits subserving peripersonal space representation can be distinguished, as described below.

#### **4 *DISTINCT, BUT FUNCTIONALLY COUPLED VIP HEAD-CENTERED AND F4 ARM-CENTERED PERIPERSONAL SPACES.***

The first peripersonal space representation circuit is formed by parietal area VIP and premotor area F4 (figure 2b, Rizzolatti and Luppino, 2001; Matelli and Luppino, 2001). Importantly, in spite of their strong anatomical connections and functional homologies, a key functional difference needs to be highlighted between these two cortical regions. The visual information in F4 is anchored to the limbs. As a result, both the tactile and the visual receptive fields of F4 neurons match each other, irrespectively of eye position and the location of the object in space (Graziano et al., 1994). As discussed above, in area VIP, visual and tactile information matches for a significant fraction of VIP neurons, essentially representing the near space around the face and head. For the remaining neurons, the spatial position of the VIP visual receptive fields is influenced by the gaze (Duhamel et al., 1997; Avillac et al., 2005). The tactile and visual receptive fields match is essentially described for VIP neurons

representing the peripersonal space around the head (Duhamel et al., 1997). As a result, F4 visual information is anchored onto the arm/hand while in VIP, visual information is anchored to the head (figure4). Interestingly, a recent study (Chen et al., 2014) describes that, under large-field, multi-patch, random-dot motion visual stimulations, virtually all VIP neurons represented visual information in an eye centered and not in a head centered frame of reference. This contrasts with the seminal Duhamel et al. (1997) observations, suggesting that the spatial reference frames of visual responses in VIP may depend on the visual stimulation conditions, i.e. on the ongoing sensory context, thus hinting towards a context-dependent, dynamic space representation.



**Figure 4:** Head and arm/hand peripersonal spaces have a privileged representation as compared to the rest of the body.

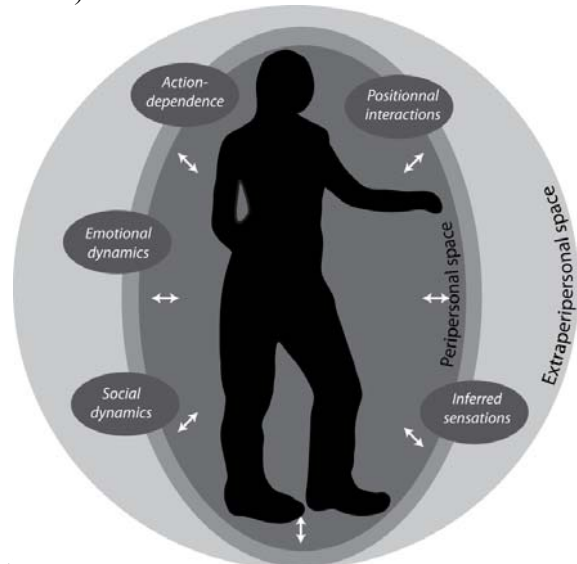
#### 4.1 *Defense, avoidance and margin of safety around the body.*

The VIP-F4 network thus processes all the necessary information to bind together the localization of objects around our body, and specifically around the head, with actions towards these objects. Specifically, VIP represents the relative movement between the environment or its sub-elements and the

subject's the body, while it does not encode the 3D structure of objects in the vicinity of the body (Durand et al., 2007). This contrasts with adjacent anterior intraparietal area AIP, whose neurons discharge during the fixation of graspable objects, during their grasping both in the light and in the dark (Sakata and Taira, 1994; Murata et al., 2000), as well as to the fine 3D structure of close by graspable objects (Durand et al., 2007). As a result, one can hypothesize that VIP's function is more about perceiving and locating objects in space than providing F4 with information about how to grasp them. In this context, electrical microstimulation studies provide insight about a possible functional role of this parieto-premotor VIP-F4 network. Specifically, the electrical microstimulation of area VIP produces eye blinking and squinting (this in spite of the fact that spontaneous eye blinks do not activate fundal IPS, Guipponi et al., 2014), ear folding back against the head and shoulder shrugging (Thier and Andersen, 1998), as well as lifting the upper lip in a face grimace, the retraction of the face from the contralateral side of space and the lifting of the contralateral arm and movement of the hand into lateral or upper lateral space (Cooke and Graziano, 2003; Graziano et al., 2005; Stepniewska et al., 2005), a movement repertoire that is also observed following air puffs delivered to the face (Cooke and Graziano, 2003; Graziano and Cooke, 2006). In F4, at sites with visual and tactile receptive fields encoding peripersonal space close to the head, a similar motor repertoire as that observed in VIP is also elicited by electrical microstimulations (Cooke and Graziano, 2004; Graziano et al., 2002; Graziano and Cooke, 2006). At sites with visual and tactile receptive fields encoding peripersonal space close to the arm or hand, fast withdrawal of the hand to a protective posture behind the back is elicited (Cooke and Graziano, 2004; Graziano et al., 2002; Graziano and Cooke, 2006). However, mirroring the distinct functional response properties of these two regions, distinct

contributions of area VIP and area F4 to defense and avoidance seem to co-exist, as highlighted by the comparative electrical microstimulation study performed by Graziano and colleagues (Cooke and Graziano, 2004; Graziano et al., 2002; Graziano and Cooke, 2006). While the above described motor repertoire could be elicited from the premotor cortex with thresholds as low as  $20\mu\text{A}$ , both in the awake and anesthetized monkey, in the parietal cortex, current intensities of  $100\mu\text{A}$  or more had to be used and the frequency and amplitude of this motor repertoire were greatly reduced by anesthesia. Another important difference needs to be highlighted. The electrical microstimulation of F4 systematically disrupts ongoing behavior (by the above described motor repertoire), but this ongoing behavior is abruptly resumed when the stimulation is interrupted. In VIP, the evoked defensive repertoire often diminishes over repeated electrical stimulation trials, indicating an adaptation to the stimulation. In addition, the complex movement pattern generated by the stimulation continues after the end of the stimulation (i.e. the monkey does not abruptly resumes the behavior it was performing prior to the stimulation), possibly indicating that the percept at the origin of the motor response is still active (Graziano and Cooke, 2006). Overall, these observations suggest a contribution of this VIP-F4 network to defense and obstacle avoidance behavior, the parietal pole of this network being more involved in the construction of a perception of the environment anchored to the head, and the premotor pole being more involved in the production of reflexive, rapid, complex defensive motor patterns aimed at protecting the body by producing defensive (e.g. closing of the eye lid, lifting the arm/hand in front of the head) or avoidance responses (moving the head away to the side, retrieving the arm and placing it behind the back). In other words, this network is proposed to sub-serve the representation and protection of near peripersonal space or safety margin around the

body, with a specific emphasis on two vulnerable body parts, the head and the arm/hand unit (figure 5, Graziano and Cooke, 2006).



**Figure 5:** The boundary between far and near space representations is plastic and dynamic, under the influence of a variety of endogenous and exogenous factors.

#### 4.2 *Looming stimuli and the dynamic intrusion into the peri-personal safety margin.*

When considering the concept of a safety margin, stable stimuli close to our body (e.g. a tree, a cup) do not have the same ecological significance as dynamic stimuli looming towards us. Indeed, looming stimuli are potentially more dangerous than other visual stimuli, including dynamic stimuli with no predicted impact to the body. Think in this respect of a predator or an aggressive conspecific jumping on us, or of a branch coming onto us at high speed. Such looming stimuli are known to trigger stereotyped defense responses (in monkeys: Schiff et al., 1962; in human infant: Ball and Tronick, 1971). Interestingly, threatening looming stimuli are perceived as having a shorter time-to-impact latency as compared to non-threatening objects moving at the same objective speed (Vagnoni et al., 2012). In a recent study (Ben Hamed et al., 2013), we

show that tactile sensitivity is enhanced at the predicted location and predicted time of impact of a looming visual stimulus to the face as compared to 1) baseline tactile sensitivity (average increase in  $d' = 0.44$ ,  $n=10$ ,  $p<0.01$  at corrected level), 2) the tactile sensitivity observed when the looming stimulus is temporally predictive but not spatially predictive (average increase in  $d' = 0.25$ ,  $n=10$ ,  $p<0.01$  at corrected level), and 3) the tactile sensitivity observed when the looming stimulus is spatially predictive but presented during the looming stimulus rather than at its expected time of impact (average increase in  $d' = 0.20$ ,  $n=10$ ,  $p<0.05$  at corrected level). Tactile perception is also enhanced as compared to baseline tactile sensitivity when the looming stimulus brushes past the face without however predicting an impact to the face (average increase in  $d' = 0.75$ ,  $n=10$ ,  $p<0.001$ ). This suggests a cross-modal processing of visual stimuli potentially impacting the face.

Interestingly, and in direct relation with these observations, the visual response occasionally observed in parietal tactile neurons (and more generally in bimodal visuo-tactile neurons) was initially interpreted as an “anticipatory activation”, predictive of touch in the corresponding skin (Hyvärinen and Poranen, 1974). Amongst the several areas discussed above as hosting bimodal neurons, the selectivity of VIP and F4 neurons appears as optimally tuned for the detection of dynamic looming visual stimuli (Colby et al., 1993; Bremmer et al., 2002a, 2002b; Rizzolatti et al., 1981; Graziano et al., 1997), corroborating their possible role in the definition of a border-of-self safety zone. Accordingly, in a recent non-human primate fMRI experiment (figure 3, horizontal panels 3 and 4, Cléry et al., 2013, 2014), we present low luminosity looming stimuli predicting an impact to the face while monkeys fixated a central fixation point. These degraded visual looming stimuli were either presented on their

own, or in conjunction with a very weak tactile stimulus (air puff), either in temporal coincidence with the looming visual stimuli (figure 3, horizontal panel 4) or in temporal offset, such that the visual stimuli are actually predicting the tactile stimuli (which are thus presented at the predicted time of impact of the looming stimulus to the face, figure 3, horizontal panel 3). This experiment is designed to identify the cortical sites that are maximally activated by the predictive bimodal stimuli. These robustly include striate and extrastriate visual cortical sites (not shown). Areas VIP (figure 3b3) and F4 (figure 3c3) are also robustly activated, bilaterally. Most importantly, these activations are systematically significantly higher when the looming stimulus is predictive of the tactile stimulus than when these two stimuli are presented simultaneously, a condition which hardly elicits any parietal (figure 3b4) or periarculate activation (figure 3c4). Overall, these observations indicate that the peripersonal defense network described above is also involved in the prediction of intrusive impact prediction to the body. In addition, they strongly suggest that this parietal premotor VIP-F4 network, most probably belongs to a larger functional network involving lower level visual areas.

#### 4.3 *The parieto-premotor VIP-F4 network and social cognition.*

Ishida et al., (2010) describe, in parietal area VIP, “body-matching neurons” that respond to visual stimuli presented near a specific body part of the monkey being recorded from (as classically described), but also to visual stimuli presented near the corresponding body part of the human experimenter. The response of the majority of these neurons depends on the position of the experimenter with respect to the monkey, though some of them are, to a certain extent, independent of this spatial relationship between the monkey and the observed

experimenter. In humans, a shared representation for the space near oneself and near others has recently been described by Brozzoli et al. (2013). This suggests that, at minimum, the parietal node of the discussed parieto-premotor VIP-F4 network possibly contributes to the construction of both a representation of one own's body and of the body of others. This is to be contrasted with the description of the representation of others' actions in the parieto-premotor network for action described below.

In conclusion, as stated above, the peripersonal representation subserved by this parieto-premotor network, though serving the definition of a safety body margin contributing the definition of self (as a whole) with respect to the external world, over-represents two vulnerable body parts, namely the head and the arm/hand unit (figures 2 and 3). This network is tightly associated with defensive behavior, protecting the body margin from external aggression, and the prediction of intrusive impact to the body. Because of these specific properties, we predict that the peripersonal space representation subserved by this functional network dynamically adjusts to the general emotional and social context the subject is experiencing (see discussion below).

## **5 THE PARIETO-PREMOTOR NETWORK FOR ACTION.**

The second circuit is formed by parietal areas AIP and 7b and premotor area F5 (figure 2b). As will be detailed below, while areas 7b and F5 share sensory visual and tactile properties as well as motor hand-related properties subserving their central role in grasp planning and execution within a motor peripersonal space defined as the reachable space (see sections 2.2 and 3), area AIP does not appear to contribute to peripersonal space representation per se (though it does represent 3D objects structure and thus possibly contributes to the definition of the motor

affordances of objects, see section 2.1). However, given the strong anatomical connections and otherwise functional homologies between these three cortical regions (Matelli and Luppino, 2001; Rizzolatti and Luppino, 2001), the contribution of areas F5 and 7b to grasping in peripersonal space cannot be discussed without also discussing the contribution of area AIP to this network.

### **5.1 Grasping.**

The second parieto-premotor network is formed by parietal areas 7b and AIP (not that this latter cortical region is not described to contain bimodal visuo-tactile neurons), and premotor area F5 (figure 2b, Rizzolatti and Luppino, 2001; Matelli and Luppino, 2001; Rizzolatti and Matelli, 2003). It is functionally specialized in the visuomotor transformation that subserves the grasping of objects in our environment, i.e. the online adjustment of the hand and finger configuration for a secured interaction with the objects. The neurons of area AIP can be classified into three different categories (see Sakata and Taira, 1994; Murata et al., 2000). "Visual-dominant" neurons discharge during object fixation and when this object is grasped in the light, but not in the dark. "Visual-and-motor" neurons discharge during grasping both in the light and in the dark, but their response is higher when the grasped object is visible. These neurons also respond to the mere presentation of a graspable object. "Motor-dominant" neurons discharge during grasping whether in the dark or in the light but are not responsive to the presentation of an object. A specific coding for the 3D structure of objects is also described in this region (Durand et al., 2007). The reversible inactivation of this cortical region induces an inability for the monkey to correctly shape its hand and finger to grasp the presented object (Gallese et al., 1994). A high proportion of area 7b neurons respond not only to visual and tactile stimulations but also to motor activity (Hyvärinen, 1981; Hyvärinen



and Poranen, 1974; Hyvärinen and Shelepin, 1979; Leinonen, 1980; Leinonen et al., 1979; Leinonen and Nyman, 1979; Robinson et al., 1978). These neurons respond for simple actions (e.g. grasping a specific object) as well as to complex sequences of actions, though differently (e.g. grasp to bring to the mouth, Fogassi et al., 2005; Fogassi and Luppino, 2005). Last, as is the case for AIP neurons, 20% of area F5 neurons discharge in response to the visual presentation of 3D objects (Murata et al., 1997). The so-called “canonical neurons” are selectively activated by the vision of objects of a specific size, shape and orientation. Their visual specificity matches their motor specificity and their visual response is independent of whether an action is being planned or performed towards the object or not (Murata et al., 1997). Its inactivation leads to deficit similar to the one observed following AIP inactivations (Fogassi et al., 2001).

## 5.2 *Objects, one’s action and others’ actions.*

The monkey ventral premotor visuomotor neurons of area F5 are classically subdivided into two categories of neurons. “Canonical” neurons, as described above, respond to visually presented objects and to actions generated towards these objects, both in the dark and in the light and are proposed to underlie visuomotor transformation for grasping (Murata et al., 1997; Raos et al., 2006). “Mirror” neurons respond during both the generation of an action and the observation of someone else performing the same action, and are proposed to play a role in action understanding (Gallese et al., 1996; Rizzolatti et al., 1996; Rizzolatti and Matelli, 2003; Rizzolatti and Fogassi, 2014). In a recent study, Bonini et al. (2014) show that neurons with canonical and mirror properties are often present at the same cortical sites. A subset of F5 neurons actually share both canonical and mirror properties (canonical-mirror neurons). In addition, the authors show that responses of

canonical and canonical-mirror neurons to the presentation of graspable objects typically require the stimulus to be in peripersonal space. In other words, these neurons require the grasping action called for by the object to be feasible. In contrast, the action observation responses of mirror and canonical-mirror neurons are present irrespectively of whether the observed action is performed in the peripersonal or in the extrapersonal space. As a result, in this cortical region, space constrained responses to objects mostly rely on an action possibility rather than actual distance from the body. Interestingly, mirror-neurons can also be found in parietal area 7b (Fogassi et al., 2005; Fogassi and Luppino, 2005). These neurons, like the “canonical” 7b neurons, respond differentially to simple acts and to complex goal-directed sequences of acts specifying an action. Fogassi et al. suggest that these neurons not only code the observed act but also the intention of the agent when performing the whole sequence specifying the action. A further comparison between the properties of parietal 7b and premotor F5 mirror neurons suggests that the inferior parietal cortex plays an important role in the organization of natural ecological actions (Bonini et al., 2010). Because of these specific properties, we do not expect this functional network to be dynamically adjusts to the general emotional and social context the subject is experiencing. Rather, in addition to its dependence of its responses on whether an object is graspable, we predict a dynamical adjustment of these responses to the emotional and social nature of the object to be grasped (e.g. graspable object on fire, see discussion below).

## 6 **PLASTIC AND DYNAMIC PERIPERSONAL SPACE REPRESENTATIONS**

All throughout this review, we have considered peripersonal space as a static functional representation, determined by fixed body constraints such as the within reach

space around the body or around the head. However, there is an ever growing body of evidence that peripersonal space should rather be considered as extremely dynamic and rapidly adjusting to both endogenous and exogenous factors (figure 5). Here, we distinguish two types of changes in peripersonal space representation. Plastic changes are defined as changes that occur following training or learning. In contrast, dynamic changes are defined as abrupt changes due to a correlated change in the environment or in the internal state of the individual. These two types of changes are expected to be mediated by different mechanisms (see below). Whenever monkey driven evidence is available, this will be discussed in priority (section 6.1). In the absence of such experimental evidence, human data will be put forward, in order to stimulate future research on the neural bases of peripersonal space plasticity and dynamics in the non-human primate.

### 6.1 Action-dependence.

Near space is not rigidly defined by the space at hand-reaching distance. Far space can indeed become included in near peripersonal space when subjects manipulate tools that allow them to act in a larger space around their body (Farnè and Ládavas, 2000; Berti and Frassinetti, 2000). This tool incorporation into the body schema and the correlated plastic expansion of peripersonal space representation cannot be solely based on the passive perceptual observation of the tool in the hand, but requires active repeated use of the tool to reach objects in far space (Farnè et al., 2005). This tool remapping of peripersonal space has been reviewed by several authors and is beyond the scope of the present work (Maravita et al., 2003; Maravita and Iriki, 2004; Ládavas and Serino, 2008; Cardinali et al., 2009; Makin et al., 2012; Brown and Goodale, 2013; Brozzoli et al., 2014; but see Holmes, 2012). We would just like to highlight

here the fact that training, i.e., repeated action, appears to be important for tool remapping to take place, though this training does not need to be long in order to produce measurable effects on peripersonal space representation (Maravita et al., 2002; Sengül et al., 2012). Overall this suggests that tool remapping of peripersonal space relies on motor knowledge (Brown and Goodale, 2013). This is supported, amongst, other evidence, by the fact that peripersonal space representation dynamically adapts to the action the subject is actually performing (e.g. a reach versus a grasping movement, Brozzoli et al., 2010). In a set of monkey electrophysiological recording studies, Iriki et al. elegantly explore the neural bases of tool remapping of peripersonal space. In particular, they describe bimodal neurons, in the medial anterior intraparietal sulcus and in the post-central gyrus, whose visual receptive fields expand following tool use training so as to encompass the tool in addition to the hand or arm (Iriki et al., 1996; Maravita and Iriki, 2004). This was the case for both “distal” cells, whose tactile receptive field was on the skin of the hand, and “proximal” cells, whose tactile receptive field was on the skin of the shoulder. Importantly, these changes required active tool use. Using positron emission tomography (PET), Obayashi et al. (2001) further describe the activation, at the cortical level, of the pre-supplementary motor area and the premotor cortex at locations matching F4 and F5 areas discussed above. The increased corticocortical afferents to the intraparietal sulcus (Hihara et al., 2006) and the increased expression of neuronal plasticity markers in this cortical region (Ishibashi et al., 2002a, 2002b) following the learning of tool-use but not following its execution confirm that training on tool-use activates parietal neuronal plasticity mechanisms.

However, there is yet more to action-dependent plasticity of peripersonal space. For example, Lourenco and Longo (2009) show that changing the arm-related proprioceptive

signals by wearing weights to the wrists results in a contraction of peripersonal space, indicating that peripersonal space does not exclusively rely on visuo-motor interactions, and supporting the idea of a functional link between peripersonal space representation and body schema (Cardinali et al., 2009). For example, Bassolino et al. (2010) show that an extension of peripersonal space can be achieved not only by using a solid tool acting onto the far space environment, but also with a tool that acts onto far space without being physically connected to it (e.g. a mouse). This suggests that the driving information in tool-use remapping might actually be the perceptual resultant of the action onto far space rather than the action itself. In addition, the authors show that the subject's peripersonal space representation adjusts to whether the subjects are manipulating the mouse or not, suggesting that there is no such thing as a "near space" representation but rather, that it is dynamical in essence, constantly incorporating sensory, motor and higher-order elements (see below) in time.

## 6.2 *Inferred sensations.*

In most daily life situations, visual stimuli are physically perceived and analyzed with respect to our self. However, some artificial situations lead us to infer the presence of a visual stimulus close to our body. For example, when facing a mirror, we see a visual image of our body projected somewhere in extrapersonal space. A visual stimulus seen through the mirror as close to our body will be referred to a real stimulus close to our actual body, though this stimulus is physically perceived in far space, and will be incorporated into our peripersonal space representation (Maravita et al., 2000; Holmes and Spence, 2006). To our knowledge, there is a unique experimental account of the putative neural bases of this mirror inferential effect. Iriki et al. (2001) show that the bimodal visuo-tactile neurons in the lateral anterior

intraparietal cortex of the monkey respond both when a visual stimulus is presented within their visual receptive field close to the body, or when the animals viewed a video in which a visual stimulus is presented close to their filmed body, at a location matching their visual receptive field. Another example is the case of body shadow. Several experiments suggest that the space round our body shadow is partially remapped as peripersonal space (Pavani and Castiello, 2004; Bonfiglioli et al., 2004; Galfano and Pavani, 2005). This ability to extend peripersonal space representation to other spaces referring to the body is proposed to serve defense and protective behaviors. Think of yourself drinking at a water pound, in the savanna, on the watch for any predator ready to jump on you. Both a change in the visual information from the water reflection and the body shadow limits are strong indicators of danger. However, the neural bases of such inferred peripersonal space are still scarce.

## 6.3 *Positional interactions.*

Head and arm peripersonal spaces are often considered as independent spaces, however, recent evidence suggests that depending on the relative position of one with respect to the other, these peripersonal spaces can actually interact and merge. Sambo et al. (2012b) show that the hand blink reflex that is elicited by an electrical stimulation of the median nerve is dramatically increased when the hand is placed within the face peripersonal space. The authors suggest that this is due to a top down modulation exerted by the VIP-F4 parieto-motor network and having as effect to change the response thresholds of the medial nerve. Interestingly, the eye blink reflex that is elicited by an electrical stimulation of the trigeminal nerve is not affected by the proximity of the hand to the face, suggesting that the hand is being incorporated into the head peripersonal space and not the reverse. In addition, the hand blink reflex is highly

dependent onto cognitive expectations and inferences. Indeed, it is enhanced only when participants expect to receive stimuli on the hand (placed close to the face, Sambo et al., 2012a). Last, this enhancement is abolished when a thin wooden screen is placed between the participants' face and their hand, creating a virtual separation between the face and hand peripersonal space representations. Again, the neural bases of such positional interaction in peripersonal spaces are scarce.

#### 6.4 *Social and emotional plasticity of peripersonal space.*

Last, several higher-order variables have been described to dynamically influence perceptual processes and the representation of peripersonal space. For example, Markman and Brendl (2005) demonstrate an interaction between word valence (positive words and negative words) and the representation of self, whereby subjects are faster at pulling a lever than at pushing it when presented with a positive word and faster at pushing than pulling when presented with a negative word. Likewise, positive objects induce an extension of the peripersonal space, such that they are perceived closer to the body than neutral or negative objects, as if they were included in the peripersonal space (Valls-Solé et al., 1997). As a result, not only the nature of the action one is performing is important in the definition of peripersonal space (Brozzoli et al., 2010), but also the emotional valence of the target as well as the emotional consequences of the actions. This is all the more marked in the context of social interactions (Teneggi et al., 2013). Indeed, Teneggi et al. (2013) describe that our peripersonal space is smaller when we are facing another individual standing in far space, as compared to when we are facing a mannequin placed at the same location. Importantly, the peripersonal boundary changes as a function of the social experience we are having with the individual facing us. Teneggi et al. show that, following an

economic game, peripersonal space boundaries between our self and the other individual merge, but only if this person behaved cooperatively. Overall, this indicates a link between low-level sensorimotor processing shaping a core peripersonal space representation and high-level social and emotional cues dynamically adjusting this core representation. This type of dynamic adjustment of peripersonal space is proposed to serve defense and protective behaviors. Corroborating this putative function of peripersonal space dynamics induced by emotions, claustrophobic fear is positively correlated with a larger peripersonal space (Lourenco et al., 2011). These observations suggest that the enlarged peripersonal space might actually be at the origin of claustrophobia, anxiety to enclosed spaces and physically restrictive situations arising from the higher rate of objects and agents perceived as intruding into these subjects' peripersonal space.

## 7 **PUTATIVE MECHANISMS SUBSERVING DYNAMIC PERIPERSONAL SPACE REPRESENTATIONS**

### 7.1 *Domain specific social and emotional dynamics in the processing of peripersonal space*

As described in section 6.1, action-dependent changes in peripersonal space representation is proposed to essentially involve the core 7b-AIP-F5 parieto-premotor network (and possibly other functionally coupled cortical and subcortical regions). A major property of this functional network is the dependence of its visual responses to the operational quality of the presented objects, i.e. to whether they are graspable or not. Emotional and social cues can alter the graspability of an object. For example, a graspable object on fire is no more graspable. Likewise, in the presence of a dominant

conspecific, a graspable apple may become ungraspable for social peace motivations. As a result, we predict that the peripersonal space representation subserved by this functional network will dynamical adjust to the emotional and social nature of the object to be grasped. In contrast, we propose that the positional and inferential changes in peripersonal space representation described in section 6.2 and 6.3 essentially involve the core VIP-F4 parieto-premotor network, due to its central role in the definition of a protective margin of self. Likewise, we expect this functional network to be involved in the dynamics in peripersonal space representations following changes in the emotional and social global context experienced by the subjects. This proposal does not exclude functional interactions between these two networks (and hence these two types of peripersonal spaces), as perception and action are not independent cortical functions (for a review, Rizzolatti and Matelli, 2003).

## 7.2 *Plastic and dynamic*

As stated in section 6, plastic cortical changes are defined as changes taking place following training or learning. In contrast, dynamic changes are defined as abrupt changes in response to a change in the environment or in the internal state of the individual. Overall, peripersonal space appears to be not only plastic (section 6.1), that is to say affected by training and repeated exposure to a given sensori-motor context, but also dynamic, that is capable of an instantaneous adjustment to the ongoing low-level (sensory and motor) and higher order (inferential, emotional, social) context (sections 6.2, 6.3 and 6.4). Several groups have provided important insights on the neural basis of tool-induced plasticity in the non-human primate. However, in the face of the growing number of neuropsychological and psychological studies describing the dynamic properties of peripersonal space representations in humans,

non-human primate studies describing its possible neural bases remain rare. Several studies have characterized the dynamic changes in the visual receptive fields of individual MT visual extrastriate (Womelsdorf et al., 2006, 2008; Anton-Erxleben et al., 2007) and parietal cortex (Ben Hamed et al., 1997, 2002) as a function of attention, demonstrating the highly dynamic context-dependent nature of the visual space representation. These attention-driven dynamic adjustments of how individual cells represent visual information are proposed to allow for an adjustment of spatial processing to the requirements of the ongoing behavior, corroborating the psychophysical evidence for an effect of attention on size and distance perception (Anton-Erxleben et al., 2007, 2010; Anton-Erxleben and Carrasco, 2013; Wardak et al., 2011). We propose that similar dynamic neuronal mechanisms underlie the overt dynamic changes in peripersonal space representation described above and result from the weighted integration, by local networks, of context-dependent incoming information (visual, tactile, proprioceptive, attention, emotional, social, cognitive, motor,...). Consequently, space representation dynamically is proposed to change as a function of the nature of processed information, while the unified space perception is proposed to be achieved via the fact that it arises from stable cortical networks. Like it has been described for attention (Buschman and Miller, 2007; Gregoriou et al., 2009, 2012), long-range top-down synchronization mechanisms in the functional networks highlighted above are expected to play a crucial role in the continuous adjustment of the core peripersonal space representation (as defined by low level cues) to the cognitive context. The peripersonal space dynamics induced by emotional and social situation are expected to involve long-range synchronization mechanisms between these core functional networks and such structures as the amygdala or the orbitofrontal cortex.

Future experiments will allow to directly test this hypothesis.

**Acknowledgments:** O.G. was funded by the French education ministry. S.BH was funded by the French Agence nationale de la recherche (Grant #ANR-05-JCJC-0230-01)

## References

- Ackroyd, K., Riddoch, M.J., Humphreys, G.W., Nightingale, S., Townsend, S., 2002. Widening the sphere of influence: using a tool to extend extrapersonal visual space in a patient with severe neglect. *Neurocase* 8, 1–12. doi:10.1093/neucas/8.1.1
- Aimola, L., Schindler, I., Venneri, A., 2013. Task- and response related dissociations between neglect in near and far space: A morphometric case study. *Behavioural Neurology* 27, 245–257. doi:10.3233/BEN-2012-110243
- Akao, T., Kurkin, S.A., Fukushima, J., Fukushima, K., 2005. Visual and vergence eye movement-related responses of pursuit neurons in the caudal frontal eye fields to motion-in-depth stimuli. *Exp Brain Res* 164, 92–108. doi:10.1007/s00221-004-2213-6
- Akbarian, S., Grüsser, O.J., Guldin, W.O., 1993. Corticofugal projections to the vestibular nuclei in squirrel monkeys: further evidence of multiple cortical vestibular fields. *J. Comp. Neurol.* 332, 89–104. doi:10.1002/cne.903320107
- Akbarian, S., Grüsser, O.J., Guldin, W.O., 1994. Corticofugal connections between the cerebral cortex and brainstem vestibular nuclei in the macaque monkey. *J. Comp. Neurol.* 339, 421–437. doi:10.1002/cne.903390309
- Alkan, Y., Biswal, B.B., Alvarez, T.L., 2011. Differentiation between vergence and saccadic functional activity within the human frontal eye fields and midbrain revealed through fMRI. *PLoS ONE* 6, e25866. doi:10.1371/journal.pone.0025866
- Alvarez, T.L., Alkan, Y., Gohel, S., Douglas Ward, B., Biswal, B.B., 2010. Functional anatomy of predictive vergence and saccade eye movements in humans: A functional MRI investigation. *Vision Research* 50, 2163–2175. doi:10.1016/j.visres.2010.08.018
- Anton-Erxleben, K., Abrams, J., Carrasco, M., 2010. Evaluating comparative and equality judgments in contrast perception: attention alters appearance. *J Vis* 10, 6. doi:10.1167/10.11.6
- Anton-Erxleben, K., Carrasco, M., 2013. Attentional enhancement of spatial resolution: linking behavioural and neurophysiological evidence. *Nat. Rev. Neurosci.* 14, 188–200. doi:10.1038/nrn3443
- Anton-Erxleben, K., Henrich, C., Treue, S., 2007. Attention changes perceived size of moving visual patterns. *J Vis* 7, 5.1–9. doi:10.1167/7.11.5
- Avillac, M., Ben Hamed, S., Duhamel, J.-R., 2007. Multisensory integration in the ventral intraparietal area of the macaque monkey. *J. Neurosci.* 27, 1922–1932. doi:10.1523/JNEUROSCI.2646-06.2007
- Avillac, M., Denève, S., Olivier, E., Pouget, A., Duhamel, J.-R., 2005. Reference frames for representing visual and tactile locations in parietal cortex. *Nat. Neurosci.* 8, 941–949. doi:10.1038/nn1480
- Ball, W., Tronick, E., 1971. Infant responses to impending collision: optical and real. *Science* 171, 818–820.
- Bassolino, M., Serino, A., Ubaldi, S., Làdavas, E., 2010. Everyday use of the computer mouse extends peripersonal space representation. *Neuropsychologia* 48, 803–811. doi:10.1016/j.neuropsychologia.2009.11.009
- Ben Hamed, S., Cléry, J., Guipponi, O., Wardak, C., 2013. Multisensory integration for looming visual. *Société française des Neurosciences*. Poster 156. Personnel Communication.
- Ben Hamed, S., Duhamel, J.-R., Bremmer, F., Graf, W., 1997. Attentional modulation of visual receptive fields in the posterior parietal cortex of the behaving macaque. *Experimental Brain Research Series* 25, 371–384.
- Ben Hamed, S., Duhamel, J.R., Bremmer, F., Graf, W., 2001. Representation of the visual field in the lateral intraparietal area of macaque monkeys: a quantitative receptive field analysis. *Exp Brain Res* 140, 127–144.
- Ben Hamed, S., Duhamel, J.-R., Bremmer, F., Graf, W., 2002. Visual receptive field modulation in the lateral intraparietal area during attentive fixation and free gaze. *Cereb. Cortex* 12, 234–245.
- Berti, A., Frassinetti, F., 2000. When far becomes near: remapping of space by tool use. *J Cogn Neurosci* 12, 415–420.
- Beschin, N., Robertson, I.H., 1997. Personal versus



- extrapersonal neglect: a group study of their dissociation using a reliable clinical test. *Cortex* 33, 379–384.
- Bhattacharyya, R., Musallam, S., Andersen, R.A., 2009. Parietal reach region encodes reach depth using retinal disparity and vergence angle signals. *J. Neurophysiol.* 102, 805–816. doi:10.1152/jn.90359.2008
- Bisiach, E., Perani, D., Vallar, G., Berti, A., 1986. Unilateral neglect: personal and extrapersonal. *Neuropsychologia* 24, 759–767.
- Bjoertomt, O., Cowey, A., Walsh, V., 2002. Spatial neglect in near and far space investigated by repetitive transcranial magnetic stimulation. *Brain* 125, 2012–2022.
- Bjoertomt, O., Cowey, A., Walsh, V., 2009. Near space functioning of the human angular and supramarginal gyri. *J. Neuropsychol* 3, 31–43. doi:10.1348/174866408X394604
- Bonfiglioli, C., Pavani, F., Castiello, U., 2004. Differential effects of cast shadows on perception and action. *Perception* 33, 1291–1304.
- Bonini, L., Maranesi, M., Livi, A., Fogassi, L., Rizzolatti, G., 2014. Space-Dependent Representation of Objects and Other's Action in Monkey Ventral Premotor Grasping Neurons. *J. Neurosci.* 34, 4108–4119. doi:10.1523/JNEUROSCI.4187-13.2014
- Bonini, L., Rozzi, S., Serventi, F.U., Simone, L., Ferrari, P.F., Fogassi, L., 2010. Ventral premotor and inferior parietal cortices make distinct contribution to action organization and intention understanding. *Cereb. Cortex* 20, 1372–1385. doi:10.1093/cercor/bhp200
- Bremmer, F., Duhamel, J.-R., Ben Hamed, S., Graf, W., 1997. The representation of movement in near extra-personal space in the macaque ventral intraparietal area (VIP)., in: Thier, P., Karnath, H.-O. (Eds.), *Parietal Lobe Contributions to Orientation in 3D Space*, Experimental Brain Research Series, Vol 25. Springer, pp. 619–630.
- Bremmer, F., Duhamel, J.R., Ben Hamed, S., Graf, W., 2000. Stages of self-motion processing in primate posterior parietal cortex. *Int. Rev. Neurobiol.* 44, 173–198.
- Bremmer, F., Duhamel, J.-R., Ben Hamed, S., Graf, W., 2002a. Heading encoding in the macaque ventral intraparietal area (VIP). *Eur. J. Neurosci.* 16, 1554–1568.
- Bremmer, F., Graf, W., Ben Hamed, S., Duhamel, J.R., 1999. Eye position encoding in the macaque ventral intraparietal area (VIP). *Neuroreport* 10, 873–878.
- Bremmer, F., Klam, F., Duhamel, J.-R., Ben Hamed, S., Graf, W., 2002b. Visual-vestibular interactive responses in the macaque ventral intraparietal area (VIP). *Eur. J. Neurosci.* 16, 1569–1586.
- Bremmer, F., Schlack, A., Duhamel, J.R., Graf, W., Fink, G.R., 2001. Space coding in primate posterior parietal cortex. *Neuroimage* 14, S46–51. doi:10.1006/nimg.2001.0817
- Bremmer, F., Schlack, A., Kaminiarz, A., Hoffmann, K.-P., 2013. Encoding of movement in near extrapersonal space in primate area VIP. *Front. Behav. Neurosci.* 7, 8. doi:10.3389/fnbeh.2013.00008
- Breveglieri, R., Hadjidimitrakis, K., Bosco, A., Sabatini, S.P., Galletti, C., Fattori, P., 2012. Eye position encoding in three-dimensional space: integration of version and vergence signals in the medial posterior parietal cortex. *J. Neurosci.* 32, 159–169. doi:10.1523/JNEUROSCI.4028-11.2012
- Brown, L.E., Goodale, M.A., 2013. A brief review of the role of training in near-tool effects. *Front. Psychol.* 4, 576. doi:10.3389/fpsyg.2013.00576
- Brozzoli, C., Cardinali, L., Pavani, F., Farnè, A., 2010. Action-specific remapping of peripersonal space. *Neuropsychologia* 48, 796–802. doi:10.1016/j.neuropsychologia.2009.10.009
- Brozzoli, C., Ehrsson, H.H., Farnè, A., 2014. Multisensory representation of the space near the hand: from perception to action and interindividual interactions. *Neuroscientist* 20, 122–135. doi:10.1177/1073858413511153
- Brozzoli, C., Gentile, G., Bergouignan, L., Ehrsson, H.H., 2013. A shared representation of the space near oneself and others in the human premotor cortex. *Curr. Biol.* 23, 1764–1768. doi:10.1016/j.cub.2013.07.004
- Brozzoli, C., Makin, T.R., Cardinali, L., Holmes, N.P., Farnè, A., 2012. Peripersonal Space: A Multisensory Interface for Body–Object Interactions, in: Murray, M.M., Wallace, M.T. (Eds.), *The Neural Bases of Multisensory Processes*, Frontiers in Neuroscience. CRC Press, Boca Raton (FL).
- Buschman, T.J., Miller, E.K., 2007. Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science* 315, 1860–1862. doi:10.1126/science.1138071
- Cardinali, L., Brozzoli, C., Farnè, A., 2009. Peripersonal space and body schema: two labels for the same concept? *Brain Topogr*

- 21, 252–260. doi:10.1007/s10548-009-0092-7
- Chen, A., DeAngelis, G.C., Angelaki, D.E., 2011a. A comparison of vestibular spatiotemporal tuning in macaque parietoinsular vestibular cortex, ventral intraparietal area, and medial superior temporal area. *J. Neurosci.* 31, 3082–3094. doi:10.1523/JNEUROSCI.4476-10.2011
- Chen, A., DeAngelis, G.C., Angelaki, D.E., 2011b. Representation of vestibular and visual cues to self-motion in ventral intraparietal cortex. *J. Neurosci.* 31, 12036–12052. doi:10.1523/JNEUROSCI.0395-11.2011
- Chen, X., DeAngelis, G.C., Angelaki, D.E., 2013. Diverse spatial reference frames of vestibular signals in parietal cortex. *Neuron* 80, 1310–1321. doi:10.1016/j.neuron.2013.09.006
- Chen, X., DeAngelis, G.C., Angelaki, D.E., 2014. Eye-centered visual receptive fields in the ventral intraparietal area. *Journal of Neurophysiology* 112, 353–361. doi:10.1152/jn.00057.2014
- Cléry, J., Guipponi, O., Odouard, S., Wardak, C., Ben Hamed, S., 2014. Neural bases of impact prediction in the non-human primate. 9th FENS Forum of Neuroscience. Poster D003. Personnel Communication.
- Cléry, J., Guipponi, O., Wardak, C., Ben Hamed, S., 2013. Multisensory integration of dynamic stimuli in the non-human primate: a functional Magnetic Resonance Imaging (fMRI) study. Société française des Neurosciences. Poster 142. Personnel Communication.
- Colby, C.L., Duhamel, J.R., Goldberg, M.E., 1993. Ventral intraparietal area of the macaque: anatomic location and visual response properties. *Journal of Neurophysiology* 69, 902–914.
- Cooke, D.F., Graziano, M.S.A., 2003. Defensive movements evoked by air puff in monkeys. *J. Neurophysiol.* 90, 3317–3329. doi:10.1152/jn.00513.2003
- Cooke, D.F., Graziano, M.S.A., 2004. Sensorimotor integration in the precentral gyrus: polysensory neurons and defensive movements. *J. Neurophysiol.* 91, 1648–1660. doi:10.1152/jn.00955.2003
- Coslett, H.B., Schwartz, M.F., Goldberg, G., Haas, D., Perkins, J., 1993. Multi-modal hemispatial deficits after left hemisphere stroke. A disorder of attention? *Brain* 116 (Pt 3), 527–554.
- Cowey, A., Small, M., Ellis, S., 1994. Left visuo-spatial neglect can be worse in far than in near space. *Neuropsychologia* 32, 1059–1066.
- Cowey, A., Small, M., Ellis, S., 1999. No abrupt change in visual hemineglect from near to far space. *Neuropsychologia* 37, 1–6.
- Duhamel, J.R., Bremmer, F., Ben Hamed, S., Graf, W., 1997. Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature* 389, 845–848. doi:10.1038/39865
- Duhamel, J.-R., Colby, C.L., Goldberg, M.E., 1998. Ventral Intraparietal Area of the Macaque: Congruent Visual and Somatic Response Properties. *Journal of Neurophysiology* 79, 126–136.
- Durand, J.-B., Nelissen, K., Joly, O., Wardak, C., Todd, J.T., Norman, J.F., Janssen, P., Vanduffel, W., Orban, G.A., 2007. Anterior regions of monkey parietal cortex process visual 3D shape. *Neuron* 55, 493–505. doi:10.1016/j.neuron.2007.06.040
- Durand, J.-B., Peeters, R., Norman, J.F., Todd, J.T., Orban, G.A., 2009. Parietal regions processing visual 3D shape extracted from disparity. *Neuroimage* 46, 1114–1126. doi:10.1016/j.neuroimage.2009.03.023
- Farnè, A., Iriki, A., Làdavas, E., 2005. Shaping multisensory action-space with tools: evidence from patients with cross-modal extinction. *Neuropsychologia, Movement, Action and Consciousness: Toward a Physiology of Intentionality A Special Issue in Honour of Marc Jeannerod* 43, 238–248. doi:10.1016/j.neuropsychologia.2004.11.010
- Farnè, A., Làdavas, E., 2000. Dynamic size-change of hand peripersonal space following tool use. *Neuroreport* 11, 1645–1649.
- Ferraina, S., Paré, M., Wurtz, R.H., 2000. Disparity sensitivity of frontal eye field neurons. *J. Neurophysiol.* 83, 625–629.
- Fogassi, L., Ferrari, P.F., Gesierich, B., Rozzi, S., Chersi, F., Rizzolatti, G., 2005. Parietal lobe: from action organization to intention understanding. *Science* 308, 662–667. doi:10.1126/science.1106138
- Fogassi, L., Gallese, V., Buccino, G., Craighero, L., Fadiga, L., Rizzolatti, G., 2001. Cortical mechanism for the visual guidance of hand grasping movements in the monkey: A reversible inactivation study. *Brain* 124, 571–586.
- Fogassi, L., Gallese, V., Fadiga, L., Luppino, G., Matelli, M., Rizzolatti, G., 1996. Coding of peripersonal space in inferior premotor cortex (area F4). *J. Neurophysiol.* 76, 141–157.

- Fogassi, L., Luppino, G., 2005. Motor functions of the parietal lobe. *Curr. Opin. Neurobiol.* 15, 626–631. doi:10.1016/j.conb.2005.10.015
- Galfano, G., Pavani, F., 2005. Long-lasting capture of tactile attention by body shadows. *Exp Brain Res* 166, 518–527. doi:10.1007/s00221-005-2392-9
- Gallese, V., Fadiga, L., Fogassi, L., Rizzolatti, G., 1996. Action recognition in the premotor cortex. *Brain* 119, 593–609. doi:10.1093/brain/119.2.593
- Gallese, V., Murata, A., Kaseda, M., Niki, N., Sakata, H., 1994. Deficit of hand preshaping after muscimol injection in monkey parietal cortex. *Neuroreport* 5, 1525–1529.
- Gamlin, P.D., Yoon, K., 2000. An area for vergence eye movement in primate frontal cortex. *Nature* 407, 1003–1007. doi:10.1038/35039506
- Genovesio, A., Ferraina, S., 2004. Integration of retinal disparity and fixation-distance related signals toward an egocentric coding of distance in the posterior parietal cortex of primates. *J. Neurophysiol.* 91, 2670–2684. doi:10.1152/jn.00712.2003
- Gentilucci, M., Fogassi, L., Luppino, G., Matelli, M., Camarda, R., Rizzolatti, G., 1988. Functional organization of inferior area 6 in the macaque monkey. I. Somatotopy and the control of proximal movements. *Exp Brain Res* 71, 475–490.
- Gentilucci, M., Scandolaro, C., Pigarev, I.N., Rizzolatti, G., 1983. Visual responses in the postarcuate cortex (area 6) of the monkey that are independent of eye position. *Exp Brain Res* 50, 464–468.
- Gnadt, J.W., Mays, L.E., 1995. Neurons in monkey parietal area LIP are tuned for eye-movement parameters in three-dimensional space. *J. Neurophysiol.* 73, 280–297.
- Graziano, M.S.A., Aflalo, T.N.S., Cooke, D.F., 2005. Arm movements evoked by electrical stimulation in the motor cortex of monkeys. *J. Neurophysiol.* 94, 4209–4223. doi:10.1152/jn.01303.2004
- Graziano, M.S.A., Cooke, D.F., 2006. Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia* 44, 2621–2635.
- Graziano, M.S.A., Taylor, C.S.R., Moore, T., 2002. Complex movements evoked by microstimulation of precentral cortex. *Neuron* 34, 841–851.
- Graziano, M.S., Hu, X.T., Gross, C.G., 1997. Visuospatial properties of ventral premotor cortex. *J. Neurophysiol.* 77, 2268–2292.
- Graziano, M.S., Yap, G.S., Gross, C.G., 1994. Coding of visual space by premotor neurons. *Science* 266, 1054–1057.
- Gregoriou, G.G., Gotts, S.J., Desimone, R., 2012. Cell-type-specific synchronization of neural activity in FEF with V4 during attention. *Neuron* 73, 581–594. doi:10.1016/j.neuron.2011.12.019
- Gregoriou, G.G., Gotts, S.J., Zhou, H., Desimone, R., 2009. High-frequency, long-range coupling between prefrontal and visual cortex during attention. *Science* 324, 1207–1210. doi:10.1126/science.1171402
- Gross, C.G., Graziano, M.S.A., 1995. REVIEW ■: Multiple Representations of Space in the Brain. *Neuroscientist* 1, 43–50. doi:10.1177/107385849500100107
- Guariglia, C., Antonucci, G., 1992. Personal and extrapersonal space: a case of neglect dissociation. *Neuropsychologia* 30, 1001–1009.
- Guipponi, O., Odouard, S., Pinède, S., Wardak, C., Ben Hamed, S., 2014. fMRI Cortical Correlates of Spontaneous Eye Blinks in the Nonhuman Primate. *Cereb. Cortex*. doi:10.1093/cercor/bhu038
- Guipponi, O., Wardak, C., Ibarrola, D., Comte, J.-C., Sappey-Mariniér, D., Pinède, S., Ben Hamed, S., 2013a. Multimodal convergence within the intraparietal sulcus of the macaque monkey. *J. Neurosci.* 33, 4128–4139. doi:10.1523/JNEUROSCI.1421-12.2013
- Guipponi, O., Wardak, C., Odouard, S., Pinède, S., Ben Hamed, S., 2013b. Identification of the visuo-tactile convergence network: a functional magnetic imaging (fMRI) study in awake monkeys. *Société française des Neurosciences. Poster 134. Personnel Communication.*
- Hadjidimitrakis, K., Breveglieri, R., Bosco, A., Fattori, P., 2012. Three-dimensional eye position signals shape both peripersonal space and arm movement activity in the medial posterior parietal cortex. *Front Integr Neurosci* 6, 37. doi:10.3389/fnint.2012.00037
- Hadjidimitrakis, K., Breveglieri, R., Placenti, G., Bosco, A., Sabatini, S.P., Fattori, P., 2011. Fix your eyes in the space you could reach: neurons in the macaque medial parietal cortex prefer gaze positions in peripersonal space. *PLoS ONE* 6, e23335. doi:10.1371/journal.pone.0023335
- Halligan, P.W., Fink, G.R., Marshall, J.C., Vallar, G., 2003. Spatial cognition: evidence from visual neglect. *Trends Cogn. Sci. (Regul.*

- Ed.) 7, 125–133.
- Halligan, P.W., Marshall, J.C., 1991. Left neglect for near but not far space in man. *Nature* 350, 498–500. doi:10.1038/350498a0
- Hepp-Reymond, M.C., Hüsler, E.J., Maier, M.A., Ql, H.X., 1994. Force-related neuronal activity in two regions of the primate ventral premotor cortex. *Can. J. Physiol. Pharmacol.* 72, 571–579.
- Hihara, S., Notoya, T., Tanaka, M., Ichinose, S., Ojima, H., Obayashi, S., Fujii, N., Iriki, A., 2006. Extension of corticocortical afferents into the anterior bank of the intraparietal sulcus by tool-use training in adult monkeys. *Neuropsychologia* 44, 2636–2646. doi:10.1016/j.neuropsychologia.2005.11.020
- Holmes, N.P., 2012. Does tool use extend peripersonal space? A review and re-analysis. *Exp Brain Res* 218, 273–282. doi:10.1007/s00221-012-3042-7
- Holmes, N.P., Spence, C., 2006. Beyond the Body Schema: Visual, Prosthetic, and Technological Contributions to Bodily Perception and Awareness, in: Knoblich, G., Thornton, I.M., Grosjean, M., Shiffrar, M. (Eds.), *Human Body Perception from the inside out: Advances in Visual Cognition*, Advances in Visual Cognition. Oxford University Press, New York, NY, US, pp. 15–64.
- Hyvärinen, J., 1981. Regional distribution of functions in parietal association area 7 of the monkey. *Brain Res.* 206, 287–303.
- Hyvärinen, J., Poranen, A., 1974. Function of the Parietal Associative Area 7 as Revealed from Cellular Discharges in Alert Monkeys. *Brain* 97, 673–692. doi:10.1093/brain/97.1.673
- Hyvärinen, J., Shelepin, Y., 1979. Distribution of visual and somatic functions in the parietal associative area 7 of the monkey. *Brain Res.* 169, 561–564.
- Iriki, A., Tanaka, M., Iwamura, Y., 1996. Coding of modified body schema during tool use by macaque postcentral neurones. *Neuroreport* 7, 2325–2330.
- Iriki, A., Tanaka, M., Obayashi, S., Iwamura, Y., 2001. Self-images in the video monitor coded by monkey intraparietal neurons. *Neurosci. Res.* 40, 163–173.
- Ishibashi, H., Hihara, S., Takahashi, M., Heike, T., Yokota, T., Iriki, A., 2002a. Tool-use learning selectively induces expression of brain-derived neurotrophic factor, its receptor trkB, and neurotrophin 3 in the intraparietal multisensory cortex of monkeys. *Brain Res Cogn Brain Res* 14, 3–9.
- Ishibashi, H., Hihara, S., Takahashi, M., Heike, T., Yokota, T., Iriki, A., 2002b. Tool-use learning induces BDNF expression in a selective portion of monkey anterior parietal cortex. *Brain Res. Mol. Brain Res.* 102, 110–112.
- Ishida, H., Nakajima, K., Inase, M., Murata, A., 2010. Shared mapping of own and others' bodies in visuotactile bimodal area of monkey parietal cortex. *J Cogn Neurosci* 22, 83–96. doi:10.1162/jocn.2009.21185
- Jeannerod, M., Arbib, M.A., Rizzolatti, G., Sakata, H., 1995. Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends in Neurosciences* 18, 314–320. doi:10.1016/0166-2236(95)93921-J
- Keller, I., Schindler, I., Kerkhoff, G., von Rosen, F., Golz, D., 2005. Visuospatial neglect in near and far space: dissociation between line bisection and letter cancellation. *Neuropsychologia* 43, 724–731. doi:10.1016/j.neuropsychologia.2004.08.003
- Làdavas, E., Farnè, A., 2004. Visuo-tactile representation of near-the-body space. *Journal of Physiology-Paris, Representation of 3-D Space Using Different Senses In Different Species* 98, 161–170. doi:10.1016/j.jphysparis.2004.03.007
- Làdavas, E., Serino, A., 2008. Action-dependent plasticity in peripersonal space representations. *Cogn Neuropsychol* 25, 1099–1113.
- Leinonen, L., 1980. Functional properties of neurones in the posterior part of area 7 in awake monkey. *Acta Physiol. Scand.* 108, 301–308. doi:10.1111/j.1748-1716.1980.tb06536.x
- Leinonen, L., Hyvärinen, J., Nyman, G., Linnankoski, I., 1979. I. Functional properties of neurons in lateral part of associative area 7 in awake monkeys. *Exp Brain Res* 34, 299–320.
- Leinonen, L., Nyman, G., 1979. II. Functional properties of cells in anterolateral part of area 7 associative face area of awake monkeys. *Exp Brain Res* 34, 321–333.
- Lourenco, S.F., Longo, M.R., 2009. The plasticity of near space: evidence for contraction. *Cognition* 112, 451–456. doi:10.1016/j.cognition.2009.05.011
- Lourenco, S.F., Longo, M.R., Pathman, T., 2011. Near space and its relation to claustrophobic fear. *Cognition* 119, 448–453. doi:10.1016/j.cognition.2011.02.009
- Luppino, G., Ben Hamed, S., Gamberini, M., Matelli, M., Galletti, C., 2005. Occipital (V6) and parietal (V6A) areas in the anterior wall of the parieto-occipital sulcus of the macaque: a

- cytoarchitectonic study. *Eur. J. Neurosci.* 21, 3056–3076. doi:10.1111/j.1460-9568.2005.04149.x
- Luppino, G., Murata, A., Govoni, P., Matelli, M., 1999. Largely segregated parietofrontal connections linking rostral intraparietal cortex (areas AIP and VIP) and the ventral premotor cortex (areas F5 and F4). *Exp Brain Res* 128, 181–187.
- Makin, T.R., Holmes, N.P., Brozzoli, C., Farnè, A., 2012. Keeping the world at hand: rapid visuomotor processing for hand-object interactions. *Exp Brain Res* 219, 421–428. doi:10.1007/s00221-012-3089-5
- Maravita, A., Clarke, K., Husain, M., Driver, J., 2002. Active tool use with the contralesional hand can reduce cross-modal extinction of touch on that hand. *Neurocase* 8, 411–416. doi:10.1076/neur.8.5.411.16177
- Maravita, A., Iriki, A., 2004. Tools for the body (schema). *Trends Cogn. Sci. (Regul. Ed.)* 8, 79–86. doi:10.1016/j.tics.2003.12.008
- Maravita, A., Spence, C., Clarke, K., Husain, M., Driver, J., 2000. Vision and touch through the looking glass in a case of crossmodal extinction. *Neuroreport* 11, 3521–3526.
- Maravita, A., Spence, C., Driver, J., 2003. Multisensory integration and the body schema: close to hand and within reach. *Curr. Biol.* 13, R531–539.
- Markman, A.B., Brendl, C.M., 2005. Constraining theories of embodied cognition. *Psychol Sci* 16, 6–10. doi:10.1111/j.0956-7976.2005.00772.x
- Martinez-Trujillo, J.C., Medendorp, W.P., Wang, H., Crawford, J.D., 2004. Frames of reference for eye-head gaze commands in primate supplementary eye fields. *Neuron* 44, 1057–1066. doi:10.1016/j.neuron.2004.12.004
- Matelli, M., Luppino, G., 2001. Parietofrontal circuits for action and space perception in the macaque monkey. *Neuroimage* 14, S27–32. doi:10.1006/nimg.2001.0835
- Murata, A., Fadiga, L., Fogassi, L., Gallese, V., Raos, V., Rizzolatti, G., 1997. Object representation in the ventral premotor cortex (area F5) of the monkey. *J. Neurophysiol.* 78, 2226–2230.
- Murata, A., Gallese, V., Luppino, G., Kaseda, M., Sakata, H., 2000. Selectivity for the shape, size, and orientation of objects for grasping in neurons of monkey parietal area AIP. *J. Neurophysiol.* 83, 2580–2601.
- Obayashi, S., Suhara, T., Kawabe, K., Okauchi, T., Maeda, J., Akine, Y., Onoe, H., Iriki, A., 2001. Functional brain mapping of monkey tool use. *Neuroimage* 14, 853–861. doi:10.1006/nimg.2001.0878
- Olson, C.R., 2003. Brain representation of object-centered space in monkeys and humans. *Annu. Rev. Neurosci.* 26, 331–354. doi:10.1146/annurev.neuro.26.041002.131405
- Olson, C.R., Gettner, S.N., 1995. Object-centered direction selectivity in the macaque supplementary eye field. *Science* 269, 985–988.
- Ortigue, S., Mégevand, P., Perren, F., Landis, T., Blanke, O., 2006. Double dissociation between representational personal and extrapersonal neglect. *Neurology* 66, 1414–1417. doi:10.1212/01.wnl.0000210440.49932.e7
- Pavani, F., Castiello, U., 2004. Binding personal and extrapersonal space through body shadows. *Nat. Neurosci.* 7, 14–16. doi:10.1038/nn1167
- Pitzalis, S., Di Russo, F., Spinelli, D., Zoccolotti, P., 2001. Influence of the radial and vertical dimensions on lateral neglect. *Exp Brain Res* 136, 281–294.
- Pitzalis, S., Sereno, M.I., Committeri, G., Fattori, P., Galati, G., Tosoni, A., Galletti, C., 2013. The human homologue of macaque area V6A. *NeuroImage* 82, 517–530. doi:10.1016/j.neuroimage.2013.06.026
- Pouget, A., Sejnowski, T.J., 1994. A neural model of the cortical representation of egocentric distance. *Cereb. Cortex* 4, 314–329.
- Quinlan, D.J., Culham, J.C., 2007. fMRI reveals a preference for near viewing in the human parieto-occipital cortex. *Neuroimage* 36, 167–187. doi:10.1016/j.neuroimage.2007.02.029
- Raos, V., Umiltà, M.-A., Murata, A., Fogassi, L., Gallese, V., 2006. Functional properties of grasping-related neurons in the ventral premotor area F5 of the macaque monkey. *J. Neurophysiol.* 95, 709–729. doi:10.1152/jn.00463.2005
- Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G., Matelli, M., 1988. Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Exp Brain Res* 71, 491–507.
- Rizzolatti, G., Cattaneo, L., Fabbri-Destro, M., Rozzi, S., 2014. Cortical Mechanisms Underlying the Organization of Goal-Directed Actions and Mirror Neuron-Based Action Understanding. *Physiological Reviews* 94, 655–706. doi:10.1152/physrev.00009.2013
- Rizzolatti, G., Fadiga, L., Fogassi, L., Gallese, V.,

1997. The Space Around Us. *Science* 277, 190–191. doi:10.1126/science.277.5323.190
- Rizzolatti, G., Fadiga, L., Gallese, V., Fogassi, L., 1996. Premotor cortex and the recognition of motor actions. *Brain Res Cogn Brain Res* 3, 131–141.
- Rizzolatti, G., Fogassi, L., 2014. The mirror mechanism: recent findings and perspectives. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* 369, 20130420. doi:10.1098/rstb.2013.0420
- Rizzolatti, G., Fogassi, L., Gallese, V., 2002. Motor and cognitive functions of the ventral premotor cortex. *Curr. Opin. Neurobiol.* 12, 149–154.
- Rizzolatti, G., Luppino, G., 2001. The cortical motor system. *Neuron* 31, 889–901.
- Rizzolatti, G., Luppino, G., Matelli, M., 1998. The organization of the cortical motor system: new concepts. *Electroencephalogr Clin Neurophysiol* 106, 283–296.
- Rizzolatti, G., Matelli, M., 2003. Two different streams form the dorsal visual system: anatomy and functions. *Exp Brain Res* 153, 146–157. doi:10.1007/s00221-003-1588-0
- Rizzolatti, G., Matelli, M., Pavesi, G., 1983. Deficits in Attention and Movement Following the Removal of Postarcuate (area 6) and Prearcuate (area 8) Cortex in Macaque Monkeys. *Brain* 106, 655–673. doi:10.1093/brain/106.3.655
- Rizzolatti, G., Scandolara, C., Matelli, M., Gentilucci, M., 1981. Afferent properties of periarculate neurons in macaque monkeys. II. Visual responses. *Behav. Brain Res.* 2, 147–163.
- Robinson, C.J., Burton, H., 1980. Somatotopographic organization in the second somatosensory area of *M. fascicularis*. *J. Comp. Neurol.* 192, 43–67. doi:10.1002/cne.901920104
- Robinson, D.L., Goldberg, M.E., Stanton, G.B., 1978. Parietal association cortex in the primate: sensory mechanisms and behavioral modulations. *J. Neurophysiol.* 41, 910–932.
- Romero, M.C., Pani, P., Janssen, P., 2014. Coding of Shape Features in the Macaque Anterior Intraparietal Area. *J. Neurosci.* 34, 4006–4021. doi:10.1523/JNEUROSCI.4095-13.2014
- Romero, M.C., Van Dromme, I.C.L., Janssen, P., 2013. The Role of Binocular Disparity in Stereoscopic Images of Objects in the Macaque Anterior Intraparietal Area. *PLoS ONE* 8, e55340. doi:10.1371/journal.pone.0055340
- Sakata, H., Shibutani, H., Kawano, K., 1980. Spatial properties of visual fixation neurons in posterior parietal association cortex of the monkey. *J. Neurophysiol.* 43, 1654–1672.
- Sakata, H., Taira, M., 1994. Parietal control of hand action. *Curr. Opin. Neurobiol.* 4, 847–856.
- Sakata, H., Taira, M., Kusunoki, M., Murata, A., Tanaka, Y., Tsutsui, K., 1998. Neural coding of 3D features of objects for hand action in the parietal cortex of the monkey. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* 353, 1363–1373. doi:10.1098/rstb.1998.0290
- Sambo, C.F., Forster, B., Williams, S.C., Iannetti, G.D., 2012a. To blink or not to blink: fine cognitive tuning of the defensive peripersonal space. *J. Neurosci.* 32, 12921–12927. doi:10.1523/JNEUROSCI.0607-12.2012
- Sambo, C.F., Liang, M., Cruccu, G., Iannetti, G.D., 2012b. Defensive peripersonal space: the blink reflex evoked by hand stimulation is increased when the hand is near the face. *J. Neurophysiol.* 107, 880–889. doi:10.1152/jn.00731.2011
- Schiff, W., Caviness, J.A., Gibson, J.J., 1962. Persistent fear responses in rhesus monkeys to the optical stimulus of “looming.” *Science* 136, 982–983.
- Sengül, A., van Elk, M., Rognini, G., Aspell, J.E., Bleuler, H., Blanke, O., 2012. Extending the body to virtual tools using a robotic surgical interface: evidence from the crossmodal congruency task. *PLoS ONE* 7, e49473. doi:10.1371/journal.pone.0049473
- Srivastava, S., Orban, G.A., Mazière, P.A.D., Janssen, P., 2009. A Distinct Representation of Three-Dimensional Shape in Macaque Anterior Intraparietal Area: Fast, Metric, and Coarse. *J. Neurosci.* 29, 10613–10626. doi:10.1523/JNEUROSCI.6016-08.2009
- Stepniewska, I., Fang, P.-C., Kaas, J.H., 2005. Microstimulation reveals specialized subregions for different complex movements in posterior parietal cortex of prosimian galagos. *Proc. Natl. Acad. Sci. U.S.A.* 102, 4878–4883. doi:10.1073/pnas.0501048102
- Teneggi, C., Canzoneri, E., di Pellegrino, G., Serino, A., 2013. Social modulation of peripersonal space boundaries. *Curr. Biol.* 23, 406–411. doi:10.1016/j.cub.2013.01.043
- Theys, T., Srivastava, S., Loon, J. van, Goffin, J., Janssen, P., 2012. Selectivity for three-dimensional contours and surfaces in the anterior intraparietal area. *Journal of Neurophysiology* 107, 995–1008. doi:10.1152/jn.00248.2011
- Thier, P., Andersen, R.A., 1998. Electrical Microstimulation Distinguishes Distinct



- Saccade-Related Areas in the Posterior Parietal Cortex. *Journal of Neurophysiology* 80, 1713–1735.
- Vagnoni, E., Lourenco, S.F., Longo, M.R., 2012. Threat modulates perception of looming visual stimuli. *Curr. Biol.* 22, R826–827. doi:10.1016/j.cub.2012.07.053
- Valls-Solé, J., Valldeoriola, F., Tolosa, E., Martí, M.J., 1997. Distinctive abnormalities of facial reflexes in patients with progressive supranuclear palsy. *Brain* 120 ( Pt 10), 1877–1883.
- Verhoef, B.-E., Vogels, R., Janssen, P., 2010. Contribution of Inferior Temporal and Posterior Parietal Activity to Three-Dimensional Shape Perception. *Current Biology* 20, 909–913. doi:10.1016/j.cub.2010.03.058
- Vuilleumier, P., Valenza, N., Mayer, E., Reverdin, A., Landis, T., 1998. Near and far visual space in unilateral neglect. *Ann. Neurol.* 43, 406–410. doi:10.1002/ana.410430324
- Wardak, C., Denève, S., Ben Hamed, S., 2011. Focused visual attention distorts distance perception away from the attentional locus. *Neuropsychologia* 49, 535–545. doi:10.1016/j.neuropsychologia.2010.12.008
- Wardak, C., Ibos, G., Duhamel, J.-R., Olivier, E., 2006. Contribution of the monkey frontal eye field to covert visual attention. *J. Neurosci.* 26, 4228–4235. doi:10.1523/JNEUROSCI.3336-05.2006
- Weiss, P.H., Marshall, J.C., Wunderlich, G., Tellmann, L., Halligan, P.W., Freund, H.J., Zilles, K., Fink, G.R., 2000. Neural consequences of acting in near versus far space: a physiological basis for clinical dissociations. *Brain* 123 Pt 12, 2531–2541.
- Weiss, P.H., Marshall, J.C., Zilles, K., Fink, G.R., 2003. Are action and perception in near and far space additive or interactive factors? *Neuroimage* 18, 837–846.
- Womelsdorf, T., Anton-Erxleben, K., Pieper, F., Treue, S., 2006. Dynamic shifts of visual receptive fields in cortical area MT by spatial attention. *Nat. Neurosci.* 9, 1156–1160. doi:10.1038/nn1748
- Womelsdorf, T., Anton-Erxleben, K., Treue, S., 2008. Receptive field shift and shrinkage in macaque middle temporal area through attentional gain modulation. *J. Neurosci.* 28, 8934–8944. doi:10.1523/JNEUROSCI.4030-07.2008
- Yang, Y., Liu, S., Chowdhury, S.A., DeAngelis, G.C., Angelaki, D.E., 2011. Binocular disparity tuning and visual-vestibular congruency of multisensory neurons in macaque parietal cortex. *J. Neurosci.* 31, 17905–17916. doi:10.1523/JNEUROSCI.4032-11.2011