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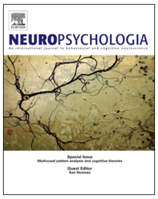

Research Report

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

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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 extrapersonal 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 periarcuate 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 periarcuate 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 extrapersonal 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 (Fig. 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 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;

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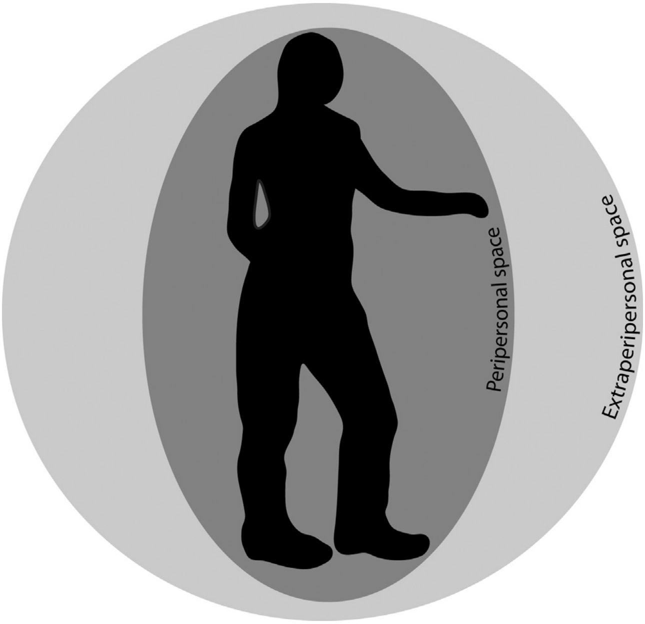

Fig. 1. Spaces around the body. The *peripersonal space* is the space that directly surrounds us and with which we can directly interact whereas the *extrapersonal space* is the space that is far away from the subject and that cannot be directly acted upon by the body.

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 understanding of 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 is 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 periarcuate 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 periarcuate 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 others' 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 others' 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 by providing the brain with information about where the eyes are fixating in space at the same time, carry 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

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