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Invited Review

Peripersonal space in the brain

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ABSTRACT

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

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1. Introduction

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

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

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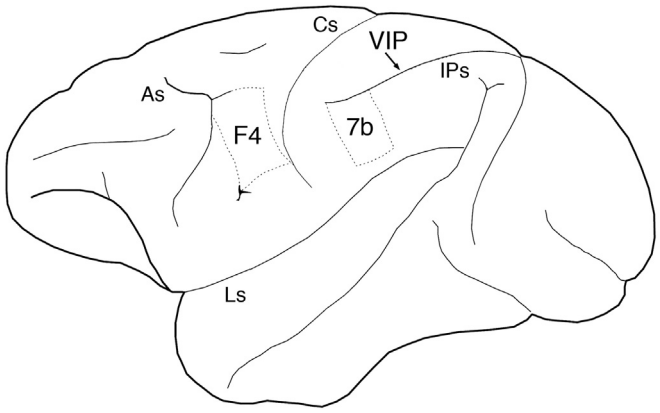

Fig. 1. Lateral view of the monkey cerebral cortex showing three regions containing neuronal populations that selectively encode peripersonal space: area F4 in the frontal lobe, area 7b and the Ventral Intraparietal Area (VIP), which is buried in the depth of the intraparietal sulcus (IPs), in the parietal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

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

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

2. Neurophysiological studies of peripersonal space in animals

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

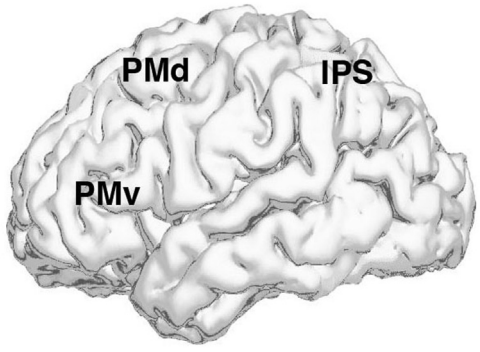

Fig. 2. Lateral view of the human cerebral cortex showing three regions revealing modulation of the BOLD signals specific to visual stimuli presented in peripersonal space: dorsal premotor (PMd) e ventral premotor (PMv) areas in the frontal lobe, and the anterior portion of the intraparietal sulcus (IPS)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

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

In the macaque monkey, the inferior aspect of the premotor cortex (area 6), particularly its caudal portion (i.e., the histochemical area F4 where proximal arm movements are represented; Matelli et al., 1985), contains neurons that reliably respond to tactile stimulation. These neurons are characterized by relatively large tactile receptive fields (RFs), located primarily on the monkey's face, neck, arm, hand (or both hands) and face (i.e., in the peribuccal region; Rizzolatti et al., 1981a), and arranged to form a crude map of the body surface. A large proportion of neurons in area F4 are bimodal, discharging in response to both tactile and visual stimuli. Critically, unlike classical visual neurons, F4 neurons respond poorly to light stimuli far from the animal, but are effectively triggered mostly by real three-dimensional objects moving near the animal, in its peripersonal space (Gentilucci et al., 1983, 1988; Rizzolatti et al., 1981a). Some F4 neurons respond only to stimuli very close to the body surface (less than 10 cm away; pericutaneous neurons), while others can be triggered by stimuli located further away, but always within the animal's reaching distance (e.g., distant peripersonal neurons). The visual and tactile RFs of F4 neurons are in spatial register with one another, thus forming a single responsive region mapping the bodily surface and the space immediately adjacent to it. More recently, Graziano et al. (1999) showed that F4 neurons integrate not only tactile and visual but also auditory information about the location of objects within PPS, thereby indicating that premotor area F4 instantiates a multimodal representation of nearby space.

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

These results provide strong evidence that, unlike brain areas related to the control of eye movements, F4 neurons do not code space in a coordinate system centered on the retina (Andersen 1987; Goldberg et al., 1990). Rather, F4 neurons appear to code the location of a visual stimulus with respect to the face, arm, hand, or other body parts. This type of body part-centered reference frame appears to be extremely appropriate for organizing head and arm movements toward or away from visual objects, since head and arm movements are also programmed in body part-centered coordinates (Cohen and Andersen, 2002).

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

Second, some bimodal, visual–tactile neurons were shown to respond to visual objects presented near a fake monkey arm prepared by a taxidermist and placed in a realistic posture (Graziano, 1999). In this study, a stuffed monkey arm was placed above a