Organization of space perception: neural representation of three-dimensional space in the posterior parietal cortex

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The representation of perceptual space in the posterior parietal cortex can be divided into at least two categories: far space, beyond arm's reach, and peripersonal space, within arm's reach. These are encoded by different groups of neurons that are closely related to the control of gaze and the guidance of arm and hand movement, respectively.

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Introduction

Space perception provides information about where objects are in the environment and how they move. It may be dissociated from pattern perception, which provides information about what the objects are and how they are characterized. The dissociation of these two modes of perception is particularly clear in the visual system, as demonstrated by Mishkin and his associates in monkeys on the basis of lesion studies and anatomical studies with 2-deoxyglucose [1,2]. Recently, Haxby *et al.* [3•] have dissociated object and spatial visual processing in human cerebral cortex using the positron emission tomography method. Since the 1970's neurophysiological studies of association cortices in alert monkeys have continued to provide evidence supporting the idea that posterior parietal cortex may be concerned with space perception as well as spatial control of movements [4–7]. This review will focus on recent findings concerning the neural representation of spatial location and motion in the parietal cortex and its vicinity, with a particular emphasis on new insights provided by studies of visually guided movements.

Neural representation of visual space in the parietal cortex

One of the fundamental problems of visual space perception is how the retinotopic signal of position is transformed into the head coordinate system and eventually into body-centered coordinates. To accomplish this, the perceptual system must take into account the extraretinal signal of eye position [8]. The posterior parietal cortex is the most likely area of the brain involved in such transformations, as lesions in this area in humans cause visual disorientation [9]. Monkeys with lesions of the inferior parietal cortex also show disturbance in visuospatial discrimination tasks [10].

Eye position-dependent visual neurons

The remarkable effect of eye position upon the visual response of light-sensitive (visual) neurons in area 7a was first noted by Andersen and Mountcastle [11]. They found that the receptive fields of area 7a neurons did not change their retinotopic position as a function of eye position, but their excitability altered [12]. This interaction of eye and retinal position produces a neural code of the locations of visual targets in head-centered coordinates (for a review, see [13]). The responses of most of these neurons were modulated linearly with change in eye position along the horizontal, vertical or diagonal axes [14•], in the same way as the discharge rate of visual fixation neurons [15]. Thus, area 7a neurons do not have receptive fields for restricted locations in head-centered space, suggesting that the code for spatial location is distributed. This feature of the neurons has been demonstrated with a neural network model [16]. Similar types of gaze-dependent visual neurons have also been found in area V3A [17]. The receptive fields of V3A neurons are much smaller than those of area 7a neurons. As area V3A sends a cortico–cortical projection to area 7a by way of the dorsal prelunate (DP) area [18], it is possible that the eye position effects are initially produced in area V3A and then transferred to area 7a.

Neural code of body-centered coordinates

In order to produce a body-centered representation of spatial location, head position would need to be incorporated into the activity of eye-position dependent visual neurons in area 7a. Brotchie and Andersen (*Soc Neurosci Abstr* 1991, 17:1218) have studied the effect of both head and eye positions on the visual or saccade-related

Abbreviations

DP—dorsal prelunate area; **LIP**—lateral intraparietal area; **MT**—middle temporal area; **STP**—superior temporal polysensory area; **Tpt**—temporo-parietal area; **VIP**—ventral intraparietal area.

activity of area 7a and lateral intraparietal (LIP) neurons. The monkey was trained to orient either its head or eyes toward a fixation target, and make visually guided saccades from different initial eye and head positions. The responses of the majority of neurons recorded during this task were modulated as a linear function of gaze position rather than just head position or eye position.

Neural code of egocentric distance

There are a number of visual cues for the perception of depth in the visual world, but extraretinal signals of convergence and accommodation play crucial roles in estimating absolute distance in egocentric space [19]. Many visual fixation neurons in area 7a are selective with respect to the distance of the fixation point, suggesting that these neurons mediate the extraretinal signals [4,15]. Gnadt and Mays (*Soc Neurosci Abstr* 1989, 15: 313.4) have found that some parietal eye-position dependent visual neurons are modulated by both conjugate and disjunctive eye position. This suggests that at least some visual neurons in the parietal cortex receive extraretinal signals of convergence to code three-dimensional position in egocentric space.

Integration of polysensory signals to represent space around the body

We perceive the space around our body not only with visual signals but also with tactile and auditory signals. Neural representations of space in these different sensory modalities need to be integrated into a common frame of reference in order to orient the body and guide limb movements. Such a process of multimodal integration seems to take place in and around the parietal cortex.

Convergence of visual and somatosensory signals in areas 7b and VIP

Polysensory neurons that respond to visual and somatosensory stimuli are found in area 7b (the anterolateral part of the inferior parietal lobule) [20]. Many of these neurons respond to visual stimuli that move towards the cutaneous receptive field or at a close distance (5–10 cm) to it, and their response does not change with a change in the direction of gaze [21]. Recently, Duhamel *et al.* [22•] found a similar type of neuron in the ventral intraparietal (VIP) area, which is located in the fundus of the intraparietal sulcus. Because area VIP receives input from the middle temporal (MT) area of the prestriate cortex [23,24], most of the neurons in area VIP are sensitive to visual movement and are directionally selective. The majority of these neurons also respond to somatosensory stimulation and are therefore truly bimodal. The authors found a striking correspondence between the locations and sizes of visual and somatosensory receptive fields, and there was also a matching in directional selectivity in the two sensory modalities. Many of the neurons in area VIP were selective for depth, and some of them preferred 'ultra-near' stimuli (within 5 cm of the monkey's face). These bimodal neurons may represent immediate extrapersonal space or the 'peripersonal' space around the skin or within arm's reach.

Visual and somatosensory neurons of the premotor cortex and the representation of peripersonal space

Rizzolatti *et al.* [25] have found that in monkeys many neurons of the postarcuate cortex of the premotor area respond to both visual and somatosensory stimuli. About half of the visual receptive fields of these neurons were located near the skin of the animal and were called 'pericutaneous' receptive fields. The other half were within reach of the hand and were called 'distant peripersonal' receptive fields. A large number of these bimodal (visual and somatosensory) neurons had visual receptive fields that were not retinotopic and which remained in register with the tactile receptive fields even if the eyes moved [26].

In contrast to premotor neurons, neurons of the prearcuate cortex (frontal eye field) respond to visual stimuli presented far from the animal. A dichotomy of peripersonal and 'far' space has also been suggested by lesion studies of periarcuate cortex [27]. Lesions of the inferior premotor area cause visual neglect in peripersonal space but not in far space, whereas lesions of the frontal eye field caused neglect in far space but not in pericutaneous space.

Because there are reciprocal cortico–cortical connections between the postarcuate cortex and the posterior bank of the intraparietal sulcus [28], it is likely that the neural representation of peripersonal space is formulated in areas 7b and VIP and transferred to the premotor cortex to be used for motor control. Similarly, the gaze-dependent area 7a or LIP neurons may represent far space and send their signals to the frontal eye field to be used for the control of the direction of gaze.

Recently, Halligan and Marshall [29•] reported a case of right hemisphere damage that included posterior parietal cortex. The patient exhibited a severe left visuo-spatial neglect within peripersonal space but not in far space. Large errors were made by the patient in line bisection using a pen at a distance of 0.45 m, but performance was nearly normal in line bisection using a pointing light at a distance of 2.44 m. This suggests that in the human brain there may also be functional dissociation of near (peripersonal) and far visual space.

Multimodal neurons in the superior temporal polysensory area

The cortex of the dorsal bank and fundus of the superior temporal sulcus is called the superior temporal polysensory (STP) area, because many neurons in this area respond to more than one sensory modality [30,31]. Hikosaka *et al.* [32] have studied the receptive fields of neurons in the caudal part of STP. This area is just posterior to the temporo-parietal (Tpt) area in which Leinonen *et al.* [33] found many auditory neurons with receptive fields around the head of the animal. Whereas area Tpt is likely to represent auditory space, caudal STP is thought to be concerned with the integration of visual and auditory signals around the body. The large majority of unimodal cells were either visual or auditory and most of the multimodal cells were both visual and auditory.

Because both the visual and auditory receptive fields are large, the caudal STP cells are not likely to be coding the precise location of stimuli in space, but they may play an important role in the coordination of visual and auditory space perception. For most visual/auditory cells, the visual receptive fields overlap with the auditory receptive fields. For other cells, however, the auditory receptive fields are juxtaposed to the periphery of the visual receptive fields. The latter type of receptive field seems to be important for representing space behind the body as a continuation of the visible space in front of the body.

Neural coding of spatial characteristics related to hand and arm movement

In earlier studies of the parietal cortex, in both areas 5 and 7, many neurons were found to be related to active movements of the hand and arm [5, 6]. Recent studies of parietal neurons related to hand manipulation demonstrate their remarkable selectivity for the spatial characteristics of these movements.

Hand-movement related neurons of the inferior parietal lobule

Taira *et al.* [34•] found a group of neurons in the posterior bank of the intraparietal sulcus that were specifically related to the active movement of the hand. Many of them had both visual and motor components in their activity, and were selective for the spatial characteristics of the object to be manipulated, such as shape, size, orientation of axis, and spatial arrangement. These characteristics are all crucial for the adjustment of shape and orientation of the hand. Some of the neurons in this area were purely visual and responded to the appearance of the target object or even to simpler stimuli, such as a luminous bar in a particular orientation [35]. Thus, a study of hand-movement related neurons discloses features of visual information processing underlying visually-guided movement. It appears that parietal neurons in this area selectively extract visual information concerning spatial characteristics that is necessary to guide the hand movement.

Dissociation of visual motor guidance from visual perception

Recently Goodale *et al.* [36] and Milner *et al.* [37•] described a patient with visual agnosia following carbon monoxide poisoning, who showed accurate guidance of hand movement, despite an inability to recognize the size, shape and orientation of visual objects. Although magnetic resonance imaging revealed diffuse brain damage, the major damage was on the lower aspects of the lateral occipital cortex. In contrast, patients with optic ataxia have difficulty in adjusting the orientation of the hand to that of a target, although none of them show any disturbance of visual space perception [38]. The patients with optic ataxia had lesions in the posterior parietal cortex, which always included the intraparietal sulcus. On the basis of these observations in human patients, Goodale and Milner [39•] argue that the parietal cortex is mainly concerned with the visual guidance of actions, but not with visual space perception *per se*. An alternative interpretation is that the parietal lobe mechanisms of space perception are supramodal and dissociable from modality-specific visual perception, in the same way that spatial attention is supramodal [40] and visual imagery is dissociable from spatial imagery [41]. In any case, it is clear that the parietal cortex houses a neural representation of space that can guide the actions necessary for manipulating real objects in the environment.

Conclusion

The recent neurophysiological and neuropsychological evidence summarized in this review suggests that the neural substrates of space perception and spatial control of movements are inseparably connected within the parietal cortex. The location of visual objects in space is represented by parietal visual neurons receiving extraretinal signals of eye and head position. These neurons may be concerned mainly with far space, beyond the arm's reach, and may send their signals to the frontal eye field to guide eye movements. Many of the visual fixation neurons, on the other hand, are selective for the distance of the fixation point, and may represent egocentric distance of the visual target, which is necessary to guide reaching. Bimodal (visual and somatosensory) neurons of areas 7b and VIP are likely to represent peripersonal space, within reach of the hand. Most of them have visual receptive fields that are independent of eye position and related to somatotopic location. They may send their signals to the premotor cortex to guide hand and arm movements. Visual signals to the hand-movement related neurons in the posterior bank of the intraparietal sulcus appear to represent spatial characteristics of the target object other than spatial location, which are necessary to guide hand actions.

Further studies of the neural mechanisms underlying space perception may be based on the hypothesis that space perception is organized in such a way as to be relevant to the guidance of movements and actions in the environment.

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