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Where am I and how will I get there from here? A role for posterior parietal cortex in the integration of spatial information and route planning

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ABSTRACT

The ability of an organism to accurately navigate from one place to another requires integration of multiple spatial constructs, including the determination of one's position and direction in space relative to allocentric landmarks, movement velocity, and the perceived location of the goal of the movement. In this review, we propose that while limbic areas are important for the sense of spatial orientation, the posterior parietal cortex is responsible for relating this sense with the location of a navigational goal and in formulating a plan to attain it. Hence, the posterior parietal cortex is important for the computation of the correct trajectory or route to be followed while navigating. Prefrontal and motor areas are subsequently responsible for executing the planned movement. Using this theory, we are able to bridge the gap between the rodent and primate literatures by suggesting that the allocentric role of the rodent PPC is largely analogous to the egocentric role typically emphasized in primates, that is, the integration of spatial orientation with potential goals in the planning of goal-directed movements.

1. Introduction

This review examines the role the posterior parietal cortex (PPC) plays in spatial orientation and navigation. The successful act of navigation likely requires the integration of a number of different spatial constructs, including location and directional heading, the perception of linear and angular movement, the updating of spatial orientation after movement using idiothetic and landmark cues, and finding one's way along a route – often referred to as wayfinding. We argue that one role of the PPC in this behavior is to integrate the organism's perceived spatial orientation (i.e., the perception of current location and directional heading relative to the immediate surrounding environment) with the overall spatial view of the world (i.e., the spatial relationships of landmarks and goals with one another) in order to formulate an accurate route or trajectory to a goal. To expand on this concept further, consider the process of memory. It is often described as consisting of three major processes: (1) encoding, (2) consolidation, and (3) retrieval. A deficit in any one of these three functions will result in impaired performance on a memory task. Similarly, navigation can be thought of as composed of three processes: (1) spatial orientation, (2) manipulation of spatial representations to enable the computation of a planned route, and (3) execution of the plan. Like memory, a deficit in any one of these processes would result in poor output – in this case inaccurate navigation. In this review, we contend that navigational deficits seen after damage to the PPC are largely due to an inability to integrate spatial orientation with the spatial position of the final goal and in formulating a plan to attain that goal. In this view, it is thus possible to have a deficit in navigation without an impairment in the individual's perceived spatial orientation.

This view is consistent with a number of observations about the types of spatial deficits experienced by subjects with parietal damage. For example, one of the more well-known parietal disorders is Balint's syndrome – an ataxia where the subject is unable to make an accurate limb movement to a target location (Balint, 1909; Damasio & Benton, 1979; Holmes, 1918). The deficit is usually characterized as an inability to integrate visual spatial information about the target with the necessary motor movements required to attain it. Note, however, that the patient may have a normal perception of their own spatial orientation, and that they can execute a movement to the goal, albeit an inaccurate one. Thus, the deficit appears to lie in understanding the spatial relationships between the body and the target and/or in computing an accurate limb movement from one spatial position to another. In many ways, the problem these patients have is analogous to the navigational deficits seen in rodents with parietal damage, with the primary difference being one of scale. The primate literature has mainly focused on tasks requiring the manipulation of spatial relationships within the personal space of the subject (i.e., Balint's syndrome) (e.g., Buneo & Andersen, 2006; Colby & Goldberg, 1999; Snyder, Grieve, Brotchie, & Andersen, 1998) or the use of functional-imaging tech-

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niques with subjects that are stationary and performing a spatial task (Aguirre & D'Esposito, 1997; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Maguire, Spiers, & O'Keefe, 2001; Maguire et al., 1998; Merriam, Genovese, & Colby, 2003). In contrast, rodent studies have emphasized tasks on a much larger scale addressing issues of whether an animal can accurately navigate from one location to another (e.g., Parron & Save, 2004; Save, Guazzelli, & Poucet, 2001; Save & Moghaddam, 1996). In both cases, the deficits are similar in the sense that there is an inability to manipulate spatial relationships to formulate a plan to accurately move the body or limb to another place in space. In this review, we argue that one of the major roles of the PPC is to perform this integration of spatial information in the planning of goal-directed movements. We will provide further evidence that humans and animals with PPC damage retain the ability to perceive their spatial orientation and execute a movement, but have deficits in understanding the spatial relationships amongst different elements in the environment, which then leads to errors in determining an accurate route to a goal.

2. Two forms of navigation

Animals appear to use two basic and complementary processes for localization of position and directional heading while navigating. Path integration (also known as dead reckoning) is the process by which current position is estimated by performing an integration of movement velocity (direction and speed of movement) over time since the last known position (Gallistel, 1990; Mittelstaedt & Mittelstaedt, 1980). During locomotion, movement velocity can be estimated using self-movement (idiothetic) cues such as vestibular signals of linear and angular head velocity, proprioceptive cues, optic-flow, and motor efference copy. While Darwin (1873) himself hypothesized that animals may navigate in this way, Mittelstaedt and Mittelstaedt (1980) provided some of the first documented evidence of this in a mammal, by showing that if gerbil pups are displaced from their nest in total darkness, the mother upon finding them can take a direct route back to the nest in the absence of orienting landmarks, despite taking a meandering path in her outward search. While the idiothetic cues used for path integration are readily available during self-motion, this process does have shortcomings as accuracy is dependent on the continually updated, error free, storage of movement information. Any errors occurring during this process will tend to accumulate, leading to increasingly larger inaccuracies in position estimation over the course of an excursion. A second method of estimating one's position, landmark navigation (also known as piloting or place recognition), relies upon the presence of stable allothetic (landmark) cues in the environment (Gallistel, 1990). Perhaps the best example of this technique in the laboratory is the classic Morris water maze (Morris, 1981), where the animal is placed in a pool of opaque water at random positions and must learn to locate the position of a hidden platform based on the constellation of visual cues in the surrounding room. While landmark navigation would appear to be more accurate than path integration (or at least less prone to error accumulation), the availability of familiar landmarks on a given excursion may be limited, and so a compromise is to use the process of landmark navigation to locate one's position when landmarks are available, and path integration to accurately navigate in the absence of available landmarks.

3. The role of posterior parietal cortex in navigational behavior

While much attention has been given to the navigational role of subcortical limbic structures and associated limbic cortex, we know much less about the role of the neocortex in this behavior, despite the fact that the sensory and motor signals necessary for path integration and landmark navigation may readily occur there. Clinical case studies have long recognized the importance of the parietal cortex for spatial orientation, as several studies have shown that parietal damage leads to topographic disorientation (De Renzi, 1982; Hublet & Demeurisse, 1992). Similarly, a number of investigators have suggested that the posterior parietal cortex (PPC) may be an important area in the rat neocortex for navigation (Arbib, 1997; McNaughton, Leonard, & Chen, 1989; Save & Poucet, 2000a). The origin of this view mostly arises out of the role of the primate PPC in spatial orientation and subsequent attempts to identify a rat homologue to this area.

In the earliest electrophysiological investigation of the primate PPC, Mountcastle and colleagues described PPC (equivalent to Broadman's areas 5 and 7) as a multisensory area involved in directing attention to and exploration of space close to the body (Mountcastle, Lynch, Georgopoulous, Sakata, & Acuna, 1975). While Ungerleider and Mishkin (1982) considered PPC as visual association cortex, and included it as an element of the dorsal visual stream important for processing the "where" aspect of visual perception, Goodale and Milner (1992) modified this view to the role of processing visually guided actions. Human patients with damage to PPC show deficits such as unilateral neglect and errors in reaching for a visual target (Critchley, 1953), deficits that cannot be described as strictly sensory or motor, but rather a combination of these two functions. In accordance with this view, recent conceptualizations of this area in the primate give it an important role in sensory–motor transformation, providing multiple action-specific reference frames from which spatial targets close to the body are transformed into egocentric[1] coordinates for the planning and/or guidance of movements (Buneo & Andersen, 2006; Colby & Goldberg, 1999; Medendorp, Beurze, Van Pelt, & Van Der Werf, 2008).

Early attempts at characterizing the rat cerebral cortex did so largely on the basis of cytocharchitecture and there was much disagreement as to the extent and location of the associative parietal areas (for a review, see Corwin & Reep, 1998). In one of the earliest descriptions of the rat cortex, Krieg (1946) identified the equivalent of Broadman's area 7 distinct from the more rostral somatosensory cortex and caudal occipital cortex. Subsequent authors either verified (Kolb & Walkey, 1987) or disputed (Chandler, King, Corwin, & Reep, 1992; Zilles & Wree, 1985) the ability to distinguish on cytoarchitectural grounds a true area 7 or PPC from visual association cortex. This lack of anatomical clarity as to the location and extent of rat PPC has led to methodological differences among researchers using a lesion approach to study the function of this area. In localizing their lesion sites most investigators have used similar coordinates for PPC in the medial–lateral dimension, beginning 1.5–2 mm lateral to the midline and spanning 3–4 mm to the side; however, there are wide variations in the anterior–posterior placements of PPC lesions across studies. For instance, DiMattia and Kesner (1988) localized PPC as a 4 mm long strip with the rostral border beginning 0.5 mm anterior to Bregma. In contrast, Kolb and Walkey (1987) and Save and Poucet (2000b) used an area of similar dimensions, but marked the rostral border 2 mm posterior to Bregma. Finally, Ward and Brown (1997) utilized a 2 mm long lesion beginning approximately 4 mm behind Bregma. A more recent strategy is to localize PPC on the basis of the unique connections of this area to thalamic and cortical structures (e.g., Corwin & Reep, 1998; Save & Poucet, 2000a). In addition to potentially being less subjective than the earlier cytoarchitectural studies, this ap-

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[1] Egocentric space is defined by using the organism as the reference frame. In contrast, allocentric space uses the external world as the reference frame. For example, an animal utilizing a rule to always turn right at the choice points in a maze is using an egocentric reference frame while an animal that uses landmarks to guide itself to go north, south, east, or west is using an allocentric reference frame.