The Posterior Parietal Cortex

The posterior parietal cortex, along with temporal and prefrontal cortices, is one of the three major associative regions in cortex. It is situated between the visual cortex at the caudal pole of the brain and somatosensory cortex just behind the central sulcus. Technically, any cortex that is covered by the parietal bone is referred to as "parietal cortex", but the posterior sector, formally referred to as posterior parietal cortex (PPC), is indeed its own functional section of cortex, consisting of Brodmann's areas 5, 7, 39, and 40, in humans, areas 5 and 7 in macaques, and area 7 in rodents (Figure 1). While the anterior parietal cortex in humans comprises primary somatosensory areas, the PPC has several higher-order functions. It is labeled as an "associative" cortical region since it is neither strictly sensory nor motor, but combines inputs from a number of brains areas including somatosensory, auditory, visual, motor, cingulate and prefrontal cortices, and it integrates proprioceptive and vestibular signals from subcortical areas. By virtue of its vast connectivity (Figure 2), different portions of PPC participate in multiple cognitive processes including, but not limited to, sensorimotor integration, spatial attention, spatial navigation, decision making, working memory, early motor planning, and more complex behaviors such as pantomiming the use of objects. It also mediates some abstract and symbolic cognitive capacities, including the representation of real and imagined spatial relationships, as well as numerical quantity and mathematical abilities. Though each function listed above currently comprises a proper sub-field in neuroscience (and therefore cannot be discussed at length here), it was not always clear that PPC performed such a diverse panoply of cognitive feats.

Our current understanding of the many types of neural representations in PPC is founded primarily on neurophysiological recordings from animal models, starting in the 1970's in non-human primates, followed by a smaller number of rodent studies beginning in the 1980's. In addition to neurophysiology, a number of labs now use genetically encoded calcium indicators to image the activity of hundreds to thousands of neurons at a time in behaving animals. Long before the development of modern recording techniques, however, the first insights into PPC function came from clinical observations of human patients recovering from stroke or head injuries. Thus, some of the more illuminating (and bizarre) clinical cases will be discussed before returning to the modern state of the field.

Clinical deficits: spatial coding and embodiment

One of the earliest characterizations of behavioral deficits following damage to PPC came from the Austro-Hungarian physician Rezsö Bálint. In 1909 he published a study detailing the symptoms of patients with bilateral stroke damage to PPC and the parieto-visual border areas. His patients presented three major common symptoms: *simultagnosia* (the inability to perceive more than one item in the visual field), *oculomotor apraxia* (difficulty in making targeted eye movements), and *optic ataxia* (the inability to make visually-guided arm and hand movements). In the case of optic ataxia, for example, a patient could look directly at an object in front of them, name it, but not be able to grasp it. The trio of deficits, referred to as "Bálint's Syndrome", provided the first major clues that PPC was critical to the construction of a map of peripersonal space and the coordination of actions in it. Contemporaneous work by British neurologists Henry Head and Gordon Holmes reported that damage to parietal cortex was often associated with a profound lack of awareness of bodily posture or the position of limbs, leading them to propose the concept of "body schema". Body schema, according to them, represent an individual's continuous awareness of how the body and its parts are configured in 3D space, providing a "standard against which all subsequent changes of posture are measured before they enter consciousness... every new posture or movement is recorded on this plastic schema." The essential role of PPC in generating body image was later confirmed and expanded upon in Macdonald Critchley's definitive clinical text, "The Parietal Lobes", published in 1953. In it, Critchley discussed not only patients with disturbances in body image and various motor apraxias, but a broader spectrum of neurological disorders including sensory disturbances, deficiencies in symbolic thought, mathematical abilities and visuospatial attention. A few patients exhibited *autotopagnosia*, or the inability to correctly locate a body part when instructed, while others showed a total loss of awareness of body parts altogether, often the fingers. In rare of cases patients were unaware that they were paralyzed on the left or right half of the body, while others exhibited hemispatial neglect, ignoring either their left or right visual hemifields altogether. Together these studies crystallized the notion that PPC played a critical role generating and guiding spatial awareness, as well as one's sense of orientation, limb location and how their statuses co-varied during movement. The neural representation of this last feature—the representation of body parts relative to one another—was precisely measured during neurophysiological recordings in monkeys and termed "gain modulation", more than 70 years after the work of Head and Holmes.

Modern day clinical investigations continue to underscore the importance of PPC in generating the sense of embodiment. Several insights have been gleaned through studying the effects of evaluative brain stimulation in open-skulled epileptic patients prior to surgery. In a fascinating study published by Blanke et al. in 2002, neurosurgeons applied focal electrical stimulation to different sectors of cortex including the ventral-most part of PPC, near the occipital border in the right hemisphere. Much to the surprise of the surgeons, stimulating this part of the brain induced an out of body experience in one female patient who, upon stimulation, reported "I see myself lying in bed, from above, but I only see my legs and lower trunk." Subsequent stimulation induced similar feelings of "lightness" and "floating" near the ceiling of the room, two meters above the bed. In 2006, Blanke's team published another study in which they applied stimulation to the junction of the left temporal and parietal lobes, which caused that patient to report the presence of a "shadow person" hovering just behind her, mimicking her body positions and movements. When she leaned forward and grasped her knees, for example, she sensed that he leaned forward as if to embrace her around the waist. In both studies the locations of the stimulations were in the very ventral regions of PPC, which is a site of massive confluence for visual, tactile, proprioceptive and vestibular signals. Both classical and modern-day clinical observations support the interpretation that our sense corporeal awareness and self-localization arise from an amalgamation of co-registered sensory signals: we feel like we are in our own bodies because our brains tell us so, and we remain unaware of this fact unless the process of sensory integration is perturbed.

PPC and navigation

The role of PPC in representing bodily position and spatial orientation is not limited to peripersonal space, but includes movement over larger spatial scales during navigation. Spatial navigation is a complex behavior that involves the interaction of multiple brain systems, and though PPC likely contributes in multiple ways, several lines of evidence point toward a role in formulating navigational routes. One of the key early insights into this came from a study by Eleanor Maguire and others, who measured levels of brain activity using functional magnetic resonance imaging (fMRI) while subjects navigated through a virtual town. They found that several cortical and sub-cortical areas showed heightened activation over the course various tasks, with inferior and medial parietal areas showing the highest activation when subjects computed sequences of turns and movements to reach a goal. The

hippocampus, on the other hand, was engaged during allocentric, or map-like, spatial processing and navigation. A subsequent study in Maguire's lab imaged the brains of London taxi drivers in an fMRI while they took pretend passengers to specific destinations in a "virtual London". The taxi drivers then watched videos of their performance after the task and gave post-hoc reports of what they were thinking at various stages of each journey. In line with previous findings, it was found that medial PPC was activated during "movement" planning in the immediate environment, such as changing lanes, while lateral areas of PPC were most active when drivers performed extended route planning beyond the present location. The functional imaging studies also resonated with a parallel line of work investigating PPC-damaged patients' abilities to perform "mental space travel" through familiar remembered landscapes. In this work, from the lab of Morris Moscovitch, it was reported that long-term residents of Toroto, Canada who suffered prior PPC damage had no problems recalling a detailed image of the city, but that they could not navigate mentally between known locations. Their subjective experience of imagined navigation was described as "impoverished and disembodied" relative to controls. Together, these and other studies have led to the interpretation that PPC is critically involved in transforming world-based spatial information from landmarks into first-person (i.e. egocentric) movement sequences required to reach a goal.

The work in humans is paralleled marvelously by multiple recording studies in animal models, including rats and macaque monkeys. In the case of rats, clear evidence of route mapping in PPC was reported in a 2006 paper by Douglas Nitz, in which PPC cells were recorded while freely behaving animals traversed irregular multi-part tracks (Figure 3A). It was found that many PPC neurons fired only when a particular movement (e.g. a left turn) was made at a certain point along the journey, and that the movement correlates of the cells changed depending on which path the animals ran. The firing fields were the same whether the lights were on or off, indicating that the cells followed the animals' internally generated sense of "route" as opposed to visual landmarks in the room. Further evidence of first-person based route mapping came from experiments by Whitlock et al., which showed that the "route" to which PPC cells were tuned did not even have to be physical. They found that simply having rats run in north-south sequences in an open arena was sufficient to elicit the same firing patterns recorded in PPC when the animals ran in a real maze consisting of north-south alleys. This is not to say that PPC does not make use of external landmarks when they are available—on the contrary, a recent paper by Wilber et al. found that subsets of cells in PPC in rats encoded movement types as well as the direction of goal locations

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relative to the animal's heading. First-person route-mapping functions have also been described in the medial parietal region in monkeys. In a 2006 study by Sato et al., neurons in the medial parietal region were recorded in macaques while they used a joystick to navigate through a virtual house to reach instructed end-locations. More than 75% of the PPC neurons that were active in the task appeared to encode certain "movements" (e.g. a right turn) made at specific locations (e.g. before the stairs). Similar to the findings in rats, the firing fields in this task were specific to the different routes the animals took, and pharmacological inactivation of the medial parietal region caused the animals to become lost during navigational trials. And much like monkeys, disruption of PPC in rats and mice also results in navigational deficits, often in selecting the correct trajectory to reach a goal. Thus, studies in humans, monkeys and rats point to a key role for PPC in constructing first-person route maps which can be calibrated against external landmarks, a function at the interface between egocentric and allocentric frames of reference.

Gain modulation in PPC

The co-registration of signals across reference frames in general, whether they are body-based or world-based, is a cardinal feature of neural coding in PPC. Take, for example, swatting a fly buzzing just above your head. When you first hear the sound of the fly you move your eyes and head up to spot it, and without hesitation you can swing at it with your hand. In order for the sensory information regarding the fly's location to be of service to your hand, visual and auditory signals must first be transformed into reference frames that are intelligible to your motor system. This process of coordinate transformation occurs over several steps, including the co-registration of the location of the fly image on your retina with where your eyes are in their orbits, which is in turn co-registered with head position relative to your shoulders and the horizon, which is co-registered with your shoulder position relative to your torso, and so on. Each step is an example of a neural computation termed "gain modulation", in which the coding of one variable (the image of the fly on your retina) is multiplied by an independent variable (the orbital position of your eyes relative to your head), leading to a single signal encoding both features simultaneously. As pointed out earlier, the concept of gain modulation was evident already at the turn of the 20th century, but it was not recorded in the brain until the 1980's, when Richard Andersen and Vernon Mountcastle showed that the coding of a visual stimulus in the monkey PPC varied dramatically depending on where the animal's eyes were fixated. This elegant form of sensory interweaving has been reported during a variety of spatially guided behaviors,

including movements of they eyes, head, arm, hand, whole body and even the locus of one's attention. Previous work specifically demonstrated that cells in PPC can encode the end goals of hand movements relative to where the animals' eyes were fixated (Figure 3C)—a computation which would indeed come in handy when trying to swat away a flying pest. In light of these and many other electrophysiological studies, the neural mechanisms underlying spatially targeted action and attention have become much clearer in recent decades, providing an increasingly detailed framework for understanding the symptomologies described in both early and ongoing clinical studies.

Imitation and mirror neurons

Perhaps one of the most unusual features of PPC is its involvement in coordinating not only actions in first-person, but in imitating actions observed of others. To borrow the earlier parlance of Henry Head, PPC enables one to map their own "body schema" onto that of another individual, and damage to PPC can impair this ability in a condition referred to as *visuo-imitative apraxia*. The inability to imitate observed movements is part of the larger family of motor apraxias observed following PPC damage, and has been best documented as deficits in mimicking hand positions and hand gestures. For example, patients with left PPC damage have been reported as having difficulty in pantomiming the use of various objects, such as hammering a nail, whether they were instructed to do so verbally or by visual demonstration. Such patients could still use a real hammer and nail, and they could identify such behaviors performed by someone else, but they lacked the ability conjure up the motor program using sensory or verbal input. Conversely, functional imaging work by Frey and Gerry (2006) revealed that the brains of normal individuals showed heightened activation in the inferior parietal cortices and ventral pre-motor cortices when passively viewing hand-object interactions, and that the level of activation was larger when viewing with the intention to imitate the movements afterward.

At the cellular level, sensory-motor matching has been recorded directly in the form of "mirror" neurons, which are neurons that fire whether a particular action is made or merely observed. Mirror neurons were discovered in the monkey pre-motor cortex in the lab of Giacomo Rizzolatti, where it was found that neurons that fired when the animal grabbed a piece of food also fired when the monkey simply watched one of the experimenters do the same. Since then, mirror neurons have been described in other areas of the cortical motor system, including the inferior parietal lobe and primary motor cortex,

as well as other areas which process emotions and facial expressions. As far as PPC is concerned, a cleverly designed study by Fogassi et al. recorded from neurons in the inferior parietal lobe of macaques while they grasped a piece of food and either it or placed in a cup by their mouth. Subsets of cells were modulated by the end-goal of the action, firing only when grasping was followed by eating or placing the food in a cup. Incredibly, they recorded from mirror neurons that showed similar goal-specificity for observed actions— that is, the cells encoded what the monkey *expected the demonstrator to do* with the grasped object. There are few examples in the field that provide such a direct window on the intersection of motor neurophysiology and social cognition. Outside of monkeys, mirror neurons have been recorded in humans prior to neurosurgery, and very elegant work in birds has directly recorded changes in the "mirror" properties of pre-motor neurons in juvenile birds when they learned a new song. While it has not yet been causally demonstrated that mirror neurons enable imitative learning in mammals, the unique coding properties of the cells would provide a logical mechanism for teaching a "blind" motor system new behaviors using visual or other sensory information. What remains a matter of great debate, however, is the broader role of the mirror neuron system in understanding the conceptual meaning of observed behaviors, and other processes such as emotional cognition and social awareness.

Conclusions

As evidenced by the diversity of literatures and sub-areas of research, PPC clearly participates in a manifold of cognitive functions, and just a few were touched upon here. While the present discussion was centered around the theme of body schema and neural coding in first-person, PPC also plays a major role in shaping how we see the world "out there". For example, the deficiencies in spatial attention seen after PPC damage extend well beyond corporeal awareness, and include features and images in the outside world. Nowhere is this more clearly evidenced than in patients with hemispatial neglect who, when asked to copy a picture of a clock or house, will only copy the right half of the picture. Fascinating neurophysiological recordings have also shown that the locus of visual receptive fields in PPC will pre-emptively shift in the direction of an impending eye movement, again illustrating the quintessential role for PPC in linking together the "inside" and "outside" worlds. Other major topics of study in PPC include selective attention, evidence accumulation, decision making and working memory, and entire reviews on those topics are listed below in "Further Reading." As modern experimental tools advance and enable increasingly sophisticated questions, the field will continue to dissect the functions of different cell types, microcircuits, and anatomical connections which link PPC with other

areas. For example, what are the inputs that a mirror cell in PPC receives that make it a mirror cell, but not the cell next to it? As recording techniques advance we also stand to gain deeper insights into network-level computations implemented in PPC when solving tasks with different cognitive or behavioral demands. If we neuroscientists are successful, common computational principles will begin to emerge which link PPC functions that were previously taken as unrelated, and perhaps those computations will be surprisingly similar across mice, monkeys and humans.

Further Reading

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Figure Legends

Figure 1. Topography of PPC relative to other cortical areas
Lateral view of human, macaque and rat brains, showing the organization of visual, posterior parietal, somatosensory and primary motor areas of cortex. The ordering of cortical areas is the same for all mammals, with the visual areas furthest posterior, PPC lying between visual and somatosensory areas, and primary motor areas in front of somatosensory cortex.
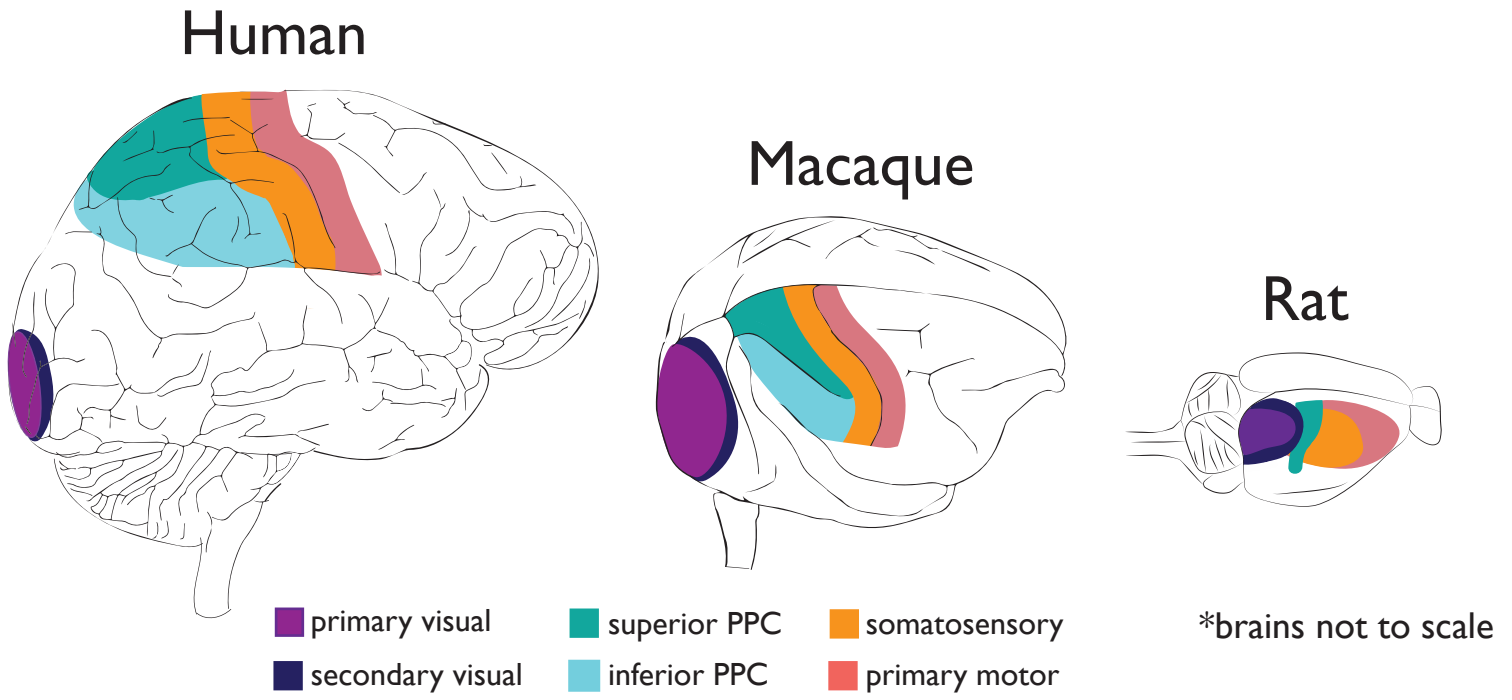
Figure 2. Cortical and sub-cortical connections of PPC
Shown in schematic form, a given neuron in PPC can receive input and send output to a large number of areas in different systems of the brain. The diversity of connections speaks to the variety of behaviors in which PPC participates, including decision-making, spatial attention, working memory, movement planning, navigation, as well as processing visual, somatosensory and auditory signals.
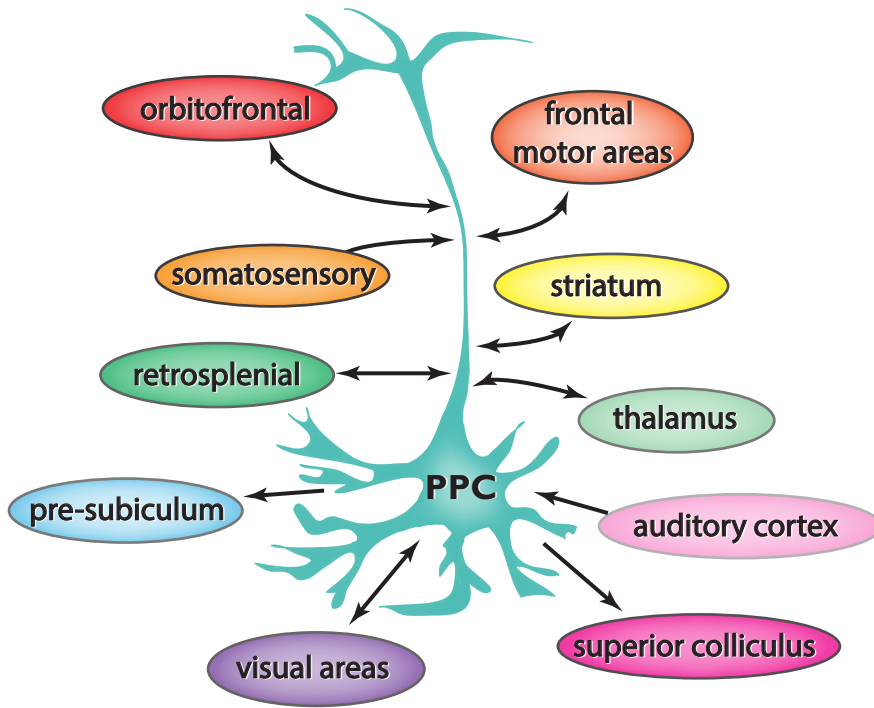
Figure 3. Behavioral paradigms for studying PPC
Common animal models used for studying PPC include monkeys, rats and mice, though PPC anatomy and physiology have been studied in several species, including cats, bats, ferrets, pro-simian galagos, and new-world monkeys. Different species bring different advantages depending on the experimental question. **A**) Rodents are a popular model for studying spatial navigation since neural activity can be recorded in freely-behaving subjects as they move about different environments. Route-tracking functions were described in PPC in rats running irregular paths as shown. **B)** Rats and mice have also been studied in evidence accumulation and decision making-task. Here, instructional auditory and visual stimuli are delivered at a certain frequency while the rat keeps its nose in a center port; based on the frequency, the animal must decide to orient left or right to get a liquid reward. **C)** Studies in head-fixed primates have provided the foundation for understanding the behavioral neurophysiology of PPC. Shown here is an example of a visually-instructed reaching task, in which the animal moves its hand to where a stimulus was flashed on the screen (middle). The hypothetical neuron (spikes shown below) fires maximally when the hand moves to the target directly above where they eyes are looking. It illustrates the findings of Batista et al., which showed that reach-related neural spiking was co-modulated by where the hand moved to relative to the eye.

Figure 1

Human

Macaque

Rat

*brains not to scale

- ■ primary visual
- ■ secondary visual
- ■ superior PPC
- ■ inferior PPC
- ■ somatosensory
- ■ primary motor

Figure 2

Figure 3

A

B

visual + auditory cues

Choose left   Choose right

C

Fixate   Cue for reach   Reach

neural firing

time   time   time