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Neural correlates of learning and working memory in the primate posterior parietal cortex

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Abstract

The posterior parietal cortex has been traditionally associated with coordinate transformations necessary for interaction with the environment and with visual-spatial attention. More recently, involvement of posterior parietal cortex in other cognitive functions such as working memory and task learning has become evident. Neurophysiological experiments in non-human primates and human imaging studies have revealed neural correlates of memory and learning at the single neuron and at the brain network level. During working memory, posterior parietal neurons continue to discharge and to represent stimuli that are no longer present. This activation resembles the responses of prefrontal neurons, although important differences have been identified in terms of the ability to resist stimulation by distracting stimuli, which is more evident in the prefrontal than the posterior parietal cortex. Posterior parietal neurons also become active during tasks that require the organization of information into larger structured elements and their activity is modulated according to learned context-dependent rules. Neural correlates of learning can be observed in the mean discharge rate and spectral power of neuronal spike trains after training to perform new task sets or rules. These findings demonstrate the importance of posterior parietal cortex in brain networks mediating working memory and learning.

Keywords

Monkey; area 7a; intraparietal sulcus; attention; neurophysiology

1. Introduction

Experiencing the world is dependent upon an observer's ability to amalgamate disjunct waves of sensation into a cohesive internalized model that depicts the surrounding environment. From this internalized representation, the viewer can extract the necessary information to effect meaningful interaction with the environment and its component objects. The brains of higher animals adapted to handle the increasing sensory load by diversifying and distributing processing. In the primate visual system, segregated streams emerged to convey different aspects of each stimulus to be processed in parallel. The ventral visual pathway encodes physical attributes of a stimulus important for recognition and identification such as its color and shape, whereas the dorsal visual pathway tracks its location and movement (Ungerleider

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& Mishkin, 1982). The posterior parietal cortex (PPC) sits at the apex of the dorsal pathway and it is recognized as an important association area that acts as an interface between the external world and the actions of an animal. Functions of the PPC can be grouped in four domains: sensorimotor transformations, selective attention, working memory, and learning. We will provide a brief overview of these functions next, and focus on the latter two for the remainder of this review.

An important role of the PPC, recognized very early, is its function in receiving and integrating information across multiple sensory areas, and transforming it into a common reference system from which goal-directed motor movements can be computed (Batista, Buneo, Snyder, & Andersen, 1999; Seal, 1989; Stricanne, Andersen, & Mazzoni, 1996). To do this, it must take into account the changing alignment of body parts during movement. Eyes, head, trunk, and limbs move independently, each with its own intrinsic coordinate reference system that places items relative to itself. For example, an object tracked on a region of the observer's retina will be in a different location with respect to the head when the eyes are deviated within the orbits than when the eyes are oriented straight ahead. A turn of the head will produce a different frame of reference with respect to the trunk, limbs and so on. An ongoing series of computations must continuously update the body's internal model in order to maintain the fluid dynamic of interaction with the environment. These coordinate subsystems are encompassed by two larger points of view within the world schema: that of the egocentric observer, who understands the disposition of surrounding space and its contents in relationship to itself, and that of the allocentric point of view in which spatial maps are constructed based upon landmarks or relationships of objects relative to one another; the latter has emerged only recently in the phylogenetic lineage and also develops fairly late in adolescence in humans (Mathews, 1992; Pine, Grun, Maguire, Burgess, Zarahn, Koda, Fyer, Szeszko, & Bilder, 2002). Posterior parietal cortex has been implicated in mediating sensory motor behavior with reference to both viewpoints.

In spite of its level of development, the primate brain cannot process all sensory stimuli simultaneously. Instead, it must allocate resources to a particular stimulus or region in space in which a relevant event is occurring, or expected to occur. A second important function of the posterior parietal cortex is to act as a mediator of this process, known as selective attention. PPC has been shown under different experimental paradigms to be activated when an organism directs its attention towards or away from a specific location, as well as when the organism is actively maintaining attention on a locale (Constantinidis, 2006a).

Closely tied with the function of selective attention is working memory, or the ability to keep pieces of pertinent information temporarily available during ongoing execution of a mental operation. Working memory has traditionally been ascribed to the prefrontal cortex (PFC), but a wealth of recent research demonstrates that posterior parietal cortex is not only activated during working memory, but that inactivation of, or damage to posterior parietal regions can cause specific working memory deficits. This newfound role of PPC is not entirely surprising in view of the fact that this region has dense reciprocal connections with frontal cortex and limbic areas, thus placing it within a distributed network with other areas known to participate in the working memory circuit (Constantinidis & Procyk, 2004). The role of PPC in working memory will be the first focus of this review.

Selective attention and working memory are subservient to learning and long-term memory. Some prior experience must govern where an animal attends, what stimulus is to be remembered, and ultimately how to act with respect to that stimulus in order to achieve a result. Learning imparts the ability to react to a stimulus differently depending on the behavioral context and according to a desired goal. The effects of learning on PPC have received relatively less attention until recently, and will make up the second focus of this review.

2. Anatomical Organization

A gross overview of anatomical connections reveals that PPC receives inputs from primary and secondary sensory modalities and has extensive reciprocal connections with prefrontal association areas, frontal regions, limbic structures, as well as superior colliculus and basal ganglia. The triad of network modules comprised by the parietal association, the prefrontal association cortices and limbic regions defines one of the mainstays of higher cognitive behavior. Within PPC, there exists differential connectivity within these larger networks and diverse interconnectivity among distinct sub-regions, each with its own specialization.

The human posterior parietal region occupies the largest percentage of cortical area compared to any other primate (Hyvarinen, 1982). It lies within and along either side of the intraparietal sulcus (IPS), bounded anteriorly by the postcentral sulcus. It is comprised of Brodmann's areas (BA) 5, 7, 40 and 39 (Figure 1). Functional and anatomical studies that map posterior parietal function from the macaque onto human cortical analogues confirm that the PPC is relatively well aligned across species (Astafiev, 2003). Two general functional gradients can be identified, one running anterior to posterior and the other medial to lateral (Grefkes, 2005). Anterior structures, closest to somatosensory and motor brain regions, are involved in sensorimotor processing, whereas posterior structures in PPC, located next to extrastriate visual areas, are visually related. Areas situated within the medial bank of intraparietal sulcus are more closely associated with arm movement whereas regions along the lateral bank are mostly eye-movement related (Grefkes, 2005).

Though the human PPC is considerably more specialized than that of other primates, the monkey PPC is phylogenetically similar and can account for a wide range of functions observed in the human. As in the human brain, macaque PPC centers around the IPS and occupies areas 5 and 7 on either side of it (Figure 2). One can loosely define the boundary delineated by the Sylvian Sulcus (SS), the Superior Temporal Sulcus (STS) and the bend in the Lunate Sulcus, as the posterior-lateral edge of the PPC (Brodmann, 1909). Various subregions of PPC have been proposed (Pandya, 1982; Vogt & Vogt, 1919; von Bonin & Bailey, 1947; von Economo & Koskinas, 1925). Areas 5 and 7 have been further subdivided based on cytoarchitectonics and functional specialization. Within IPS, anterior, ventral, lateral, medial, and caudal intraparietal divisions have been identified, each also handling a different aspect of neural processing (Cavada & Goldman-Rakic, 1989a; Cavada & Goldman-Rakic, 1989b; Colby, 1999; Grefkes, 2005).

A source of confusion regarding PPC organization and function involves the correspondence between human and monkey PPC subdivisions. The first part of this dilemma arises from the discrepancy of area assignments from one species to another and the various naming schemes that have been applied by the pioneering anatomists. The gross level differences in area placements between species are immediately obvious in the anatomical atlases. In the human, Brodmann's areas 5 and 7 reside within the superior temporal lobule while areas 40 and 39 occupy most of the inferior parietal lobule. In monkeys, area 5 is found in the superior parietal lobule whereas areas 7a and 7b fall in the inferior parietal lobule. Brodmann's Areas 39 and 40 have not been identified in the monkey. An equivalent arrangement has been proposed by Von Economo and Koskinas for the human brain. In this nomenclature human area PG is roughly equivalent to Brodmann's human area 39, PF is in register with area 40, PE corresponds to area 7, and PA to area 5. Von Bonin and Baily adapted Von Economo's and Koskinas' terminology to the macaque brain. In their scheme, monkey area PG is best aligned with (monkey) area 7a, PF with 7b, and PE with area 5.

This anatomical ambiguity has impeded the establishment of a functional correspondence between human and monkey parietal areas, though some insights have been gained recently.

Activation of the human superior parietal gyrus has been observed during spatial attention shifts and visually guided saccades (Vandenberghe, Gitelman, Parrish, & Mesulam, 2001). Based on observations of activation to selectivity for saccade direction, others have ascribed macaque LIP as homolog to this area, (Koyama, Hasegawa, Osada, Adachi, Nakahara, & Miyashita, 2004; Nakahara, Adachi, Osada, & Miyashita, 2007; Sereno & Maunsell, 1998). Corbetta and colleagues have characterized activation of the temporoparietal junction (TPJ) in redirecting attention to behaviorally relevant stimuli in novel or unexpected locations (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Corbetta & Shulman, 2002), in analogy to area 7a activation in the monkey (Constantinidis & Steinmetz, 2001; Steinmetz & Constantinidis, 1995). However, few monkey neurophysiological studies have directly compared neuronal responses in multiple cortical areas in order to establish clear functional differences between them. Therefore, the functional correspondence between monkey and human areas remains unclear.

Despite this uncertainty, cytoarchitectonic and physiological studies in the macaque brain have determined a number of well-defined cortical areas. A brief overview of these areas is presented next, along with their major cortical patterns of connectivity and physiological properties that offer insights on their main functions.

2.1 Area 5 and MIP (PRR)

Area 5 (Figure 2) lies anterior to the intraparietal cortex and is interconnected with the primary and secondary somatosensory cortex, other parietal areas, as well as motor, premotor and supplemental motor cortices (Jones, 1978; Jones, 1969; Jones, 1970; Kunzle, 1978; Lynch, 1980; Petrides M, 1984; Strick & Kim, 1978). It additionally sends efferents to the corticospinal tract (Peele, 1942; Toyoshima K, 1982; Weisendanger, 1979). Adjacent to area 5, lining the medial bank of the Intra-Parietal Sulcus is the Medial Intraparietal area (MIP). This anatomical area corresponds to the functionally-defined Parietal Reach Region (PRR), although the latter may extend into area V6a as well (Cohen & Andersen, 2002). Both area 5 and PRR have been identified as part of a fronto-parietal network involved in generating reaching movements (Caminiti, Ferraina, & Mayer, 1998; Wise, Boussaoud, Johnson, & Caminiti, 1997). The Parietal Reach Region coordinates hand movements to visual targets within reaching distance, encoding impending arm movements in eye-centered coordinates (Batista et al., 1999; Snyder, Batista, & Andersen, 2000) and is activated during delay periods before memory guided arm movements (Snyder, Batista, & Andersen, 1997; Snyder et al., 2000). A gradient of neurons with strictly visual to strictly sensorimotor response properties runs from the fundus of the intraparietal sulcus to the outer edge within MIP, with bimodal neurons bridging the two pools (Colby & Duhamel, 1991). Activity during saccades is proposed to facilitate hand-eye coordination or maintain eye-centered object representation during reaching movements as eye movements are being made (Snyder, 2000). Neurons in the area 5 encode target location before and during a movement in both hand and the eye-centered reference frame (Andersen & Buneo, 2002). Within the network, the transformation from eye to hand coordinates arises simultaneously without intermediary steps relative to the head or body (Buneo, Batista, Jarvis, & Andersen, 2008).

2.2 VIP

The Ventral Intra-Parietal area has been implicated in motion detection across sensory modalities including tactile, visual and vestibular (Bremmer, Duhamel, Ben Hamed, & Graf, 2002; Colby, Duhamel, & Goldberg, 1993; Duhamel, Colby, & Goldberg, 1998). Neurons in this area are sensitive to stimulus speed and direction, as can be hinted by their anatomical connection with areas MT and MST (Boussaoud, Ungerleider, & Desimone, 1990; Rosa, Soares, Fiorani, & Gattass, 1993; Ungerleider & Desimone, 1986). Multisensory neurons that respond to both visual and tactile stimuli are head-centered and demonstrate alignment of the

receptive fields such that a correspondence exists between regions of space with analogously placed body parts; a neuron that is activated by a visual stimulus presented in the upper left quadrant of a screen will also react to a tactile stimulus on the upper left part of the head (Duhamel et al., 1998). Another distinguishing feature of VIP is sensitivity for the distance of stimuli, with “ultranear” neurons encoding visual stimuli only when they come within 5 cm of the face (Colby et al., 1993). This area is interconnected with parietal areas including LIP, MIP and 7b, somatosensory areas including 5 and S2, and projects to premotor area F4, which has been implicated in the encoding of head and mouth movements (Gentilucci M, 1988; Lewis, 2000; Luppino, 1999; Rizzolatti G, 1988).

2.3 Area 7b

Area 7b is mainly connected with the primary and secondary somatosensory cortex, parietal area 5, dorsal premotor, and orbital prefrontal cortex (Andersen, Asanuma, Essick, & Siegel, 1990a; Cavada & Goldman-Rakic, 1989a; Neal, Pearson, & Powell, 1990). Area 7b has a rough motor somatotopic organization, and neurons are activated both by a motor act and during observation of the act performed by a different individual, in analogy to “mirror neurons” first described in the premotor cortex (Fogassi, Ferrari, Gesierich, Rozzi, Chersi, & Rizzolatti, 2005).

2.4 AIP and CIP

The Anterior Intraparietal (AIP) and Caudal Intraparietal (CIP) areas, both in the lateral bank of the IPS, are involved in the transformation of visual 3D information into appropriate hand movement for grasping objects (Fogassi, Gallese, Buccino, Craighero, Fadiga, & Rizzolatti, 2001; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Rizzolatti, 1998; Sakata, 2003). Different populations of neurons in area AIP respond to either object manipulation alone, simultaneous visual and tactile stimulation, or 3-D visual stimulation (Sakata, Taira, Murata, & Mine, 1995). Some neurons also demonstrate sustained discharges to 3-D objects after viewing before handling, interpreted to encode memory for shape or motor preparation to grasp (Murata, Gallese, Kaseda, & Sakata, 1996). The anterior intraparietal area (AIP) has connections with the inferior parietal lobule, area LIP, and secondary somatosensory area (SII), as well as the lower bank of STS, ventral premotor area F5, and prefrontal areas 12 and 46 (Borra, 2008; Matelli, Camarda, Glickstein, & Rizzolatti, 1986; Murata et al., 2000; Nakamura, Kuroda, Wakita, Kusunoki, Kato, Mikami, Sakata, & Itoh, 2001; Rizzolatti, 1998). Like area AIP, CIP is involved with processing 3D attributes. It responds to 3D visual cues and surface orientation and is involved in stereopsis, or the computation 3D surfaces from binocular disparity (Tsutsui, Jiang, Yara, Sakata, & Taira, 2001). It is thought to combine feature and location information relevant to guiding hand movement (Tsutsui, Jiang, Sakata, & Taira, 2003). Neurons here also show sustained discharges after stimulus presentation when a surface orientation feature must be remembered in order to complete a task (Tsutsui et al., 2003). The Caudal Intraparietal area receives afferents from visual areas V3, V3A and projects to AIP (Adams, 1997; Nakamura et al., 2001).

2.5 LIP

Area LIP is located between AIP and CIP within the lateral bank of the intraparietal sulcus and has been shown to guide saccades to both visual and auditory targets (Barash, Bracewell, Fogassi, Gnadt, & Andersen, 1991; Linden, Grunewald, & Andersen, 1999). An extensive literature has implicated area LIP in visual attention (reviewed by Gottlieb in this issue). LIP neurons continue firing after the offset of a behaviorally relevant stimulus, implying a function in working memory (Gnadt & Andersen, 1988). LIP is connected with visual extrastriate regions, parietal areas AIP, VIP, 7a, and the Frontal Eye Fields (Andersen et al., 1990a; Blatt, Andersen, & Stoner, 1990; Nakamura et al., 2001; Stanton, Bruce, & Goldberg, 1995).

2.6 Area 7a and DP

Area 7a is connected with visual cortical areas including area MST and PO, other parietal areas, including areas LIP and 7m, and the dorsolateral prefrontal cortex, with connections most heavily concentrated in the posterior part of the principal sulcus (Cavada & Goldman-Rakic, 1989a; Cavada & Goldman-Rakic, 1989b). Its limbic connections encompass the parahippocampal gyrus, the presubiculum, ventral posterior cingulate cortex, agranular retrosplenial cortex, and the caudomedial lobule, while it sends direct connections to CA1 of hippocampus (Rockland, 1999). Neurons in area 7a have large and often bilateral visual receptive fields (Lynch, Mountcastle, Talbot, & Yin, 1977; Motter & Mountcastle, 1981). A large literature also exists regarding the modulation of area 7a responses by attention (Constantinidis, 2006a). The dorsal prelunate (DP) is continuous with area 7a, and has similar visual properties (Andersen et al., 1990a; Siegel, Raffi, Phinney, Turner, & Jando, 2003). Both areas exhibit gain fields such that the amplitude of the neural response is modulated as a function of eye position of the orbit. Furthermore neurons in both areas are responsive to optic flow, which provide motion cues for navigation (Motter & Mountcastle, 1981; Read & Siegel, 1997; Siegel & Read, 1997).

2.7 Area 7m

Area 7m lies in the medial surface of the parietal lobe; the human homologue is often referred to as the precuneus area (Liu, Slotnick, Serences, & Yantis, 2003; Serences, Schwarzbach, Courtney, Golay, & Yantis, 2004). Area 7m is interconnected mainly with visual cortical areas PO and MST, parietal area 7a, dorsal prefrontal cortex, and the Frontal Eye Fields (Cavada & Goldman-Rakic, 1989a; Leichnetz, 2001). Cingulate sulcus and granular retrosplenial cortex comprise the major limbic constituents of the network connected with area 7m (Cavada & Goldman-Rakic, 1989a).

3. Clinical Relevance and Pathology

An understanding of the importance of posterior parietal cortex was initially derived from the deficits observed in human lesion patients. Perhaps the signature effect of PPC damage is the neglect syndrome, typically occurring after a lesion in the right hemisphere. Disturbances include the inability to detect an object in the contralateral (left) visual hemifield (egocentric neglect) or to perceive the left side of objects, regardless of where they appear within the visual field (allocentric neglect). Related conditions involve constructional apraxia and extinction, which can occur after lesions on either side of PPC. These conditions are characterized by inability to reconstruct a visual scene (apraxia) and to attend to stimulus in the hemisphere contralateral to the lesion when a stimulus in the ipsilateral hemifield appears at the same time (extinction). The most severe effects of bilateral parietal lesions produce Balint's syndrome, characterized by the inability to perceive more than one visual stimulus at a time, to direct visual attention outside the fovea, to scan visual space, and to coordinate hand movements to visual targets (Constantinidis, 2006b).

Although the study of parietal lesions has emphasized the attentional character of the deficits, spatial working memory performance and capacity can also be affected. An interaction between working memory deficits and neglect may exacerbate the effect of neglect, possibly by interfering with the ability to keep track of what spatial locations have already been searched (Husain, Mannan, Hodgson, Wojciulik, Driver, & Kennard, 2001; Wojciulik, Husain, Clarke, & Driver, 2001). Additionally, damage to the right Temporal-Parietal Junction (TPJ), which has been implicated in neglect (Heilman KM, 1983; Leibovitch FS, 1998; Vallar, 2001; Vallar & Perani, 1986) has also been shown to produce spatial working memory deficits (Malhotra, 2005). In the latter study, modified versions of the Corsi blocks task were used to dissociate the working memory aspect of the pathology from neglect; viewers had to remember the order

of a series of highlighted discs whose locations were restricted to the vertical midline, thus eliminating the attentional bias towards the ipsilesional visual field. Damage to the Temporal-Parietal Junction was associated with poor performance in the task. Interestingly, poor performance was also observed in two patients with right lateral frontal lesions who showed no neglect (Malhotra, 2005), confirming that a dissociation can exist between spatial working memory and neglect in some cases. While the symptoms of neglect often attenuate over time, sustained attention and visual memory problems have been found in long-term neglect patients as well (Maguire & Ogden, 2002). These studies support the idea that when important nodes in the spatial working memory network are compromised or deafferented, an inability to keep track of previously searched locations in the ipsilateral hemifield may contribute to the failure to attend to the contralateral one (Driver, 2002; Malhotra, 2005).

Recent neuropsychological research provides more details about the nature of memory deficits produced by parietal damage (Berryhill, 2008a; Berryhill, 2008b; Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007; Davidson, 2008; Finke, 2006; Haramati, 2008; Pisella, 2004). For a comprehensive review, see Olson and Berryhill (Olson, 2008). Visual working memory impairment in both location and object working memory has been shown in patients with right and bilateral parietal lesions (Berryhill, 2008a; Berryhill, 2008b), though these deficits may depend on the particular demands of the task (Finke, 2006; Pisella, 2004). Work by Berryhill and Olson has pointed specifically to a deficit in retrieval of information from Working Memory (Berryhill, 2008a; Berryhill, 2008b). Quite unexpectedly, recent work has also pointed to a deficit in long-term, episodic memory after parietal lesions. For example, one study reported that bilateral damage decreases the amount of detail with which patients describe autobiographical events during free recall, but not when prompted by specific questions (Berryhill et al, 2007). In another study employing a source memory task, recalling the correct answer when cued was unimpeded, whereas recognition that an item was encountered before was impaired and remembering subjective details was found to be significantly diminished (Davidson et al, 2008). Episodic memory deficits described in free recall tasks may be attributed to a failure of bottom up processes to capture attention, a phenomenon termed “memory neglect” (Cabeza, 2008; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008). Specific probe questions may provide top-down cues that induce patients to recall details that they would otherwise miss. A related possibility is that this disruption in internal attention is caused by “memory simultanagnosia”, an inability to pay attention to more than one memory at once (Cabeza, 2008; Cabeza et al., 2008).

4. Neural correlates of working memory

Neurophysiological recordings in monkeys have been instrumental for the investigation of cognitive functions given the monkey brain’s close structural homology with the human brain and the monkeys’ ability to perform complex behavioral tasks. The role of the PPC in working memory has been investigated in this fashion. The bulk of physiological studies related to working memory have been conducted in areas LIP and 7a and these will be the basis of our review. It is instructive to discuss the concept of working memory in the psychological literature and its correlates in posterior parietal neuronal activity.

4.1 Characteristics of working memory

Short-term memory, lasting for a period of a few seconds, was first addressed in primates by testing them in delayed-response tasks. These types of tasks require subjects to remember a cued location or object in the absence of its continued physical presence for short periods of time in order to receive a reward. Lesions to the prefrontal cortex produced deficits in performance (Jacobsen, 1936). Failure to perform the task in lesioned animals was attributed to a disruption in the ability to maintain an internalized representation of the cue and early investigators deduced that the anatomical correlate of this internalized representation must be

localized in prefrontal cortex. Early neurophysiological studies provided neural correlates for such an internalized representation in the form of sustained discharges for neurons in the macaque prefrontal cortex and mediodorsal nucleus of the thalamus (Fuster & Alexander, 1971; Kubota & Niki, 1971). Fuster further described the attributes of this sustained activity as being dependent on a goal-directed need to hold information in memory, not induced simply by reward expectancy, being correlated with ability to remember the information, and being susceptible to distracting influences (Fuster, 1973; Fuster, 2003). Cells exhibiting working memory characteristics have subsequently been found distributed throughout many other areas including, inferotemporal cortex, somatosensory and posterior parietal cortices (Andersen, Bracewell, Barash, Gnadt, & Fogassi, 1990b; Constantinidis & Steinmetz, 1996; Fuster & Jervey, 1981; Miller & Desimone, 1993).

The concept of working memory also emerged in the psychological literature (Baddeley, 1986; Baddeley & Hitch, 2000; Baddeley, 1974; Pascual-Leone, 1970). Working memory does not refer to a memory system that differs from that of short-term memory; the term rather emphasizes that this type of memory does not function simply as a passive storage of information but it allows integration of remembered information with current contingencies and future goals. Recent models propose four subsystems of working memory, a “central executive,” responsible for controlling and coordinating information through “slave” systems called the visual-spatial sketchpad for manipulation of visual objects, the phonological loop for verbal rehearsal, and the latest addition, an episodic buffer, that allows for temporal storage and binding of information within the other subsidiary subsystems (Baddeley & Hitch, 2000). It should be made clear however that these working memory subsystems refer to functional rather than anatomical units (Constantinidis & Procyk, 2004; Goldman-Rakic, 1995). For example, the prefrontal cortex seems a logical functional neural analogue to the central executive. However, physiological evidence indicates that prefrontal neurons in area 46 represent spatial and object attributes of visual memoranda in correspondence to the visual-spatial sketchpad (Rao, Rainer, & Miller, 1997) while at the same time they provide neural correlates of executive functions such as rule execution and category classification (Freedman, Riesenhuber, Poggio, & Miller, 2001; Wallis, Anderson, & Miller, 2001). Additionally, each of the working memory “subsystems” activates multiple brain areas: Smith and Jonides identify selective attention and task management as two of the main components of executive control and cite examples of related activity in both prefrontal and anterior cingulate cortices (Smith, 1999). Contrary to the buffer concept, Miller and Cohen propose that activity sustained in PFC may represent a goal along with an associated plan of action, rather than a memory trace for a particular item (Miller & Cohen, 2001). It has also been posited that instead of being maintained in dedicated modality-specific buffers, information held in working memory is represented by the activity of those processes within the current focus of attention (Cowan, 1988). Along similar lines, the idea has evolved that working memory is an emergent property of cognition and the network of brain regions that mediate it (D’Esposito, 2007; Hazy, 2006; Postle, 2006).

4.2 Neural mechanisms mediating working memory

One obvious question is how might the neural activity seen in working memory networks be maintained during the representation of the memoranda. Computational models have been instructive in that respect and spiking neural network with recurrent connections have been shown to achieve a remarkably close approximation to actual neurons recorded in monkey cortex (Zipser, 1993). Reverberating activity within recurrent circuits is a characteristic of this type of architecture: pyramidal neurons form reciprocal, excitatory connections between them and transmit action potentials to each other so that, even when the original stimulus is no longer present, discharges continue to reverberate in the network. A critical property revealed by models is that discharges can be sustained if the postsynaptic neuron continues to be in an excited state at the time presynaptic inputs accumulate. Given the fairly low firing rate of

cortical pyramidal neurons, postsynaptic receptors with fairly slow time constants are essential for this function. The NMDA receptor has therefore been proposed as a critical element of cortical circuits involved in working memory (Lisman, Fellous, & Wang, 1998). Reverberatory networks, when left unperturbed, will settle into an attractor state defined by a stereotyped pattern of activity within the network (Hopfield, 1982). Attractor models may undergo spontaneous oscillations, although network instantiations have also been shown to be capable of mediating sustained responses without oscillatory discharges (Compte, Brunel, Goldman-Rakic, & Wang, 2000). These models emphasize the importance of spiking mechanisms as a means for the maintenance of working memory, however it is possible that intracellular and synaptic mechanisms may also play a role (Egorov, Hamam, Franssen, Hasselmo, & Alonso, 2002; Mongillo, Barak, & Tsodyks, 2008).

4.3 Posterior parietal contributions to working memory

Although working memory has been traditionally associated with the prefrontal cortex and neural correlates of working memory were first described there, the posterior parietal cortex is closely associated with the prefrontal cortex via reciprocal connections and shares many of its functional properties. In fact, prefrontal and parietal regions are almost invariably activated simultaneously in human imaging studies of working memory (Bunge, Ochsner, Desmond, Glover, & Gabrieli, 2001; Courtney, Ungerleider, Keil, & Haxby, 1997; Jonides, Smith, Koeppe, Awh, Minoshima, & Mintun, 1993; Marshuetz, Smith, Jonides, DeGutis, & Chenevert, 2000; Munk, Linden, Muckli, Lanfermann, Zanella, Singer, & Goebel, 2002; Owen, Stern, Look, Tracey, Rosen, & Petrides, 1998; Raye, Johnson, Mitchell, Reeder, & Greene, 2002; Stern, Sherman, Kirchhoff, & Hasselmo, 2001; Ungerleider, Courtney, & Haxby, 1998). A meta-analysis of imaging studies involving working memory tasks revealed that area 7 was reliably activated by all aspects of executive function examined (ordering, updating, and manipulating items held in working memory), as well as the spatial content of working memory (Wager & Smith, 2003).

Initial reports of working memory activity in the posterior parietal cortex described discharges in monkey area LIP that followed the offset of a visual stimulus which was to be a target for a planned eye movement (Gnadt & Andersen, 1988). Later studies in area 7a demonstrated that posterior parietal neurons represent the remembered locations of visual stimuli, independent of a planned motor response (Constantinidis & Steinmetz, 1996). Activity of area 7a neurons was directionally tuned but independent of a directional motor movement, suggesting that the activity is indicative of a memory signal rather than a motor preparation signal. Two types of neural activity were revealed: The first was a sustained response during the delay period following a stimulus presentation that evoked a strong response. This activity remained elevated or gradually decreased until a stimulus at a new location was presented. The second type was an anticipatory response that was observed in some neurons as a ramping up of activity before a following stimulus, a type of activity also observed during the planning of a motor response (Quintana & Fuster, 1992).

The similarity in patterns of activity between prefrontal and parietal neurons was also confirmed by neurophysiological studies in both areas. Virtually identical percentages of neurons exhibiting working memory responses were observed in parietal areas 7a and LIP and prefrontal areas 46 and FEF (Chafee & Goldman-Rakic, 1998). The importance in the interaction between the two areas was revealed by deactivation of either PPC or PFC by cortical cooling which was shown to produce a profound effect on the output of neurons in the other area (Chafee & Goldman-Rakic, 2000).

Despite these similarities between PPC and PFC, important differences have also emerged (Constantinidis & Procyk, 2004). Memory-related activity in the parietal cortex differs from the memory trace held in frontal cortical neurons in that it is disrupted by intervening,

distracting stimuli; the activity of parietal neurons represents the most recent stimulus to appear, whether it was behaviorally relevant or not (Constantinidis & Steinmetz, 1996). In contrast, frontal neurons continue to discharge even after the presentation of intervening stimuli, representing the behaviorally relevant stimulus held in memory (di Pellegrino & Wise, 1993; Miller, Erickson, & Desimone, 1996). These results suggest that posterior parietal cortex encodes the memory of the last stimulus location whereas prefrontal areas are critical for mental operations that span multiple items of a sequence of stimuli. This idea has been supported by human fMRI studies which revealed that while parietal and prefrontal areas are activated during spatial working memory, prefrontal activation is critical for memory of sequences of items and predictive of error trials (Sakai, Rowe, & Passingham, 2002). Similarly, right Transcranial Magnetic Stimulation (TMS) applied over both prefrontal and posterior parietal cortex during the delay phase of a spatial working memory task increased reaction times whereas TMS applied during the decision phase of the task disrupted performance only when applied over the prefrontal, but not PPC (Koch, Oliveri, Torriero, Carlesimo, Turriziani, & Caltagirone, 2005). These results clearly demonstrate a specialization in working memory function for posterior parietal compared to prefrontal cortex. It should be noted however that this specialization does not correspond to distinct components or subsystems of the Baddeley model, as both visual-spatial and executive functions have been described in both parietal and prefrontal areas.

A series of recent imaging studies has indicated posterior parietal activation during recall of information from long-term memory (Cabeza et al., 2008; Wagner, 2005). Wagner and his coworkers put forward three hypotheses about episodic memory retrieval (Wagner, 2005): first, the parietal cortex may subserve attention to an internal representation, shifting, or maintaining attention on internally derived mnemonic representations; second, parietal cortex may function as a mnemonic accumulator such that memory strength signals are accrued until they reach a decision criterion; or third, the parietal cortex may provide a working memory buffer, holding a readily-accessible transient memory trace available to decision making processes analogous to the working memory buffers of Baddeley's model (Baddeley, 1998). The first of these theories directly links attention to the memory retrieval process. An earlier model of attention processing, the dual attention process (DAP) hypothesis, proposes that there is an interaction in top-down attention mediated by dorsal fronto-parietal networks with bottom-up attention mediated by ventral frontal-temperoparietal networks (Corbetta & Shulman, 2002). Similar processes may occur not just for attention to external events, but also to internally derived memory of events (Cabeza, 2008; Cabeza et al., 2008).

5. Neural correlates of learning

Learning encompasses cognitive phenomena that traditionally have also not been associated with the posterior parietal cortex. However, recent evidence suggests parietal involvement in a number of cognitive tasks that require, or depend on learning. Even if it is not the sole brain area mediating these effects, the activity of parietal cortical neurons reflects learned tasks and associations.

5.1 Human imaging studies

As already discussed, working memory does not involve simple buffering of prior information, but relies on executive processes to organize, monitor, and use it. Information can be re-coded in a structured way to make it easier to remember and utilize in the course of ongoing operations—or for retrieval and use at any given time later on. A strategy known as “chunking” (Miller, 1956) takes small pieces of information and combines them into meaningful groups that constitute larger, single units of information. This type of manipulation is used in reading, language acquisition and many types of expert learning e.g. chess (Gobet, Lane, Croker, Cheng, Jones, Oliver, & Pine, 2001). In humans, the use of structured grouping strategies in working

memory can help reduce the working memory load and allow far greater amounts of information to be retained simultaneously (Bor, 2004; Bor, Duncan, Wiseman, & Owen, 2003). When structured grouping is utilized during learning, both short- and long-term memory systems are engaged to add new information along previously learned patterns or paradigms. Organizational strategies that encode information, including chunking as well as more generalized grouping of information into organizational and spatial relational structures revealed involvement of both the prefrontal and posterior parietal cortex (Bor, 2004; Bor et al., 2003; Bor & Owen, 2007; Wendelken, Bunge, & Carter, 2008).

In addition to mediating some of the more complex forms of working memory utilized during generalized learning, posterior parietal cortex is also recognized for its role in motor learning and retrieval of acquired motor skills including highly developed, complex motor skills (Gallese V, 1994; Goodale & Milner, 1992; Haaland, Harrington, & Knight, 2000; Rushworth, Nixon, Wade, Renowden, & Passingham, 1998). A compelling demonstration of the latter was provided in an fMRI experiment where human subjects were presented with pictures of hand tools. Common or familiar tools, in comparison to ones with which the observer was unfamiliar or had little experience, elicited supramarginal and superior parietal lobule activation, consistent with the recall of motor programs for the use of the tool (Vingerhoets, 2008). Another recent study demonstrated that training and execution of a visual motor task in humans engaged separate areas of posterior parietal areas for different components of motor learning (Grafton, Schmitt, Van Horn, & Diedrichsen, 2008). These investigators showed that acquisition of the ability to produce predictive feedforward commands in response to external input activated areas within the left supramarginal gyrus and intraparietal sulcus while response and modification of feedback control elements of the task produced bilateral activation in the superior parietal lobule and anterior intraparietal sulcus (Grafton et al., 2008).

Expert learning and the development of specific motor and tool-use skills rely upon building on knowledge gained from previous experience. These are not simply the result of transient organization of neural activity for the completion of a short-term goal nor are they limited to sequences of learned procedures to be applied in a stereotypic manner. Skills and knowledge can be built on over the course of a lifetime, and new approaches to old problems can emerge by the integration of previous experience into new behaviors.

5.2 Neurophysiological studies of learning in posterior parietal cortex

In recent years, neuronal activity in the monkey posterior parietal cortex has also been shown to depend on prior experience and training in a behavioral task. These studies provide insights on the neural correlates underlying learning. PPC neurons typically have low selectivity for color; only a small percentage of area 7a neurons demonstrate significantly different responses to green and red stimuli of equal luminance (Constantinidis & Steinmetz, 2001). However when animals execute a behavioral task for which color is important because it signifies eye movements, a larger percentage of PPC neurons exhibit selectivity for the color of the stimuli (Toth & Assad, 2002).

Similarly, responses to visual stimuli can differ based on the sensorimotor association or rule that the monkey is trained to perform (Stoet & Snyder, 2004). In its simplest form, a rule can be explicitly stated about how a task is to be executed by a cue at the beginning of the trial or it can be implicitly deduced by the presence or lack of reinforcement in consequence to a given action. Behavior involving rule updating under changing task demands is known as set shifting and one of the most striking deficits observed is in patients suffering from frontal lobe lesions is the inability to do this successfully. Human studies indicate that set shifting involves posterior parietal regions as well (Asari, 2005; Lie, 2006; Ng, 2007). These results suggest that learning the contingencies of a behavioral task can modify the responses of PPC neurons to identical stimuli.

A more fundamental effect of learning was revealed by comparing responses of PPC neurons in animals trained to perform a behavioral task (Constantinidis & Steinmetz, 2001) with responses in animals naïve to behavioral training (Constantinidis & Steinmetz, 2005). These studies revealed that although the overall pattern of responses was similar, neuronal activity in monkeys trained to detect a salient stimulus in a visual display reflected the target faster, and produced a more discriminable level of activation. In an attempt to understand the underlying neural mechanisms mediating learning, a later study investigated neural response patterns in naïve and trained monkeys (Joelving, Compte, & Constantinidis, 2007). The results demonstrated that active attention and maintenance of a stimulus in working memory was characterized by distinct firing patterns, most notably a decrease in spectral power in the 5–10 Hz frequency range. These studies suggest that learning to perform a behavioral task induces profound and enduring changes in neuronal processing.

6. Conclusions

The research reviewed here demonstrates that the primate PPC plays a central role in the mediation of cognitive functions, in agreement with the cognitive deficits following PPC lesions. More specifically, the activity of PPC neurons plays a role in the maintenance of working memory, at least for the most recent stimulus. Posterior parietal activity could provide a physiological correlate to the “visual-spatial sketchpad” in Allan Baddeley’s model of working memory by allowing for the manipulation of items held in working memory into larger organized structures. At the same time, PPC activity is modulated by experience and learning, contributing to the acquisition of new skills and rules. Neural correlates of learning are reflected in the activity of parietal neurons and performance of different tasks is critically dependant on PPC.

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Figure 1. Outline of the human posterior parietal cortex. Abbreviations: IPS, intraparietal sulcus; BA, Brodmann's area.

Figure 2.

Outline of the macaque monkey posterior parietal cortex. Abbreviations: AIP, anterior intraparietal area; CIP, caudal intraparietal area; DP, dorsal prelunate area; IPS, intraparietal sulcus; LIP, lateral intraparietal area; LS, lunate sulcus; MIP, medial intraparietal area; STS, superior temporal sulcus; VIP, ventral intraparietal area. Inset shows the intraparietal sulcus unfolded to view areas along the banks. Area 7m lines the medial surface of the parietal lobe (not visible in lateral view).