CHAPTER 14

The role of posterior parietal cortex in the regulation of saccadic eye movements

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Abstract

The posterior parietal cortex (PPC) is a node within the cerebral 'higher-order' network that has no clear homologue in non-primate mammals and is fully defined only in catarrhine primates, which include old world monkeys and hominoids. The late coming of the PPC in the eye movement circuit and the absence of an unequivocal role in saccade preparation and production suggests that the PPC should only be viewed as an innovation to enhance the sensory guidance and flexible control of visual behaviour. In line with this idea is the evidence that the lateral intraparietal area integrates sensory and goal-directed information into a map wherein representations of spatial locations can be maintained and selected as saccade targets through decision processes.

Evolutionary considerations

A wealth of data from neuroanatomical, neurophysiological, lesion, and imaging studies has yielded several hypotheses regarding the functions subserved and the operations performed by the several areas of the PPC. Advances on the role of PPC in space coding, coordinate transformation, visual attention, movement planning, and multisensory integration have been reviewed previously, and the reader is invited to consult this rather large literature. Together, many of these hypotheses form the outline of a PPC visuomotor theory (e.g. Goodale and Milner, 1992; Wise et al., 1997), but a full integration is wanting before we have a complete theoretical grounding. Towards that end, we think that there is one important area of investigation to integrate and develop further, namely, the evolutionary perspective.

Comparative studies, as reviewed by Kaas (2008), suggest that the neocortex of early mammals was composed of a limited number of distinct areas, mostly primary and secondary sensory fields. The growing predominance of vision in early primates was associated with an expansion of the occipital and temporal cortices. Concomitantly, the organization of the somatosensory areas in parietal cortex underwent a significant expansion of the forepaw representation, which may partially be related to the high manual dexterity demands of arboreal life (see for review Ross and Martin, 2007). The PPC

came about from the concerted expansion of the somatosensory and visual cortices, linking the latter with motor fields of the frontal cortex (Fang et al., 2005). These evolutionary considerations provide supportive evidence for the basic role of the PPC in visually-guided behaviour, but they also indicate that it may be to confer primates with skilled visuomanual behaviour, including eye–hand coordination and grasping (see for review Disbrow et al., 2007; Preuss, 2007a; Ross and Martin, 2007). The more recent evolution of a fully opposable thumb in humans, clearly a prerequisite for tool use, certainly coincided with further expansion of the PPC in this species (Frey, 2007; Ramayya et al., 2010). This capability may have built upon phylogenetically older neural circuits controlling skilled forelimb movements, such as in food handling behaviour (see for review Iwaniuk and Whishaw, 2000; Whishaw, 2003), and perhaps also on existing visual processing circuits associated with navigation and locomotion-related obstacle avoidance, which are evident in rodents (Kolb and Walkey, 1987) and cats (see for review McVea and Pearson, 2009).

Consistent with the above hypothesis, sustained electrical stimulation of the anterior PPC in prosimian galagos evokes what look like 'primitives' of ethologically significant behaviours, such as reaching-and-grasping, hand-to-mouth movements, and coordinated defensive body movements (Stepniewska et al., 2005)—such defensive movements have also been observed following sustained electrical stimulation of the ventral intraparietal area of the macaque monkey PPC (Cooke et al., 2003). Although these coordinated movements certainly result from the activation of distributed neural circuits extending beyond the PPC, they seem to be topographically organized within the PPC: moving the stimulation electrode from the most ventral part of the PPC to its most dorsal part progressively evokes eye movements, facial expressions, grasping, reaching, and hind-limb movements. Overall, the specific PPC role in regulating eye movements, which is the topic of this chapter, may well be only understood in the context of this larger sensory-motor map with perhaps special consideration to complex behaviour, such as eye–hand coordination (Land, 2006; Johansson and Flanagan, 2009). The hypothesized role of the PPC in space coding and coordinate transformation is particularly relevant in this context (see for review Cohen and Andersen, 2002; Husain and Nachev, 2007).

The distinctive visual ability of primates is conferred, in part, by a fairly large ocular motility and a retina equipped with a well-defined fovea requires a sophisticated eye movement system to gather useful, detailed visual information. The large oculomotor range that primates possess appears to be evolutionarily recent. The human oculomotor range spans about ±50° of visual angle (Guitton and Volle, 1987; Stahl, 1999) and is comparable to that of the macaque monkey (Tomlinson and Bahra, 1986) and baboon (Marchetti et al., 1983). In contrast, the oculomotor range of early primates such as prosimians (Shepherd and Platt, 2006) as well as that of the new world squirrel monkey (McCrea and Gdowski, 2003) is limited to 20–25°. Limited ocular motility is commonly reported in frontal-eyed non-primates that lack a distinct fovea, such as the tree shrew (Remple et al., 2006) and the cat (Guitton et al., 1984). This augmented oculomotor facility may have paralleled an increasing involvement of the PPC in regulating eye movements. Anatomical studies have shown that the PPC is heavily interconnected with the prefrontal cortex (PFC) and the superior temporal sulcus cortex, as well as with the dorsal pulvinar and the superior colliculus (SC), and thus a node is what is best described as a 'higher-order' network (Preuss, 2007b). This network has no clear homologue in non-primate mammals and is fully defined only in catarrhine primates (Preuss, 2007a, 2007b), which include old world monkeys and hominoids. In comparison, the high-order saccade centre, the frontal eye field (FEF), is common to all primates (Kaas, 2008; Preuss, 2007a), as the optic tectum (the SC homologue) is to vertebrates. In addition, the projections to the SC that originate from the PPC have been shown to be negligible in platyrrhine primates (Collins et al., 2005), the new world monkeys that are extant members of the oldest branch of the anthropoid radiation. It is therefore reasonable to assume that the role of PPC in regulating orienting in general and eye movements in particular is also evolutionarily recent.

The link between PPC and behaviour is certainly much more indirect than that implied by the above electrical stimulation studies. The PPC is an ideal interface between the different sensory fields and the frontal cortex motor fields and it is an undeniably important player in the frontoparietal network that endows us with several of our cognitive abilities. Nevertheless, the PPC does not have

direct access to the motor circuitry, per se. As evidenced in the rest of this chapter, oculomotor research suggests that PPC neuronal activity is not directly associated with the production of movements. A more accurate view is that PPC only provides signals that can regulate potential actions in the form of representations from which specific goals can be selected. With respect to eye movements, these regulatory signals could reflect several cognitive processes and their origins would be predominantly visual.

There is a vast literature on the role of PPC in regulating eye movements and related cognitive processes. Significant advances have been made in studying human patients and healthy subjects using many different approaches, such as psychophysics, functional brain imaging (see for review Curtis, Chapter 20, this volume), and transcranial magnetic stimulation (see for review Müri and Nyffeler, Chapter 21, this volume). A complete review of these findings is beyond the scope of this chapter, and we opted to focus this review on work conducted on the saccadic eye movement system in our best animal model, the macaque monkey. This chapter also emphasizes work, framed by work conducted in our laboratories, on saccade-related processes investigated with single-neuron recording in the lateral intraparietal (LIP) area, an area within the PPC vision-for-action processing stream with the strongest connections to the saccadic eye movement system. Along with evolutionary considerations, the advances in our understanding of the neuronal activity in this particular cortical area in the macaque monkey provide a framework to guide our general understanding of PPC and to interpret data from different approaches.

A vision-for-saccade interface

The primate PPC contains many subdivisions (Fig. 14.1) (Lewis and Van Essen, 2000a), several of which appear homologous in monkeys and humans (Grefkes and Fink, 2005; see also Shikata et al., 2008; Arcaro et al., 2011). The intraparietal sulcus divides this cortical region into superior and
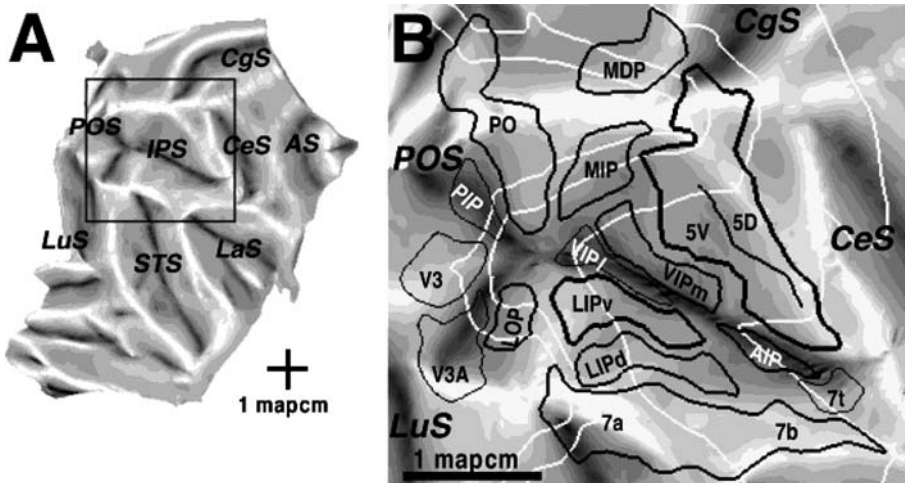

Fig. 14.1 Macaque posterior parietal cortex. **A.** Flat map of the macaque cerebral cortex showing the entire sulcal pattern and major subdivisions: arcuate sulcus (*AS*), central sulcus (*CeS*), cingulated sulcus (*CgS*), intra-parietal sulcus (*IPS*), the lateral sulcus (*LaS*), the lunate sulcus (*LuS*), the posterior-parietal sulcus (*POS*) and the superior temporal sulcus (*STS*). Anterior is to the right. **B.** Expanded view of the intra-parietal sulcus (*IPS*), showing the location of the dorsal (*LIPd*) and ventral (*LIPv*) portion of the lateral intraparietal area along with fifteen other architectonically identified subdivisions. White lines are layer IV contours. Adapted from Journal of Comparative Neurology, vol. 428, Lewis, J. W. & Van Essen, D. C., Mapping of architectonic subdivisions in the macaque monkey, with emphasis on parieto-occipital cortex. pp. 79-111, 2000, with permission from John Wiley and Sons.

inferior lobules, whose primary inputs are somatosensory and visual, respectively. One particular subdivision within the lateral bank of the intraparietal sulcus was found to contain neurons with both visually evoked responses and saccade-related activity (Andersen et al., 1987). Figure 14.2 illustrates the basic discharge properties of these neurons, including the sustained and persistent activity they often exhibit in delayed response tasks. All types of activity are spatially co-registered (Barash et al., 1991; Johnston et al., 2009) and give these neurons circumscribed, yet large response fields. Together, the neurons—located in what is now referred to as the LIP area—are organized into a coarse representation of the contralateral visual field (Ben Hamed et al., 2001; Blatt et al., 1990).

Anatomical studies have found that area LIP receives converging inputs from numerous visual areas and sends projections to the two brain regions necessary for saccade production, namely, the FEF within the anterior bank of the arcuate sulcus (see for review Johnston and Everling, Chapter 15, this volume) and the intermediate layers of the midbrain SC (see for review White and Munoz, Chapter 11, this volume) (Andersen et al., 1990; Baizer et al., 1991). Tracing of retrograde labels injected in FEF (Schall et al., 1995a) and SC (Lynch et al., 1985) confirmed this direct access to the saccadic eye movement system, and antidromic activation studies have identified that many of these projection neurons have saccade-related activity (Ferraina et al., 2002; Paré and Wurtz 1997, 2001). Lastly, there are also reciprocal connections from FEF (Ferraina et al., 2002; Lewis and Van Essen, 2000b; Schall et al., 1995a; Stanton et al., 1995) as well as from the SC (Clower et al., 2001), though the latter are via the inferior pulvinar and primarily from the more sensory superficial layers of the SC.
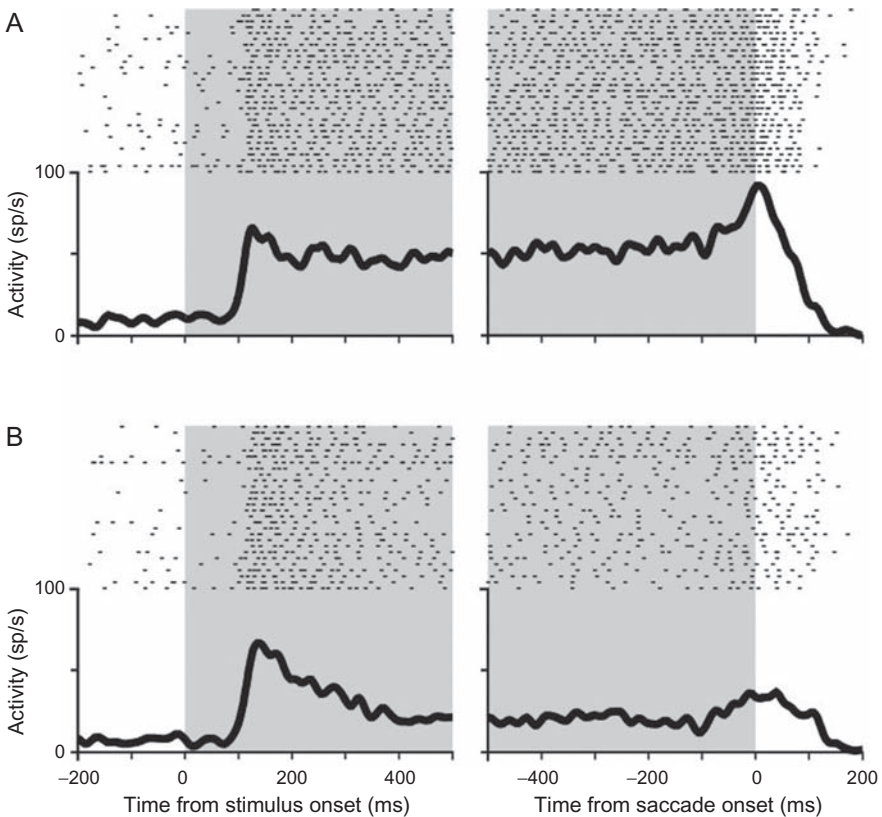

Fig. 14.2 LIP neuronal activity in delayed saccade tasks. Rasters and spike densities from one representative LIP neuron are shown for visual (**A**) and memory (**B**) delayed saccade tasks. [Paré M., & Wurtz, R. H., Journal of Neurophysiology, 1997, Am Physiol Soc, modified with permission.]

Area LIP itself may also be subdivided into an anterio-dorsal (LIVd) and posterio-ventral (LIPv) portion (Fig. 14.1), the latter being identified by its dense myelination (Blatt et al., 1990; Lewis and Van Essen, 2000a; Seltzer and Pandya, 1980). The stronger connections of LIPv with FEF and SC (Blatt et al., 1990; Lynch et al., 1985; Schall et al., 1995a) suggest that this portion of the lateral bank of the intraparietal sulcus is the main interface between the visual and saccadic eye movement systems. In contrast, the more exclusive connections of LIPd with visual areas of the temporal cortex (Blatt et al., 1990; Lewis and Van Essen, 2000b) suggest that this portion has a more sophisticated role in visual processing, perhaps at the expense of eye movement processing (but see Liu et al., 2010 for a different account). Consistent with this scheme, Bakola et al. (2006) have shown with C-deoxyglucose imaging that LIPv is recruited during both visually guided and memory-guided saccades, whereas LIPd is recruited primarily during visual fixation and visually-guided saccades. From this work, it is plausible that some of the different hypotheses regarding the functions of area LIP stemmed from results obtained from two distinct populations of neurons. For instance, the visual feature sensitivity identified in some LIP studies (Sereno and Amador 2006; Sereno and Maunsell, 1998; see also Janssen et al., 2008) could be limited to LIPd (Ogawa and Komatsu, 2009).

In summary, the role of PPC in regulating saccadic eye movements may be best investigated by examining the properties of area LIPv. In addition, given the general hypothesis that the PPC receives predominantly visual inputs, investigations should make particular considerations for visually guided eye movements.

Saccade production

The direct projections of area LIP to FEF and SC suggest that its neurons directly participate in the production of saccadic eye movements, but this is now proven not to be a tenable hypothesis. The first evidence for this original hypothesis is the original observation made by Mountcastle and colleagues of pre-saccade increase in activity in neurons of area 7—including portion of the lateral bank of the intraparietal sulcus, from which LIP neurons would likely have been sampled (Lynch et al., 1977; Yin and Mountcastle, 1977). This discharge patterns was subsequently attributed to neurons within area LIP (Andersen et al., 1987; Barash et al., 1991). More recent evidence suggests, however, that area LIP is not directly involved in saccade production. First, the magnitude of LIP pre-saccade activity shows visual dependence and is significantly reduced when saccades are made in the absence of a visual stimulus (Ferraina et al., 2002; Paré and Wurtz, 1997, 2001; see also Gottlieb and Goldberg, 1999) as well as when several stimuli are present (Thomas and Paré, 2007). In addition, large amount of electrical current is necessary to elicit saccadic eye movements when stimulating area LIP (Keating et al., 1983; Kurylo and Skavenski, 1991; Shibutani et al., 1984; Thier et al., 1998). Lastly, ablation of this cortical area does not impair saccade production (Lynch and McLaren, 1989). This body of evidence contrasts with the demonstration of the critical role of FEF and SC in the production of saccades. First, removal of both FEF and SC severely and irreversibly impairs the ability of monkey to produce saccades (Schiller et al., 1980). Second, low-current microstimulation of these brain regions produces saccades of predictable amplitudes and directions (Bruce et al., 1985; Robinson, 1972; Robinson and Fuchs, 1969). Third, SC and FEF contain neurons with pre-saccade increase in activity (Bruce and Goldberg, 1985; Wurtz and Goldberg, 1971) that is correlated with saccade occurrence (Hanes et al., 1998; Paré and Hanes, 2003; Sparks, 1978; see also Mohler and Wurtz, 1976). In light of these major differences, it appears premature to take the pre-saccadic increase in the activity of LIP neurons as evidence that this cortical area is directly involved in the production of saccades.

For any brain region hypothesized to be involved in saccade production, it is imperative to determine whether its neuronal activity is actually closely linked to saccade occurrence, i.e. sufficient to account for saccade production. One definitive test is provided by the countermanding paradigm, which has been adapted for monkeys making saccadic eye movements (Hanes and Schall, 1995, 1996). This paradigm tests one's ability to inhibit the initiation of a response when an infrequent stop signal follows the go signal, and modelling of task performance can estimate the length of time

needed to cancel the commanded response (Logan and Cowan, 1984). In this context, for neurons to be involved in the process of saccade production, they must change their activity when a saccade is cancelled instead of executed, and they must do so before the saccade is cancelled. This has been found to be the case for nearly all SC movement neurons tested (Paré and Hanes, 2003) as well as for about half of such neurons in FEF (Hanes et al., 1998).

We recently conducted a study in which LIP neurons with saccade-related activity were submitted to the countermanding test (Brunamonti et al., 2008). Unlike what was observed in SC and FEF neurons, LIP neurons were found to change their activity when saccades were countermanded instead of executed only infrequently. In addition, this change in activity nearly always occurred later than when the saccade was cancelled, as estimated from the behaviour collected in the very same trials. This finding provides solid evidence that area LIP does not contain neurons with the signals necessary to control whether a saccade is to be produced. Similar result has been obtained in the supplementary eye field, despite the presence of pre-saccade activity observed in this PFC area since its discovery (Stuphorn et al., 2010). Figure 14.3 contrasts the results obtained from area LIP, FEF, and SC.

Altogether, the mere existence of a pre-saccadic increase in the activity of a neuron cannot be taken as evidence that this neuron is involved in saccade production. For example, some neurons in striate and extrastriate visual cortex have been shown to increase their activity just prior to a saccade made to a stimulus presented in their visual receptive fields (Moore, 1999; Nakamura and Colby, 2000; Supèr et al., 2004), but most would be cautious about describing this pre-saccade activity as playing a role in triggering saccades (see also Schiller and Tehovnik, 2001). Such activity can instead be interpreted as guiding saccades, and the strong dependence of LIP pre-saccade activity on visual stimulation is consistent with this interpretation. The evolutionary late emergence of PPC in the eye movement circuit may have limited its role in saccade regulation to processes that can only influence saccade production. This account agrees with the principle that the basic organization of neural
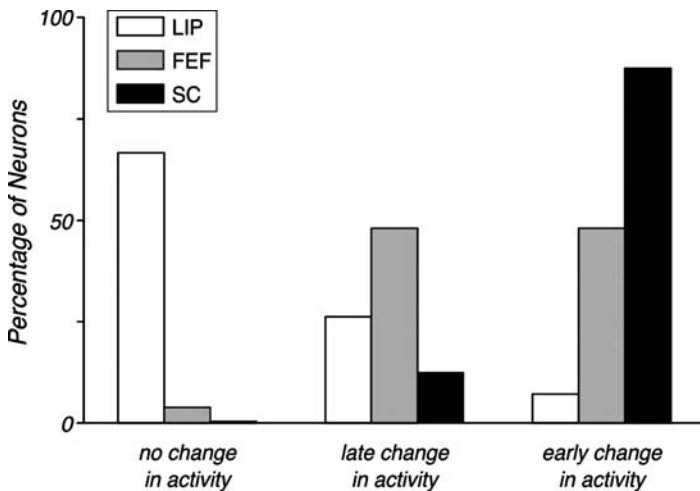

Fig. 14.3 Comparison of LIP, FEF, and SC neuronal responses associated with saccade countermanding. Graph shows the percentage of neurons with: 1) no significant change in activity around the time of saccade cancellation (no change in activity); 2) a significant change in activity, but occurring after saccade cancellation or after the efferent delay (late change in activity); and 3) a significant change in activity occurring early enough to account for saccade cancellation, i.e., within the efferent delay (early change in activity). Data are from samples of movement neurons: 42 in LIP (white), 51 in FEF (striped), and 32 in SC (dark). The shortest efferent delay is the minimal conduction time needed for signals from LIP, FEF, and SC to reach the eye muscles: 10 ms for both LIP and FEF, and 8 ms for SC (Paré & Hanes 2003). FEF data are from Hanes et al. (1998), SC data from Paré and Hanes (2003), and LIP data are from Brunamonti et al. (2008).

circuits is evolutionarily conservative, but that changes in behaviour can occur through adaptive changes in modulatory inputs to the control circuits (Katz and Harris-Warrick, 1999).

The evidence provided here argues against the idea that area LIP constitutes a parietal eye field (Andersen et al., 1992). The next sections consider the several hypotheses that LIP neuronal activity reflects more covert processes.

Saccade preparation and initiation

Response preparation refers to the neural processes by which response goals are specified and the execution of a specific response is facilitated (Riehle and Requin, 1989, 1993; Requin et al., 1990; see also Schall, 2004). For neurons to be involved in saccade preparation they must therefore: 1) change their activity in advance of an upcoming saccade, and the strength of their activity must predict both 2) the probability of occurrence, and 3) the timing of the saccade.

The involvement of area LIP in saccade preparation was first suggested by the observation that LIP neurons display a sustained activity during an imposed delay period between visual stimulation and saccade initiation. Andersen and colleagues (Andersen et al., 1987; Barash et al., 1991; Gnadt and Andersen, 1988) first showed that LIP neurons discharge long before specific saccadic vectors that correspond to their response fields. Specifically, the delay activity is maintained, albeit at a reduced level, when visual stimulation is interrupted or when the saccade is made within the response field without recent visual stimulation. These activity patterns meet the first operational criterion for response preparation, namely, that the activity must occur in advance of action.

Regarding the second criterion, some evidence suggests that LIP neuronal activity is predictive of an impending saccade in a neuron's response field. Several studies using various behavioural tasks have shown that LIP activity is sensitive to the information content of advanced instructions specifying whether or which saccade will be produced (Gottlieb et al., 1998; Paré and Wurtz, 2001; Platt and Glimcher, 1997; Shadlen and Newsome, 1996, 2001; Toth and Assad, 2002). Such activity has also been shown to be independent of the sensory modality and closely related to the occurrence of the next saccade (Mazzoni et al., 1996). Nevertheless, when compared with SC delay activity recorded in a Go/Nogo response task, the LIP activity is much less dependent on advanced instruction (Paré and Wurtz, 2001).

The third and highest-level operational criterion for response preparation refers to the predictive value of the neuronal activity for response initiation, i.e. the activity level should be related to the timing of the response. Neuronal activity can hardly be considered as preparatory if it does not affect the process for which it presumably prepares. This last criterion is been largely neglected in previous LIP studies. To date, studies have found relatively inconsistent and, at best, very weak evidence that the sustained activity of LIP neurons is predictive of saccade latency (e.g. Bendiksby and Platt, 2006; Dorris and Glimcher, 2004; Pesaran et al., 2002; Platt and Glimcher, 1999; Shadlen and Newsome, 2001; Roitman and Shadlen, 2002). These results contrast greatly with the preparatory nature of the activity of SC neurons recorded in a warned response task (Dorris and Munoz, 1998; Dorris et al., 1997; Paré and Munoz, 2001). In the gap saccade task, the early pre-target activity of SC neurons observed during the warming preparation period correlates with saccade latency. Our observations from the recording of LIP neurons in identical tasks are that these neurons generally lacked this early activity. Although some LIP neurons can display some activity in the absence of visual stimulation (Ben Hamed and Duhamel, 2002), they appear to reflect processes only once activated by sensory inputs.

In any given saccade task, response latency varies from trial to trial, and a useful framework to understand this variability is provided by accumulator models of response time performance (see for review Smith and Ratcliff, 2004). Studies in both FEF (Hanes and Schall, 1996) and SC (Dorris and Munoz, 1998; Dorris et al., 1997) have shown that saccades are initiated when the variable growth of pre-saccade activity reaches a fixed threshold (see for review Stuphorn and Schall, 2002). This saccade trigger threshold is reached very late in the response time interval, approximately 10–12 ms before saccade initiation (Paré and Hanes, 2003) and consistent with the anatomy and physiology of the

premotor circuitry of the saccadic eye movement system (Hanes and Schall, 1996). Evidence for a similar rise-to-threshold pattern of activity in area LIP remains, however, limited. In the study conducted by Roitman and Shadlen (2002), a variable rate of growth in LIP neuronal activity was observed, but the timing of when it reaches threshold was estimated to be 70 ms before saccade initiation. This timing is at odds with the FEF and SC estimates of trigger activation threshold. It is, however, more in line with what is referred to as the saccade target selection threshold—when a visual stimulus is selected as the saccade goal—which has been estimated to have a comparable timing in both FEF (Thompson et al., 2005a) and SC (Shen and Paré, 2007).

These neurophysiological data provide only partial evidence regarding the existence of saccade preparation signals in area LIP. Data from human studies have provided converging evidence in showing that unilateral lesions of the parietal lobe do not result in enduring changes in saccade latency (Machado and Rafal, 2004; Pierrot-Deseilligny et al., 1991; Rafal, 2006). It has also been suggested the observed increases in latency of saccades made to visual, contralesional stimuli rather reflect a deficit in visual spatial attention (Rafal, 2006). The same interpretation may apply to data from monkeys with intraparietal lesions (Lynch and McLaren, 1989). Results from inactivation of area LIP with injections of the GABA$_A$ agonist muscimol have also been inconclusive. Some mild increases in saccade latency in the memory delayed response task were observed by Li et al. (1999), but subsequent single (Schiller and Tehovnik, 2003) and multiple injections (Wardak et al., 2002) failed to reproduce reliably these effects. In contrast, much more reliable increases in saccade latency following LIP inactivation are observed when monkeys perform alternative choice tasks (Wardak et al., 2002). Together with the decreases in saccade latency observed when LIP is microstimulated during choice tasks (Hank et al., 2006), these findings suggest that LIP neuronal activity reflects covert processes only indirectly related to saccade initiation.

Overall, the neuronal population in area LIP does not appear to carry the necessary neural signals to regulate when a saccade will be produced, i.e. it is most probably not involved in saccade preparation per se. The next sections examine whether area LIP participate in the covert processes that maintain saccade goal representations and select saccade goals.

Visual working memory

Saccadic eye movements can be directed not only to visual stimuli but also to their remembered location. Our ability to maintain information temporarily is critical for goal-driven behaviour, including eye movements. This cognitive process is referred to as working memory and significant experimental and theoretical advances have been made regarding its substrate. First, neural activity that persists in the absence of a sensory stimulus has been identified in a network of cortical areas, including the PPC (see for review Curtis, Chapter 20, this volume). Second, likely candidates for the underlying mechanism have been suggested to include the reverberatory process provided by the recurrent projections of cortical pyramidal neurons (Amit, 1995) and the slow dynamic of the NMDA glutamate receptor (Lisman et al., 1998), both of which playing predominant roles in our current models (see for review Durstewitz et al., 2000; Wang, 2001, 2010).

A large body of work on the neuronal persistent activity associated with working memory has been conducted within the PFC in delayed response tasks involving either skeletomotor (Fuster and Alexander, 1971; Kubota and Niki, 1971) or ocumolotor responses (Bruce and Goldberg, 1985; Funahashi et al., 1989). Persistent activity has also been observed in PPC (Fig. 14.1) (see for review Constantinidis and Procyk, 2004; Rawley and Constantinidis, 2009), and it is frequently used as a defining characteristic of neurons in area LIP, but not frequently studied as a mnemonic process (but see Mazzoni et al., 1996). As indicated in the section above, Andersen and colleagues were first to show that PPC neurons in area LIP and 7a discharge during the delay period (retention interval) intervening between the presentation of a stimulus in a neuron's receptive field and the ensuing eye movement made to that remembered location (Andersen et al., 1987; Gnadt and Andersen, 1988; Barash et al., 1991). This delay activity in area LIP has since most often been interpreted as being associated with saccade-related processes. Given the lack of strong evidence directly linking area LIP

to movement processing, it is important to test the alternative hypothesis that its persistent activity reflects the process of retaining in memory the sensory stimulus presented in delayed response tasks.

There are extensive interconnections between PPC and PFC, including LIP and FEF, respectively (Andersen et al., 1990; Cavada and Goldman-Rakic, 1989; Petrides and Pandya, 1984; Schall et al., 1995a; Schwartz and Goldman-Rakic, 1984; Stanton et al., 1995). And the persistent activity of LIP neurons in the memory delayed saccade task is very similar to that found in PFC (Chafee and Goldman-Rakic, 1998). Furthermore, it has been shown that persistent activity in these areas is interdependent (Chafee and Goldman-Rakic, 2000), which suggests a cooperative role in working memory processes. The specific role of LIP persistent activity in working memory is, however, not as well established as for PFC (see for review Johnston and Everling, Chapter 15, this volume). For instance, correlational evidence that PFC persistent activity is mnemonic in nature has been provided by Funahashi et al. (1989), who showed that this activity is reduced, or absent, when monkeys incorrectly perform the delayed saccade task. Similar observations have yet to be made in area LIP. More causal evidence has also been provided in the demonstration that PFC deactivation impairs working memory performance (Funahashi et al., 1993). Again, such impairments have yet to be consistently observed following PPC deactivation (Chafee and Goldman-Rakic, 2000) or inactivation (Li et al., 1999; Wardak et al., 2002).

Nevertheless, some important observations have been made regarding the nature of LIP persistent activity in the memory delayed saccade task. First, LIP neurons have greater visually evoked responses than saccade-related activity in this task (Barash et al., 1991; Paré and Wurtz, 1997, 2001), and the directional tuning of their delay activity is better aligned with their visually evoked responses than their saccade activity (Barash et al., 1991). These data suggest that the LIP persistent activity reflects more retrospective than prospective representations. Second, the neural activity during the delay period possesses a temporal structure, which is not present during fixation and which include broadband oscillations within the gamma frequency range (Pesaran et al., 2002). These oscillations are comparable to those observed in human EEG during short-term memory (Tallon-Baudry et al., 1998; see for review Jensen et al., 2007; Wang, 2010) and consistent with the dynamics of slow reverberation networks capable of maintaining persistent activity (Wang, 1999; Compte et al., 2000; see for review Wang, 2010). Third, it was shown that the persistent activity of LIP pyramidal neurons that project to FEF does not differ from that of pyramidal neurons that project to SC (Ferraina et al., 2002). Because cortico-cortical and cortico-tectal neurons are nearly all confined to cortical layer III and V, respectively, this finding indicates that the persistent activity in both layers may rest on similar reverberatory processes. This may contrast with the emphasis on layer III microcircuitry within PFC as a substrate for working memory. Lastly, compared to the activity displayed by in response to prolonged visual stimulation, the rate of persistent activity of LIP neurons is both lower (Fig. 14.1) (Ferraina et al., 2002; Paré and Wurtz, 1997, 2001) and more irregular (Johnston et al., 2009), which suggest that LIP mnemonic representations are low-fidelity signals. It remains to be tested whether the limited information contained in LIP persistent activity accounts for the limited capacity of visuospatial working memory of macaque monkeys (Heyselaar et al., 2011).

The approach taken so far to study the neurophysiological basis of visual working memory has been almost exclusively limited to single-stimulus delayed response tasks, which obviously fail in manipulating working memory demands. It has therefore been difficult to establish a strong linking proposition between persistent activity and working memory content. Much stronger evidence that PPC plays an important role in visual working memory has been obtained in human studies using multiple-stimulus sequential comparison tasks while measuring brain activation with evoked related potentials (Vogel and Machizawa, 2004) and blood-oxygen-level dependent signals (Todd and Marois, 2004). These experiments have found that changes in activation localized to PPC to predict successful performance, to be modulated by the memory load imposed by the task (i.e. the number of objects being held in memory), and to saturate for memory arrays that meet or exceed the subject's memory capacity limit. Several pieces of evidence suggests that area LIP contain neurons carrying signals sufficient to maintain temporarily the goal of a saccade in the absence of visual

stimulation, but new data and experimental approaches are needed to support unequivocally this hypothesis.

Visual attention

Visual attention relates to the neural processes by which visual information is filtered and selected, so that it can be more fully processed and possibly brought into perceptual awareness. In most natural situations, vision is active and visual processing involves the sequential sampling of details accomplished by overtly shifting perceptual resources, i.e. by reorienting the line of sight. Saccades are thus 'overt' shifts of visuospatial attention (see for review Kristjánsson, Chapter 25, this volume). Furthermore, experimental evidence suggests that saccade processing is closely related to 'covert' visuospatial attention. Shifting visual attention covertly to a spatial location facilitates the processing of saccades directed to that location, whereas planning a saccade to a spatial location facilitates perceptual processing of objects at that location (see for review Awh et al., 2006; Moore et al., 2003). Such a functional coupling between covert and overt shifts of visuospatial attention may result from the overlapping of their respective neural circuits (Corbetta et al., 1998; Nobre et al., 1997) and from the massive connections between brain areas with visual and oculomotor functions (e.g. Schall et al., 1995a). Consistent with this interconnectivity, voluntary shifts in visual attention are associated with enhanced activity not only in visual cortical areas (see for review Maunsell and Treue, 2006) but also in FEF and SC (see for review Awh et al., 2006; Moore et al., 2003).

Attention-related modulation in neuronal activity has also been observed in PPC (see for review Constantinidis, 2006; Goldberg et al., 2006). Early recording in area 7—including portion of the lateral bank of the intraparietal sulcus, from which LIP neurons would likely have been sampled—showed that the visually evoked responses of neurons are enhanced when a visual stimulus presented in their receptive fields specifies the goal of a saccade (Robinson et al., 1978; Yin and Mountcastle, 1977) or of a reaching arm movement (Bushnell et al., 1981). These findings paralleled those of Lynch et al. (1977), who recorded in the same PPC region neurons that showed enhanced activity during active fixation or tracking of a visual stimulus. Similar enhancements were observed when monkeys performed a peripheral attention task, which required detecting the dimming of a visual stimulus placed within the neuron's receptive field by releasing a lever, i.e. without making a saccade to that stimulus (Bushnell et al., 1981; see for review Colby and Goldberg, 1999). The independence of this enhancement from the animal's response is in line with the hypothesis that PPC provides guidance signals for actions in general as well as with the hypothesis that LIP neuronal activity reflects covert visuospatial attention, which is not necessarily associated with any action; see also Thompson et al. (2005b) for a similar account in the FEF. In summary, area LIP does appear to contain neural signals that are sufficient to regulate which stimulus is selected for further perceptual processing, which may then be used for guiding an action.

A significant body of work on visual attention has used the visual search paradigm, in which the ability of a subject to find a target within a multistimulus display can inform us about that subject's allocation of attentional resources (see for review Wolfe and Horowitz, 2004). This approach most often requires subjects to indicate the presence of the search target with a manual response without them being instructed to foveate that stimulus, but several studies have also monitored where subjects look while performing this task (e.g. Binello et al., 1995; Maioli et al., 2001; Scialfa and Joffe, 1998; Williams et al., 1997; Zelinsky and Sheinberg, 1995). As stressed above, the natural exploration of the visual world involves visuospatial attention being deployed by reorienting the line of gaze and the monitoring gaze fixations during visual search therefore provides almost a moment-by-moment measure of a subject's allocation of attention. The high rate of saccades in natural tasks such as visual search, text reading, and scene perception suggests that there are few attentional shifts besides those associated with the execution of saccades when the eyes are free to move (for a review see Findlay and Gilchrist, 2003). Covert shift of spatial attention may only assist overt shifts and the additional analysis of the visual periphery that it provides during each fixation contribute to the selection of the visual

detail that will become the goal of the next saccade (see Henderson, 1992; Schall 2004; Schall and Thompson, 1999; Schneider, 1995).

The process of selecting a saccade target among the several alternatives available in a visual search display has been studied at the neural level (see for review Schall and Cohen, Chapter 19, this volume). For neurons to be involved in saccade target selection, they must discharge differently when a saccade target versus a distractor stimulus is presented in their receptive fields and they must do so in advance of saccade initiation. Such neurons have been recorded in both the FEF (Bichot and Schall, 1999; Sato and Schall, 2003; Schall and Hanes, 1993; Schall et al., 1995b; Thompson et al., 1996) and the SC (McPeek and Keller, 2002; Shen and Paré, 2007) as well as in visual cortical areas (area V4: Bichot et al., 2005; Chelazzi et al., 2001; Mazer and Gallant, 2003; Ogawa and Komatsu, 2004, 2006; area TEO: Chelazzi et al., 1993).

Several pieces of evidence indicate that the PPC in general and area LIP in particular participates in the process of selecting saccade targets during visual search. First, functional brain imaging studies have shown blood flow increases in human PPC during difficult visual search (Corbetta et al., 1993; Donner et al., 2000, 2002; Gitelman et al., 2002; Nobre et al., 2003). Interestingly, the location of this activation matches very closely a region previously associated with both covert and overt shifts of attention (Corbetta et al., 1993, 1998; Nobre et al., 1997). Second, transcranial magnetic stimulation of PPC selectively impairs performance in difficult visual search (Ashbridge et al., 1997; Hodsoll et al., 2009; Kalla et al., 2008; Muggleton et al., 2008). Third, human patients with PPC lesions show marked deficits in difficult visual search when targets fall in their contralesional visual field (Arguin et al., 1993; Eglin et al., 1989; Karatekin et al., 1999; Riddoch and Humphreys, 1987). In the monkey, the role of area LIP in the process of saccade target selection was first demonstrated by Wardak and colleagues (Wardak et al., 2002), who observed deficits in visual search following LIP inactivation; similar deficits in covert attention were also observed (Wardak et al., 2004).

Consistent with the visual search studies on saccade target selection cited above, LIP neurons were shown to discriminate a saccade target from distracter stimuli in advance of saccade initiation (Ipata et al., 2006; Mirpour et al., 2009; Ogawa and Komatsu, 2009; Thomas and Paré, 2007). The time at which LIP neuronal activity discriminates the saccade target was found to correlate with the latency of the search saccades (Ipata et al., 2006; Thomas and Paré, 2007). This finding is comparable to observations made in distinct neuronal populations within FEF (Sato and Schall, 2003; Thompson et al., 1996) and SC (McPeek and Keller, 2002), and it has been interpreted as evidence for the role of LIP in saccade generation (Bisley and Goldberg, 2010). This interpretation is, however, difficult to reconcile with previous findings that LIP neuronal activity does discriminate visual stimuli substantially in advance of saccade initiation in instructed, delayed saccade tasks (Paré and Wurtz, 2001; Platt and Glimcher, 1997; Toth and Assad, 2002). Furthermore, other studies have reported evidence for a similar visual selection in the complete absence of saccades (Balan and Gottlieb, 2006; Balan et al., 2008; Oristaglio et al., 2006). We have also argued elsewhere against such an interpretation, on the basis of the differences between the tasks performed by the monkeys in these studies (Paré et al., 2009). Visual and saccade selection processes may be more difficult to dissociate temporally in the LIP studies because the unconstrained nature of their search tasks emphasizes speed over accuracy. The correlation between the timing of LIP neuronal discrimination and saccade initiation may rather be evidence for a direct association between covert shift in visual attention and the selection of the next saccade in natural situations, when saccades are not associated directly with a reward or punishment (Findlay and Gilchrist, 2003). It remains to be tested whether this correlation is also manifest when FEF and SC neurons are recorded in unconstrained visual search tasks. Recent evidence suggests that it is the case in the SC (Shen et al., 2011).

Altogether, this collection of data implicates area LIP in selective visual processes guiding both covert and overt shifts in attention. The map of visual space within area LIP may thus instantiate the visual salience map postulated by models of visual search and selective attention (Cave and Wolfe, 1990; Findlay and Walker, 1999; Glimcher et al., 2005; Hamker, 2006; Itti and Koch, 2001; Logan, 1996; Treisman, 1988; Treisman and Gelade, 1980; Wolfe, 1994). According to these models, the stimulus-driven outputs from individual feature maps, which can be instantiated by extrastriate

cortical areas, are integrated with goal-directed signals into a map of representations, whose magnitudes reflect the relative importance of each stimulus. Despite many similarities between the neuronal activity observed in FEF, area LIP, and SC (see for review Schall et al., 2007), it is unlikely that the visual salience map is simply replicated across these brain regions. With respect to saccade target selection, we posit that this process results from the progressive filtering of distracter representations and amplifying of target representations from area LIP to FEF onto SC. This is supported by our comparative analysis showing that the reliability of the target/distracter discrimination improves from cortex to SC (Thomas and Paré, 2007). Continuous flow of information between these brain regions could account for the discriminating activity observed simultaneously across these brain regions.

In summary, area LIP does appear to contain neurons carrying signals sufficient and perhaps necessary to regulate where a saccade will be directed.

Saccade decision

Saccade target selection in visual search implies a perceptual decision, which is the process by which a specific item is selected as the next target of an action. Anatomically, area LIP is ideally situated to integrate diverse sources of evidence that are involved in visual decision-making and to send guiding signals to saccade generating centres like the FEF and SC. Although some evidence suggests that LIP neuronal activity accumulates towards a bound (Churchland et al., 2008; Kiani et al., 2008), as we have outlined previously, it is unlikely that a saccade trigger threshold exists in LIP. Rather we argue that area LIP provides a map where evidence supporting the saliency of competing visual items accumulates. Decisional processes can then assist visual attention, visual working memory, saccade preparation and, if required, saccade execution (see for review Ludwig, Chapter 23, this volume).

Broadly speaking, evidence that favours one visual item over others can come in the form of immediate sensory cues or economic variables that are learned through experience. Researchers have developed tasks that employ instructive cues of varying quality or economic outcomes that are uncertain to examine how such forms of evidence are represented in LIP activity and related to one's choices. Recent evidence also suggests that decision processes in LIP are strongly modulated by the expected timing of environmental cues and required responses.

The motion discrimination task (Britten et al., 1992) has been particularly useful to study decision-making based on sensory evidence. In this task, monkeys view a random dot kinetogram, in which a minority of the dots is moving in a coherent direction amongst randomly moving dots. The monkey then indicates the overall perceived direction of motion by directing a saccade to one of two peripheral saccade targets. The location, size, speed, and direction of the random dot kinetogram are optimized to best activate the LIP neuron under study. Results from this work have demonstrated that LIP neuronal activity accumulates for preferred direction motion, the rate of which depends on the quality of the sensory evidence, i.e. motion coherence (Shadlen and Newsome, 1996, 2001). Moreover, the accumulation process continues with longer exposure, but like behavioural performance, tends to asymptote (Shadlen and Newsome, 2001). Together, these LIP properties are consistent with bounded accumulator models of simple decision-making, which provide a mechanism for integrating incoming sensory information over time.

LIP neuronal activity also encodes more economic variables that are not immediately sensory in nature but are learned through experience. Rather than base their decisions on sensory instructions, monkeys are required to choose based on the relative reward rates between options or through strategic competition. LIP neuronal activity is influenced by the probability of a saccade target yielding a reward, the magnitude of reward associated with that option and the degree of confidence in the decision (Fig. 14.4A) (Churchland et al., 2008; Dorris and Glimcher, 2004; Kiani and Shadlen, 2009; Platt and Glimcher, 1999; Rorie et al., 2010; Yang and Shadlen, 2007). Unlike the FEF and SC (Basso and Wurtz, 1998; Dorris and Munoz, 1998; Ikeda and Hikosaka, 2003; Roesch and Olson, 2003), economic information is not represented in baseline LIP activity but is only revealed immediately after target presentation (Fig. 14.4A). This finding strongly suggests that LIP is not where economic variables are stored; instead representations in area LIP are modulated by their potential economic impact from external sources.
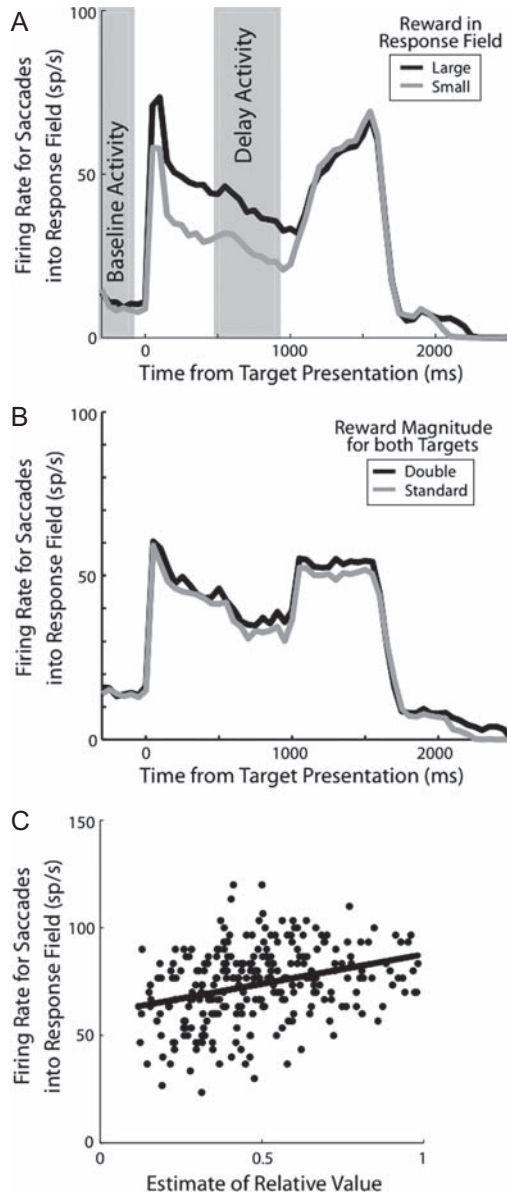
Fig. 14.4 LIP represents the relative value of potential visual targets. **A.** Population firing rate (n=30) when saccades were instructed to response field targets of differing reward. Note that there is no difference in firing rate during the baseline period preceding target presentation even though the location of the large and small rewarded targets are fixed throughout a block of trials. In addition, the difference in firing rate only occurs during the first 1000 ms after target presentation when the monkey is uncertain which target will be instructed. Once a cue indicates that the target in the response field is the target (approx. time 1000 ms) then uncertainty is removed and the neurons fire at the same rate regardless of reward magnitude. **B.** Trial by trial correlations between firing rate and an estimate of relative value during a strategic game. Activity was sampled for a single neuron during the delay period highlighted in **A. C.** Relative not absolute value is represented in LIP. Population firing rate (n=22) during a strategic game when standard reward magnitudes were used or the rewards for both targets were doubled. Adapted from Neuron, vol. 44, Dorris, M. C., & Glimcher, P. W., Activity in posterior parietal cortex is correlated with the relative subjective desirability of action, pp. 365-78, 2004, with permission from Elsevier.

More recently, a case has been made that LIP neuronal activity is not influenced by either probability or reward in isolation but something closer to their product, expected value. More specifically, activity is a function of relative expected value, i.e. the expected value of the neuron's preferred target divided by the sum of the expected values for the other potential visual targets (Fig. 14.4B) (Dorris and Glimcher, 2004; Platt and Glimcher, 1999; Rorie et al., 2010). This normalization of value across LIP is ideal from a decision-theoretic standpoint because it allows many multiple potential options to be represented simultaneously and compared across a wide range of values.

These decision processes do not evolve at a fixed rate but are strongly influenced by the expected timing of environmental events. For example, LIP neurons adjust their activity to reflect whether the duration of sensory events are shorter or longer than a standard time (Leon and Shadlen, 2003). LIP activity can also represent sophisticated probabilistic time distributions of when salient events are likely to occur (Janssen and Shadlen, 2005). Such timing signals are potentially important for initiating voluntarily actions especially those constrained by strict deadlines for choosing (Churchland et al., 2008; Maimon and Assad, 2006).

If area LIP is involved in the decision process, its activity must not only be influenced by sensory, economic, and timing evidence but also it must predict the choices that subjects ultimately make. Indeed, in the motion discrimination task, while LIP activity is clearly influenced by the coherence of the motion stimulus it also predicts whether the animal will choose correctly for a given coherence (Shadlen and Newsome, 1996, 2001). Particularly telling, when the monkey viewed motion stimuli below their psychophysical thresholds, LIP activity is predictive of upcoming choice. Lastly, artificially increasing LIP activity with electrical micro-stimulation manipulates perceptual decision formation as evidenced by decreases in the latency and increases in the proportion of choices in favour of the option associated with the site of stimulation (Hanks et al., 2006). Similarly, when saccadic choices are based on more economic considerations, LIP activity is influenced by the relative value of the options but also predicts the overall allocation of choices (Coe et al., 2002; Dorris and Glimcher, 2004; Seo et al., 2009; Sugrue et al., 2004). Similar to the ambiguous motion coherence, when the subjective values of the targets are, on average, equal during a strategic equilibrium, LIP activity is predictive of upcoming choices on a trial-by-trial basis (Fig.14.4C).

Together, the dynamic representation of both sensory and economic forms of evidence on the same maps can provide downstream structures with important information regarding which of the potential targets is the most salient at any moment in time. Decision theory posits that overt choice should be directed towards the most salient item, which would be the point of highest activity on the LIP map. Covert processes such as visual attention and saccade preparation, however, may be allocated in proportion to the salience representation of multiple options on this LIP map. Bounded integration models, influenced in large part by empirical findings, have been successful in reproducing patterns of behavioural choice (Huk and Shadlen, 2005; Kiani et al., 2008; Mazurek et al., 2003; Wong et al., 2007). Although further empirical and theoretical work is required to understand the rules by which sensory, economic and timing evidence are weighted and combined within this single map for the vast majority of decisions in the real world rely on all considerations (e.g. Feng et al., 2009; Gold and Shadlen, 2002). An initial examination of how sensory and reward information is integrated in LIP by Rorie et al. (2010) suggests that reward biases the starting position of the accumulation process but does not the affect the rate of accumulation which is determined by the quality of sensory information.

In summary, area LIP appears to contribute to saccade decision processes based on incoming sensory evidence, economic variables, and the expected timing of salient events.

Conclusion and future directions

We have reviewed the role of PPC in regulating saccadic eye movements. Our focus has been on area LIP, an evolutionarily recent outcropping of the PPC in primates presumably in response to their reliance on high acuity foveal vision and extended oculomotor range. Anatomically, area LIP is situated at the nexus between sensory and motor processing stages related to visual behaviour.

LIP neuronal activity is not as directly involved in the production of saccades as compared to the FEF and SC, but it forms representations about potential saccade targets. In sum, area LIP appears to be a recent innovation that supplements the saccadic eye movements system with guidance signals, thereby allowing primates more flexible behavioural control.

The guidance signal that LIP provides has been termed 'saliency', which is a subjective perceptual quality that causes some items to 'jump' out from their settings—the use of this term can be traced back to conditioning theory (see for review Rescorla, 1988; Rumbaugh, 2007). Saliency is a multifactorial quantity composed of diverse sensory and cognitive signals. We have reviewed how sensory evidence contributes to a saliency representation in area LIP during the discrimination of visual stimuli from alternatives. We have also reviewed cognitive evidence that are less immediate in nature but are gathered through experience. These include the relative value of potential targets, timing signals and a role for sensory working memory. In keeping with its evolutionary emergence, the salience map in area LIP should also be considered to regulate other behaviours, e.g. visual perception and visuomanual behaviour, including eye–hand coordination and grasping.

Future advances about the role of area LIP in saccade-related processes may be provided by new data from comparative studies that address the evolution of the PPC and of the 'high-order' network of which it is a constituent. This review highlighted the benefits of comparing results obtained in area LIP with those obtained in FEF and SC. This comparative approach is necessary to gain a comprehensive understanding of the neural circuit regulating saccadic eye movements. Further distinction between data collected from LIPd and LIPv will help resolve an already large and growing body of data. Substantially more data are needed to understand the role of LIP persistent activity in visual working memory, and new approaches are recommended to advance our understanding of the neural basis of this process within and beyond the PPC. Area LIP continues to be a model area to study decisional processes, but the study of selective visual attention in the context of visual search still deserves more attention.

Acknowledgements

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