

Chapter 12

The Role of the Pulvinar in Spatial Visual Attention

There are at least two general mechanisms in which the pulvinar seems to be instrumental for spatial visual attention (Fig. 12.1). The first aspect concerns the pattern of pulvinar connectivity with brain regions known to be playing a role in attentional mechanisms. The reciprocal and profuse nature of these projections indicates that the pulvinar is in a strategic position for coordinating activity across large neuronal networks. Therefore, the pulvinar could serve as a hub for brain communication and thereby gate the flow of information across different brain regions. Notably, these connectivity patterns follow a precise visuotopic organization, which is particularly useful for the spatial aspect of visual attention. In addition to its coordinating role, the pulvinar seems to also participate in the selection process of attention. Rafal and Posner (1987) proposed a model for the posterior attention system, which deals with spatial visual attention (Posner and Petersen 1990). They used a very simple attention task that was tested in patients with cortical (i.e., parietal) and subcortical (i.e., pulvinar and SC) lesions. According to these authors, attention is a continuous process with four operational steps: disengage, move, engage, and inhibit (Fig. 12.1). The first step is thereby to disengage from the undesired location and then to redirect attention to the new target location. The previously attended location is now disfavored by the attention system, and the subject responds more slowly at that location than to any other location in the visual field. This tendency to make slower responses to the previously attended location is called “inhibition of return.”

Patients with lesions in the parietal cortex show a primary deficit in the disengage operation of spatial visual attention. These patients were unable to move their attention toward the hemifield contralateral to the lesion site (designated as the “bad” visual hemifield). Midbrain lesions involving the SC impaired the ability to redirect the attentional focus. Patients with such lesions lacked an effective “inhibition of return” as they had difficulty moving their eyes and shifting their attention covertly. In patients with pulvinar lesions, one observed a deficit in the ability to hold attention on the target stimulus when competing information was also present

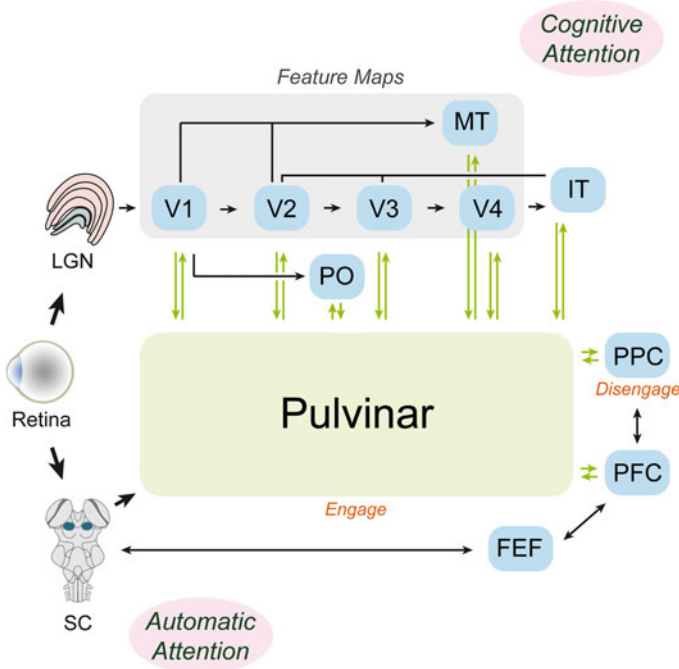


Fig. 12.1 Schematic diagram of the neuroanatomical circuit underlying automatic and cognitive spatial visual attention. An attempt was made to correlate the anatomical structures to the basic attentional mechanisms of disengaging, moving, engaging and inhibiting the focus of attention. V1, V2, V3, V4, PO and MT are cortical visual areas; *LGN* lateral geniculate nucleus, *FEF* frontal eye field, *PFC* pre-frontal cortex, *PP* posterior parietal, *SC* superior colliculus [modified from Gattass and Desimone (1996)]

in the visual field. Therefore, monkeys and patients with pulvina lesions seem to have a great deal of difficulty filtering out or ignoring irrelevant stimuli that occur at locations other than the one to which they are attending (Desimone et al. 1990; Petersen et al. 1985, 1987). In this sense, these individuals are more distractible and have difficulty engaging their attentional focus (Gattass and Desimone 1996). This scheme incorporates the distinction of at least two attentional mechanisms: one automatic, mediated by the SC, and another central or cognitive, not related to the SC but rather to cortical visual areas with a potential role played by the pulvina.

From the perceptual point of view, when the eyes are fixed, attention can be covertly directed to another location other than fixation, and information processing at that location will be accordingly enhanced. From the oculomotor perspective, attention at that location can help to determine where to move the eyes (Gattass and Desimone 2014). In normal behavior, the eyes will usually move to that location. Following the eye movement, novel locations, which have not been attended to in the last few seconds, are favored over previously attended locations. Posner's model of attention assumes that attention precedes the eye movement. In this

respect, this model is different from the one proposed by Goldberg and Wurst (1972) in which signal programming of the eye movement, coming from the deep layers of the SC, propagates upward to the superficial layers and engages spatial visual attention. The projection of the SC to the cortex, via the pulvinar nucleus, contributes to the visual and attentional properties of cortical visual areas (Gross 1991; Treue and Maunsell 1996).

Although the specific proposals differ, a role for the pulvinar in visual attention has been a recurrent hypothesis (e.g., Chalupa et al. 1976; Gattass et al. 1979; Crick 1984; LaBerge and Buchsbaum 1990; Robinson and Petersen 1992; Olshausen et al. 1993; Shipp 2000). More recent work finds that attentional modulation of activity is pervasive within the pulvinar and as significant as in any area of the cortex (Bender and Youakim 2001). The model presented by Shipp (2003) corroborates this idea. Shipp (2003) reviewed the published data on the topography and connectivity of the pulvinar with the cortex and proposed a simplified, global model for the organization of cortico-pulvinar network. According to this model, connections between the cortex and pulvinar are topographically organized, and as a result, the pulvinar contains four topographically ordered “maps.” Shipp (2003) proposed a replication principle of central-peripheral-central projections that operates at and below the level of domain structure. He hypothesized that cortico-pulvinar circuitry replicates the pattern of cortical circuitry, but not its function, thereby playing a more regulatory role instead. The projecting cells in V4 and their termination in the pulvinar suggest that the cortical-pulvinar-cortical connections define a pathway by which deep layers of cortical visual areas affect, via pulvinar, the superficial layers of coupled cortical areas.

In our study of the cortical connections of V4, we found a central-peripheral asymmetry in the projections to the temporal and the parietal cortices (Ungerleider et al. 2008). We concluded that peripheral field projections from V4 to parietal areas could provide a direct route for rapid activation of circuits serving spatial vision and attention, while the predominance of central field projections from V4 to inferior temporal areas could provide the necessary information needed for detailed form analysis for object vision. In the study of the subcortical connections of V4, Gattass et al. (2014) found no evidence for central-peripheral asymmetry. Instead, we found both topographical and non-topographical projections to subcortical structures. These data led us to propose a segregation of topographical bidirectional projections to the four fields of the pulvinar, to two subdivisions of the claustrum, and to the interlaminar portions of the LGN, structures that may operate as gates for spatial attention. The topographical efferent projections to the superficial and intermediate layers of the SC, to the thalamic reticular nucleus, and to the caudate nucleus suggest that these structures may also be involved in the processing of visual spatial attention.

Consistent with this role of the pulvinar in regulating effects of spatial attention in V4, deactivation of this portion of the pulvinar causes spatial attention deficits in monkeys (Desimone et al. 1990). Accordingly, joint electrophysiological recordings in V4 and PL reveal synchronized activity between the two structures during spatial attention tasks (Saalmann and Kastner 2011). However, several open

questions remain regarding the neurophysiological basis and dynamics of pulvinar-cortical interactions. Saalman et al. (2012) reported that neuronal oscillations of predominately lower frequencies (<30 Hz) would be responsible for synchronizing the pulvinar with cortical visual areas. However, lower-frequency oscillations have been largely associated with inactive states and sleep. Indeed, Zhou et al. (2016) used GABA to inactivate the pulvinar in monkeys performing a visual spatial task while simultaneously recording the neuronal activity of the pulvinar and V4. They observed that pulvinar inactivation drove the cortex into an “inactive” state, including reduced higher-frequency oscillations and synchronization in V4, increased lower-frequency oscillations in V4, and substantial behavioral deficits in the affected portion of the visual field. One of the established effects of attention is an enhanced synchrony in the gamma frequency band, presumably for the facilitation of neuronal communication (Fries et al. 2001; Fries 2005, 2015; Womelsdorf et al. 2007). Accordingly, Zhou et al. (2016) tested for pulvinar-V4 synchronization by measuring the spike-LFP coherence between both regions during a visual attention task. Indeed, spike-LFP coherence was found to be enhanced between the pulvinar and V4 when attention was directed to a location that fell within the recorded receptive fields. However, the authors reported that area V4 systematically led the pulvinar in terms of gamma synchrony (at least for the spatial attention task they employed). This result begs the question as to what special role (if any) the pulvinar might play in coordinating larger networks of cortical activity, as initially proposed by Shipp (2003). On the other hand, and despite the overlap in neuronal properties between V4 and the ventrolateral pulvinar, inactivation of the latter results in profound neuronal and behavioral deficits. Resolving the functional role of the pulvinar and how it interacts with the cortex in order to organize behavior will be fundamental questions to tackle in future research.