

Corticocortical and thalamocortical information flow in the primate visual system

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Abstract: Visual cortex in primates contains a mosaic of several dozen visual areas that collectively occupy a large fraction of cerebral cortex (~50% in the macaque; ~25% in humans). These areas are richly interconnected by hundreds of reciprocal corticocortical pathways that underlie an anatomically based hierarchy containing multiple processing streams. In addition, there is a complex pattern of reciprocal connections with the pulvinar, which itself contains about 10 architectonically distinct subdivisions. Information flow through these corticocortical and corticothalamic circuits is regulated very dynamically by top-down as well as bottom-up processes, including directed visual attention. This chapter evaluates current hypotheses and evidence relating to the interaction between thalamocortical and corticocortical circuitry in the dynamic regulation of information flow.

Introduction

Numerous anatomical and neurophysiological studies of primate visual cortex during the 1980s and early 1990s led to several broad hypotheses about cortical organization and function. (1) *Multiplicity of areas.* Cerebral cortex includes a complex mosaic of several dozen visual areas that differ from one another in cortical architecture, connectivity, visual topography, and/or functional characteristics (Maunsell and Van Essen, 1983; Van Essen, 1985; Desimone and Ungerleider, 1989; Kaas, 1997). (2) *Distributed hierarchical organization.* Visual areas can be arranged into an anatomically defined hierarchy (Maunsell and Van Essen, 1983) that includes 10 levels of cortical processing (Felleman and Van Essen, 1991). This hierarchical scheme is based on feedforward,

feedback, and lateral directions of information flow suggested by the laminar patterns of connectivity among several hundred identified corticocortical pathways. However, not all anatomical data fit perfectly with this scheme (Felleman and Van Essen, 1991), and there are alternate schemes involving different numbers of hierarchical levels (Hilgetag et al., 2000). Hence, it may be more appropriate to consider the cortex as “quasi-hierarchical” in its organization. (3) *Multiple processing streams.* At each hierarchical level there are multiple processing streams, manifested by anatomically distinct yet intertwined compartments at early cortical levels (areas V1 and V2) and by physically separate dorsal and ventral streams at higher levels (DeYoe and Van Essen, 1988; Desimone and Ungerleider, 1989; Goodale and Milner, 1992; Van Essen and Gallant, 1994). More recent studies have highlighted that cross-talk between streams is extensive at multiple levels (Yabuta et al., 2001; Sincich and Horton, 2002). (4) *Dynamic routing of information.* The control of

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information flow is highly dynamic within the anatomically defined hierarchy and is powerfully regulated by visual attention. Directed visual attention constitutes an information bottleneck that allows only a tiny fraction (<1%) of the information passing through the optic nerve to reach conscious perception (Van Essen et al., 1992; Olshausen et al., 1993; Anderson et al., 2005). The attentional system requires circuitry for deciding where to attend and at what spatial scale. In addition, there must be circuitry that implements these decisions rapidly, perhaps by way of pulvinarcortical circuits that selectively gate corticocortical information flow (Olshausen et al., 1993). While this model provides an attractive framework that accounts for many aspects of attention, many other models of attention have been proposed that differ in a variety of ways (Itti and Koch, 2001; Itti et al., 2005).

With this background in mind, the present chapter addresses several general issues relating to the flow of information within the primate visual system. The overarching objective is to compare the nature of information flow through corticopulvinarcortical (CPC) circuits versus that through corticocortical (CC) pathways. Sherman and Guillery (1998, 2005 (this volume)) have suggested that in general (i) cortico-thalamo-cortical circuits may be a major if not the dominant route for “driving” ascending sensory information and that (ii) direct corticocortical circuits may be largely modulatory rather than driving in their function. This hypothesis is essentially the opposite of the hypothesis that CPC pathways modulate the flow of visual information carried by direct CC pathways (Olshausen et al., 1993; Anderson et al., 2005). As argued in Corticocortical vs. corticopulvinarcortical information flow, consideration of the numbers of neurons available to represent the results of successive stages of cortical processing make the extreme form of the CPC driver hypothesis very unlikely. Nonetheless, the fundamental issue of whether the pulvinar and CPC circuits have a driving or a modulatory role is a central but unresolved issue.

The number of neurons present in any given structure or pathway places strong constraints on the amount of information that can be communicated and in the options available for representing this information. Individual neurons are fundamentally

“noisy” devices, generally capable of conveying only a few (3–10) bits of information per second (Eliasmith and Anderson, 2002). For this reason, the 10^6 axons in each optic nerve constitute a fundamental early bottleneck, restricting information flow to $3\text{--}10 \times 10^6$ bits/sec rather than the far greater information rate encoded by retinal photoreceptors. This information is packaged into three major retinal ganglion cell classes, each acting as a distinct “channel” that efficiently conveys information associated with a restricted portion of spatio-temporo-chromatic space (Van Essen and Anderson, 1995). The encoding at this stage is compact, or “dense”, in the sense that retinal ganglion cells and LGN (lateral geniculate nucleus) neurons have relatively high spontaneous firing rates and have stereotyped center-surround receptive fields that are modulated by a broad range of stimuli encroaching on the classical receptive field.

Beyond the optic nerve bottleneck, the amount of information encoded about a visual scene cannot increase, even though the number of neurons in visual cortex is vastly greater. Instead, the increased neuronal numbers allow for extensive reformatting of the visual representation, in order to make it more useful for subsequent computations. This is at the heart of cortical information processing strategies (Van Essen and Anderson, 1995). The next two sections summarize key aspects of the functional organization of visual cortex and pulvinar in the macaque monkey. The section on visual cortex considers the arrangement and size of different visual areas, patterns of corticocortical connectivity and receptive field characteristics. The section on the pulvinar considers the arrangement of its subdivisions, the pattern of pulvinarcortical connectivity, and the total number of pulvinar neurons.

Cortical areas and surface-based atlases

Primate cortex contains dozens of distinct areas that are largely or entirely visual in function. A combination of obstacles has made it very difficult to chart the arrangement of these areas and to establish their identities unequivocally. (i) *Subtle transitions*: Except for a few areas (e.g., areas V1 and the middle temporal area, MT), the boundaries between visual areas are difficult to discern over most of cortex,

because the transitions are often subtle by any of the anatomical and physiological methods available and because there is internal heterogeneity within each area. (ii) *Cortical convolutions*: The extensive convolutions of macaque cortex (and even more so in humans) have been a major impediment to many aspects of analyzing and making comparisons across individuals. (iii) *Individual variability*: Well defined areas such as V1 and MT vary by two- or three-fold in surface area across individual hemispheres (Van Essen et al., 1984; Maunsell and Van Essen, 1987; Sincich et al., 2003). The variability in location of each area relative to gyral and sulcal boundaries, while far less in the macaque than in humans, is nonetheless on the order of 2–3 mm and thus a major fraction of the dimensions of most areas. Moreover, the precise pattern of convolutions is variable from one individual to the next.

Dozens of partitioning schemes for part or all of cerebral cortex have been described over the past

century, starting with Brodmann and other classical neuroanatomists. For visual cortex alone in the macaque, a dozen schemes remain in current use, and numerous schemes exist for other regions in frontal, parietal, and temporal cortex. Comparisons between these schemes have been impeded by the fact that the various schemes have generally been presented on different atlases or individual brains using a variety of display formats (e.g., brain slices, hemisphere views, views of schematically inflated hemispheres, and flat maps generated manually or by computerized methods).

In order to facilitate comparisons and help resolve discrepancies, this “tower of Babel” of partitioning schemes needs to be brought into a common spatial framework that provides flexible visualization options. To this end, a surface-based atlas of macaque cortex and associated visualization and analysis software has been developed. To illustrate the general approach, Fig. 1 shows fiducial, inflated, and flat map

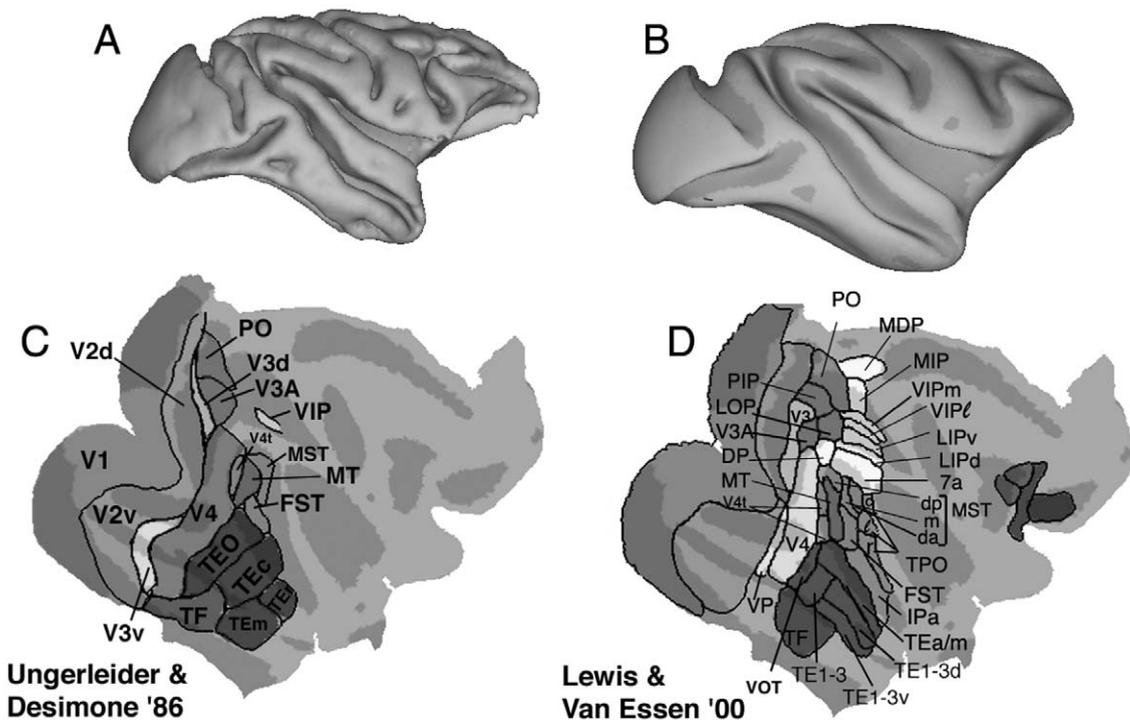


Fig. 1. A surface-based atlas of macaque cortex right hemisphere. A. Lateral view of fiducial surface. B. Lateral view of the inflated atlas surface. C. Ungerleider and Desimone (1986) partitioning scheme on the atlas flat map: D. Lewis and Van Essen (2000a) partitioning scheme. Data sets can be visualized online or downloaded for offline visualization using Caret by accessing <http://sumsdb.wustl.edu:8081/sums/archivelist.do?archivid=685946>.

representations of the right hemisphere of a macaque atlas (the “F99UA1” atlas, based on high resolution structural MRI). Fourteen different partitioning schemes have been mapped to this atlas, in most cases using surface based registration in which geographical landmarks (sulci and gyri) are used to constrain the registration (Van Essen et al., 2001; 2004; Van Essen, 2004a). In the two examples shown in Fig. 1, there are numerous differences between the Desimone and Ungerleider (1986) scheme (Fig. 1C) and the Lewis and Van Essen (2000a) scheme (Fig. 1D). These differences reflect a combination of factors, including the criteria used to identify boundaries, experimental errors in changing areal boundaries, individual variability across monkeys, and distortions introduced in the registration process.

More generally, there is concordance across many studies regarding the existence, location, and approximate extent of seven visual areas: V1, V2, V3d (or V3), V3v (or VP), V3A, V4, and MT (V5), as discussed elsewhere (Van Essen, 2004a,b). For the rest of macaque visual cortex, there is much uncertainty and debate regarding the fundamental subdivisions. Indeed, it is conceivable that some high-level regions in temporal and parietal cortex may not be subdivided into genuinely distinct areas. Such regions might instead be heterogeneous on the basis of gradients or fluctuations in connectivity and function that do not admit to sharply delimited parcellation. Comparisons among the complete set of areal partitioning schemes mapped to the atlas can be made using the SumsDB database (<http://sumsdb.wustl.edu:8081/sums>) by visualizing results online using the WebCaret interface or by downloading the data sets for offline analysis and visualization using Caret software (<http://brainvis.wustl.edu/caret>).

Human visual cortex occupies about 20–30% of total cortical surface area and contains numerous subdivisions, based mainly on topographic and functional criteria (Van Essen, 2004). Most of the visuo-topic areas identified in the macaque have also been charted in human visual cortex, but some are controversial, and many higher level regions have yet to be thoroughly mapped (Van Essen, 2004a,b; Van Essen et al., 2004).

Altogether, the current status of cortical cartography is arguably similar in important respects to that

of 17th century earth cartographers, who were forced to choose among many competing versions of the basic arrangement of earth’s geographic and political subdivisions. Progress in resolving these issues will require extensive additional data that can be analyzed at high spatial resolution and in a way that allows accurate registration across individuals.

Cortical numbers

Cortical areas in the macaque range widely in size and thus in the number of constituent neurons. Area V1 occupies $\sim 1000\text{--}1300\text{ mm}^2$ of surface area (Van Essen et al., 1984; Sincich et al., 2003) and has an estimated 1.6×10^8 neurons in each hemisphere (O’Kusky and Colonnier, 1982). Area V2 is about 1000 mm^2 in surface area (Sincich et al., 2003) but is like the rest of neocortex in having a lower neuronal density than in V1. Assuming 10^5 neurons per mm^2 surface area (Rockel et al., 1980), V2 contains about 10^8 neurons on average. (Given the individual variability in surface area of each area noted above, there is presumably twofold or more variability in neuronal numbers for each area.) The remainder of extrastriate visual cortex occupies about 2400 mm^2 and contains about 2.4×10^8 neurons, for an approximate total of 5×10^8 neurons in macaque visual cortex.

Corticocortical pathways

Among the hundreds of known visual corticocortical pathways, most have been described only in qualitative or at best semiquantitative fashion. Typically, estimates of connection strengths must be assessed by viewing selected histological sections (or drawings thereof) on which retrograde or anterograde connections are displayed. In such cases it is difficult to be more precise than simply characterizing any particular pathway as strong, moderate, or weak (Felleman and Van Essen, 1991). Even in studies that report quantitative aspects of connectivity (e.g., Lavenex et al., 2002), it is generally difficult to make detailed comparisons of the complex spatial patterns of connectivity that are observed in different experiments on different hemispheres.

Surface-based atlases provide a valuable approach for bringing connectivity data, both quantitative

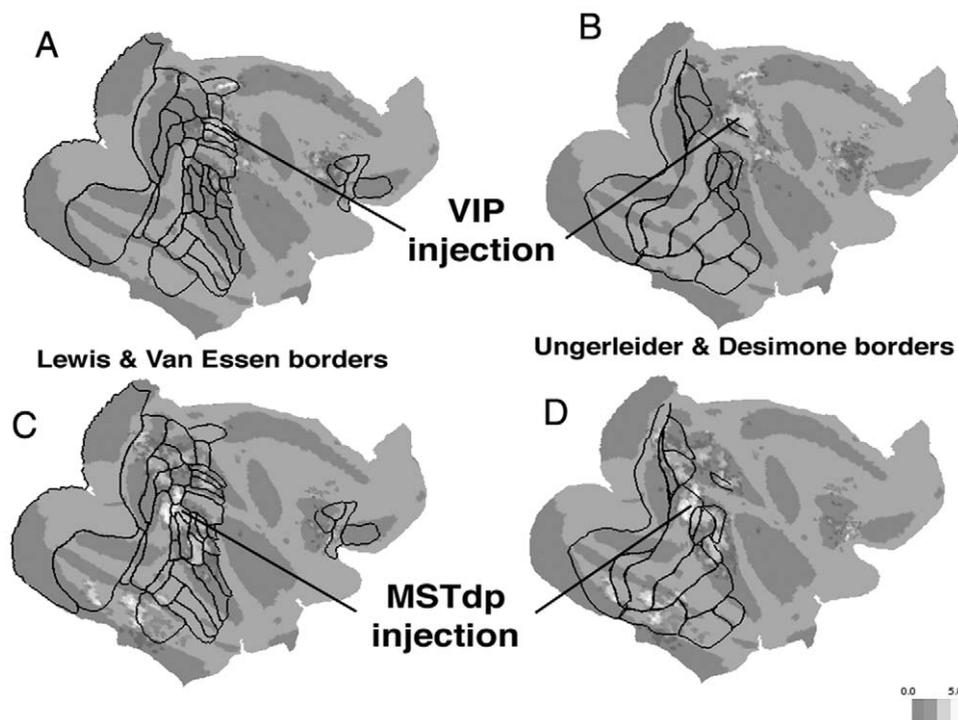


Fig. 2. Connectivity patterns in relation to partitioning schemes. A. VIP injection, with [Lewis and Van Essen \(2000a,b\)](#) areas overlaid. B. Same VIP injection, but with [Ungerleider and Desimone \(1986\)](#) areal boundaries. C. MSTdp injection with Lewis and Van Essen areas. D. Same MSTdp injection with Ungerleider and Desimone areas. Cell densities are indicated as $\log(\text{cells}/\text{mm}^2)$.

and qualitative, into a common spatial framework. [Figure 2](#) illustrates results from two experiments involving injections of retrograde tracers into different cortical locations (areas VIP and MSTdp) in different monkeys ([Lewis and Van Essen, 2000b](#)). The pattern of retrogradely labeled cells was charted quantitatively (as labeled cells/ mm^2) in the individual experimental hemispheres, and the data were then registered to the macaque surface-based atlas using geographical landmarks to constrain the registration ([Van Essen et al., 2004](#)). Once in the atlas framework, the injection patterns can be compared with one another and also with any of the partitioning schemes available on the atlas. This is illustrated by overlaying the [Lewis and Van Essen \(2000a\)](#) scheme on the connectivity for injections of VIP (ventral intraparietal area) and MSTdp (medial superior temporal area, dorso-posterior subdivision) in [Fig. 2A](#) and [2C](#), respectively, and by overlaying the [Ungerleider and Desimone \(1986\)](#) scheme over these same injections in

[Fig. 2B, D](#). In this way, one can assign connection strengths (as percent of total labeled neurons) to each area for each partitioning scheme of interest. In addition, the same data can be described/analyzed more objectively by expressing connection strengths for cortical locations encoded by surface-based coordinates (e.g., polar coordinates on the atlas spherical map), thereby circumventing the need to use areal assignments that may not stand the test of time.

The most powerful single pathway, and one of the best studied to date, is the reciprocal link between V1 and V2, the two largest areas. The projection to V2 arises from layers 2, 3, and 4B of V1, which collectively contain about 6×10^7 neurons per hemisphere ([O’Kusky and Colonnier, 1982](#)). About 80% of these (5×10^7) are pyramidal cells, but only about half of them (2.5×10^7) have extrinsic projections ([Callaway and Wiser, 1996](#)), the great majority of which target V2. Thus, the direct projection from V1 to V2 is about 20–25-fold greater numerically than the

LGN inputs to V1. An important issue is whether direct corticocortical feedforward projections can be categorized as “drivers” or “modulators” by the morphological and physiological criteria proposed by Sherman and Guillery (1998) and Sherman (2001). Morphological studies of V1 axons projecting to V2 are inconclusive, but the axons from V1 to MT are anatomically distinctive and suggestive of a “driver” morphology (Rockland and Virga 1990; Anderson et al., 1998; Rockland, 2002).

Receptive field characteristics in the ventral stream

Neuronal response characteristics of visual cortical neurons differ from their LGN precursors dramatically and in numerous ways. For area V1, the most striking general characteristic is that the majority of neurons (especially outside layer 4C) are highly selective along multiple stimulus dimensions. The types of selectivity encountered in the population include tuning for orientation, spatial frequency, binocular disparity, direction of motion, luminance, color, and orientation contrast (Van Essen and Gallant, 1994). In general, the neuronal representation in V1 is far “sparser” than in the LGN, insofar as most neurons are responsive over a much smaller portion of the overall stimulus space than for LGN neurons (Olshausen and Field, 2004). This obviously demands a large number of neurons if all featural dimensions and all of visual space are to be represented at high resolution. Another important consideration is that significant neuronal redundancy is necessary in order to provide a good signal-to-noise ratio for information carried at spatial frequencies coarser than the maximum visual acuity associated with any given retinal location (Anderson and DeAngelis, 2004). Viewed from this perspective, the 20–25-fold greater numbers of V2-projecting neurons compared to LGN inputs hardly seems excessive.

Neurons in V2 preserve (or regenerate) selectivity along the many stimulus dimensions explicitly encoded in V1. In addition, many V2 cells show complex spatial properties that are absent or rare in V1. This includes tuning for stereoscopic depth edges (von der Heydt et al., 2000), relative rather than absolute binocular disparity (Thomas et al., 2002), and subjective contour responsiveness (Peterhans and

von der Heydt, 1989). In addition, many neurons show dual orientation preferences (Hegde and Van Essen, 2000; Anzai and Van Essen, 2002; Ito and Komatsu, 2004) or border ownership properties (Zhou et al., 2000).

Among the many intermediate visual areas along the ventral stream, the best studied is area V4. Many V4 neurons show selectivity for complex gratings (Gallant et al., 1993) and boundary contours relative to object centers (Pasupathy and Connor, 2001). These properties become even more complex in the posterior inferotemporal area (PIT), (Brincat and Connor, 2004), and in more anterior inferotemporal areas (Kobatake and Tanaka, 1994; Booth and Rolls, 1998).

In extrastriate cortex, one general observation is that receptive field sizes at a given eccentricity increase progressively at successive stages of the anatomically defined hierarchy (see Felleman and Van Essen, 1991), reflecting the anatomical convergence associated with feedforward anatomical pathways. This presumably requires specialized neural circuits in each area devoted to generating selectivity to low level dimensions (e.g., orientation) at a coarser spatial scale than at lower hierarchical levels. A more striking set of characteristics relates to the emergence of progressively stronger scale invariance and position invariance at higher cortical levels. In parallel, the degree of attentional modulation increases at progressively higher cortical levels (Maunsell and Cook, 2002). The issue of how attentional scale and position are controlled is discussed further in Attentional control and the pulvinar.

The latency of visual responses varies widely within the neuronal population in each visual area but shows systematic differences across areas. For V1 and V2 the earliest latencies (~40 ms and ~50 ms, respectively) and the median latencies correlate with their position in the anatomical hierarchy, but for higher areas the correlation is poor (Bullier, 2001). This presumably reflects the fact that many pathways jump across multiple hierarchical levels and some are also notably fast conducting (e.g., the V1 to MT projection). While of major importance for understanding temporal aspects of information processing, these findings do not constitute strong evidence against the notion of hierarchical processing per se.

Functional organization of the pulvinar

The primate pulvinar is much larger than the neighboring LGN yet is far less well understood. Progress in elucidating the functional organization of the pulvinar has been impeded by a combination of technical obstacles that differ from those facing investigators of cerebral cortex. (1) *Non-coextensive subdivisions*: The pulvinar contains many architectonic subdivisions revealed most clearly using a combination of immunocytochemical and histochemical methods, though the number is not nearly as great as for cerebral cortex. However, while architectonic transitions in the pulvinar are generally more robust than the subtle transitions between most cortical areas, the relationship of pulvinar architectonic subdivisions to those defined by connectivity and visual topography is more complex. (2) *Lack of layers*: The pulvinar lacks well defined internal layers or other anatomical features that are suitable for making 2-dimensional maps of the type that have been extremely useful for cortical studies and have also been successfully applied to the LGN (Connolly and Van Essen, 1984). (3) *Lack of a high resolution electronic atlas*: Comparisons across studies would be greatly facilitated if a high resolution electronic atlas of the pulvinar were available and if methods were available for registering data from individuals to the atlas. Progress towards this goal has been impeded by the fact that the pulvinar and its constituent subdivisions are difficult to visualize using conventional structural MRI. In the meantime, an image based online database, XANAT (Press et al., 2001) and 3-dimensional computerized reconstructions of the pulvinar (Shipp, 2001) represent useful steps forward.

Architectonic subdivisions

As with cerebral cortex, many different architectonic partitioning schemes have been proposed for the macaque pulvinar. The classical scheme of inferior, lateral, medial, and anterior subdivisions (Jones, 1985) has been superseded by schemes based heavily on calbindin and parvalbumin immunocytochemistry and on acetylcholinesterase staining (Gutierrez et al., 1995, 2000; Stepnowski and Kaas, 1997; Adams et al., 2000; Shipp, 2001). This includes four

subdivisions of the inferior pulvinar (PI_P, PI_M, PI_{CM}, and PI_{CL}) (Stepnowski and Kaas, 1997), two subdivisions of the lateral pulvinar (PL_{VM} and PL_{VL}) (Adams et al., 2000), and four subdivisions of the dorsal (medial/oral) pulvinar complex (PL_d, PM_I, PM_m, and PM_{m-c}) (Gutierrez et al., 2000). Although some discrepancies remain to be resolved, this suggests that the pulvinar contains approximately 10 architectonic subdivisions.

Topography, connections, and physiology of ventral pulvinar

The classical physiological mapping study by Bender (1981) revealed two topographically organized areas within ventral and lateral pulvinar, now identified as the P1 and P2 fields by Adams et al. (2000) and the VP1 and VP2 fields by Shipp (2003). Bender (1981) suggested that the P1 field included all of the inferior pulvinar plus part of the lateral pulvinar, but Adams et al. (2000) consider P1 to include only PI_{CL} and PL_{VM}. The P2 field corresponds to PL_{VL}. The P3 field includes PI_P, PI_M, and PI_{CM} within the inferior pulvinar, but its visuotopic organization remains unclear.

Numerous retrograde and anterograde labeling studies indicate that each pulvinar subdivision has a distinctive pattern of reciprocal projections with multiple cortical visual areas (Baizer et al., 1993; Adams et al., 2000; Shipp, 2001; Weller et al., 2002 and references therein). In general, the inferior and lateral pulvinar are extensively connected with V1, V2, and ventral stream areas (including V4 and inferotemporal cortex). The dorsal pulvinar complex is extensively connected with dorsal stream areas and with non-visual areas; and overlap between dorsal and ventral streams is strongest in PM_I.

For the inferior and lateral pulvinar, Adams et al. (2000) report that PL_P projects into V4 and MT, but not into V1 or V2; PI_M projects into V2 and more heavily to MT, but not into V1 or V4; PI_{CM} projects into V2, V4, and MT, but not into V1; and PI_{CL}, PL_{VM}, and PL_{VL} project into all four areas, but most heavily into V4. Shipp (2001, 2003) reports little overlap between the MT-projecting and V4-projecting portions of these subdivisions (PI_{CM}, PI_{CL}, PL_{VM}, and PL_{VL}).

The various subdivisions of dorsal pulvinar (PLd, PMI, PMm, and PMm-c) have a differential pattern of connections with frontal, parietal, and temporal regions, including non-visual (superior temporal gyrus) as well as visual (V4; intraparietal sulcus and inferior parietal lobule, dorso-lateral prefrontal cortex, and inferotemporal) regions (Bayle and Morel, 1992; Baizer et al., 1993; Adams et al., 2000; Gutierrez et al., 2000). Most relevant to the current focus is that PMI is strongly connected with area V4 and with posterior parietal, and inferotemporal regions; within this region there is some segregation but also some direct convergence of dorsal and ventral streams.

Two other important aspects of pulvinar circuitry are its inputs from other subcortical structures and its intrinsic circuitry. The superior colliculus provides a major source of visual inputs to the pulvinar (Jones, 1985), though it apparently is not a driving input (Bender, 1983). As in other thalamic nuclei, intrinsic connections within pulvinar are sparse and local (Ogren and Hendrickson, 1977, 1979). While intrinsic circuits offer relatively little opportunity for integration within or across pulvinar subdivisions, the adjacent reticular nucleus provides an important substrate for such interactions (Guillery and Harting, 2003).

Pulvinar receptive field characteristics

In the inferior and lateral pulvinar, neurons in P1 and P2 have small receptive fields that are comparable to those in V1 and V2 at any given eccentricity (Bender, 1981; 1982). This suggests a driving role for V1 (Bender, 1983) and perhaps V2 inputs and a modulatory role for other corticopulvinar inputs. Many pulvinar neurons are selective for orientation and/or direction of motion, but the tuning for these dimensions is considerably broader on average than in V1 or V2. Response latencies for neurons in the P1 map range from 44 to 70 ms (Bender, 1982), well within the ranges reported for V1 and V2 neurons. In the dorsal pulvinar, visually responsive neurons tend to be more difficult to drive, even in the alert monkey, and are often modulated by visual attention (Petersen et al., 1985; Bender and Youakim, 2001).

Pulvinar size and neuronal numbers

Surprisingly, estimates of the size of the macaque pulvinar (its volume and neuronal number) have not been reported in the literature. There are even major discrepancies in the overall extent of the pulvinar (and other thalamic nuclei, including the medial dorsal nucleus) in different macaque atlases (e.g., Paxinos et al., 2000; Kusama and Mabuchi, 1970). Nonetheless, rough approximations can be made indirectly by combining data for other structures (the medial dorsal nucleus of the thalamus, MD) and other species (human). Such estimates are important because they provide strong constraints on hypotheses about pulvinar function.

The macaque MD nucleus contains an estimated 1.2×10^6 neurons in a volume of 75 mm^3 (Dorph-Petersen et al., 2004; volume not corrected for within-plane section shrinkage). This implies a neuronal density of $1.6 \times 10^4/\text{mm}^3$, much lower than the cell density in primate neocortex. In humans, the pulvinar is about twice the size of MD (680 to 990 mm^3 for MD and 840 – 1640 mm^3 for pulvinar (Byne et al., 2001; Danos et al., 2003; Kemether et al., 2003)). If the ratio of pulvinar to MD volume is the same in macaque and humans, and if neuronal density is comparable in the pulvinar and MD (as appears to be the case from inspection of the Paxinos et al., 2000 atlas) then the macaque pulvinar contains about 2.4×10^6 neurons. The percentage of these that are projection neurons is 60–75% (Arcelli et al., 1997; Dorph-Petersen et al., 2004), so the total number of macaque pulvinar projection neurons is unlikely to exceed 2 million in each hemisphere. Of these, only a subset are the parvalbumin-positive type that are putative “driver” projection neurons (Jones, 2002).

Corticocortical vs. corticopulvinarcortical information flow

It is instructive to consider two extremes on a spectrum: (i) *The CPC driver hypothesis*: the pulvinar is the sole source of driving influences on extrastriate visual areas, with corticocortical pathways playing a purely modulatory role. (ii) *The CC driver hypothesis*: corticocortical pathways are the sole source of driving

influences on extrastriate visual areas; the pulvinar plays a purely modulatory role. These extreme hypotheses can be evaluated by considering V1 and V2, which are the largest visual areas and where many key data are available.

The projection from V1 to the pulvinar arises exclusively from layer 5 and includes only about 20% of the 2×10^7 neurons in this layer, for a total of about 4×10^6 neurons (Callaway and Wiser, 1996; O’Kusky and Colonnier, 1982). This projection terminates in the main visuotopic fields P1 and P2, though not in their most posterior portions (Ungerleider et al., 1983; Shipp, 2001). Fields P1 and P2 constitute perhaps half of total pulvinar volume and hence only about 1 million pulvinar projection neurons in total. Given these numbers, it is not possible for the V1-recipient portions of the pulvinar to preserve an explicit representation of many stimulus dimensions with the same fine-grained spatial resolution encountered in V1. Rather, it is evident from the neurophysiological characteristics described above that the pulvinar has opted to retain a fine-grained spatial representation in its P1 and P2 fields and in exchange to represent orientation and other dimensions much more coarsely.

By the CPC driver hypothesis, the sharp tuning for orientation and other dimensions that occurs commonly in V2 would need to be regenerated essentially de novo from a set of pulvinar inputs that are concentrated in the P2 field (PL_{VL}) but also include some inputs from the P1 and P3 fields. Since each of these fields has stronger projections into other visual areas, the total number of pulvinar neurons projecting into V2 is not known but is probably well under 1 million; the number of candidate “driver” neurons (parvalbumin-containing) must be even smaller. Moreover, these pulvinar inputs are generally not very orientation selective or direction selective. The sharply tuned CC inputs from V1 would by the CPC driver hypothesis only be available as modulatory rather than driving inputs. It would be particularly challenging to generate V2 receptive fields having subfields with different (and sharply tuned) orientation preferences. In contrast, it is relatively straightforward to account for the multiorientation tuning characteristics of V2 cells (at least qualitatively) if one assumes such cells receive driving inputs from V1

neurons that differ in orientation and receptive field location. Altogether, the CC driver hypothesis provides an attractive (albeit unproven) framework to account for many important V2 properties. In contrast, the CPC driver hypothesis places severe computational burdens on a relatively small population of pulvinar neurons whose characteristics appear to be poorly suited for such tasks. Note that this argument regarding neuronal numbers is based on a fundamentally different logic than the synaptic numbers argument raised by Sherman and Guillery (1998, 2004), who note very appropriately that the driving inputs to a structure (e.g., the LGN or V1) can be successfully mediated by a rather small percentage of its total synaptic inputs.

If one accepts the argument that pulvinar neurons are unlikely to be the sole, or even the primary source of driving inputs to extrastriate visual cortex, what alternatives should receive prime consideration? Pulvinar inputs might nonetheless still be drivers, while remaining relegated to a backseat by virtue of their small numbers relative to CC projections. The alternative that they play a strong modulatory role is more attractive in several respects, especially in relation to hypotheses about visual attention.

Attentional control and the pulvinar

Lesion studies provide some support for the hypothesis that the pulvinar plays a role in visual attention (Petersen et al., 1985, 1987; Desimone and Ungerleider, 1989; Danziger et al., 2004). However, the remarkable complexity of corticocortical and corticopulvinar circuitry reviewed above poses interesting challenges for thinking about the precise functional role of the pulvinar. In an earlier hypothesis for a role of the pulvinar in visual attention (Olshausen et al., 1993), it was formulated in the overall context of a tripartite division of labor conceptualized for the attentional system. For the first stage of this process, it was hypothesized that bottom-up cues (e.g., salient stimuli) and top-down influences (e.g., verbal instructions) combine to form a single “saliency map”, in which a winner-take-all mechanism (e.g., Koch and Ullman, 1985) determines

the location and spatial scale for the next attentional shift. In the second stage, the output from the saliency map (putatively located in parietal cortex) is transmitted to the pulvinar and converted into control signals. In the third stage, these pulvinar control signals are used to regulate information flow into inferotemporal cortex, thereby providing the inputs needed to perceive objects within the attended location.

As originally noted, there are two problems with this hypothesis that suggest an alternative formulation. First, as noted above, the anatomical interactions between dorsal (parietal) streams and ventral streams is mainly restricted to a limited portion of the dorsal pulvinar. For this reason, the outputs of a parietal saliency map would not have access to the entire pulvinar, and would instead need to operate mainly through a single dorsal pulvinar subnucleus (PMI). Another issue is that when visual stimuli are presented as isolated objects without the normal background clutter of natural visual scenes, “involuntary” attentional shifts driven by highly salient stimuli appear to occur very rapidly (Nakayama and Meckebien, 1989) — probably more rapidly than could be mediated by a system that required obligatory activation of a parietal saliency map.

An alternative speculation proposed here is that the ventral pulvinar mediates involuntary attentional shifts and the dorsal pulvinar mediates voluntary attentional shifts. In theory, this division of labor offers the advantage of speed for the involuntary process and flexibility for the voluntary process. On the other hand, it poses significant implementation challenges for how attentional shifts would be controlled under the frequent conditions where voluntary and involuntary cues interact.

Conclusion

Progress in solving major questions of systems neuroscience is increasingly dependent on a combined neurobiological, computational, and behavioral cognitive approach. Nowhere is this more evident than in the fascinating phenomena of visual perception and visual attention. It is vital that hypotheses about perception and attention be based on sound neurobiological principles and closely grounded in hard

neuroanatomical and neurophysiological facts. Access to these facts will be greatly facilitated by further advances in atlases and databases that provide efficient access to information in formats that are most informative. It is equally critical that these hypotheses be formulated in a way that reflect good engineering principles at the level of single neurons, small circuits, and system-wide organization (Eliasmith and Anderson, 2002) and that they respect the overall system performance revealed by psychophysical studies. A compelling resolution to the question of what role the pulvinar plays in vision is still unattained. Prospects for deeper insights will benefit from consistent application of the strategies outlined in this chapter.

Abbreviations

V1–V4	visual areas 1-4
CC	corticocortical
CPC	corticopulvinar cortical
LGN	lateral geniculate nucleus
MT	middle temporal area
MRI	magnetic resonance imaging
MSTd	medial superior temporal area, dorsal
VIP	ventral intraparietal area
MSTdp	medial superior temporal area, dorsal, posterior
PI _{CL}	inferior pulvinar, central-lateral subdivision
PI _P	inferior pulvinar, posterior subdivision
PI _M	inferior pulvinar, medial subdivision
PI _{CM}	inferior pulvinar, central-medial subdivision
PL _{VM}	lateral pulvinar, ventro-medial subdivision
PLd	lateral pulvinar, dorsal subdivision
PMI	medial pulvinar, lateral subdivision
PMm	medial pulvinar, medial subdivision
PMm-c	medial pulvinar, medial-central subdivision
MD	medial dorsal nucleus

Acknowledgments

Work from the author’s laboratory was supported by grants from NEI (EY02091), joint funding from the

National Institutes of Mental Health, National Institute of Biomedical Imaging and Bioengineering, and the National Science Foundation (MH60974) and the Mathers Foundation. The author would also like to thank Susan Danker for help in manuscript preparation.

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