

Chapter 13

Views of the Visual Cortex

Introduction to the visual system in cats and primates; involvement of about 1/2 of the brain; different major complexes and the concept of pathway. At what level of abstraction should we think about something as complex as 1/2 of the brain?

13.1 Introduction

What is required for a tree-dwelling mammal, such as a tarsier, to navigate through its world, to locate food, and to prey upon it? While flies needed to avoid obstacles, the tarsier needs to locate branches in trees with sufficient accuracy that it can leap from one to another without making a mistake and quickly enough that prey cannot escape; see Fig. 13.5.

The visual system in primates (and other higher mammals, such as the cat and the ferret) is significantly more complex than those we have been considering thus far. It is larger and, as is clear from gross anatomy, elaborated into several distinct structures; see Fig. 13.2. The outward appearance of the human brain is dominated by the visual cortex, a thin sheet of neurons that is about the size of a pizza when spread out. It surrounds a number of midbrain and “interior” structures, such as the cerebellum and the hippocampus, which play major roles in planning movements (cerebellum) and memory (hippocampus). However, while mice and men have such differently sized brains, they both consist of neural networks and both are capable of an array of visual behaviours. Our challenge is to build upon the background that we have developed thus far, to explain how this can be the case despite the gross size and articulation differences.

In this lecture we provide an overview of certain basic organizational features and how these inspired various informal characterizations. We begin with an historical view and develop this in concert with certain of the key anatomical features.

While insects and amphibians illustrate a substantial level of complexity in their behaviour, and hence in the brain structure that subserves it, we now move to the visual system in primates. It is key to notice how much more organized these structures



Figure 13.1: (left) Tarsier preying on a lizard. What tasks does its visual system need to solve to accomplish this? (right) A student at the University of Rochester making a peanut butter sandwich. To do so, the observer needs to look around the room to find the necessary ingredients and tools; shown are the locations at which his eyes dwell (fixations are yellow circles; diameter proportional to the duration of fixation) and the saccades — or movement between fixations. (Mary Hayhow and Dana Ballard, Eye movements in natural behavior. *Trends in Cognitive Sciences*, 9(4), 2005, 189 - 194.

are than those we've already seen. Understanding this organization – and why it is essential – will set the stage for the work we have remaining.

13.2 An Historical View

The antidote to complexity is organization, and any notion of organization has to begin with modularity. To ancient philosophers, sensation and cognition are uniquely human; they reside in the soul. But they do provide a basis for organization.

To quote Leonardo da Vinci (see Fig. 13.3:

The Common Sense *senso comune*, is that which judges of things offered up to it by the other senses. ... And they say that this Sense is situated in the centre of the head between Sensation and Memory. ... This Common Sense is acted upon by means of Sensation which is placed as a medium between it and the senses. Sensation is acted upon by means of the images of things presented to it by the external instruments, that is to say the senses which are the medium between external things and Sensation. In the same way the senses are acted upon by objects. Surrounding things transmit their images to the senses and the senses transfer them to the Sensation. Sensation sends them to the Common Sense, and by it they are stamped upon the memory and are there more or less retained according to the importance or force of the impression. ... Experience tells us

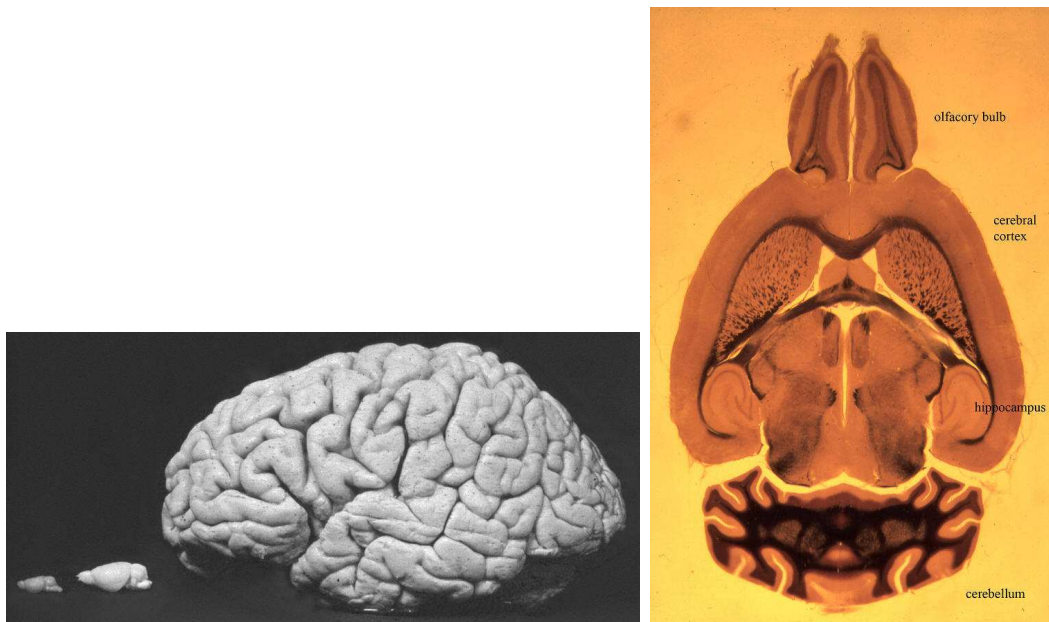


Figure 13.2: Brain size varies significantly across species. (left) Mouse, rat, and human brains shown to size. (right) Section through the mouse brain. It has a small cerebral cortex, which can be seen in relative size to it's olfactory bulb. By contrast, the human cerebral cortex is nearly 1 square meter in size.

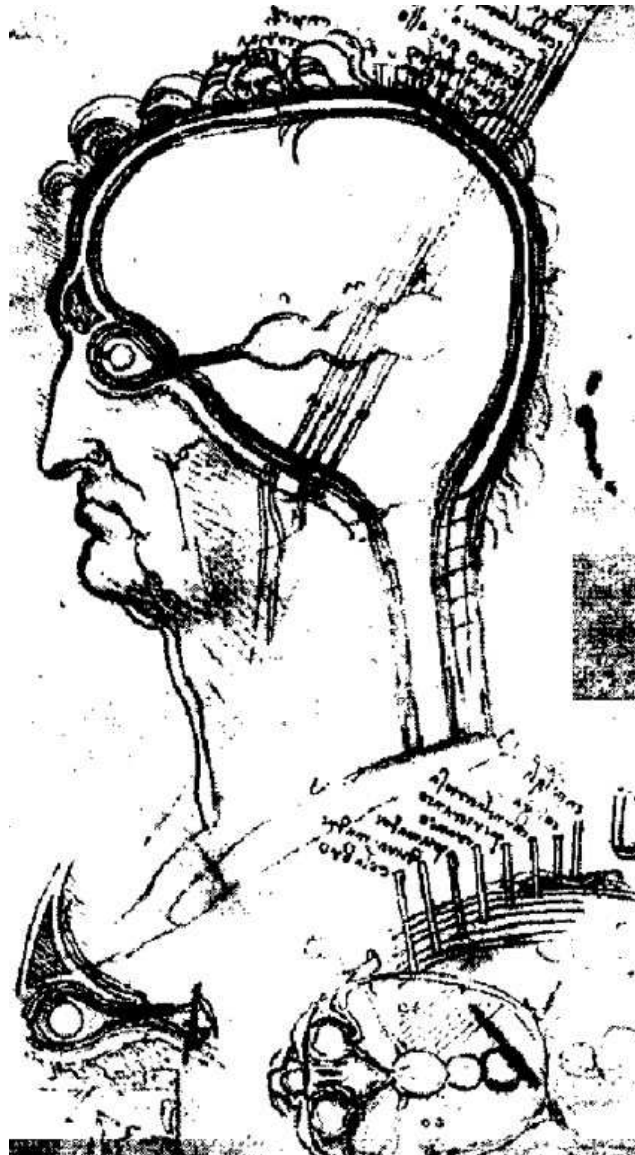


Figure 13.3: Leonardo da Vinci's drawing of the brain. Three lobular structures that he discovered by anatomical exploration are shown, organized into a feedforward circuit. While we now know that these are the ventricles, da Vinci conjectured that they provide a locus for the soul. Interpretation: the anterior vesicle houses the *senso comune*, the next a vesicle to mediate "cognition," and the third (posterior) one to subserve memory. What a beautiful attempt to integrate an organizational theory with anatomical "facts."

that the eye apprehends ten different natures of things, that is: Light and Darkness, one being the cause of the perception of the nine others, and the other its absence:—Colour and substance, form and place, distance and nearness, motion and stillness.

Quoted from Richter no 836 (www.davinciandthebrain.org/neuro.jsp)

da Vinci already exhibited the foundations of modern science. He conducted anatomical explorations to provide a foundation, and then sought an explanation for them.

Jumping several centuries forward in time, the scientific method became much more direct. Franz Josef Gall and Johann Spurzheim published *Anatomie et Physiologie du Système Nerveux*, 1810, in which they claimed the brain consists of organs manifesting such personality traits as pride, vanity, humor, benevolence, and tenacity (Allman p 29). See Fig. 13.4(left) This leads to phrenology which, while tested by removal of different brain areas was never actually confirmed.

A much more modern view involved working inside the brain. With electrical stimulation, Sherrington was able to map those locations on cortex which, when stimulated, would cause motor movement (or perceived sensation) in different parts of the body; see Fig. 13.4(right). People with brain injuries and lesions of different loci also suggested an assignment of function to areas – this suggested where the “primary visual cortex” might be, or the locus of processing where vision “begins” in the brain.

13.3 From Cytoarchitecture to Anatomy

The modern view labels cortical and sub-cortical structures by anatomical coordinates. Words to learn: Lateral view, medial view, occipital lobe, parietal lobe, temporal lobe, etc.

Need some discussion of hemispheres, corpus collosum, etc.

Big anatomical advances: staining allows one to “see” the cortical architecture by highlighting differences. This reveals both the differences as you “move along” the cortex – what have become to be called an area – plus the differences between layers; see Figs. 13.6 and 13.7.

The first visual area, V1, in the occipital lobe, is shown in Fig. 13.8; it differs from other visual areas Fig. 13.9 and across species.

13.3.1 Developmental and Evolutionary Considerations

Need some embryology and developmental neurobiology here.

Eyes moving forward gives the advantage of stereo but at the cost of a more restricted field-of-view. How could this have evolved?

13.3. FROM CYTOARCHITECTURE TO ANALYSIS OF THE VISUAL CORTEX

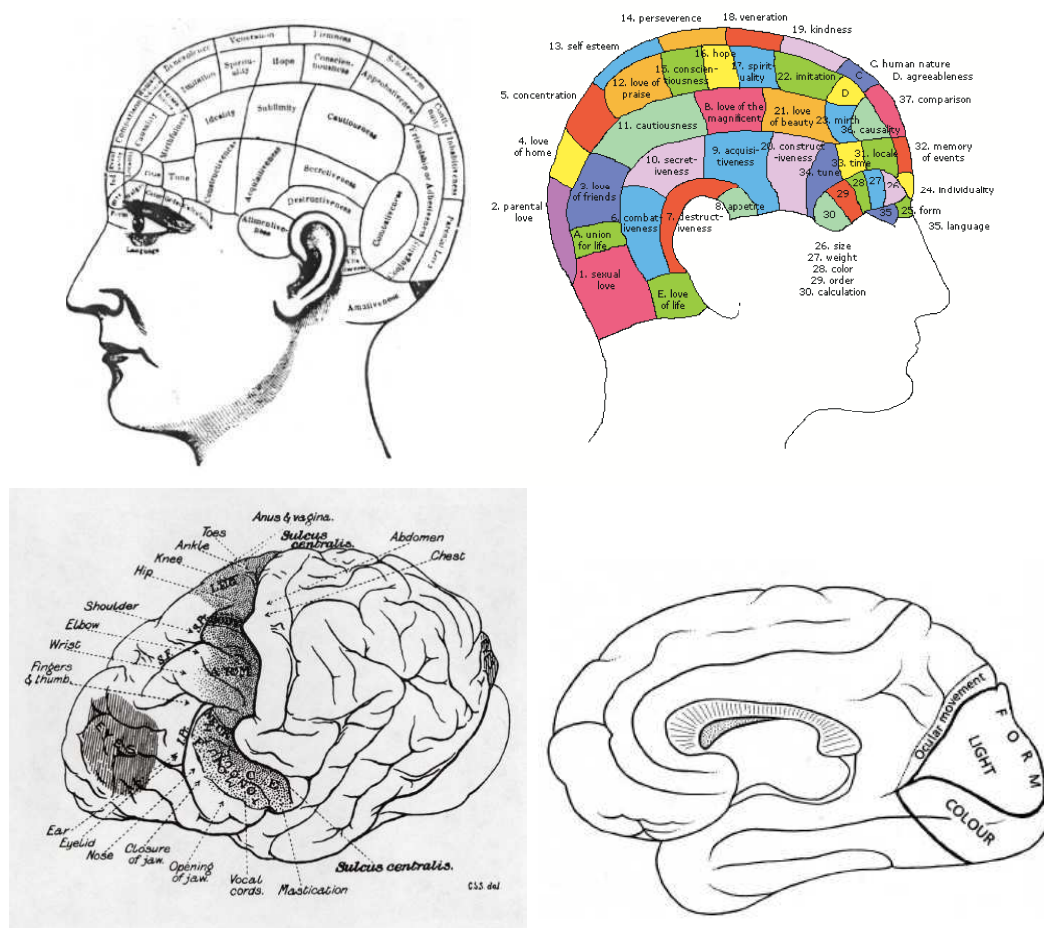


Figure 13.4: Steps along the way to assigning “function” to different brain areas. (top left) In the early 19-th century Gall established phrenology, in which different personality areas were expressed in different portions of the brain) (top right) This thinking still persists (map from www.phrenology.com/phrenology.html). (bottom left) A.S.F. Grunbaum and Charles Sherrington mapped the motor cortex in the left hemisphere in 1902, establishing how different regions of cortex were responsible for movement of different parts of the body. This only illustrates a portion of the cortical function, however. (bottom right) Different visual functions assigned to primary visual cortex circa 1906 (C. K. Mills, *The eye and the nervous system*, (zeki p 34).

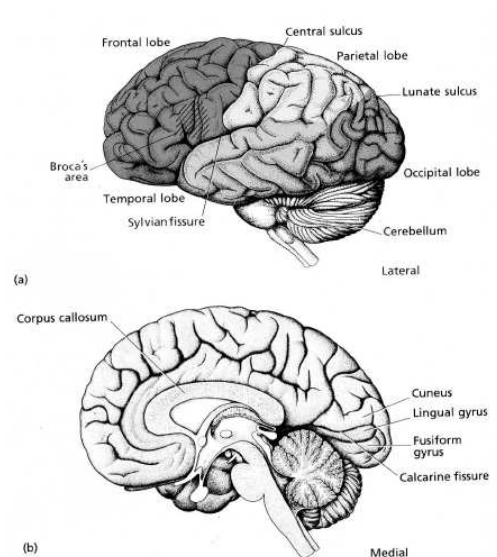


Figure 13.5: Illustration of the modern anatomical landmarks. Lateral view: imagine a person looking forward (to the left) and you're looking right through her ear. Medial view: imagine the same positions, but now you've cut away that half of the brain and are looking at the other half from the "inside." Figure from Zeki.

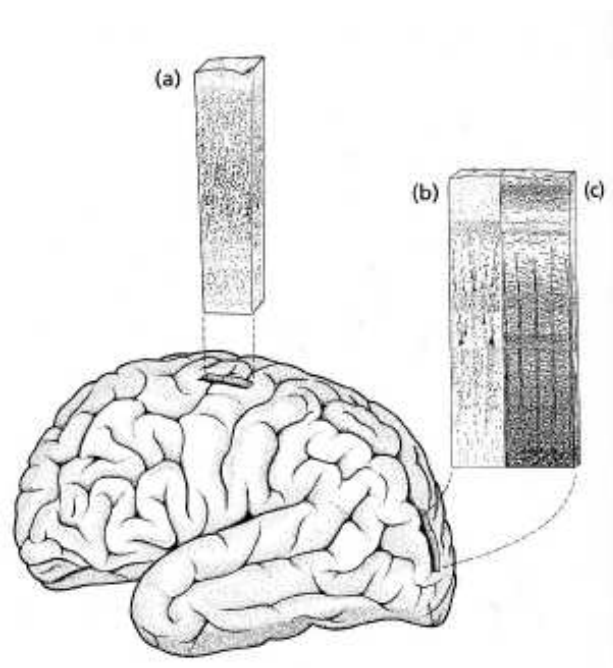


Figure 13.6: vertical slices - zeki

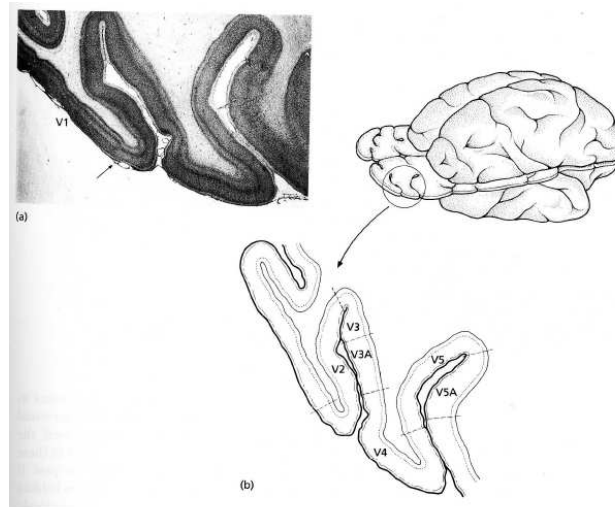


Figure 13.7: Horizontal section - zeki

13.4 Overview of the Visual System

An overview of the visual system is shown in Fig. 13.11. The primary projection with which we shall be concerned proceeds from the RETINA through an intermediate area called the LATERAL GENICULATE NUCLEUS of the thalamus to the cortex. Notice how visual processing begins in the “back” of the brain, in the first visual area (V1 in primates; AREA 17 in cats; PRIMARY VISUAL CORTEX in many books and articles) in the OCCIPITAL LOBE., and then proceeds forward into the rest of the brain. About half of the cortex is involved in processing visual information; see Fig. 13.12. We shall discuss this main pathway in this lecture, with the goal of understanding some of its main structural components.

Recall: there are perhaps 10^{12} neurons in our brain, each making about 10^3 synapses so, from what we’ve learned before, our task is to understand a network of about one-half of 10^{15} units!

It is interesting to study the different ways the retinal information is organized on its way to the next station: the Lateral Geniculate Nucleus, a part of the thalamus. See Fig. 13.13.

Other pathways, e.g., involving the SUPERIOR COLLICULUS, are involved in eye movements, which we shall not discuss at this point.

13.5 A hierarchical view of visual areas

A more detailed view of the different areas and how they relate to anatomy is provided in the following figures, summarized mostly from the work of David van Essen and his

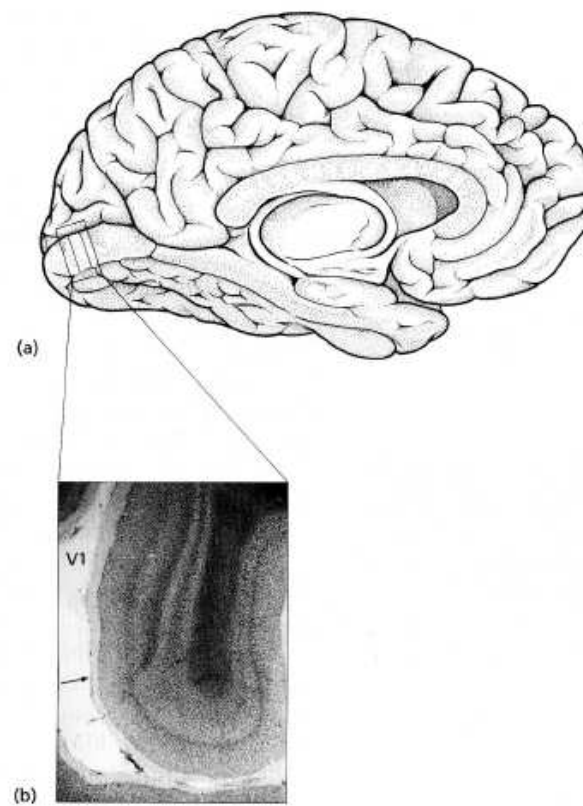


Figure 13.8: V1 section - zeki

13.5. A HIERARCHICAL VIEW OF THE VISUAL CORTEX

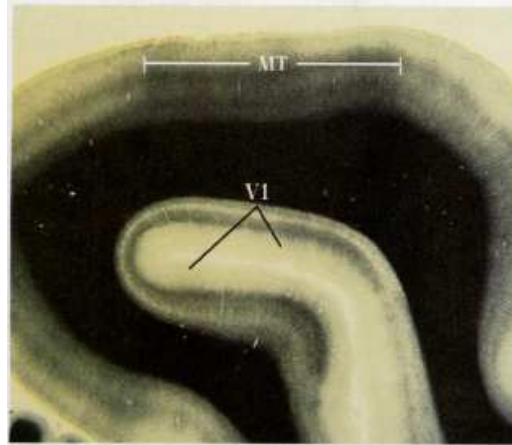
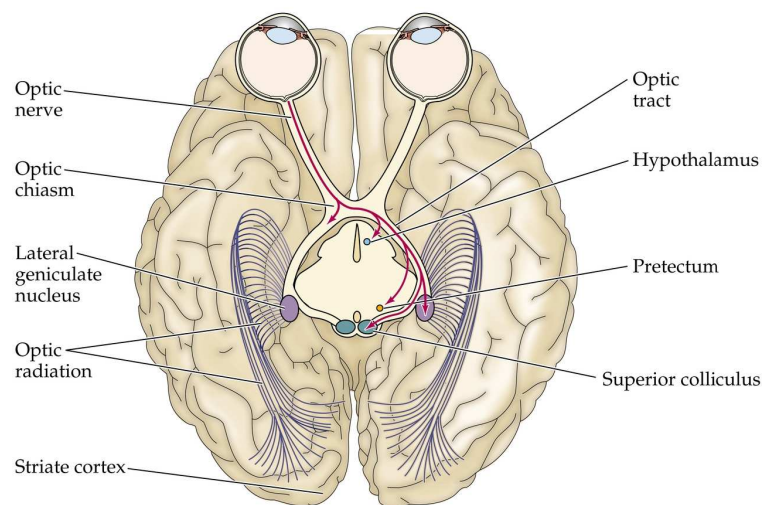


Figure 13.9: section through the brain of an owl monkey showing the distinct staining that defines V1 and MT, from Allman. This is a stain for the myelin that forms a sheath around the axons.



Figure 13.10: Development of stereo overlap, from hedgehog, a mammal that resembles early primitive ones, to *Loris gracilis*, a prosimian and immediate precursor to primates.

CHAPTER 13. VIEWS OF THE HUMAN VISIONAL SYSTEM



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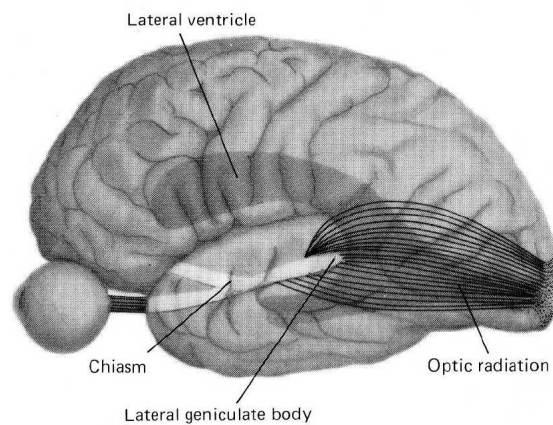


Figure 13.11: Overview of visual system in primates. Top Figure from Purves et al. bottom from Kandel

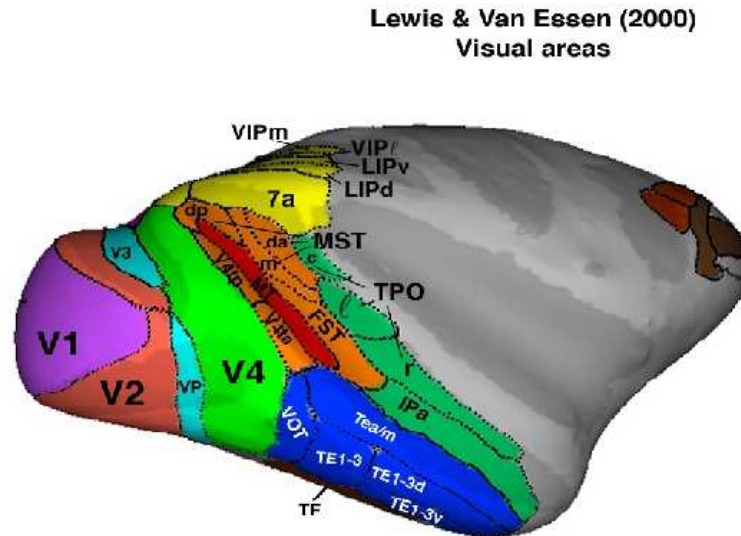


Figure 13.12: The visual system comprises nearly half of the brain. While the brain is a convoluted structure, in this projection from David van Essen the indentations have been “blown out” so that the entire surface area is visible.

colleagues. We begin with Fig. 13.14 which shows basic landmarks on the macaque brain and how it “unfolds” to a sheet.

We next label the different areas; Fig. 13.16

Finally, we show which areas are connected to which; Fig. ??

The model that emerges here is a classical one: hierarchy manages complexity; more abstract, “higher-level” features are built out of a composition of earlier, “low-level” features. The rules of composition for the hierarchy are also simple and testable. We shall take up these tests in the next chapter.

Beyond the retina, this lecture is highly introductory; We shall revisit virtually all of this material in subsequent lectures.

13.6 A pathways view of visual areas

dorsal vs ventral streams

what vs where

Visual system is very complex. Others have attempted to summarize this complexity with different processing streams – the “what” vs. the “where” pathways; see Fig. 13.17.

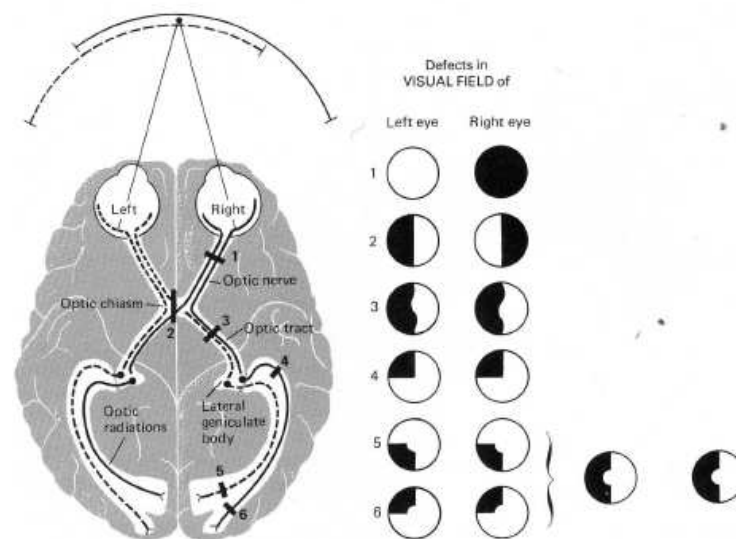


Figure 13.13: The basic projections in the visual system from the eye to the brain. If lesions are made at the differently numbered sites, then lesions in the appropriate visual field are induced. Notice how eye-of-origin information and location are not independent of one another. How do hemi-fields in retinotopic coordinates correspond to hemispheres for processing? (I.e., is the left side of the “world” processed by the left side of the brain? Does this matter?

13.6. A PATHWAYS VIEW OF THE VISUAL CORTEX

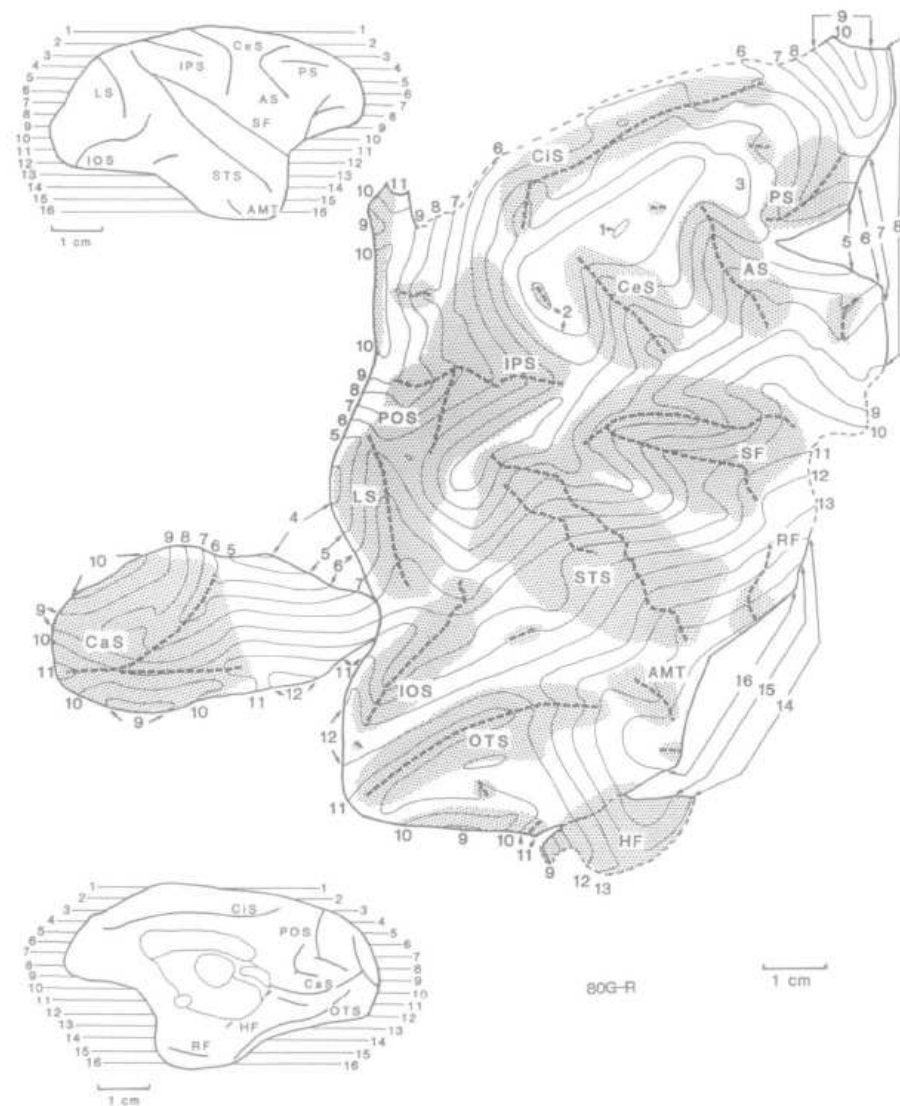


Figure 1. A 2-D map of cerebral cortex in macaque monkey, prepared by the method of Van Essen and Maunsell (1980). *Fine solid lines* represent the contours of layer 4 from a series of 16 horizontal sections taken at 2-mm intervals through the cortex. *Numbers* along the margins of the map correspond to the different section levels indicated in the lateral (upper left) and medial (lower left) views of the hemisphere. *Shading* indicates cortex lying within various sulci, and the fundus of each sulcus is indicated by *heavy dashed lines*. *Solid lines* along the perimeter of the map indicate regions where artificial cuts have been made to reduce distortions. *Dashed lines* along the perimeter represent the margins of the cortex, where it adjoins various noncortical structures: the corpus callosum/indusium griseum (top), olfactory tubercle and amygdalar nuclei (right), and dentate gyrus of the hippocampus (bottom). The scale on the map has been adjusted to correct for the estimated 18% shrinkage that occurs during histological processing (cf. Van Essen and Maunsell, 1980; Van Essen et al., 1986). *AMT*, anterior middle temporal sulcus; *AS*, arcuate sulcus; *CaS*, calcarine sulcus; *CeS*, central sulcus; *CIS*, cingulate sulcus; *HF*, hippocampal fissure; *IOS*, inferior occipital sulcus; *IPS*, intraparietal sulcus; *LS*, lunate sulcus; *OTS*, occipitotemporal sulcus; *POS*, parieto-occipital sulcus; *PS*, principal sulcus; *RF*, rhinal fissure; *SF*, sylvian fissure; *STS*, superior temporal sulcus.

Figure 13.14: Van essen unfolding of macaque cortex.

CHAPTER 13. VIEWS OF THE VISUAL AREAS VIEW OF VISUAL AREAS

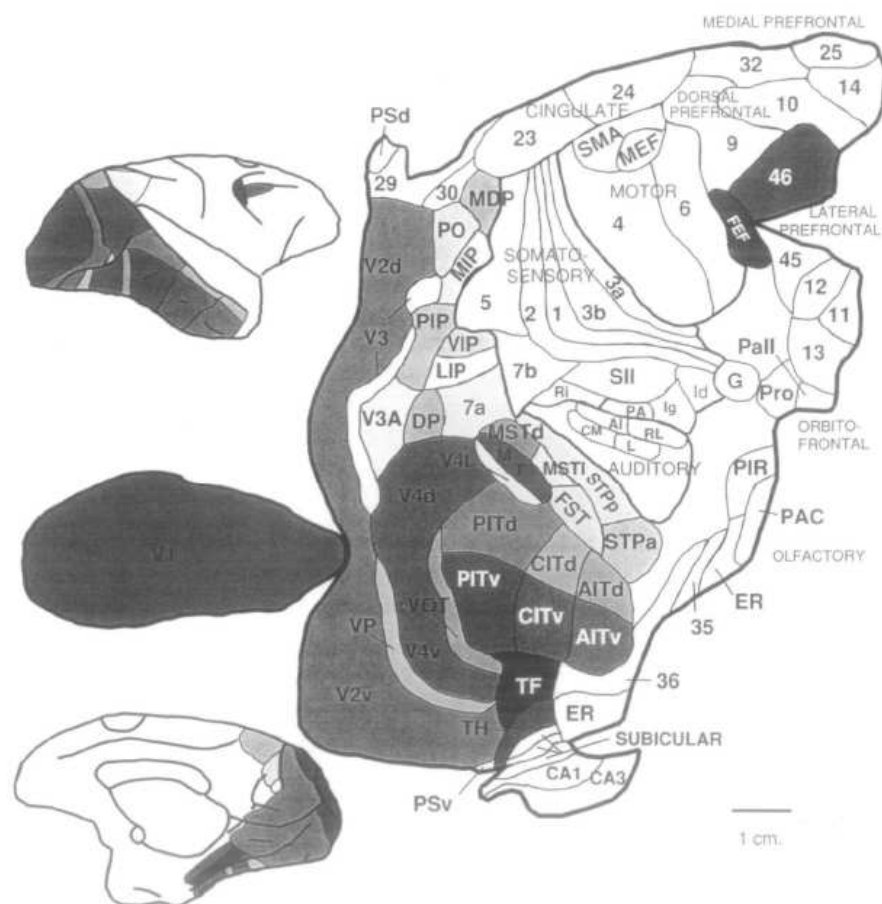


Figure 2. Map of cortical areas in the macaque. The locations of 32 visual areas are indicated with colors that indicate whether they are in the occipital lobe (purple, blue, and reddish hues), parietal lobe (yellow, orange, and light brown hues), temporal lobe (green hues), or frontal lobe (brown hues). The references used in placement of boundaries for the different visual areas are listed in Table 1. The scale applies only to the map; the brain drawings are smaller by 20% (cf. Fig. 1). The specific studies used in estimating the border of the various nonvisual areas are as follows: Somatosensory areas 3a, 3b, 1, 2, 5, 7b, SII, RI (retroinsular), PI (postauditory), AI (auditory granular), and AII (auditory dysgranular) were based on Jones and Burton (1976), Jones et al. (1978), Robinson and Burton (1980), Friedman et al. (1986), Huerta et al. (1987), and Andersen et al. (1990). Note that, in this scheme, areas 1 and 2 intervene between SII and area 3b. In other primates, including the marmoset and the owl monkey, SII appears to directly adjoin area 3b, and it has been suggested that more detailed mapping will reveal the same arrangement in the macaque (Cusick et al., 1989; Krubitzer and Kaes, 1990). Auditory areas AI (primary auditory), RI (retroinsular), CM (caudomedial), and L (lateral) were based on Merzenich and Brugge (1973). The postauditory area (PI) is described as a somatosensory area by Robinson and Burton (1980) and as an auditory area by Friedman et al. (1986). We have included it as part of the auditory cortex in our analysis, but obviously this issue merits further investigation. Areas of the hippocampal complex (HC), including the entorhinal cortex (ER), areas 35 and 36, presubiculum, prosubiculum, subiculum, and fields CA1 and CA3, were based on Amaral et al. (1987), Insausti et al. (1987), and Saunders et al. (1989). Olfactory areas, including the piriform cortex (PIR) and periamygdaloid cortex (PAC), were based on Insausti et al. (1987). Orbitofrontal areas 11, 12, and 13, preoccipital (Pro), perilocomotor (Pall), lateral prefrontal area 45, dorsal prefrontal areas 9 and 10, and medial prefrontal areas 14, 25, and 32 were based on Barbas and Pandya (1989) and Insausti et al. (1987). Motor areas 4 (primary motor) and 8 (premotor and arcuate premotor, or 6s and 6l), supplementary motor area (SMA), and medial eye field (MEF, or supplementary eye fields, SEF) were based on Brodmann (1905), Matsui et al. (1986), Insausti et al. (1987), Schlag and Schlag-Rey (1987), Hutchins et al. (1988), and Merin et al. (1988). Finally, cingulate and other limbic areas 23, 24, 29 (retrosplenial), 30 (PGie or 7m), and prostriate (PS, divided by an artificial cut into dorsal (d) and ventral (v) sectors) were based on Insausti et al. (1987) and Sanides (1970). A few regions in the posterior orbitofrontal, lateral prefrontal, and anterior sylvian cortices have not been closely studied and are left unspecified here.

Figure 13.15: Labelled areas of macaque cortex.

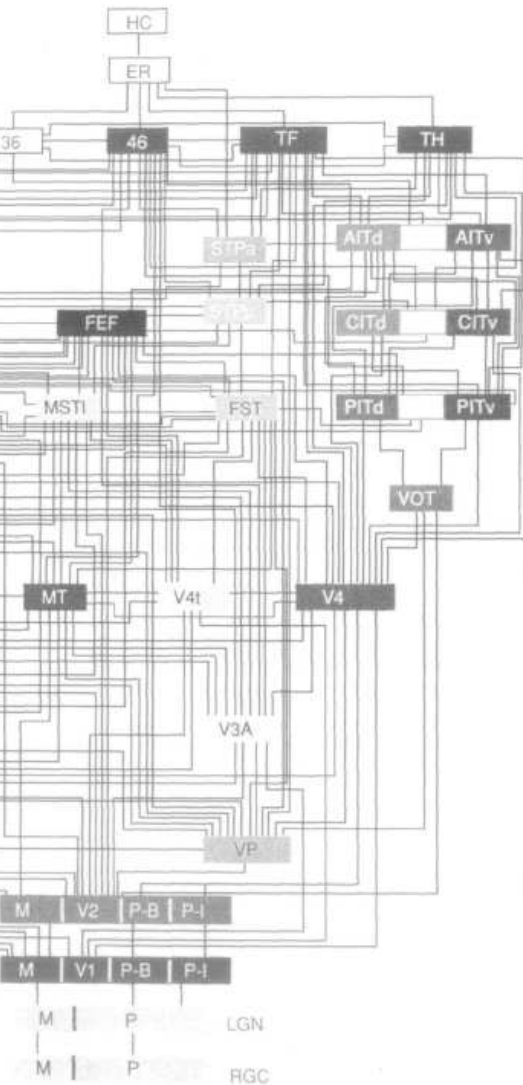


Figure 13.16: Connections between visual areas of macaque cortex. It is essential to realize that for each of these connection “wires” it is actually a rich projection of many thousands of axons and that, for each “forward” projection to a “higher” visual area, there is a “backprojection” to the “lower” area. The hierarchy shown comes from an interpretation of van Essen; we shall consider this in more detail as the lectures proceed.

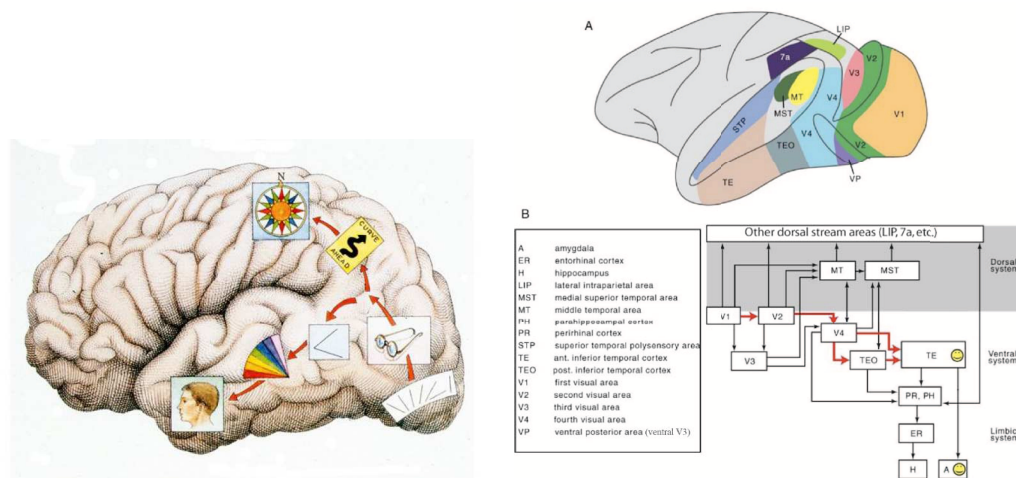


Figure 13.17: Illustration of basic pathways for information flow derived from lesion data. The pathway to the temporal cortex is thought to be used for object recognition (hence the face); the pathway to the parietal cortex for where questions (hence the compass). Is this the right abstraction for studying the visual system?

13.7 Early Vision and High-Level Vision

bottom-up vs top-down

Early vision: general purpose computations in special purpose architecture
 High-Level Vision: special purpose computation in general purpose architecture

Early vision can be automatic - it proceeds without the need for attention (see refs in Kastner)
 Early vision is cognitively unpenetrable (Pylyshyn)

Somehow we're going to need to make sense of this difference. It's important to note that the cytoarchitecture remains pretty much the same.

we'll see some examples of kanizsa subjective figures – these seem to happen regardless of whether one wants them to or not.

Visual illusions.

13.8 The Road Ahead

but also, in a sense, more organized. We shall have to consider the complexity of the tasks that these systems are seek to accomplish in light of their organization. Our plan will be to provide an increasingly detailed look at this organization over subsequent lectures while, as structure is revealed, we develop it into information processing theories. The nature and structure of such theories will develop as a theme as well.

Pevsner, J. Leonardo da Vinci's contributions to neuroscience TINS 25(4), 2002, 217 - 220.

13.8. THE ROAD AHEAD CHAPTER 13. VIEWS OF THE VISUAL CORTEX

Chapter 14

The Eye, The Retina, and the Lateral Geniculate Nucleus

Structure of the retina; different layers; sensor design; coding information for transmission to cortex; adaptation to brightness

14.1 Introduction

The eye is a beautiful optical instrument in which the lens forms an (inverted) image on the retina; Fig. 14.1. The retina is itself an extremely complex neural network. We are thinking of this as the “input” device that sends information to the cortex, so it’s also important to consider the channels as a communication system. Each of these parts is dealt with in turn.

14.2 Optical Properties of the Eye

The sensory input is given by the RODS and CONES which are distributed non-uniformly across it. The rods are primarily distributed in the periphery and the cones in the central portion (along the optical axis).

need to add discussion of blur function; see Fig. 14.2. Gaussian. Good discussion of this in Wandell, Chaps 2, 3. Also includes aliasing effects.

14.3 The Retina

The cones contain the long, medium, and short wavelength pigments and are thus responsible for color vision as well as high-resolution spatial vision. The rods are specialized for photon capture in low-light situations, and for rapid, non-linear responses to movement in the periphery. (This helps in avoiding flying objects coming from the

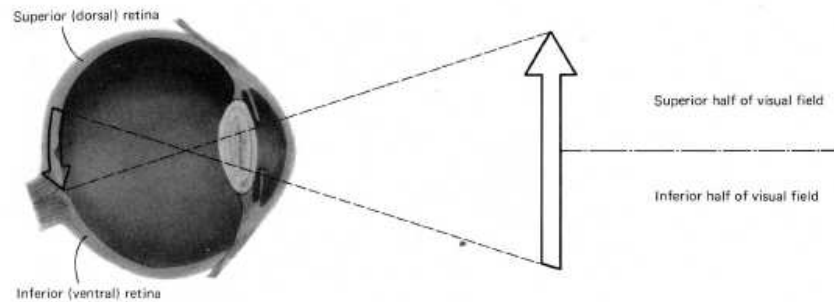


Figure 14.1: The eye. Figures from KANDEL

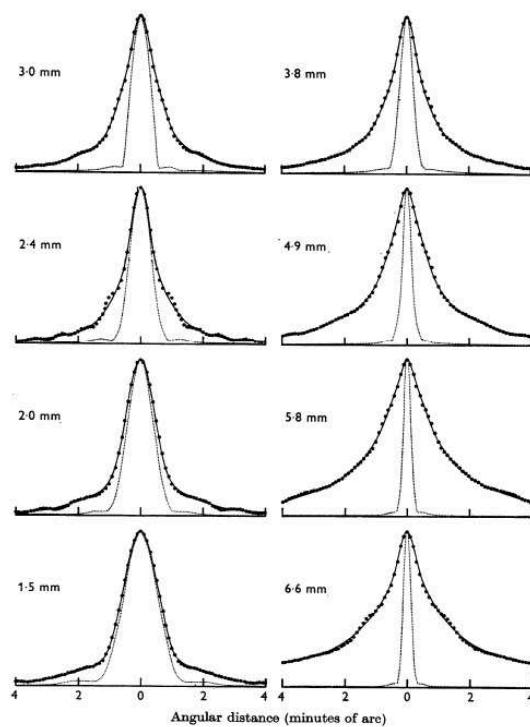


Figure 14.2: Dark lines: Linespread functions from the human eye, measured at different pupil diameters. (The thin curve is the diffraction image of a line at that diameter. Figure from Campbell and Gubish

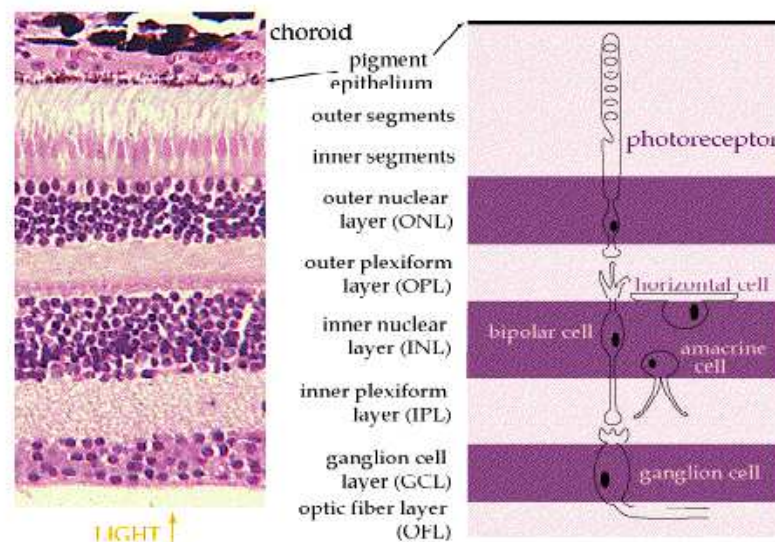


Figure 14.3: The structure of the retina. It consists of several layers of neurons organized in a horizontal and vertical fashion. There is a structural resemblance to the lateral inhibitory networks we have been studying, although the structure here is more elaborate. The output layer contains the retinal ganglion cells. These have “center-surround” receptive fields that adapt to different ambient light conditions. Figures from WUSTL

side!) We shall concentrate in these lectures on the input from the cones. For now we shall ignore the spectral component to their response.

The neural network of the retina is organized into layers. Signals from the rods/cones are integrated by layers of horizontal, bipolar, and amacrine cells into the ganglion, or output layer. Some of the horizontal structure resembles the lateral inhibitory networks we have been studying, although the structure here is more elaborate. While the RGC's have "center-surround" receptive fields, these change as a function of adaptivity. Loosely speaking, in low-light situations when integration of photons is more important the inhibitory surround is reduced; in bright-light situations the inhibitory surround is elaborated. See Fig. 14.5.

It is important to notice that the retina is built inversely to what one might expect: the light hits the photoreceptor layer last. It must first pass through the blood vessels and other retinal layers, although these are reduced significantly in the fovea; see Fig. 14.6. There are about 2 photoreceptors for each RGC in the fovea.

There are different pathways from the retina to the cortex; we shall focus on the X PATHWAY which originates in the cones and proceeds in a roughly linear fashion to encode information. (The Y-pathway is rod dominated; highly nonlinear and very fast in conduction velocity. There is also a W pathway.)

14.3.1 Wiring of the Retina

In discussing how responses are built up, it is essential to refer back to the OFF response for the barnacle shadow-reflex.

14.3.2 ON and OFF cells

Our first task in understanding retinal ganglion cells is to increase our understanding of their response to light; see Fig. 14.8.

14.3.3 Sensitivity of the Retina

What functions might the retina be designed to implement? Certainly there is an issue of light capture and phototransduction, and the retina is specialized to adapt to ambient conditions in an optimal fashion.

The famous experiment of Hecht, Schlaer and Pirenne¹ in 1942 demonstrated sensitivity to single quanta of light, just above the thermal noise level in dark-adapted situations. (If your head was ever abruptly struck so that you could "see stars", then you can appreciate the thermal sensitivity of the rhodopsin pigment molecules.) In fact, in the dark-adapted state the rods are about 10,000 times more sensitive to light than the cones.

¹S. Hecht, S. Schlaer and M.H. Pirenne, "Energy, Quanta and vision." *Journal of the Optical Society of America*, 38, 196-208 (1942)

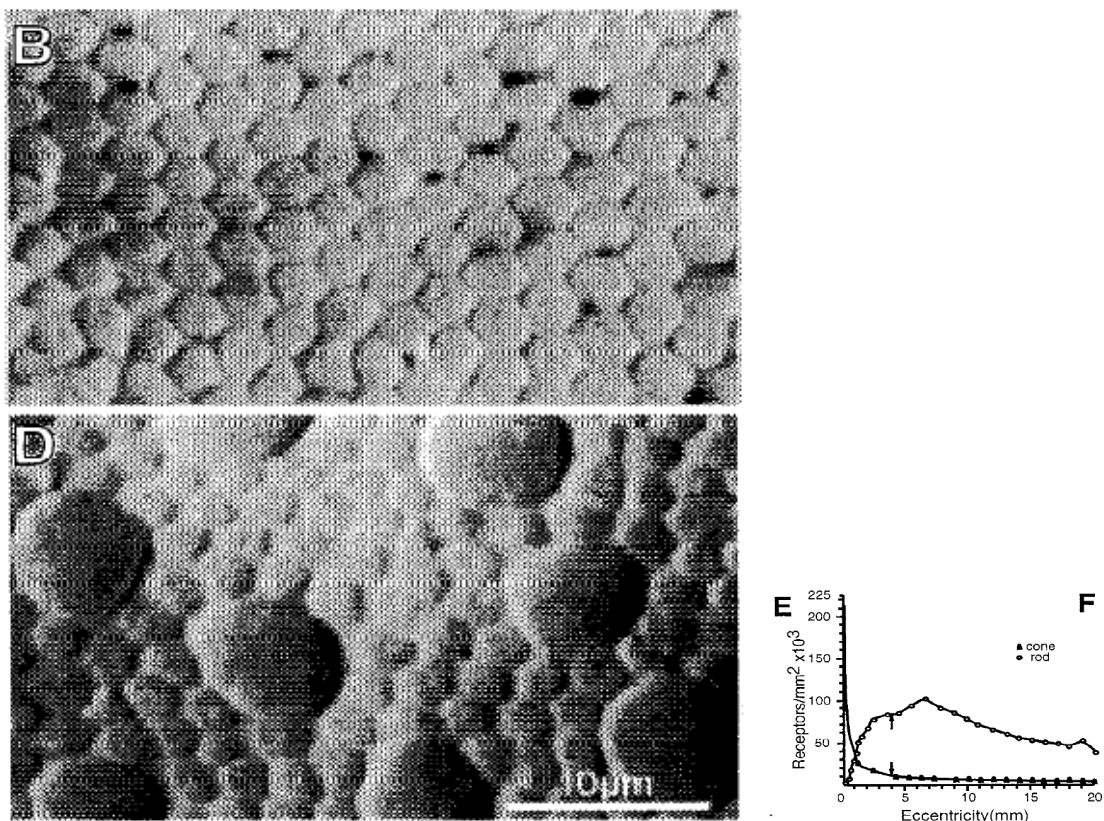


Figure 14.4: (LEFT) Packing of cones (top) and rods (bottom) in the retina. The top figure is a tangential view of the human fovea through the inner segments. Notice the almost perfect hexagonal packing (is there a better way to do this?) There are no rods in this portion of the fovea. (bottom) Human retina 20 degrees nasal. Notice that there are a few cones mixed with the rods. These help in photon capture at night although the mechanisms are complex. (RIGHT) Number of rods and cones across the retina. Figures from Sterling

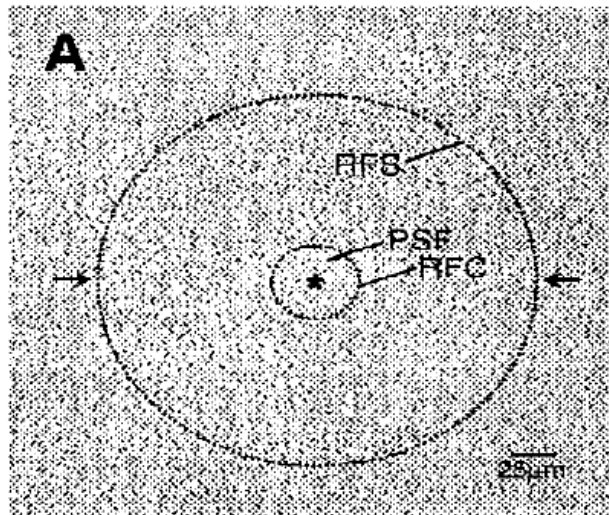


Figure 14.5: Retinal (center surround) receptive field from the cat to illustrate an order-of-magnitude display over the retinal cones. In the cat there are about 24,000 cones/mm² and there is no fovea. Optical blur in the cornea spreads a point of light to cover about 10 cones (the optical PSF: Point Spread Function). The central excitatory region (around cone *) spreads influence over about 50 cones. This is the Receptive Field Center. The RF Surround is built up by the horizontal cells with inhibition; this covers about 1200 cones. Figures from Sterling



Figure 14.6: The specialized structure of the fovea. It is visible to opticians and is called the macula. Figure from WUSTL

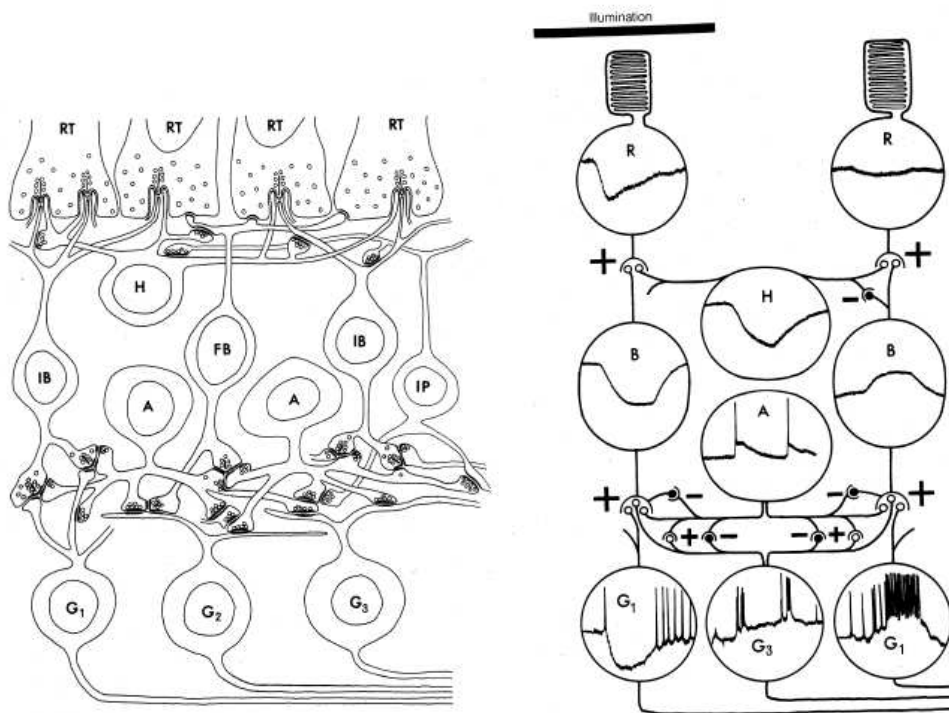


Figure 14.7: A composite sketch of the retina in some detail. (left) Wiring diagram with the different types of synapses. (right) Composite assembly of the different potentials recorded from the different retinal layers. Notice how the first few layers are graded; the latter ones are spiking. See text for discussion. Figure from J. Dowling, *The Retina*, HUP.

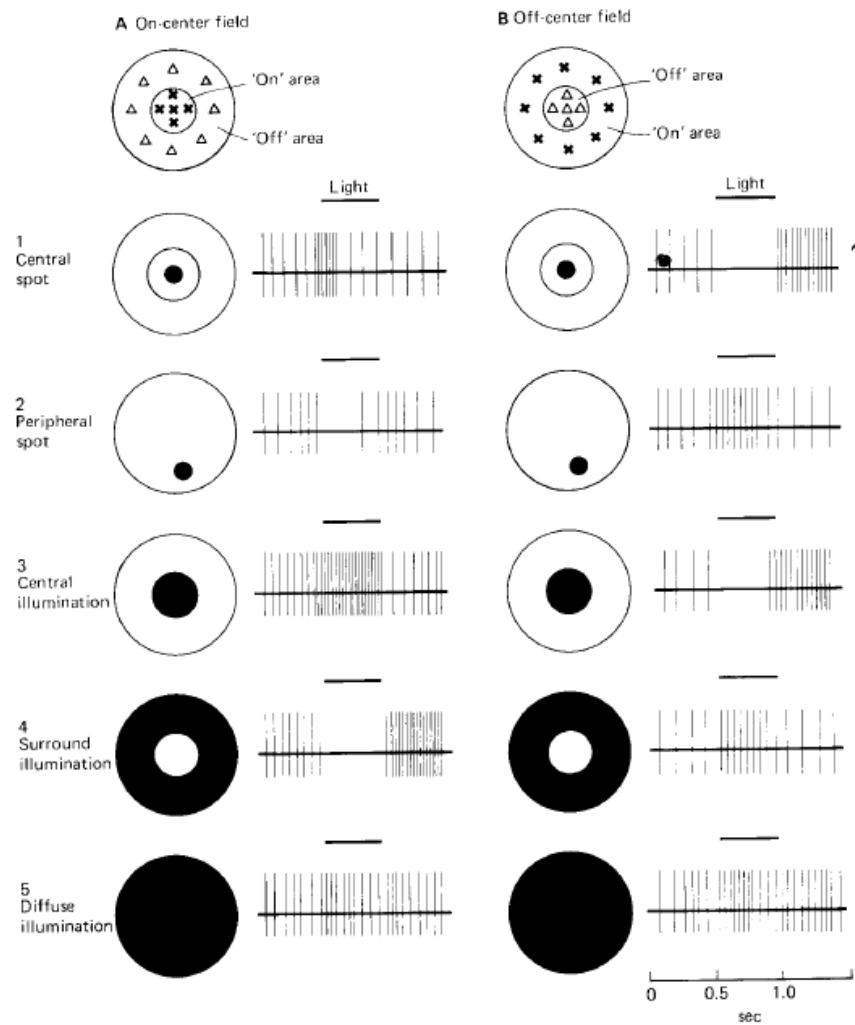


Figure 14.8: ON and OFF responses in the retina. Figure from Kandell and Schwartz

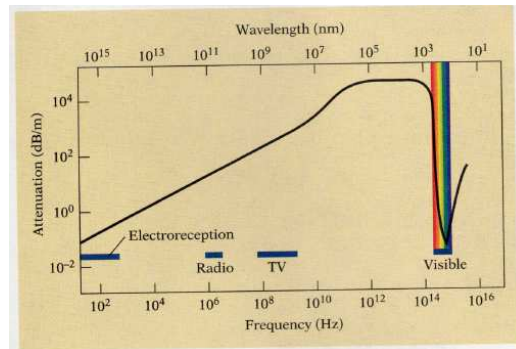


Figure 14.9: The visible spectrum evolved while animals were underwater. This plot of attenuation vs wavelength showed how the narrow range of “visible” light emerged from animals that needed to see underwater. From Fernald.

Barlow, H., B., Fitzhugh, R., and Kuffler, S.W., Change of organization in the receptive fields of the cat’s retina during dark adaptation, J. Physiol. 1957, 137, 338 - 354.

14.4 Color, Cones and Coordinates

Earliest evolution of photoreceptors may have involved a sensitivity to energy – two possibilities: (i) move toward warmth (sensitivity to IR) or (ii) move away from damaging UV radiation (possibly relevant to fish)

color evolution

14.4.1 Photopigments and Spectral Absorption

14.4.2 Distributed Coding

Color Opponency

14.5 Predictive Coding and the Retina

Given the sensitivity of the retina, how many distinct levels of brightness can be encoded given noise? This requires an introduction to coding and information theory.

As a sensor, however, the retina must also function as a communications device, sending information to the cortex for processing as efficiently and as accurately as possible. This brings up the question of how intensity (number of photons per unit time) is encoded. In a simple spike-rate encoding there is a limited dynamic range; i.e., the range of intensity values that can be encoded. Moreover, in bright situations

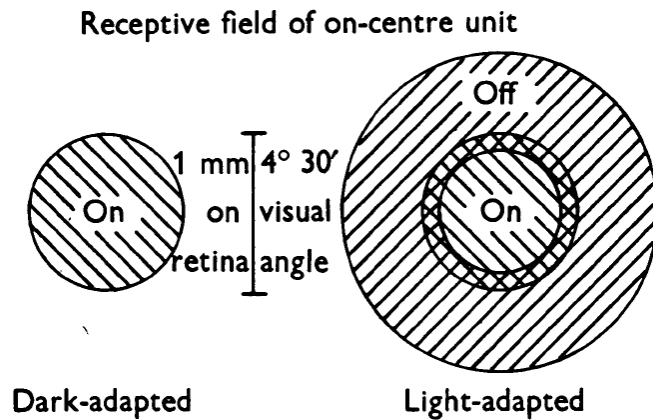


Figure 14.10: Light adaptation and receptive field configuration. Classical drawing from Barlow Fitzhugh and Kuffler of how a receptive field varies with adaptation. When dark adapted the inhibitory surround effectively disappears.

the RGC's will be firing extremely rapidly, an energetically very expensive encoding strategy.

Another interpretation of the center:surround RGC receptive field structure is to form the difference between the intensity at the center of the RF and in the surround; i.e., to calculate how the central value differs from its context. Normally this is thought of as a measure of contrast, which is one way to think about it.

Another way is to think of contrast as an encoding strategy, in which only the *difference* between the center and the surround is encoded, rather than the absolute value of the center. Since we are viewing RGC receptive fields as roughly linear, a kind of LINEAR PREDICTIVE CODE is established, in which the surround “predict” the center value and only the error term is communicated over the optic nerve. This can clearly extend the dynamic range and can vary the metabolic load frequently with eye movements. (Rarely would the same retinal point land on a scene location with the same contrast.) Fro more see ²

A more advanced model takes noise more fundamentally into account; see Atick, J., and Redlich, A. N., Towards a theory of early visual processing, Neural Computation, 1990, 2, 308 - 320.

See also Shapley-Enroth-Cugell, 1984.

²Srinivasan MV, Laughlin SB, Dubs A., Predictive coding: a fresh view of inhibition in the retina. Proc R Soc Lond B Biol Sci. 1982 Nov 22;216(1205):427-59.

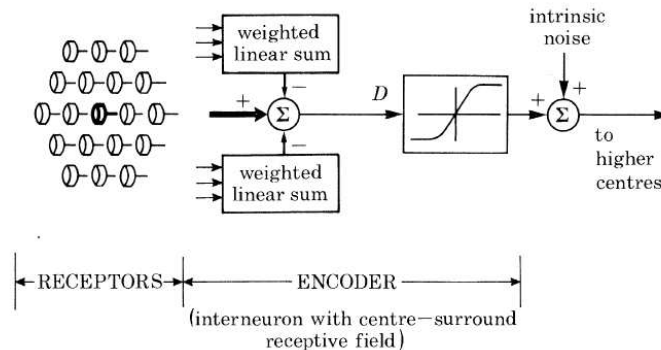


Figure 14.11: A simplified model for viewing the retina as an encoder, from the original paper by sreenivasan et al.

14.6 Lateral Geniculate Nucleus

The optic nerve passes through the LGN which also is organized into layers. The key distinction here is PARVOCELLULAR vs MAGNOCELLULAR layers: the X pathway is mainly parvo; the Y is magno.

Receptive fields are again circular surround (as in RGC's), with smaller ones for the parvo layers and larger for magno. Spatial resolution and color sensitivity are higher for parvo, while temporal resolution is faster and contrast sensitivity is higher for magno.

The eye of origin distinction is maintained.

Really important feedback from V1 to LGN; what function do such loops support?

14.6.1 Cortical Circuits for Image Stability

(this represents some of the myriad functions that must be accomplished by the visual cortex, but which we will not discuss in the rest of the lectures.)

Nature 444, 374-377 (16 November 2006)

Influence of the colliculus via thalamus on spatial visual processing in frontal cortex

Marc A. Sommer and Robert H. Wurtz

see also Sommer and Wurtz, Ann Rev Neurosci, 2008

Carol Colby: about moving receptive fields that shift ahead of eye movements
abstract:

Each of our movements activates our own sensory receptors, and therefore keeping track of self-movement is a necessary part of analysing sensory input. One way in which the brain keeps track of self-movement is by monitoring an internal copy, or corollary discharge, of motor commands^{1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13}. This concept could explain why we perceive a stable visual world despite our frequent quick,

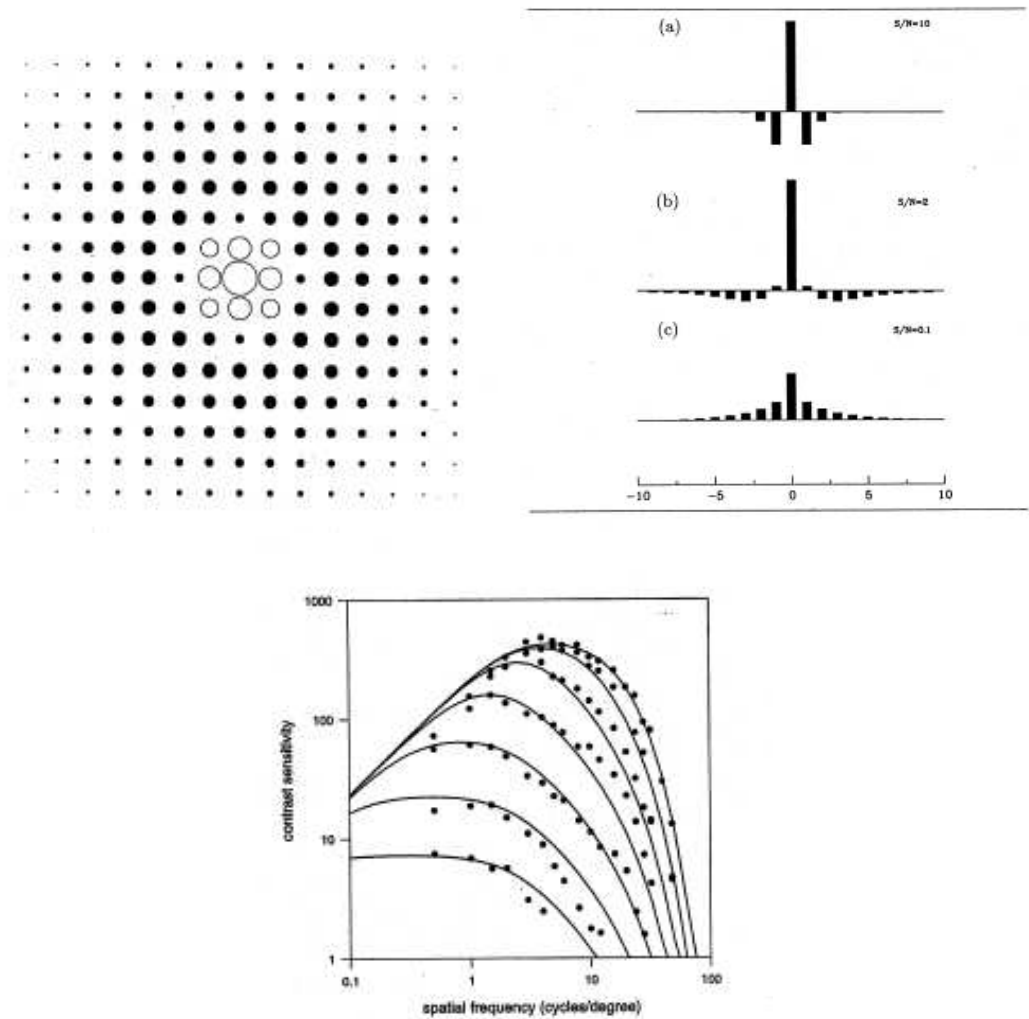


Figure 14.12: Atick encoder as a model for the retina. (left) array of inputs and their relative weight; solid discs are inhibitory; open discs are excitatory. (right) Synaptic “weights” as a function of signal-to-noise level. Note that as signal decreases relative to noise much more averaging is required and the system does more smoothing. In the smoothing regime for high enough noise the inhibitory surround can disappear. (bottom) Spectral view of the encoding filter. When dark adapted, the system is low-pass; when adapted to high intensities the system is band pass.

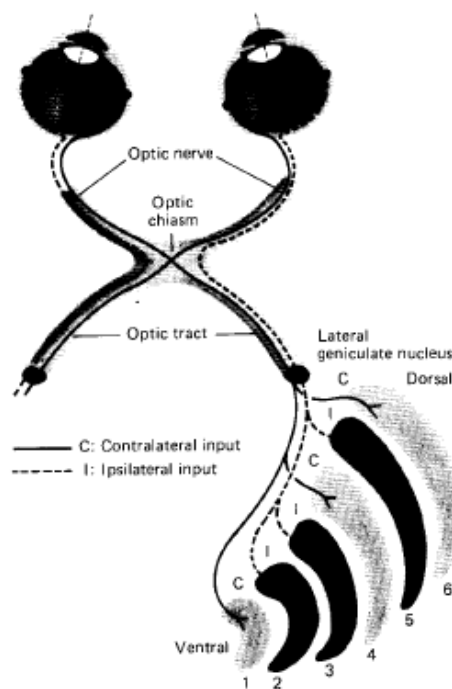


Figure 14.13: The lateral geniculate nucleus is a layered structure; it keeps the different types of RGC's organized. It also receives an important feedback from the first visual area.

or saccadic, eye movements: corollary discharge about each saccade would permit the visual system to ignore saccade-induced visual changes^{6, 7, 8, 9}. The critical missing link has been the connection between corollary discharge and visual processing. Here we show that such a link is formed by a corollary discharge from the thalamus that targets the frontal cortex. In the thalamus, neurons in the mediodorsal nucleus relay a corollary discharge of saccades from the midbrain superior colliculus to the cortical frontal eye field^{10, 11, 12}. In the frontal eye field, neurons use corollary discharge to shift their visual receptive fields spatially before saccades^{14, 15}. We tested the hypothesis that these two components a pathway for corollary discharge and neurons with shifting receptive fields form a circuit in which the corollary discharge drives the shift. First we showed that the known spatial and temporal properties of the corollary discharge predict the dynamic changes in spatial visual processing of cortical neurons when saccades are made. Then we moved from this correlation to causation by isolating single cortical neurons and showing that their spatial visual processing is impaired when corollary discharge from the thalamus is interrupted. Thus the visual processing of frontal neurons is spatiotemporally matched with, and functionally dependent on, corollary discharge input from the thalamus. These experiments establish the first link between corollary discharge and visual processing, delineate a brain circuit that is well suited for mediating visual stability, and provide a framework for studying corollary discharge in other sensory systems.

Recently it has been discovered the FEF neurons are also shape selective, so this says that these systems are not totally independent from what we will be studying; see Peng X, Sereno SC, Silva A, Lehky SR, Sereno AB. Shape selectivity in primate frontal eye field. *Journal of Neurophysiology*, 100: 796-814, 2008.(papers/sereno/shape-fef.pdf)

14.7 Conclusions