

Chapter 15

An Introduction to Visual Cortex

[Intro V1]

Continuining the introduction to the visual system in primates; organization of V1; simple, complex hypercomplex cells; hierarchy; layers

15.1 Introduction

A first look at visual cortex is that it's large; to what functions might this amount of cortical space be dedicated? A first answer – image reconstruction – does not seem plausible, since the “encoding” side was done with simple center-surround operators.

15.2 The First Visual Area of Cortex

The first visual area is one of the largest in the cortex. It contains perhaps 200 million cells, more than 100 times the number in the geniculate and, when spread out, its area covers several in² and is about 2 mm thick. It is here that the first abstraction from the visual image arises.

15.2.1 Cortex is a Layered Structure

Our first observation about cortex in most primates is that it is a convoluted structure, with some portions buried and others exposed to the outer surface. We will not be concerned with the different convolutions for now; but rather should think of it simply as a sheet. (This is incorrect in the sense that the convolutions change the topological relationships between areas, a subtle point when wiring considerations are taken into account.)

The second observation about cortex is that it is a layered structure; see Fig. 15.1.

The input enters “in the middle”, layer IVc, and proceeds superficially to the upper layers and deeper to the lower layers. It comes primarily from the dorsal

15.2. THE FIRST VISUAL AREA OF CONDUCTION TO VISUAL CORTEX

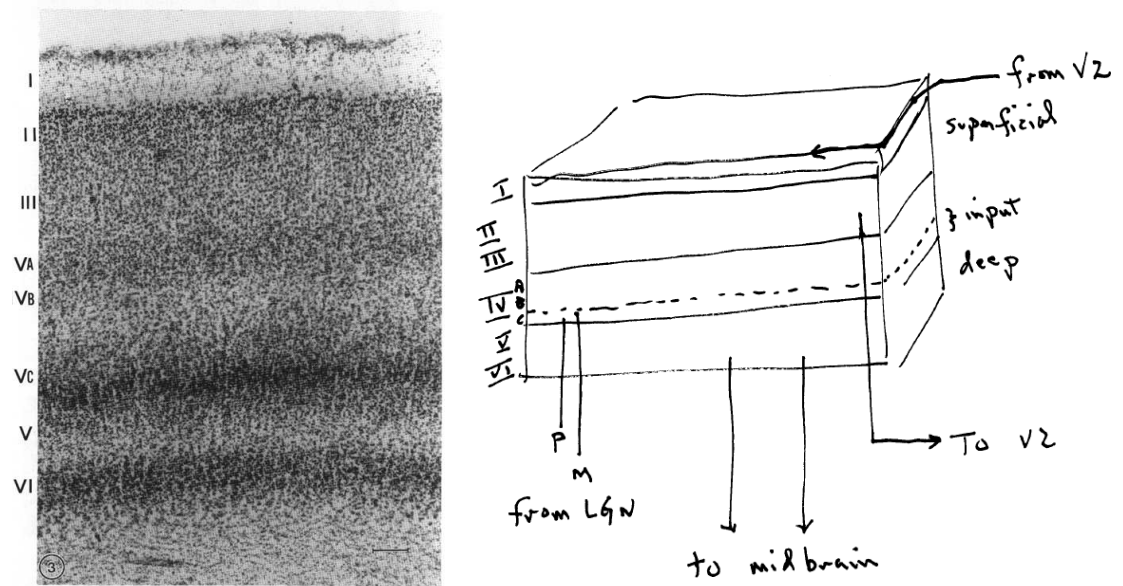


Figure 15.1: Microscopic views of visual cortex. (LEFT) Cross section through cortex. Note that it consists of 6 layers, some of which have multiple sub-layers. The input enters layer IVc. W indicates white matter and the lower VI and V are the deep layers of a buried fold from a different area of cortex. Cresyl violet stain shows cell bodies. Layers are anatomically defined, in this case by density of cell bodies. Image from Hubel and Wiesel, 1977. (RIGHT) Input/output organization of V1. The input from the dLGN enters the middle (layer IVc). It is there that the first neurons with cortically-distinct properties are found. The axons of these neurons then project into both the superficial (upper) layers and the deep layers. Projects to V2 arise from layers II-III, and the return project from V2 synapses in layer I. There is also a projection back to the midbrain from layers V and VI.

lateral geniculate nucleus (dLGN) of the thalamus, and projects directly into layer IV.

The layers are themselves complex structures, often organized into sub-layers. The input layer IV, for example, has three divisions into IVA, IVB, and IVC, the latter of which is the input layer. Recalling that there are multiple projections from the retina (in cat, X and Y; in primate α and β) and that these remain segregated in the dLGN (the parvo and magno layers), we observe that they remain separate into cortex as well, arriving in layers IVC α and IVC β , respectively.

15.2.2 Different Projections from/to Different Layers

The magno to IVC β projection then goes to IVA and is involved mainly in visual motion analysis; it projects, in turn, to other visual areas involved in motion (MT). (There is also a smaller projection from layer VI to MT.) We shall not be concerned with this pathway for the rest of this lecture.

We shall focus a lot on the parvo to IVC α projection, especially the part that goes superficial into layers II-III. The organization of these layers will be our main focus.

The projection from V1 to V2 arises from layers II-III, and proceeds to V2, layer IV. The backprojection from V2 to V1 arrives in the superficial layer I. This layer has no cell bodies; only the apical dendrite projection of neurons in other layers.

There is also a projection back to the midbrain, the colliculus and the lateral geniculate. The former is heavily involved in eye movements.

Note that two circuits are formed: dLGN \leftrightarrow V1 and v1 \leftrightarrow V2. The size of these forward and backward projections is enormous; apart from the corpus colluseum they are among the most significant in the primate brain.

Before we work out the circuits established by these different neurons in the different layers we first consider properties that emerge in V1 at the single-cell level.

For future reference, the “output” from a typical visual area, say V1, emerges from the superficial layer II/III and proceeds to the second visual area; and from the deep layer VI and proceeds back to the dLGN. It also goes to other midbrain areas such as superior colliculus.

15.3 Orientation Selectivity

No one tells the story better than David Hubel¹; see Fig. 15.2:

...By the late 1950s very few scientists had attempted to record from single cells in the visual cortex, and those who did had come up with disappointing results. They found that cells in the visual cortex seemed to work very much like cells in the retina: they found ON cells and OFF

¹Eye, Brain, and Vision, p. 69-70, Freeman



Figure 15.2: Illustration of extra cellular recording, in which an electrode is inserted into cortex and placed near an intact neuron. D. Hubel.

cells, plus an additional class that did not seem to respond to light at all. In the face of the obviously fiendish complexity of the cortex's anatomy, it was puzzling to find the physiology so boring.

...This was the situation in 1958, when Torsten Wiesel and I made one of our first technically successful recordings from the cortex of a cat. The position of microelectrode tip, relative to cortex, was unusually stable, so much so that we were able to listen in on one cell for a period of about nine hours. We tried everything short of standing on our heads to get it to fire. (It did fire spontaneously from time to time, as most cortical cells do, but we had a hard time convincing ourselves that our stimuli had caused any of that activity.) After some hours we began to have a vague feeling that shining light in one particular part of the retina was evoking some response, so we tried concentrating our efforts there. To stimulate, we were using mostly white circular spots and black spots. For black spots, we would take a 1-by-2-inch glass microscope slide, onto which we had glued an opaque black dot, and shove it into a slot in the optical instrument Samuel Talbot had designed to project images on the retina. For white spots, we used a slide of the same size made of brass with a small hole drilled through it. (Research was cheaper in those days.) After about five hours of struggle, we suddenly had the impression that the glass with the dot was occasionally producing a response, but the response seemed to have little to do with the dot. Eventually we caught on: it was the sharp but faint shadow cast by the edge of the glass as we slid it into the slot that was doing the trick. We soon convinced ourselves that the edge worked only when its shadow was swept across one small part of the retina and that the sweeping had to be done with the edge in one particular orientation. Most amazing was the contrast between the machine-gun discharge when the orientation of the stimulus was just right and the utter lack of a response if we changed the orientation or simply shined a bright flashlight into the cat's eyes.

This account of the frustration of exploratory experimental research saved by the serendipity of discovery is exemplary, even when guided by a good insight—in this case, that of Vernon Mountcastle that one should expect visual cortex to contain interesting structure like that which he had just found in motor cortex. It opens a remarkable change in our line of approach to understanding the visual system in primates.

15.3.1 Receptive Field Structures

An illustration of the experimental set-up is shown in Fig. 15.3. In this case the animal is viewing a grating pattern, but individual edge and line stimuli are also useful.

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Note in particular that *activity (e.g., spikes/second) varies with the orientation of the underlying stimulus.*

The dependence of activity on stimulus features can be summarized in tuning curves; examples are sketched in Fig. 15.4. Each tuning curve represents a series of experiments in which a number of stimuli, designed to span the feature of interest, are shown to the subject. When the tuning curve is not flat, i.e. the neuron shows differential activity with regard to that feature, we say that the neuron is “tuned” to that feature. The maximum activity is often taken as indicating the feature value to which it is tuned, although determining whether this is optimal (over larger ensembles of stimuli) remains an issue.

Many cells in visual cortex indicate that they have a receptive field structure analogous to what we have seen earlier. Recall that the receptive field is the locus of positions (in the visual field) to which a cell is sensitive, labeled with whether this is excitatory or inhibitory. It remains important to underline, though, that receptive fields as we shall be discussing them in the next several lectures are empirical, and hence involve the experimenter’s choice of where boundaries are located. These might vary depending on whether an informal approach is employed, as Hubel and Wiesel did (they just “listened” to what the spike rate was), or whether a more quantitative approach is employed (e.g. reverse correlation).

Most of the cells with which we shall be concerned for the rest of these lectures are tuned to orientation; some have tighter tuning with respect to position of the stimulus than others. Hubel and Wiesel categorized these cells as:

- *Simple Cells*: are those which have receptive fields whose sub-domains are *simple* to separate from one another;
- *Complex Cells*: are those whose subdomains are difficult to separate from one another. This is especially clear in the spatial tuning curve but less clear in the orientation tuning curve; see Fig. 15.5.
- *Hypercomplex Cells*: most difficult to categorize; see discussion below.

Experimentally sinusoidal gratings have been used a lot to classify the cell types and receptive field structures in visual cortex. Think of a stimulus in which one cycle of a sinusoid covers the receptive field, and now imagine that the amplitude of this sin is modulated in time from +1 to 0 to -1 repeatedly. Simple cells respond to the bright component in their excitatory portion of the receptive field and the dark in the inhibitory; complex cells respond to both peaks at the same time. This has lead observers to claim that simple cells are linear in their input but complex cells are non-linear. See Fig. 15.6.

Receptive field sizes for simple cells tend to be smaller than those for complex cells and orientation tuning tends to be tighter.

Size of receptive fields vary with layer; the smallest are in layer IV (typically a degree of visual angle, or less); intermediate-sizes (a degree or two) in superficial

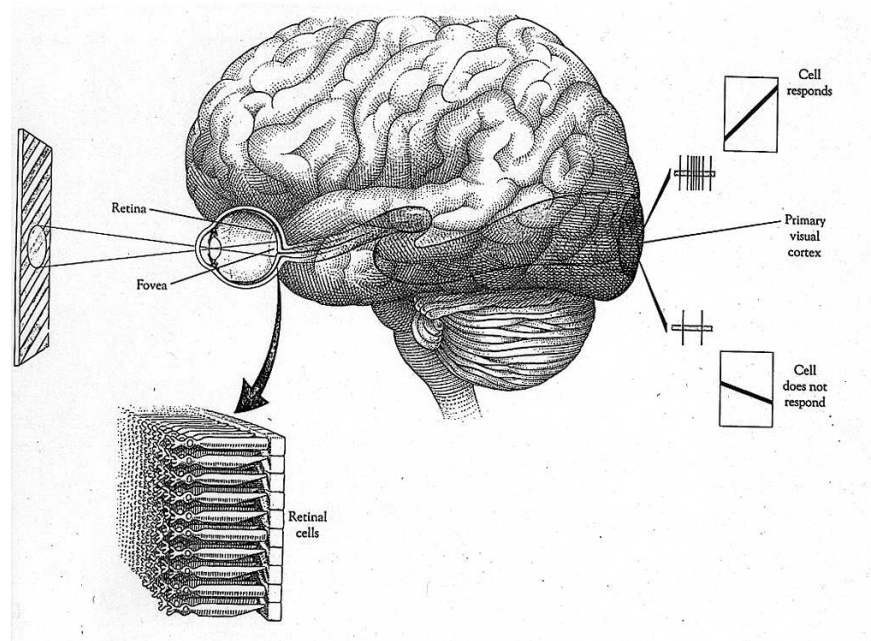


Figure 15.3: Recording from individual neurons in V1. The animal views a screen onto which visual patterns are projected, in this case a simple grating pattern. Response is a function of the orientation of the grating. Two possible recordings are shown, which indicate a high-level of spiking activity for one grating orientation and a lower-level of spiking activity for another.

layers II-III; and largest in deep layer VI (up to 10 degrees of visual angle in some primates).

A third group of receptive field structures was referred to as *Hypercomplex*; these cells indicate a complicated firing pattern which is often associated with the “corner” of a stimulus; that is to say, either the end of an extent of a stimulus or two orientations or something???; see Fig. 15.5. Because a central part of the hypercomplex response is that they tend to peak when the “end” of the stimulus is in the receptive field, they are also called *endstopped cells*. We shall have a lot more to say about endstopped neurons in subsequent lectures.

Certain cells indicate a strong variation in their length tuning, some of which sum and others of which decline (as in endstopping); see Fig. 15.8

Cells are also tuned to velocity and to ocular dominance, or how strongly their response is influenced by input from either the left eye or the right eye. Both of these tuning dimension will occupy us in later lectures, so we won't say much about them now.

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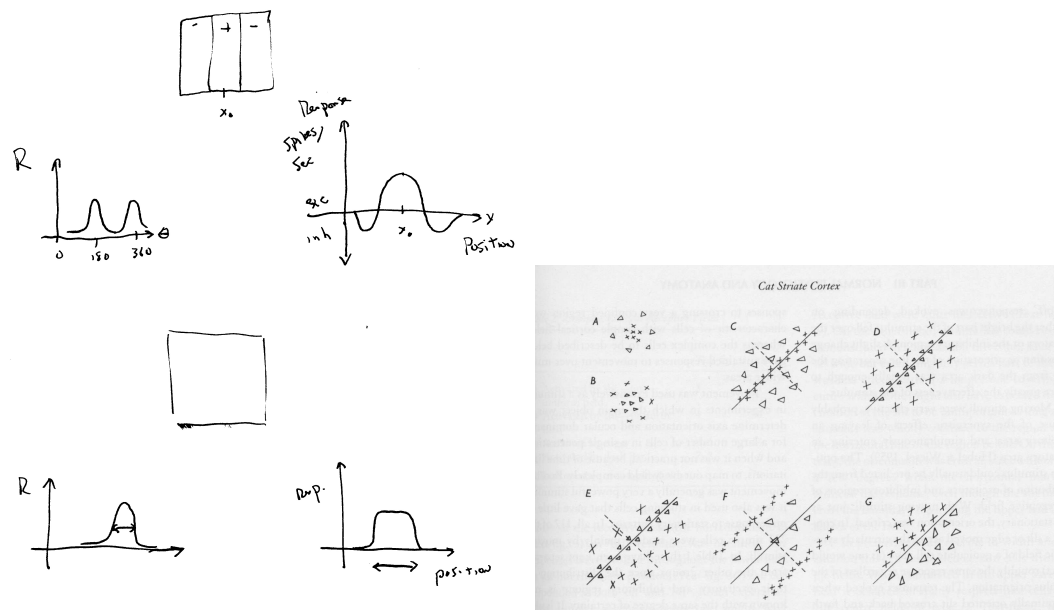


Figure 15.4: (LEFT) Tuning curves for typical neurons in which the orientation or the position (phase) of the stimulus is varied. (LEFT, TOP) Simple cells exhibit clear orientation and position tuning; (LEFT, BOTTOM) complex cells exhibit (typically less sharp) orientation tuning and much less sharp (highly-non-linear) position tuning. (RIGHT) Different simple cell receptive field profiles from Hubel and Wiesel’s original 1982 paper in cat striate cortex. Note some have even symmetry (are tuned to “lines”) and some have odd symmetry are tuned to “edges”, or step changes in intensity. The first two circular-surround receptive fields could be found either in the LGN or at the afferent terminals from the LGN in layer IVc.

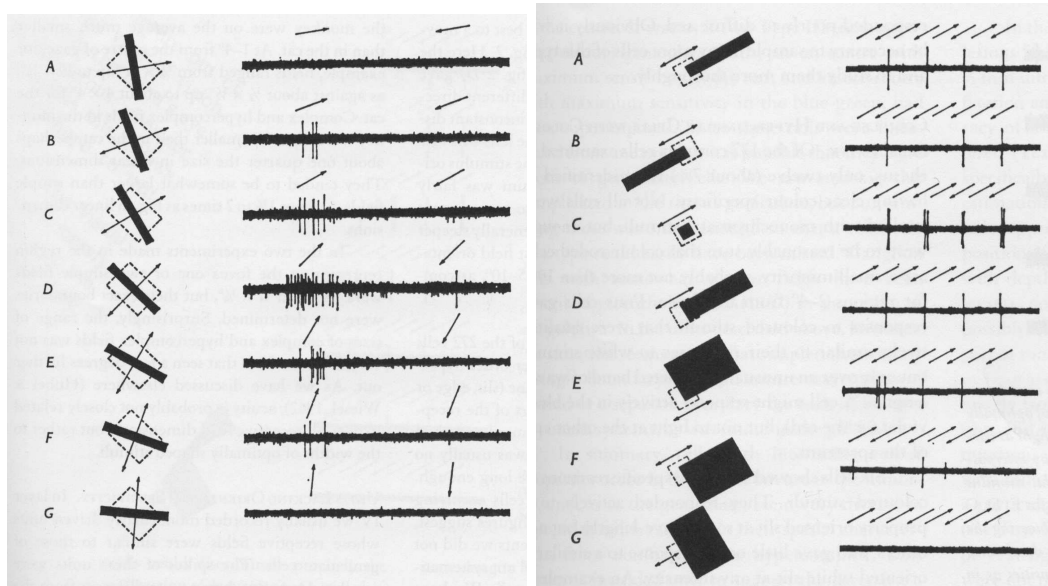


Figure 15.5: Illustration of firing patterns for different stimuli drifting across a the position on a screen corresponding to a cell's receptive field; again from Hubel and Wiesel. In these diagrams, the rough outline of a receptive field is indicated as a rectangle, and the stimulus bar is shown in dark superimposed on it. The light arrow indicates the direction of drift for the stimulus. (Stable, flashed stimuli can also be used to similar but often less robust effect.) (LEFT) The firing pattern for a complex cell; note how it is a function of stimulus orientation. It remains high while the stimulus is in the classical receptive field, thus exhibiting poor position tuning (within the receptive field). Thus it is not selective for position (within the receptive field) but drops off rapidly outside of it. The locus of positions where activity begins operationally defines the receptive field extent. (RIGHT) The firing pattern for a hypercomplex cell is more difficult to understand. Notice how short leading or trailing edges are poor stimuli, but a spot is an OK stimulus. Oddly, when the leading edge is extended into a corner on one side the cell provides a vigorous transient response. When the leading edge is rotated, however, the response declines. What is the ideal stimulus for a hypercomplex cell?

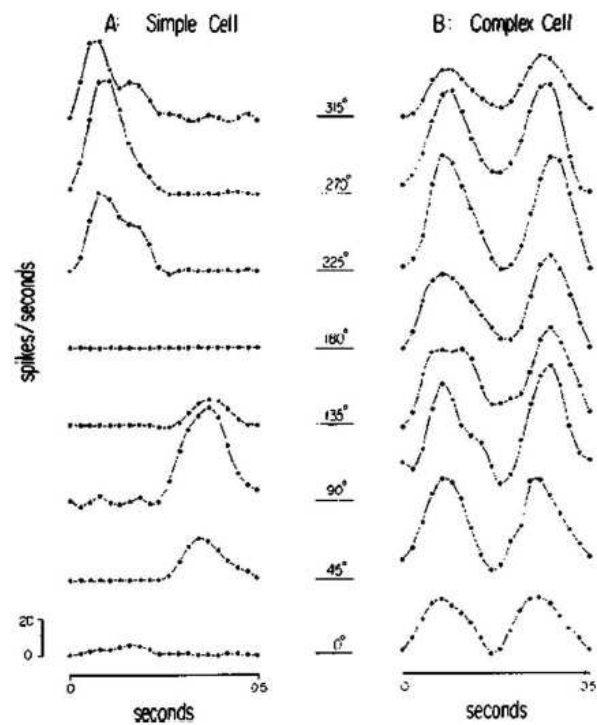


Figure 15.6: Simple cells are often described as “linear” and complex cells as “non-linear” transformations of their input stimuli. Here a reversing sinusoidal grating (or a grating in which the amplitude varies from +1 to -1 over time) shows a single peak in response for a simple cell, but multiple peaks for the complex one. DeValois 1982. That is, the ON domain of the simple cell reports the positive contrast portion of the stationary grating, while the complex cell shows both the positive and the negative contrast parts, as if they were rectified.

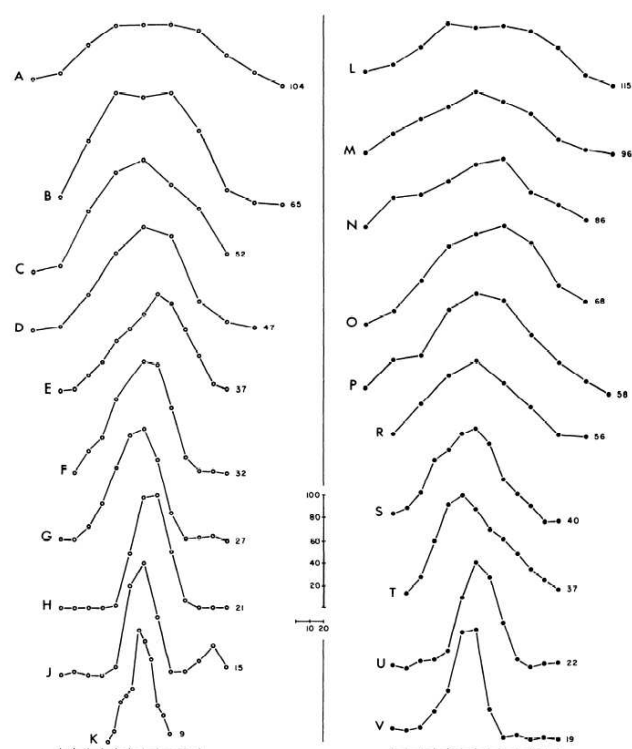


Figure 15.7: Different orientation tuning curves showing the variation in orientation tuning. The stimulus was a drifting bar or edge, varied in 10 degree steps, and the number to the right of each graph indicates an orientation tuning score. Left: simple types; right: complex type. On average, that the most tightly tuned cells are simple. Figs from Shiller, Finlay, volman, 2

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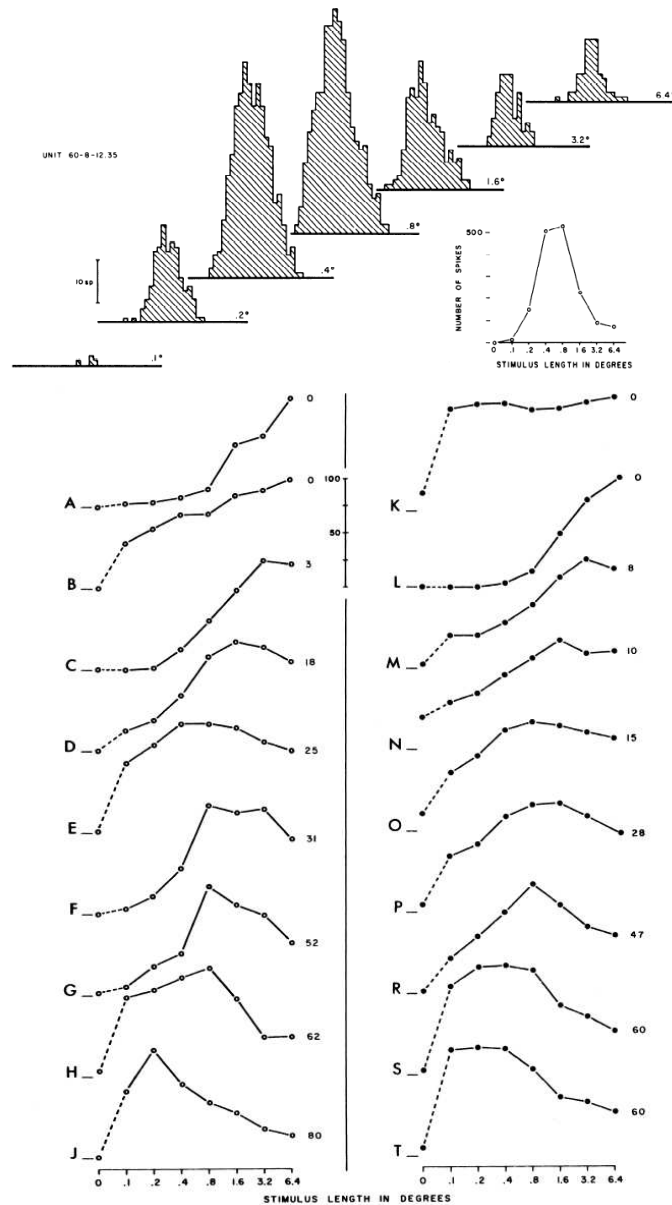


Figure 15.8: Different length summation and endstopped responses. (top) when a bar of different lengths is swept across the receptive field, spikes accumulate at different positions (in time). The histograms show the spikes for different bar lengths; note how the 0.8 degree bar give the maximum; longer bars elicit fewer spikes. The plot inset right shows the length tuning curve that summarizes the histograms; this cell is strongly endstopped. (bottom) Examples of length tuning curves for different simple (or S-type) cells (left) and complex (CX) cells (right). Note how many examples illustrate intermediate amounts of endstopping. What is the purpose of these “features?” Figs from Shiller, Finlay, volman

15.3.2 Functional Architecture

Neurons with different receptive field properties are arranged systematically in V1; this gives rise to a functional architecture. In a cartoon fashion, one can characterize the result of two different types of electrode penetration: those that are normal to the surface of cortex at a point and those that are tangential; Fig. [?]. In brief, a *normal penetration* encounters cells with receptive fields tuned to about the same orientation and position in retinotopic space but differing in size; this goes along with the layer differences mentioned above. See Fig. [?].

A short *tangential penetration* encounters cells whose receptive fields overlap onto about the same location in retinotopic coordinates but whose orientation preference varies. Extending the tangential penetration reveals a shift of position. Fig. 15.10.

Eye of origin information is clearly maintained in IVc and approximately maintained in superficial layers. That is, neurons are driven by one eye (monocular), mainly by one eye, or equally by both eyes (binocular); there may be a complete gradation in V1 between purely monocular and purely binocular. We shall discuss binocular vision two lectures hence.

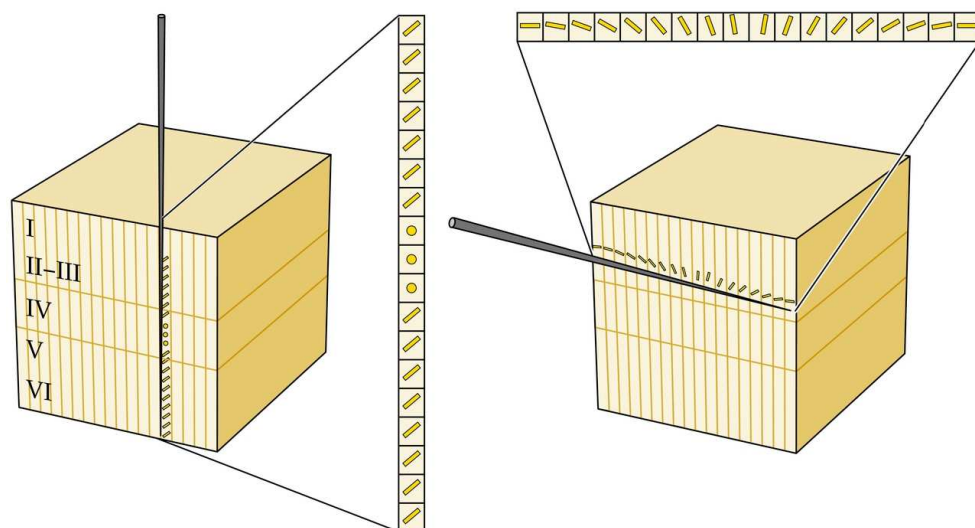
We stress that these two descriptions of the orthogonal penetrations are cartoons that capture an idealized view of cortex but one that will turn out to be useful for our purposes. In later lectures we will show more accurate description of visual cortex.

15.3.3 Cortical coordinates

Retinotopic coordinates are approximately mapped onto V1, although there is a CORTICAL MAGNIFICATION FACTOR that dedicates more processing to the “high resolution” fovea than to the periphery. This is because there are many more retinal ganglion cells per photoreceptor in the fovea than in the periphery; cortical area/RGC is approximately constant; see Fig. 15.12.

15.4 Columnar (Functional) Architecture in V1

Summary: each point in visual space (retinal coordinates) is covered by groups of cells that represent all stimulus features: i.e., they are both simple and complex; cells can be found that respond to each orientation and at each symmetry at each position; and for input from each eye. This highly redundant expansion is a key aspect of early visual structure. The famous ice-cube cartoon of this is shown in Fig. 15.13. Many have commented on the “regularity” of such a layout of structure and why it might/might not be important for function. Hubel and Wiesel named this unit of covering a HYPERCOLUMN: it consists of the ORIENTATION COLUMNS for the left and right eyes, tuned to a range of spatial frequencies.



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Figure 15.9: Electrode penetrations in V1 that are normal (LEFT) or tangential (RIGHT) to cortex encounter cell arrangements indicating different functional organization. A normal penetration encounters cells with receptive fields tuned to about the same orientation and position in retinotopic space but differing in size; a tangential penetration encounters cells whose receptive fields overlap but whose orientation preference varies.

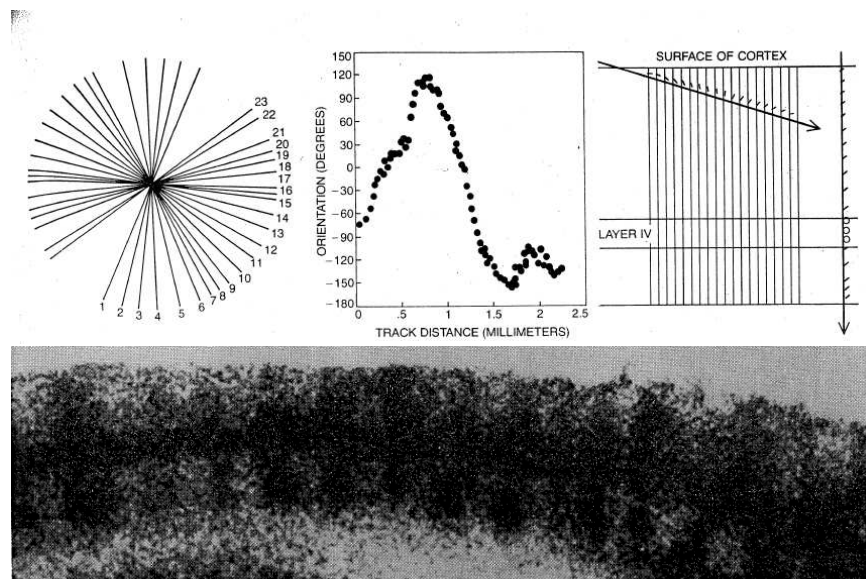


Figure 15.10: (top) Electrode penetrations in V1 that are tangential to cortex encounter cell arrangements whose orientation preference varies regularly. (left) orientation preferences of 23 neurons encountered along a penetration (middle) and cartooned at (right). From Hubel, Scientific American. (bottom) Radio-isotope shows the activity of cells tuned to vertical simulation. This is a kind of picture of the columns repeating across cortex.

15.4. COLUMNAR CHARACTERAL ARCHITECTURE OF VISUAL CORTEX

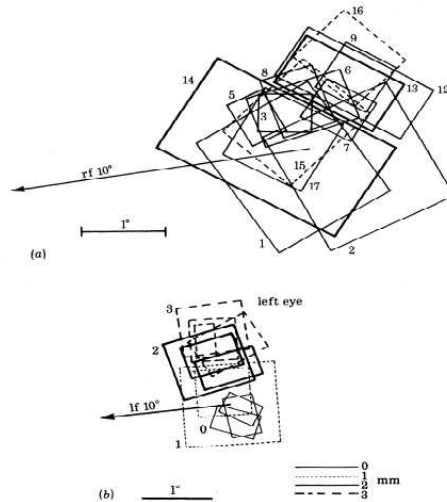


Figure 15.11: Hubel-Wiesel drawing of receptive field scatter in a normal penetration. Notice that the receptive fields overlap significantly, i.e. their “center of location” varies little, but that there is about an order of magnitude difference in their size. Given a sinusoidal grating pattern as input, the cells with large receptive fields would be tuned to lower spatial frequencies, while the cells with smaller receptive fields would be tuned to higher spatial frequencies. What is the functional role for this spatial frequency tuning?

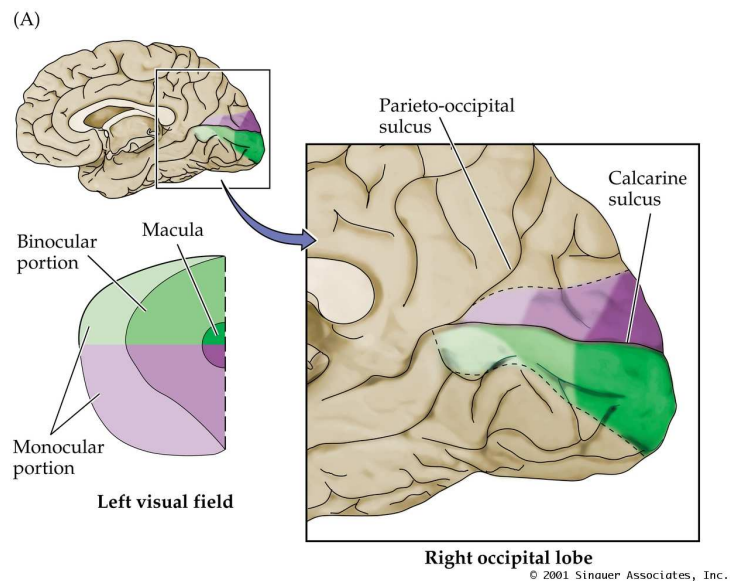


Figure 15.12: Map of retinotopic coordinates onto V1.

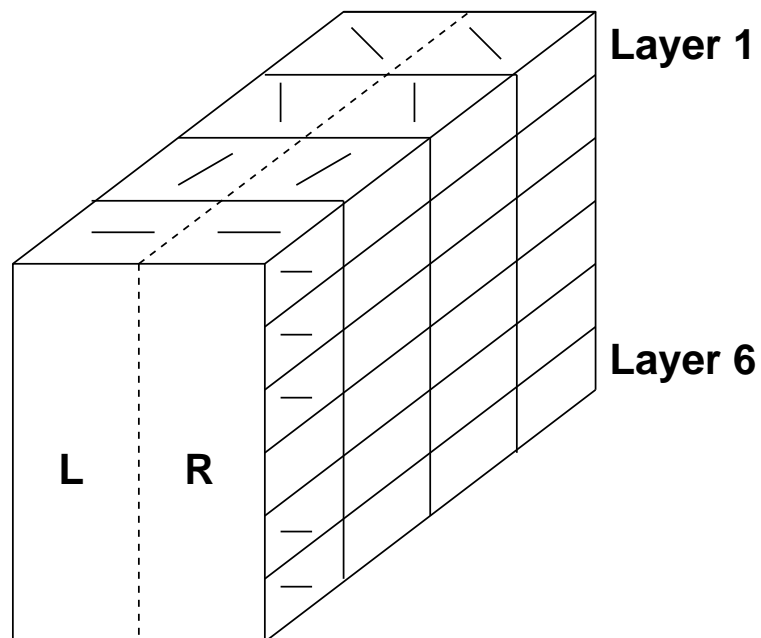


Figure 15.13: Ice cube model for a hypercolumn. It captures the regularity of cortical functional architecture in which each point in retinotopic space is covered with (the receptive fields of) neurons selective for orientation and eye-of-origin and receptive field size.

15.5 Organization of Visual Features

A classical way to organize data is with hierarchies. This is a foundation of the problem of search in theoretical computer science, where the question can be phrased in terms of books in a library.

15.5.1 Trees and Hierarchies

Suppose there are N books, with $N \approx 10^6$ just to make it concrete. If they were arranged randomly, then one might get lucky and find the book quickly; or one might be unlucky and have to search almost all of them. So it is natural to think about performing this search many times, for many different books; on average one would have to search about $N/2$ books.

Key point: to facilitate fast and efficient retrieval – and other algorithms – the main result from computer science is to build up an abstract representation that organizes the information. This way, at each step, huge portions of the space don't have to be searched.

Libraries have long faced this problem, so they have devised a number of abstract categories around which to arrange books; search through the library is then facilitated when, for each choice made (e.g. choosing physics vs. biology) a full subtree of books does not have to be searched. See Fig. 15.15.

Underlying this type of organization is a datastructure called a **TREE**. This is a collection of nodes, taken from a set of nodes, and edges that connect certain nodes (Fig. 15.16). In a tree not all nodes are connected to one another – there must be a unique path from a parent node to a child node – this is a very special property.

Formally, we say that the naive approach to searching every book in the library takes time, or in symbols, the time $T(n)$ to search n books is *on the order of* the number of books:

$$T(n) = O(n). \quad (15.1)$$

The “big Oh” notation here means that the function $T(n)$ even in the worst case is bounded by a linear function of the number of books. Normally such bounds are asymptotic: $T(n)$ is $O(n)$ if there exist constants $c > 0$ and $n_0 > 0$ such that, for all $n \geq n_0$ we have:

$$T(n) \leq c \cdot n. \quad (15.2)$$

In general, of course, one would be interested in bounds other than linear. For example, $O(n^3)$ is a cubic bound in n . Consider $f(n)$, a general function of n . “Big Oh” notation would then require $T(n) \leq c \cdot f(n)$ for all $n \geq n_0$.

The result about the Dewey decimal system indicates that it is possible to perform search in sub-linear time. This is amazing because we're not looking at most of the books. To appreciate this formally, let's assume that we're given an array of n numbers already sorted from smallest to largest. Now, to answer the question: Is the number η in the array, we could cut the array into two halves at the middle number n_{middle} .

If $\eta = n_{\text{middle}}$, we're done; otherwise we know that, if $\eta < n_{\text{middle}}$ it has to lie in the smaller half and we don't even need to look at the upper half. (Of course, if $\eta > n_{\text{middle}}$ we would only look in the upper half.)

Now, here comes a central idea in the theory of algorithms: repeat the above procedure for the smaller array of size $n/2$, which gives rise to two more subproblems of size $n/4$, and so on, until the array only has a single value in it. Mathematically, since the size of the array shrinks by a factor of 2 with each query, after k queries there are $(1/2)^k n$ elements in the array. The process stops when

$$\left(\frac{1}{2}\right)^k = O\left(\frac{1}{n}\right) \quad (15.3)$$

or when the size of the sub-array is one book. This happens when $k = \log_2 n$. Binary search has complexity $O(\log_2 n)$.

Sub-linear search is not free, however; remember that the process started with an ordered array. This is another basic result from the study of algorithms: it is often worthwhile to spend effort organizing data into a specific structure so that it can be efficiently accessed.

Divide-and-conquer can be applied again here. Suppose we're given a collection of n numbers, and we wish to organize them from smallest to largest. This is a problem of time complexity $T(n)$ in the worst case. If we break them into two groups of size $n/2$ (leaving aside issues of odd/even to make the discussion simpler), then we have to spend running time $T(n/2)$ for each one of them and, when done, we have to put these two organized lists together. Merging two sorted lists can be done in $O(n)$ time, so we have

$$T(n) \leq 2T(n/2) + \text{const} \cdot n, \text{ for } n > 2 \quad (15.4)$$

and $T(2) \leq \text{const}$.

Solving recurrence relationships like Eq. 15.4 can be done by “unrolling” it; see Fig. 15.14. Since the complexity at each level is $O(n)$ and there are k levels, the result is that any function satisfying the recurrent relation Eq. 15.4 is bounded by $O(n \log n)$.

An advantage of the “big O” notation is thus clear: the low complexity merging is absorbed into the higher-complexity bound on sorting.

Logarithmic speedup in search. Complexity theory: this speedup is a function of the size of the problem (number of books in the library).

15.5.2 Hierarchies of Visual Features

How might cells with different receptive field types arise? One of the most natural approaches is to invoke the hierarchy ideas from the beginning of this lecture. In effect, we seek to reduce a complicated and detailed “template” to a hierarchy of simpler ones, combining the earliest stages into more complex intermediate ones; and

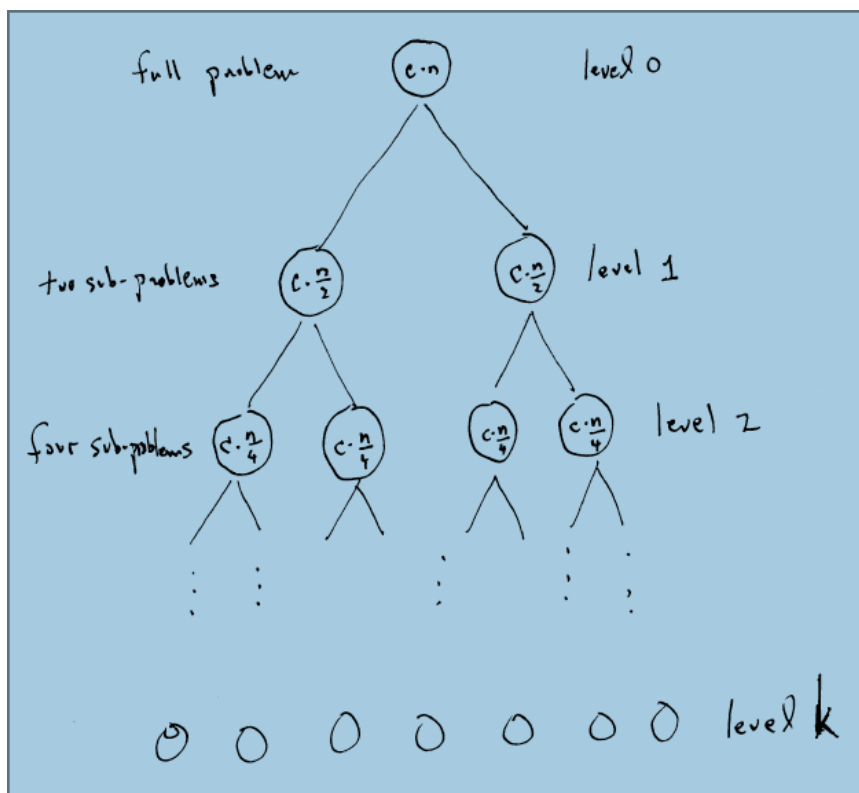


Figure 15.14: Solving the recurrence relation $T(n) \leq 2T(n/2) + O(n)$ by unrolling the recurrence. The full problem, level 0, has worst-case time complexity $T(n) = cn$; breaking it into two subproblems has complexity $2c\frac{n}{2}$ and so on until k levels of recursion have been achieved.

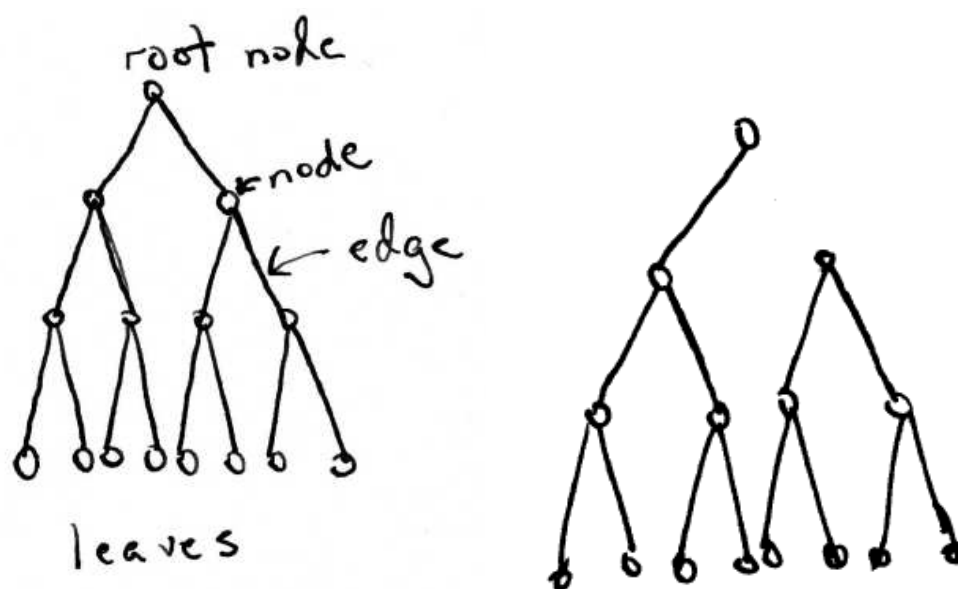


Figure 15.16: Trees are abstract combinatorial structures built from a set of nodes; some of these nodes are connected by edges. The advantage for search: if a choice is made at some level it removes a full sub-tree of items that do not need to be searched. The result is a huge speedup in searching efficiency.

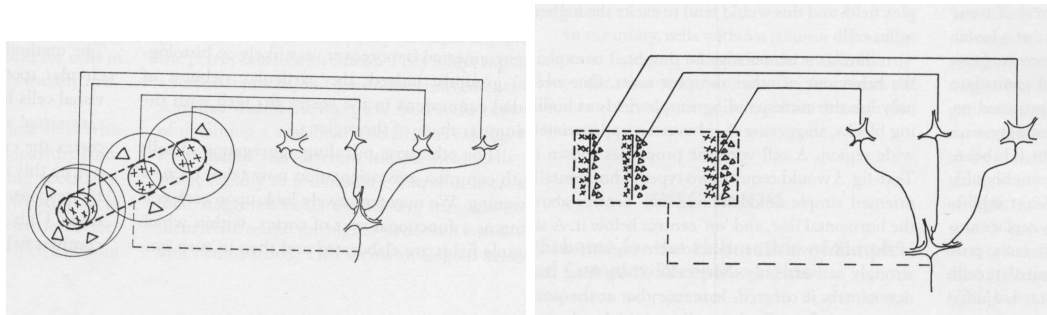


Figure 15.17: Two models for the wiring of cells with (LEFT) simple- and (RIGHT) complex-like receptive fields. In general, the idea is that more complex properties are derived from simpler ones via composition (either summation or logical OR) rules.

finally combining these intermediate ones into the full template for objects. To get such a scheme started, Hubel and Wiesel suggested:

- *entry level*: simply “add up” LGN afferents in a proper arrangement to make a simple cell (Fig. 15.17, left). This organizes retinal “points” into oriented “line” or “edge” segments.
- *middle level*: “OR” an arrangement of simple cells outputs together to make a complex cell. This groups or generalizes short “lines” and “edges” from simple cells across “position” by complex cells.
- *third level*: Finally, hypercomplex cells, which we can imagine as being composed of circuits that “AND”-together complex cells, detect “corners” and other conjunctions of features.

This is an attractively simple theory of organization for visual representations, very much in the spirit of the Dewey Decimal System for libraries. Organization certainly helps with complexity, and in this style of organization “higher” entities contain a summary of all the information relevant from “lower” ones.

The excitement generated by speculating that the primate visual system was a hierarical arrangement of the sort of feature extraction seen in the frog was fantastic. Unfortunately, as we shall see, the story is not quite so simple.

15.6 Discussion of the H-W Approach

15.6.1 The Subtlety of Receptive Field Measurements

is the 'linear' view of impulse response sufficient – shapley paper.

15.6.2 The Root Question(s) about the Hierarchy Model

These questions fall into two categories: (i) whether the H-W hierarchy notion is correct, with simple combining into Cx into HCx; and (ii) whether their circuitry model is correct. Both turn out to violate the strict H-W model although there is certainly a something to it.

- Researchers in Australia discovered that there wasn't a simple, complex, hypercomplex "hierarchy", but rather that there were both simple and complex hypercomplex-style cells. This is why researchers began to call them *simple-endstopped*, and *complex-endstopped*. To quote them:

One early observation that Henry, Dreher, and I made concerned the hypercomplex property of end-inhibition...It was a property thought only to be found in cells at a relatively high level in a simple, complex, and hypercomplex sequence. Our finding was that the property was not a later acquisition by complex cells but a general property of all the various cell types in the striate cortex. P. O. Bishop, p 100

This says that there is more to the network circuits than simple feedforward hierarchies, a question to which we shall return in some detail.

- *LGN Projections in Cat* also go directly to simple and complex cell types; this suggest more a notion of parallel pathways than of strict hierarchy. Also there are LGN projections to the first and second visual areas in the cat.
- *Response to Orientation is not a function of contrast* but rather exhibits amplitude-invariant orientation tuning.² Thus the circuitry is going to be more complicated. We shall have to worry about this in future lectures as well.
- *The Grandmother Cell* The main problem with strict hierarchies is their limit: at the top of the hierarchy tree there are "roots", or nodes at the top. The most famous example of this is the so-called "grandmother cell" or the cell in, say, temporal cortex that responds if, and only if, one is viewing one's grandmother. Not surprisingly, the concept of grandmother cell goes back to Jerry Lettvin, who saw it as the limit of "what the frog's eye tells the frog's brain." It was given great impetus by Gross's discovery of "face" and "hand" selective cells in IT cortex in the period 1969-72; see Fig. 15.18.
 - What happens if that cell dies? Do we retain memory of all the constituent properties but not of the concept?

²The Emergence of Contrast-Invariant Orientation Tuning in Simple Cells of Cat Visual Cortex Neuron, Volume 54, Issue 1, 5 April 2007, Pages 137-152 Ian M. Finn, Nicholas J. Priebe and David Ferster

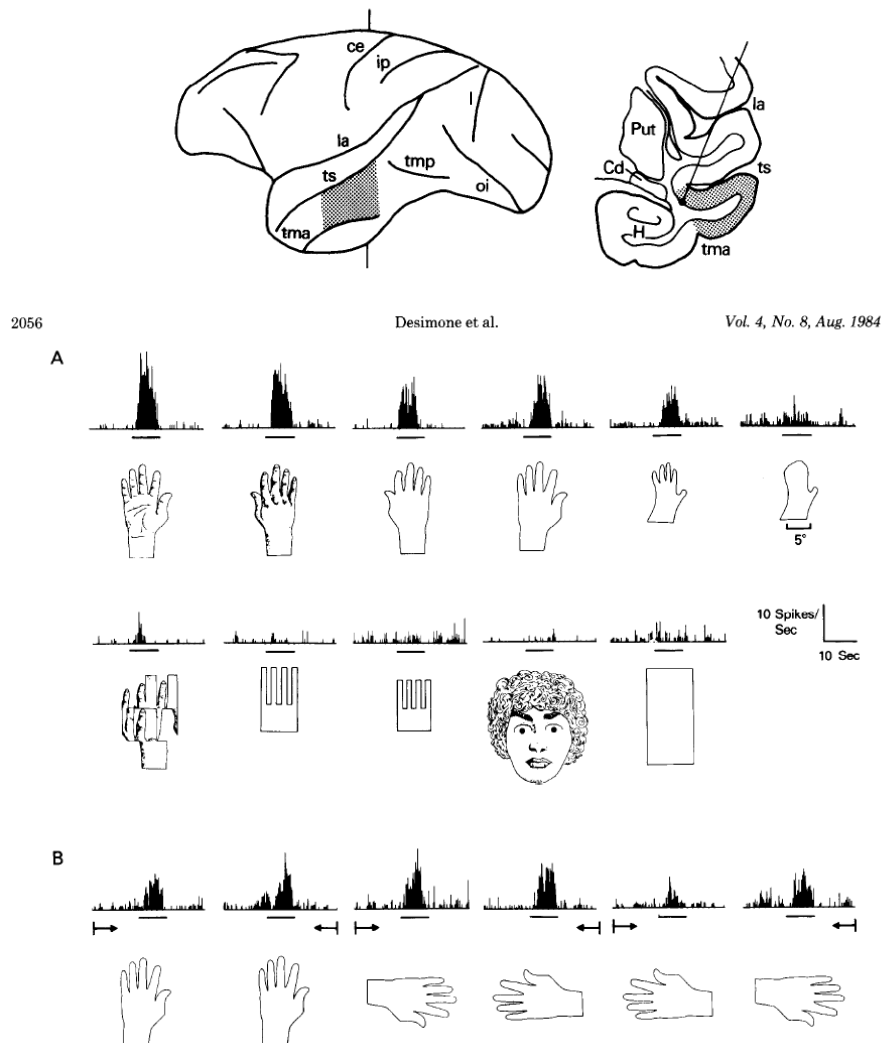


Figure 15.18: Gross et al results of finding hand and face selective cells in temporal cortex. (TOP Recording sites in IT cortex.) (BOTTOM) Results. In sampling a few dozen cells from a field of millions, what kinds of conclusions can be drawn?

- This is a code for visual properties that involves one-neuron/concept. For reliability, a network of neurons would be better.
- Since the constituents are already distributed, how will the grandmother cell “bind” them together exactly correctly?

15.7 Conclusions

Key point about abstract data structures: do some work “up front” to build it and you can then design algorithms that exploit this to run much more efficiently for actual problems. Is the design of these intermediate data structures part of what is accomplished when the visual system “wires” together?

A curious thought: could a drawing serve as such an abstraction for images? If so, how might this abstraction be computed? Notice that there is a real sense in which a drawing is simpler than an image, because the pixels are either black or white.

Key point: if there is a strict hierarchy built according to certain principles, then these principles must hold. This is the “foundation” on which we build visual representations. Do “edge detecting cells” provide this foundation?

15.8 Notes

Barlow H. (1972) Single units and sensation. *Perception* 1, 371-94. Genealogy of the “Grandmother Cell”, Charles G. Gross, *The Neuroscientist*, 2002

Desimone, R., Albright, T.D., Gross, C.G., and C. Bruce. Stimulus selective properties of inferior temporal neurons in the macaque. *J. Neurosci.*, 1984, 4: 2051-2062.