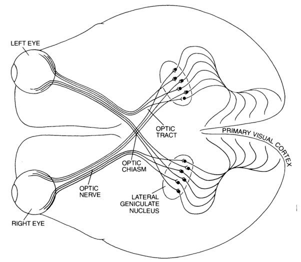
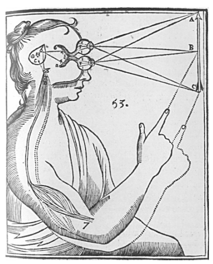
The Neuroscience of Vision I

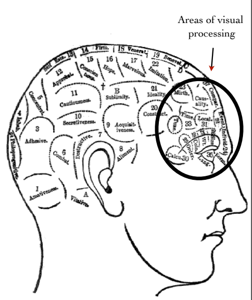


The Challenge



- Descartes understood that visual information entered through the eyes (he thought it was conveyed by particles) and is sent from the retina through fibers until, at the pineal gland, it informs the mind, which may then choose an appropriate action
- But it is a big jump from sensory input to recognizing objects so as to be able to respond appropriately to them
- How to explain the ability to see and recognize objects?
  - The mechanist gambit: different parts of the brain perform different tasks, some of them together realizing the ability to see

Remember Gall



- In addition to correlating skull shapes with traits, Gall made some seemingly plausible assumptions when it came to the senses
  - the areas that process information from a sense should be near to the sense
    - hence, vision in the frontal areas of the brain
- It wasn't until the middle of the century that researchers were able to employ techniques like lesions to investigate vision
  - And even longer before they could begin to decompose vision into subtasks that could be localized

Clicker Question

Which type of evidence did not figure in the attempts to determine the locus of vision in the brain **in the 19th century**?

Electrical stimulation of the brain region

Recording activity in brain areas while organisms performed visual tasks

Tracing neural pathways from the eyes to the brain

Determining where lesions to brain regions affected the ability to see

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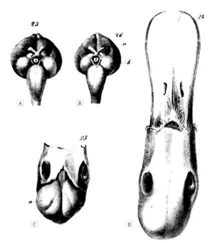
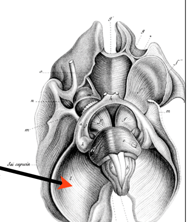
The First Experimental Localization of Vision

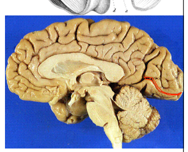
- Bartolomeo Panizza sought to follow visual processing from the eyes to the brain
  - Working in various species of fish, birds, and mammals, he employed two experimental procedures:
    - Tracing effects of destruction of the eyes
    - Destruction of brain regions and identifying corresponding deficits
  - Also examined human patients with visual pathologies to find locus of damage
- In a paper in 1855 he identified the posterior of the brain as the locus of vision
- Panizza's studies, though, were largely ignored



Following the Optic Tract

- At nearly the same time, Pierre Gratiolet traced the optic tract in monkeys and the brains of human fetuses from the lateral geniculate nucleus of the thalamus to the rear of the cortex via the radiations of Gratiolet
- Theodor Meynert identified what came to be called Meynert cells in the area surrounding the calcarine fissure as the terminus of these fibers

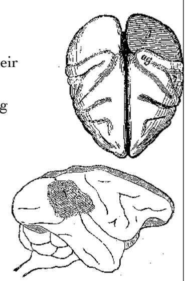




Logic of Empirical Evidence

- Tracing pathways
  - If a portion of a system is responsible for processing inputs of a given type, then there should be connections from the responsible sense organs to it
    - But the converse is not necessarily true
      - Something could receive inputs from a sense and not be responsible for processing information from it
- Lesion experiments
  - If a portion of a system is responsible for a given phenomenon, then destroying it ought to eliminate the phenomenon
    - But the converse is not necessarily true
      - Something could cause the elimination of a phenomenon without itself being responsible for it

Competing Localizations of Vision



- In the 1870s and 1880s several investigators reported visual deficits in patients with damage to the rear of their brains
  - Hermann Munk developed techniques for removing small regions of animal brains and identified the occipital lobe as the one responsible for vision
- David Ferrier, perhaps the leading neurologist of the period, claimed that the angular gyrus was the locus since lesions there seemed to generate blindness
  - And his lesions to the occipital lobe did not generate blindness
- Vast majority of findings supported Munk
  - In retrospect, Ferrier probably cut deeply into conduction pathways in lesioning the angular gyrus
    - And left much of the occipital lobe in tact in his lesions
- But such assessments can only come later once researchers settled on Munk's view

Discussion Question

Once researchers settled on the occipital lobe as the locus of vision, what further questions called out for answers?

- How did this area of the brain perform the task of vision?
- What other parts of the brain might be involved?
- Are there specialized regions within the occipital cortex that perform different tasks?
- Why is visual processing done in the rear of the brain?

But How Does Striate Cortex Work?

- The area of the occipital cortex Munk and others identified was distinguished anatomically by its striation pattern and came to be known as *striate cortex*
- The next question researchers turned to was what goes on in striate cortex?
  - Does it have parts that do different things?
- Salomen Henschen followed pathways from the retina to striate cortex and concluded that parts of the retina projected to specific regions of the striate cortex (which he termed the *cortical retina*), yielding a topological map
  - He was right about a map, but got the orientation totally reversed

Clicker Question

How did wars (the Russo-Japanese War and World War I) contributed to the development of the neuroscience of vision in the first two decades of the 20th century?

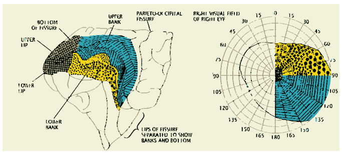
- The wars led to increased funding for researchers who investigated vision
- Armies had a high interest in improving the visual abilities of soldiers and experimented on ways to alter the visual system
- Armies had a high interest in improving the visual abilities of soldiers and developed much better optical systems that, for example, aided night vision
- The wars produced casualties who had suffered damage to particular parts of their brains and partial blindness, enabling reseachers to link specific brain areas with specific areas of blindness

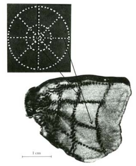
Finding Surgical Instruments Where You Can

- During the Russo-Japanese War, Tatsuji Inouye, a young Japanese ophthalmologist, was assigned to assess visual loss in Japanese soldiers who had suffered brain injury so as to determine how large their pensions would be
  - He decided to make the job more interesting and map deficits in particular parts of the visual field onto the area damaged
- The situation was set up by the fact that the Russians had developed a new high-velocity rifle (Mosin–Nagant Model 91) that fired a 7.62-mm hard-jacketed bullet.
  - This bullet pierced the skull without shattering, leaving tidy entrance and exit wounds
- This made it possible to trace the trajectory and compare the location where the occipital lobe was damaged with the part of the visual field in which the patient lost vision

Retinotopic map of the visual field

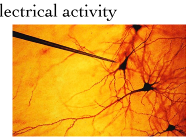
- In a study of 29 patients with focal brain injuries, Inouye correlated the parts of the visual field in which his patients were blind with areas of brain damage, and mapped the visual field onto the visual cortex
- Gordon Holmes (1918) constructed a similar map based on studies of soldiers injured during World War I
- Using radioactive markers, Tootell et al. (1982) had an anesthetized monkey look at a pattern as it died and then "developed" its brain, revealing topographic map

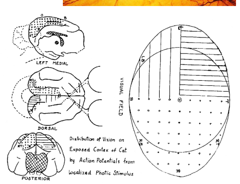




Recording From Neurons

- The recognition that neurons transmit an electrical signal motivated the search for ways to record the electrical activity of individual neurons, finally achieved in the 1930s by inserting electrodes near neurons
- Talbot and Marshall mapped the receptive fields of individual neurons by correlating locations of stimuli with individual neural response
  - Confirming the idea of topological maps developed from lesion studies



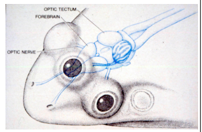


Lesion vs. Recording Studies

- Lesion studies show what ability is lost when a particular component of the mechanism is destroyed
  - But cannot show that the component is itself responsible for the ability
- Recording studies (single-cell recording, PET/fMRI) show what areas of the brain are active during a task
  - If a brain area is involved in a task, it should be active when the task is performed
    - But again, the converse is not necessarily true
- Neither type of evidence is alone conclusive, but for both types to be found by chance seems increasingly less plausible
  - Hence, enhancing the probative power of the evidence

Frogs Lead the Way to Understanding What Visual Neurons Do

- In the 1930s Haldan Hartline differentiated cells in the frog's optic nerve that responded to light in their receptive fields
  - *on cells* responded when a light was on
  - *on-off cells* responded when a light switched from on to off or vice versa
  - *off-only* cells responded only when a light was off



  and correlated responses with intensity of light
- Following up, Horace Barlow demonstrated that with *on-off cells*, the response was less if the stimulus exceeded the receptive field
  - Stimuli around the periphery of a cell's receptive field reduces response
  - Conclusion: neurons are tuned to spots of light

Discussion Question

Pretend you are a frog equipped with the ability to detect small moving spots across your visual field. How could this be useful to you?

It provides a way to detect potential mates when they are moving near you

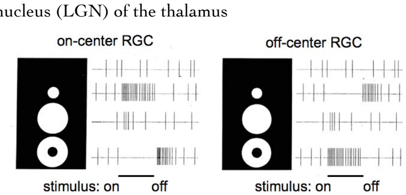
It provides a way of detecting insects that might make a nice meal

It provides a way for investigators to figure out how your vision system works

It provides a way to detect potentially dangerous projectiles so that you can duck to avoid them

Center-Surround Cells in Retina

- Turning to retinal ganglion cells in cats, Steven Kuffler found that in when the cat was in darkness or diffuse light the neurons fired at a basal rate (1-20 Hz)
  - Some cells exhibited an increased firing rate when a light spot was surrounded by darkness (*on-center*)
  - Others exhibited an increased firing rate when a dark spot was surrounded by light (*off-center*)
- Same response properties of neurons in the lateral geniculate nucleus (LGN) of the thalamus



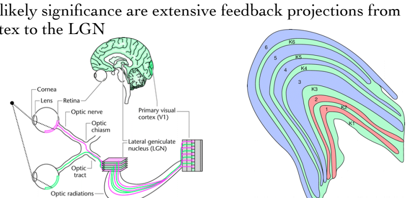
Discussion Question

Center-surrround cells register the difference in light levels, not the actual amount of light. What functional significance could this have?

- It allows organisms to detect boundaries between objects
- It allows the visual system to work at varying light levels
- It reflects the fact that our senses aren't there to paint a picture of the world, but to detect what is important in it
- Probably none. It is a crazy way to set up a visual system

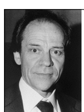
Lateral Geniculate Nucleus of the Thalamus

- The LGN is often portrayed as simply a way-station on the way to visual cortex, where the serious processing is claimed to occur
- The LGN segregates inputs by eye (layers 2, 3, 5 receive inputs from the ipsilateral eye) and type of retinal input cell (layers 1-2 receive inputs from midget cells in retina responding to detail and color)
- The true importance of the LGN, like the rest of the thalamus, is probably underestimated
  - Of likely significance are extensive feedback projections from cortex to the LGN

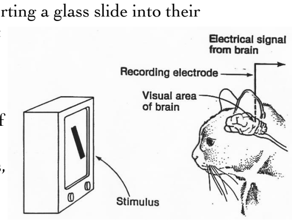


From Hooser and Nelson, Visual System, eLS

Turning to Cortex

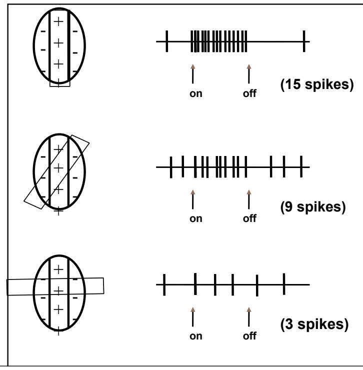


- When a technique works once, it makes sense to try it again
  - David Hubel and Thorsten Wiesel, working in Kuffler's lab, tried to replicate his achievement in the striate cortex
    - But failed, and failed, and FAILED
- One day while they were inserting a glass slide into their projecting ophthalmoscope, it stuck, creating a bar of light on the screen
- Hubel reports that "over the audiomonitor the cell went off like a machine gun"
- Bars of light (edges), not dots, activate cells in striate cortex



Hubel and Wiesel's Simple Cortical Cells

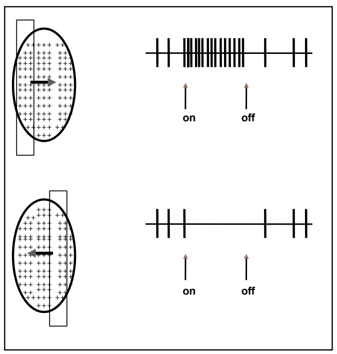
- Many of the cells Hubel and Wiesel tested in occipital lobe responded to bars of light
  - But only if they were properly oriented



Hubel and Wiesel's complex cells

- Some cells Hubel and Wiesel tested responded to bars of light anywhere in the receptive field of the cell

  or
- If they were moving in a preferred direction across the field



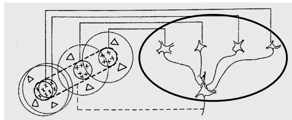
Discussion Question

Hubel and Wiesel several times emphasize that the processing in the occipital lobe is local. What does this mean?

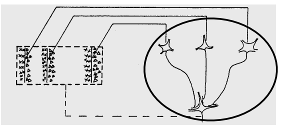
- Each neuron only responds to stimuli in particular parts of the visual field
- Individual neurons receive information from a specific source and determine their responses from that
- Information sent into cortex is sent to specific regions, not disseminated everywhere
- Processing is piecemeal. A cell only processes a restricted amount of information

How do Simple and Complex Cells do it?

- Hubel and Wiesel proposed simple model wiring diagrams to show how simple and complex cells could perform their different tasks



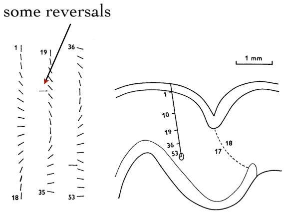
Simple cells: Fire if enough LGN cells with centers on the bar are active



Complex cells: Fire if one or another simple cell detecting a bar is active (or if several become active in sequence)

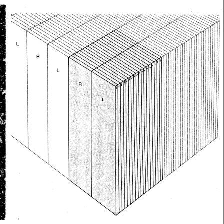
Micro-Organization of Striate Cortex

- When recording from electrodes inserted directly down through striate cortex
  - All cells responded to the same stimulus
- When recording from electrodes inserted obliquely to the surface
  - Successive cells responded to gradually rotated bars
    - With some reversals



Ocular Dominance Columns

- Radioactively labeled 2-deoxyglucose is taken up by neurons when they are active
  - Allows staining those neurons that respond to vertical stripes
  - Black versus white bands represent different eyes
- Two dimensional arrangement of columns in visual cortex



Coding Visual Inputs in Striate Cortex

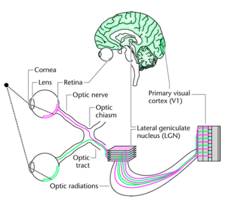
- Hubel and Wiesel's speculation (hypothesis)
  - "Why evolution has gone to the trouble of designing such an elaborate architecture is a question that continues to fascinate us. Perhaps the most plausible notion is that the column systems are a solution to the problem of portraying more than two dimensions on a two-dimensional surface. The cortex is dealing with at least four sets of values: two for the x and y position variables in the visual field, one for orientation and one for the different degrees of eye preference. The two surface coordinates are used up in designating field position; the other two variables are accommodated by dicing up the cortex with subdivisions so fine that one can run through a complete set of orientations or eye preferences and meanwhile have a shift in visual field position that is small with respect to the resolution in that part of the visual world."

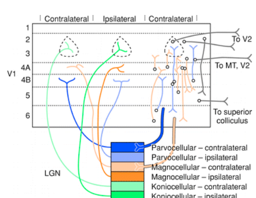
Striate Cortex (V1) is not Sufficient for Seeing

- Hubel and Weisel's results were impressive
  - Won them the 1981 Nobel Prize
- But they raised more questions than they answered:
  - "Specialized as the cells of 17 are, compared with rods and cones, they must, nevertheless, still represent a very elementary stage in the handling of complex forms, occupied as they are with a relatively simple region-by-region analysis of retinal contours. How this information is used at later stages in the visual path is far from clear, and represents one of the most tantalizing problems for the future." (Hubel and Wiesel, 1968, p. 242)
- The recognition of the need for other areas led to the labeling of striate cortex as Visual Area 1 (V1)—other areas could then be designated V2, V3, etc.

The Account So Far

- Overall, there is a processing pathway from the eyes to Striate Cortex (aka Primary Visual Cortex or V1) that involves retinal ganglion cells, LGN, and Simple and Complex Cells in V1
- But in fact the mechanism is highly interactive, involving feedback, lateral, and feedforward projections whose significance is only beginning to be understood





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