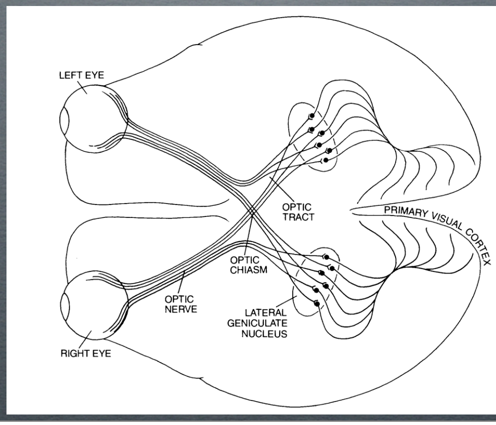
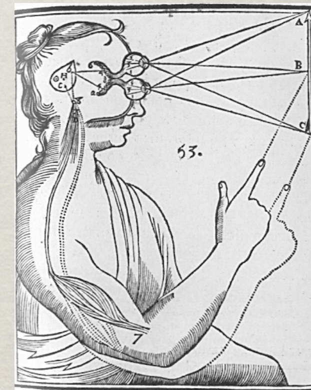
The Neuroscience of Vision I



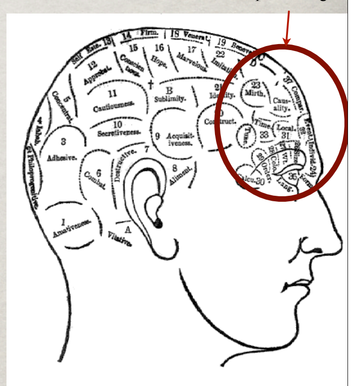
The Challenge



- 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 affects action
- But it is a big jump from sensory input to recognizing objects so as to be able to respond appropriately to them
- Where does this processing occur?
  - Researchers took the challenge to be to find the locus of visual processing

Gall and Phrenology

Areas of visual processing



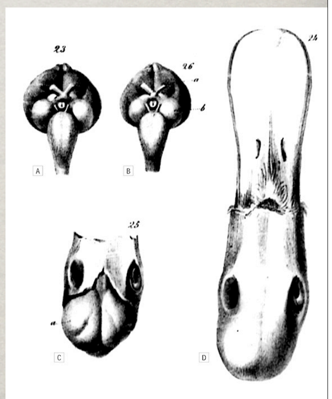
- A master anatomist, Franz Joseph Gall at the beginning of the 19th century advanced a view of how the brain supported mental activities
  - Different mental faculties are located in different parts of cortex and are responsible for the behavior associated with them
- Gall supported this hypothesis by correlating the strengths of individuals on different psychological abilities with with protrusions on their skulls
  - On the assumption that skull protrusions reflected the size of underlying brain areas
  - Correlations based on selected examples, not statistics

Holism vs. Localization

- Not everyone agreed that processing specific information would be local
  - Pierre Florens, a vigorous critic of Gall, lesioned parts of the brains of rabbits and pigeons
    - Lesions to the cerebellum produced loss of equilibrium and of motor control
    - Removal of the cortex eliminated perception and judgment
    - But destruction of parts of cortex seemed to have no specific effects—only a general loss of ability
    - Defended an early version of the principle of mass action
- The backlash to phrenology Flourens reflected resulted in a general skepticism to localization of cognitive abilities in the brain that lasted several decades

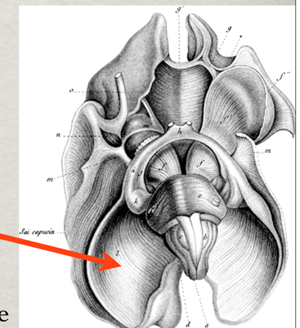
The First Experimental Localization of Vision

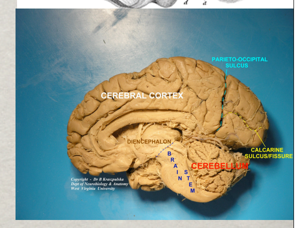
- Bartolomeo Panizza sought to follow visual processing from the eyes to the brain
  - Working in various species of fish, birds, and mammals, he employed two experimental procedures:
    - Tracing effects of destruction of the eyes
    - Destruction of brain regions
  - Also examined human patients with visual pathologies
- 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

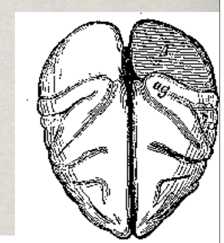


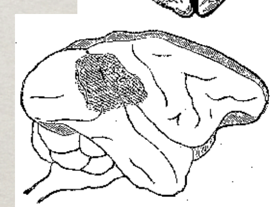


Logic of Empirical Evidence

- 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 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

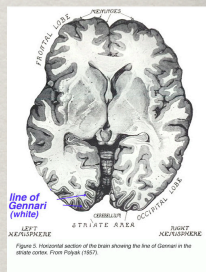




- In the 1970s and 1880s several investigators reported visual deficits in patients with damage to the rear of their brains
  - Hermann Munk developed techniques for removing small regions of animal brains and identified the occipital lobe as the one responsible for vision
- David Ferrier, perhaps the 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 his lesions there
- But such assessments can only come later once researchers settled on Munk's view

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 was what goes on it 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

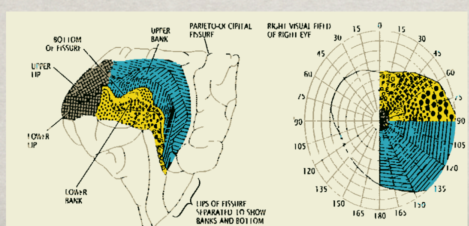


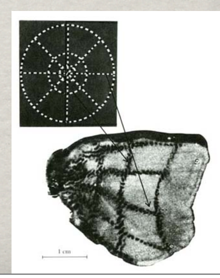
Finding Surgical Instruments Where You Can

- 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

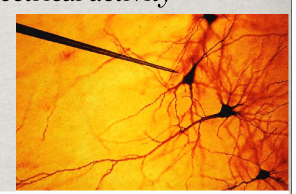
- In a study of 29 patients with focal brain injuries, Inouye correlated the parts of the visual field in which his patients were blind with areas of brain damage, and mapped the visual field onto the visual cortex
- Gordon Holmes (1918) constructed a similar map based on studies of soldiers injured 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

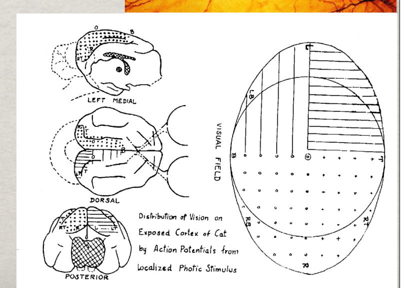




Recording From Neurons

- 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

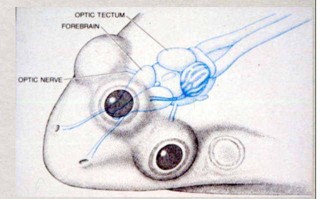




Lesion vs. Recording Studies

- 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

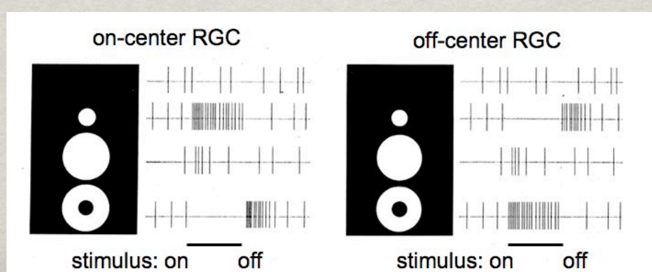


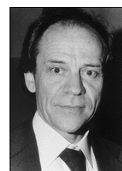
- In the 1930s Haldan Hartline differentiated cells in the frog's optic nerve that responded to light in their receptive fields
  - *on cells* responded when a light was on
  - *on-off cells* responded when a light switched from on to off or vice versa
  - *off-only* cells responded only when a light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

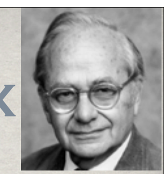
Center-Surround Cells in Retina

- Turning to retinal ganglion cells 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*)

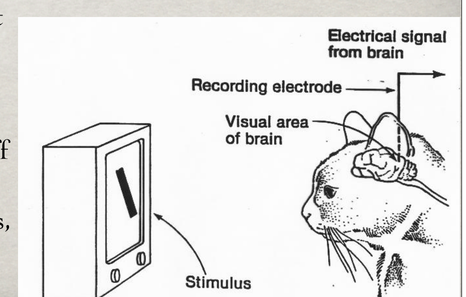




Turning to Cortex

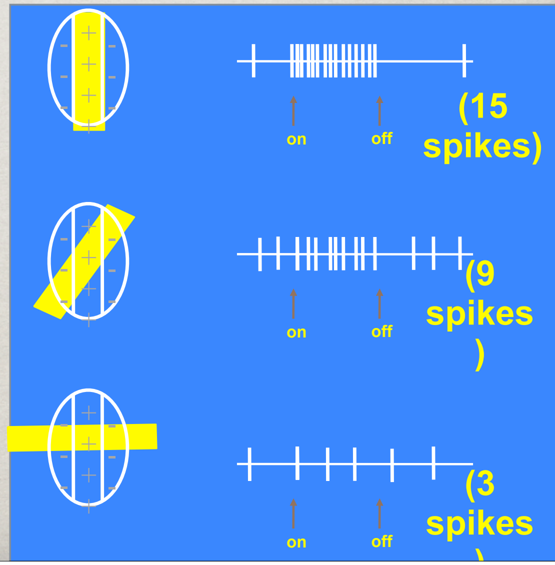


- When a technique works once, it makes sense to try it again
  - David Hubel and Thorsten Wiesel, working in Kuffler's lab, tried to replicate his achievement in the striate cortex
    - But failed, and failed, and FAILED
- One day while they were inserting a glass slide into their projecting ophthalmoscope, 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

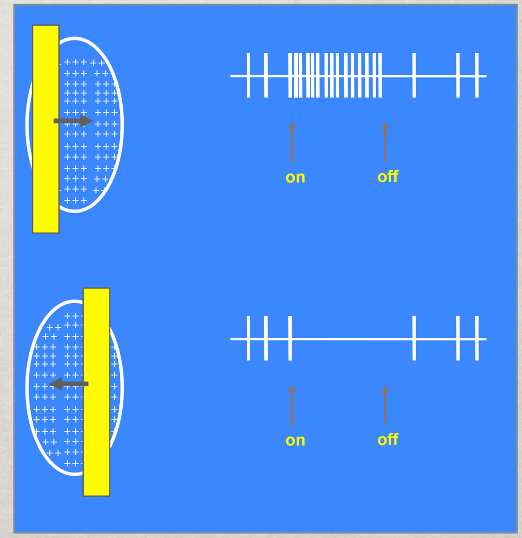
- Many of the cells Hubel and Wiesel tested in occipital lobe responded to bars of light
  - But only if they were properly oriented



Hubel and Wiesel's complex cells

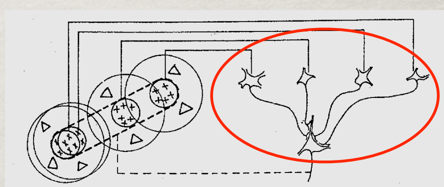
- Some cells Hubel and Wiesel tested responded to bars of light anywhere in the receptive field of the cell

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

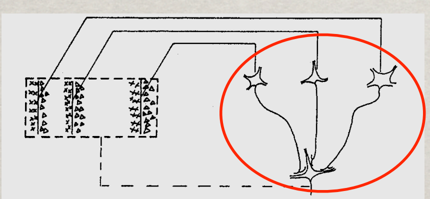


How do Simple and Complex Cells do it?

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



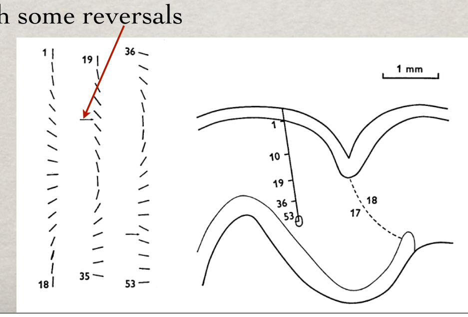
Simple cells: Fire if enough LGN cells with centers on the bar are active



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

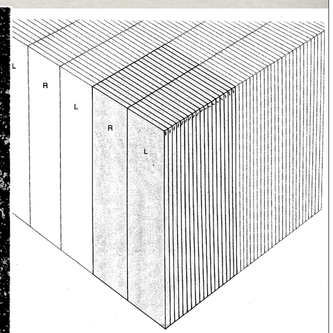
Micro-Organization of Striate Cortex

- 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.