The Neuroscience of Vision II

Striate Cortex (V1) is not Sufficient for Seeing

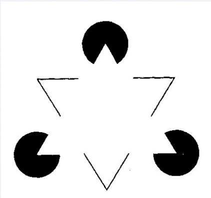
- Hubel and Wiesel conclude their 1968 paper by pointing outwards:
  - "Specialized as the cells of 17 are, compared with rods and cones, they must, nevertheless, still represent a very elementary stage in the handling of complex forms, occupied as they are with a relatively simple region-by-region analysis 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)
- A not uncommon result in science: The mechanism one thought to be responsible is not itself sufficient to produce the phenomenon

Where else is Visual Processing Performed?

- The holist challenge (initially raised by Flourens) remained
  - Karl Lashley, after failing to find a locus that would destroy particular memories, defended the principle of mass action
    - Beyond primary sensory areas, it only matters how much cortex one has
    - "visual habits are dependent upon the striate cortex and upon no other part of the cerebral cortex" (Lashley, 1950)
    - He labeled the areas outside of primary sensory and motor areas *association cortex*
      - Why *association*?

Beyond V1

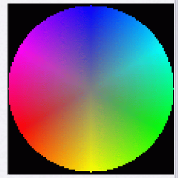
- An important step in identifying V1 as a visual processing area was the topographical mapping from it to the visual field
  - Could that criterion be used again?
- Cowley (1964) found that the area in front of V1 had another topographical map of the visual field—it became V2
  - Hubel and Wiesel showed these cells responded to binocular depth cues
  - Later demonstrated to respond to illusory contours



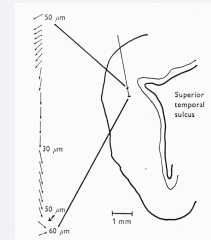
- Using their strategy of single cell recording, Hubel and Wiesel (1965) found yet another area that became V3
  - These responded to a variety of complex patterns, including edges that terminated on either one or both ends within the receptive field

Color Processing

- Semir Zeki took advantage of the fact that lesions in one area led to degeneration in the areas to which the lesioned neurons usually project to identify yet another area, V4
- With single cell recording, he found that when an electrode was inserted vertically in V4, all cells responded to light of a given wavelength, but when obliquely, successive cells cells responded to light of different wavelengths
  - Subsequent research showed that V1 was also responsive to wavelength
    - What is distinctive of V4 is that it shows color constancy, and does not respond to raw wavelength
- Lesions here could explain evidence from the 19th century of patients unable to see color (achromatopsia)



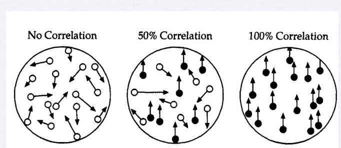
Motion Processing



- In 1974 Zeki identified another area (V5/ MT) in which cells were responsive to the direction in which a stimulus was moving
  - Some cells responded to complex patterns such as opposite direction of movement in each eye
    - What would that tell you?
- At the time there were no reports of patients unable to detect motion, but Zihl et al., 1983 described a patient who lacked motion perception
  - Only saw sequences of still life paintings
  - MT lesion could explain her deficit

Combining Methods to Determine Function

- With both V4 and V5/MT, the demonstration of function relied on the correspondence of recording and lesion studies
- Movshon and Newsome combined these with yet a third form of evidence—stimulating a brain area with a mild electrical charge
  - Trained monkeys to respond differently if stimuli were perceived as moving in the same direction or randomly



  - Then presented the test case in which 50% of the stimuli were moving in the same direction
    - Monkeys responded responded with random answers
      - Recordings from MT cells predicted their behavior
      - Microstimulation of MT cells were bias their behavior

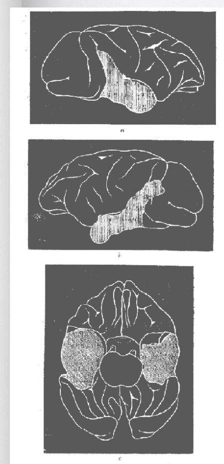
Stimulation Studies

- Stimulation was first employed by Fritsch and Hitzig in 1870 to find localized centers in the dog's brain
- Guiding idea:
  - If a brain region is responsible for a given activity, then stimulating it should affect (typically increase, but perhaps impair) that ability
    - But again, the converse doesn't hold:
      - Stimulation of an area may have a specific effect, but it not be responsible for that effect
- But if an area is active in a given task, lesioning it eliminates the ability to perform the task, and stimulating it increases that ability
  - It seems increasingly likely that it plays an important role in that task
    - Although it may not be the only area involved!

We Don’t Just See Edges, Colors and Motion

- Just as Hubel and Wiesel concluded their 1968 paper by noting that V1 was insufficient, the discovery of these extra-striate visual areas showed that they were insufficient
  - “The picture that is beginning to emerge, therefore, is one of a mosaic of areas, each with a different functional emphasis. Presumably the visual information analyzed in detail in these areas is then assembled at an even more central cortical area” (Zeki, 1974)

Further Hints from the 19th Century

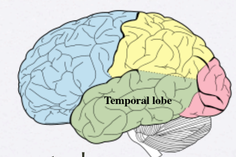


- In 1888 Schäfer reported that lesions to the temporal lobe in monkeys produced deficits in recognizing objects:
  - “the condition was marked by loss of intelligence and memory, so that the animals, although they received and responded to impressions from all the senses, appeared to understand very imperfectly the meaning of such impressions. This was not confined to any one sense, and was most evident with visual impressions. For even objects most familiar to the animals were carefully examined, felt, smelt and tasted exactly as a monkey will examine an entirely strange object, but much more slowly and deliberately. And on again, after only a few minutes, coming across the same object, exactly the same process of examination would be renewed, as if no recollection of it remained”

Klüver–Bucy Syndrome

- As part of an investigation of the area he thought was affected by mescaline, in the 1930s Klüver had Bucy remove the temporal lobes of monkeys bilaterally
  - Exhibited *psychic blindness* or *visual agnosia*: “the ability to recognize and detect the meaning of objects on visual criteria alone seems to be lost although the animal exhibits no or at least no gross defects in the ability to discriminate visually.”
  - Also, loss of emotional responsiveness and increased sexual behavior
- Suggested that recognition of visual objects might involve parts of the temporal lobe
  - Motivating inquiry directed at identifying which part

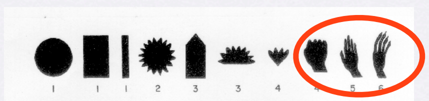
Into the Temporal Lobe



- Mortimer Mishkin found that lesions to the ventral temporal lobe (inferotemporal cortex) impaired shape discrimination
  - When cut off from earlier visual processing areas, animals experienced deficits in visual learning and memory
- Gross et al. (1967): “It is conceivable that inferotemporal cortex might be a site of further processing of visual information received from prestriate and striate cortex. If this were true, its neurons might have receptive fields and highly complex response properties”

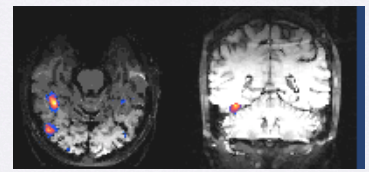
A Hand-Cell

- Initially Gross and colleagues had a difficult time finding stimuli that would generate responses from IT cells
- Then, serendipity:
  - "having failed to drive a unit with any light stimulus, we waved a hand at the stimulus screen and elicited a very vigorous response from the previously unresponsive neuron" (Gross et al., 1972)
  - Further investigation showed that a hand-shape, but only pointed upwards, elicited the strongest response



A Face Area

- Gross et al. found other cells that responded to pictures of faces or of trees, and some that responded best to three-dimensional objects than to cutout shapes
  - But his results were received skeptically
- Finally, in the 1980s other reports of cells particular responsive to faces, as well as other classes of stimuli
- Relying on fMRI, Nancy Kanwisher identified an area in the fusiform gyrus that she claims is a "face area"



Prosopagnosia

- There are human subjects who see faces, but don't recognize individual faces:
  - "When I look at a face, I see the same thing that I suspect you do. My vision works fine (other then some autistic difficulties that aren't relevant to this discussion). My brain sees a face much like any other object. The problem I have is in associating that face with a particular person I know."
  - "I recognize people by three primary methods - general body size/shape, hair, and the sound of their voice. These three methods are not nearly as effective as the normal way of recognizing people - by recognizing a face. Thus, I often mistake someone I don't know for someone that I do know or I fail to recognize someone I know. For instance, I have been unable to recognize my father on multiple occasions, since his body size and shape are not very distinctive, nor does he have long or distinctive hair."

But is the Fusiform Gyrus a Face Area?

- There is little doubt that the area Kanwisher identified responds particularly well to faces
  - But like any recording study, we don't yet know what else it might respond to
    - Some evidence that it responds to objects where detecting individual identity is important

Grandmother Cells?

- Hubel and Wiesel:
  - What happens beyond the primary visual area, and how is the information on orientation exploited at later stages? Is one to imagine ultimately finding a cell that responds specifically to some very particular item? (Usually one's grandmother is selected as the particular item, for reasons that escape us.) Our answer is that we doubt there is such a cell, but we have no good alternative to offer. To speculate broadly on how the brain may work is fortunately not the only course open to investigators. To explore the brain is more fun and seems to be more profitable."
- A Jennifer Aniston cell? (Claimed by Rodrigo Quiroga in 2005 in epileptic patients with inserted electrodes)

Parietal Lobe

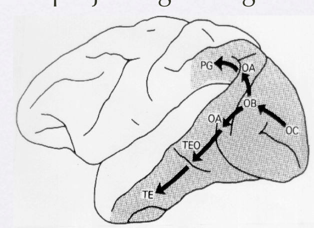
- Ferrier and Yeo (1984) reported that with damage to the angular gyrus, a monkey "was evidently able to see its food, but constantly missed laying hold of it"
- Brown and Schäfer (1988) reported that their monkey with similar damage "would see and run up to [a raisin], but then often fail to find it . . ."
- Ferrier (1990) reported that a monkey could not form the correct grasp for an object
- Rezső Bálint (1909) described a stroke patient who could not accurately reach for an object with his right hand
  - Could not use visual information to guide motor activity
  - Bálint's Syndrome

Recording from Parietal Cortex

- At first studies recording from parietal cortex seemed to yield little insight as no stimulus would activate the region when the animals were anesthetized
- When techniques were developed for recording from awake behaving animals, Juhani Hyvärinin discovered an area that responded to the conjunction of visual input and a particular attempted behavior
  - Some cells depended on eye movement
  - Others on body movements
- Richard Andersen showed that neurons in the posterior parietal cortex mapped stimuli in terms of spatial location
  - Temporal lobe cells are largely unresponsive to location
  - In lateral interparietal area (LIP) space mapped relative to head-based coordinates (not the retinal-based coordinates used in early visual areas)

Putting the Pieces Together

- Drawing upon the apparent differences in processing in the temporal lobe (object identification) and parietal lobe (spatial processing), Ungerleider and Mishkin proposed that there are two hierarchically organized visual pathways
  - A ventral *what* system projecting through V4 to the temporal lobe
  - A dorsal *where* system projecting through MT to the parietal lobe

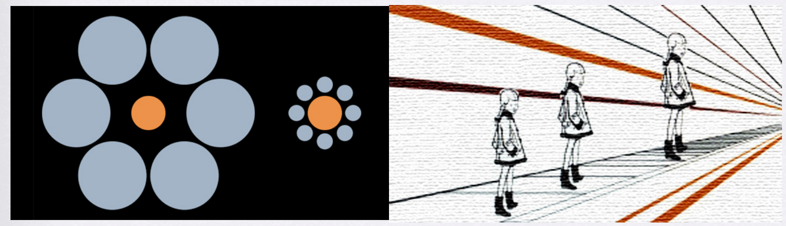


Recharacterizing the Two Pathways

- Instead of distinguishing *what* and *where*, Milner and Goodale proposed a distinction in terms of *vision for perception* and *vision for action*
  - Both pathways process *what* and *where* information
- Milner and Goodale identify the difference between the streams not in terms of inputs but the outputs they serve
  - Ventral: "enduring characteristics of objects *and* their spatial relations"
  - Dorsal: "mediate the visual control of skilled actions"
    - Crucial to implementation of action

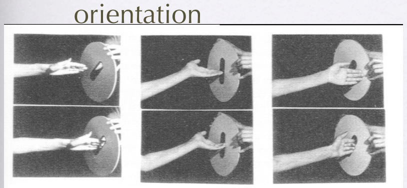
Distinguishing two Ways of Seeing

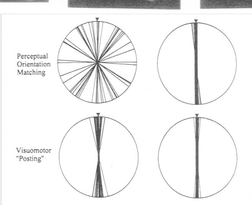
- When asked to report which yellow circle is larger, people experience the Ebbinghaus and Ponzo illusions
- But not in reaching behavior such as preparing to grip them
  - Yet effect is found if response is delayed, requiring reliance on memory

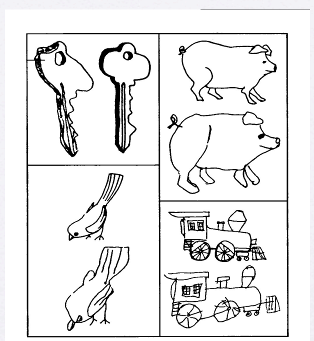


Doubled Dissociation

Optic ataxia: With damage to the parietal pathway, patients are unable to put hand through slot in correct orientation







Visual agnosia: When damage is to temporal pathway, copying is slow and slavish and patients cannot name object

Where Does It All Come Together?

- We seem to have one cohesive awareness of the world, involving both recognizing of objects, where they are located, and opportunities for doing things with them
- Suggesting that somewhere in the visual processing stream everything out to come together in one cohesive representation of what we see
  - A complete picture that some inner homunculus is looking at
- But why should the brain have been designed to work that way?
  - What is critical is that each relevant piece of information is represented and available to be employed as needed to control behavior