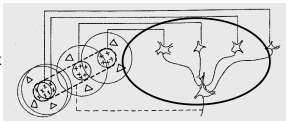


The Neuroscience of Vision II

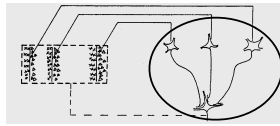


How do Simple and Complex Cells do it?

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



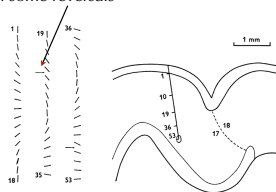
Simple cells: Fire if enough LGN cells with centers on the bar are active



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

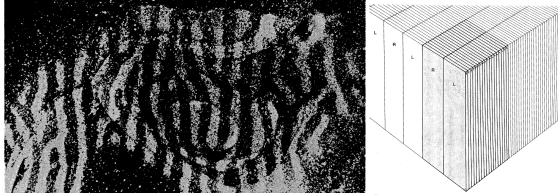
Micro-Organization of Striate Cortex

- 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 Wiesel concluded their 1968 paper by pointing outwards:
 - "Specialized as the cells of V1 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 parts of the system one thought to be responsible are not themselves sufficient to produce the phenomenon
 - And researchers must look elsewhere for the rest of the mechanism

Clicker Question

What is it to be anti-localizationist about vision?

- To deny that vision occurs in the brain
- To deny that specific brain regions perform specific tasks involved in vision
- To maintain that a single brain region is responsible for vision
- To deny that the visual system is able to establish with accuracy the location of things we see

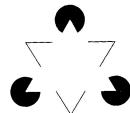
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Where else is Visual Processing Performed?

- The anti-localizationist 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

- To find visual areas beyond V1 one had to answer Lashley
- An important step in identifying V1 as a visual processing area was the topographical mapping from the visual field to it
 - 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 known as V2
 - Hubel and Wiesel showed these cells responded to binocular depth cues
 - These cells were later shown to respond to illusory contours
- Using their strategy of single cell recording, Hubel and Wiesel (1965) found yet another area that became V3
 - Cells in this region responded to a variety of complex patterns, including edges that terminated on either one or both ends within the receptive field



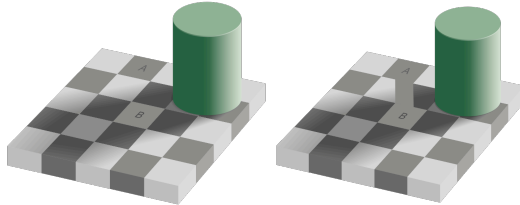
Color Processing

- 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 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)



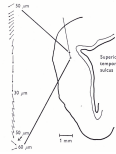
Color Constancy

- Color constancy is most powerfully revealed when the mechanism involved causes us to see the same color (even shades of grey) differently as a result of taking into account the surrounding colors



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
 - MT lesion could explain her deficit



Discussion Question

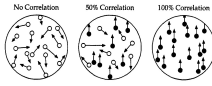
What would it be like to have a lesion in MT destroying motion perception?

- I wouldn't be able to detect objects coming at me
- It would be like seeing a series of still photographs projected rather slowly
- It would be difficult to walk around since I wouldn't be able to pick up cues from the relative motion of objects round me
- Other (be prepared to specify)

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

Discussion Question

Assume that a person has perfectly normal processing in regions V1-V5, but lacks subsequent processing. What would the person's experience be like?

Their vision would be indistinguishable from ours —they just wouldn't know what they were seeing

Their visual experience would be of moving colored shapes that lacked any coherence

Their visual experience would be a much truer portrayal of what the world really looks like since it would be unbiased by theories or hypotheses

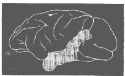
Other (be prepared to specify)

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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 what these extra-striate visual areas did showed that they were insufficient to fully explain vision
 - “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”

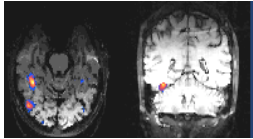
A Hand-Cell

- 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 particularly 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”



Discussion Question

If the area of your brain involved in recognizing faces were damaged, what would the experience of looking at someone be like?

I would see an empty spot where the person's face would be

I would see the shapes and colors that constitute the face, but I wouldn't recognize them as a face

I would be able to learn from a variety of experiences to call what I see a face, but I wouldn't be able to recognize different people by their face

Other (be prepared to specify)

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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 than 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 Hyvärinen discovered an area that responded to the conjunction of visual input and a particular attempted behavior
 - Some cells depended on eye movement
 - Others depended 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)

Clicker Question

When they proposed that “multiple visual areas are organized hierarchically into two separate visual pathways,” how do Ungerleider and Mishkin describe that the two pathways do?

Analyze color versus analyze shape

Process information about familiar versus unfamiliar objects

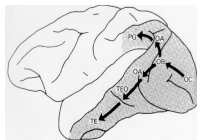
Process information about object identity versus spatial location

Process emotional responses versus objective responses

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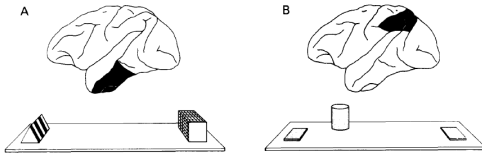
Putting the Pieces Together

- 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



Different Pathways

- In support of the *what/where* differentiation of the two pathways, Mishkin et al. focus on the types of tasks subjects with lesions in each pathway cannot perform
 - A. With temporal lobe damage, subject cannot recognize the object that matches or differs from a previous experienced sample
 - B. With parietal lobe damage, subject cannot pick object by its relation to a landmark



Clicker Question

How does Milner and Goodale's characterization of the two visual pathways differ from that of Mishkin et al.?

They viewed the ventral system not as involved in recognizing objects but in identifying how valuable they are to the viewer

They claimed that one pathway processed both object and location information while the other was actually involved in relating visual to audition

They argued that one pathway processed familiar stimuli while the other processed novel ones

They viewed the distinctive function of the dorsal stream not as spatial representation but as enabling visual control of actions

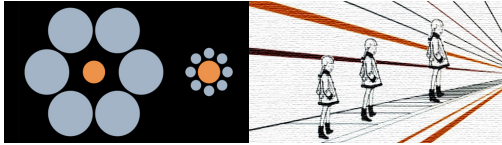
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Recharacterizing the Two Pathways

- 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

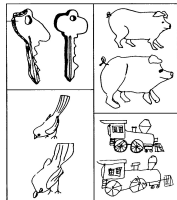
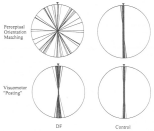
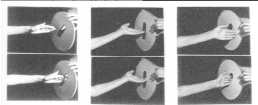
Distinguishing two Ways of Seeing

- 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 objects

Different Processing Demands for Perception and Action

- Occurrent timing is required for action since the world is undergoing change
- Action is by an agent and hence requires working in egocentric space
- Location of object in egocentric space not relevant for perceptions

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 ought 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
