WEEK 3: CONTRAST SENSITIVITY, LINEAR SYSTEMS APPROACH, AND SPATIAL SCALES

1) Structural scales: functional scales :: kernels: receptive fields
2) Peak shifts and lateral inhibition
3) Detectors and filters
4) Contrast sensitivity and spatial scales
5) A start on visual physiology

THOUGHT FOR THE DAY
Everybody wants to go to heaven, But nobody wants to die.*

Lyrics: Al Fields, Tom Delaney, & Timmie Rogers
Sung by: Ellen McIlwaine

We the People
New York: Polydor, 1973

* This is a statement about modeling.

WHY GROSSBERG (1973)?

Why discuss Grossberg (1973) at this point in CN530?

Recall: At the conclusion of Week 1’s lecture:

In the visual universe, we have:

- coherence from disconnected elements, and
- segmentations through homogeneous regions!

What kind of geometry does this?
What could possibly be its functional units?

Consider a “Miller analogy:”
uniformizing : coherence :: choice : segmentation

GROUPING: (e.g. in Glass or Bozzi patterns) perceived wholes are more uniform than their underlying luminance distributions.

SEGMENTATION: (e.g. Beck textures, Ehrenstein figures) perceived segmentations selectively cut through parts of homogeneous luminance regions.

Possible mechanism for getting around single node saturation limit (upper bound), as in:

(B-x_i)(excitatory terms).
GROSSBERG (1973) FAQ 2

Q: When can you solve directly for the equilibrium state of a differential equation by setting derivative to zero and solving resulting algebraic equation?

\[ \frac{d(\text{blah})}{dt} = 0 \]

A: First ask: Am I sure that any equilibrium exists? If so, is there only one? Moreover, is the system governed by the equation uniformly asymptotically stable, with a single attractor? This is unlikely, to say the least, for large, nonlinear, recurrent networks.

ROOTS

Many of the developments of the vision theory developed by Grossberg and colleagues from the 1980's through the present were foreshadowed in Grossberg (1983).

They can be viewed as harnessing the intuitions of theorems on recurrent (feedback) networks first explored in Grossberg (1973), but in networks with increasingly elaborate distance-dependent interactions (kernels).

STRUCTURAL AND FUNCTIONAL SCALES

The measured magnitudes of perceptual phenomena (e.g. the strength of the café wall illusion) may not be as directly “readable” from the sizes of anatomical structures, . . . as would be the case if the visual system were more “linear.”

anatomy physiology
geometry dynamics
structural scales functional scales

MODELERS AND PHYSIOLOGISTS:
“DIVIDED BY A COMMON LANGUAGE”

RECEPTIVE FIELD -- functional
Where on the retina will stimulation yield a response at this (cortical) cell?

KERNEL -- structural
Which network cells send inputs directly to this cell?

Kernels are trivial for a modeler to specify, but are generally not observable for a physiologist!
STRUCTURAL AND FUNCTIONAL SCALES AGAIN

In a network model, a kernel defines a structural scale:
e.g., a Gaussian of unit weight, \( \sigma = 2 \), truncated at
5 nodes from center.

The functional scale of this network’s response to inputs of
varying sizes might need to be determined by simulation,
if the network involves nonlinear feedback
(no analytic solution.)

i.e., how many nodes have their
activity affected (either excitation
or inhibition) as a function of bar thickness?

CONTEXT DEPENDENCE

The measured size of many cells’ receptive fields depend
on the nature of (current and prior) stimulation.

For feedforward anatomies, structural and functional scales
may be (more or less!) directly related.

Once feedback or recurrent (including lateral) connections occur,
functional scales become much more “interesting.”

FUNCTIONAL SCALES AND PEAK SHIFT

Consider Blakemore et al.’s (1970) angle expansion illusion, as
described by Levine and Grossberg (1976):

“If two lines forming an acute angle are presented to a subject and he is asked to place
a third line parallel to the other two, he will err in the direction of perceiving the angle
as larger than it really is:”

\[ \text{Line } B_p \text{ is parallel to line } B'; \text{ line } C \text{ is perceived as parallel to line } B. \]

Adapted from Fig. 1 of Levine and Grossberg (1976).

(See Simulation Assignment 1.)

Blakemore et al.’s hypothesis: Shift in perceived angle is due to
lateral inhibition among cortical neurons that are tuned to
different orientations of contrast.

LATERAL INHIBITION AND PEAK SHIFTS

Levine & Grossberg (1976): a node’s preferred angle-of-contrast is coded by
its position within network == “on-center, off-surround” in orientation space.

Response of network to a
single input at 0°.

Response of network to a
single input at 10°.

The peak responses shift
“outward” from corresponding
single-input locations
when 0° and 10° inputs
occur simultaneously.
VARIETIES OF LATERAL INHIBITION

Levine and Grossberg (1976) goals:
Classify outcomes of different kinds of “lateral inhibition:”

- additive
  \[ \frac{dx_i}{dt} = -Ax_i + \sum_{m=1}^{n} K_mC_{mi} - \sum_{m=1}^{n} K_mD_{mi} \]  
  Eq. (10), p. 486

- shunting, feedforward, no hyperpolarization

- shunting, feedforward, with hyperpolarization

- shunting, feedback

ANATOMIES OF COMETITIVE NETWORKS

Feedforward:

- With-layer (a.k.a. “horizontal” or “lateral”) feedback (recurrent)

Between-layer feedback (recurrent)

INFERENCES FROM DATA

Q: Does the empirical observation of a peak shift in vivo imply that subtractive inhibition must be occurring?

Consider L & G’s Eq. 13:

\[ x_i = \frac{\sum_{m=1}^{n} K_mC_{mi} - ED_{mi}}{A + \sum_{m=1}^{n} K_mC_{mi} + D_{mi}} \]

Of what differential equation is this the equilibrium solution?

If \( E = 0 \):
No hyperpolarization, therefore no “net” inhibition
-- i.e., “direct, subtractive” inhibition -- occurs via DOG in numerator.

Notational remark: In L & G, 1976, p. 487

\[ I_i = K_mC_{mi} \]

implies that a Gaussian weighting of inputs, (as well as of feedback signals) exists.

Also, PUN ALERT: “net inhibition”
**INFERENCES CONTINUED**

*L & G* claim: Peak shift can *still* occur . . . with only *divisive* effect of $I_2$ through $D_{mi}$.

**FEEDBACK AND TIME**

In a simulation of a recurrent network, *G & L* demonstrate the importance of *temporal factors* in the “balance” of excitation and inhibition.

“Fig 10 *Inward* peak shift [!], indicated by heavy dots in figure, becomes *outward* as recurrent inhibition “builds up” over time!”

Think about “*structural vs. functional scales*.”

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**ON THE ROAD**

**BAD NEWS:** We’re lost!
**GOOD NEWS:** We’re making good time!

- **Week 1:** Overture
- **Week 2:** Simple shunting networks
- **Week 3:** Grossberg/Marr debate
  - Structural and functional scales
  - More shunting network background
  - *X* You are here.
  - Linear systems in vision
  - Filters and detectors
- **Week 4:** Basic physiology
  - Approaches to brightness perception

When do we find out what the *units of vision* are?

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**GRAINS OF ANALYSIS**

What are the appropriate *grains* of measurement and analysis for studying intelligent processes? (See Schwartz, Bonus Reading, Week 4.)

1) *Synapse* (biochemistry, biophysics)
2) *Neuron* (and neural networks)
3) *Columns* and *maps*
4) *Behavior*

What inferences are available across grains? E.g., how can data at one grain constrain modeling at another?
SOBERING THOUGHTS


In fact, as many kinds of mathematics seem to be applied to perception as there are problems in perception. I believe this multiplicity of theories without a reduction to a common core is inherent in the nature of psychology . . ., and we should not expect the situation to change. The moral, alas, is that we need many different models to deal with the many different aspects of perception. [emphasis added]

Q: What is going on when “many different models” are applied to the same “aspect[s] of perception”? 

FEATURE DETECTION

Common theme in vision:

Scenic input is too rich in (bits of) information; the visual system has no choice but to perform some kind of image decomposition, to “extract” the important information.

Barlow (1953) introduced the idea of “trigger features” for cell responses.

Hubel & Wiesel (1959, etc.) extended the range of feature detector theories of visual processing.

Observation: Certain cortical cells appear to respond best (in some cases almost exclusively) to simple but specific image features (e.g. edges, line ends, corners).

THE “GRANDMOTHER CELL” MODEL

Hubel and Wiesel developed a hierarchical model of organization of visual cortex -- still an influential view -- in which successive layers of cells respond to specific combinations of features coded by a previous layer.

Cf: Selfridge's (1959) Pandemonium model of cognitive processes:

Thanks, Paolo!

Many of the following panels are based on notes originally developed by Paolo Gaudiano for an earlier edition of CN 530.
NEOCOGNITRON
Compare Fukushima's Neocognitron model
(shift-tolerant feature extraction and classification)

FEATURE DETECTOR HIERARCHY?
Some physiological evidence argues against the *hierarchical*
scheme. E.g., many complex cells become activated before
simple cells upon input presentation.

Seems to invalidate:

- complex
- simple
- LGN
  (center/surround)

Much of cortical organization is *parallel*.

Q: parallel *as opposed to* hierarchical, or
  parallel *in addition to* hierarchical?

* in the sense of “branching,” as well as “massively.”

MODELING AS POETRY

Is the idea of visual cortical cells as *feature detectors* the right metaphor. (Yes, I said metaphor.)

What else could they be?

*The word “feature” is used in many, and contradictory ways in the field of vision.

DETECTORS VS. FILTERS

A detector (“active”) responds only to the presence of “specific tokens” or “signature patterns” in an image.

A filter (“passive”) responds to any input token -- up to the limits of the filter's resolution or range -- but gives strongest responses to a small (?) range of token values.

Consider: You would want an “unbroken line detector” to respond to this, but not to this.

This result is hard to achieve (over variations in contrast, etc.) with a conventional (“convolution”) filter.
Is this just a question of semantics?
I.e., is the distinction a matter of definition of “specific tokens” vs. “small range of token values.”
Is a detector just a “filter with a threshold”?

Sociology of science: Whether one speaks of visual cortical cells as detectors or as filters is correlated with the field of study in which a researcher earns academic degrees!

FILTERS AND TRANSFER FUNCTIONS
Consider a filter as a “black box” that transforms each input into some output:

If the value of the output exhibits some systematic relationship with some measurable aspect of the input, we can speak of the transfer function of the filter.

CONTRAST DETECTION AND SPATIAL FREQUENCY
Cornsweet (1970) describes the visual system as consisting of a single “channel” -- which acts as a filter whose response depends (in part) on the spatial frequency content of the image.

Cornsweet writes of a modulation transfer function (MTF) because the measure of the input that is plotted against output is the modulation of the luminance of the image (“intensity”).

Historical note re: “sinusoidal grating”
A grating is a tool used in optics for the study of diffraction and interference of light; it is a surface (film) with slits etched on it.
A simple two-slit grating can be used to generate sinusoidal modulations in luminance.
Today, “sine wave gratings” are generally computer generated images.
SPATIAL FREQUENCY

*Periodic stimuli* can be classified by the *spatial frequency* of the modulation of their luminance.

**Spatial frequency:** the number of times (cycles) that luminance changes from some minimum to some maximum value over a fixed distance, given in *degrees* of visual angle.

Image regions containing only *low spatial frequencies* generally look relatively *homogeneous*; those containing only *high spatial frequencies* generally appear to have a lot of “detail” or “texture.”

Q. What is the relationship of spatial frequency to Grossberg's usage of the word “scale”?

HUMAN POINT SPREAD FUNCTION

Assume that the eye is a perfect lens, ignoring: spherical aberration, chromatic aberration, diffraction, scatter, . . .

The imperfections can be usefully “accounted for,” paving the road for *spatial frequency methods*, and attendant formalisms (e.g. linear systems theory; Fourier analysis and synthesis, wavelets, etc.)

NOTE: We can perceptually “resolve” displacements of thin lines at distances smaller than the diameter of a single photoreceptor!
SINUSOIDAL GRATINGS

The visual system can be probed by measuring its response to stimuli that contain only one spatial frequency, or a carefully controlled combination of stimuli at specific spatial frequencies.

Strategy: For measuring an unknown system, make your probe as simple as possible, and know all of the probe's characteristics with respect to dimensions of measurement.

Tradeoff: "Ecological validity" -- where did you last see (only) stripes with sinusoidal luminance modulation?

HUMAN MODULATION TRANSFER FUNCTION (MTF)

Sinusoidal stimuli are used to measure the threshold response of the human visual system as a function of spatial frequency.

To be found: minimum contrast* necessary to detect the presence of a sinusoidal modulation of luminance of a certain spatial frequency.

*lumiance

image position

image position

P

T

*Pop quiz: Write the formula for Michaelson contrast and define all the terms.

CAMPBELL-ROBSON CONTRAST- SENSITIVITY DEMO AT
http://www.bpe.es.osaka-u.ac.jp/ohzawa-lab/izumi/CSF/A_JG_RobsonCSFchart.html

Fig. 12.13 The solid curve is a describing function of the human visual system, obtained by measuring the threshold modulation at each spatial frequency. (100% modulation means that the troughs of the sine wave are completely dark.) The dashed curve is what would be expected for a lens under the same conditions of testing.

[The solid curve is from Van Nes and Bouman (1965); l = 525 nm, average intensity = 90 trolands.] (Adapted from "where else"?!)
MTF & CSF

Modulation transfer function (MTF)

Contrast sensitivity function (CSF)

The more modulation you need to detect a grating at a given frequency, the less sensitive you are to contrast at that frequency.

SIGNAL DETECTION THEORY

Instead: Consider threshold sensitivity as a stochastic process, and use concepts from signal detection theory.

The placement of the criterion level for output of positive response depends on “payoffs” for false positives vs. misses in signal-present cases.

SIGNAL DETECTION METHODS

Common assumptions:

1) Normal distribution of sensor activity
2) Same variance of sensor activity with or without signal present
3) Known receiver characteristics (e.g., transfer function)

For multi-channel detectors, add:

4) Assumptions about superposition or probability summation for responses of separate channels into a single “yes or no” output (See Graham, supplementary, Week 5)

Just as with kernels and receptive fields, “thresholds” are

- trivial to set in a network simulation, and
- difficult to measure in real life.
Query: If the visual system is so much more sensitive in the middle spatial frequencies than at the extremes, why is it that, along the bottom of the figure, where you can notice the contrast modulation across virtually the entire frequency range, the resulting modulation of brightness is essentially homogeneous throughout that frequency range?!

If you can resolve up to here in the middle, but only up to here on the sides, how come the bottom modulation of brightness looks so uniform (in amplitude)\

In other words: What are the units of brightness perception?

LEARN THIS TERMINOLOGY*!!!

Photometric measures of light intensity reaching some point (employed in neurophysiology and psychophysics) are weighted by human sensitivities (optics of cornea, lens, pigment absorption spectra, etc.) while radiometric measures (physics) do not. (Energy that does not stimulate human photoreceptors does not count for photometric measures.)

Illuminance is the amount of visually effective light falling on a surface. (That light may or may not ever reach a photoreceptor!)

Luminance is the amount of visually effective (photometric) light emitted by some source (or, in practice, reflected off some surface).

Brightness is (used by many to mean) a subjective measure of sensation associated with the magnitude of luminance of a stimulus patch viewed in isolation on a surround of zero luminance. (DIM to BRIGHT.) Related (?) usage: “Subjective estimate” of luminance (!) of an area of a scene.

Lightness is (used by many to mean) a subjective measure of the relative “gray value” of a luminance patch, viewed on a surround of nonzero luminance. (DARK to LIGHT, or BLACK to GRAY to WHITE). Related (?) usage: “Subjective estimate” of reflectance of a surface area. (Adapted from Uttal, 1976)

*Points on mid-term examination hang in the balance.

There are subtleties of usage of terms in the previous slide that I do not expect you to “get,” if for no other reason than that experts in the field use the terms in inconsistent ways. This is certainly true of brightness and lightness, as applied to perceptual phenomena.

What I do expect you to demonstrate an understanding of, through the way in which you choose words, is a sensitivity to language that is appropriate for describing a stimulus, and language that is appropriate for describing a percept.

There are anatomical and physiological techniques
2) Retinal structure and function
3) ON and OFF channels
4) Anatomy and physiology of the early visual pathways

Basic terminology
Diagrams, sketches
Historical milestones and trends
Controversies and usage of terms

Parts of what follows owe to a key historical overview:
**NEURAL NETWORKS VS. NEURON DOCTRINE**

19th century debate on brain:

*Neuron doctrine:*
**Cells** are the independent functional units of the brain.

*Neural networks:*
**Assemblies** of cells are the minimal functional units.

Cajal was a proponent of the **neuron doctrine**, basing his arguments in part on studies using the **Golgi method** of cell staining.

Golgi favored the reticular theory (*i.e.*, “net” or “net-like” theory).

**EYE OF THE BEHOLDER**

THEME 1: Knowledge of the visual system has often be determined by (advances in or limitations of) **observational techniques**.

e.g., **Golgi stain** marks almost an entire neuron, but only “one out of N” on average (depending on variations of method).

This technique isolates **individual cells** for observation.

http://biodidac.bio.uottawa.ca/thumbnails/filedet.htm?File_name=36-54&File_type=GIF

THEME 2: Data is interpreted within theories. Note that Golgi and Cajal “saw” different things when they looked at the same slides under a microscope.

**ANATOMY AND PHYSIOLOGY**

<table>
<thead>
<tr>
<th>anatomy:</th>
<th>physiology:</th>
</tr>
</thead>
<tbody>
<tr>
<td>geometry</td>
<td>dynamics</td>
</tr>
<tr>
<td>structure</td>
<td>function</td>
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Some measurement techniques can be applied, with some modification, to either anatomy or physiology:

**staining:**
- **histological** (anatomy) or **metabolic** (physiology)

**imaging:**
- **magnetic resonance imaging (MRI)** (anatomy)
- **functional magnetic resonance imaging (fMRI)** (physiology)

**ANATOMICAL TECHNIQUES**

*Multiple scales* or grains of observation:

**Gross anatomy**, using dissection, MRI, etc.

**Local circuit***, using staining, etc.

**Cytoarchitecture** (cell parts), using scanning microscopy, etc.

*E.g., **section** and **stain** to reveal cell bodies, connections, fiber passages.*
MORE ANATOMICAL TECHNIQUES

Cytochrome oxidase (mitochondrial enzyme) staining reveals structures of similar cells (e.g. “puffs” or “blobs”) in contiguous areas of cortex.

*Note:* The “grain” of the structures revealed is “between” those of local circuits and gross anatomy (inter-cortical-area connectivity).

Measurement that may be used primarily for answering “anatomical” questions may contain elements of physiological technique, as when a stain is taken up in vivo in proportion to cell activity.

E.g. How are the cells that are primarily sensitive to *monocular* (left eye, right eye) or *binocular* visual inputs physically arrayed in cortex?

PHYSIOLOGICAL TECHNIQUES

2-deoxyglucose method: taken up by cells when metabolically active, as when stimulated by a “preferred” visual input. This radioactive marker “fools” the cell; it is taken up like glucose, but cannot be excreted. *Note:* Time scale of minutes needed.

Radioactively tagged amino acids can be transynaptically transported at known rates. Autoradiography then reveals connectivity across gross structures (e.g. retinal ganglion cell to LGN cell).

Antidromic firing: potentials can travel in either direction along an axon (!), so axons synapsing at a known location can be “backfired” to determine the (distal) location of the cell body belonging to that axon.

PHYSIOLOGY: HOW ALIVE?

If the evolutionary advantage (function) of neural activity relates to control of behavior, then ask:

Is activity measured *in vitro*, or in an intact animal?

Is the animal paralyzed? ... anesthetized?... alert? ... simultaneously performing some psychophysical task?

ELECTRODE RECORDING

Single electrode recording: intracellular (can measure local, graded potentials) or exocellular (“AC” conduction can pick up action potentials over some distance.)

Multiple electrode recording

*How accurately can location of electrode(s) be determined? When* can location be determined?

*NOTE:* “Awake, behaving” preparation sacrifices knowledge of precise electrode location (and, often, cell type) for better assessment of function.

(Location can to a certain extent be “recovered” by subsequent histology.)
**OPTICAL RECORDING**

The reflectance and transmissivity of neural tissue varies -- slightly, but measurably -- as a function of mean activation in a region.

Activity in (several) superficial layers can thus be “imaged,” with or without the use of *voltage sensitive dyes*.

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**MORE TECHNIQUES**

*Neurochemistry*: Chemical *analogs* or *antagonists* of neurotransmitters can *force* or *block* firing of whole *classes* of cells at once.

*Lesions*: Experimenter-induced lesions can often be precisely localized in physiological studies.

*Human clinical*: psychophysical studies of patients with accidental or medically-mandated operative lesions, e.g. “split-brain” patients.

*Monoclonal antibodies*: These can be used to lesion highly selective structures (e.g. only cells in a lamina sensitive to specific molecules.)

*Functional magnetic resonance imaging (FMRI)*: Measure activity-dependent blood flow rate (spatial, temporal resolution...)

*Always ask yourself*: What is the *spatial and temporal resolution* of the measurement? How “*ecologically valid*” is it?

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**METHODS OF TAXONOMY OF NEURONS**

*Cell morphology*:
  - Cell body size
  - Size and shape of dendritic arborization
  - Axon length

*Conduction velocity of axons*

*Degree of depolarization or hyperpolarization*

*Chemical sensitivities to neurotransmitter analogs, antagonists,…*

*Staining* (Some cells just *look* different from others, even if functional reason is unknown.)

*Receptive field characteristics* (More on this topic later!)

*Columnar, laminar, or map structure*

*Question*: *When* and *why* is the process of making a *taxonomy* carried out in a science?

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**APPROACHING PHYSIOLOGICAL READINGS**

*Note “horizontal” and “vertical” organization . . . interleaved (and, possibly, interacting) lattices.*

Try to get used to “reading” diagrams like this with *computational questions* in mind. E.g:

1) Are there different types of *bipolar cells*? If so, how many? Why?
2) Why have *two* layers of *horizontal connectivity* in retina?
A RETINA -- NOT A PHOTOMETER

Note that even a photoreceptor's potential can be affected by "remote" quantum catches!

The "surround" antagonism is central to retina's mission.

POINTS TO PONDER

Receptors are hyperpolarized by blockage of Na+ channels that are open in the dark.

Synapse of receptors to bipolars is not thresholded. (Rate of transmitter release is proportional to degree of depolarization.)

A single transmitter (glutamate)
- inhibits ON-center bipolars, and
- excites OFF-center bipolars

There are no action potentials in the distal (outer plexiform) synaptic layer, where receptors, horizontals, and bipolars communicate.

Consider this w/r/t "standard" assumptions in many network models (e.g. McCulloch-Pitts neuron) that threshold cell potential to compute "firing rate." This issue gets worse later.

Great retina site: http://retina.umh.es/Webvision/index.html

CENTER-SURROUND GANGLION CELLS

ON-center      OFF-center

Central spot
Peripheral spot
Central illumination
Surround illumination
Diffuse illumination

Note: OFF cells tend to have higher tonic levels of activity; not indicated here.

CENTER/SURROUND ORGANIZATION

ON and OFF populations with center/surround organization were first noticed in mammalian ganglion cells.

Origin of ON and OFF was traced to bipolars.

ON and OFF "pathways" extend through LGN. What about V1?

Note: The words ON and OFF have both spatial and temporal significance . . . which took years to sort out owing to limitations of multibeam ophthalmoscope, which could not produce a rapid onset of a low luminance spot!
**ORIGINS OF CENTER/SURROUND OPPONENCY**

Learn to “read” diagrams like this one:

A single transmitter, *glutamate*, has opposite effects (excitatory, inhibitory) on synapses of different kinds (ribbon, basal).

(Difference in synapse type is not indicated graphically in this figure.)

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**RETINAL CONTROVERSY**

The 3rd edition of KSJ includes this diagram.

**Note that the possibility of cross-talk from ON bipolars to OFF ganglion cells (and vice versa) is indicated by dashed connections.**

This is consistent with a theory developed by Gaudiano concerning rapid signaling of luminance increments and decrements.

**BONUS QUESTION:** Does the absence of this dashed connection in the 4th edition mean that retinal cross-talk has been ruled out?

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**DUMBING DOWN**

Quoting from an earlier edition *KSJ3*:

“Rods and cones contact different populations of bipolar cells at synapses with distinctive morphologies* . . .”

Cones contact:
- OFF-center bipolars at basal (flat) synapses
- ON-center bipolars at ribbon (invaginating) synapses.

* This level of detail is not in KSJ4.

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Paolo Gaudiano received the first CNS Ph.D. ever awarded and is a former CNS professor.

Gaudiano’s modeling analysis indicates that:
1) if anything like a shunting “front end” exists in retina, and
2) given certain psychophysical data concerning responses to luminance increments and decrements

then: there MUST be “cross-talk” between the ON and OFF channels at some point in the pathways. (The key point is that the very factorization of pattern and energy that is touted as such an advantage for spatial pattern processing, in turn, guarantees that the simple shunting network cannot be very sensitive to large and rapid temporal fluctuations of the same underlying spatial pattern.)

Gaudiano’s hypothesis was that this occurred from bipolars to ganglion cells, but it could, in principle, be later.

I have a number of Gaudiano’s papers, and others are readily available. He is also “reachable” via email, if any of you would like to pursue this matter further.
**ON and OFF**

Brief history of “ON” and “OFF”

Adrian, 1928

First to isolate a single neuron’s response. Devised concept of “receptive field” (literally, the area on the skin which, when stimulated, results in cell's firing)

Hartline, 1938 (Limulus)

Spikes generated only at (temporal) onset or offset of stimulation

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**ARTHROPOD COMPOUND EYE**

Hartline: Evidence for (spatial) lateral inhibition (Nobel Prize)

[Image of Limulus compound eye](http://www.mbl.edu/animals/Limulus/vision/compound.eye2.jpg)

**LIMULUS PSYCHOPHYSICS**

Aside: Hartline “spent his life studying vision in a blind animal!”

[Image of Limulus](http://www.mbl.edu/animals/Limulus/vision/compound.eye2.jpg)

But see: Barlow

**ON AND OFF IN SPACE AND TIME**

Kuffler (1953) was the first to report center-surround responses from ganglion cells of mammalian retina.

[Cartoon of responses:](http://www.mbl.edu/animals/Limulus/vision/compound.eye2.jpg)

Limitations of apparatus: A multibeam ophthalmoscope can only turn small spots of light on or off; cannot “flash” a dark spot!
ON and OFF retinal ganglion cells of cat have dendrites that branch in different laminae ("stratification").

ON AGAIN, OFF AGAIN

The ON and OFF systems each provide a lattice-like coverage of the entire visual field.

Q1: Why have both ON and OFF systems?

Q2: Are they "independent" channels? (i.e., is there "cross-talk" ... in retina? ... in cortex? What happens to ON and OFF signals in "later" cortical areas, where one never hears of "ON" or "OFF" signals?)

Q3: What is the relation of the designations ON and OFF to center-surround organization?

(Part of) A: Blockage of ON bipolars by a neurotransmitter analog leaves the center-surround organization of ganglion OFF cells "largely unaffected." (Slaughter & Miller, 1981)

INTERLEAVED LATTICES

A, B & C: \(\alpha\) cells; D, E, F: \(\beta\) cells (2X magnification)

\(\alpha\) and \(\beta\): morphological classes corresponding (very) roughly to magno/parvo

B & E: ON-cells; C & F: OFF-cells; A & D both (from S & W).

ONLY CONNECT

For next week:

Read physiology with computational questions in mind, and always with a firm grip on possible connections, or lack of connections, to adaptive behavior.