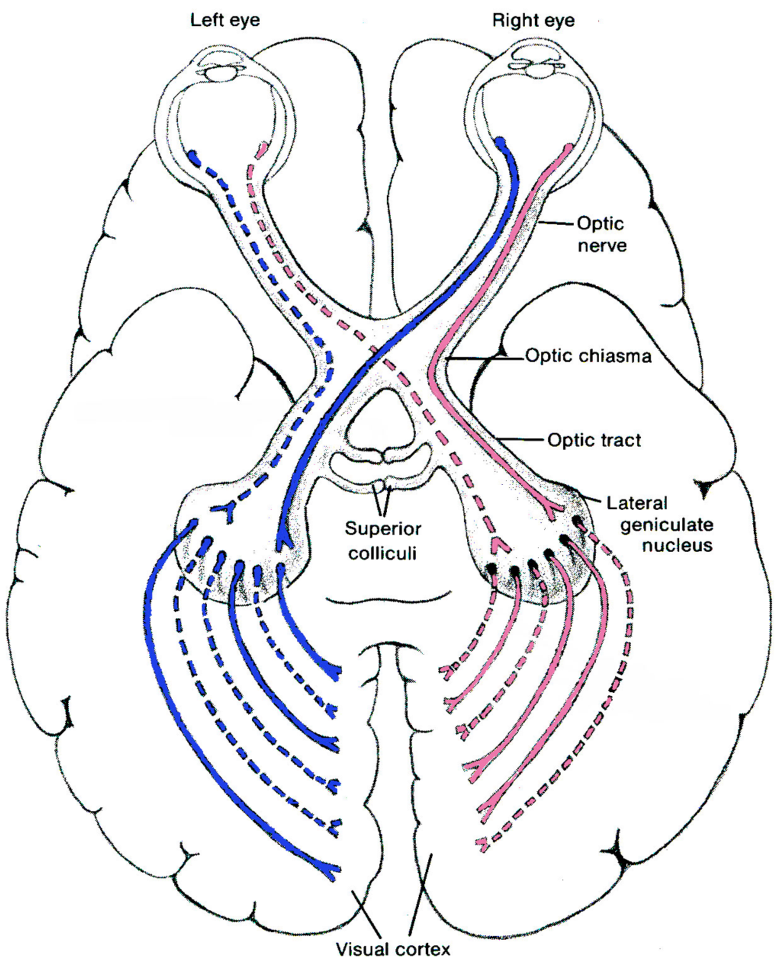
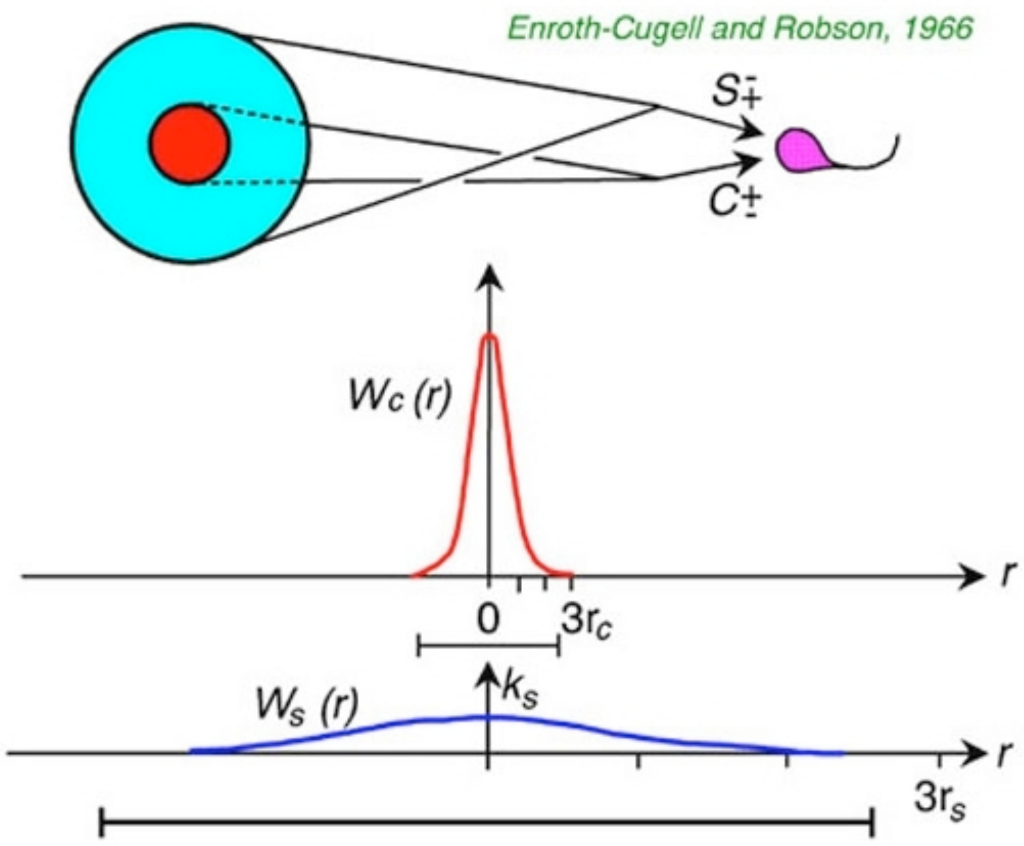
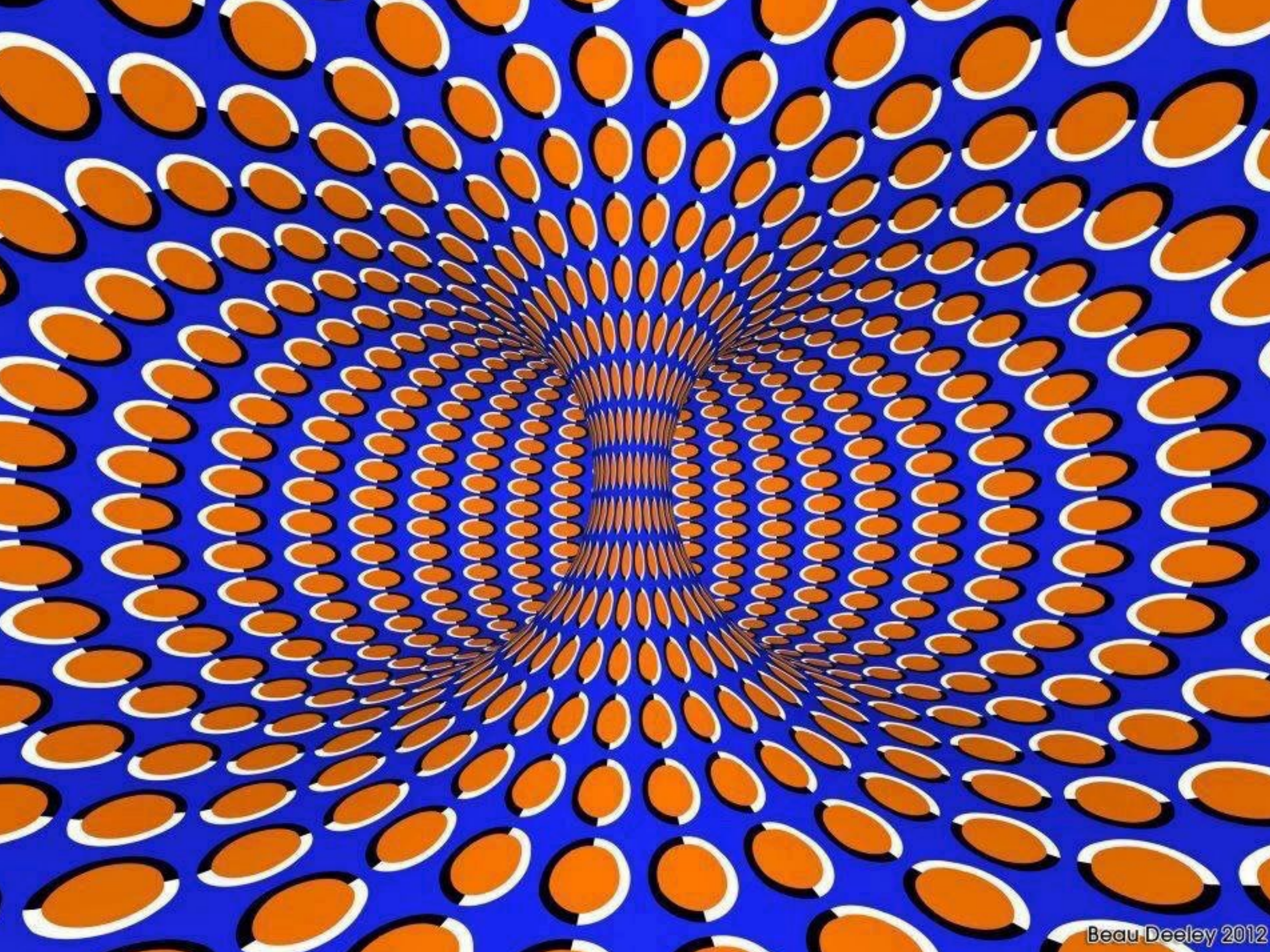
Cellular Biophysics & Modeling

Lecture 20

vision: classification of retinal ganglion cells,
parallel pathways, contrast sensitivity,
spatial frequency analysis

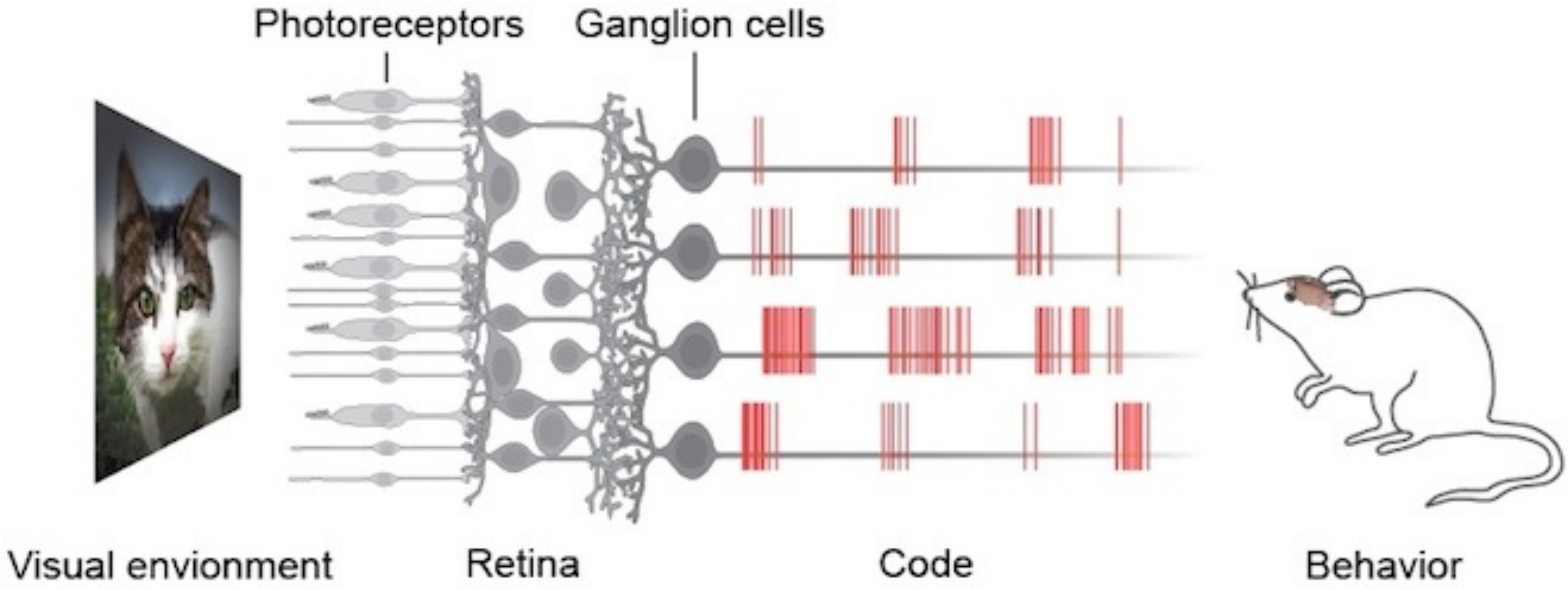


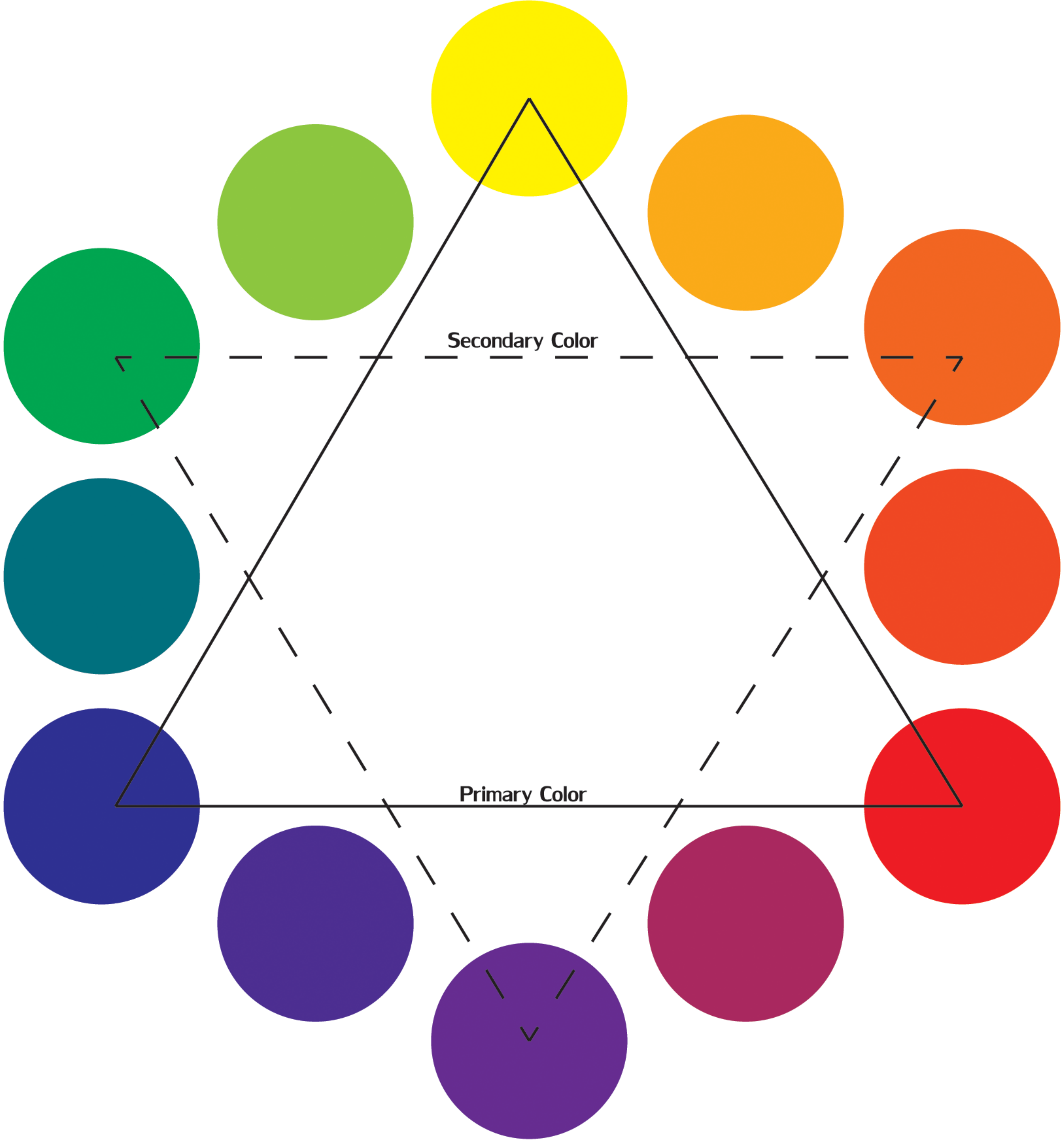

Enroth-Cugell and Robson, 1966

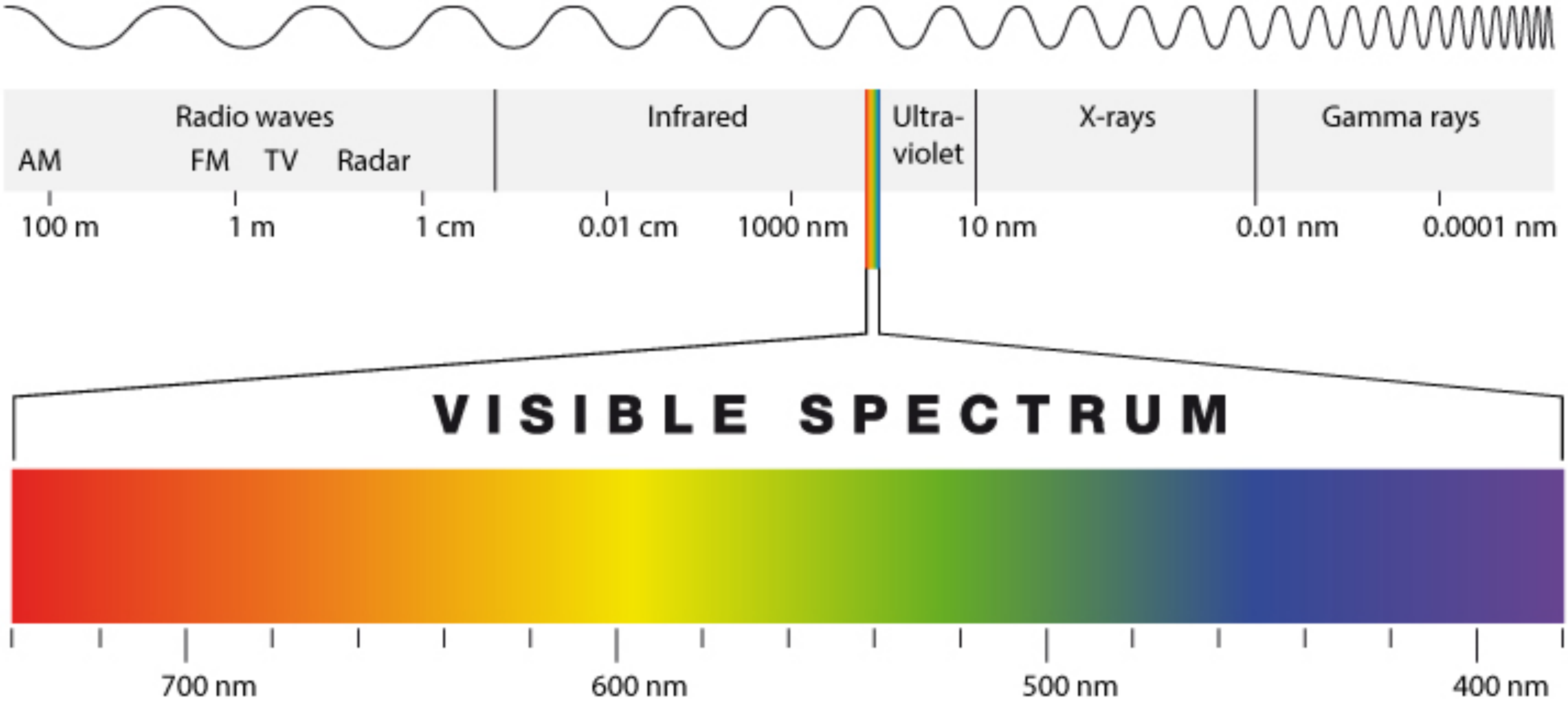

Beau Deeley 2012

optical illusions

reveal aspects of visual system function

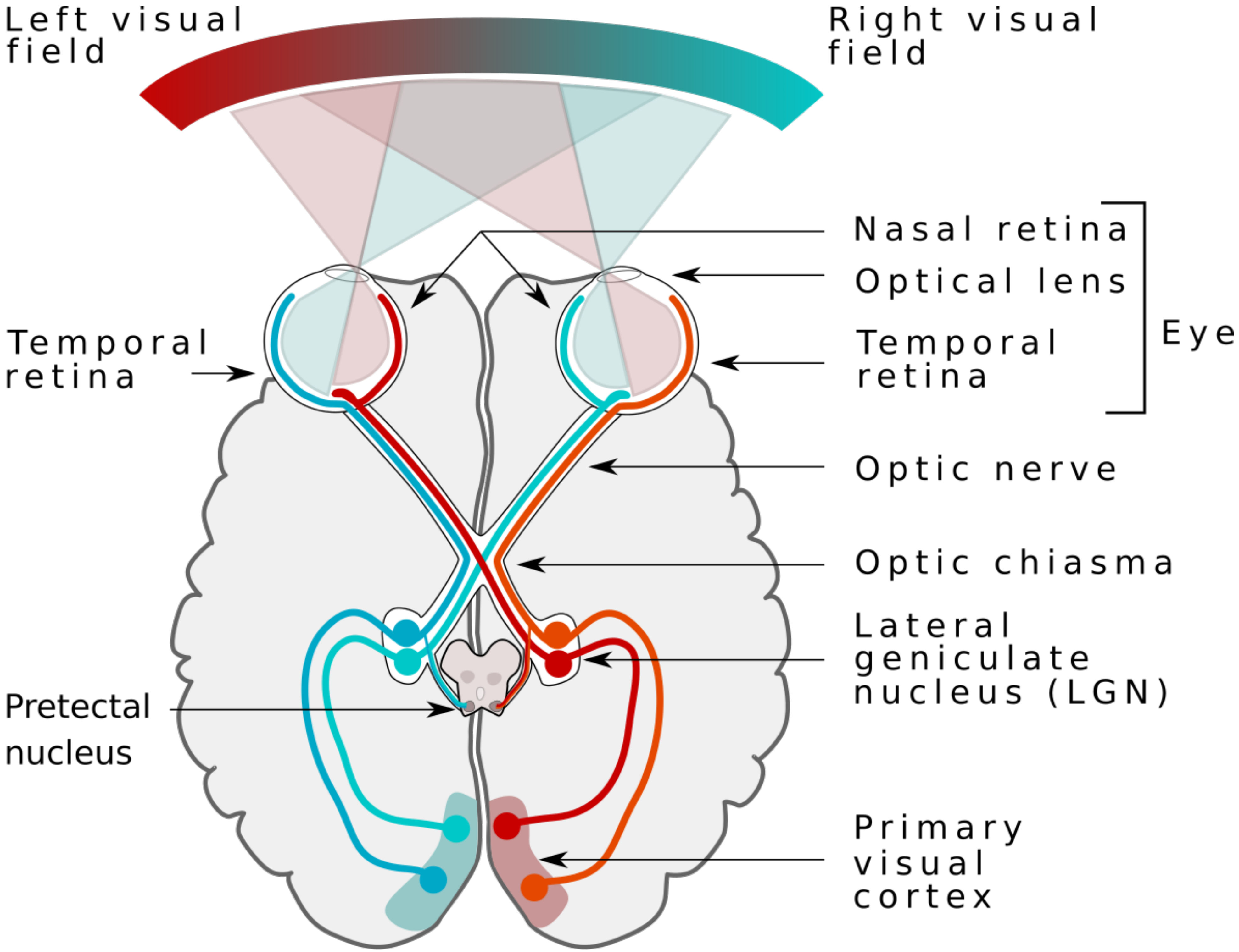



Secondary Color
Primary Color



so what does the color wheel
tell you about the visual system?

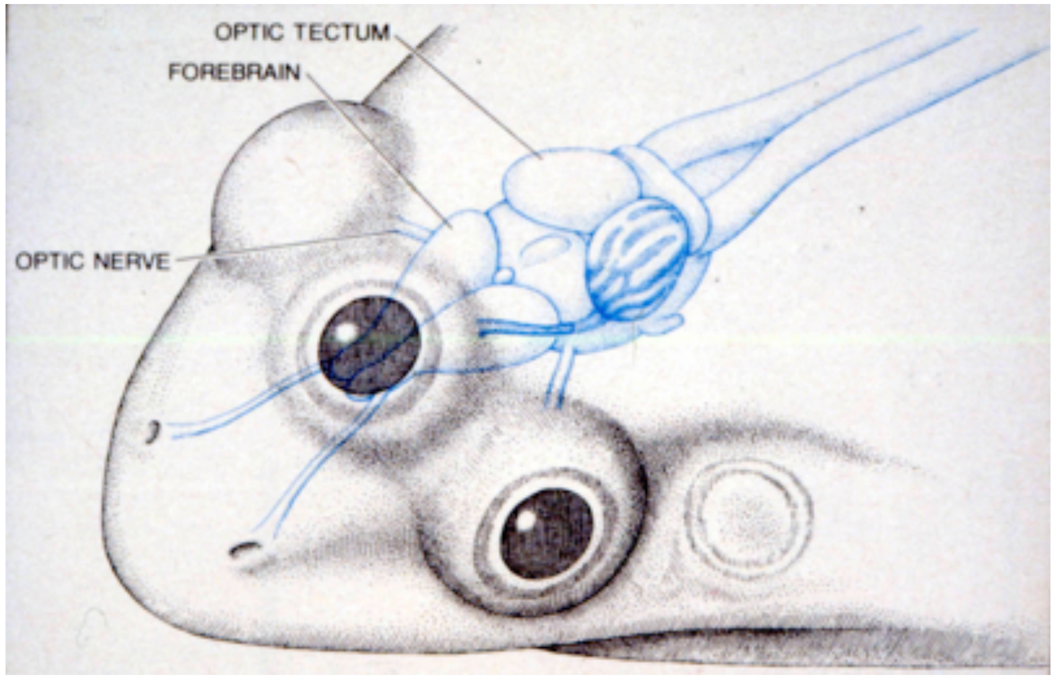
Do we know what the early visual system does?

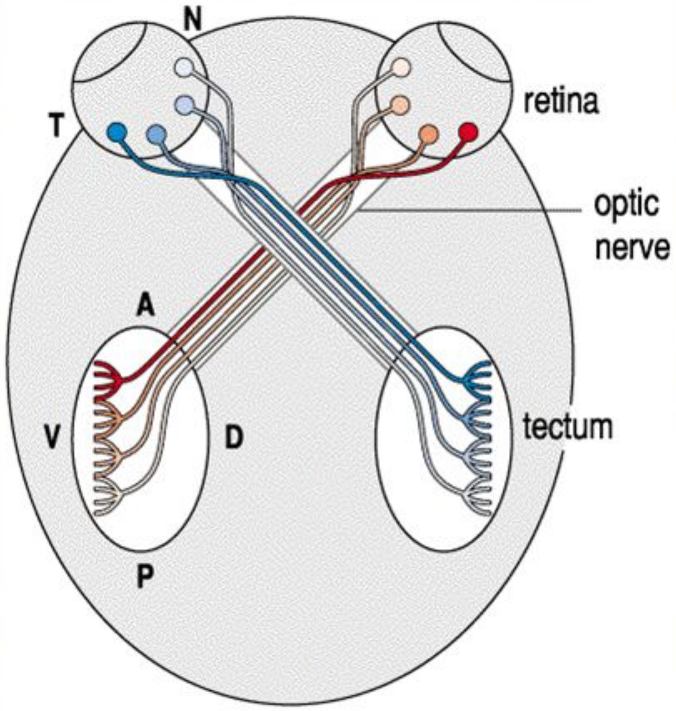


What the Frog's Eye Tells the Frog's Brain*

J. Y. LETTVIN†, H. R. MATURANA‡, W. S. McCULLOCH||, SENIOR MEMBER, IRE,
AND W. H. PITTS||

In 1959, Jerry Lettvin (trained as a psychiatrist, professor of "communications physiology" at MIT) and colleagues published an influential research article entitled "What the Frog's Eye Tells the Frog's Brain." They recorded from individual fibers (axons) in the optic nerve of frogs and discovered that many retinal ganglion cells (output layer of retina) were extremely selective for the kinds of things that frogs ought to care about.

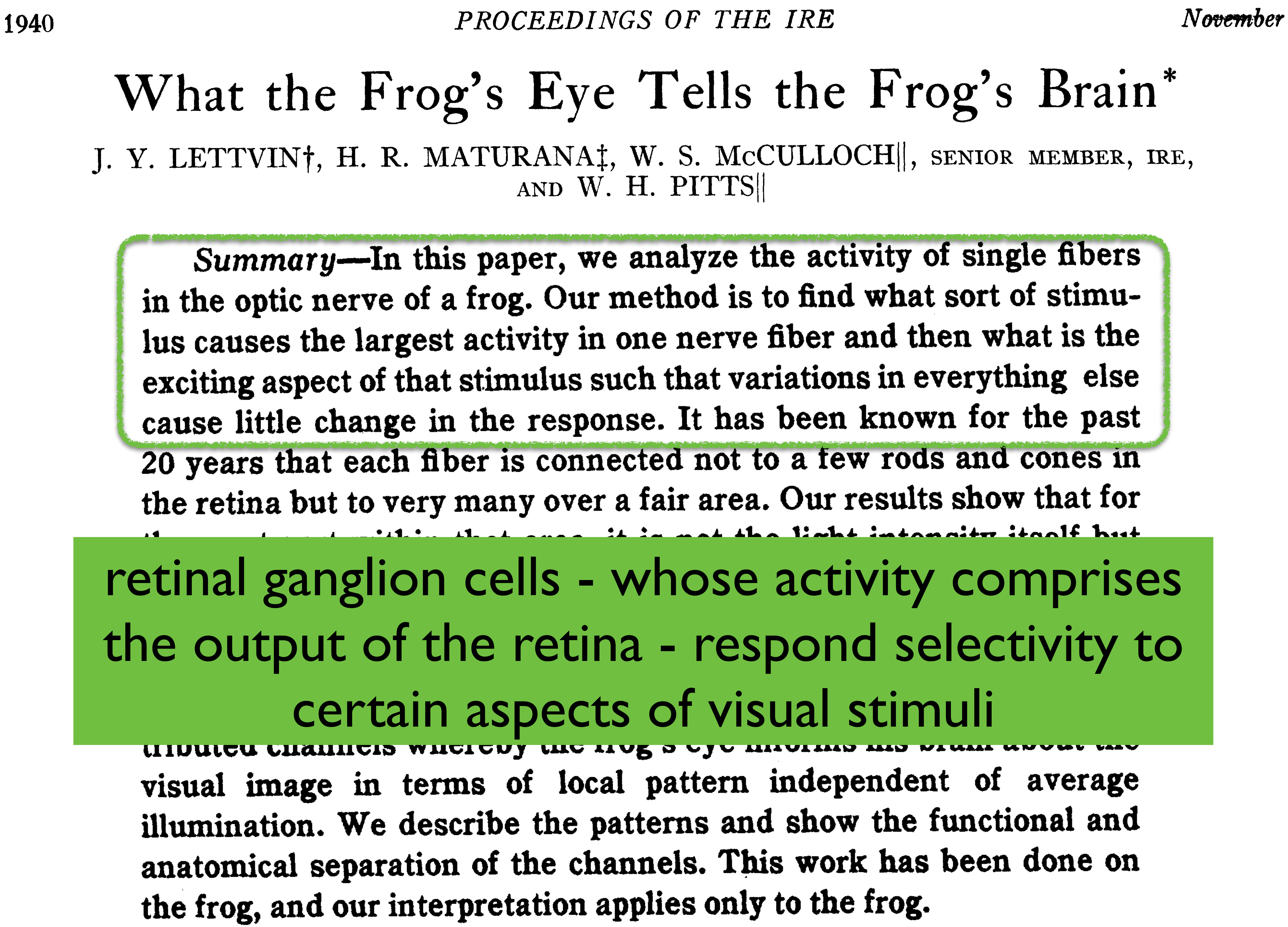




> "A frog hunts on land by vision... The frog does not seem to see or, at any rate, is not concerned with the detail of stationary parts of the world around him. He will starve to death surrounded by food if it is not moving. His choice of food is determined only by size and movement. He will leap to capture any object the size of an insect or worm, provided it moves like one."

neurobiology (the study of the nervous system)
ethology (the study of animal behavior in natural conditions).

Neuroethology is an evolutionary and comparative approach that focuses on **biologically relevant stimuli** and how the central nervous system translates these stimuli into **natural behavior**.



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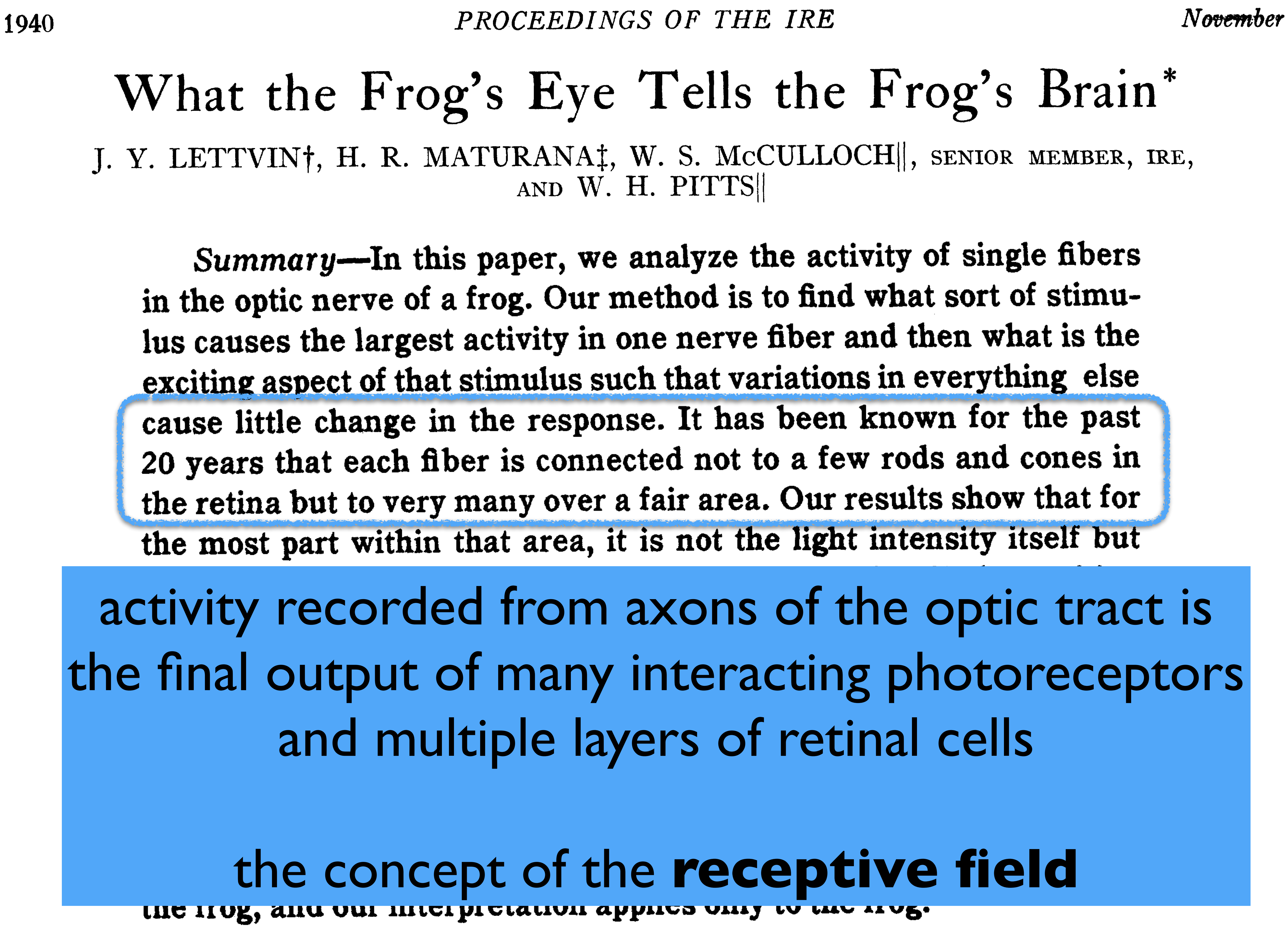
tributed channels whereby the frog's eye informs his brain about the visual image in terms of local pattern independent of average illumination. We describe the patterns and show the functional and anatomical separation of the channels. This work has been done on the frog, and our interpretation applies only to the frog.

retinal ganglion cells - whose activity comprises the output of the retina - respond selectivity to certain aspects of visual stimuli



1940 *PROCEEDINGS OF THE IRE* *November*

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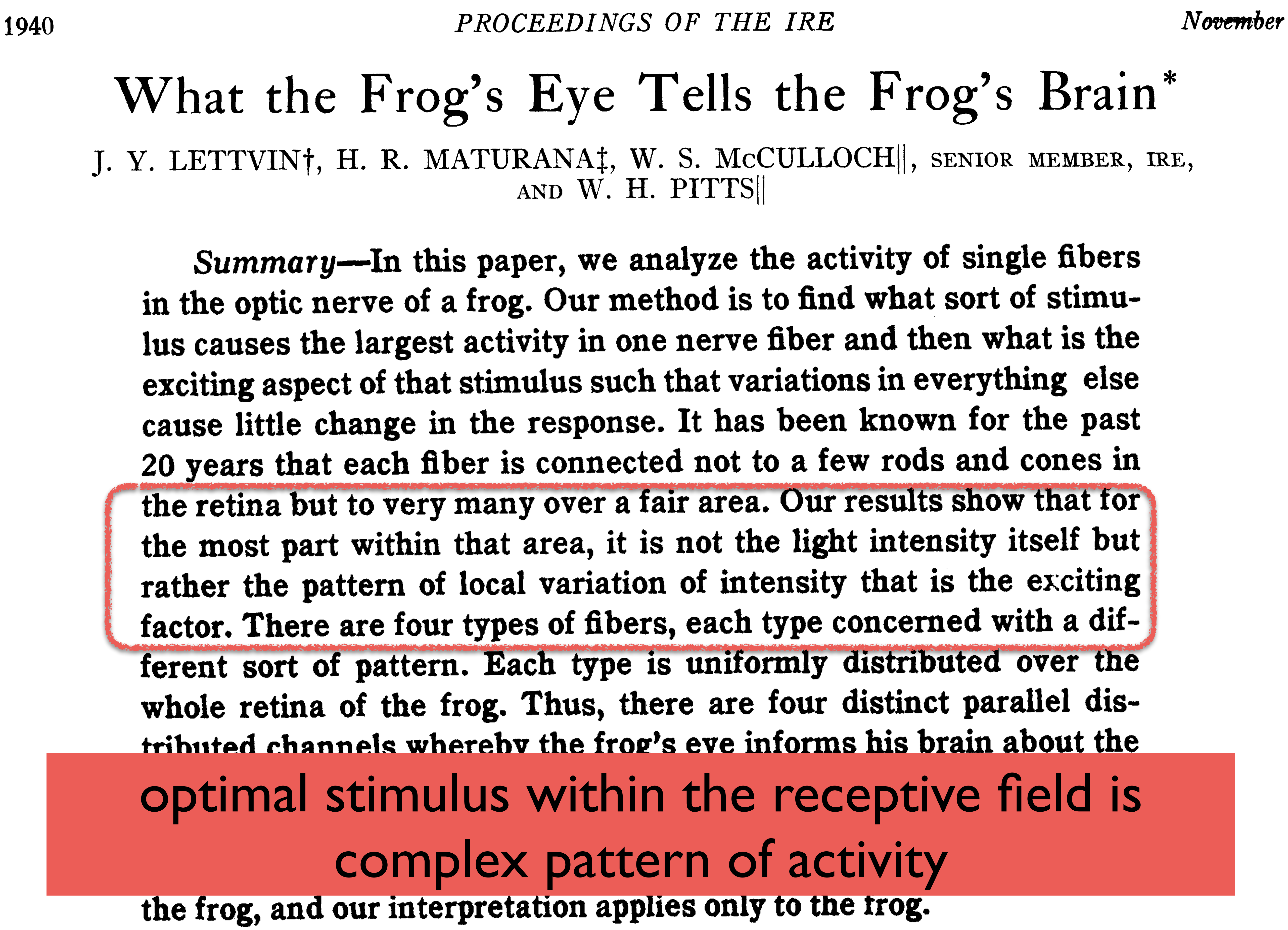
activity recorded from axons of the optic tract is the final output of many interacting photoreceptors and multiple layers of retinal cells

the concept of the **receptive field**



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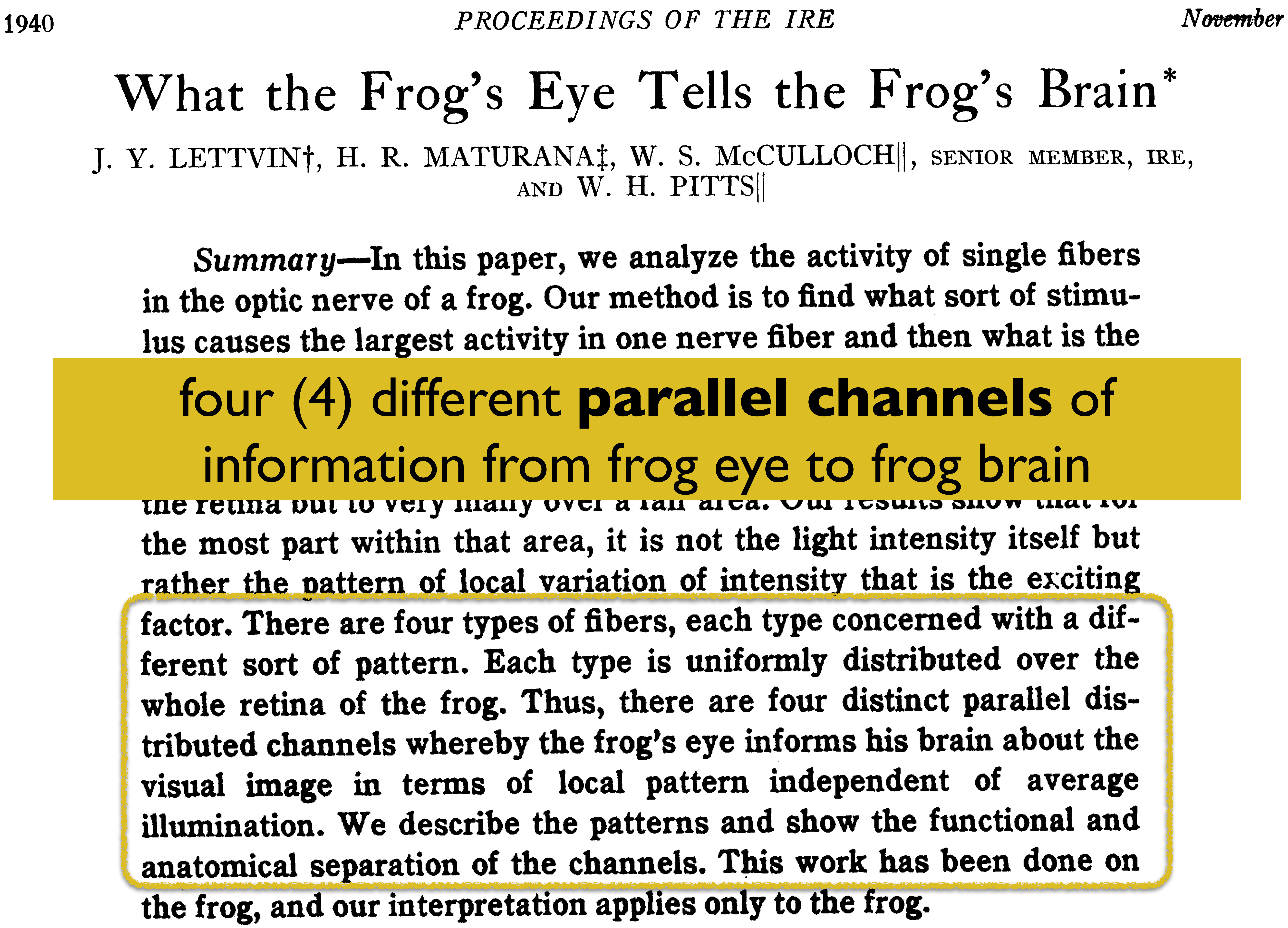
optimal stimulus within the receptive field is complex pattern of activity



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four (4) different **parallel channels** of information from frog eye to frog brain

Lettvin describes the 2nd of 4 types of fibers/channels

"**bug detectors**"

> "To our minds, this group contains the most remarkable elements in the optic nerve... We have been tempted to call them "**bug detectors**"... A delightful exhibit uses a large color photograph of the natural habitat of a frog from a frog's eye view [of course, with] flowers and grass. We can move this photograph... waving it around... and there is no response. If we perch with a magnet a fly-sized object on the... picture... and move only the object we get an excellent response. If the object is fixed to the picture... and the whole moved about, then there is none. **Could one better describe a system for detecting an accessible bug?**

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why did they feel the need to say this?

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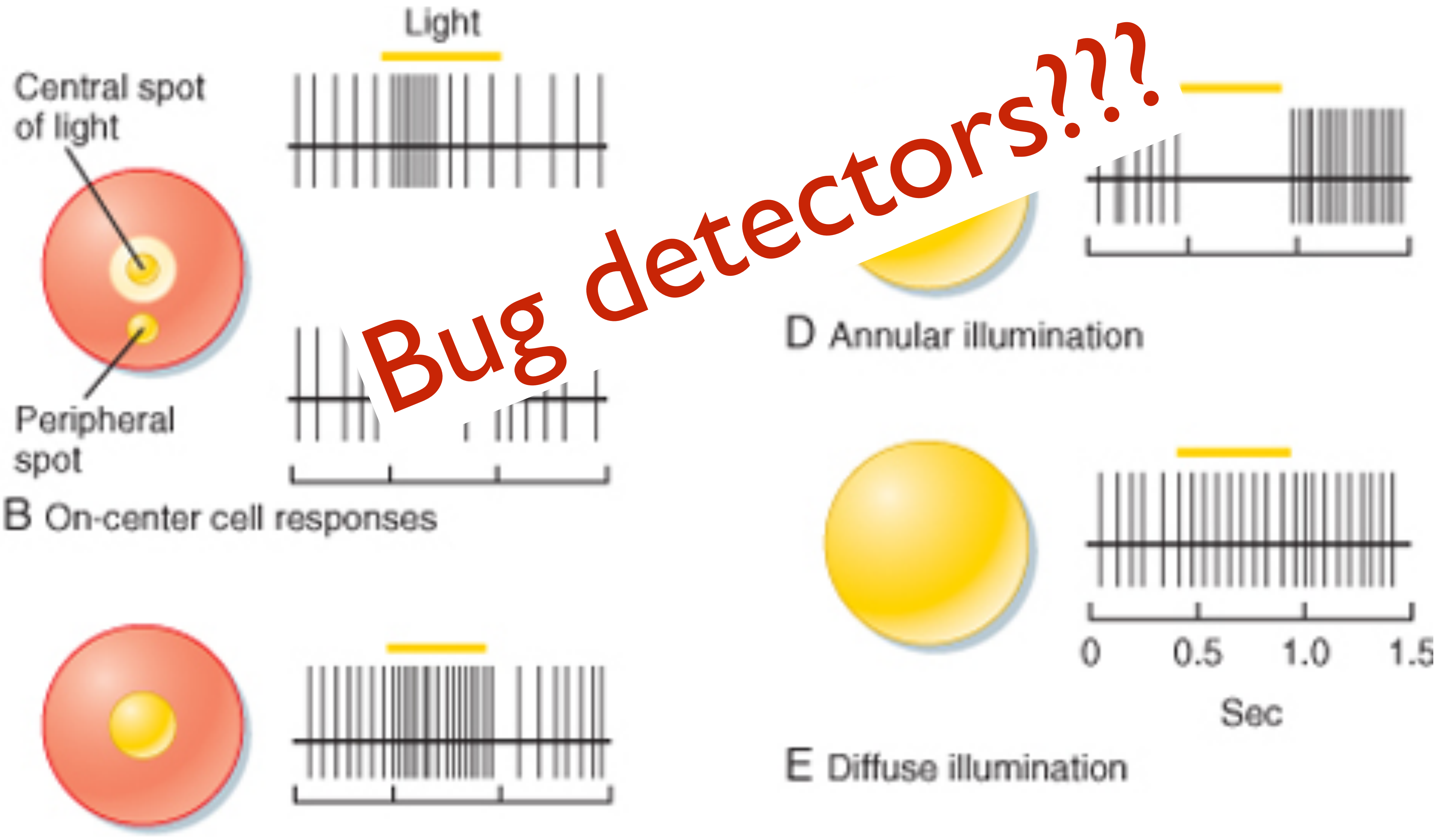
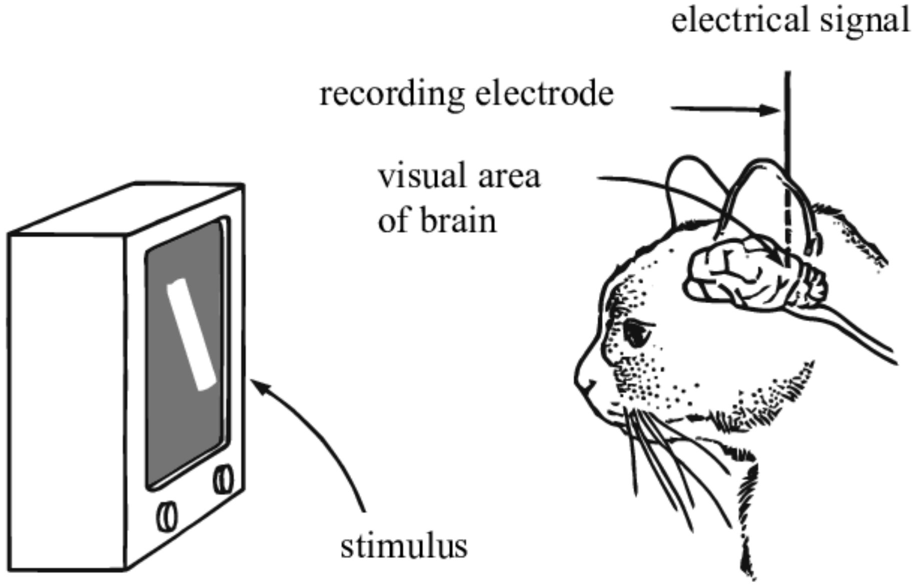
visual receptive field

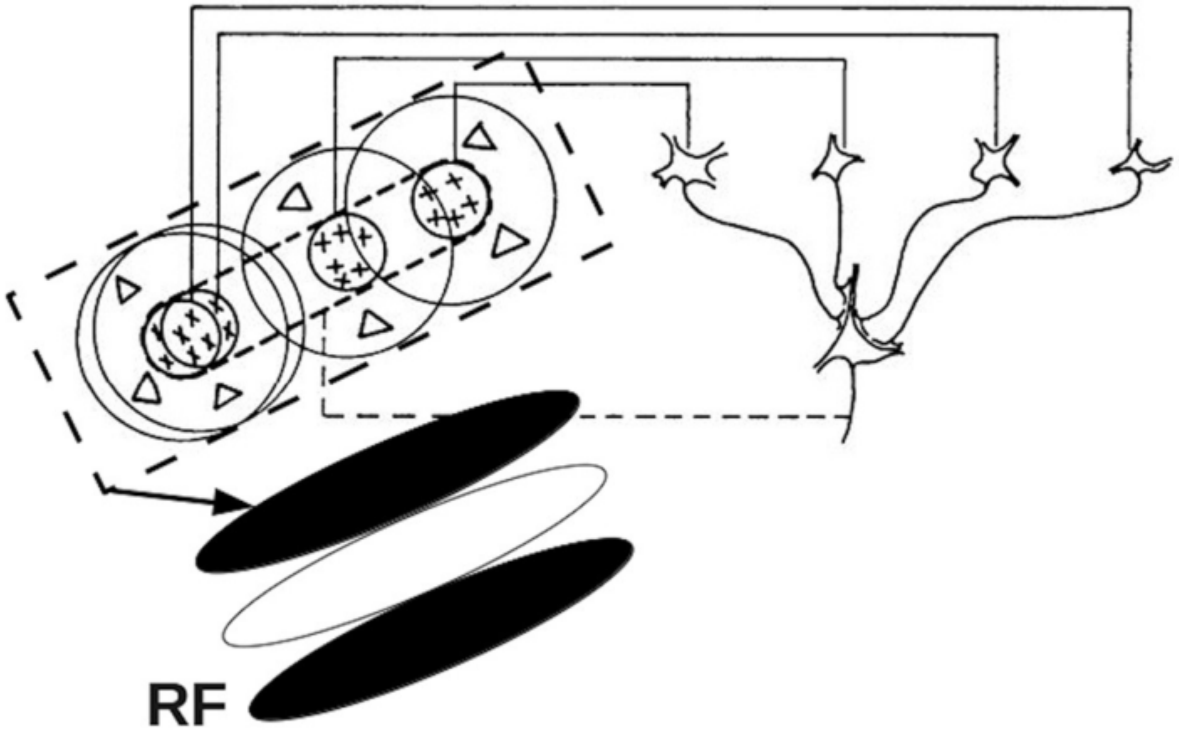
center

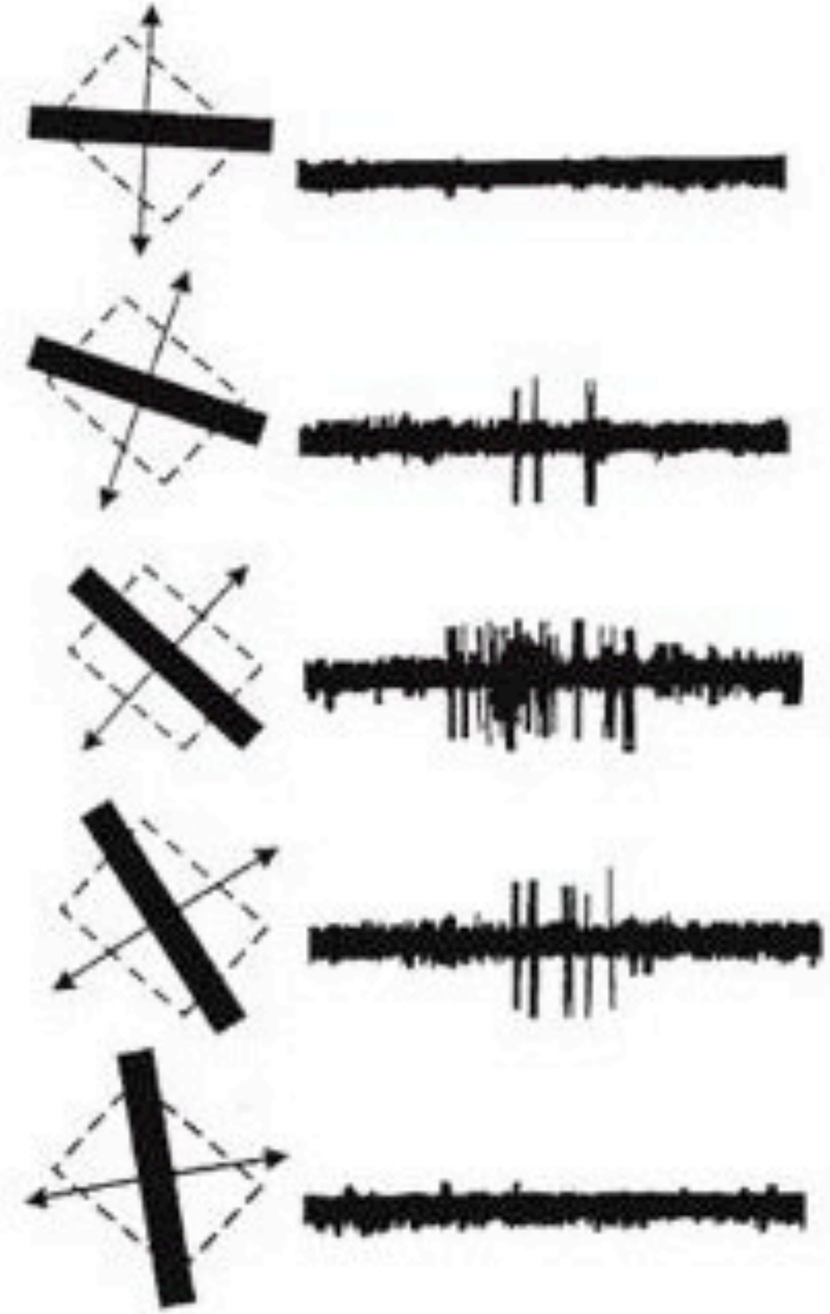
surround

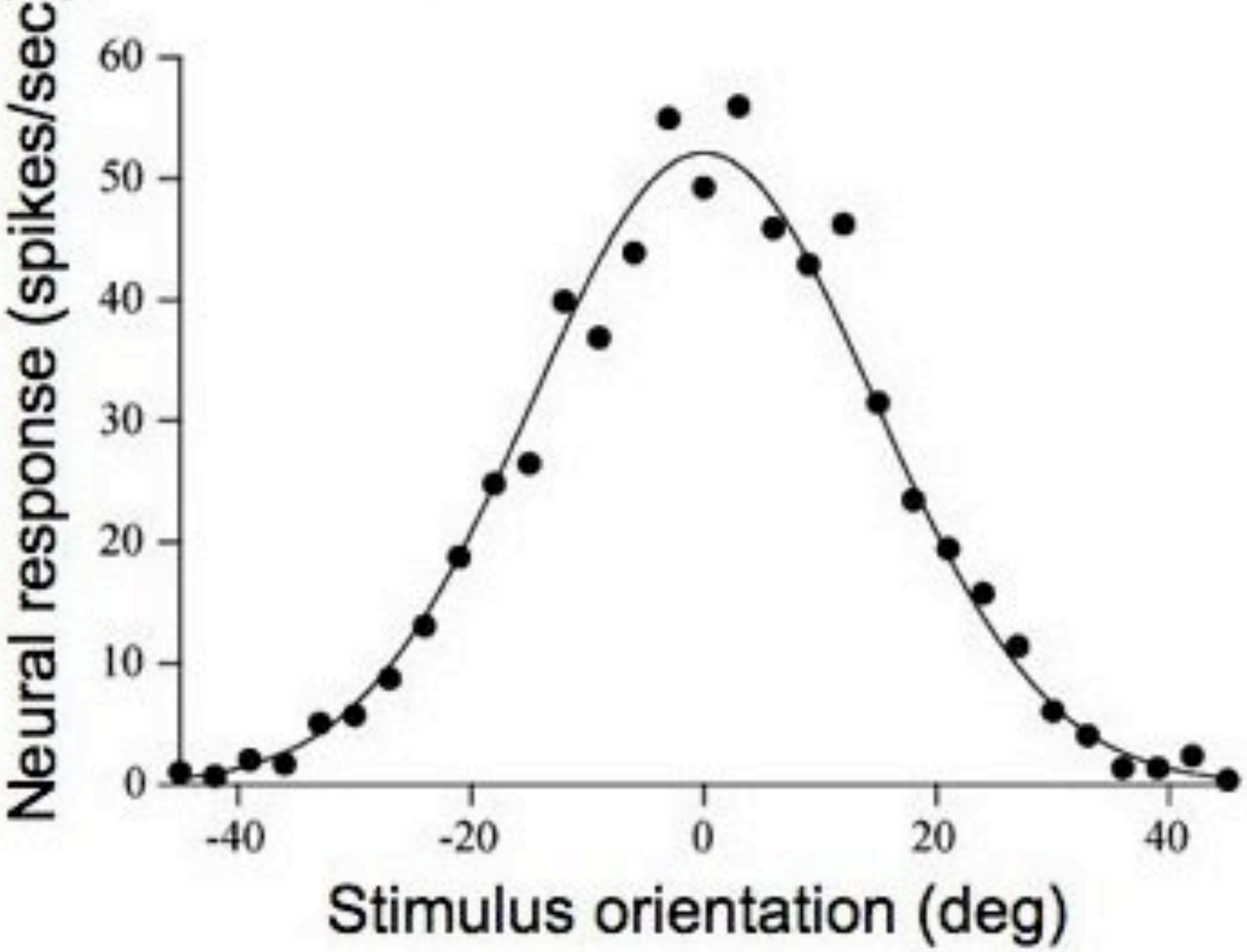


Bug detectors???









Hubel & Wiesel 1968

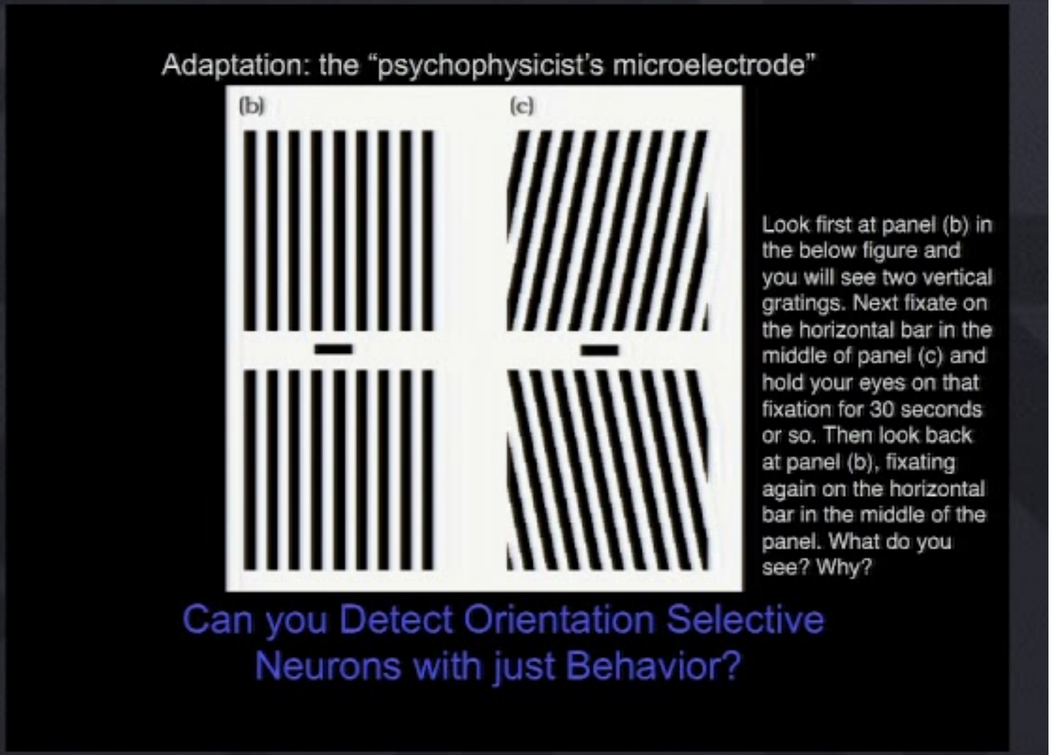
CENTER FOR
Brains
Minds+
Machines

February 21, 2018

Orientation Selectivity

Nancy Kanwisher

Massachusetts Institute of Technology



Adaptation: the “psychophysicist’s microelectrode”

Look first at panel (b) in the below figure and you will see two vertical gratings. Next fixate on the horizontal bar in the middle of panel (c) and hold your eyes on that fixation for 30 seconds or so. Then look back at panel (b), fixating again on the horizontal bar in the middle of the panel. What do you see? Why?

Can you Detect Orientation Selective Neurons with just Behavior?

Do we know what the early visual system does?

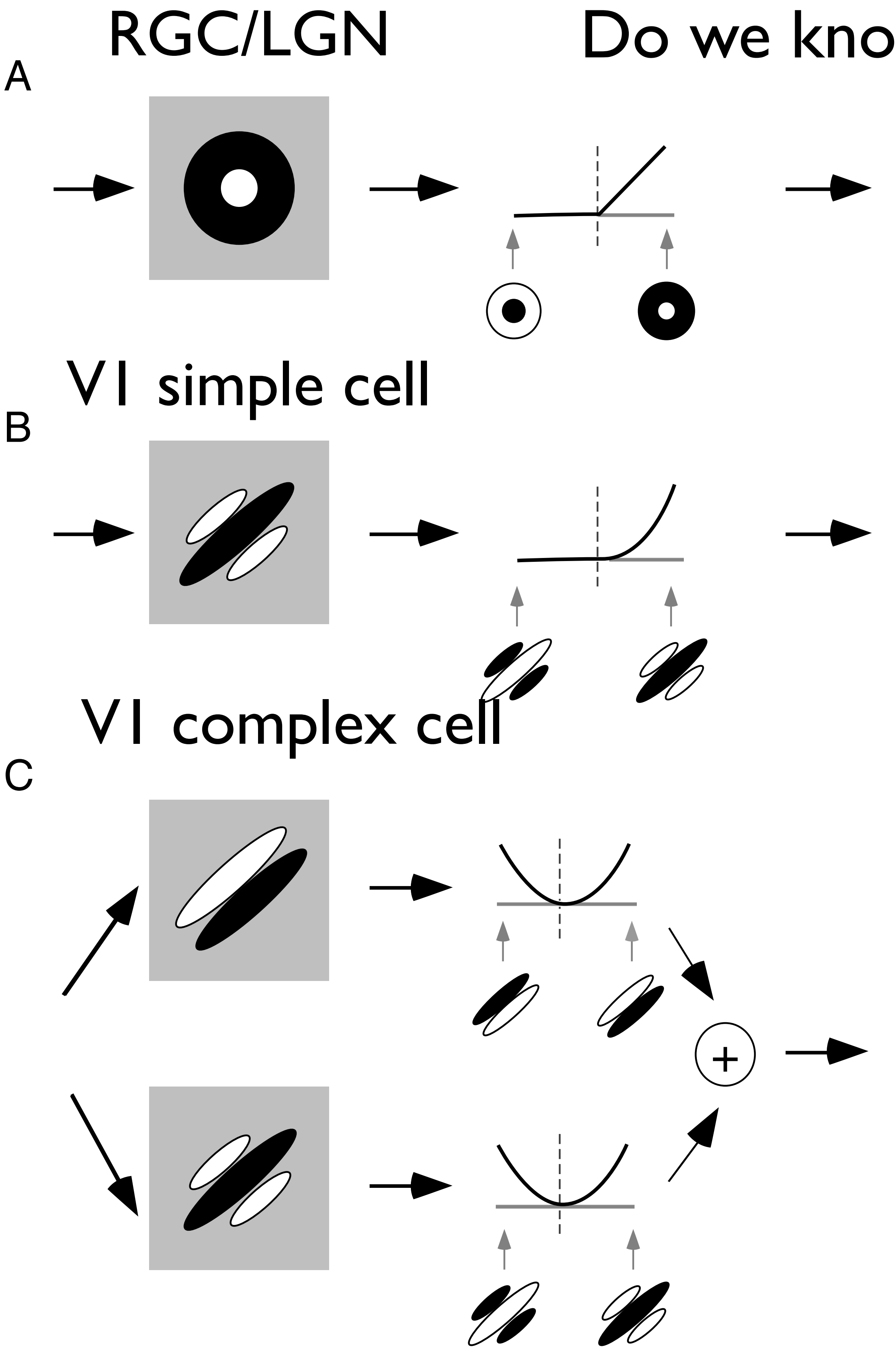
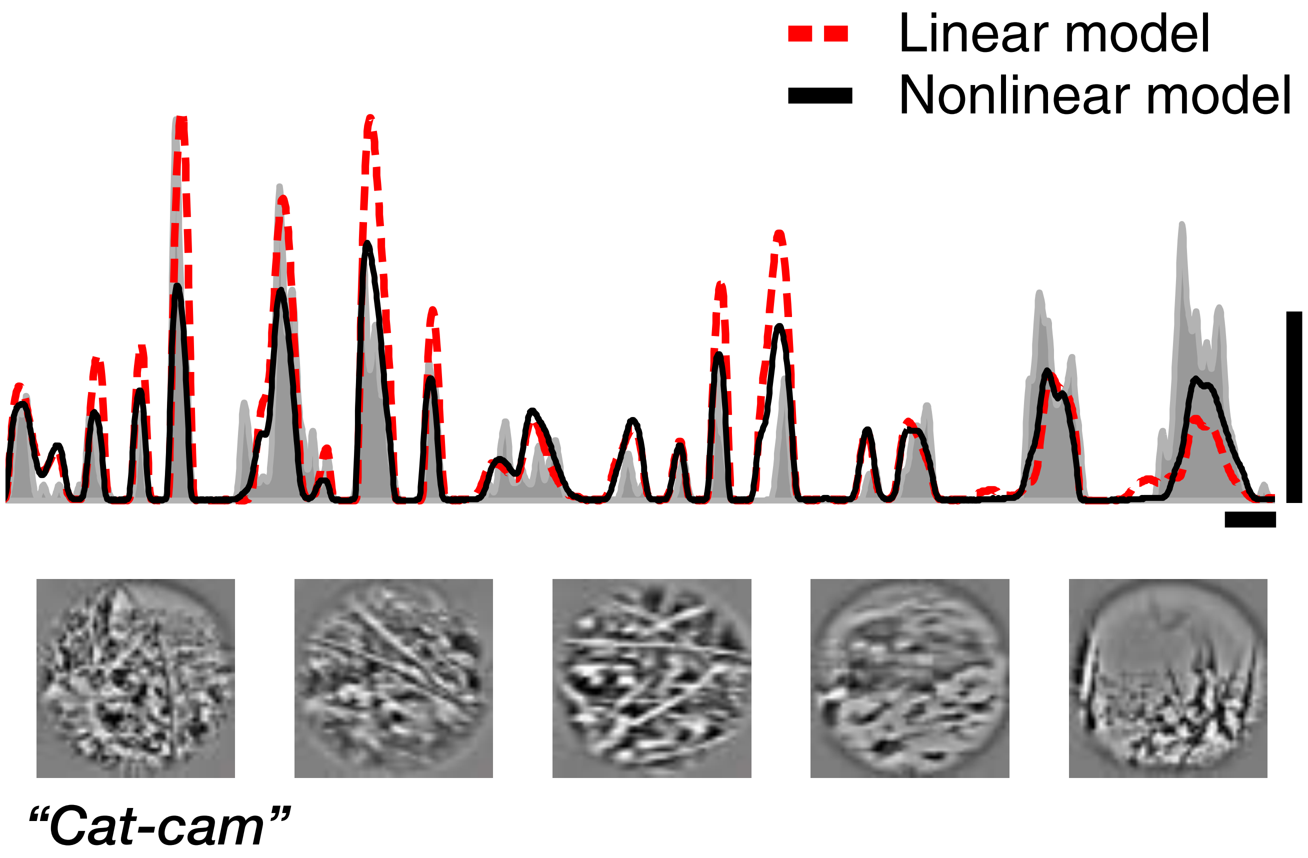


Figure 1. Basic models of neurons involved in early visual processing. In all models, the response of a neuron is described by passing an image through one or more linear filters (by taking the dot product or projection of an image and a filter). The outputs of the linear filters are passed through an instantaneous nonlinear function, plotted here as firing rate on the ordinate and filter output on the abscissa. ***A***, Simple model of a retinal ganglion cell or of an LGN relay neuron. The model includes a linear filter (receptive field) with a center–surround organization and a half-wave rectifying nonlinearity. Images that resemble the filter produce large firing rate responses, whereas images that resemble the inverse of the filter or have no similarity with the filter produce no response. ***B***, Model of a V1 simple cell as a filter elongated along one axis and a half-wave squaring nonlinearity. As in ***A***, only images that resemble the filter produce high firing rate responses. ***C***, The energy model of a V1 complex cell. The model includes two phase-shifted linear filters whose outputs are squared before they are summed. In this model, both images that resemble the filters and their inverses produce high firing rates.



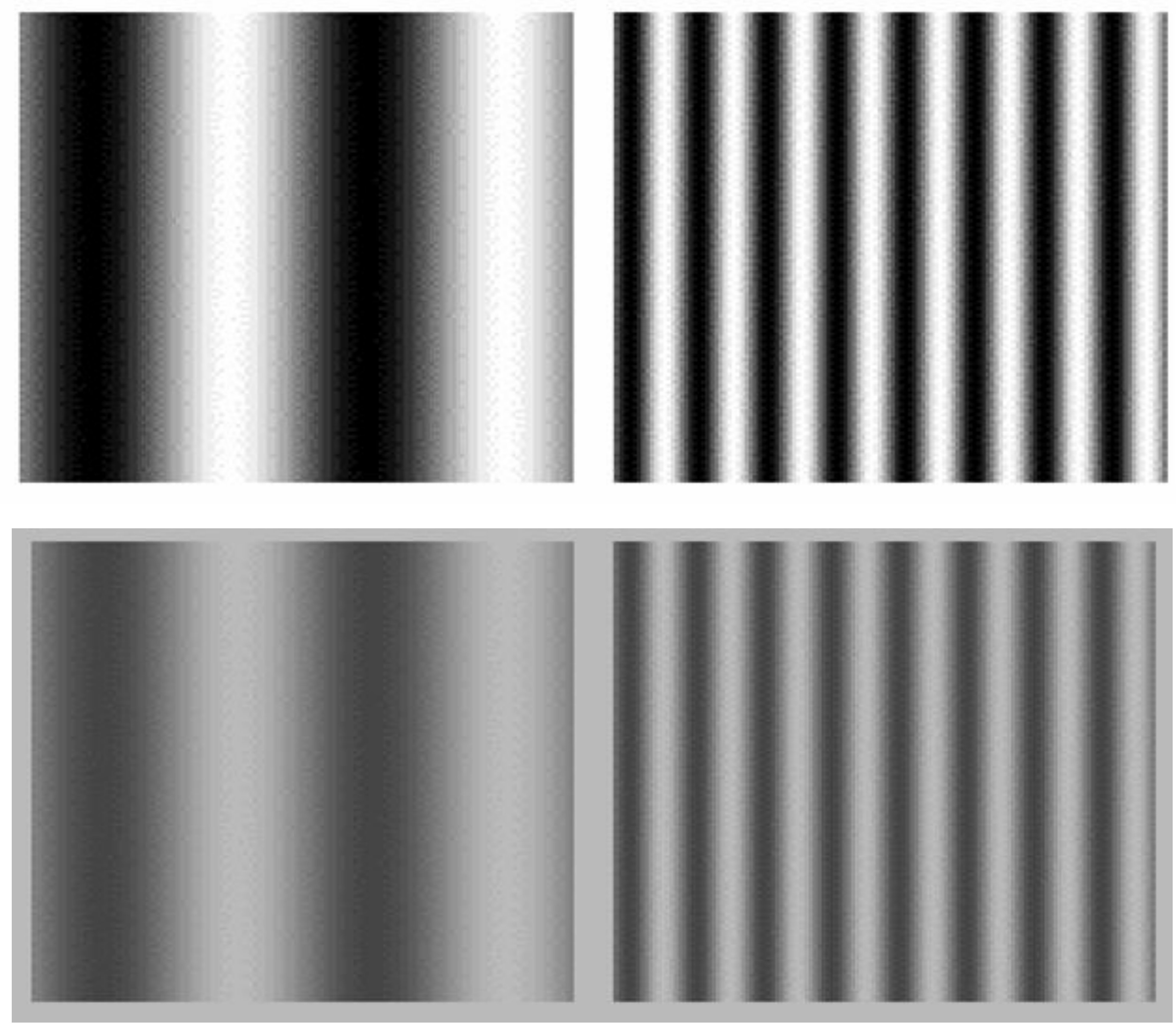
phase invariance

nonlinearities

Property	Simple Cell	Complex Cell
Orientation selective	Yes	Yes
ON/OFF subregions	Clear, linear	Lacks clear subregions
Phase sensitivity	High	Low (phase invariant)
Computational model	Linear filter + static nonlinearity	Pooling of multiple simple cells + nonlinearity
Best stimuli	Static bars/gratings aligned precisely	Moving bars/edges of proper orientation

contrast sensitivity and spatial frequency analysis of visual pathways

sinusoidal gratings



low
spatial frequency

high
spatial frequency

high
contrast

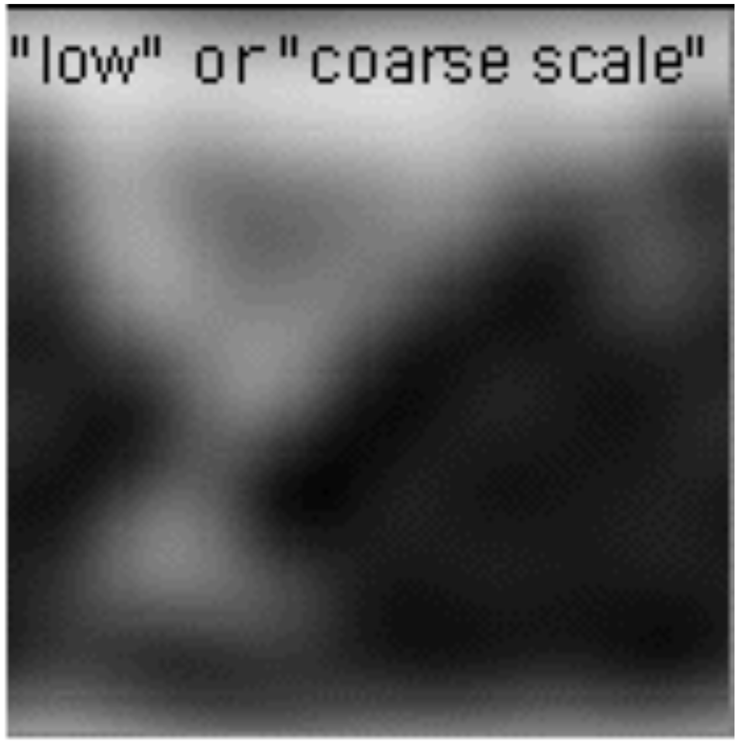
low
contrast

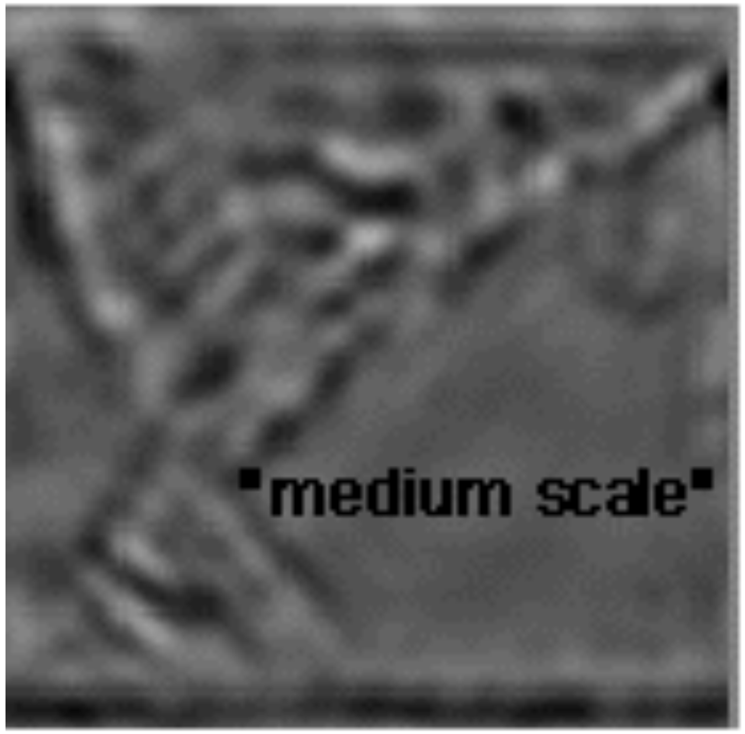
spatial frequencies of an visual image

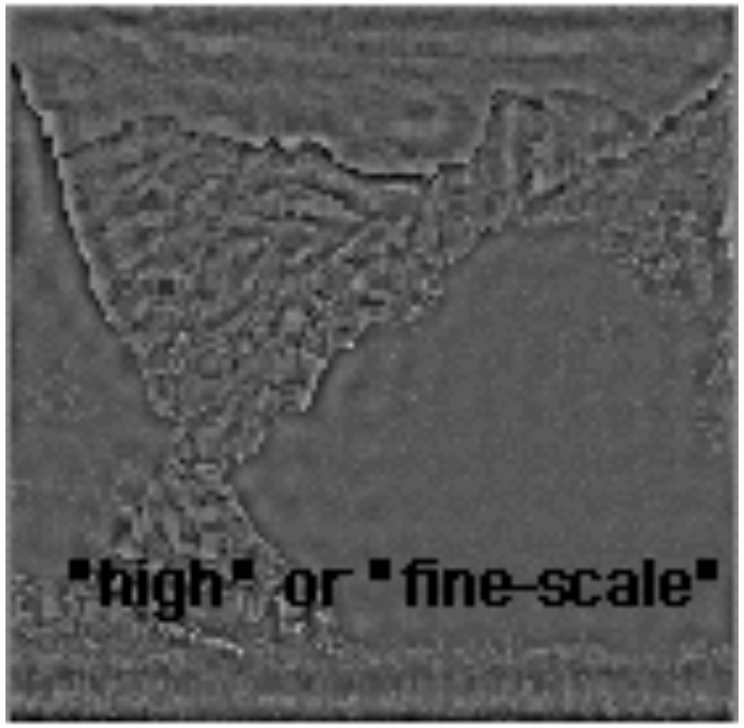
http://david.li/filtering/

low spatial frequency

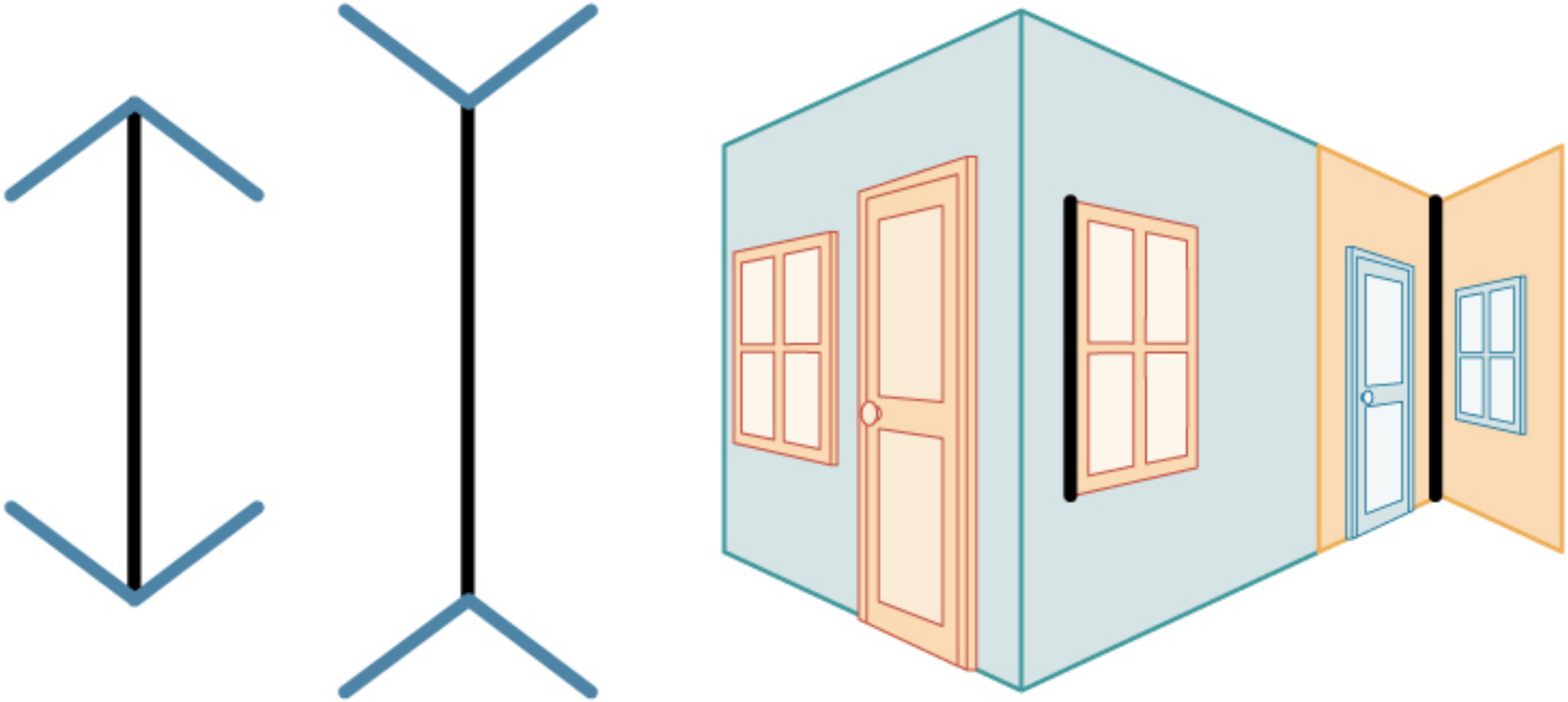
high spatial frequency



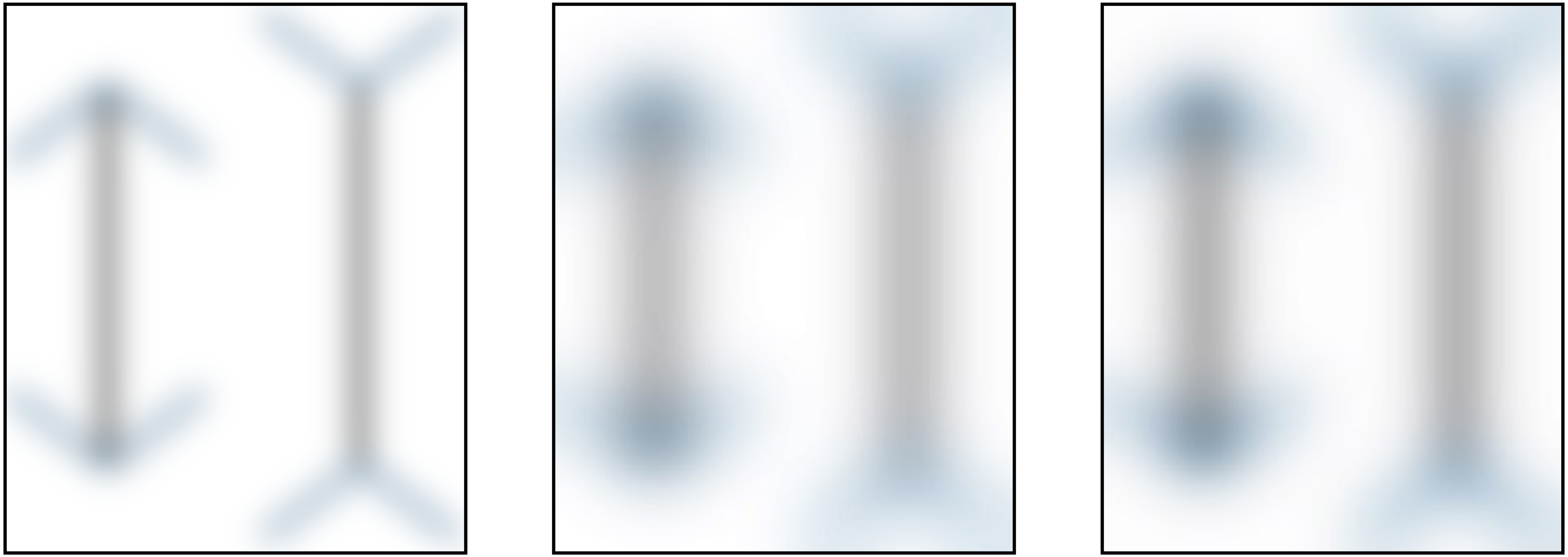




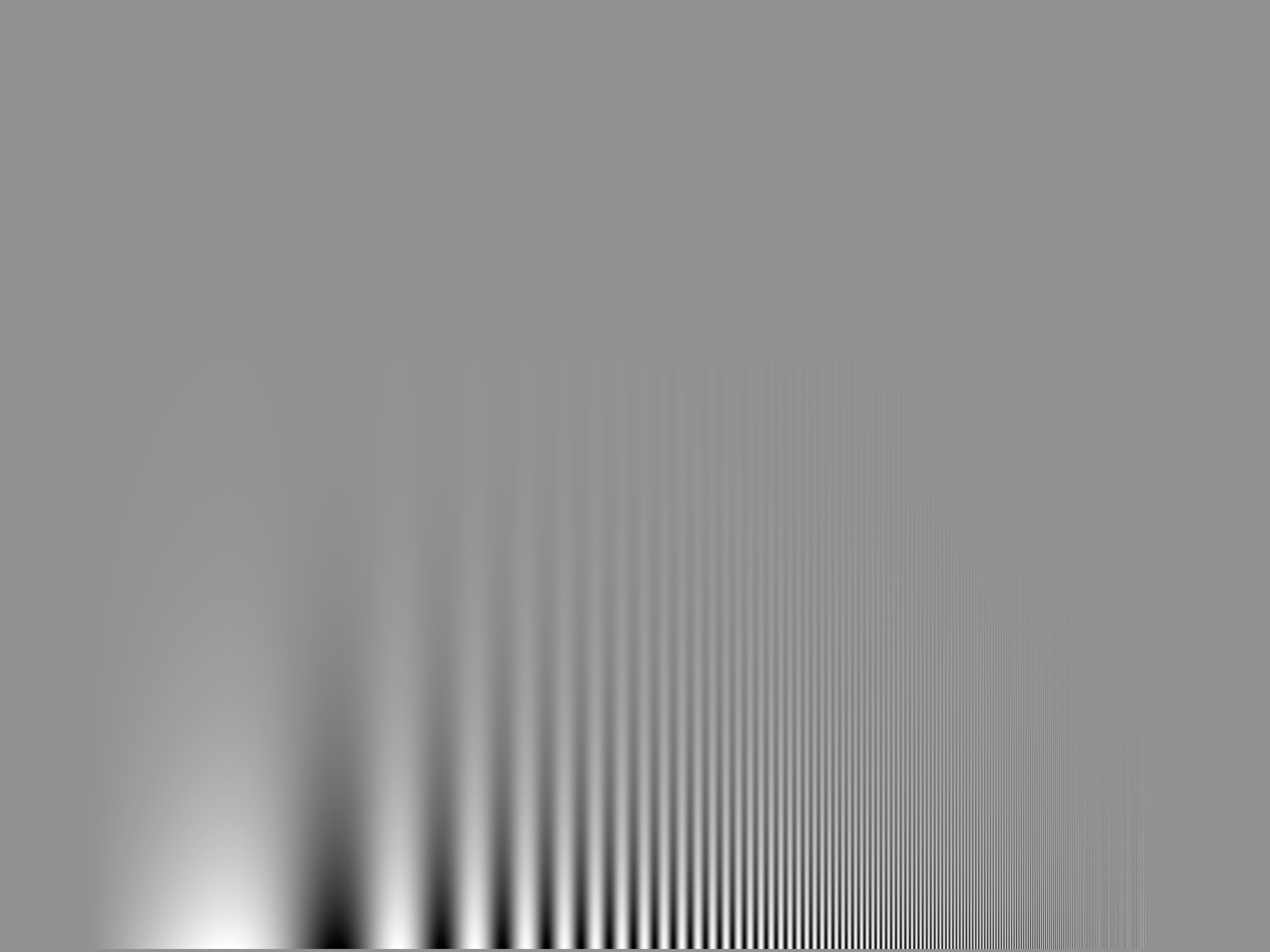
http://www.psy.vanderbilt.edu/courses/hon185/SpatialFrequency/SpatialFrequency.html



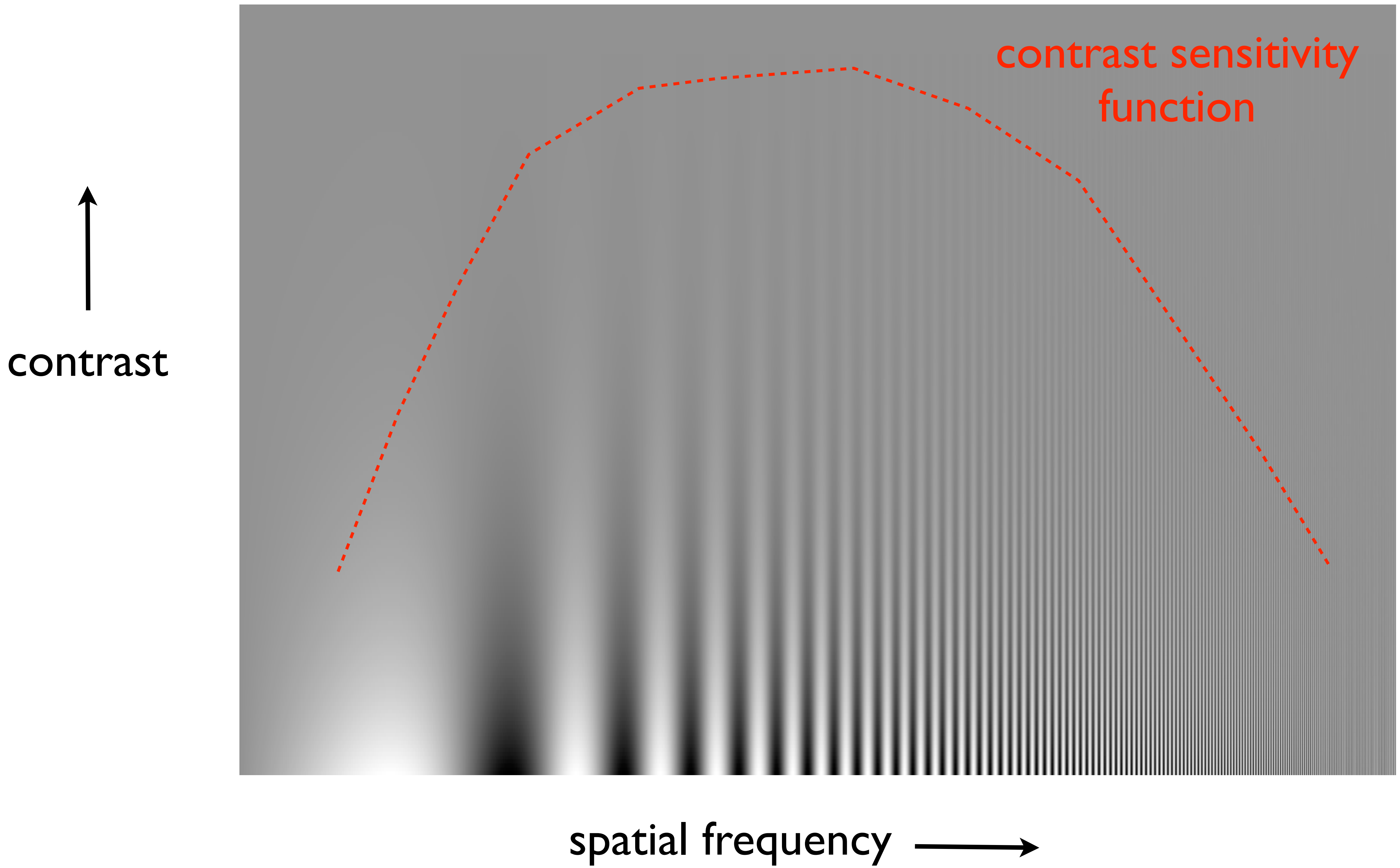
Müller-Lyer illusion: perspective explanation



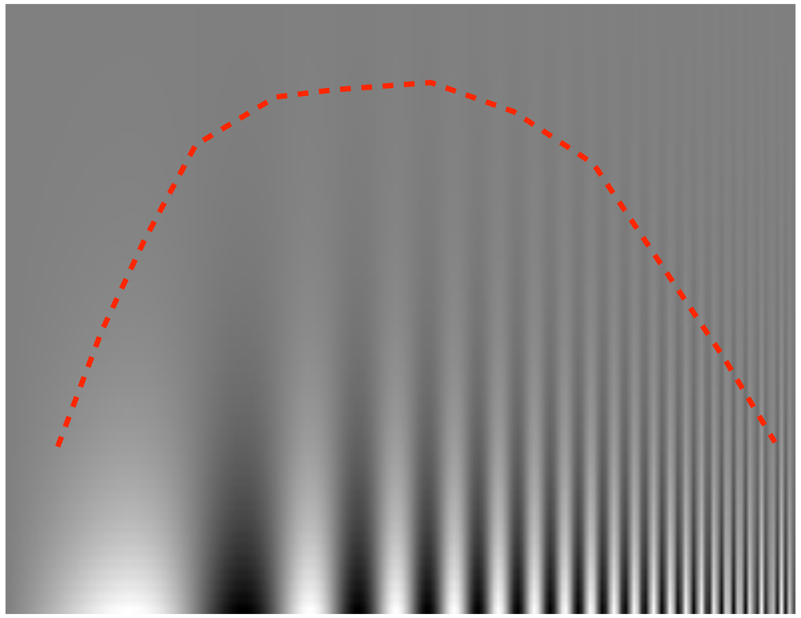
Müller-Lyer illusion: spatial frequency explanation



contrast sensitivity



sinusoidal drifting grating stimuli and contrast threshold



At different levels of the visual system, the responses of various neurons form a **neural representation** of the image falling on the retina.

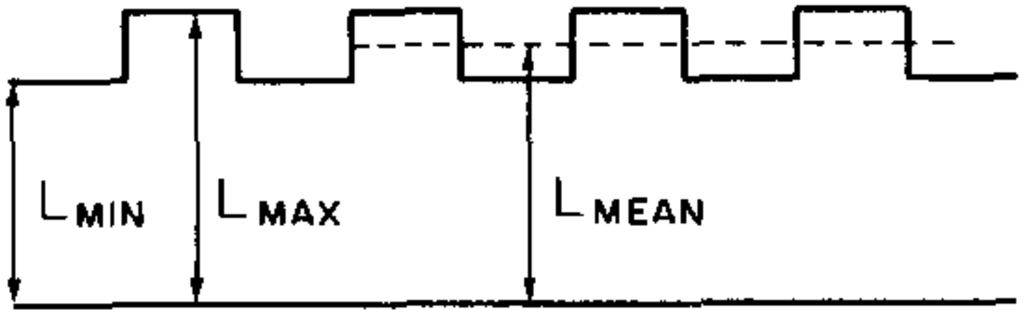
Because neurons' **receptive fields** vary in size, the responses of different subsets of neurons would constitute a neural representation at some particular **spatial scale**.

Spatial frequency analysis of the visual system uses **sinusoidal grating stimuli** because orientation, size (period of grating), and contrast (difference between brightest and darkest illumination) can be varied systematically.

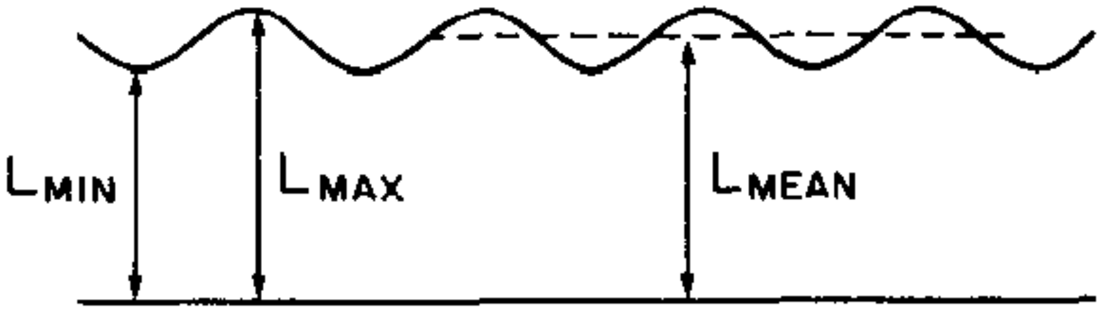
At sufficiently low contrast, the a grating appears uniform and unpatterned; at higher contrasts, the pattern would be visible.

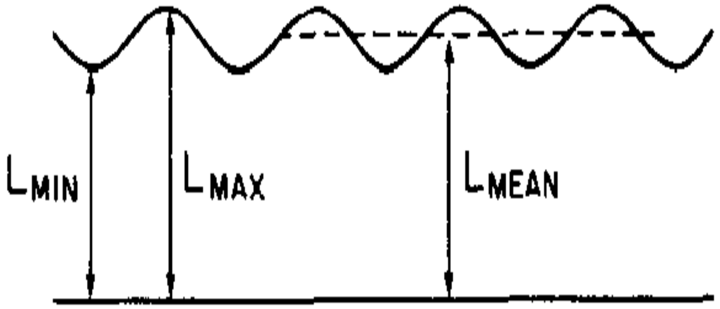
The **contrast threshold** (sensitivity to contrast) is a biphasic function of the spatial frequency of the spatial grating stimulation. This is consistent with the **center-surround properties** of retinal ganglion cells.

square pulse grating



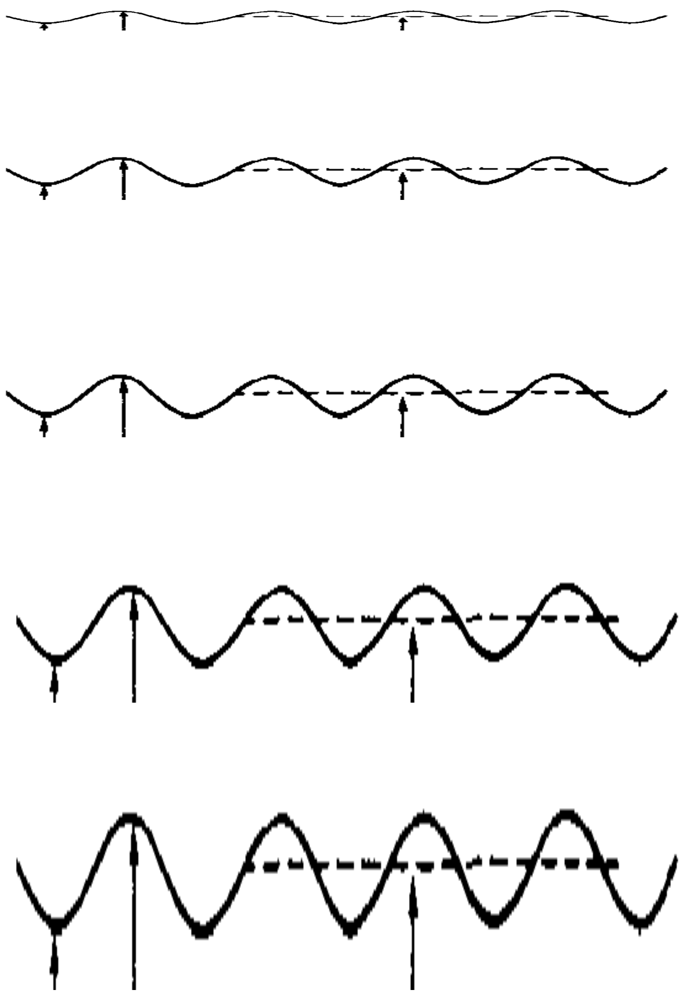
sinusoidal grating





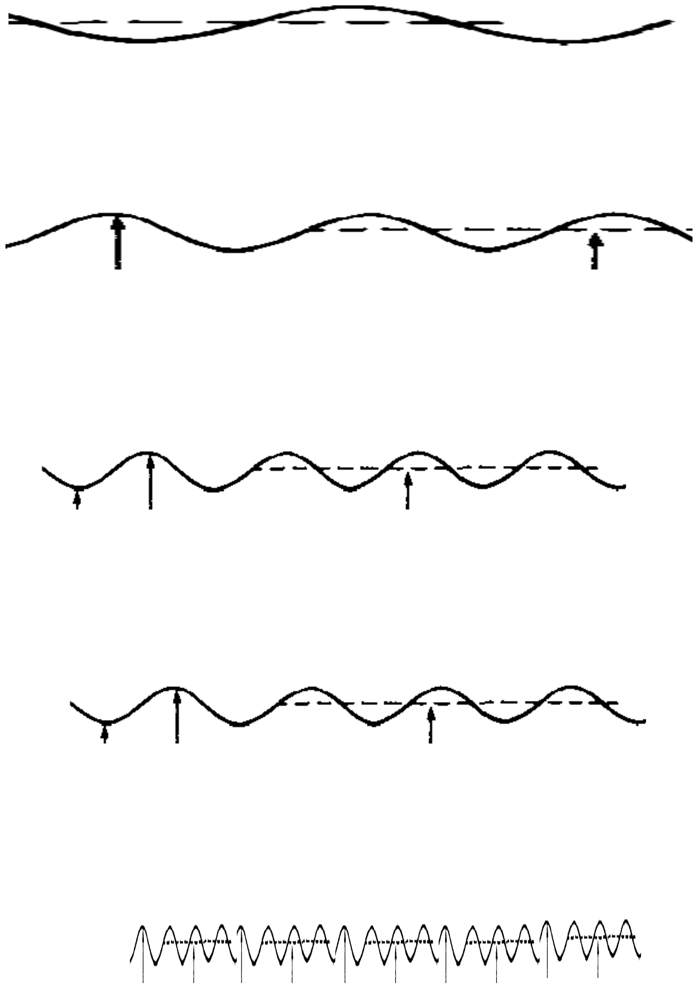
$$\text{constrast} = \frac{L_{max} - L_{min}}{L_{mean}}$$

low contrast



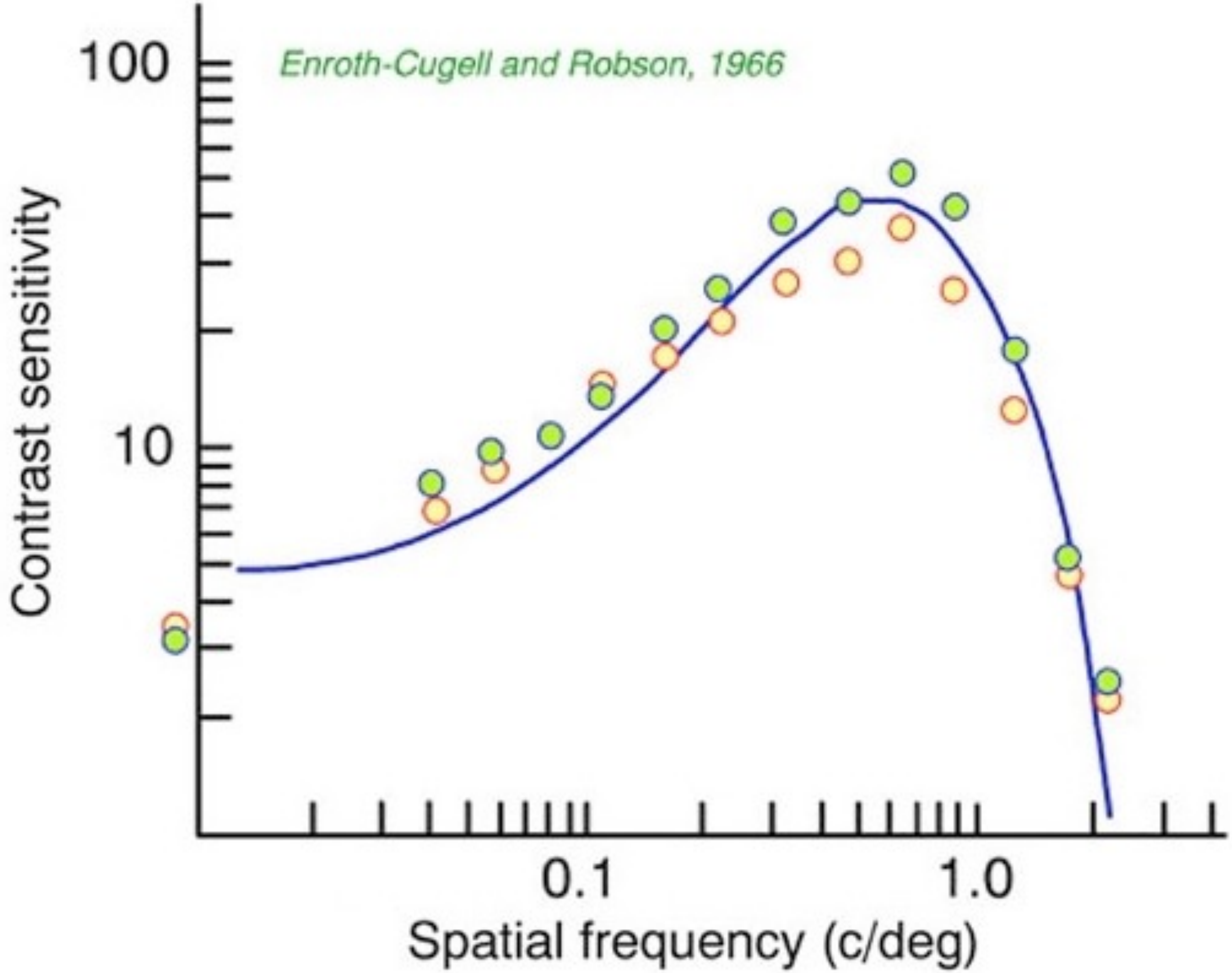
high contrast

low frequency



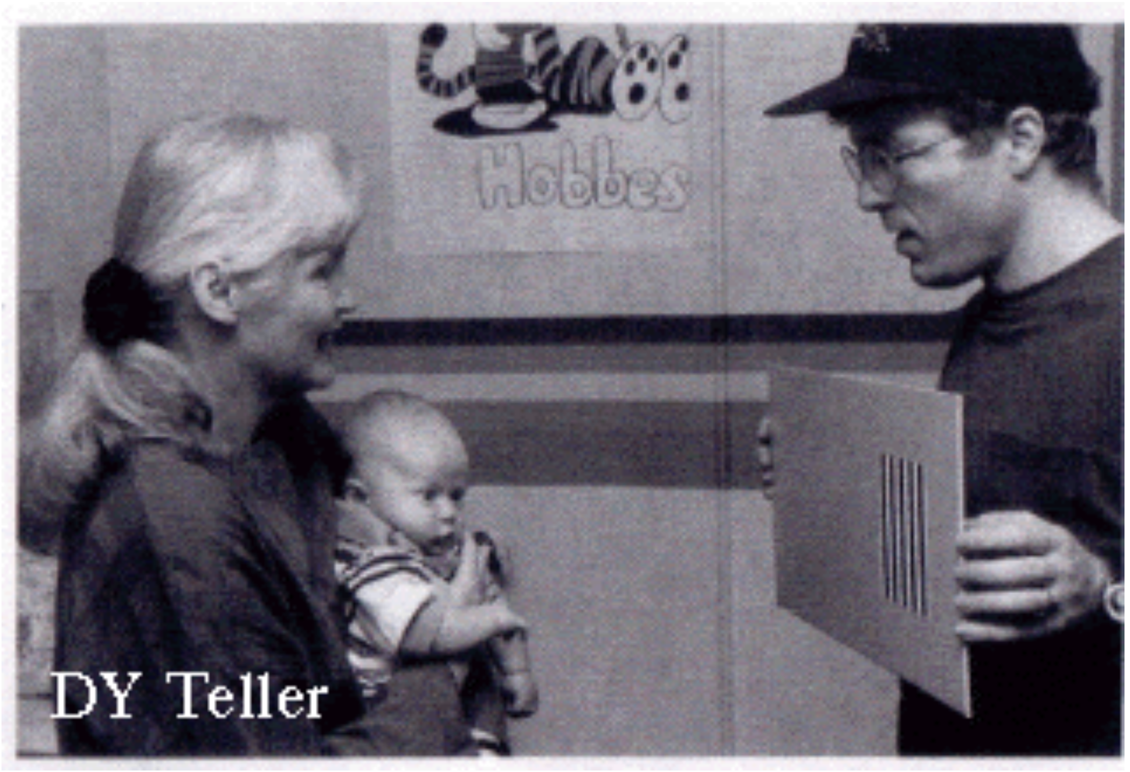
high frequency

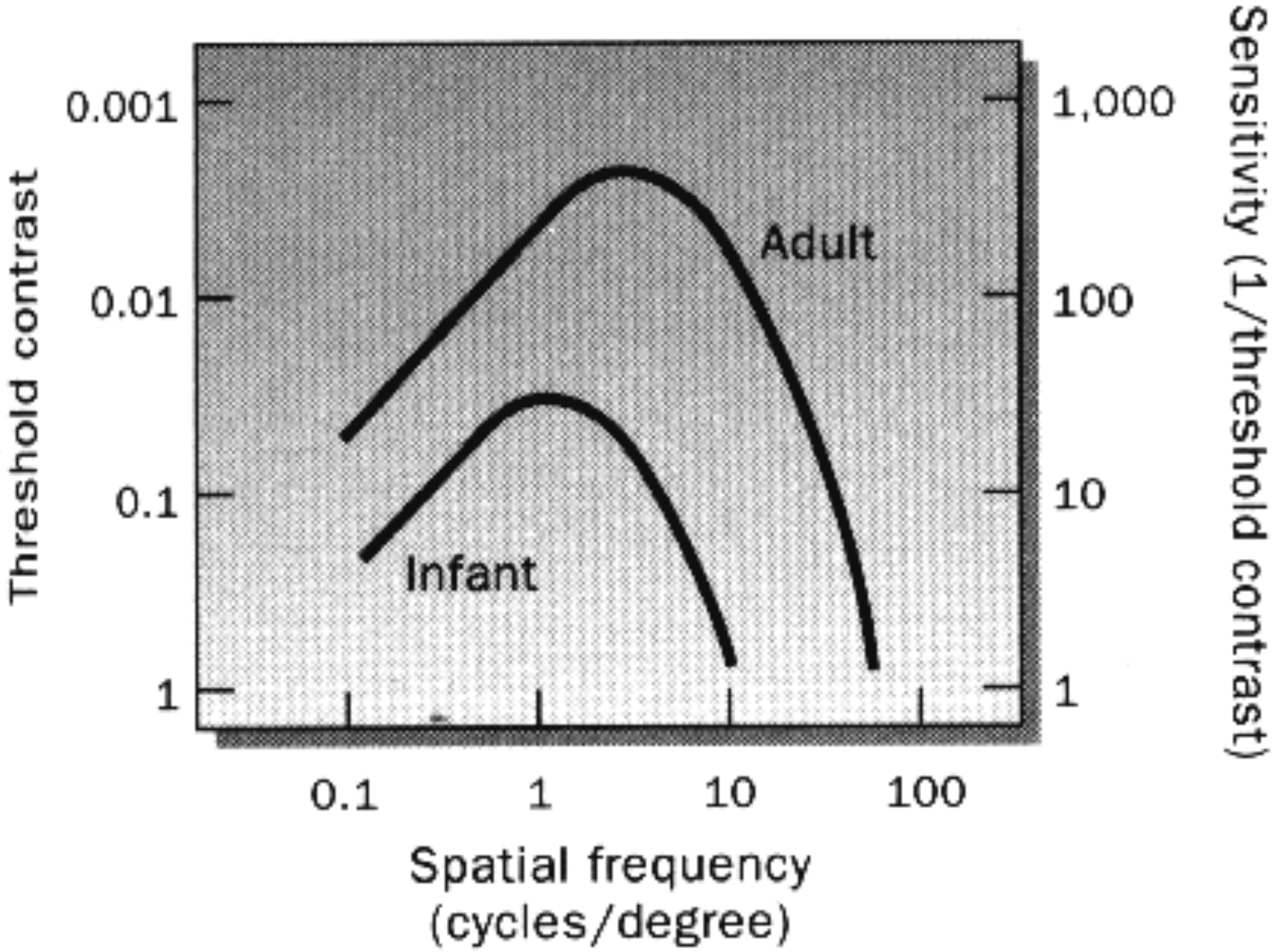
spatial tuning of ganglion cell receptive fields is reflected in peaked **contrast sensitivity** function



Each ganglion cell is "tuned" (responds best) for objects of a different size. Among the population of ganglion cells, a wide range of sizes is covered. This tuning reflects in part the variable dendritic span in ganglion cells.

contrast sensitivity functions for an infant and adult





Confronted with a patch of grating and a patch of uniform brightness, an infant will prefer to look at the grating. If the infant shows no preference for the grating over the uniform field, it is inferred that the infant cannot see the grating.

An infant held on your lap will not be able to see fine spatial details visible to you. Very young infants seem oblivious to everything except very large, high-contrast objects. The lack of sensitivity to high spatial frequencies does not stem from optical causes; rather, the infant's immature visual nervous system does not encode high spatial frequencies.

contrast sensitivity function is consistent with "difference of gaussians" model of RGC RF

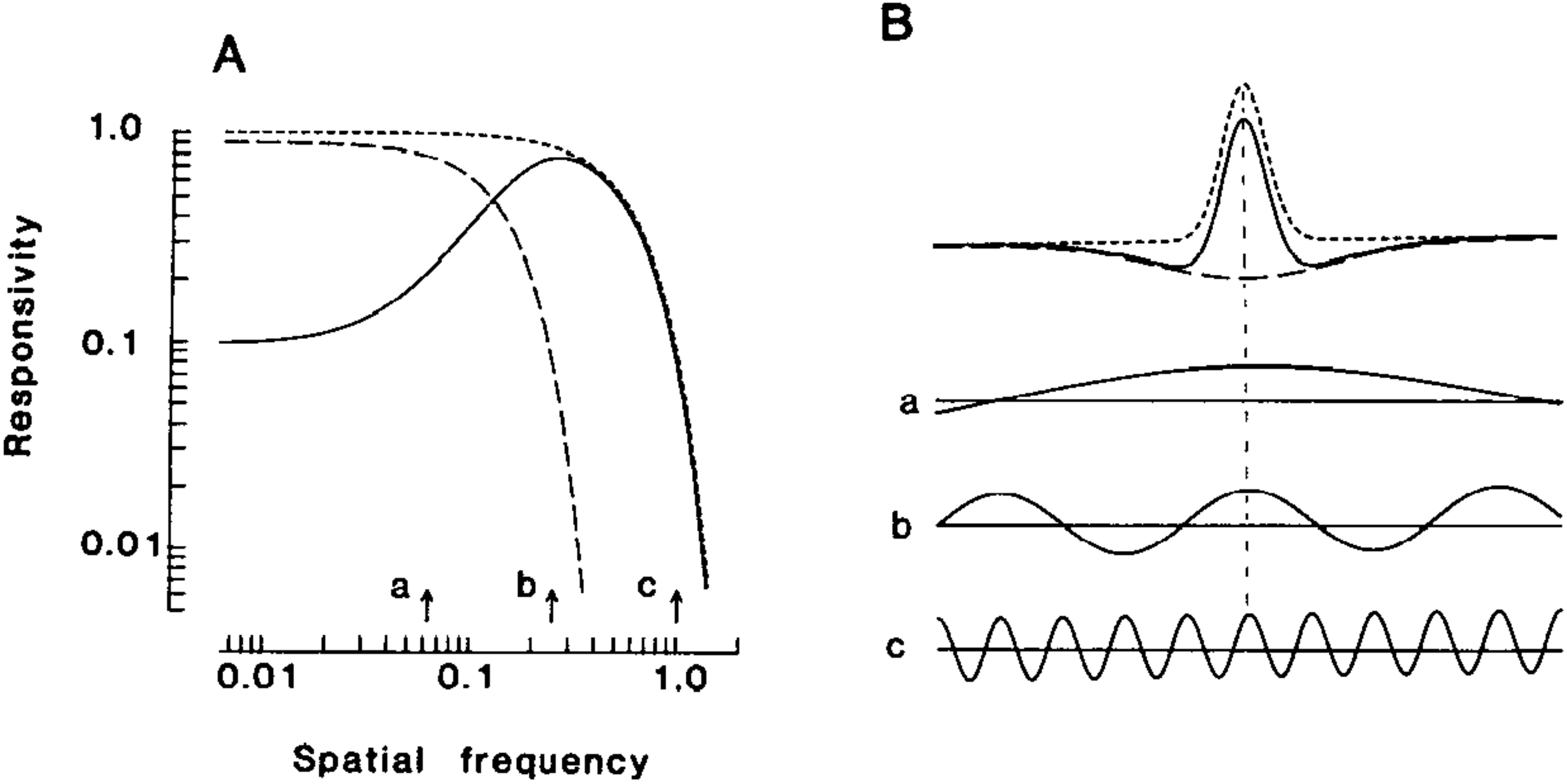
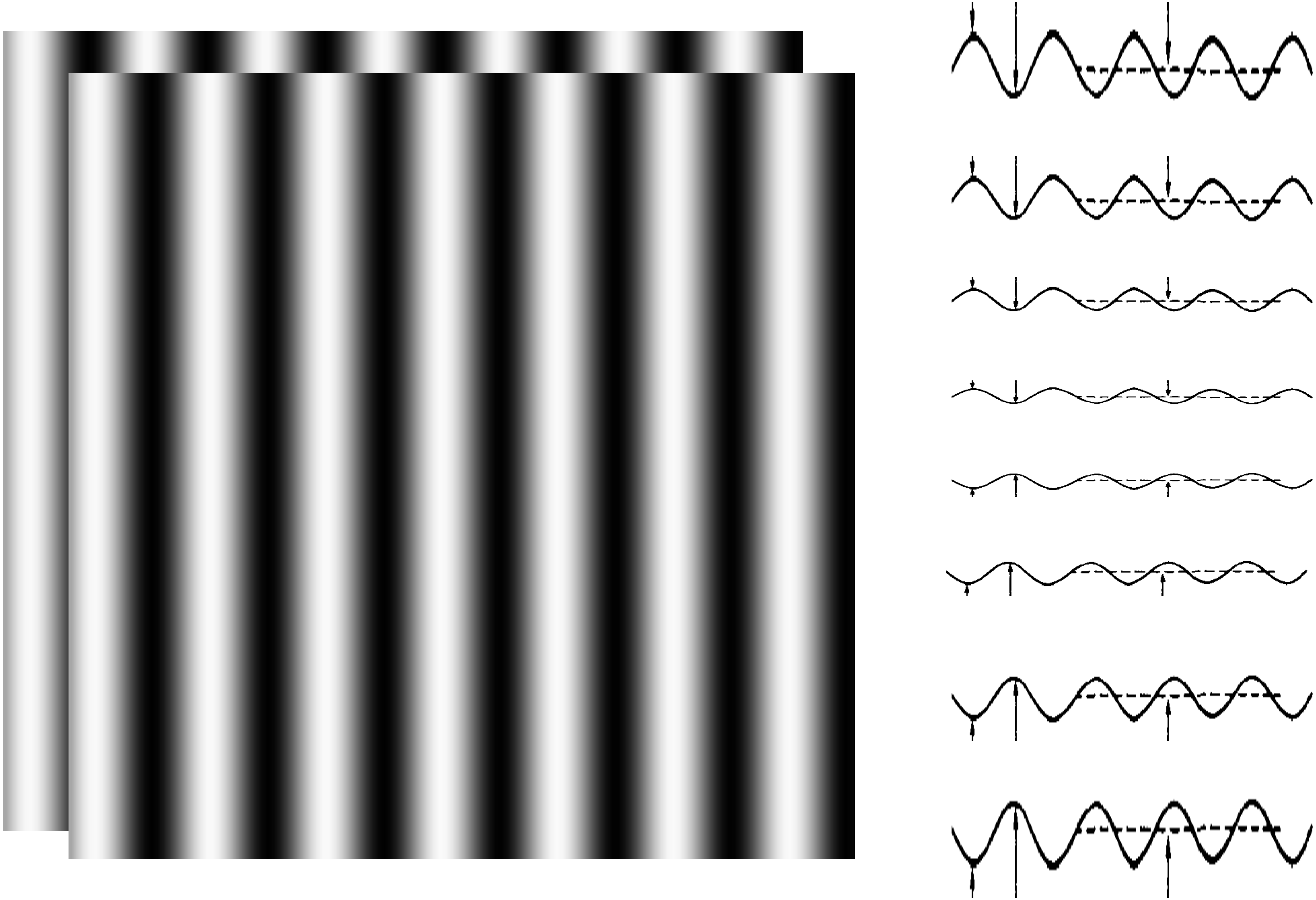
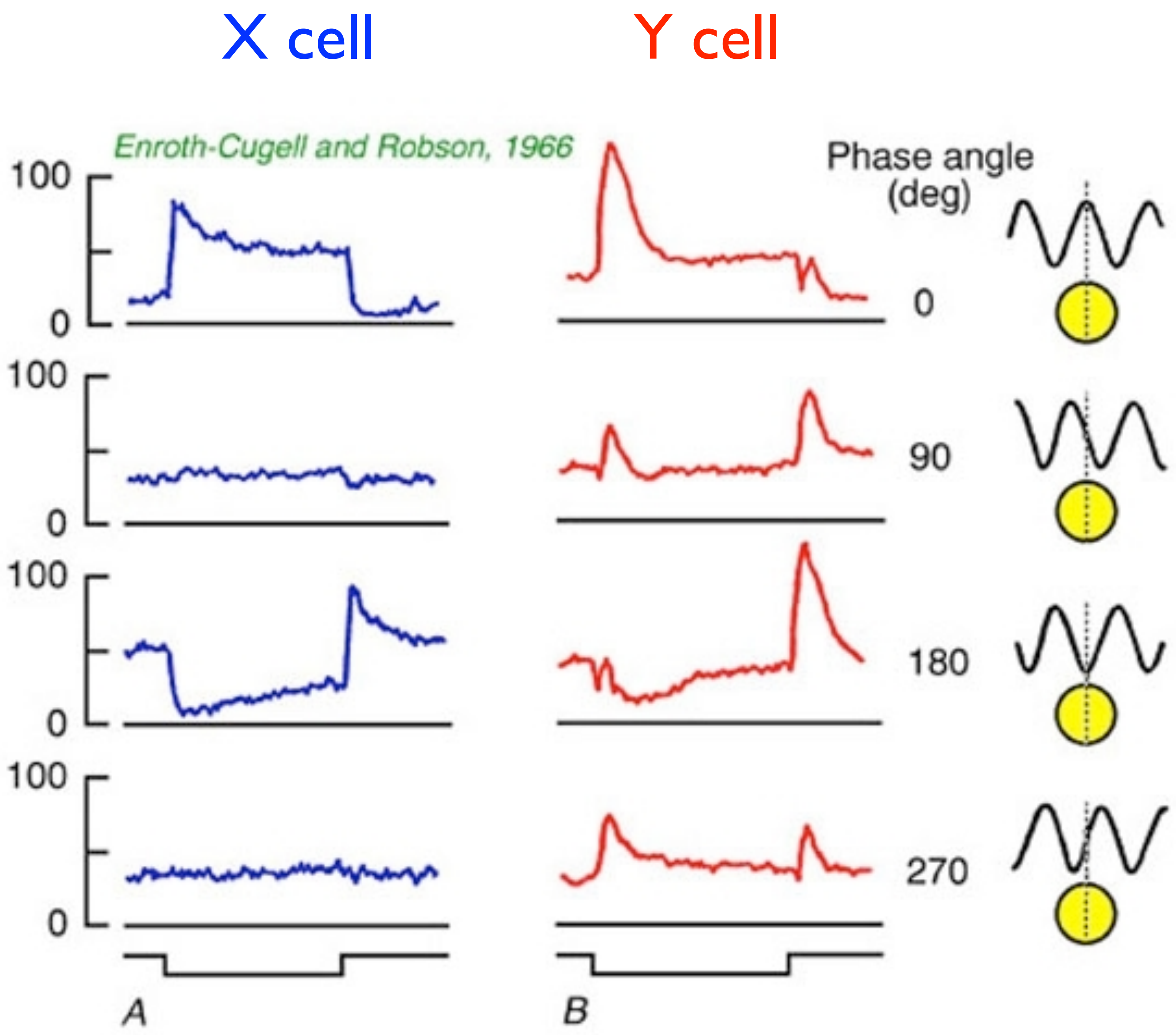


Figure 3 Difference of Gaussians model in (A) *spatial frequency* and (B) *space*. In *A*, the unbroken curve is the spatial frequency response of Rodieck's Difference of Gaussians model. The *dashed curves* show the spatial frequency responses of the center *(fine dashes)* and surround *(coarse dashes)*, each of which is a Gaussian function of spatial frequency. In this example, the ration $k_s r_s^2 / k_c r_c^2$ was 0.9, and the ratio r_s / r_c was 4. These are typical values for X-cells in the cat's retina. In *B*, the *upper set of curves* represents the Difference of Gaussians model; the *solid curve* is the sum of the narrower center Gaussian *(fine dashes)* and the broader surround Gaussian *(coarse dashes)*. These three curves are the inverse Fourier transforms of the corresponding spatial frequency responses in *A*. The three lower curves in *B* are profiles of sinusoidal gratings presented to the receptive field with even symmetry, a position of maximal response for a contrast reversal grating. The spatial frequencies of these three sinusoids, in the units in which the receptive field dimensions are expressed, are labeled a,b,c in *A*. From Enroth-Cugell & Robson (1984).

sinusoidal contrast reversing grating



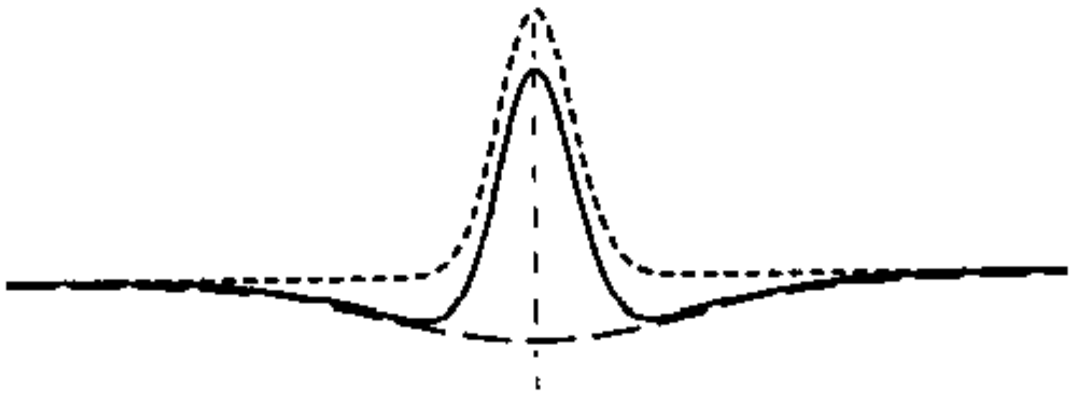
spatial frequency analysis reveals different physiological classes of RGCs



For the X-cell, when pattern is positioned so the transition from light to dark passes directly through the center of the field, a "null response" is produced (stimulus produces no effect on firing rate). The tendency of the bright bars to excite the cell is exactly compensated by the tendencies of the dark bars to reduce the firing rate. For the Y-cell, no such stimulus position can be found.

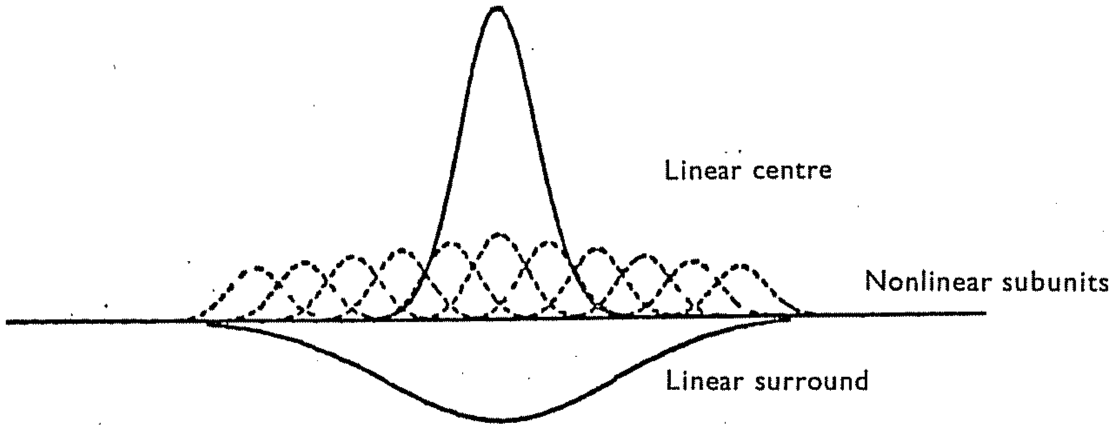
models of X- and Y-retinal ganglion cell receptive fields

X cell



difference of gaussians

Y cell



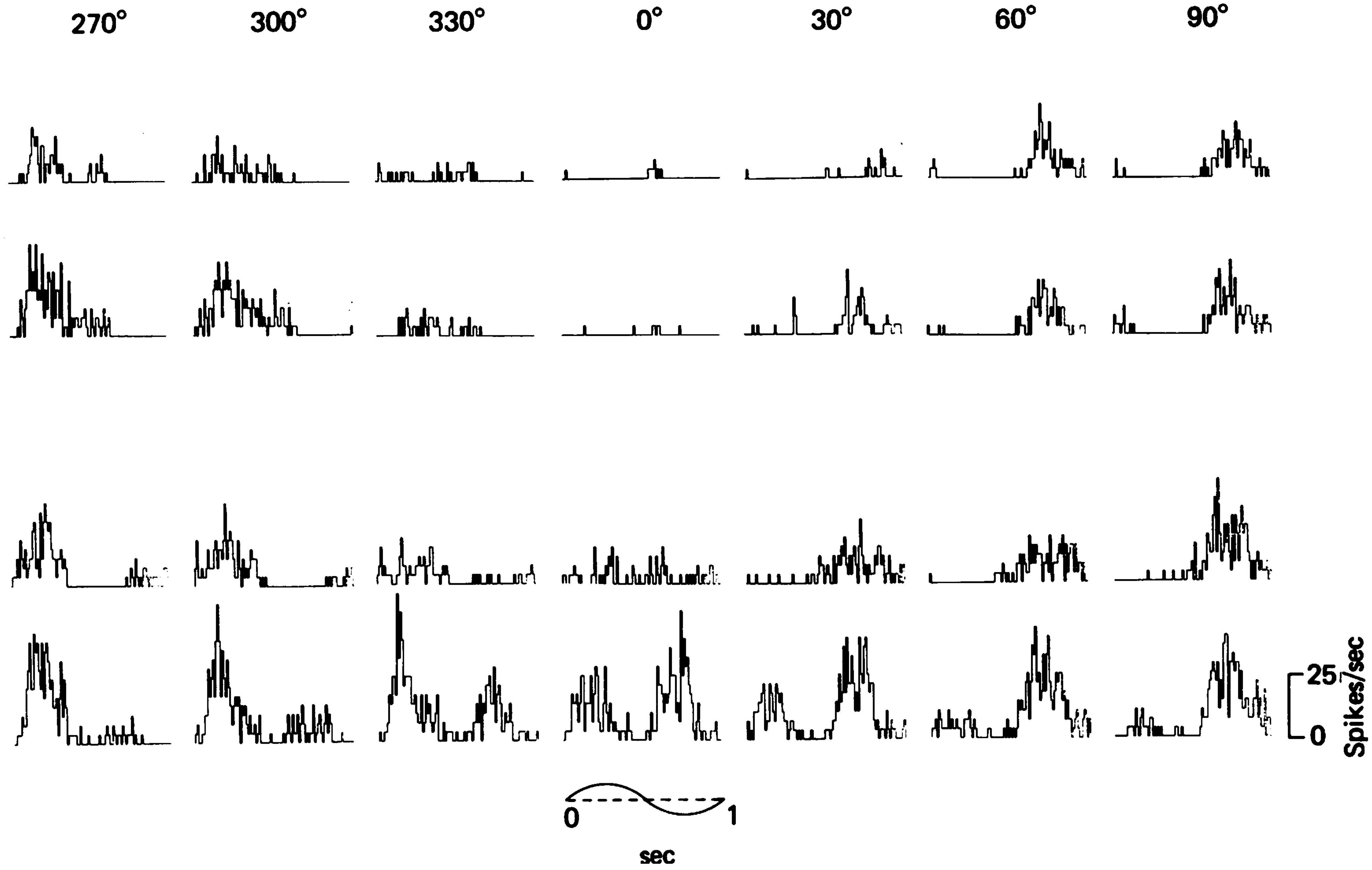
difference of gaussians
+ **nonlinear** subunits

Fig. 10. Spatial model for the Y cell receptive field. The spatial extent of elements of a Y type retinal ganglion cell are shown in this Figure. There is a centre and overlapping nonlinear subunits of the surround, each of them smaller in spatial extent than the centre. Also there is a large linear surround mechanism. The linear centre and surround are drawn with solid curves while the nonlinear subunits are drawn with a dashed curve.

SPATIAL PROPERTIES OF CELLS IN THE RABBIT'S STRIATE CORTEX

linear
simple
cell
X-like

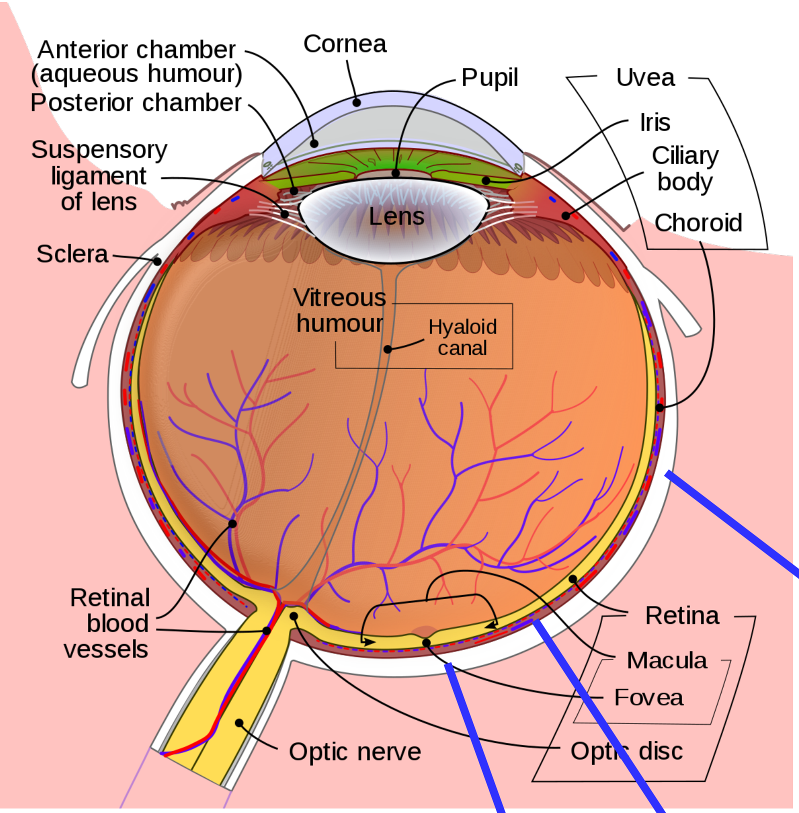
nonlinear
simple
cell
Y-like



complex
cells
(not shown)

Fig. 3. Null test results for two simple cells, one which exhibited linear spatial summation, and another which exhibited non-linear spatial summation. The first and second rows represent the linear cell's responses to gratings having spatial frequencies of 0·43 c/deg and 0·65 c/deg. The grating's contrast in each instance was 0·45. The third and fourth rows represent the non-linear cell's responses to gratings having spatial frequencies of 0·13 c/deg and 0·43 c/deg. The grating's contrast in each instance was 0·37. The gratings were all contrast-reversed at a rate of 1 Hz. Each histogram represents a cell's averaged response to twenty-six presentations of the stimulus.

morphology of beta / X and alpha / Y retinal ganglion cells at matched retinal eccentricities



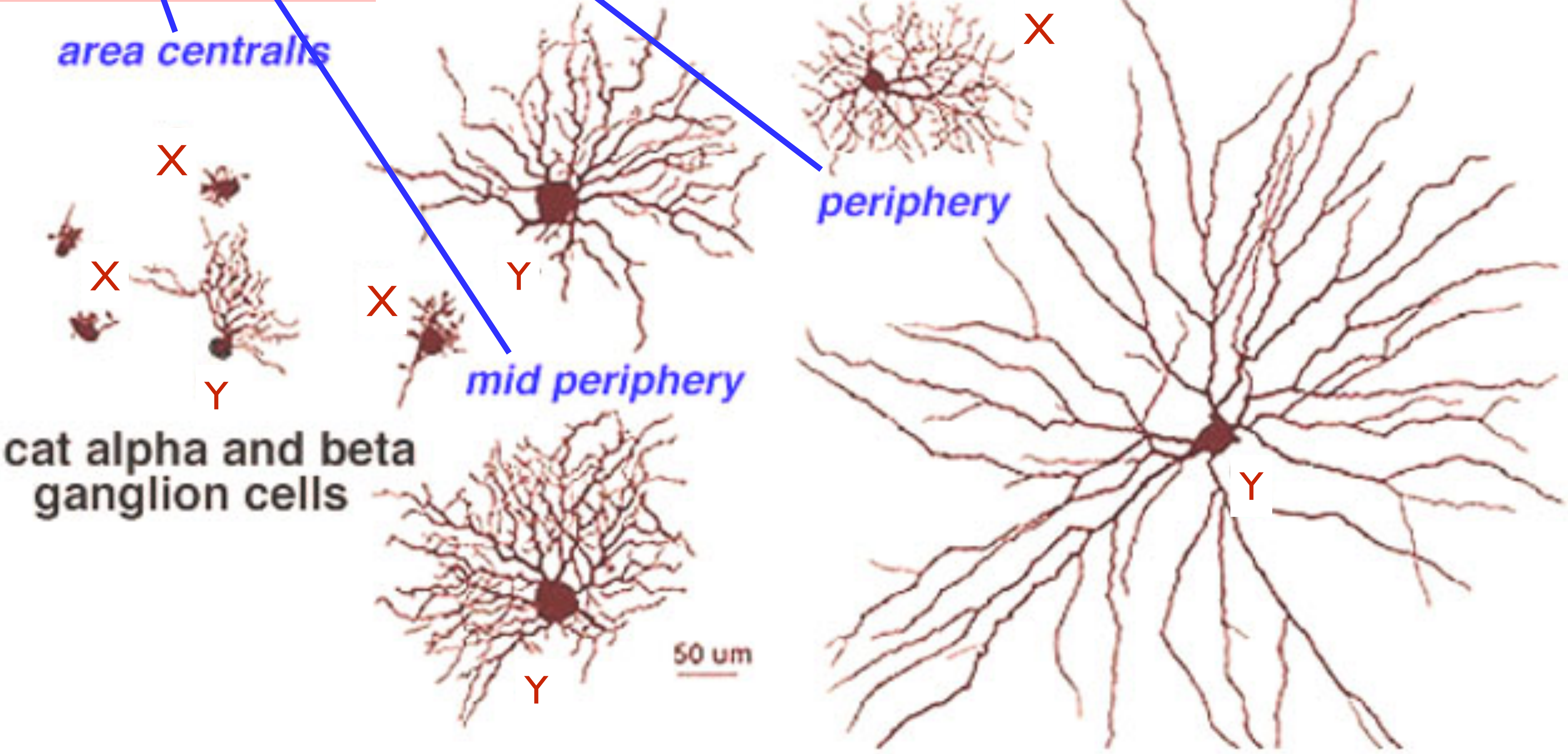
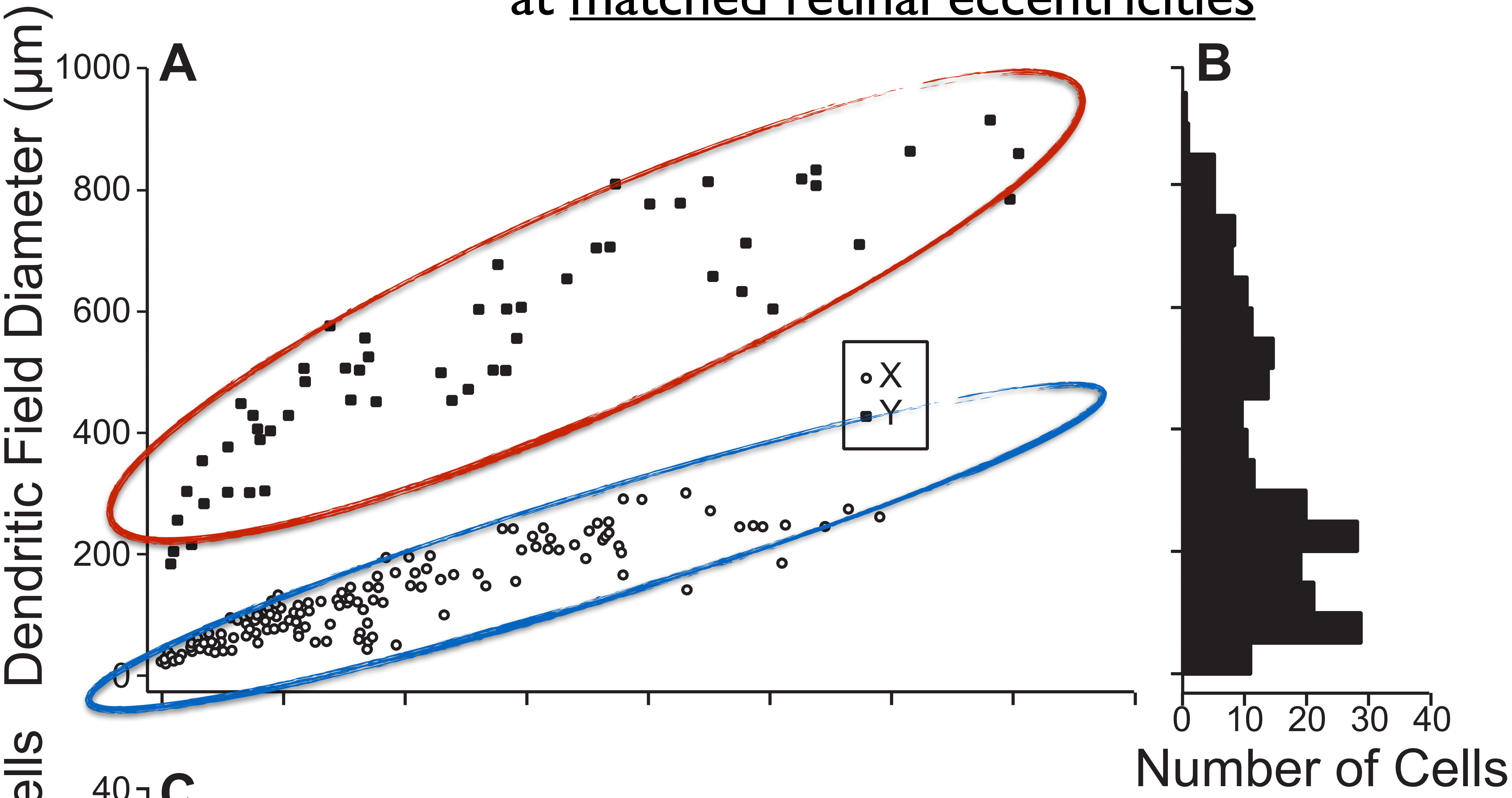


Fig. 11. Cat ganglion cells (Golgi stained wholemount views).

X and Y retinal ganglion cell receptive field size comparison at matched retinal eccentricities




S. Murray Sherman

Figure 2.3
Measures of distance from the area centralis within retina and diameter of dendritic arbor for X and Y retinal ganglion cells of the cat. *A*. Relationship of the two variables. Note the clear separation of the X and Y classes within this scatterplot. *B*. Histogram of dendritic arbor diameters for cells in *A*. C. Histogram of distances from the area centralis for cells in *A*. Note that with the single parameters of *B* and *C*, it is not possible to discern more than a single cell population. (Redrawn from Rodieck and Brening, 1983, and based on the data of Boycott and Wässle, 1974, with permission). For the functional distinction between the X and Y cells, see the legend for figure 2.5.

morphology reflects function (retinal ganglion cells)

	Y	X	W
RF center size	large	small	large
linearity	nonlinear	linear	?
soma size	large	medium	small
axon diameter	large	medium	small
conduction time	fast	medium	slow
proportion of population	10%	40%	50%
morphological correlate	alpha cells	beta cells	gamma & delta cells
responses	transient	sustained	either

W cells detect direction of movement

Adapted from Jonathan Stone "Parallel Processing in the Visual System: The Classification of Retinal Ganglion Cells and Its Impact on the Neurobiology of Vision"

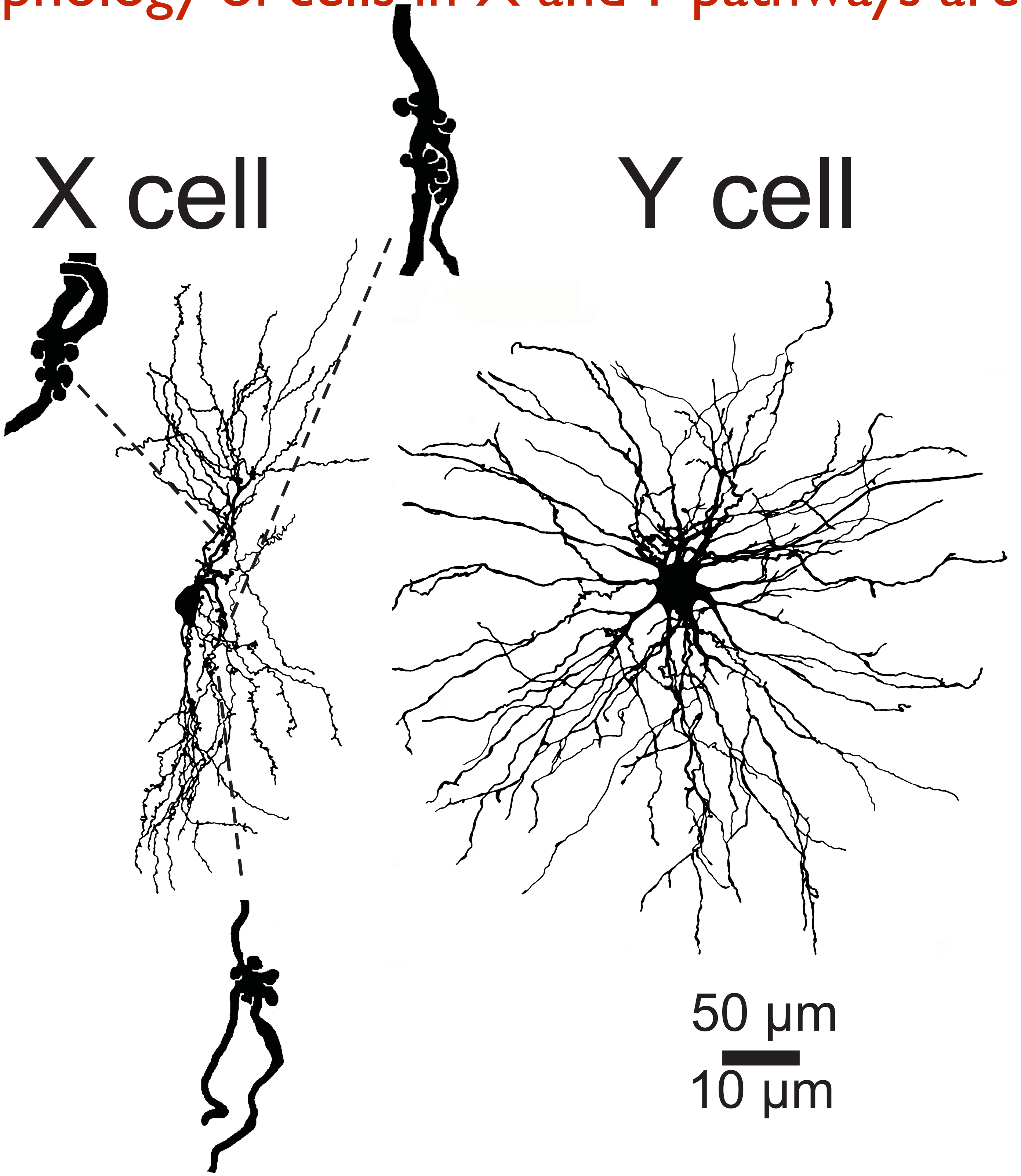
receptive field properties of **thalamic relay neurons** are similar to their afferent retinal ganglion cells and morphology of cells in X and Y pathways are different

smaller RFs

slower axons

tufted dendrites
oriented
perpendicular
to layer

"bushy"



larger RFs

faster axons

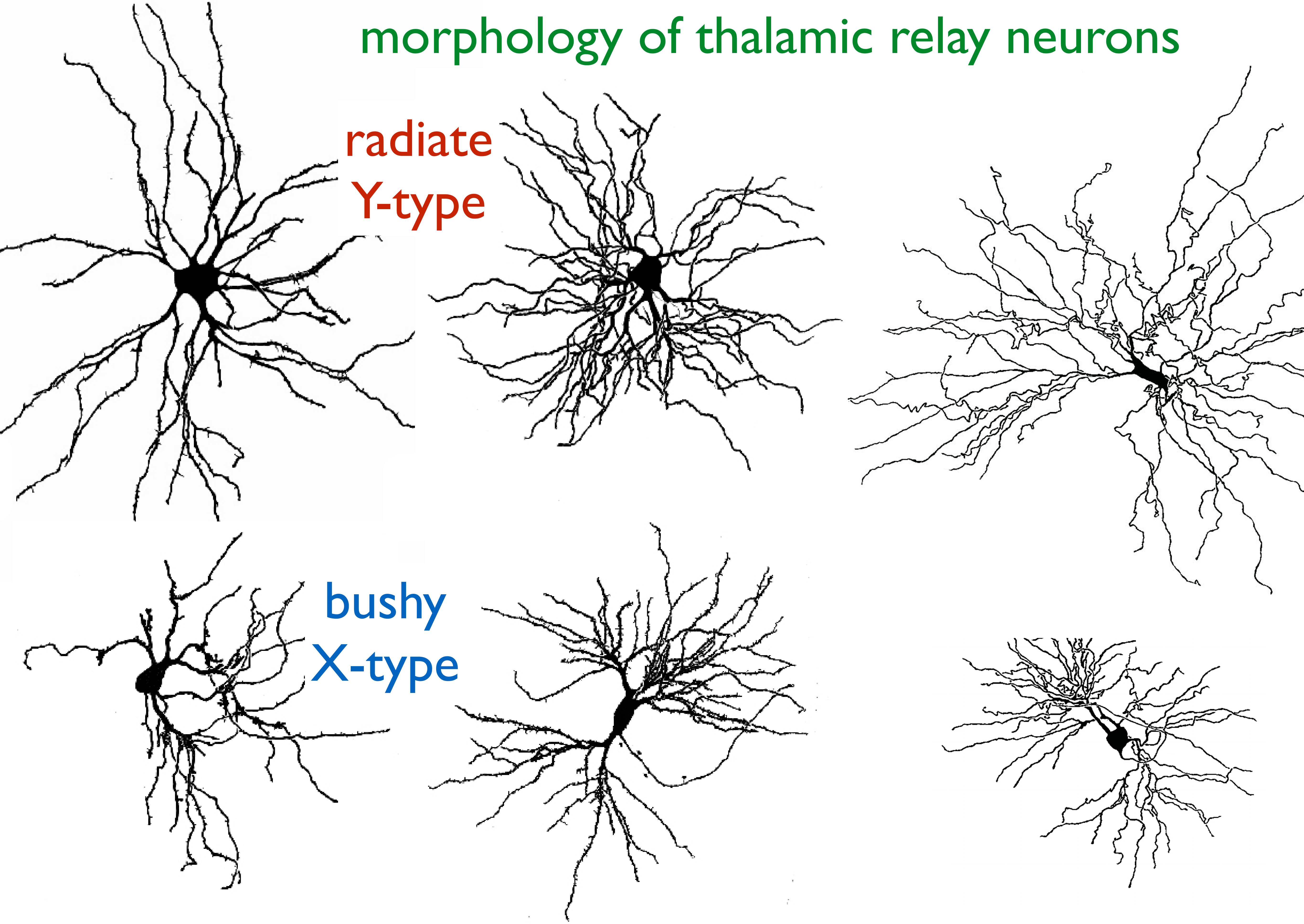
stellate
dendrites with
spherical
distribution

"radiate"

Figure 2.5

Tracings of an X cell and a Y cell from the A-laminae of the cat's lateral geniculate nucleus. The cells were identified physiologically during in vivo intracellular recording, and then horseradish peroxidase was passed from the recording pipette into the cell bodies. With minor, subtle changes, the receptive field properties of these thalamic neurons are the same as those of their retinal afferents, and thus the X/Y differences are established in the retina. Compared to X cells, Y cells have larger receptive fields at matched retinal eccentricities, faster conducting axons, better responses to visual stimuli of low spatial and high temporal frequencies, but poorer responses to low temporal and high spatial frequencies; also, Y cells respond to higher spatial frequencies with a nonlinear doubling response, whereas X cells show excellent linear summation to all stimuli (for details, see Sherman & Spear, 1982; Shapley & Lennie, 1985; Sherman, 1985). With proper histological processing, the horseradish peroxidase provides a dense stain, allowing visualization of the entire somadendritic morphology. The dendritic arbor of the X cell has the tufted pattern, is elongated, and is oriented perpendicular to the plane of the layers, whereas the Y cell dendrites show a stellate distribution with an approximately spherical arbor. The X cell also has prominent clusters of dendritic appendages near proximal branch points. These are hard to see in the cell reconstructions, so three examples are shown at greater magnification, with dashed lines indicating their dendritic locations (the scale is 50 μm for the cell reconstructions and 10 μm for the dendritic appendage examples). Data from Friedlander et al. (1981).

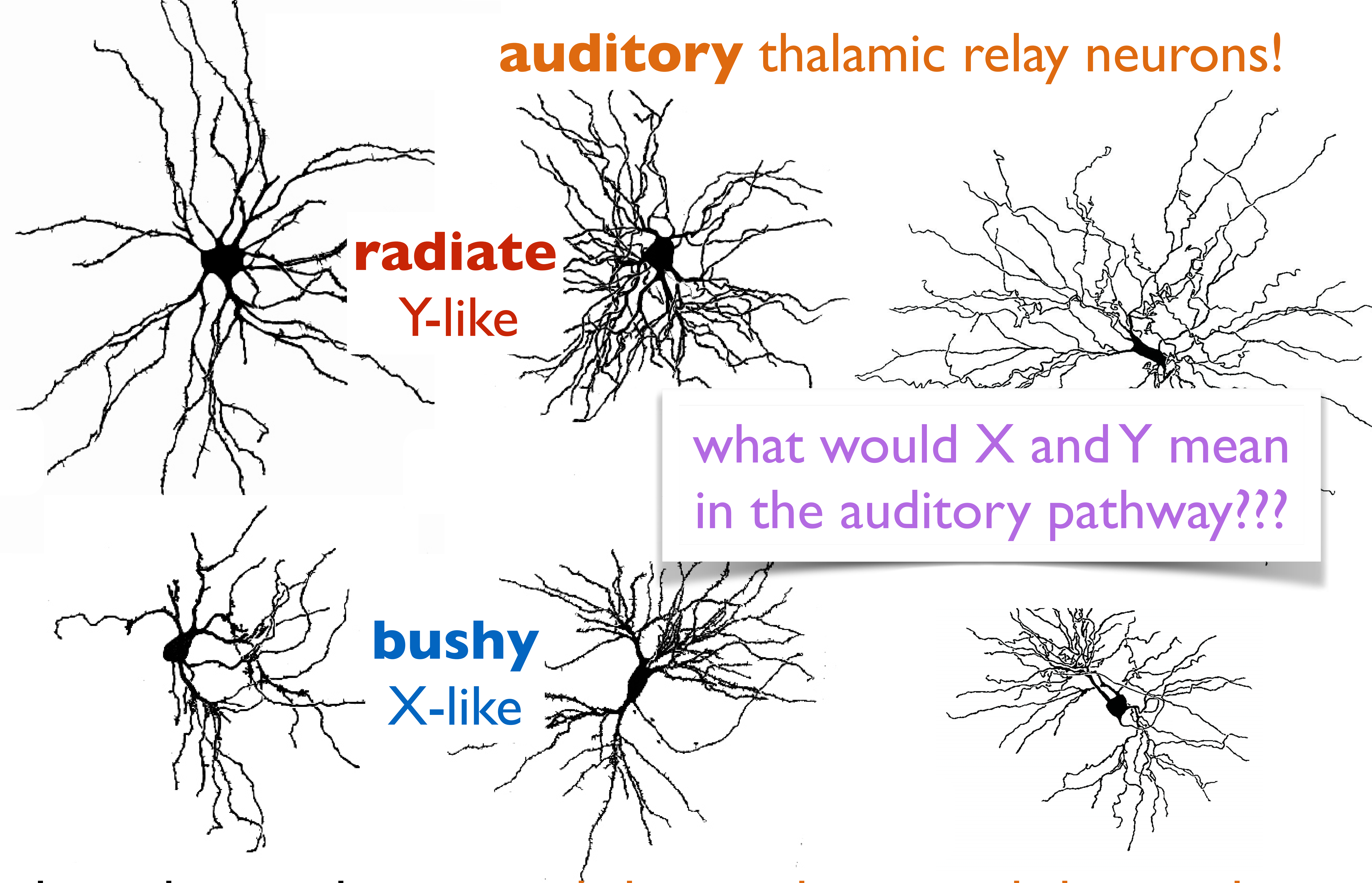
morphology of thalamic relay neurons



radiate
Y-type

bushy
X-type

auditory thalamic relay neurons!



radiate
Y-like

bushy
X-like

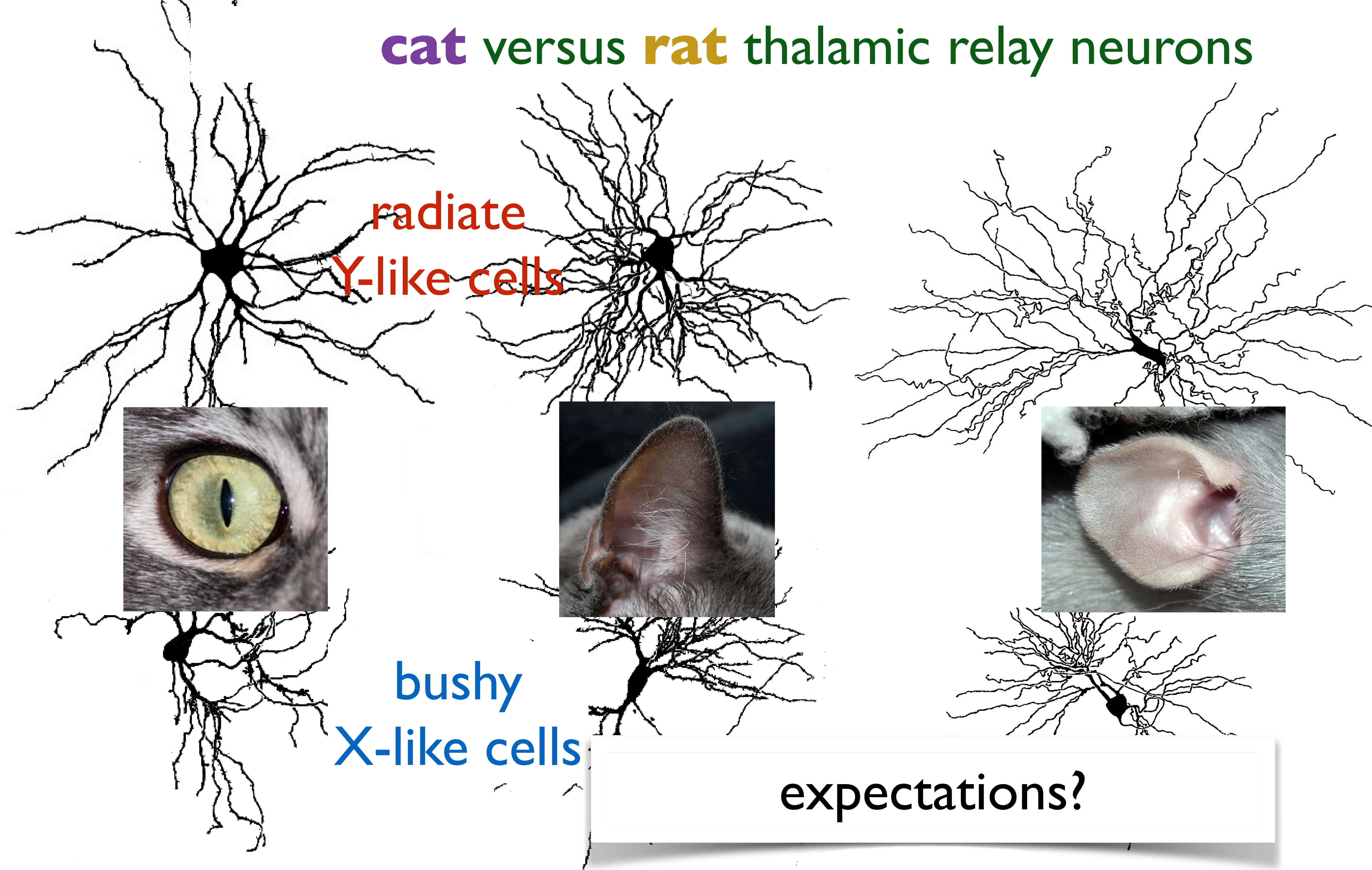
lateral geniculate
(vision)

medial geniculate
(hearing)

medial geniculate
(hearing)

what would X and Y mean
in the auditory pathway???

cat versus rat thalamic relay neurons



radiate
Y-like cells

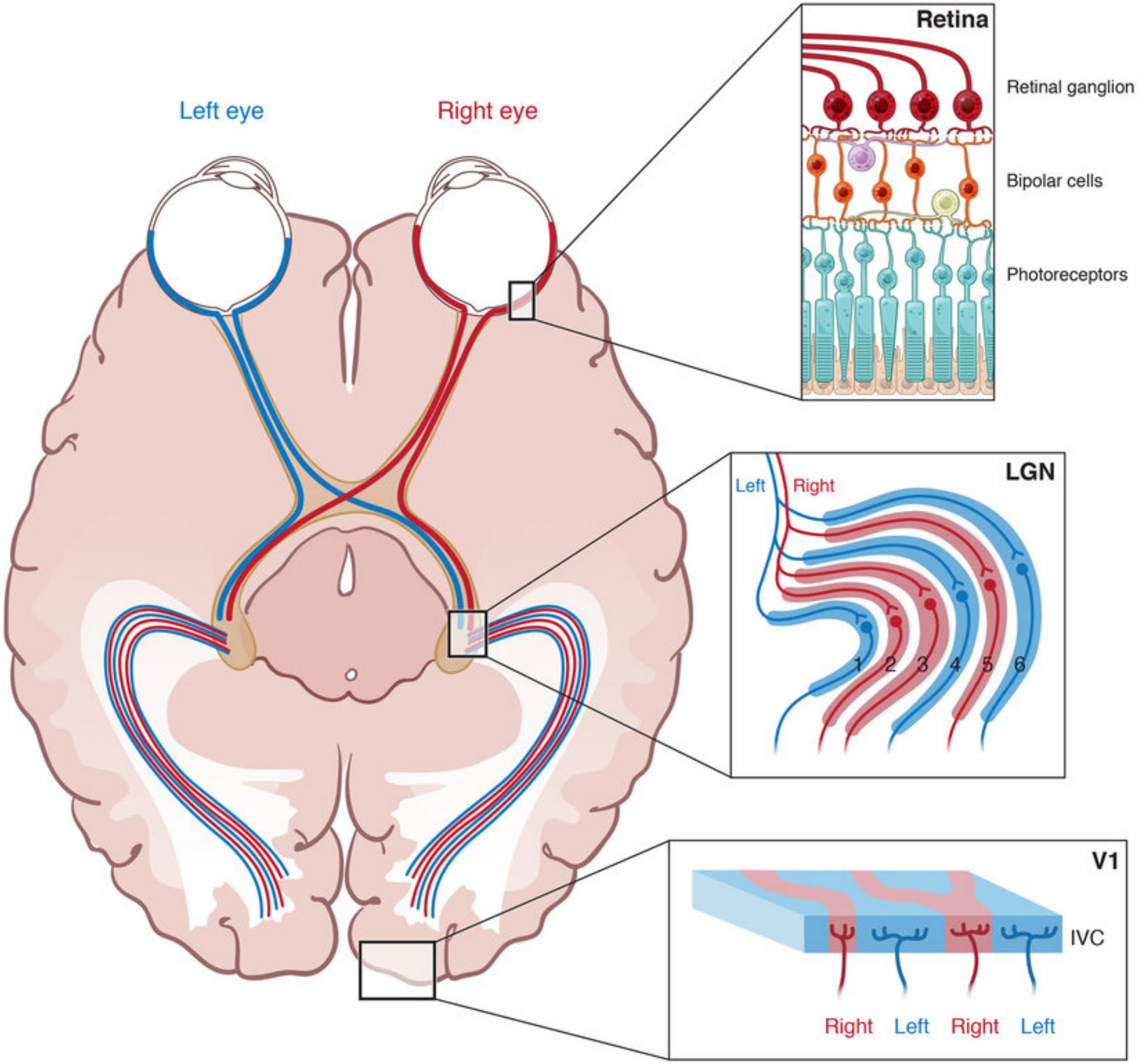
bushy
X-like cells

expectations?

lateral geniculate
(cat)

medial geniculate
(cat)

medial geniculate
(rat)



Ipsilateral

&

Contralateral

Illustration of segregation of projections from the eye. The retinal input from two eyes (blue represents left; red represents right) is segregated into distinct layers in the LGN by remodeling the axon branches and synaptic connections of RGCs. In the layer IVc of the primary visual cortex (V1), LGN neurons that respond preferentially to one eye segregate from neurons that respond preferentially to the other eye in structures called ocular dominance columns. Illustration by Sigrid Knemeyer.

parallel visual pathways - comparative neuroanatomy
cell types and layers of the lateral geniculate nucleus

MACAQUE

C P [on]
K
I P [off]
K
C P [on]
K
I P [off]
K
I M
K
C M
K

GALAGO

C P
C K
I K
I P
K
I M
K
C M
K

CAT

C X/Y
I X/Y
C Y
C W
I W
C W

FERRET
MINK

C X/Y on
X/Y off
I X/Y on
X/Y off
C Y
C W
I W
C W

TREE SHREW

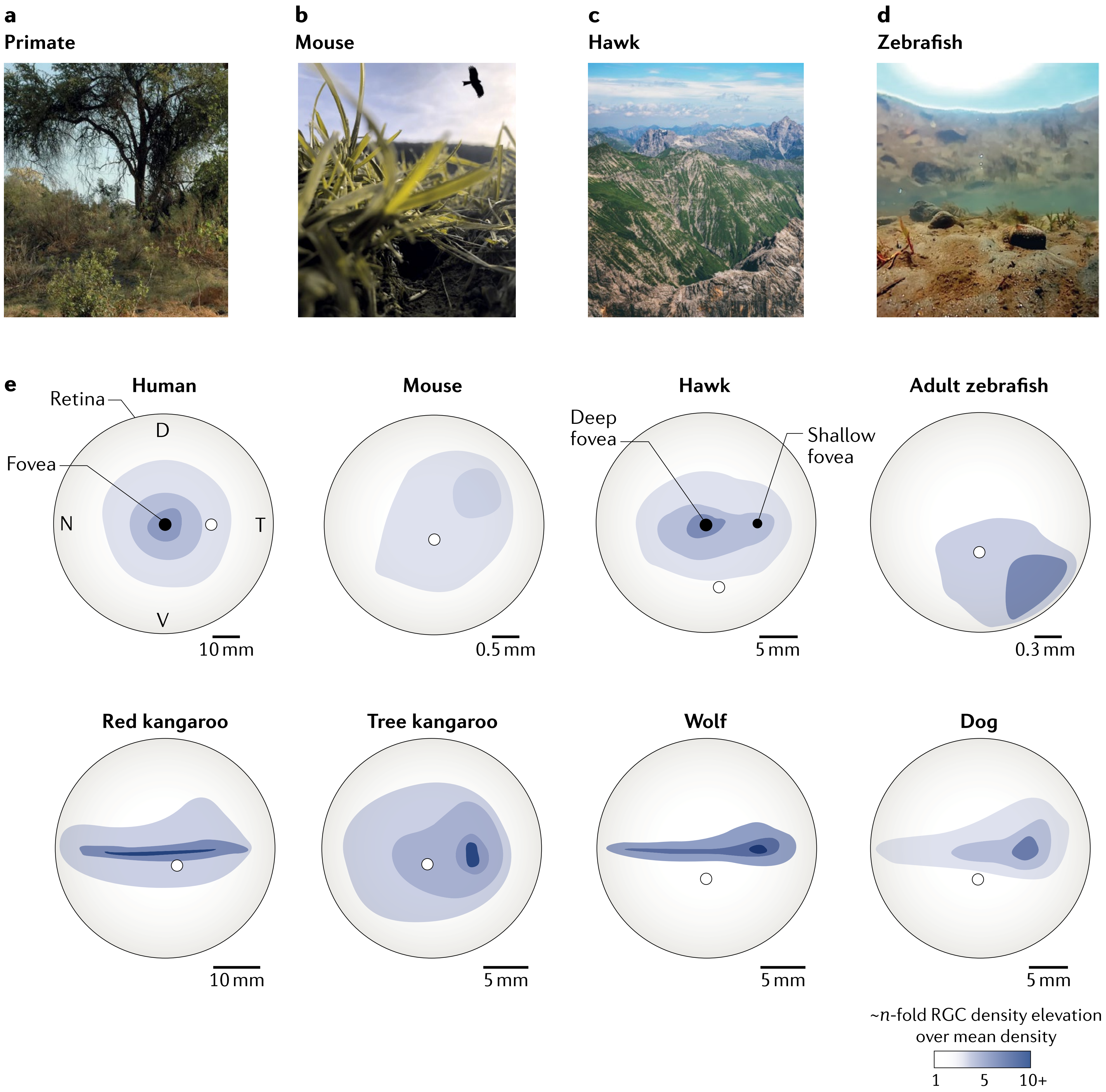
I X/Y on
C X/Y on
C (W)
C X/Y off
I X/Y off
C (W)

SQUIRREL

C X
I Y
C Y/W
I Y/W
C Y/W

Magnocellular / **P**arvocellular / **K**oniocellular
Y (alpha) / **X** (beta) / **W** (gamma, delta)
Ipsilateral & **C**ontralateral

comparative neuroscience
— retina —


a
Primate
b
Mouse
c
Hawk
d
Zebrafish
e
Human
Retina
D
Fovea
N
T
V
10 mm
Mouse
0.5 mm
Hawk
Deep fovea
Shallow fovea
5 mm
Adult zebrafish
0.3 mm
Red kangaroo
10 mm
Tree kangaroo
5 mm
Wolf
5 mm
Dog
5 mm
~n-fold RGC density elevation over mean density
1
5
10+

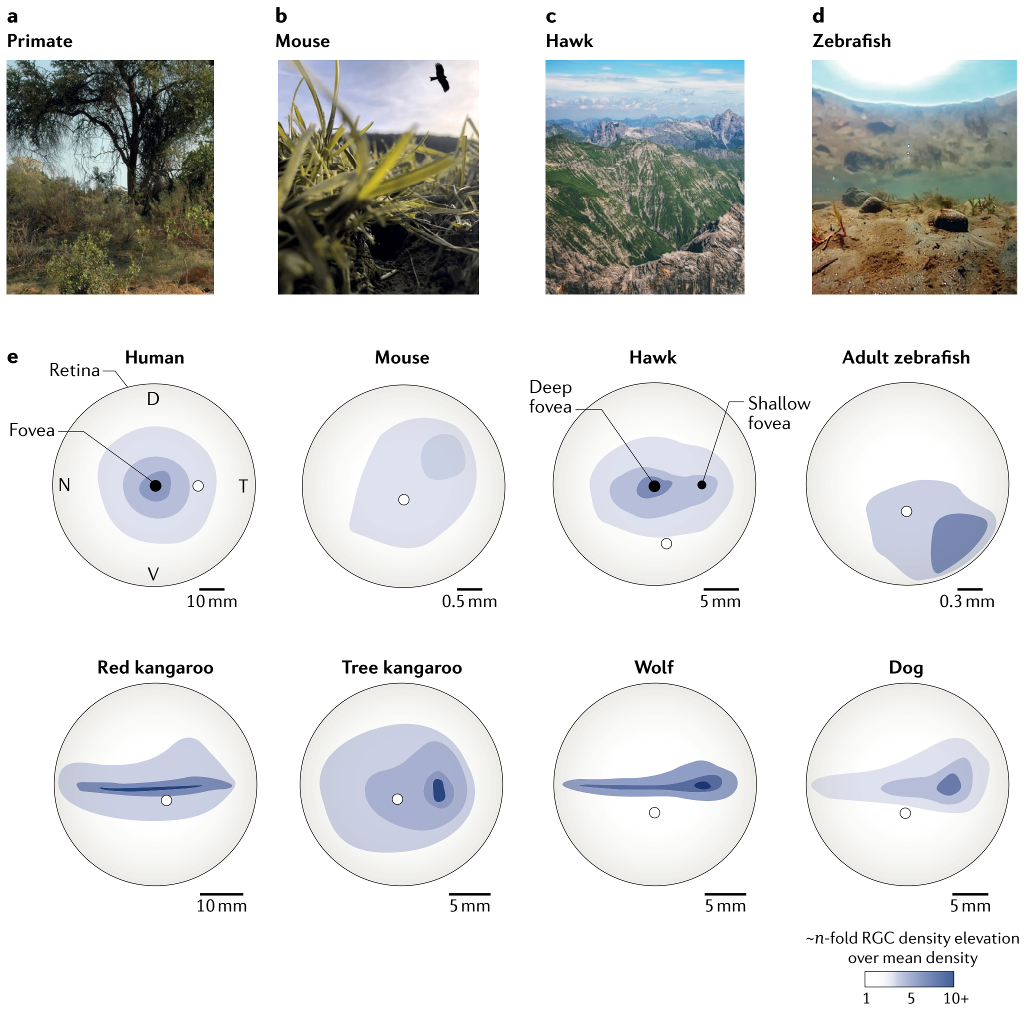
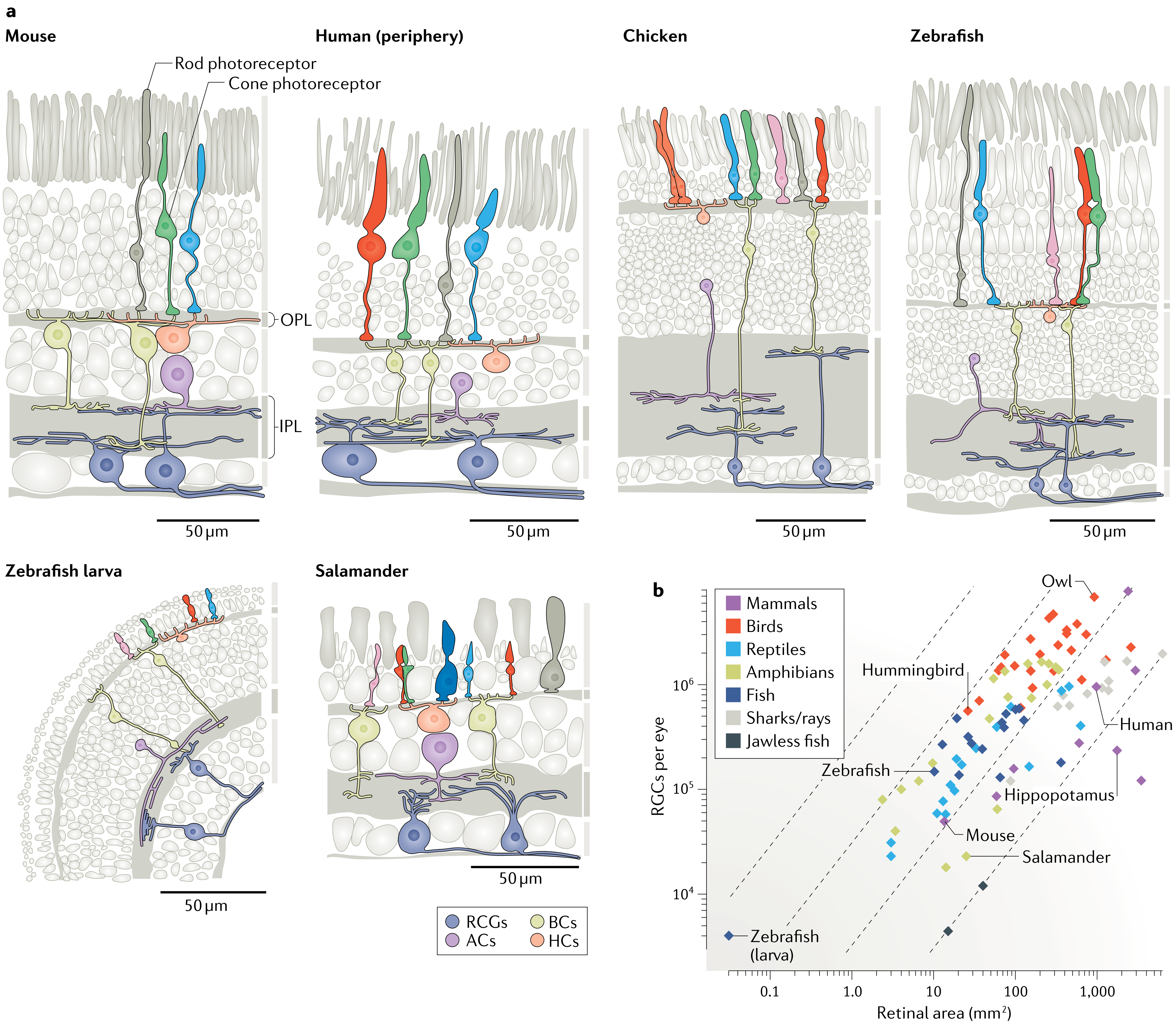


Fig. 2 | **Differential retinal ganglion cell topographies support vision in different visual environments. a–d** | Snapshots of the typical visual habitats of different animals. **e** | Representative retinal ganglion cell (RGC) density distributions across the whole retinas of different species. The schematics were created by our tracing published cell-count maps and subsequently using approximate graphical stitching to fit the images to a circular projection (human[234], adult zebrafish[198], hawk[85], red kangaroo[120], tree kangaroo[120], wolf[122] and dog[122]). The schematic of the mouse retina was sketched by hand on the basis of data in REFS[6,7,235]. For each of the published maps, we identified a number of density 'contours', for each of which we estimated the total area and RGC density. We used this information to calculate the mean RGC density across the bulk of the retina. In each schematic, areas shaded in the lightest grey are those in which RGC density corresponded to this mean density, and regions with darker shading show approximate relative elevations above this mean. The densities shown in each region are approximate, having been estimated from RGC density schematics of flat-mounted retinas depicted in the original publications. The white circles indicate the position of the optic nerve head in each retina. The optics of the eye invert the incoming image, meaning that the dorsal retina (D) surveys the ground, while the ventral retina (V) surveys the sky. N, nasal, T, temporal. Part **a** is adapted, with permission, from the database as described in REF.[167], Tkacik, G. et al., Natural images from the birthplace of the human eye. *PLoS ONE* **6,** e20409 (2011).


a
Mouse
Human (periphery)
Chicken
Zebrafish
Rod photoreceptor
Cone photoreceptor
OPL
IPL
50 μm
50 μm
50 μm
50 μm
Zebrafish larva
Salamander
50 μm
50 μm
RCGs
BCs
ACs
HCs
b
Mammals
Birds
Reptiles
Amphibians
Fish
Sharks/rays
Jawless fish
Owl
Hummingbird
Human
Zebrafish
Hippopotamus
Mouse
Salamander
Zebrafish (larva)
RGCs per eye
10^6
10^5
10^4
0.1
1.0
10
100
1,000
Retinal area (mm²)

Understanding the retinal basis of vision across species

Tom Baden[1,2]*, *Thomas Euler*[2,3] *and Philipp Berens*[2,3,4,5]

Abstract | The vertebrate retina first evolved some 500 million years ago in ancestral marine chordates. Since then, the eyes of different species have been tuned to best support their unique visuoecological lifestyles. Visual specializations in eye designs, large-scale inhomogeneities across the retinal surface and local circuit motifs mean that all species' retinas are unique. Computational theories, such as the efficient coding hypothesis, have come a long way towards an explanation of the basic features of retinal organization and function; however, they cannot explain the full extent of retinal diversity within and across species. To build a truly general understanding of vertebrate vision and the retina's computational purpose, it is therefore important to more quantitatively relate different species' retinal functions to their specific natural environments and behavioural requirements. Ultimately, the goal of such efforts should be to build up to a more general theory of vision.

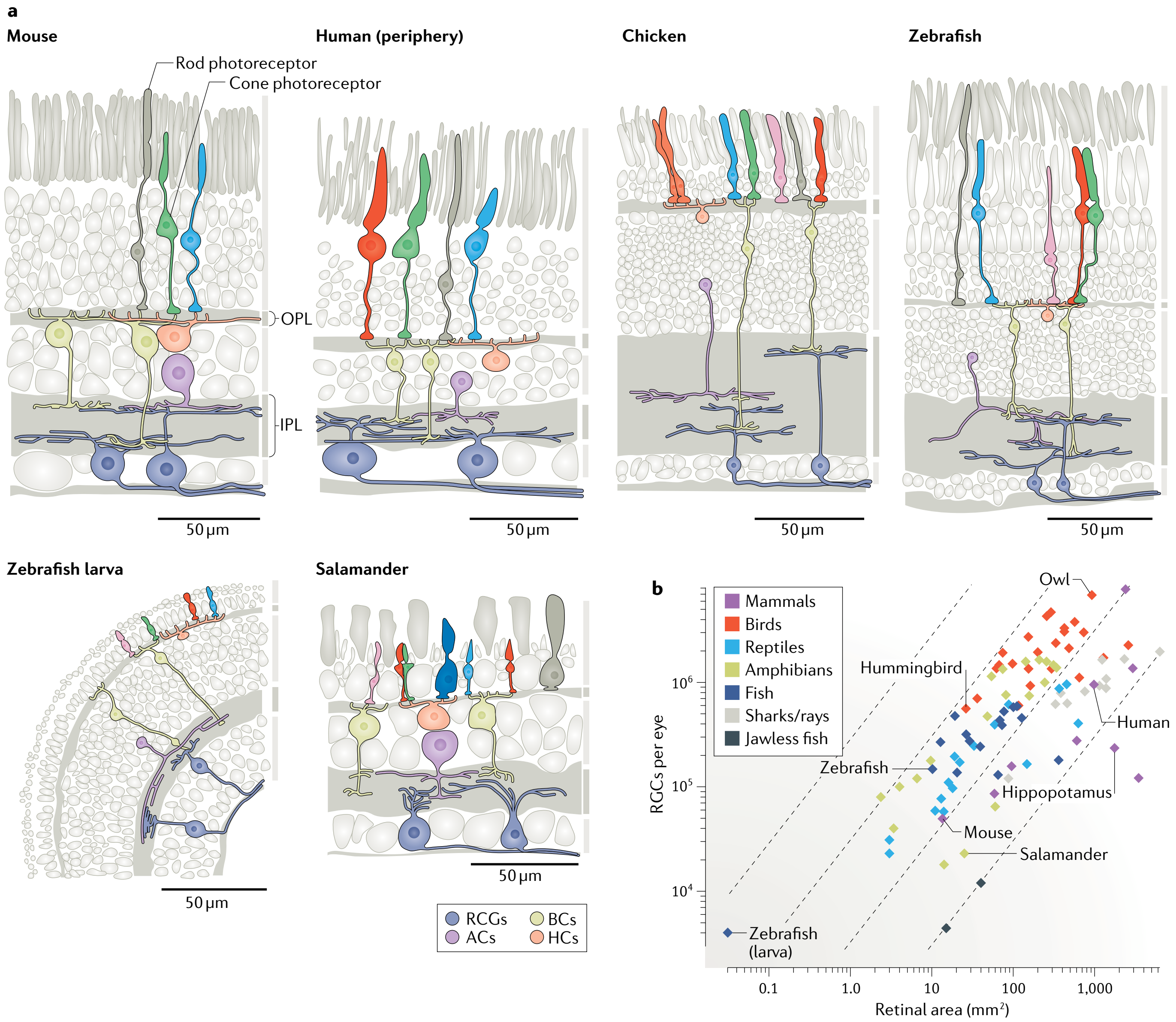
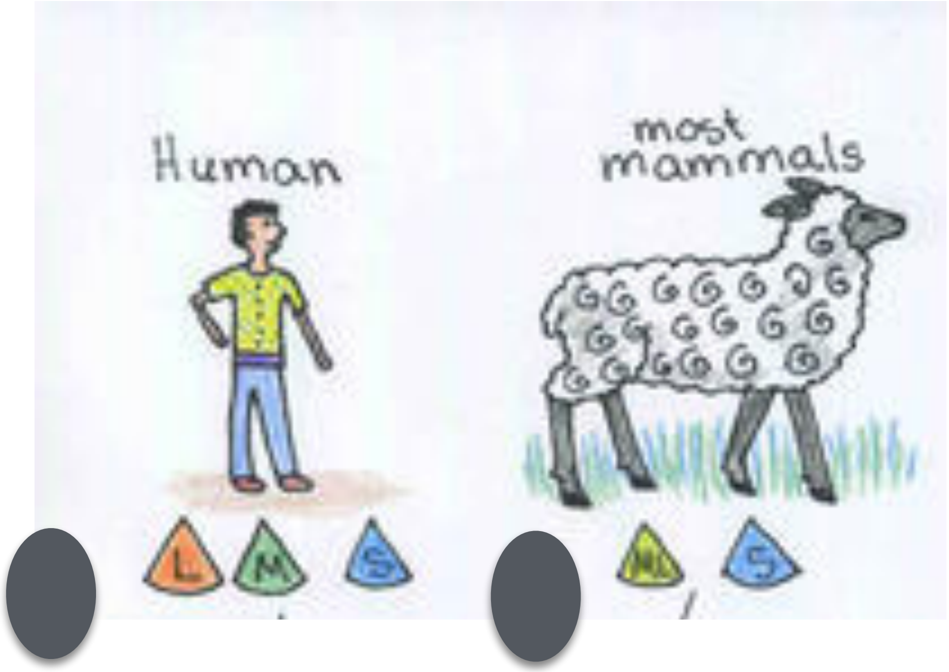


Fig. 1 | **Retinal composition across species. a** | The cell types present in the retinas of several contemporary vertebrate species (shown as transverse sections). For comparison, the plexiform (synaptic) layers (the outer plexiform layer (OPL) and inner plexiform layer (IPL)) are demarcated alongside each image. Example morphologies of different retinal neuron classes are highlighted. The schematics were created on the basis of data from the following references: mouse[191], human[192], chicken[193], zebrafish adult[194], zebrafish larva[195] and salamander[196]. **b** | Graph showing the total number of retinal ganglion cells (RGCs) present in the retinas of 105 different species versus their retinal surface area. For comparison, isodensity lines (indicating constant densities) are shown as dashed lines. The graph was created using data from REFS[3,71,85–87,89,92,104,108,124,126,173,197–234]. Species were selected for inclusion on the basis of the availability of quantitative RGC information for those species in the literature. For each clade for which such information was available, we selected one to four articles for inclusion on the basis of how readily the data could be extracted from a given study. Naturally, this list is therefore non-exhaustive. Detailed information is available in Supplementary Table 1. It can be seen that (in general) larger eyes comprise proportionally more RGCs. However, for any given eye size, RGC numbers across species vary by more than two orders of magnitude. Colours are used to distinguish between major clades of the vertebrate lineage. AC, amacrine cell; BC, bipolar cell; HC, horizontal cell.

comparative color vision (evolution of photoreceptor types and visual pigments)

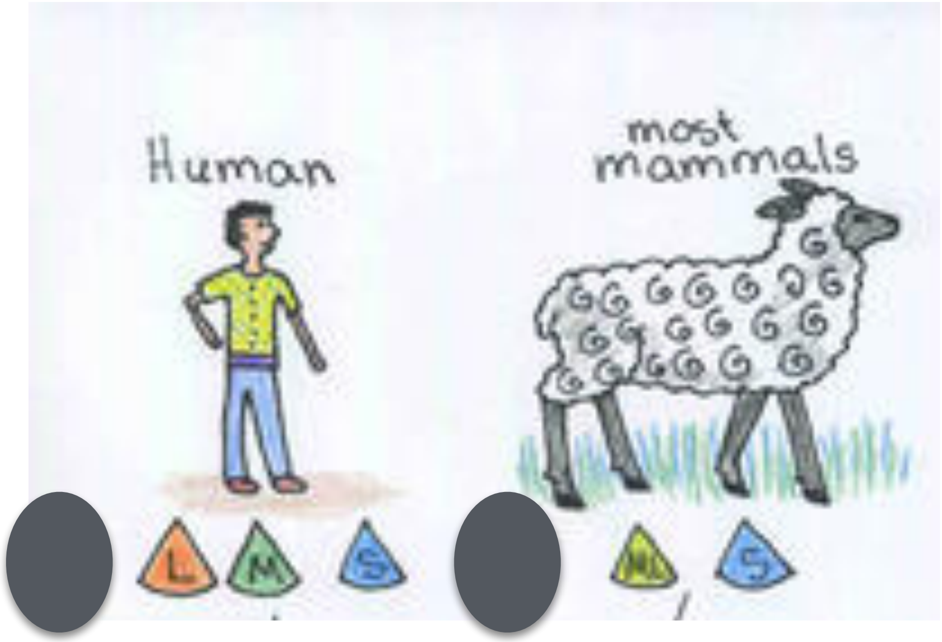


Primates have **trichromatic** color vision subserved by **three** spectral classes of cone.

Mammals have **rod-dominated retinas**. Non-primate mammals have **dichromatic** color vision subserved by **two** spectral classes of cone.

https://www.amnh.org/learn-teach/young-naturalist-awards/winning-essays2/2009-winning-essays/a-behavioral-test-to-examine-the-evolution-of-color-vision-in-vertebrates/

rod-dominated



cone-dominated

non-avian reptile

— reptilia —

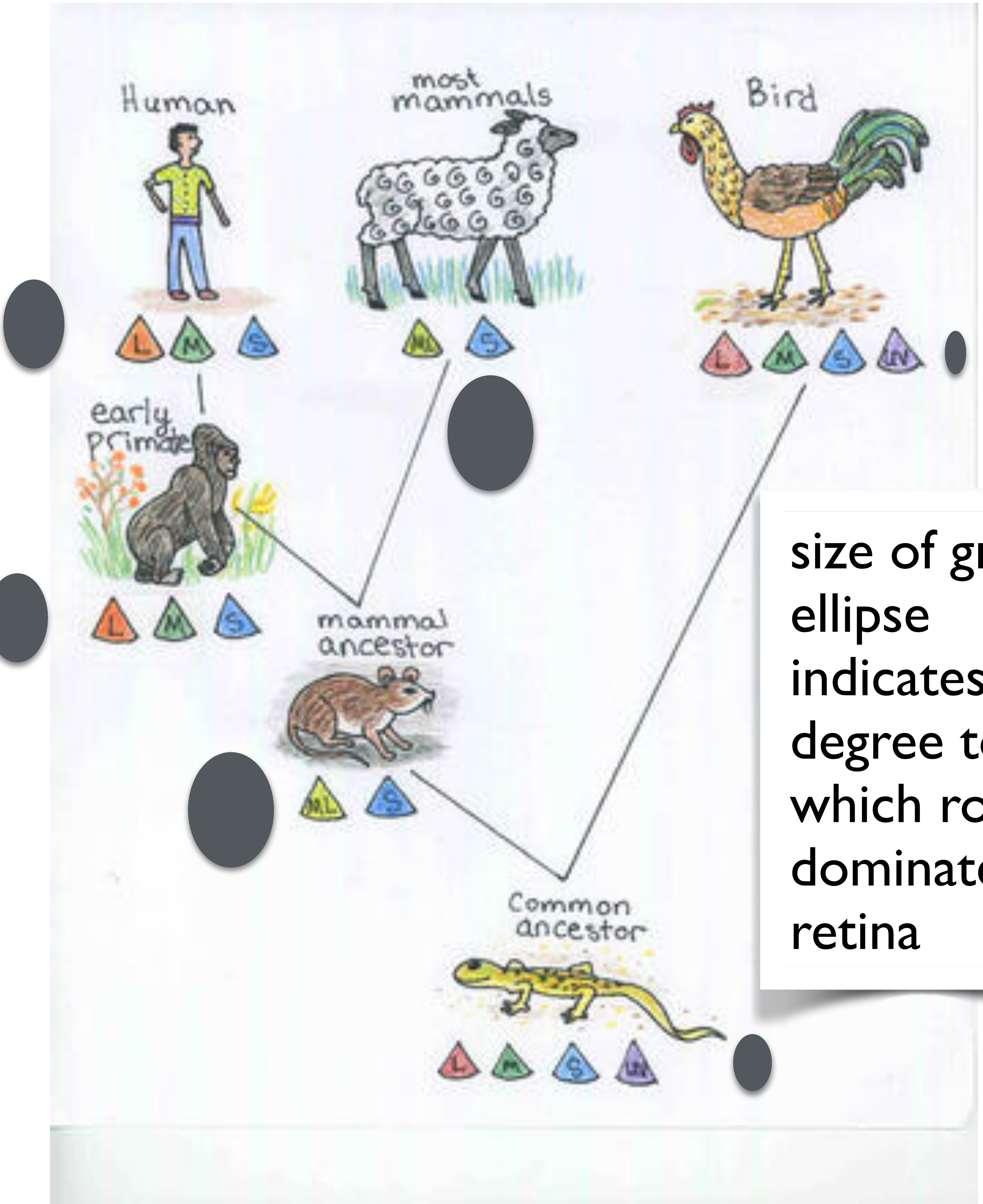
Modern teleost fish, reptiles and birds have **cone-dominated retinas**.

Many genera of teleost fish, reptiles and birds have **four** spectral classes of cones and **tetrachromatic** color vision.

https://www.amnh.org/learn-teach/young-naturalist-awards/winning-essays2/2009-winning-essays/a-behavioral-test-to-examine-the-evolution-of-color-vision-in-vertebrates/

Phylogenetic analysis of **opsin gene sequences** suggests that **ancestral pigments were cone pigments**, with rod pigments evolving last.

Mammals have **nocturnal ancestors**! Color vision requires more than moonlight. Loss of some cone pigments, and rods begin to dominate retina; also, mammals develop very good hearing.



size of gray ellipse indicates degree to which rods dominate retina

https://www.amnh.org/learn-teach/young-naturalist-awards/winning-essays2/2009-winning-essays/a-behavioral-test-to-examine-the-evolution-of-color-vision-in-vertebrates/

Evolution of colour vision in vertebrates

JAMES K. BOWMAKER

The expression of five major families of visual pigments occurred early in vertebrae evolution, probably about 350–400 million years ago, before the separation of the major vertebrate classes. Phylogenetic analysis of opsin gene sequences suggests that the ancestral pigments were cone pigments, with rod pigments evolving last. Modern teleosts, reptiles and birds have genera that possess rods and four spectral classes of cone each representing one of the five visual pigment families. The complement of four spectrally distinct cone classes endows these species with the potential for tetrachromatic colour vision. In contrast, probably because of their nocturnal ancestry, mammals have rod-dominated retinas with colour vision reduced to a basic dichromatic system subserved by only two spectral classes of cone. It is only within primates, about 35 millions years ago, that mammals 're-evolved' a higher level of colour vision: trichromacy. This was achieved by a gene duplication within the longer-wave cone class to produce two spectrally distinct members of the same visual pigment family which, in conjunction with a short-wavelength pigment, provide the three spectral classes of cone necessary to subserve trichromacy.

vision. In contrast, probably because of their