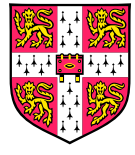
Neuroscience of vision

Guillaume Hennequin

g.hennequin@eng.cam.ac.uk

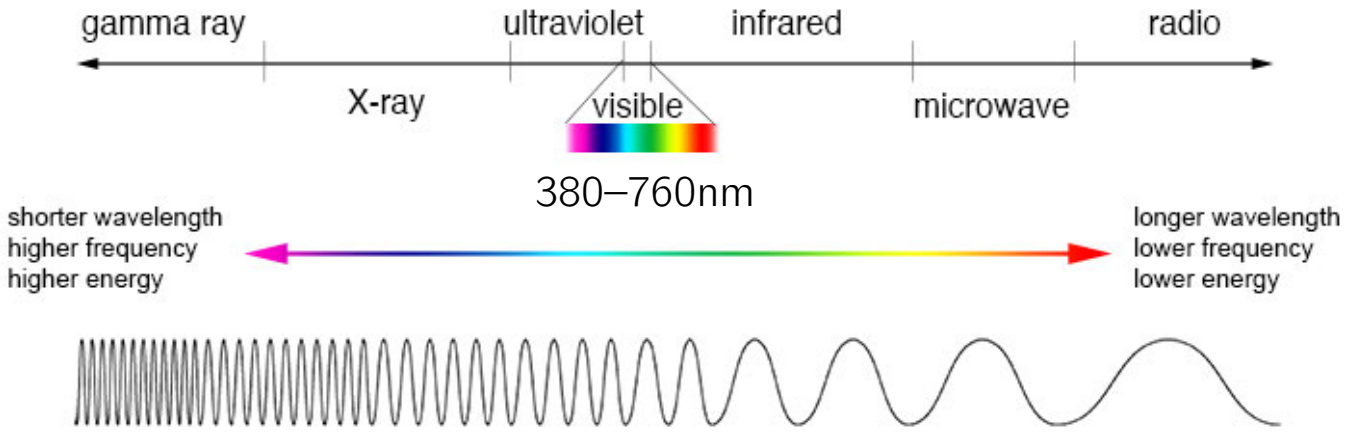
2P8 Bioengineering



UNIVERSITY OF
CAMBRIDGE

Vision

humans perceive the visible spectrum of electromagnetic radiation:



vision is our ability to infer properties of the world from the radiation it emits

this involves inferring form, motion, depth, colour (+ bind these together!)

OVERVIEW:

1. retina & visual pathway to cortex
2. spatial vision
3. depth vision
4. colour vision

Visual perception: a challenging computation

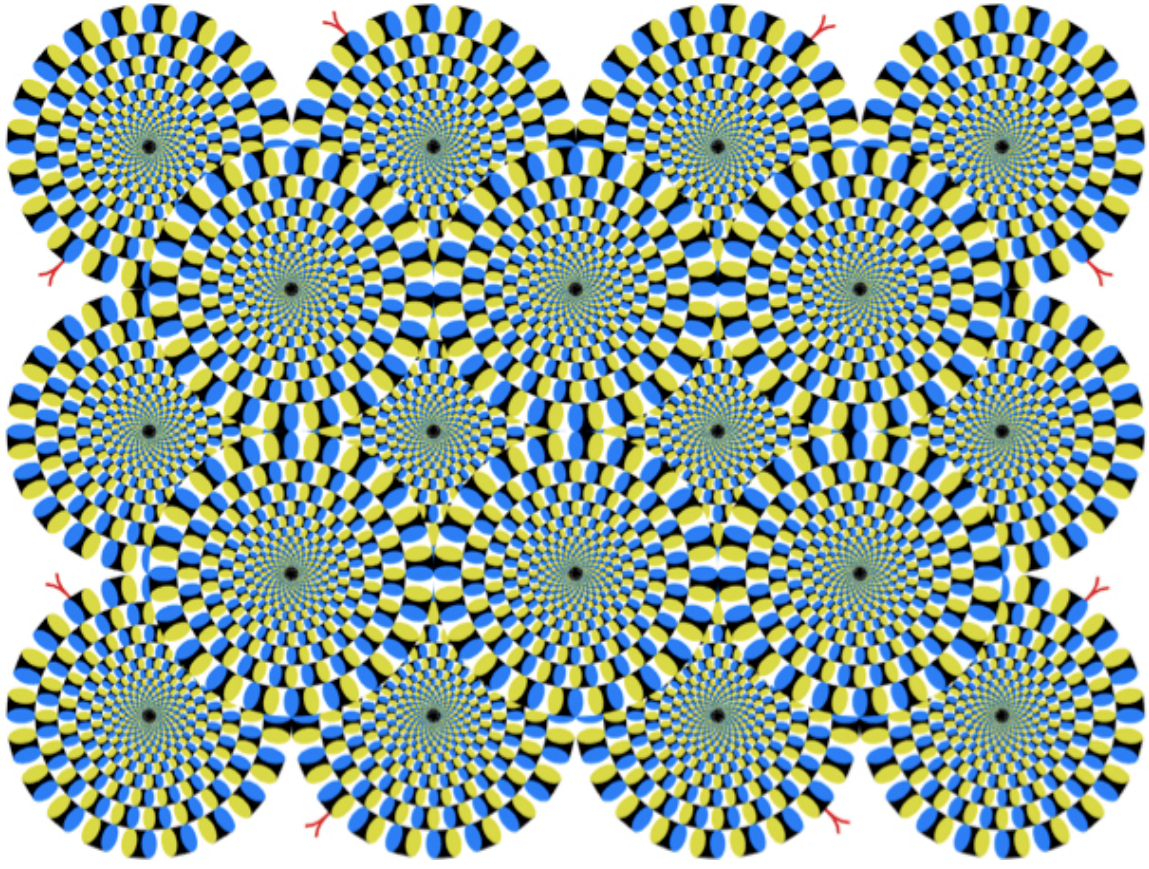
going from "raw pixel intensities" to a recognition of what's out there

problem: not a 1-1 mapping:

complementary approaches: computational, psychophysical, physiological

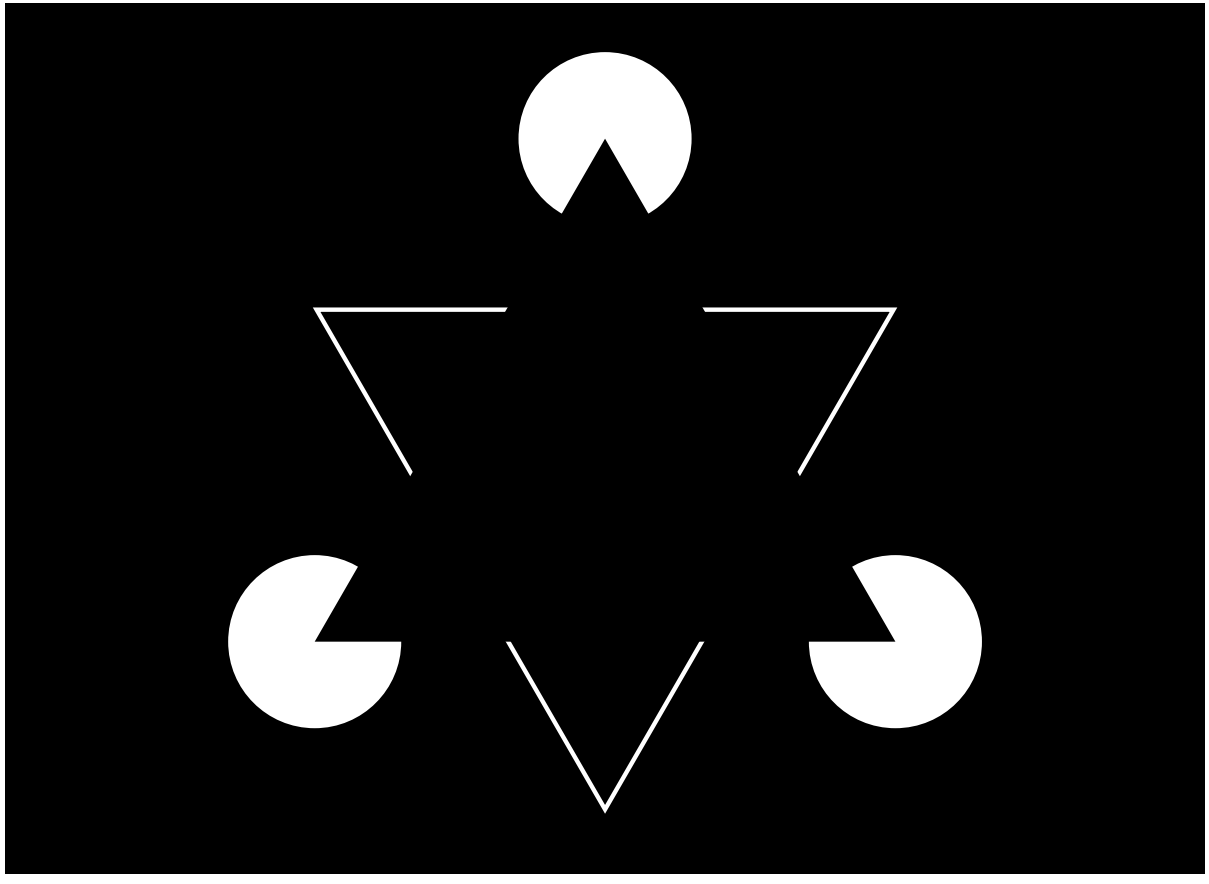
Vision is creative, not passive

vision can easily generate percepts which don't exist



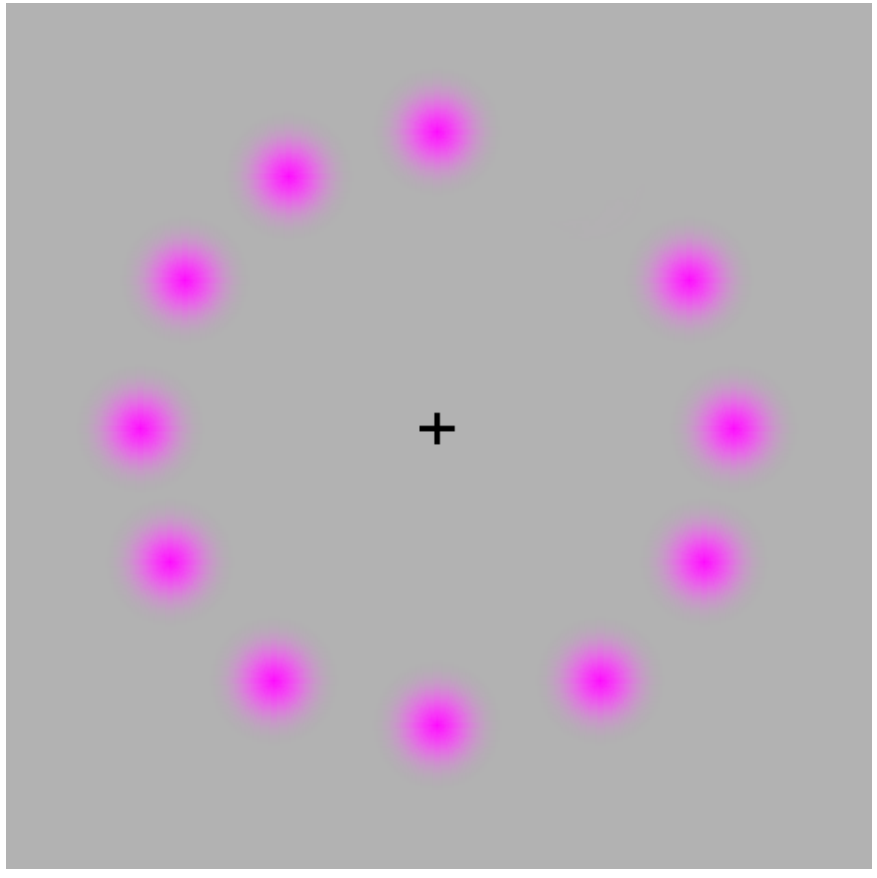
Vision is creative, not passive

vision can easily generate percepts which don't exist



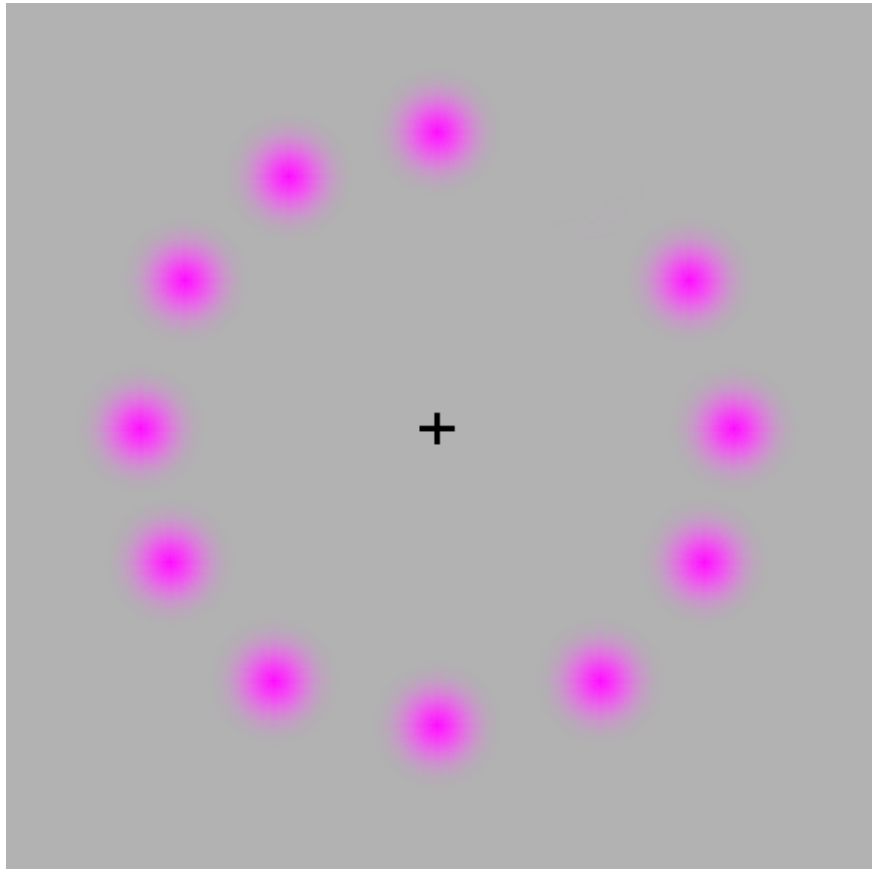
Vision is creative, not passive

vision can easily generate percepts which don't exist



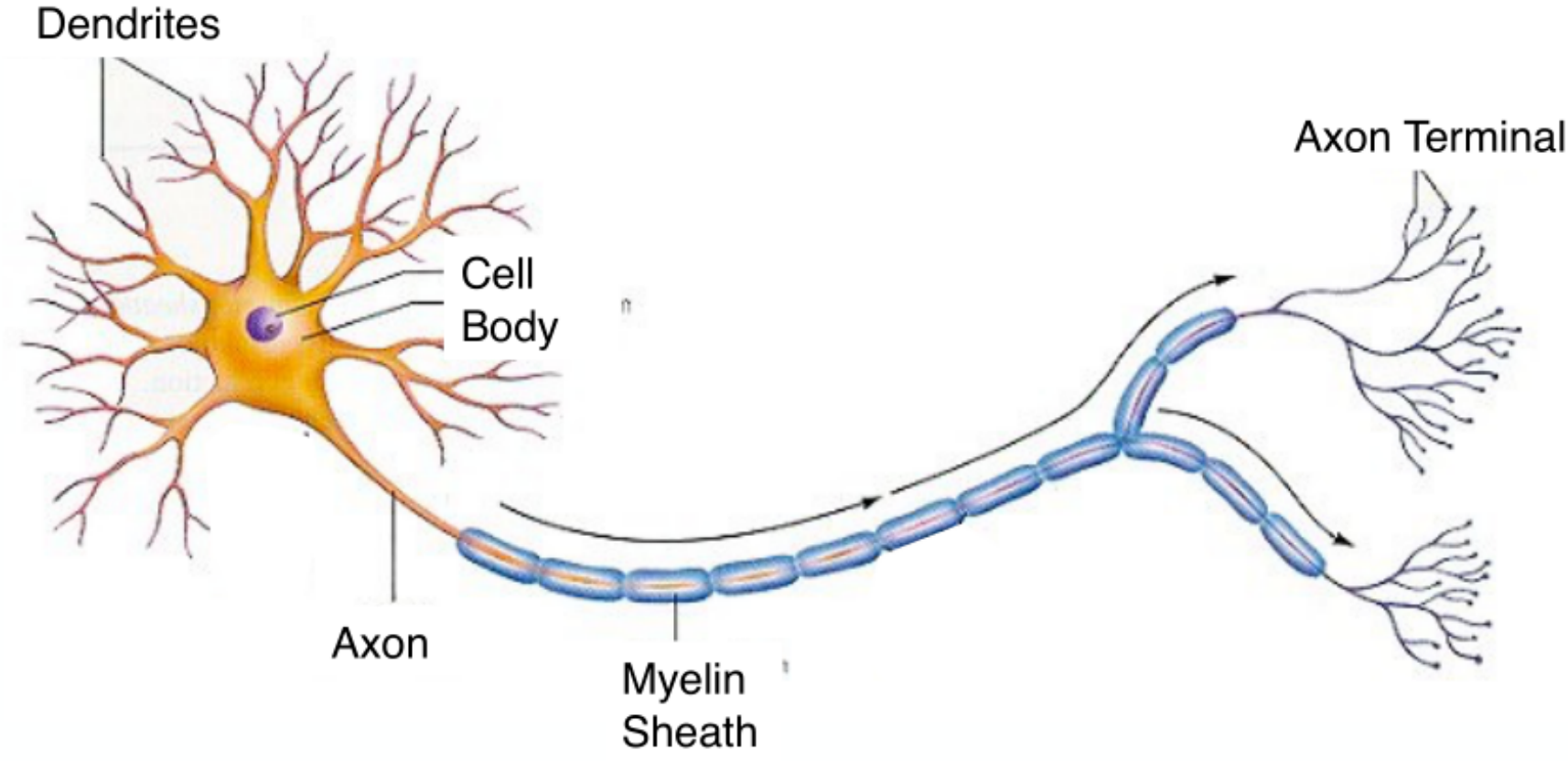
Vision is creative, not passive

vision can easily generate percepts which don't exist



+ dancing dots movie

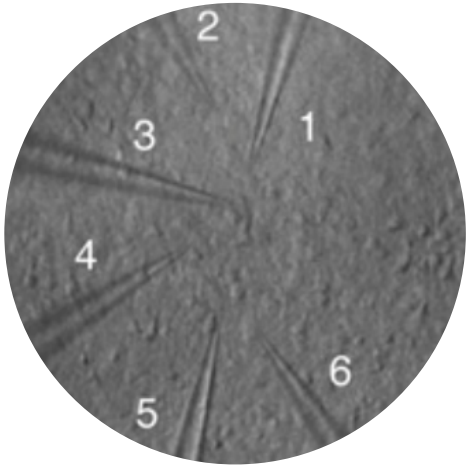
Neurons as the brain's building blocks

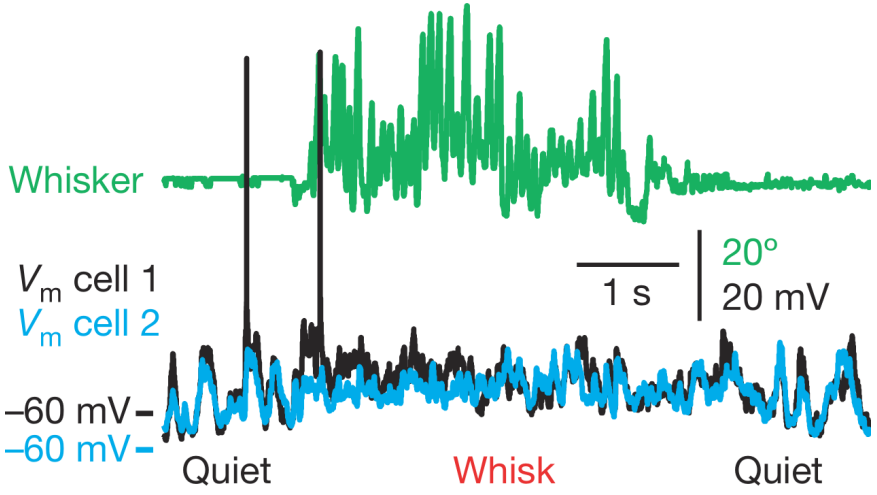


Interesting feature: **electric potential** between inside and outside of cell

Engineering problem: how can we measure it?

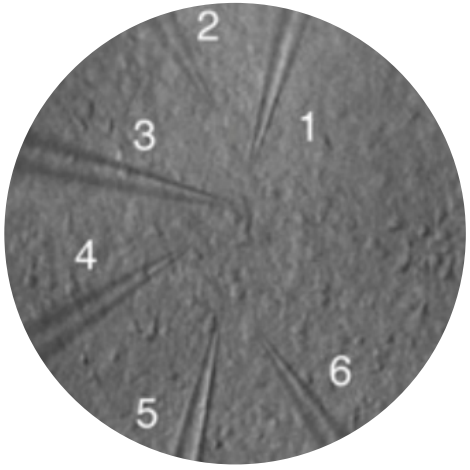
Intracellular recording

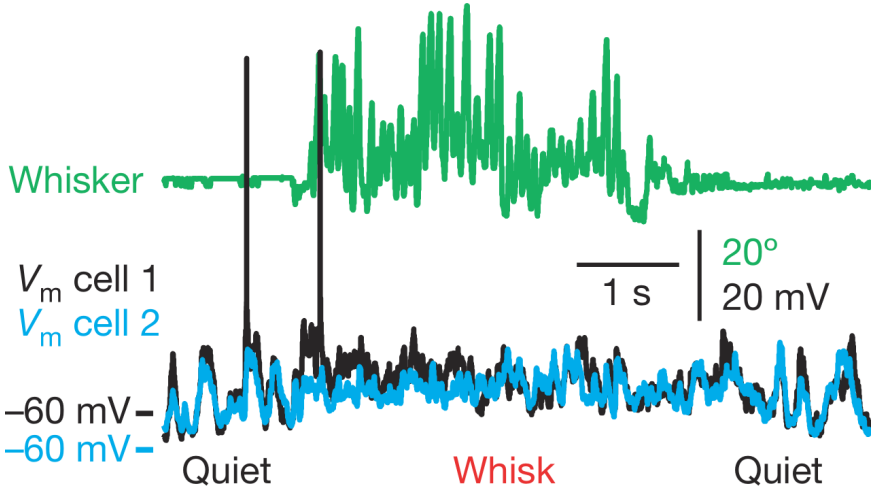




simultaneous intracellular recording of two neurons in mouse somatosensory cortex

Intracellular recording



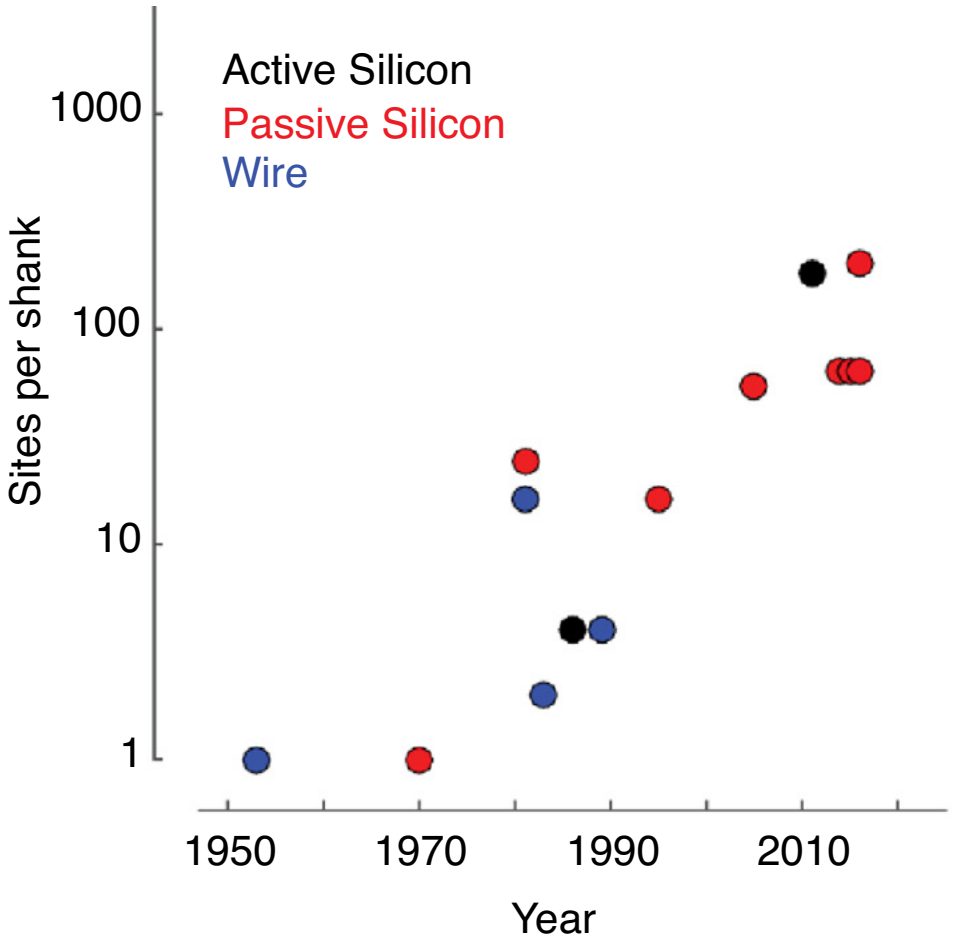


simultaneous intracellular recording of two neurons in mouse somatosensory cortex

Extracellular recording

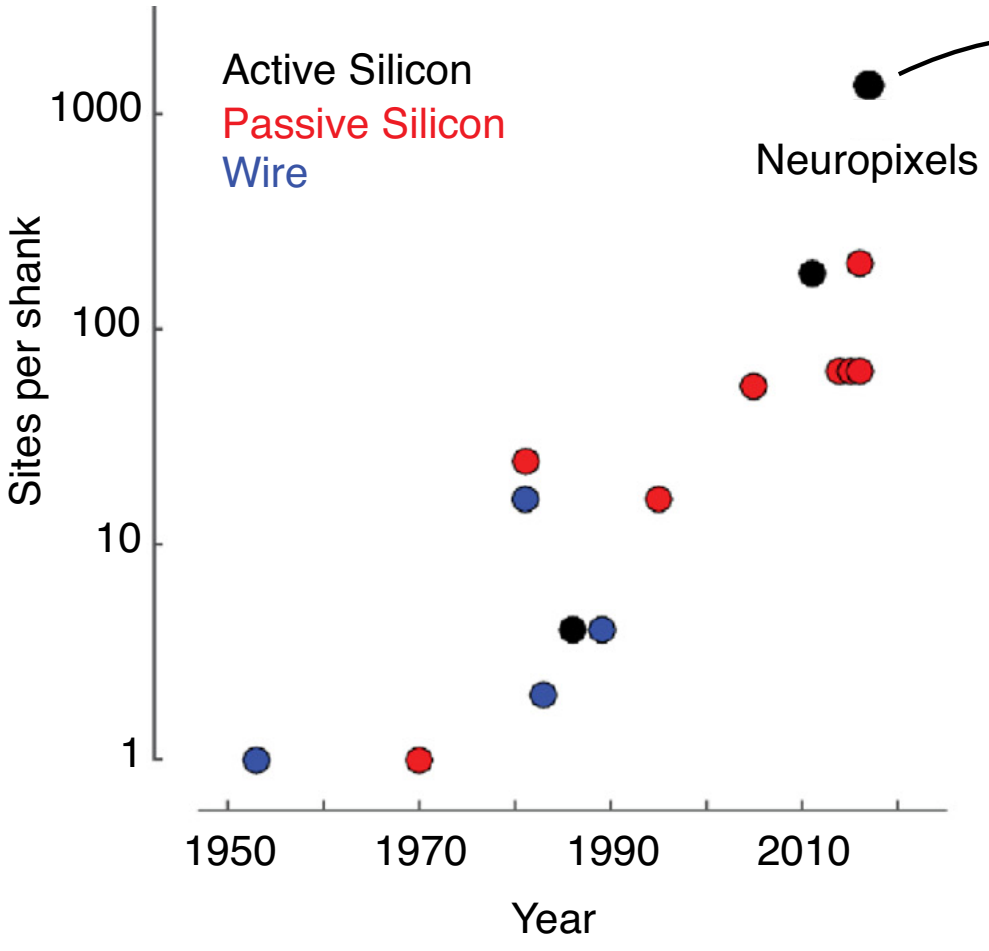
scales to whole arrays of electrodes

Technological advances in recordings



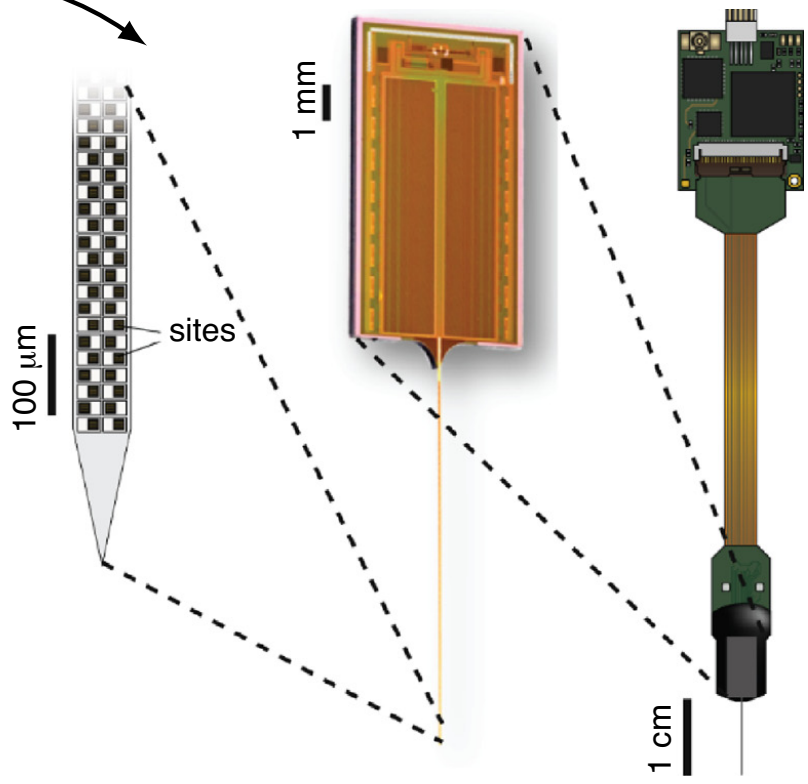
[Steinmetz et al. (2018)]

Technological advances in recordings



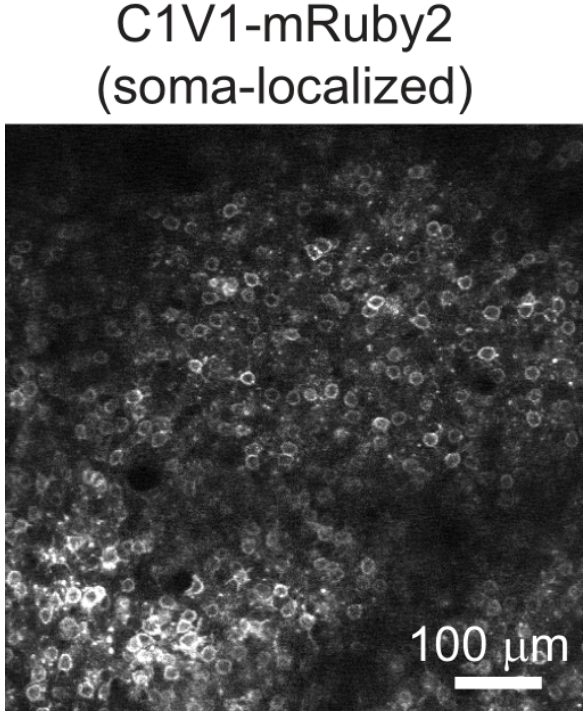
[Steinmetz et al. (2018)]

Jun et al. (2017)



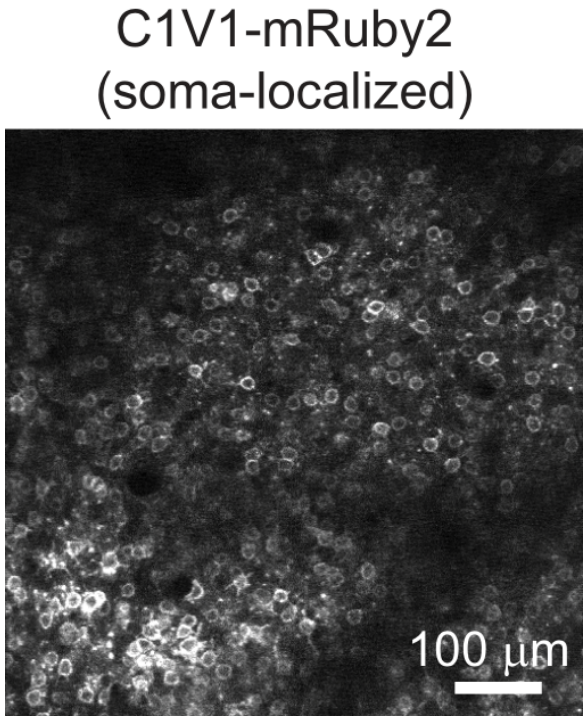
- 1000s of sites, traversing many regions
- but: neuron *location* unknown

Optics & genetics

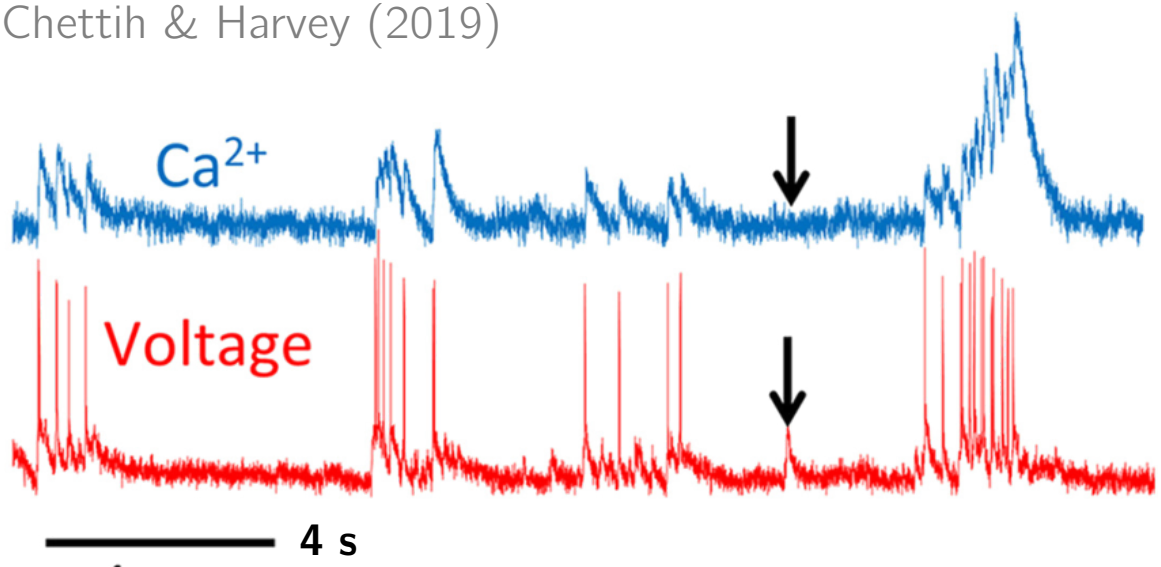


Chettih & Harvey (2019)

Optics & genetics



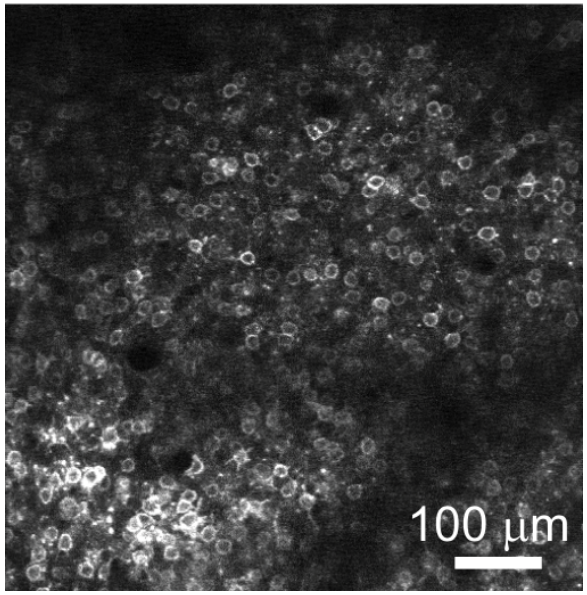
Chettih & Harvey (2019)



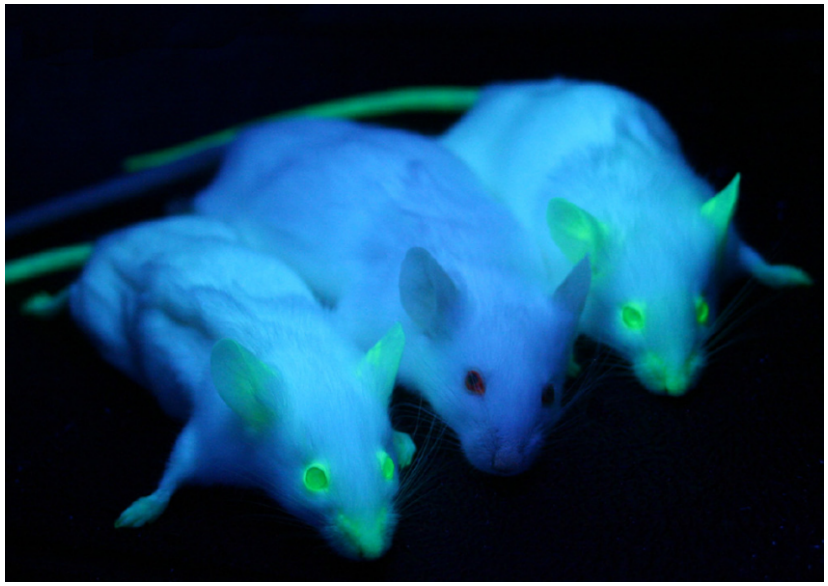
- large-scale recordings
- but slow Ca^{2+} dynamics
- needs deconvolution to extract action potentials

Optics & genetics

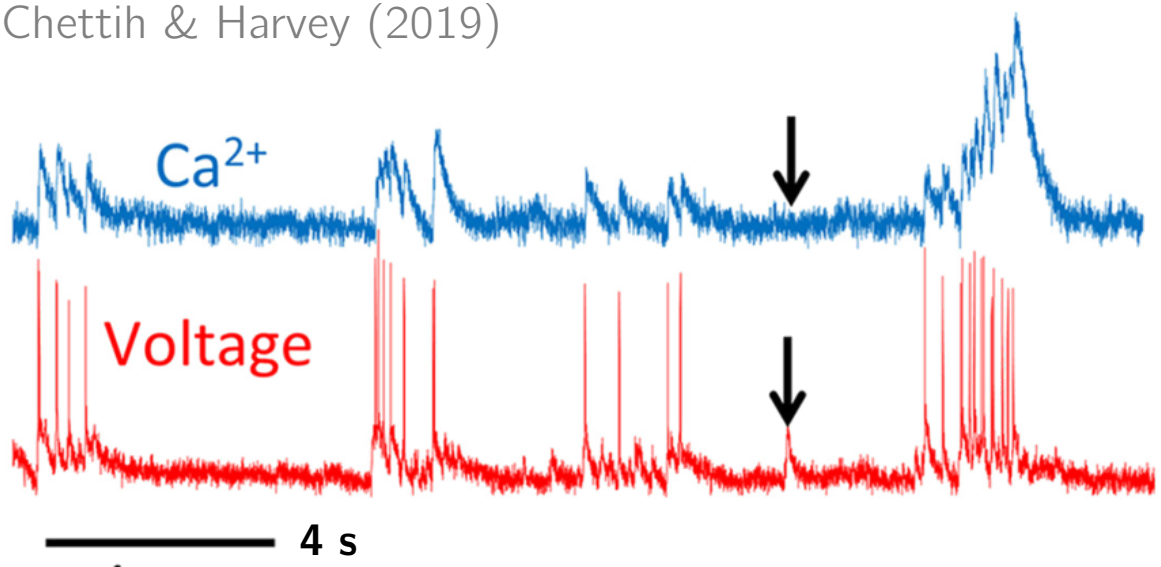
C1V1-mRuby2
(soma-localized)



Moen et al. (2012)

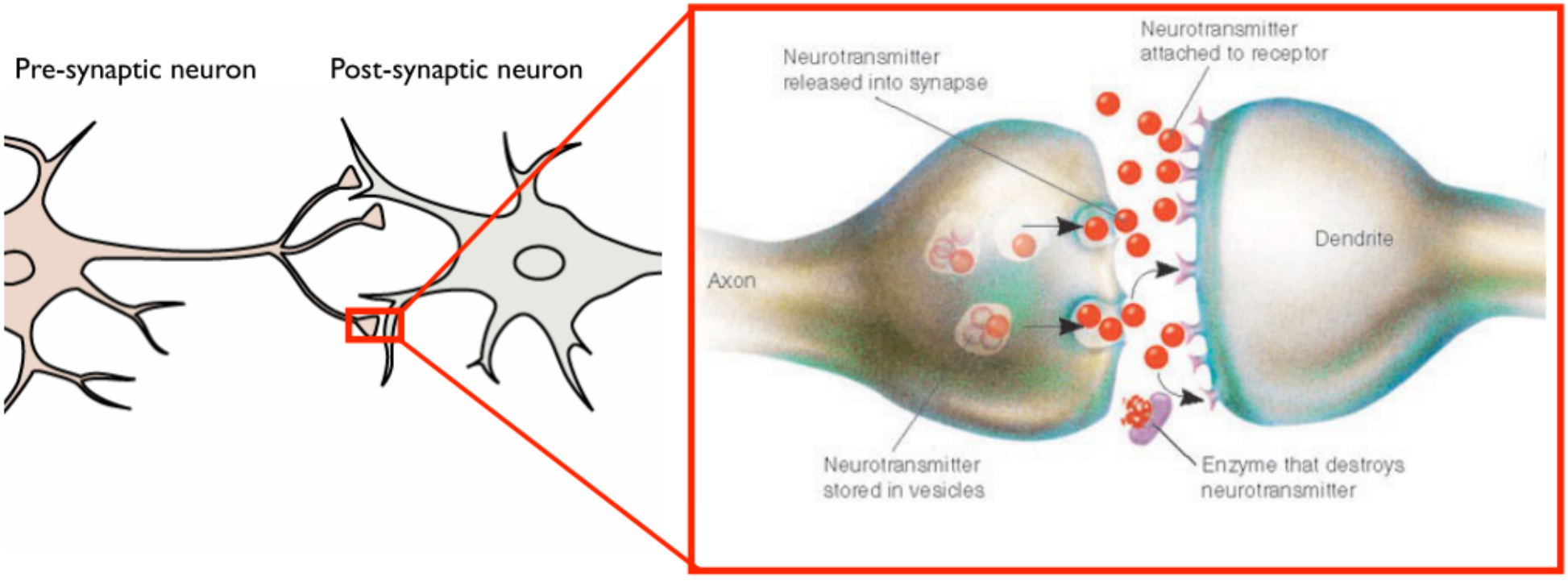


Chettih & Harvey (2019)



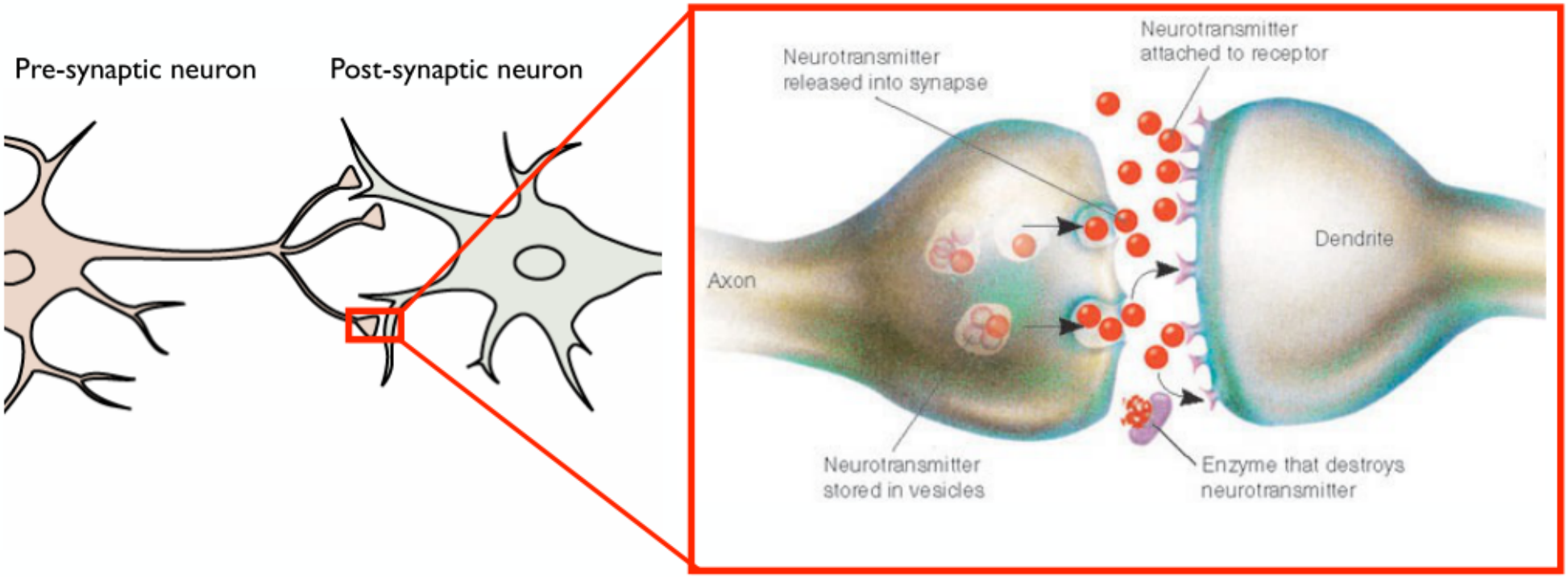
- large-scale recordings
- but slow Ca^{2+} dynamics
- needs deconvolution to extract action potentials

How neurons talk to each other: synapses



- axons contact other neurons at synapses
- neurotransmitter modules diffuse across synaptic gap
- attach to receptors and cause change in potential in post-synaptic neuron

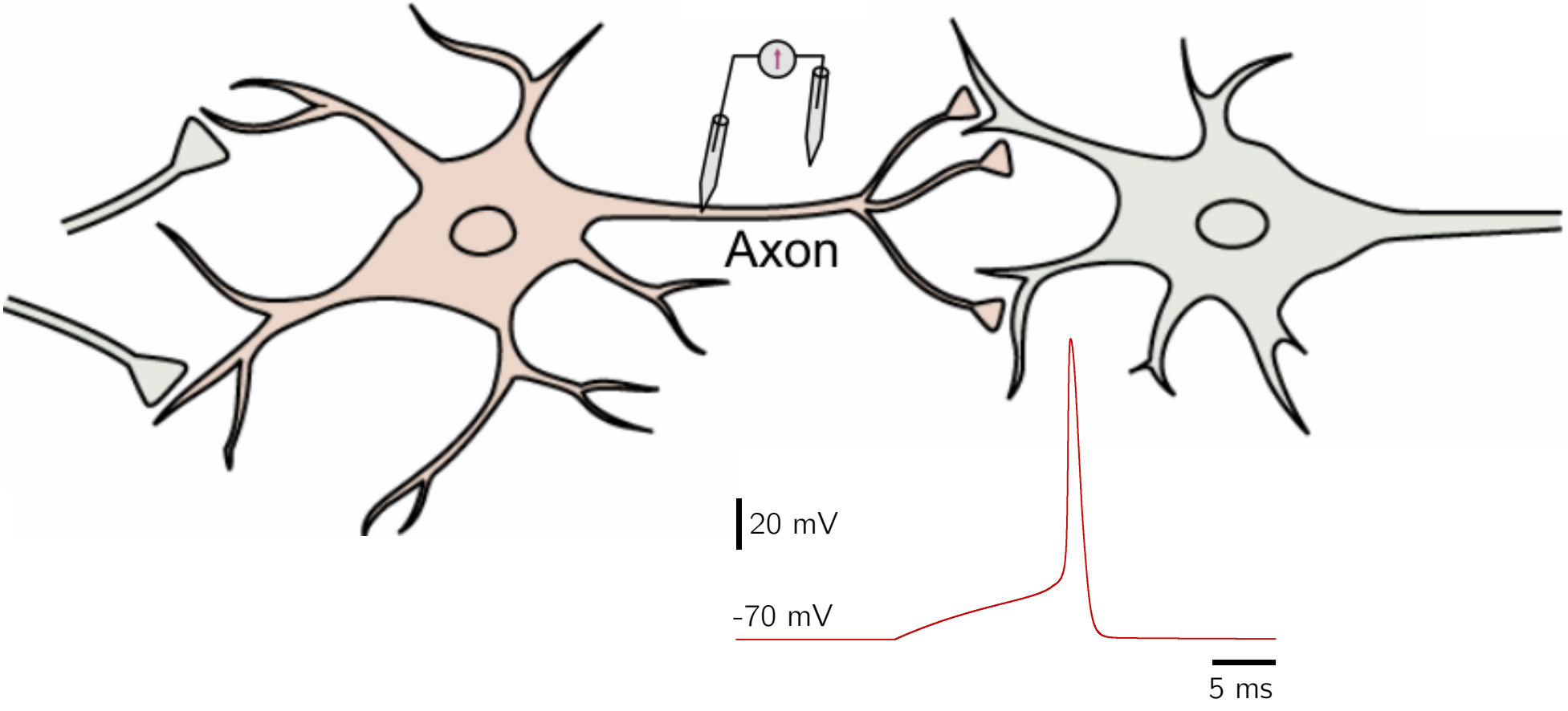
How neurons talk to each other: synapses



- axons contact other neurons at synapses
- neurotransmitter modules diffuse across synaptic gap
- attach to receptors and cause change in potential in post-synaptic neuron

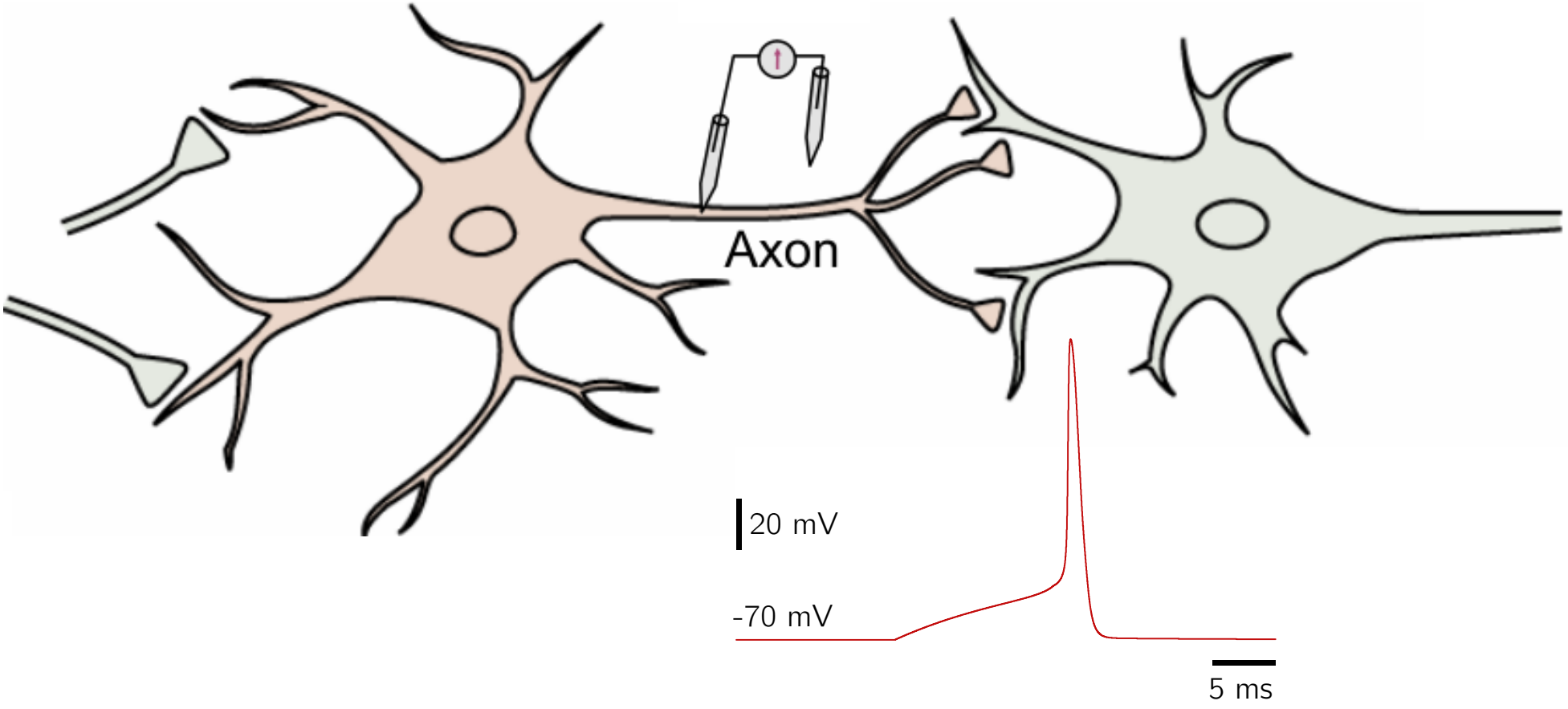
only occurs when potential is large enough at axon terminal

How neurons talk to each other: action potentials



- large membrane depolarisation initiated at beginning of axon
- propagates down the axon ("long tube")
- high voltage reaches the synapse, triggering transmission

How neurons talk to each other: action potentials

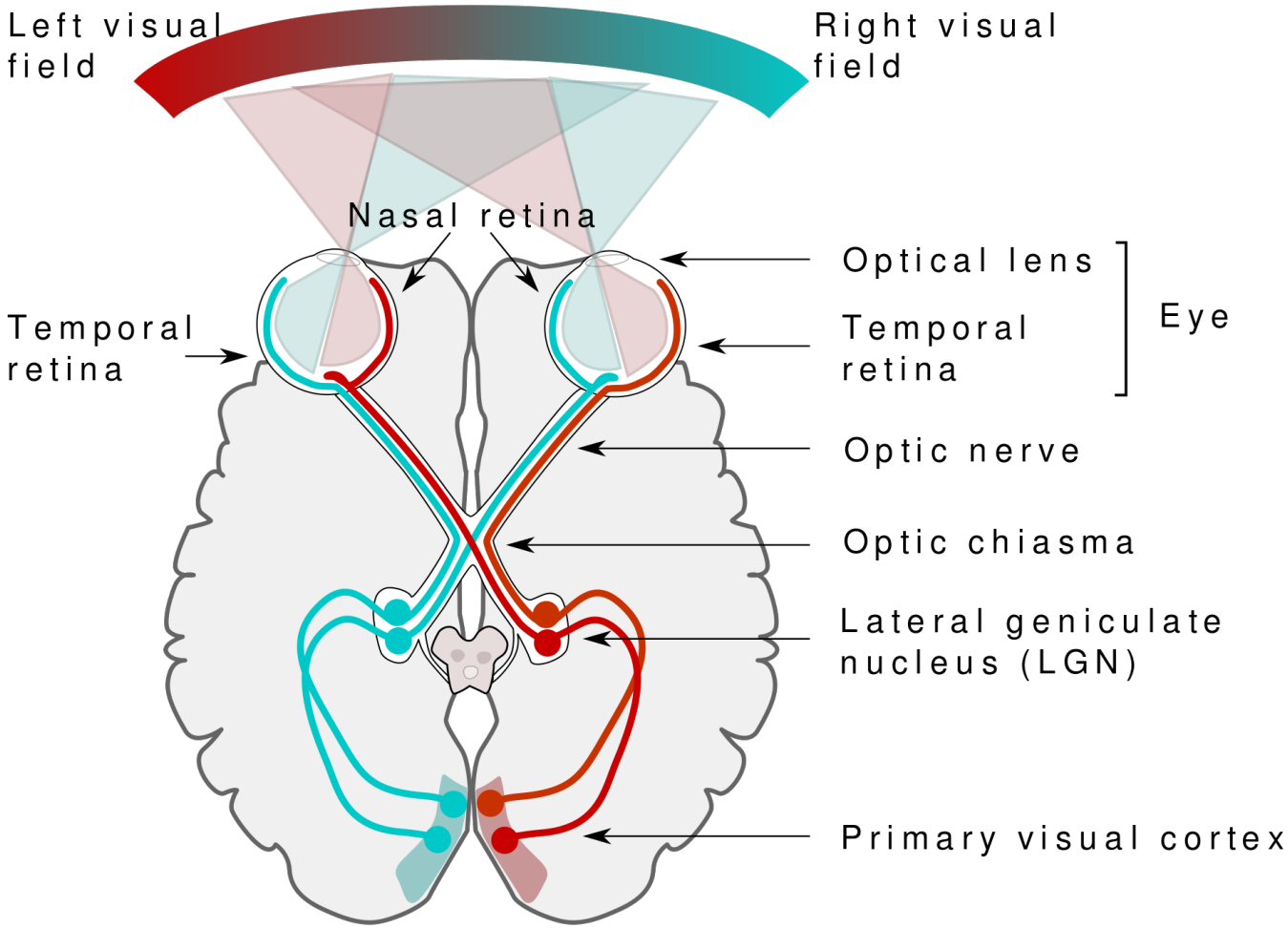


- large membrane depolarisation initiated at beginning of axon
- propagates down the axon ("long tube")
- high voltage reaches the synapse, triggering transmission

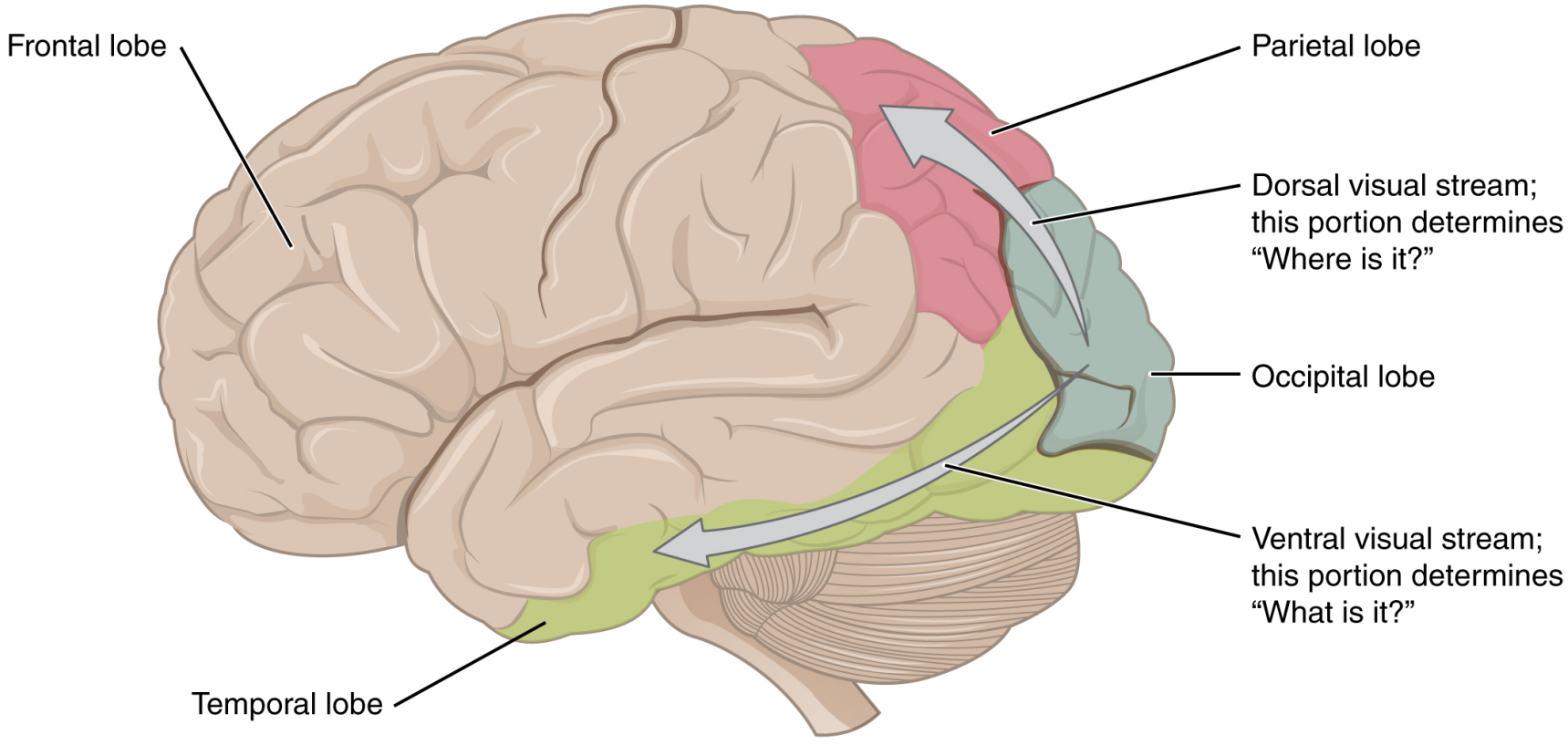
only occurs when potential is large enough at axon initial segment :)

Central visual pathway

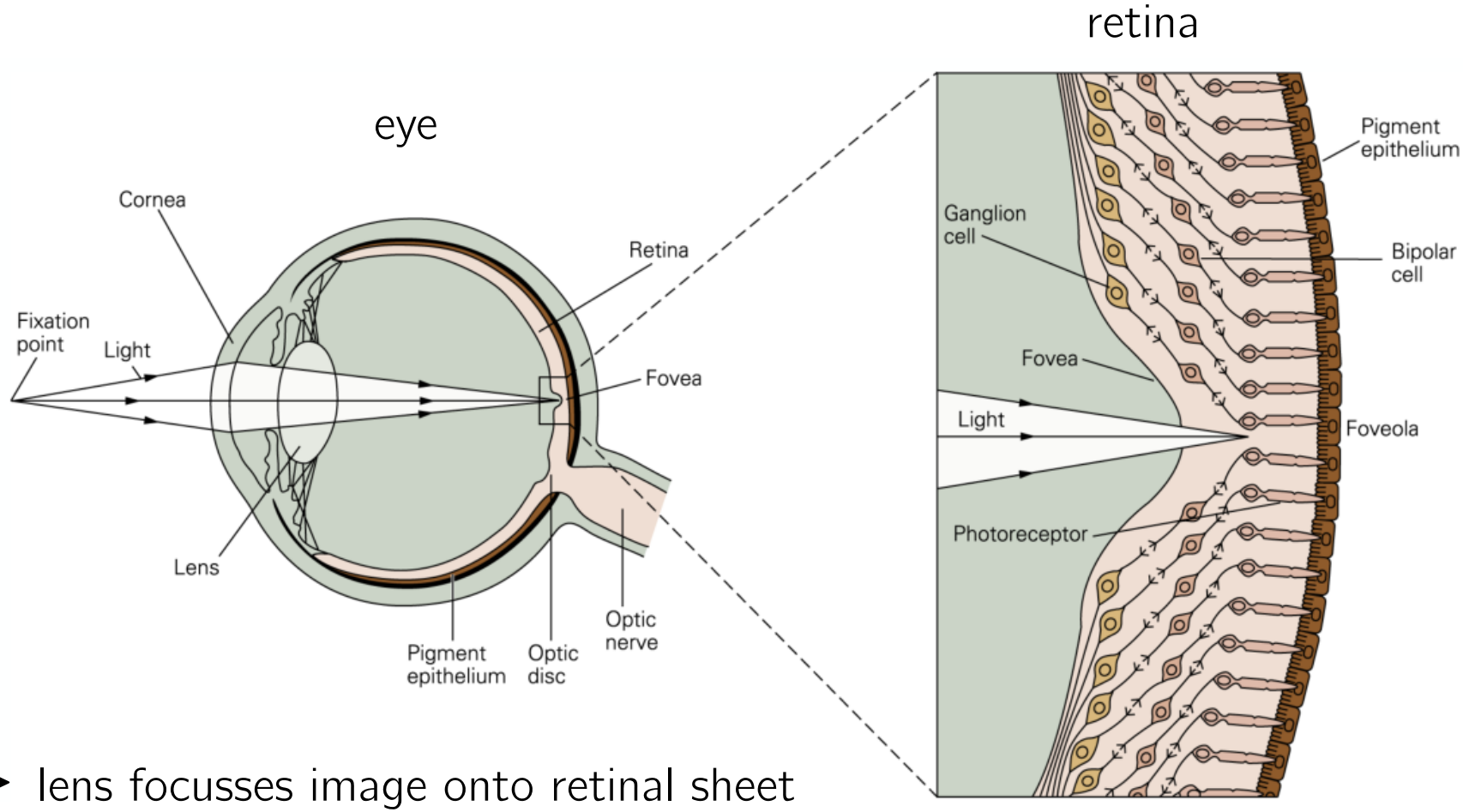
view from top:



“What” and “Where” pathways



The retina



- lens focusses image onto retinal sheet
- retina is mosaic of $\sim$ 126 million photoreceptors
- fovea has highest density of cells (and cells shifted to the side)
- axons leave retina (optic nerve, 1 million fibres), giving blind spot
- compression 1:100

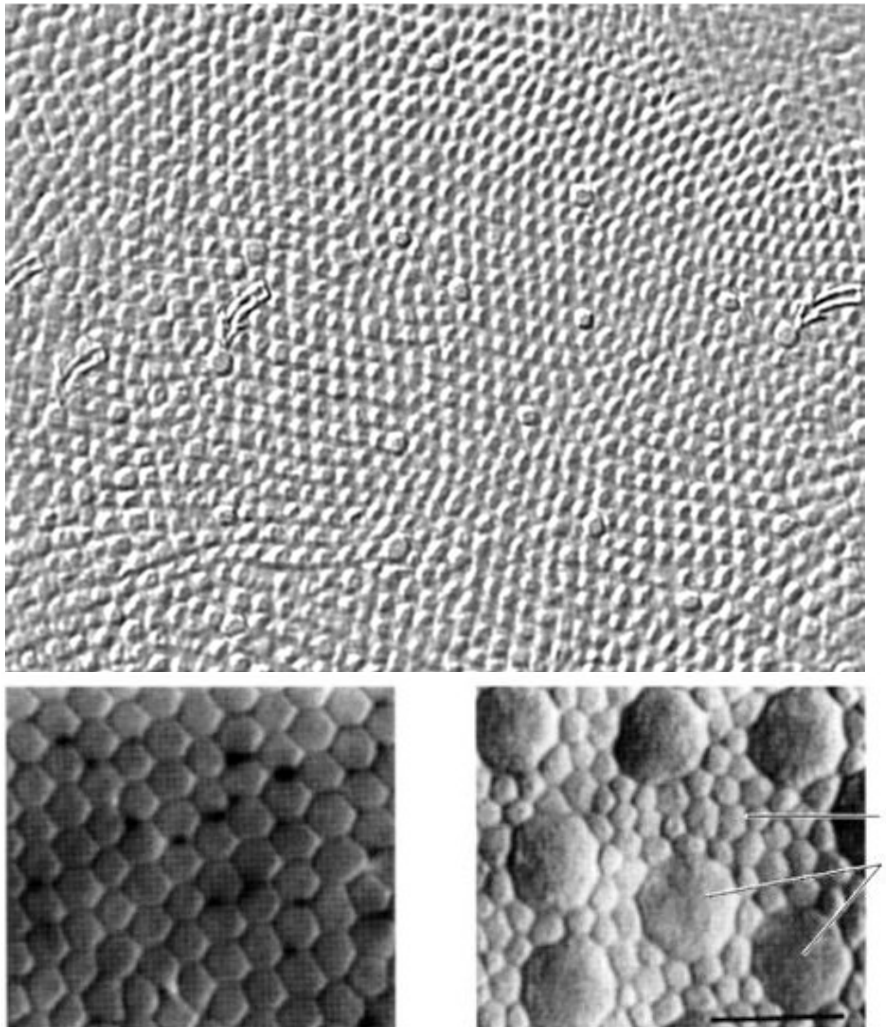
Know your blind spot

close your left eye, and look at the cross

slowly move your face forward – what happens to the black dot?

(can you explain this?)

Photoreceptors



10μm

mosaic of 126 million photoreceptors

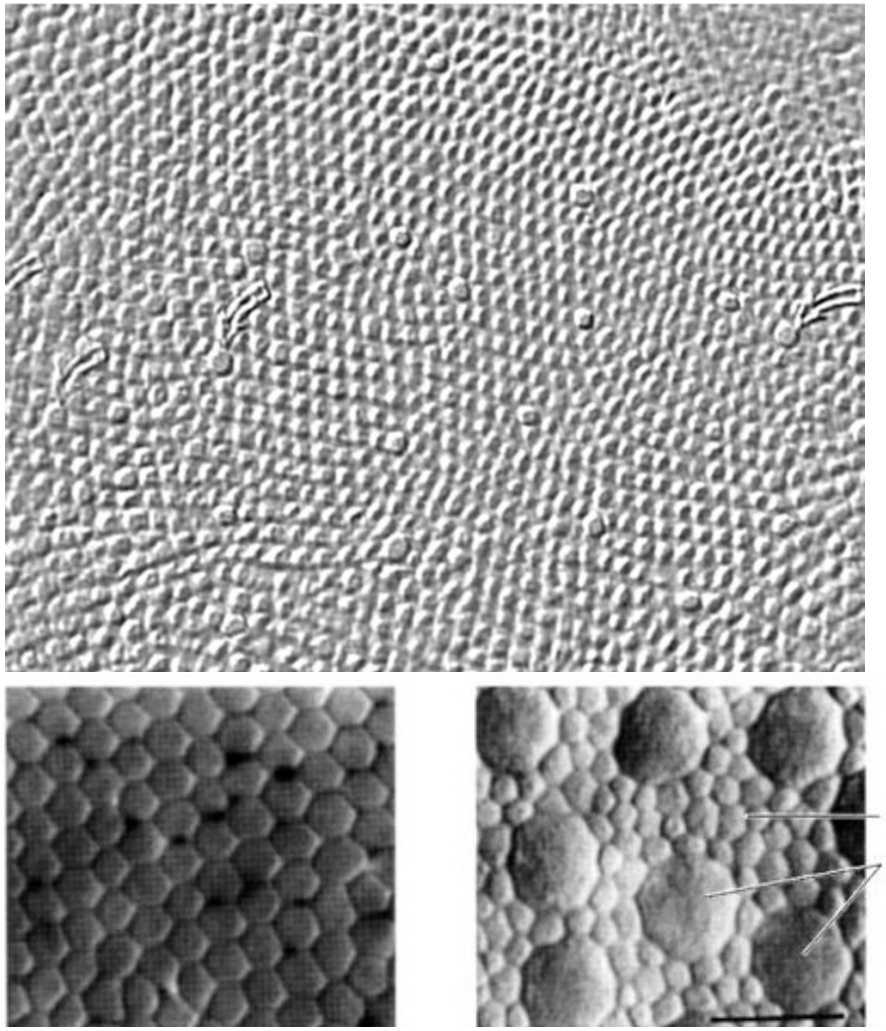
cones (6 million):

- colour & day vision
- 3 pigments
- requires 10s or 100s of photons

rods (120 million):

- greyscale & night vision
- requires only a single photon
- large convergence, spatial and temporal integration

Photoreceptors



10μm

mosaic of 126 million photoreceptors

cones (6 million):

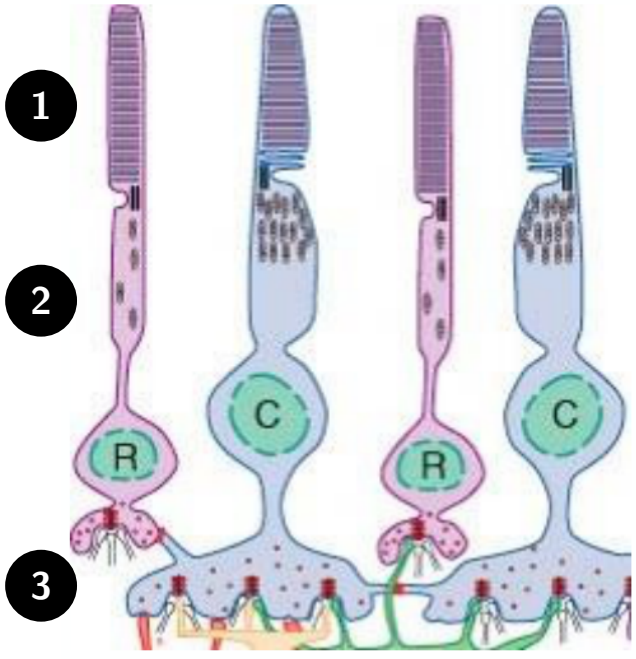
- colour & day vision
- 3 pigments
- requires 10s or 100s of photons

rods (120 million):

- greyscale & night vision
- requires only a single photon
- large convergence, spatial and temporal integration

density of cones is higher in the "fovea" (center of retina)

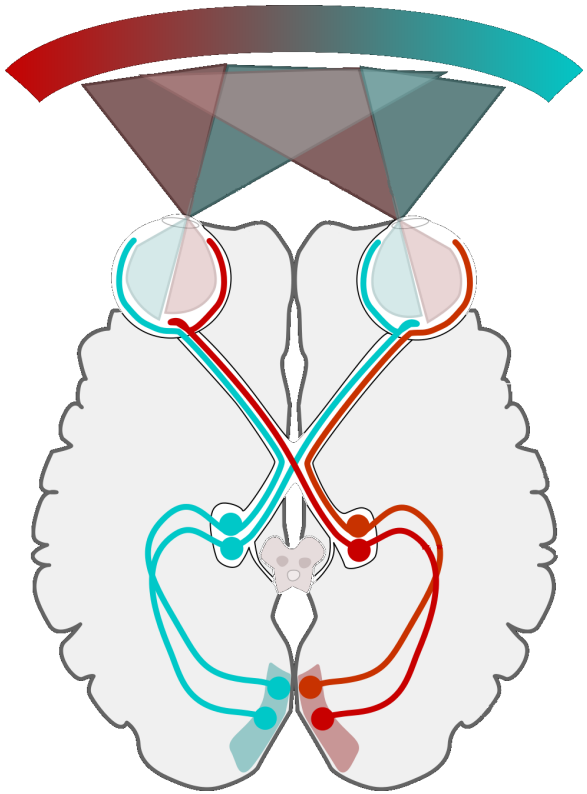
Photoreceptors



cones and rods do not fire action potentials, but respond to light with graded changes in membrane potential

1. outer segment: light-absorbing pigments; the more photons are absorbed, the *lower* the membrane voltage
2. inner segment
3. synaptic terminals: release neurotransmitters (the higher the voltage, the more gets released)

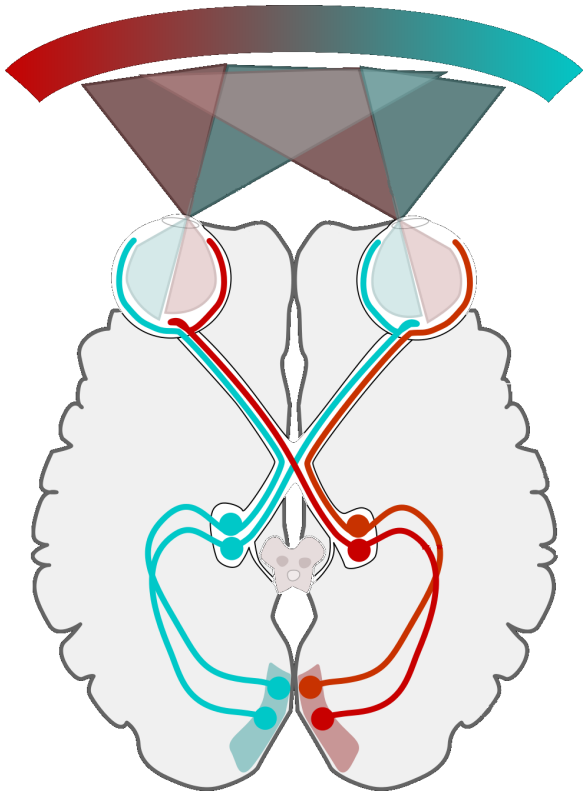
The receptive field concept



receptive field: what visual stimulus causes a given neuron to respond?

- (angular) location in visual field
- stimulus pattern, or "shape"
- color
- ...

The receptive field concept

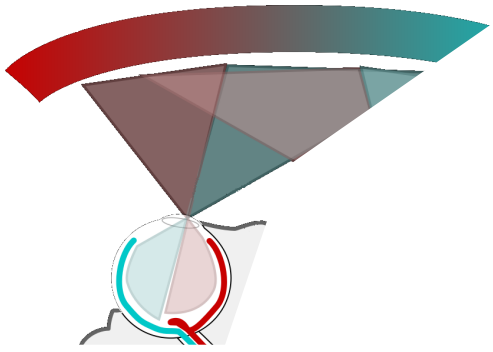


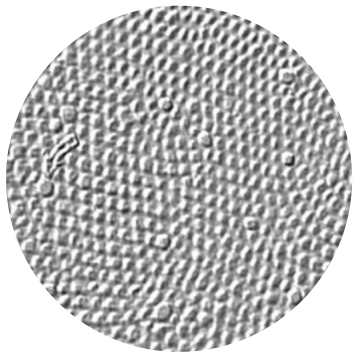
receptive field: what visual stimulus causes a given neuron to respond?

- (angular) location in visual field
- stimulus pattern, or "shape"
- color
- ...

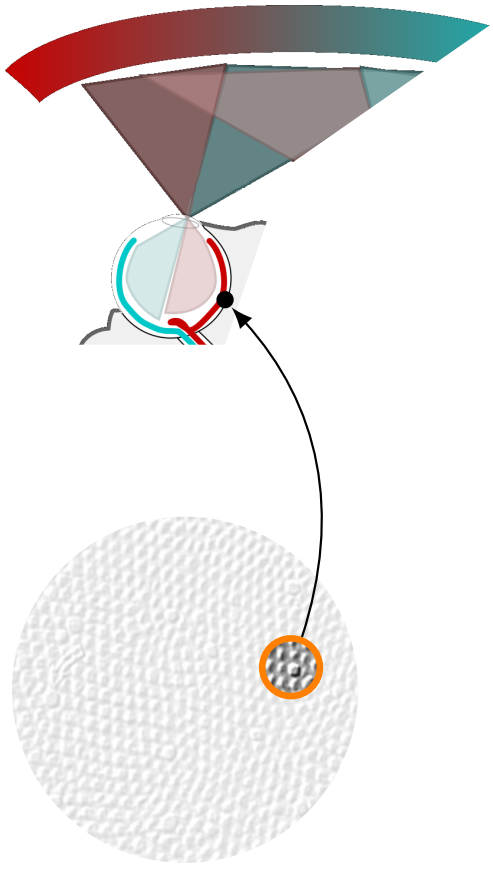
RFs are **hierarchically organised**: from photoreceptors that respond to mere points of light, to cortical neurons that respond to faces of specific people

Receptive field of a photoreceptor

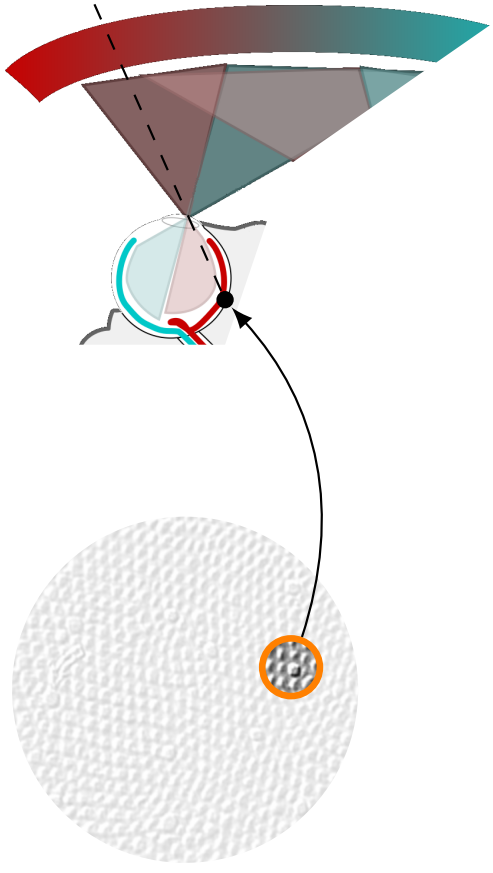




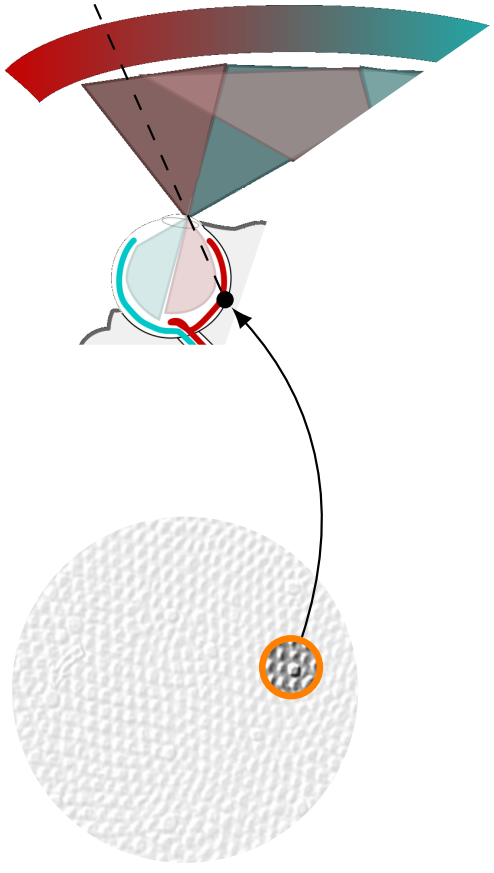
Receptive field of a photoreceptor



Receptive field of a photoreceptor

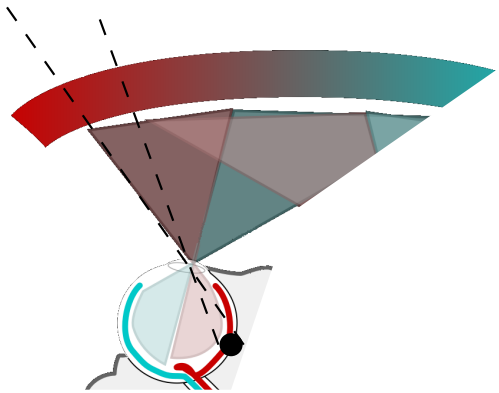


Receptive field of a photoreceptor



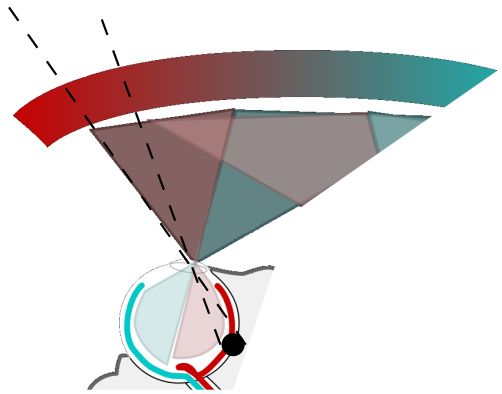
the RF of a photoreceptor is simply
the (angular) location in the visual field
(i.e. relative to center of gaze)
that maps onto the photoreceptor
through the lens

Receptive field of a retinal ganglion cell



a ganglion cell receives input from
nearby photoreceptors;
therefore, it also only responds to light in
a small (albeit larger) localised area
of visual field

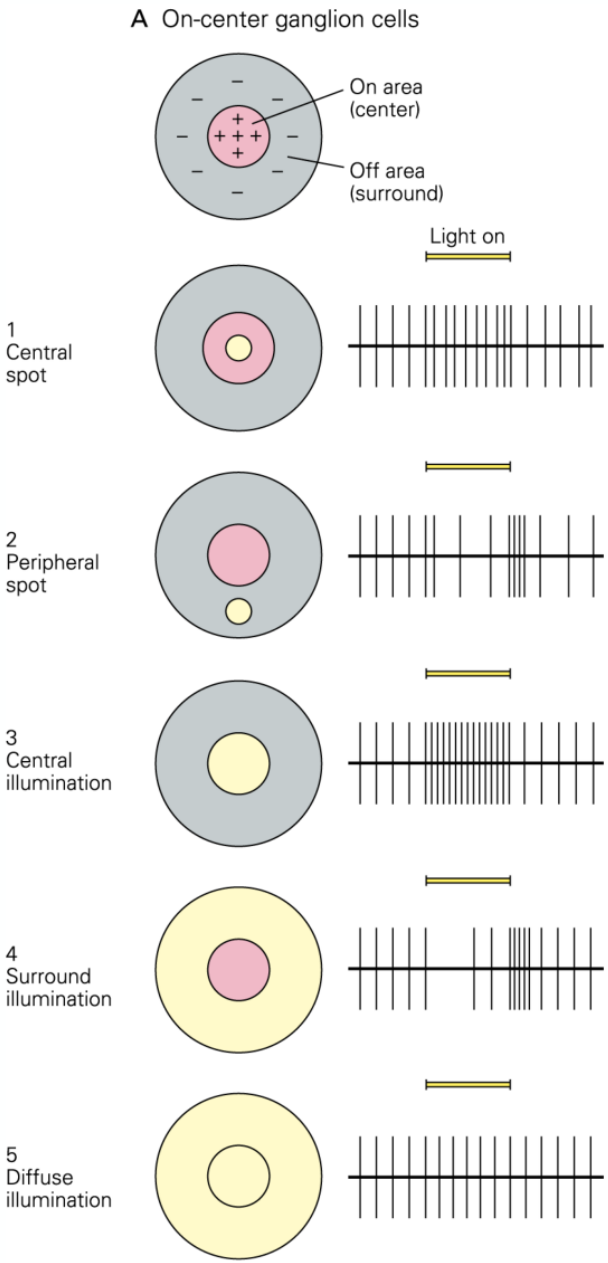
Receptive field of a retinal ganglion cell



a ganglion cell receives input from
nearby photoreceptors;
therefore, it also only responds to light in
a small (albeit larger) localised area
of visual field

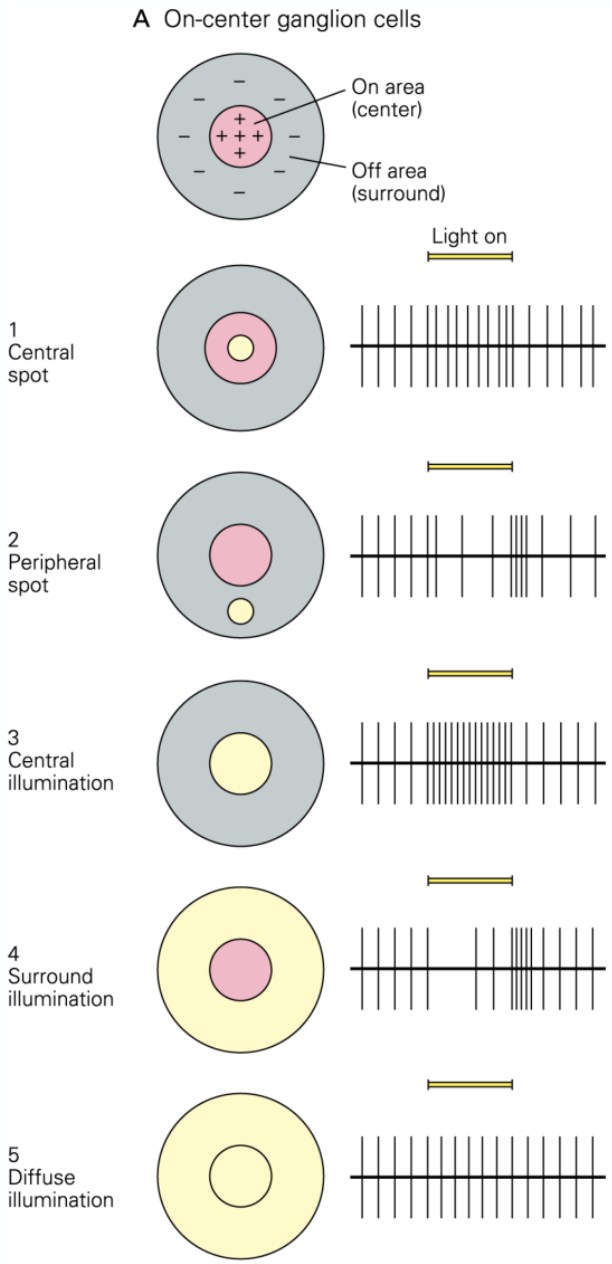
(movie)

Receptive field of a retinal ganglion cell



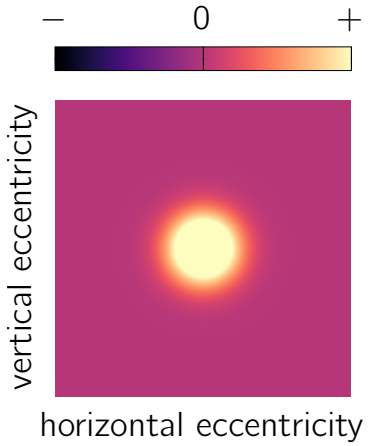
- roughly circular RFs
- few minutes of arc at fovea, few degrees at periphery
- center-surround structure (on-off, or off-on)
- responds optimally to differential illumination

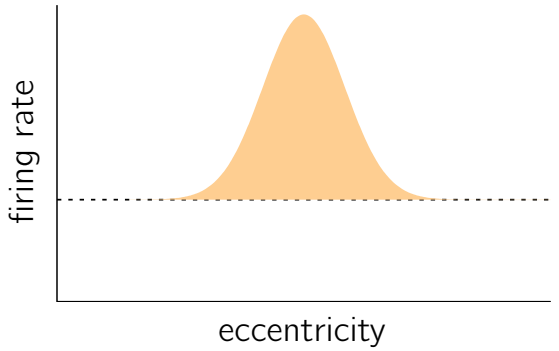
Receptive field of a retinal ganglion cell



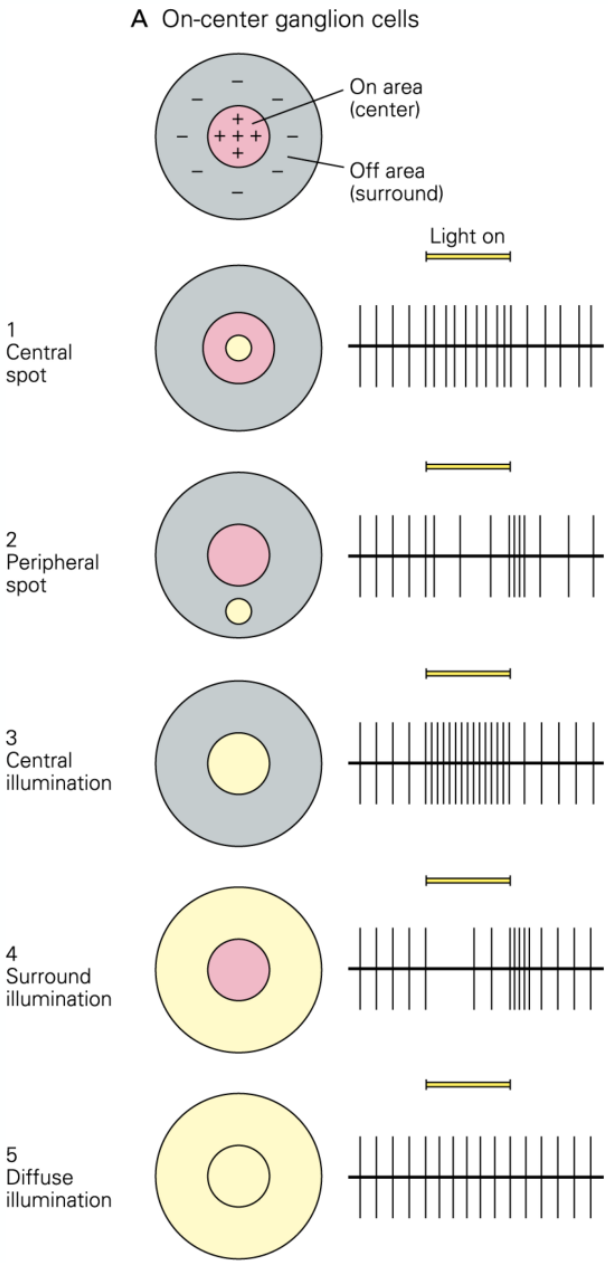
- roughly circular RFs
- few minutes of arc at fovea, few degrees at periphery
- center-surround structure (on-off, or off-on)
- responds optimally to differential illumination

difference of Gaussians model:



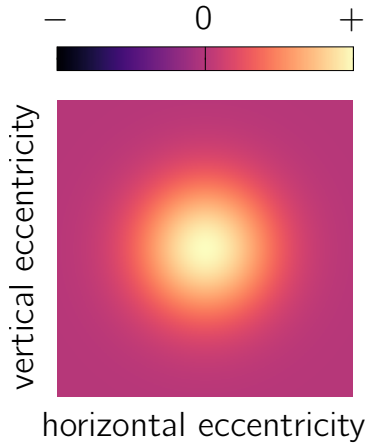


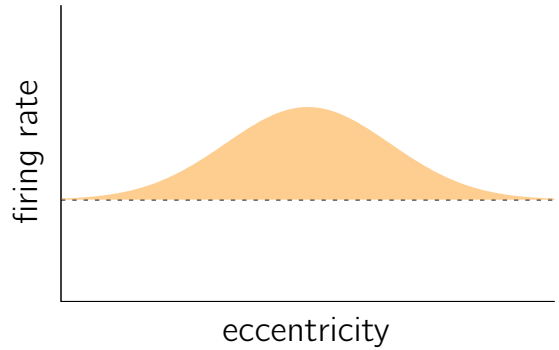
Receptive field of a retinal ganglion cell



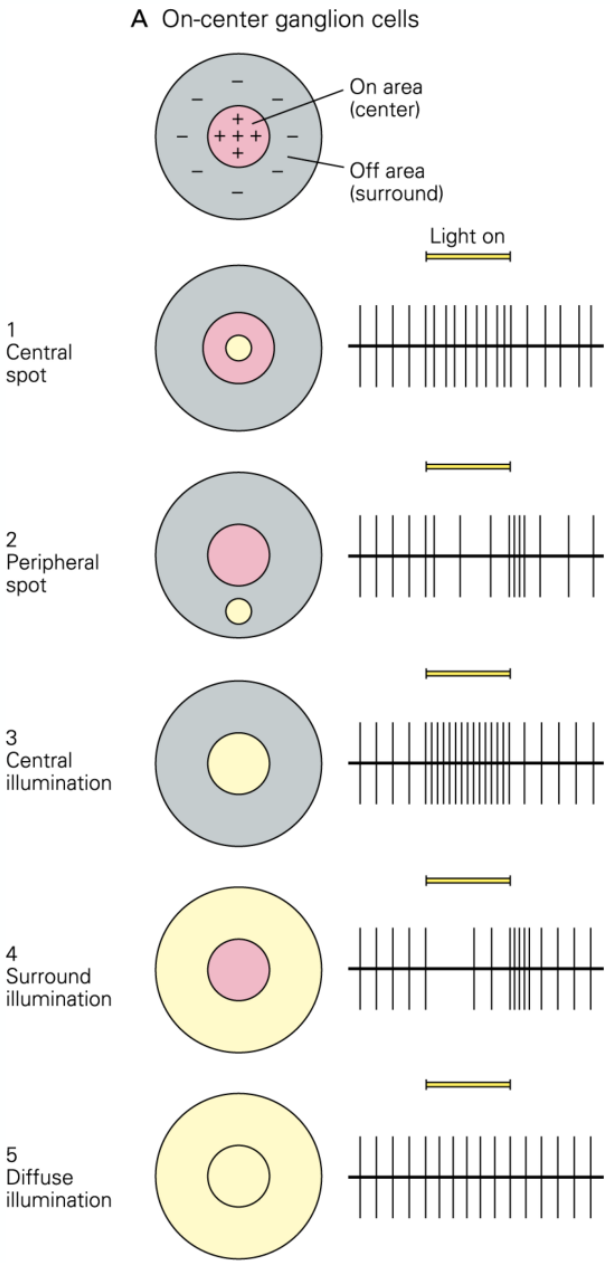
- roughly circular RFs
- few minutes of arc at fovea, few degrees at periphery
- center-surround structure (on-off, or off-on)
- responds optimally to differential illumination

difference of Gaussians model:



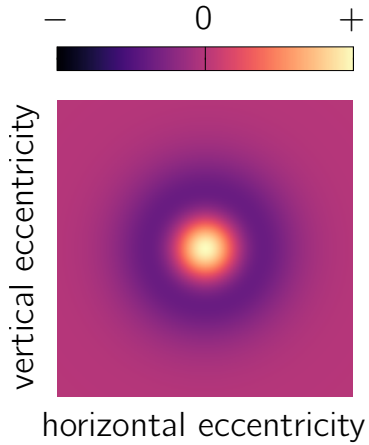


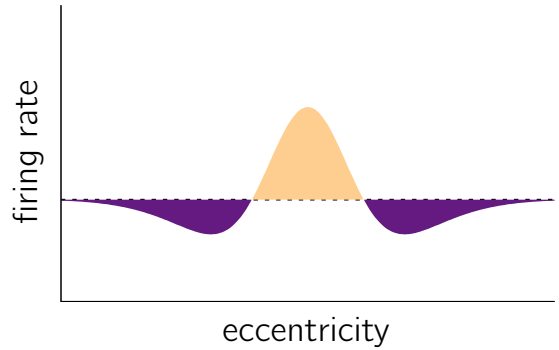
Receptive field of a retinal ganglion cell



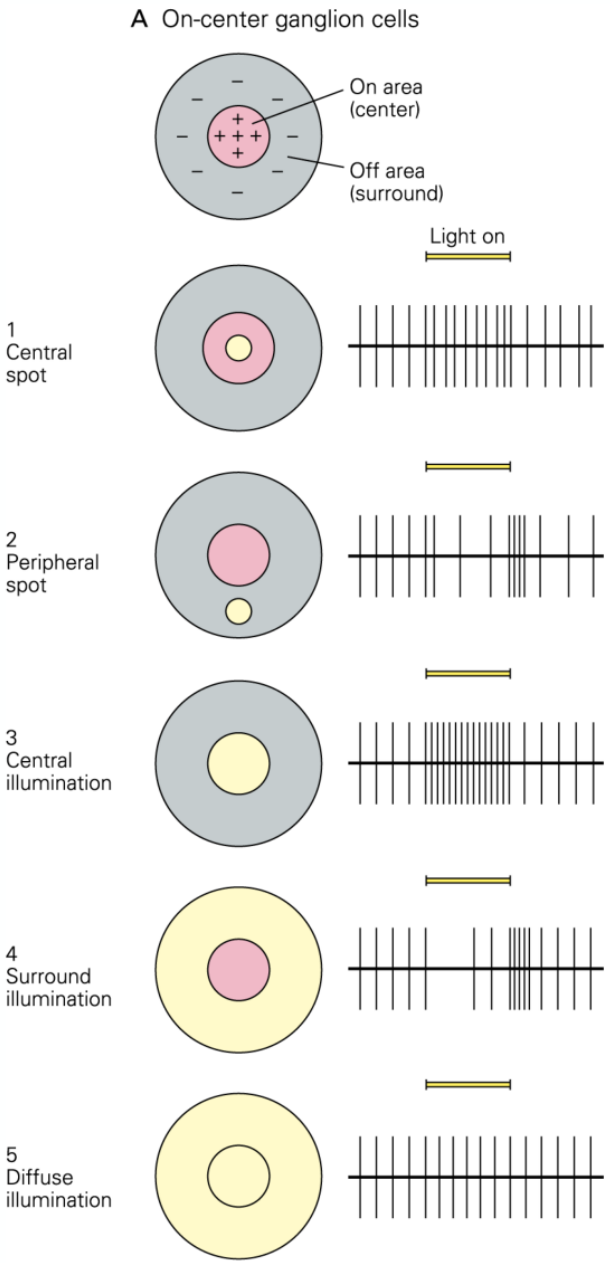
- roughly circular RFs
- few minutes of arc at fovea, few degrees at periphery
- center-surround structure (on-off, or off-on)
- responds optimally to differential illumination

difference of Gaussians model:



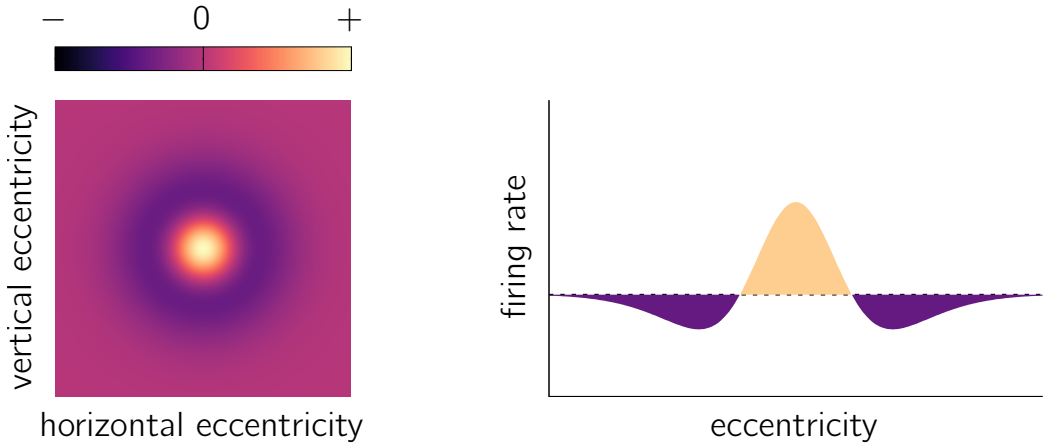


Receptive field of a retinal ganglion cell



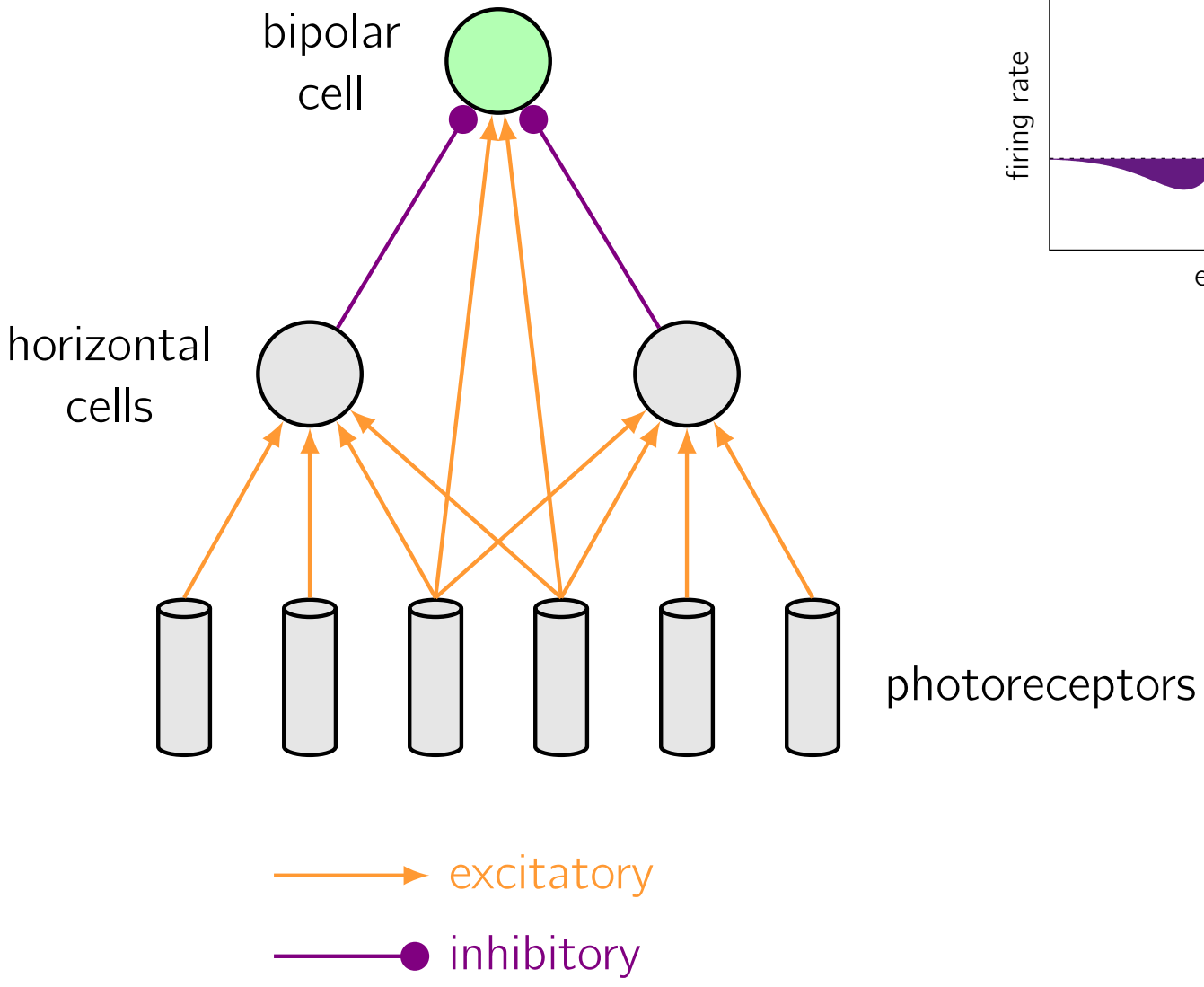
- roughly circular RFs
- few minutes of arc at fovea, few degrees at periphery
- center-surround structure (on-off, or off-on)
- responds optimally to differential illumination

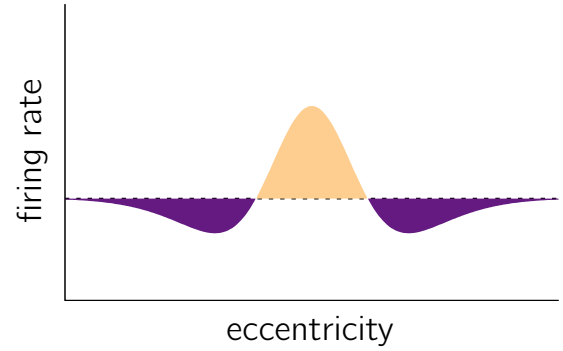
difference of Gaussians model:



responses *sum linearly*,
therefore, the above profile is also
the most effective stimulus pattern ($\equiv$ RF)

A simplified network model





Why is contrast so important?

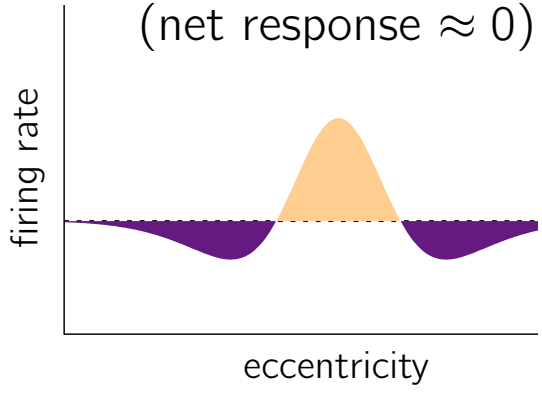
absolute light level is not important, as depends on illumination (nuisance)

contrast matters more (edges, textures, . . .)

Why is contrast so important?

absolute light level is not important, as depends on illumination (nuisance)
contrast matters more (edges, textures, . . .)

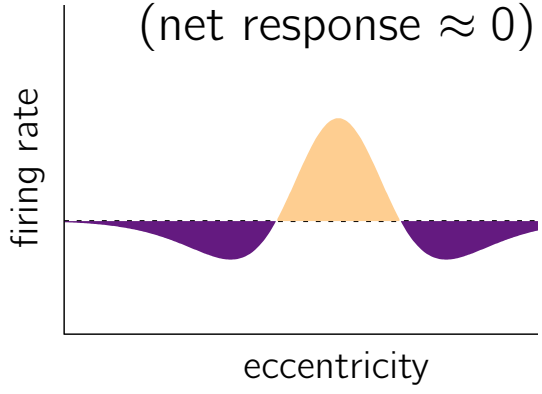
- diffuse illumination gives little response
- but a few ganglion cells respond to absolute levels (required to drive pupillary light reflex)



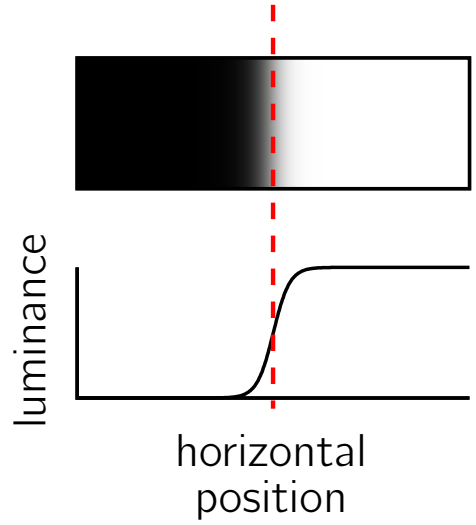
Why is contrast so important?

absolute light level is not important, as depends on illumination (nuisance)
contrast matters more (edges, textures, . . .)

- diffuse illumination gives little response
- but a few ganglion cells respond to absolute levels (required to drive pupillary light reflex)



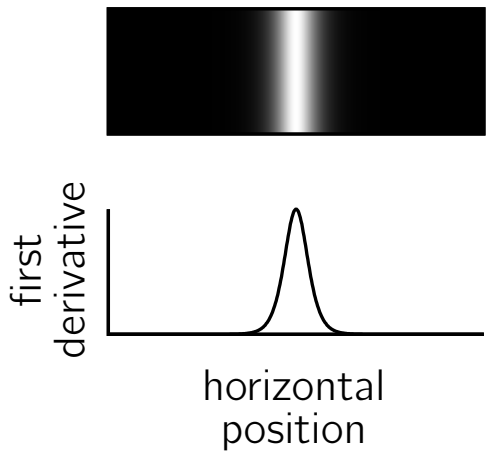
Connection to edge detection

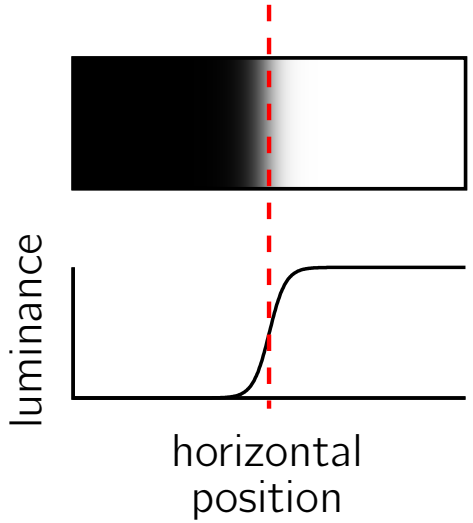


Connection to edge detection

to detect luminance edges, we could either:

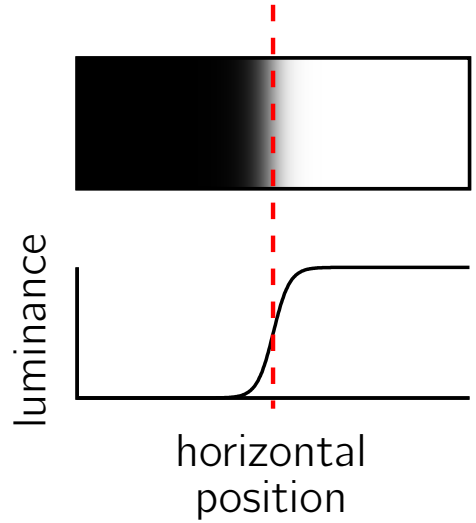
1. find peaks of first derivative



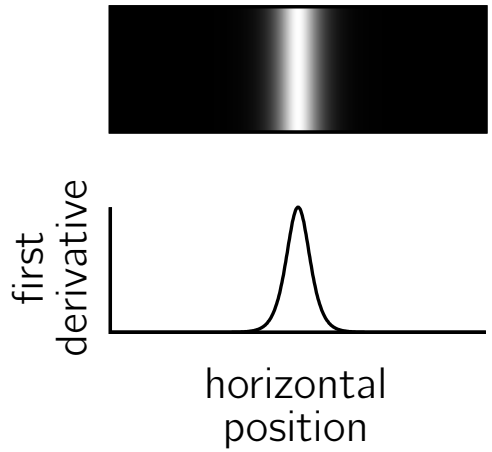


Connection to edge detection

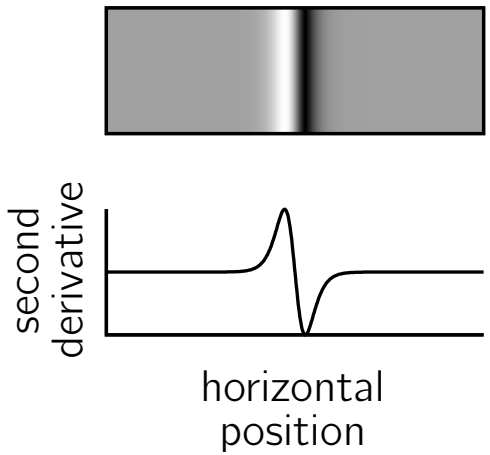
to detect luminance edges, we could either:



1. find peaks of first derivative

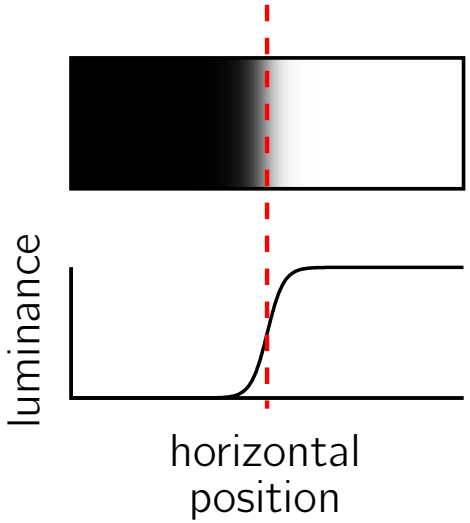


2. find zero-crossing of second derivative

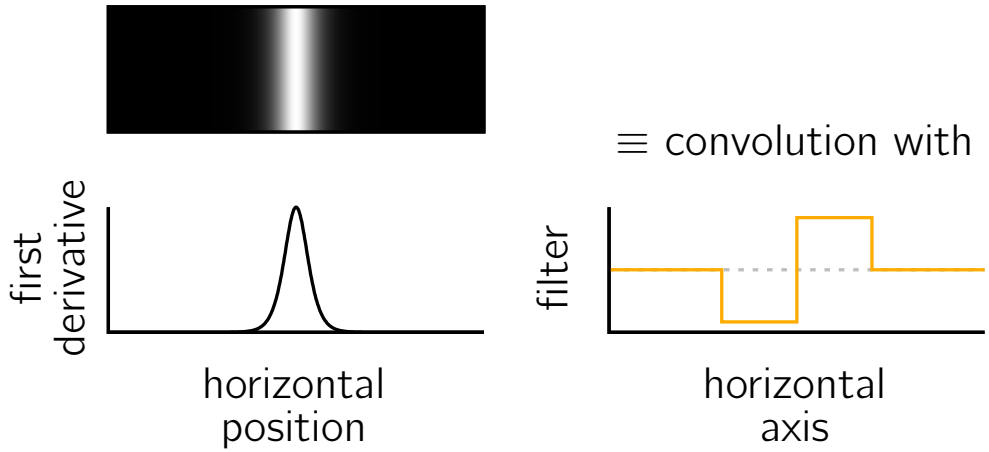


Connection to edge detection

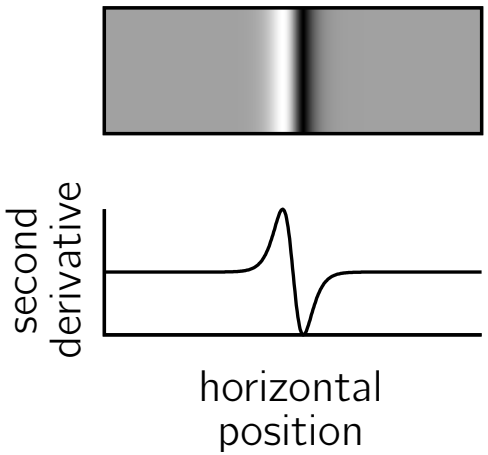
to detect luminance edges, we could either:



1. find peaks of first derivative

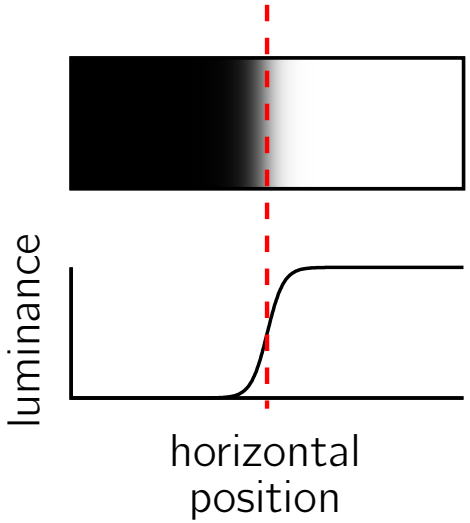


2. find zero-crossing of second derivative

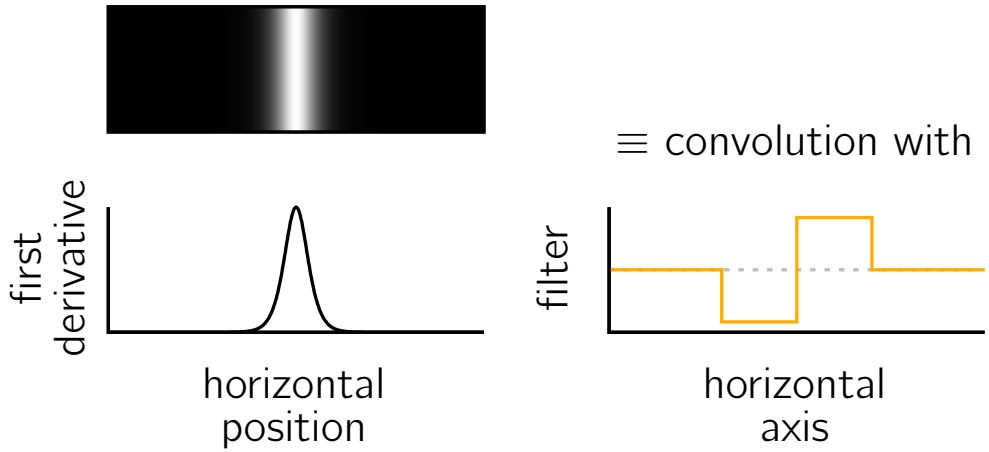


Connection to edge detection

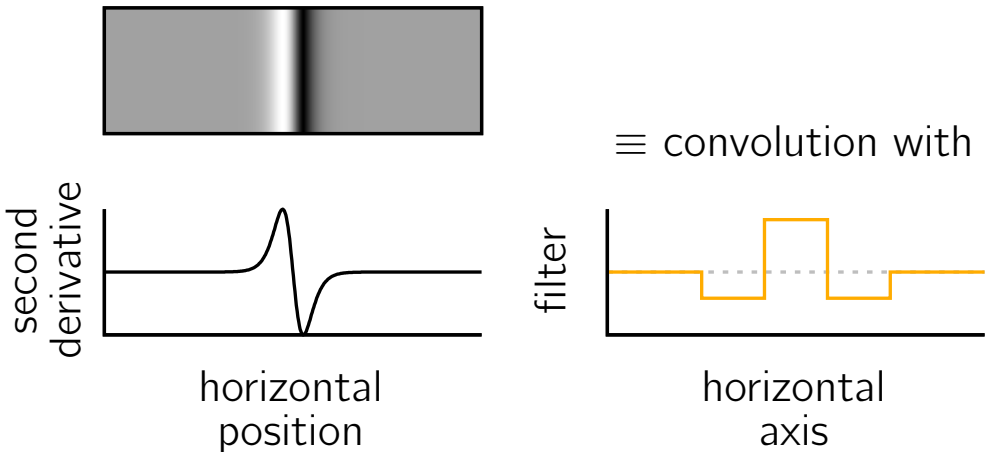
to detect luminance edges, we could either:



1. find peaks of first derivative

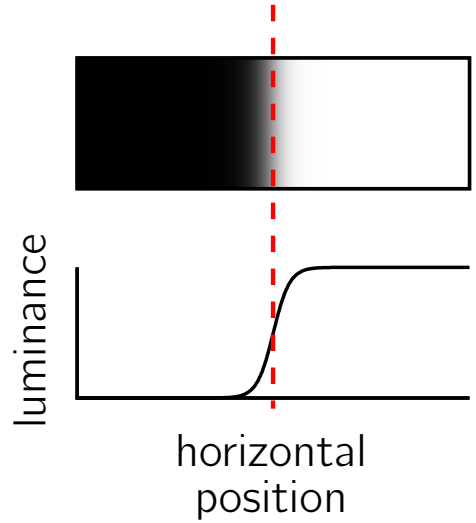


2. find zero-crossing of second derivative

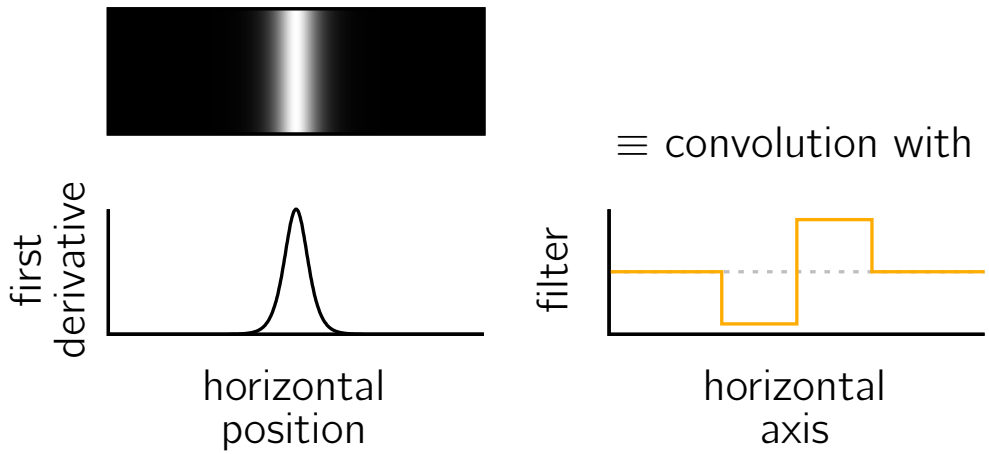


Connection to edge detection

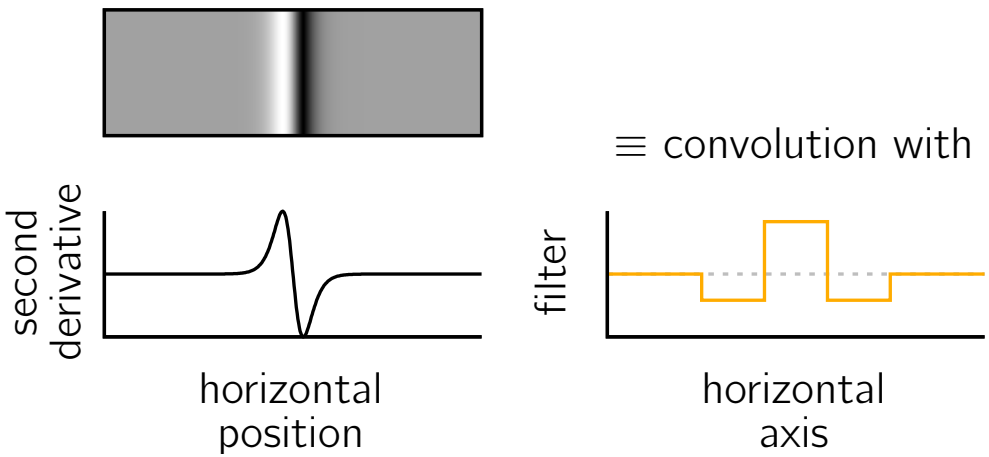
to detect luminance edges, we could either:



1. find peaks of first derivative



2. find zero-crossing of second derivative

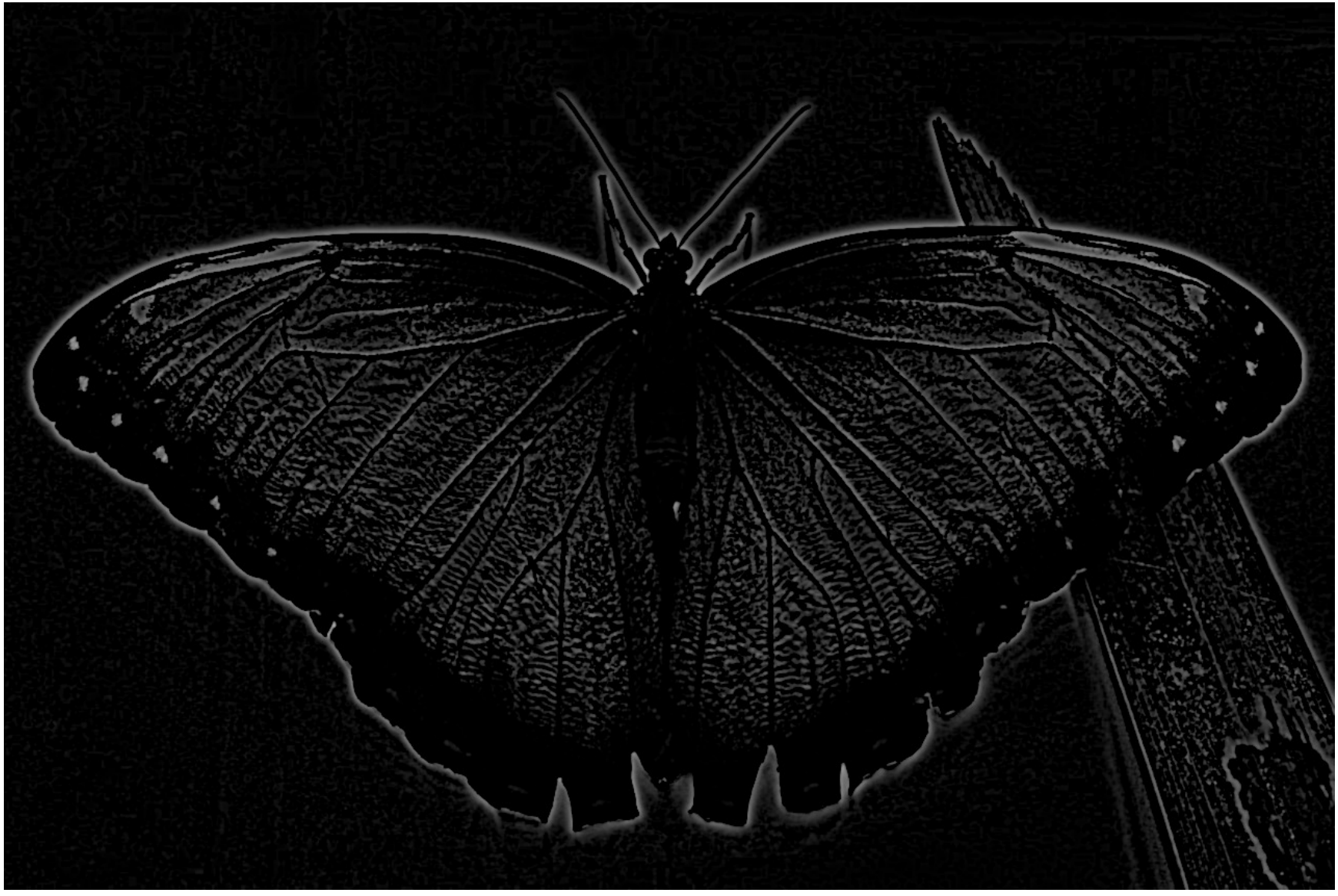


- first-order derivatives are necessarily directional
- second-order derivative operator is symmetric about mid-point, so can handle all directions at once
- in 2D, it has center-surround structure like ganglion cell RFs!
- convolution = responses of whole array of RFs tiling the visual field

Example of second-order edge detection

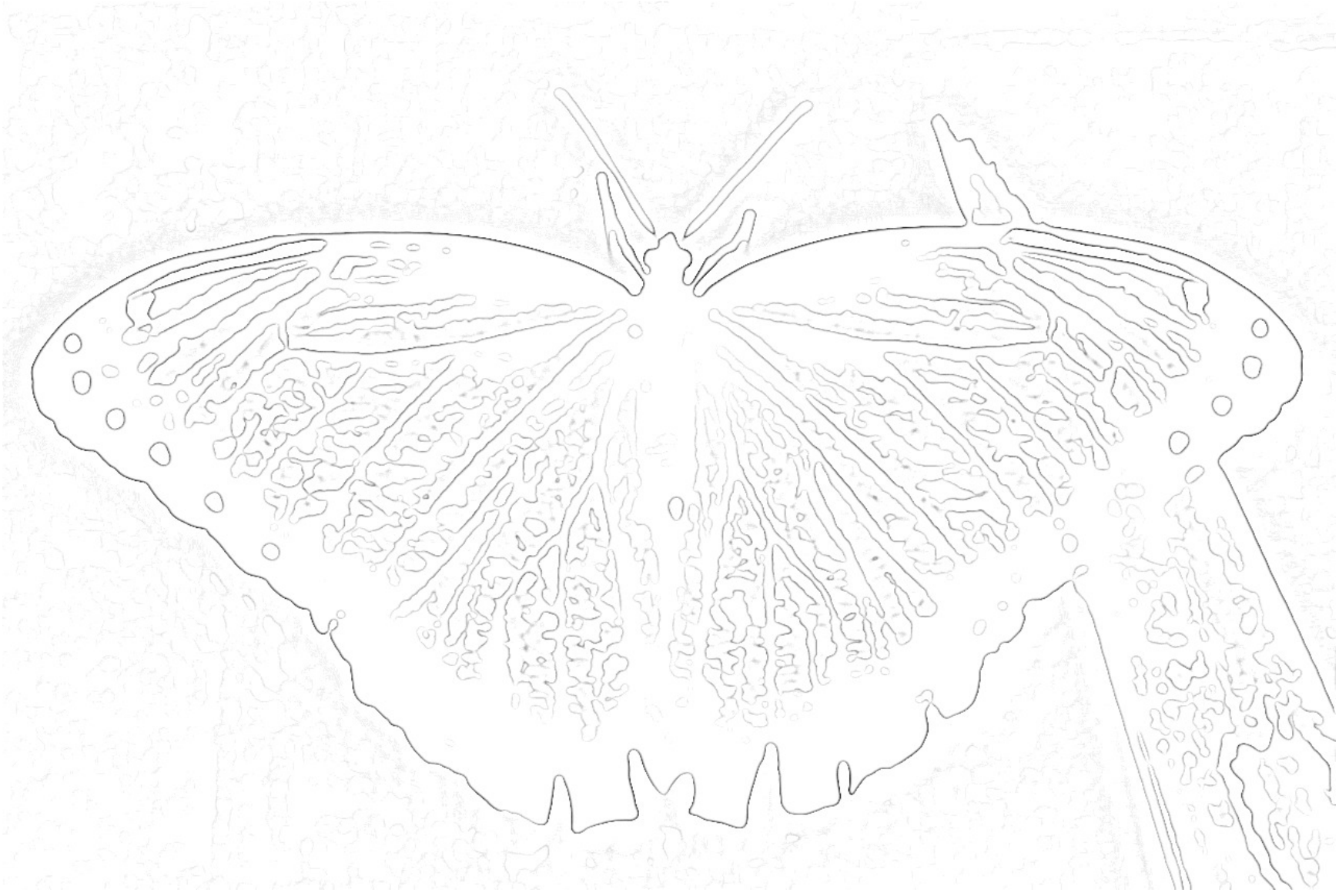
Example of second-order edge detection

convolution with difference-of-Gaussians:



Example of second-order edge detection

zero-crossing



Example of second-order edge detection

can detect edges at multiple spatial scales:

Example of second-order edge detection

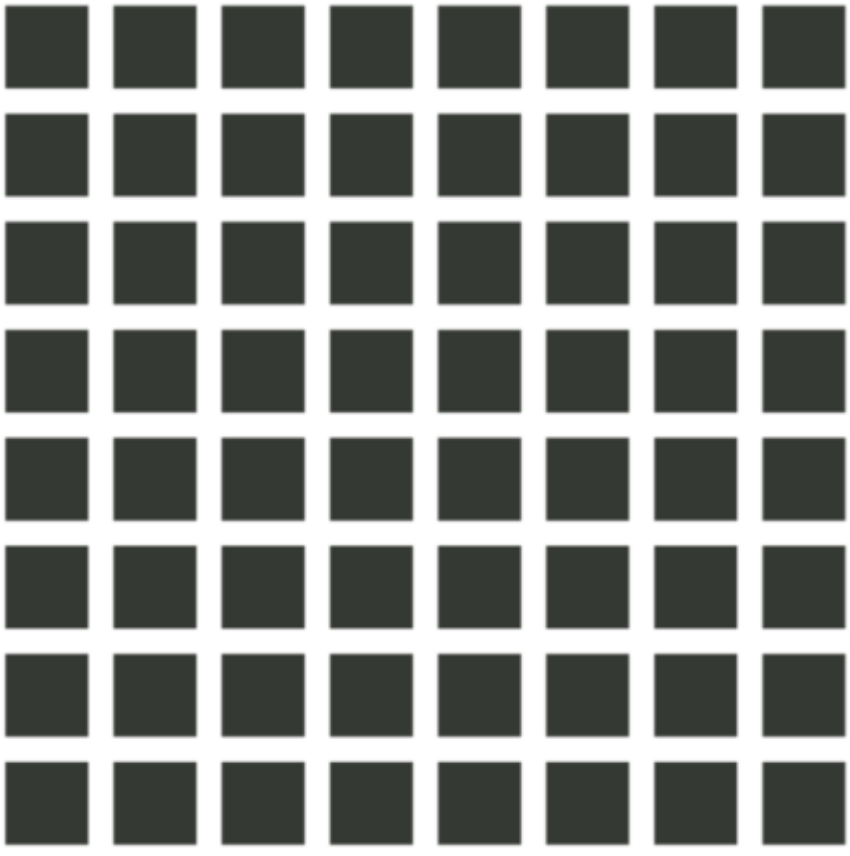
can detect edges at multiple spatial scales:

Example of second-order edge detection

can detect edges at multiple spatial scales:
accordingly, the retina has a diversity of RF sizes / spatial bandwidths

The Hermann grid illusion

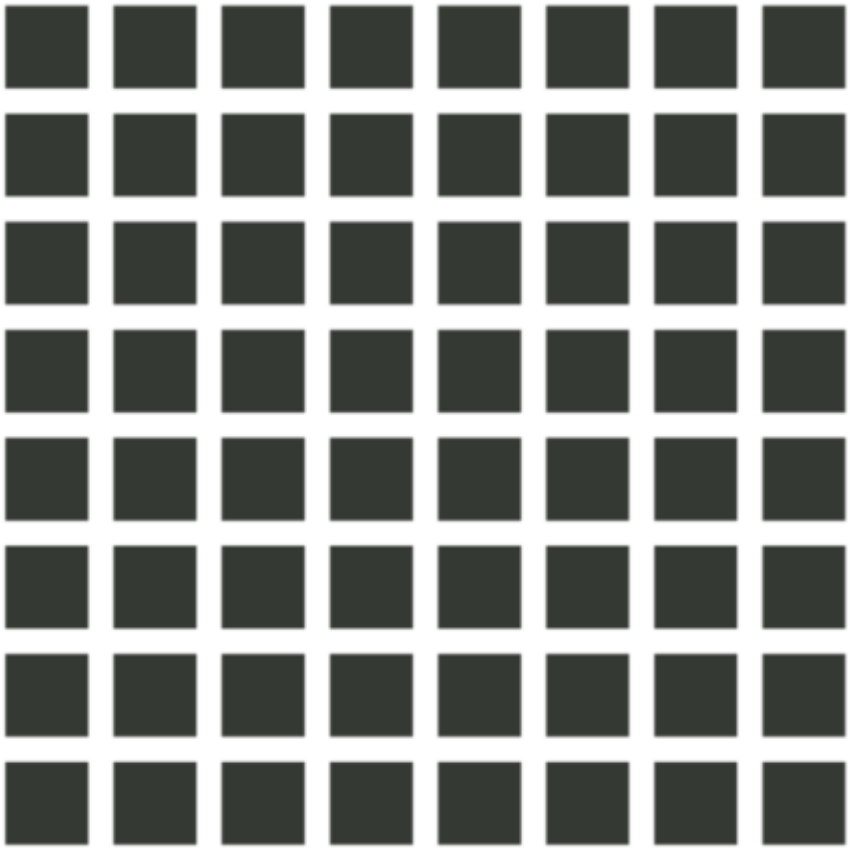
spotting signatures of retinal RF structure in psychophysics



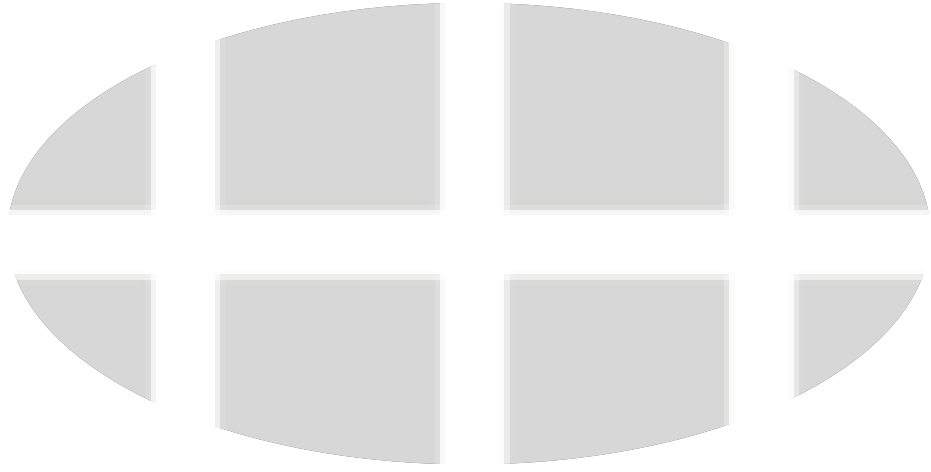
(illusory dark spots
appear at intersections)

The Hermann grid illusion

spotting signatures of retinal RF structure in psychophysics

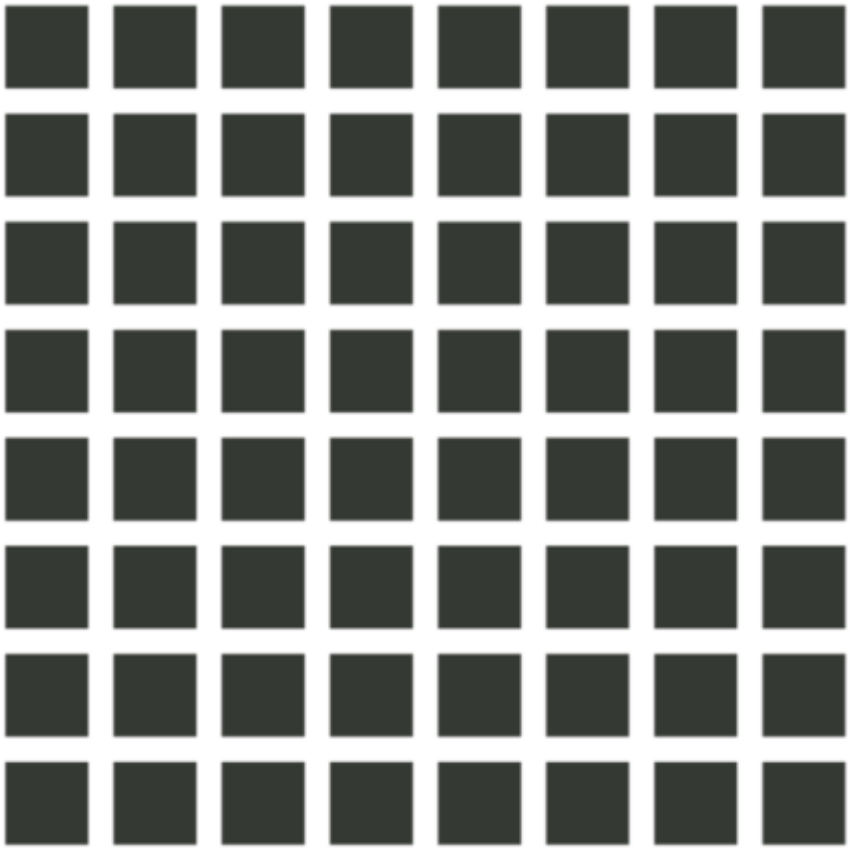


(illusory dark spots
appear at intersections)

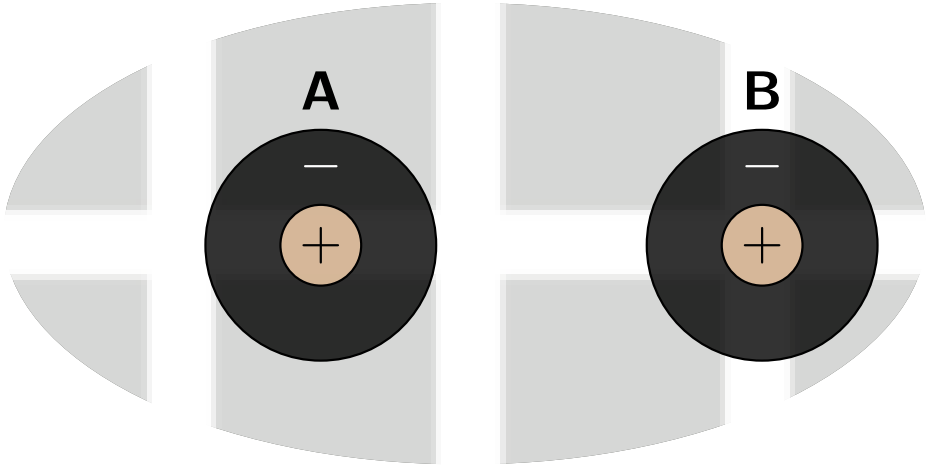


The Hermann grid illusion

spotting signatures of retinal RF structure in psychophysics

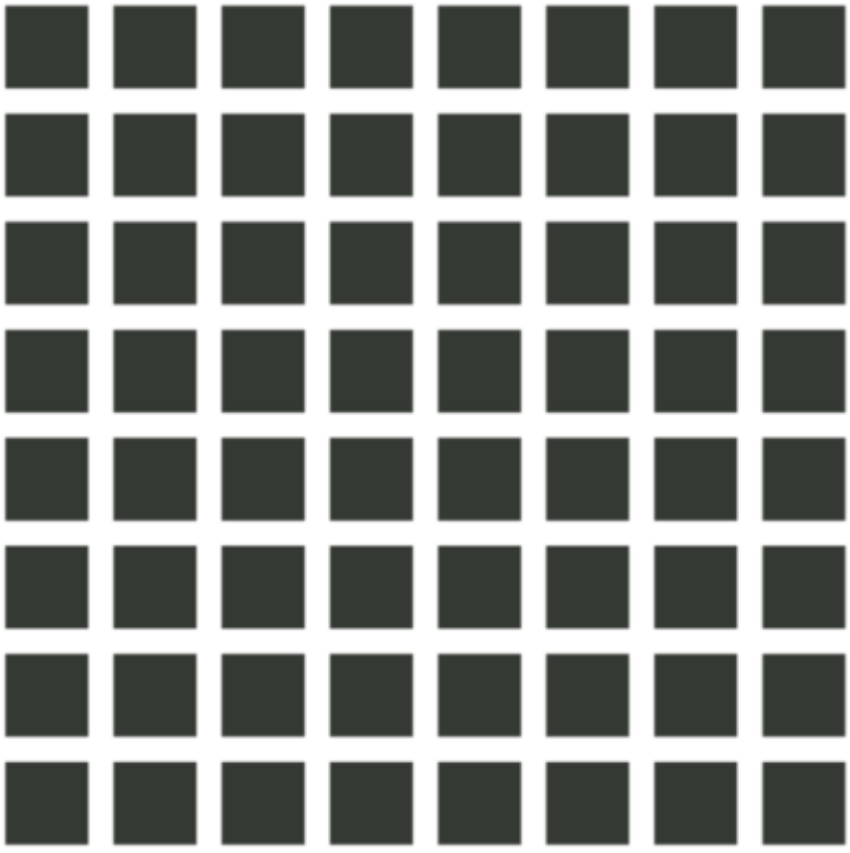


(illusory dark spots
appear at intersections)

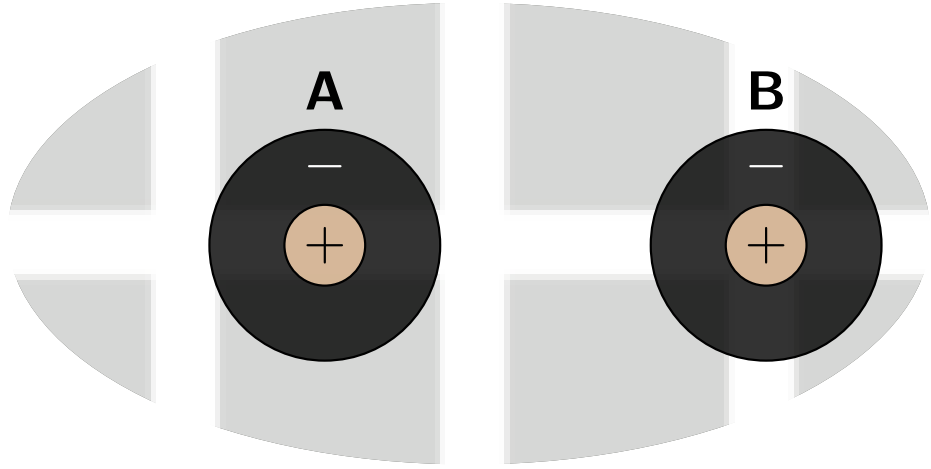


The Hermann grid illusion

spotting signatures of retinal RF structure in psychophysics

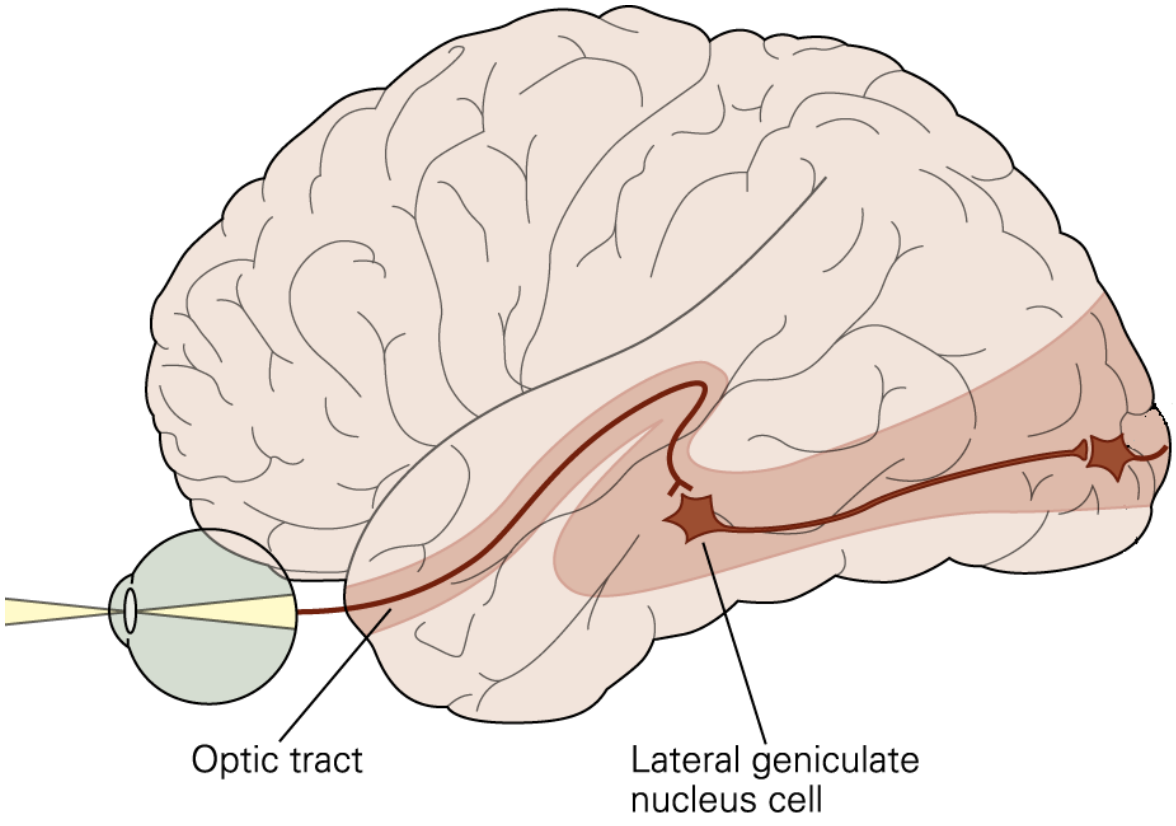


(illusory dark spots
appear at intersections)

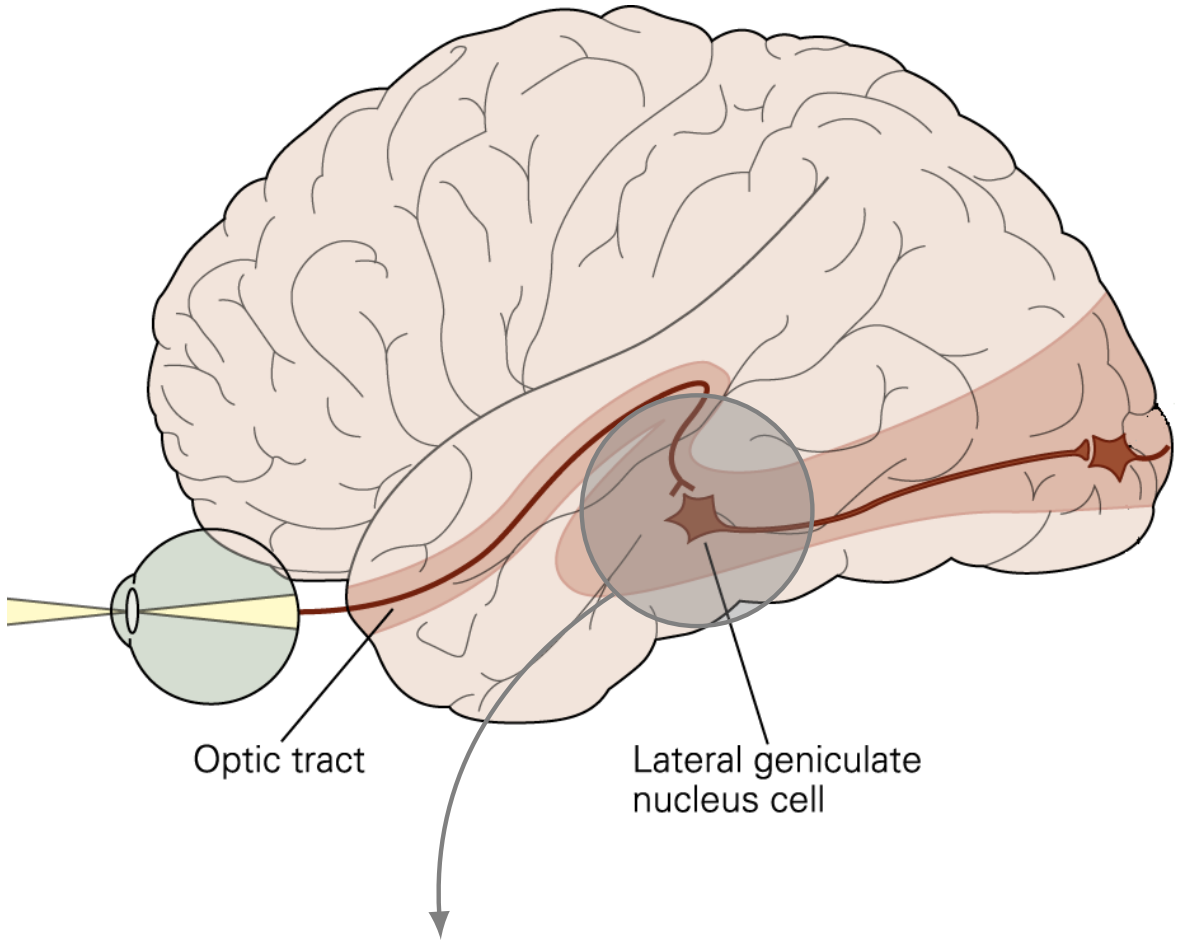


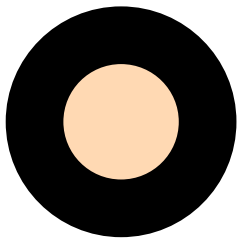
- same amount of light in RF on-center for A and B
- but in case B, more light falls in the off-center
- thus, ganglion cells with their RFs located at the intersections are less active than the others
- effect should vanish in the fovea (RFs are much smaller; check it!)

Lateral geniculate nucleus (LGN)

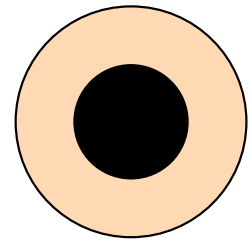


Lateral geniculate nucleus (LGN)

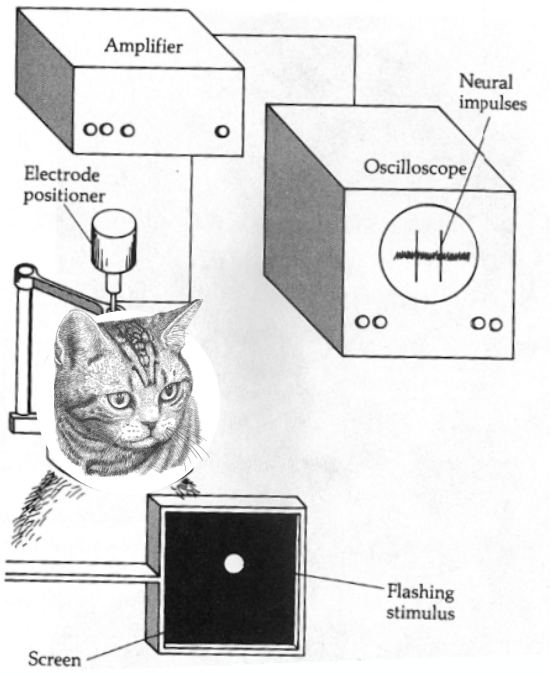




in LGN, neurons inherit the same
circular center-surround selectivity
as in the retina



Recordings from primary visual cortex (area "V1")

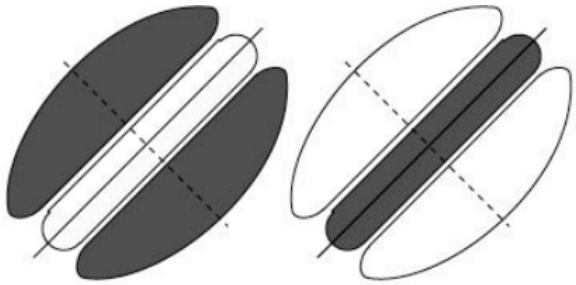


Hubel and Wiesel (1981 Nobel prize)

work performed in the late 50's, early 60's

(movie)

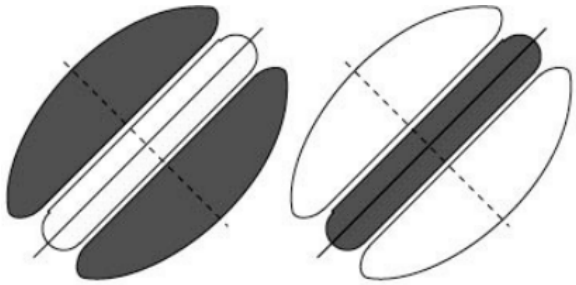
Receptive fields of V1 “simple cells”



simple cells respond maximally to:

- oriented, edge/line-like stimulus
- displayed at a specific location in visual field

Receptive fields of V1 “simple cells”

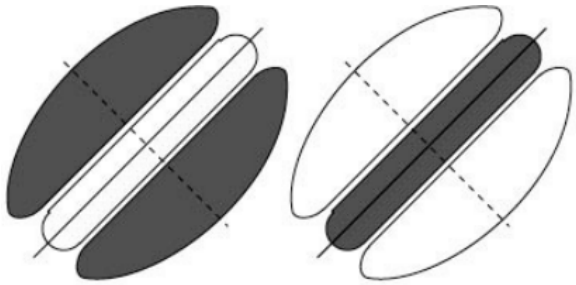


simple cells respond maximally to:

- oriented, edge/line-like stimulus
- displayed at a specific location in visual field

linear response summation, as for retinal ganglion cells: response to complex stimulus equals superposition of responses to individual spots of light

Receptive fields of V1 "simple cells"



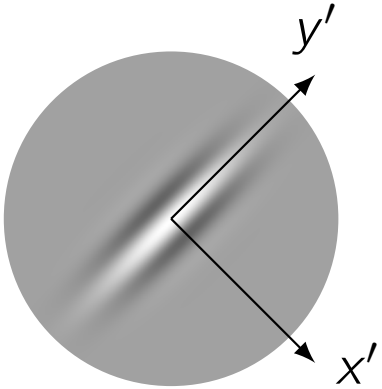
simple cells respond maximally to:

- oriented, edge/line-like stimulus
- displayed at a specific location in visual field

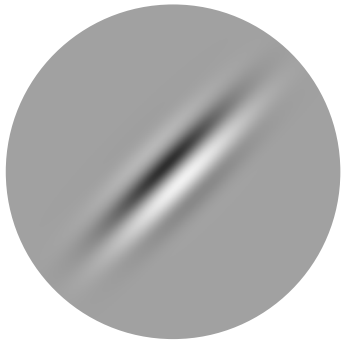
linear response summation, as for retinal ganglion cells: response to complex stimulus equals superposition of responses to individual spots of light

classic "Gabor filter" model: $f(x,y) = \exp\left(-\frac{x'^2 + (y'/\gamma)^2}{2\sigma^2}\right) \cos(\omega x' + \phi)$

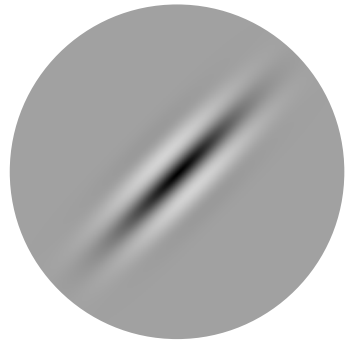
σ: width of envelope γ: elongation ω: oscillation frequency



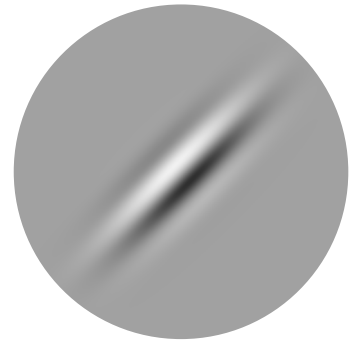
$\phi = 0$



$\phi = \pi/2$

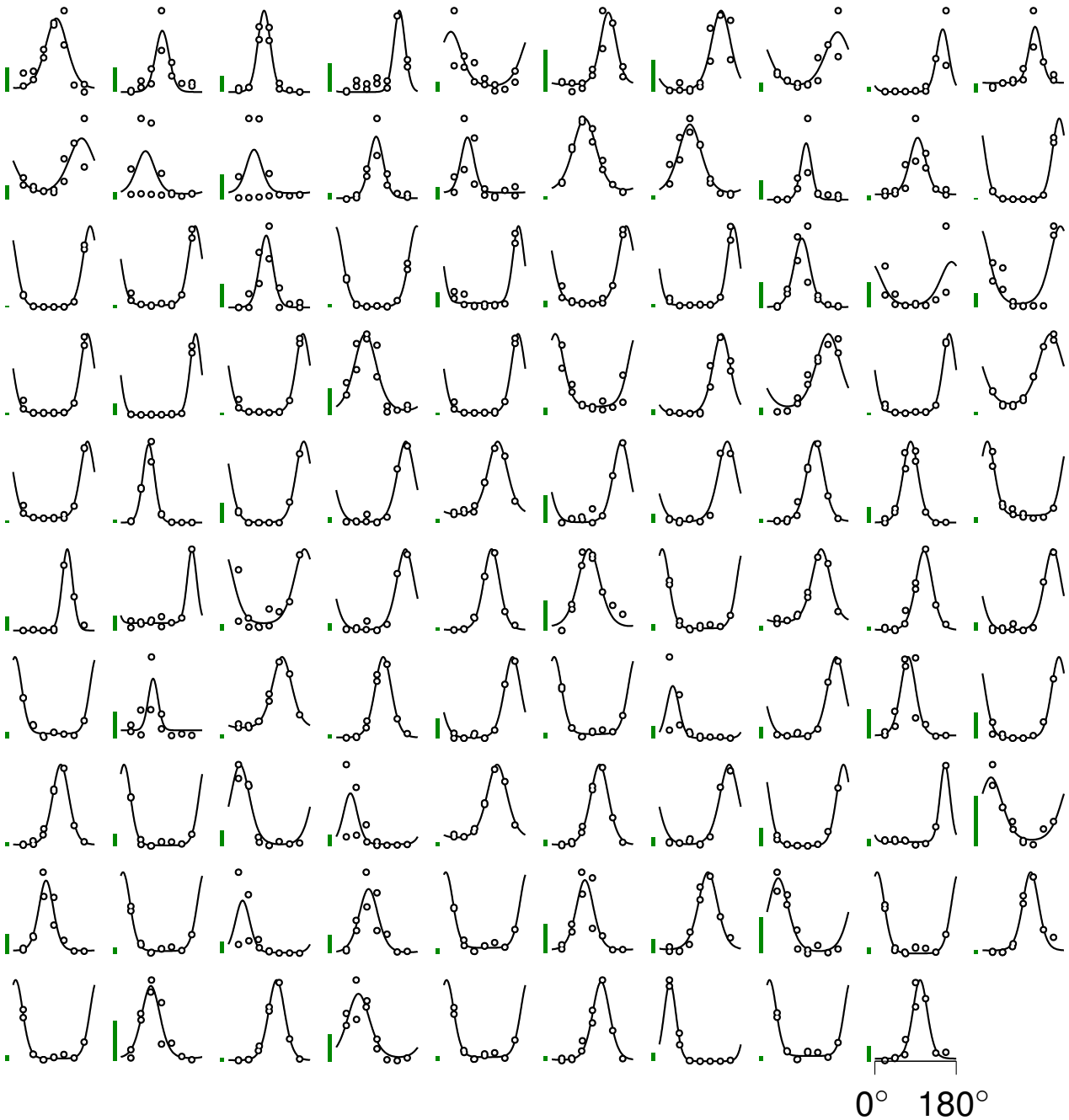


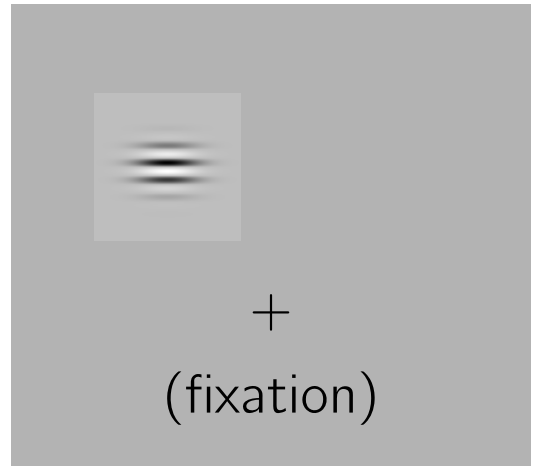
$\phi = \pi$



$\phi = 3\pi/2$

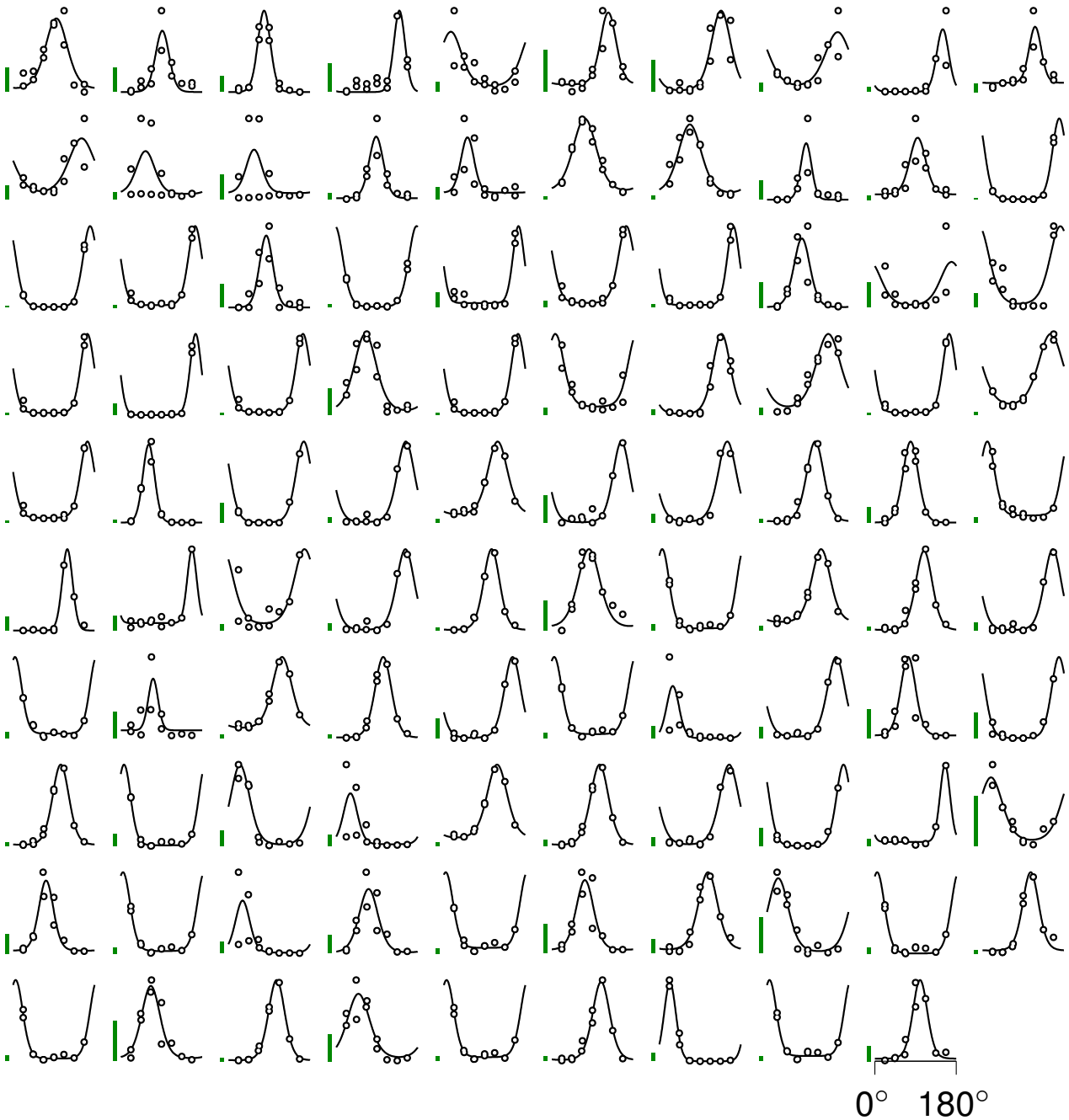
Orientation tuning curves

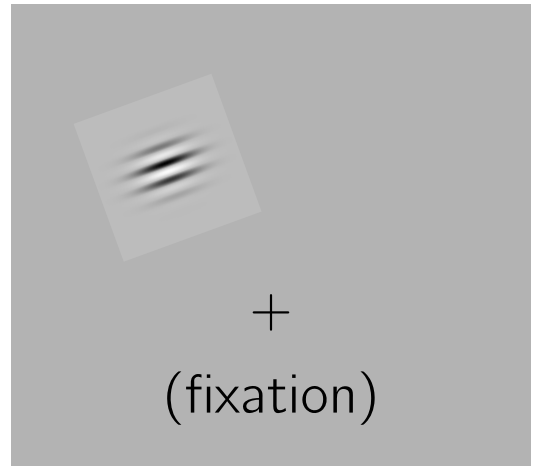




tuning curve:
firing rate (Hz)
as a function of
stimulus orientation (°)

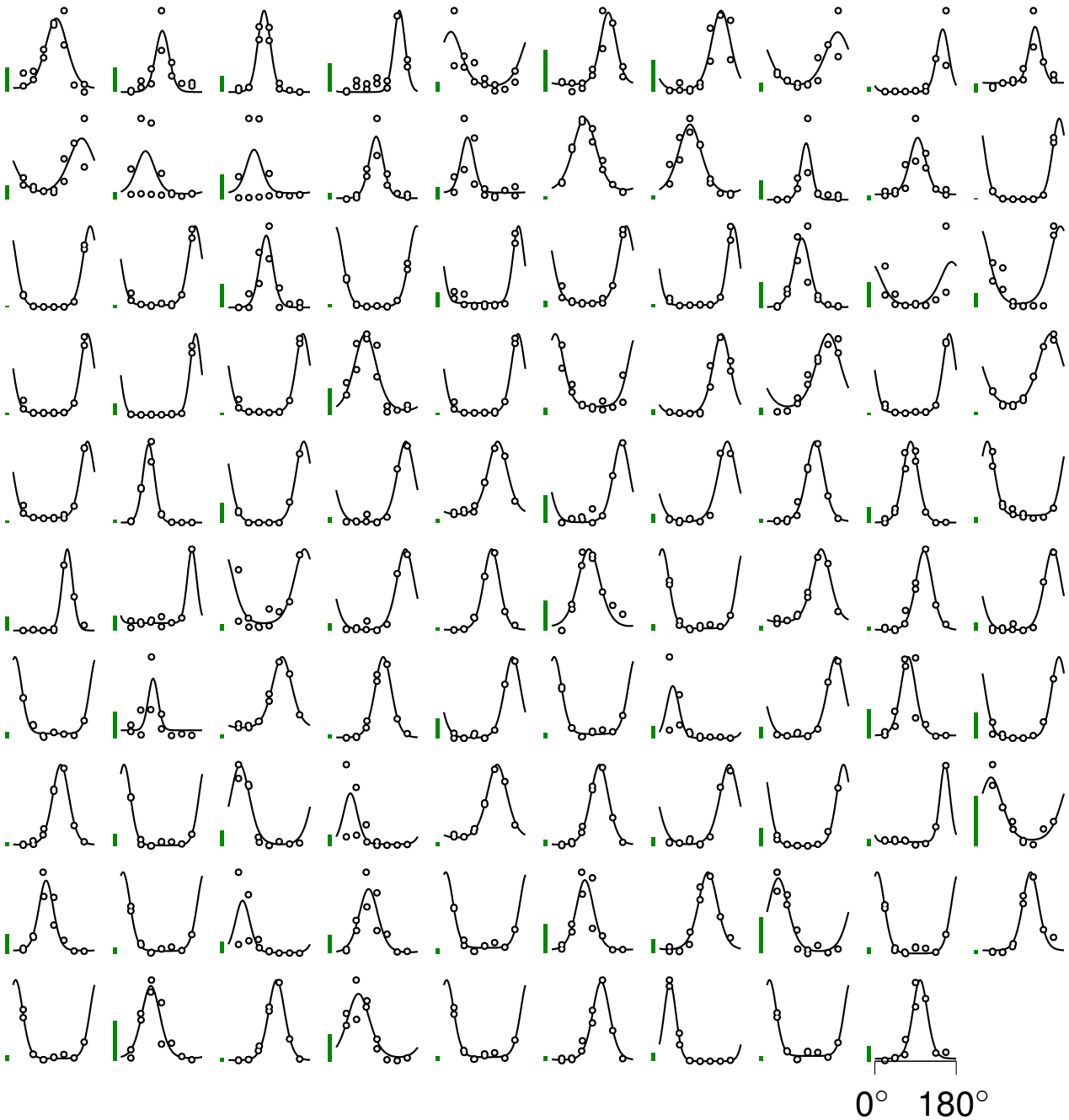
Orientation tuning curves

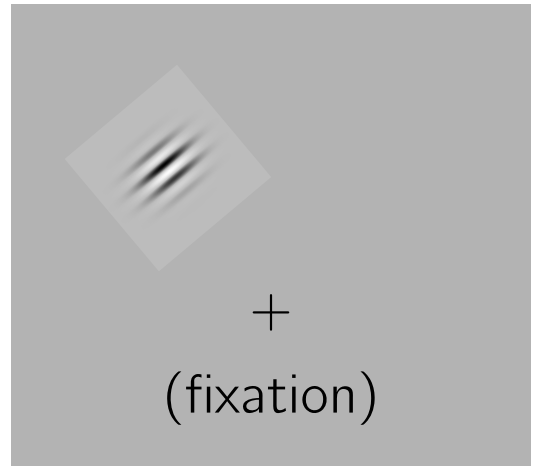




tuning curve:
firing rate (Hz)
as a function of
stimulus orientation (°)

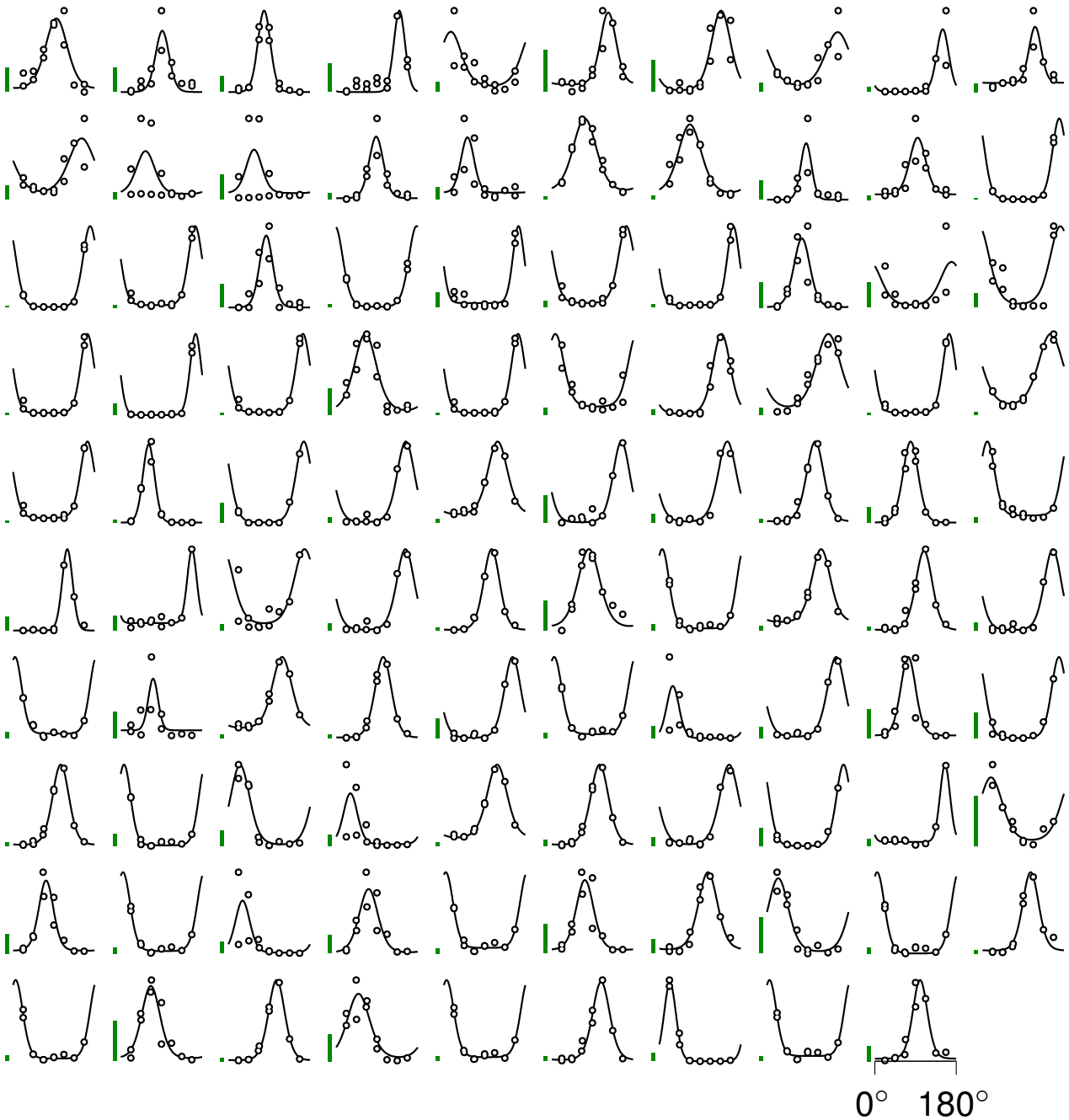
Orientation tuning curves

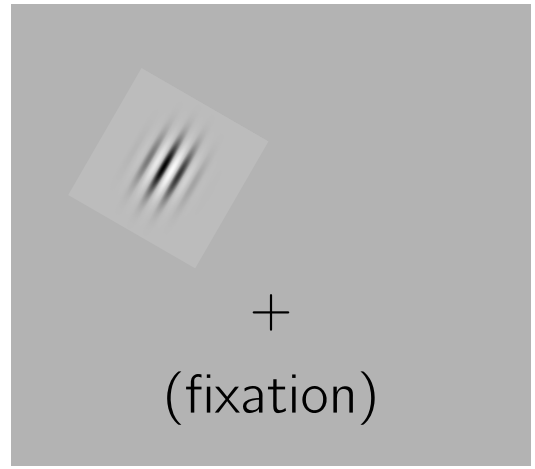




tuning curve:
firing rate (Hz)
as a function of
stimulus orientation (°)

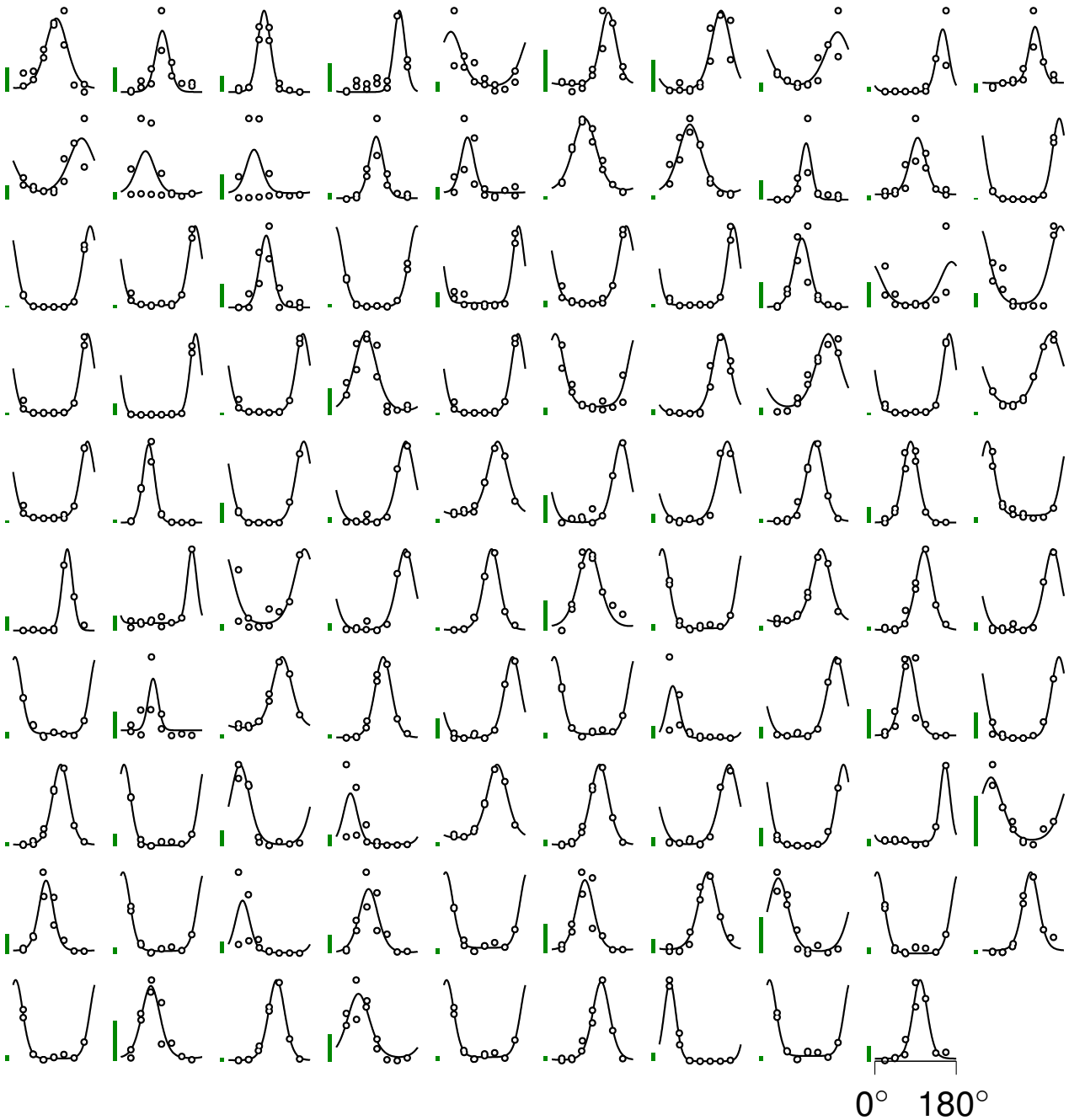
Orientation tuning curves

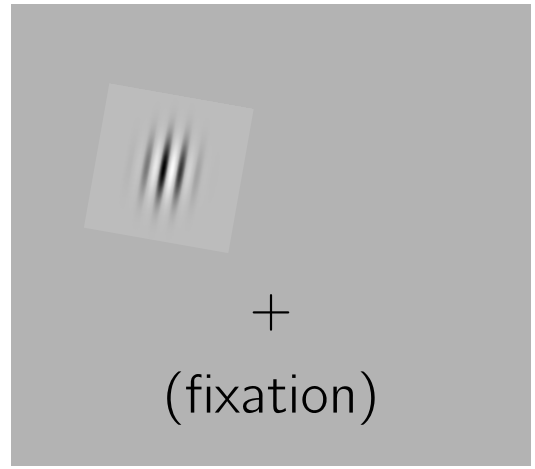




tuning curve:
firing rate (Hz)
as a function of
stimulus orientation (°)

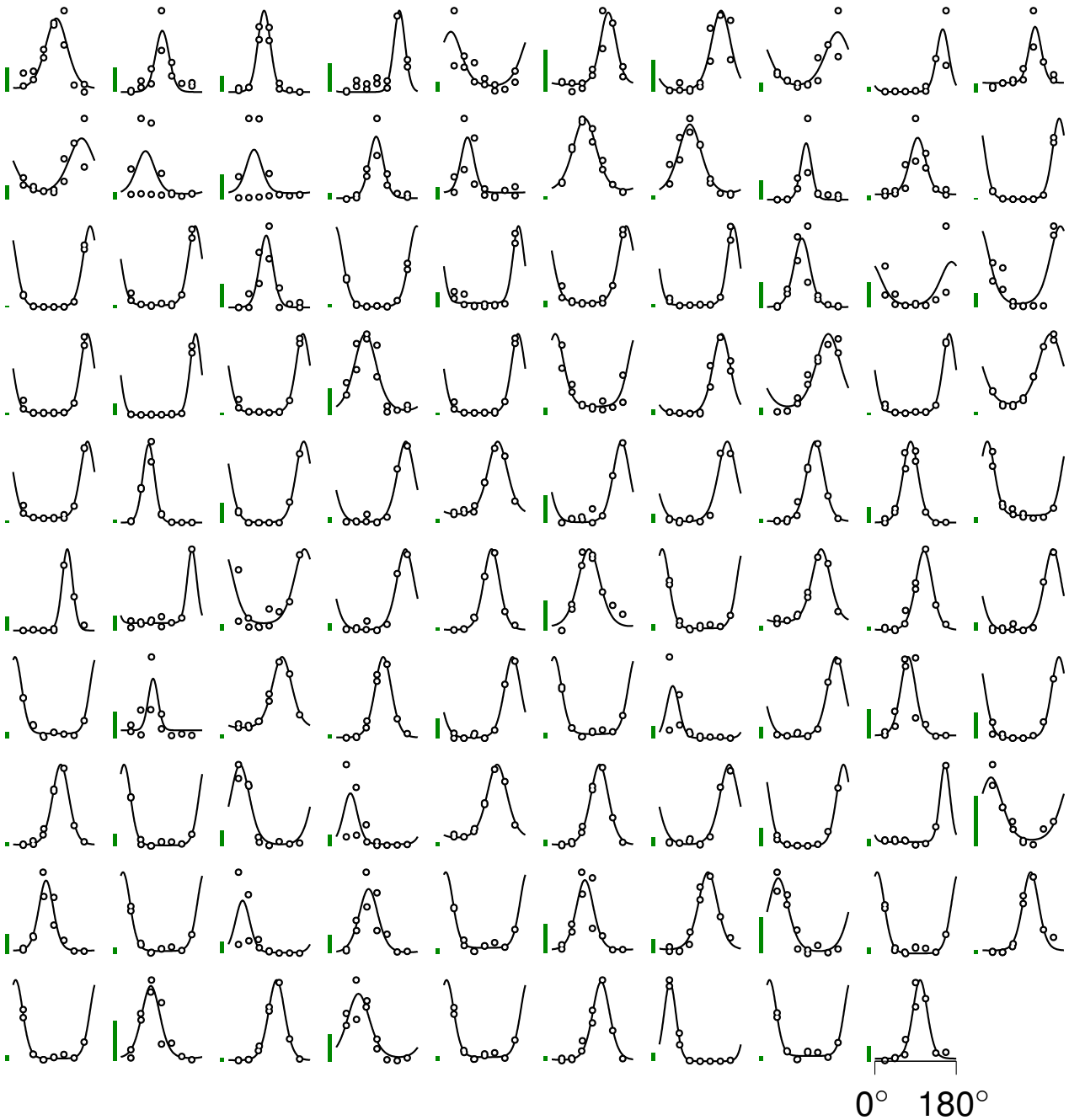
Orientation tuning curves

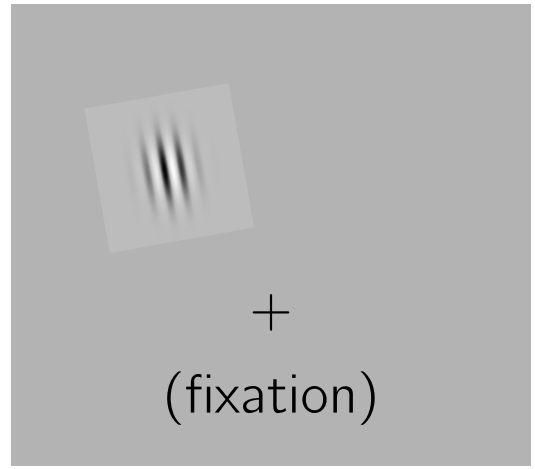




tuning curve:
firing rate (Hz)
as a function of
stimulus orientation (°)

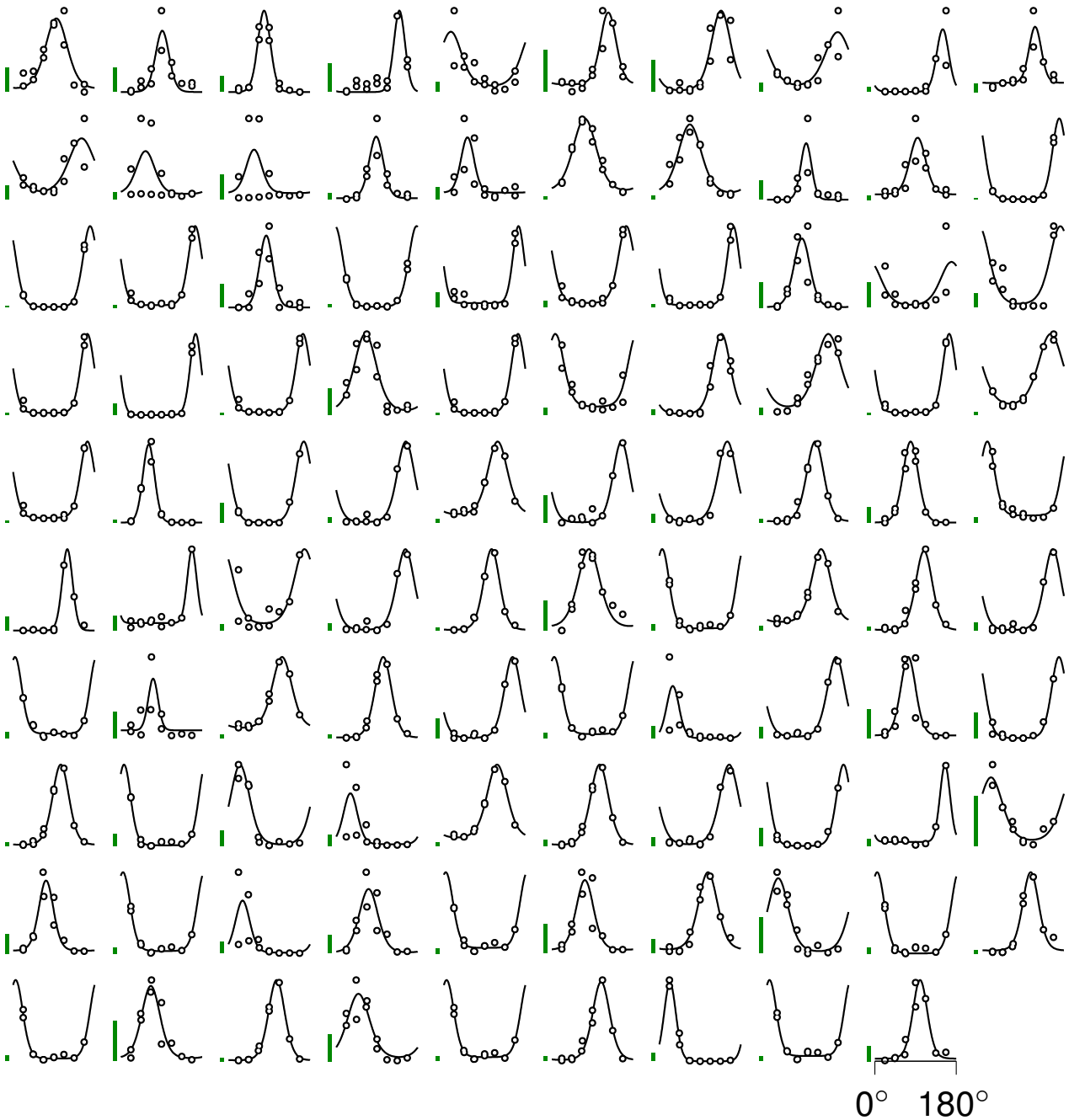
Orientation tuning curves

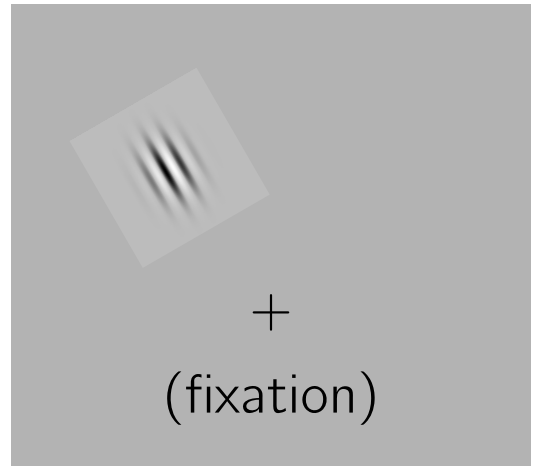




tuning curve:
firing rate (Hz)
as a function of
stimulus orientation (°)

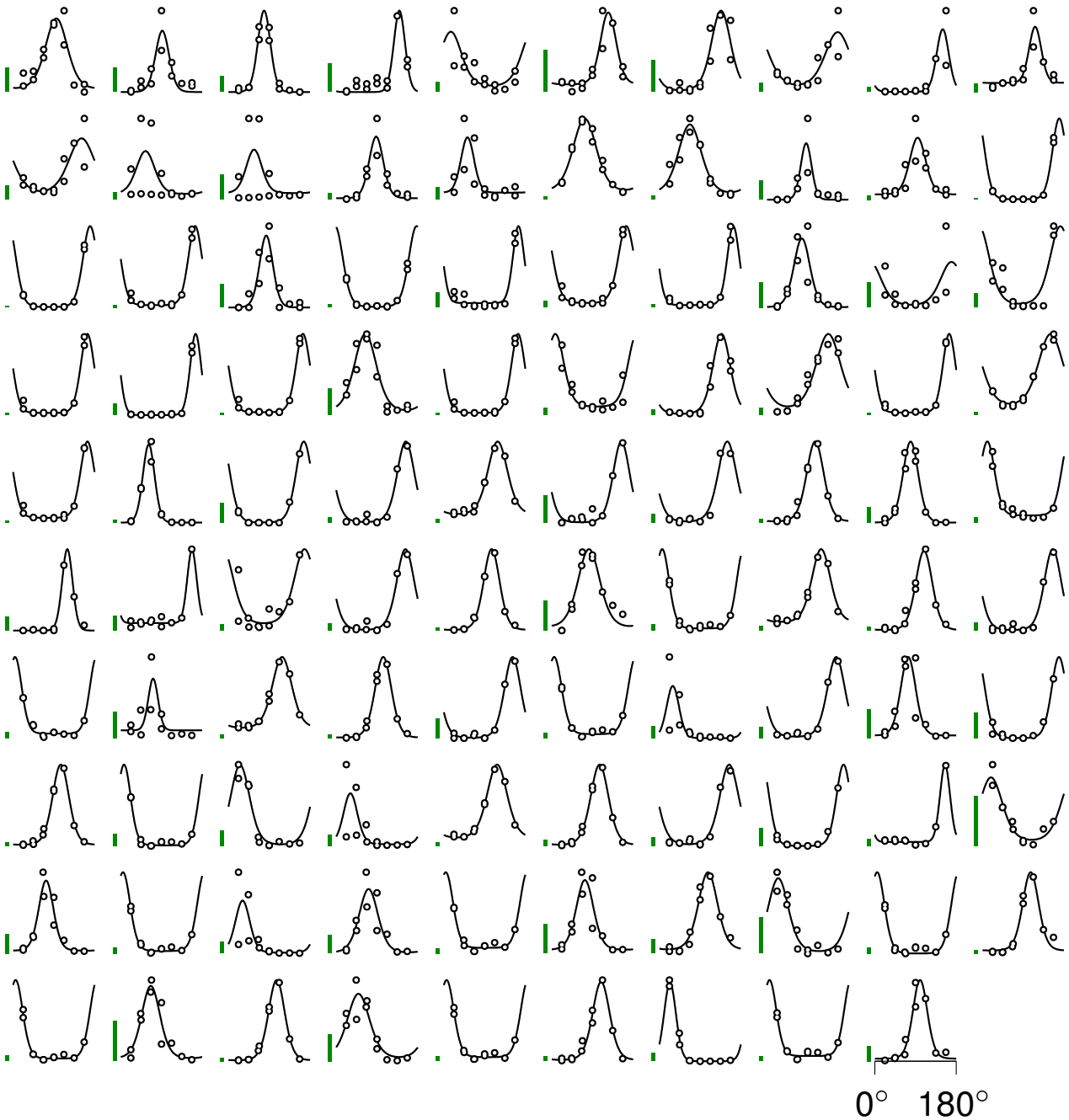
Orientation tuning curves

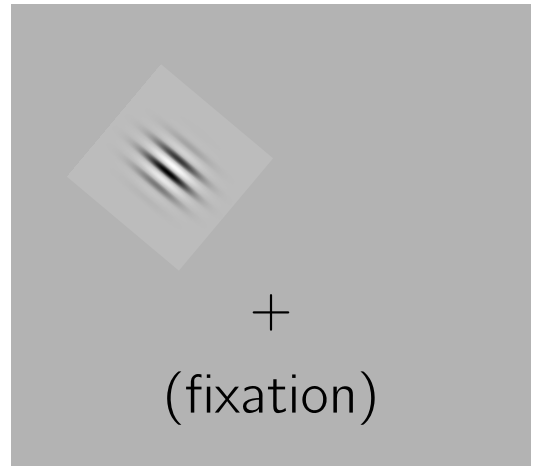




tuning curve:
firing rate (Hz)
as a function of
stimulus orientation (°)

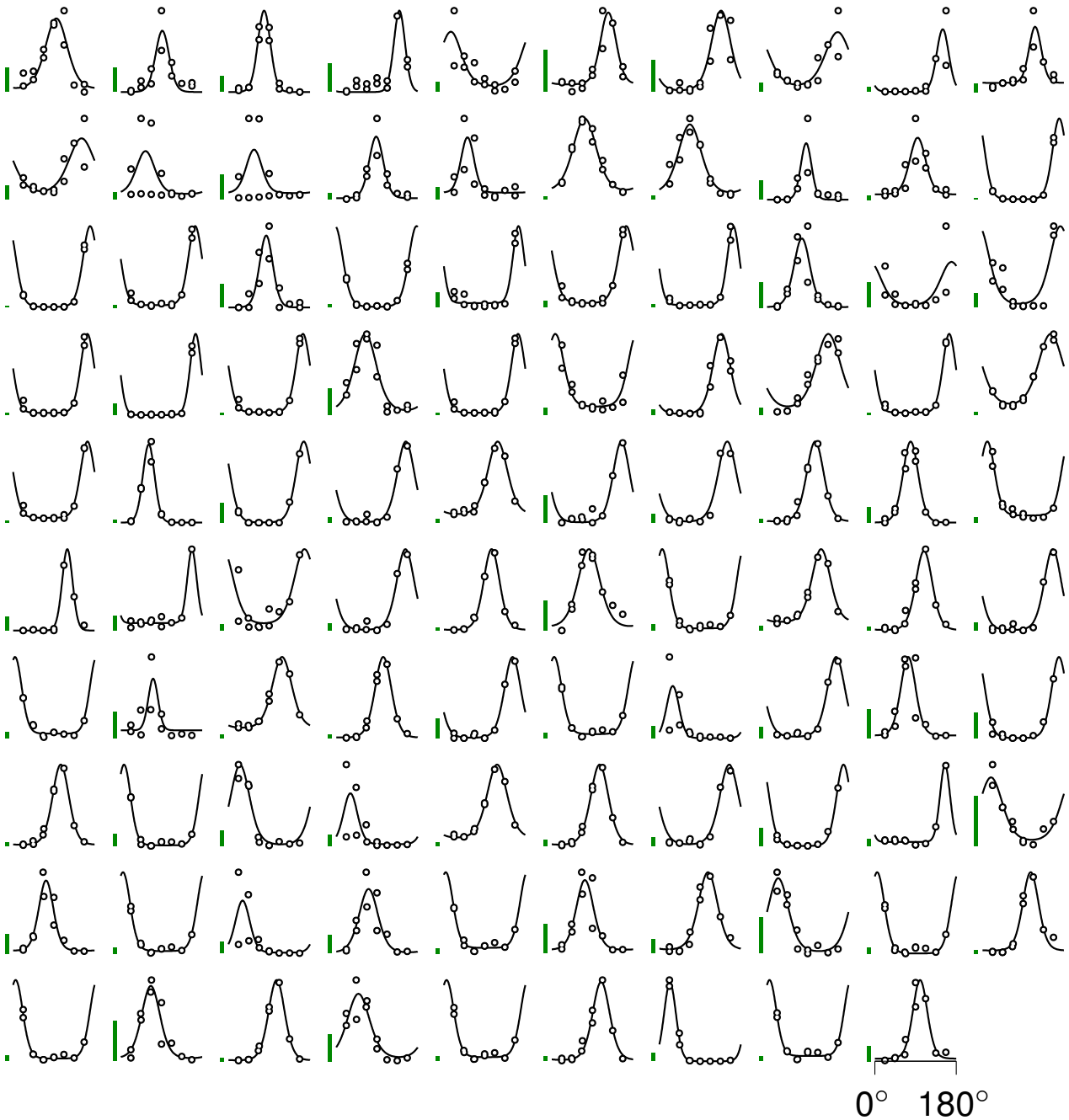
Orientation tuning curves

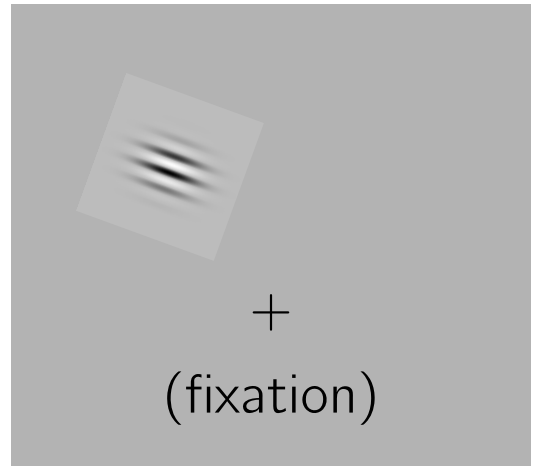




tuning curve:
firing rate (Hz)
as a function of
stimulus orientation (°)

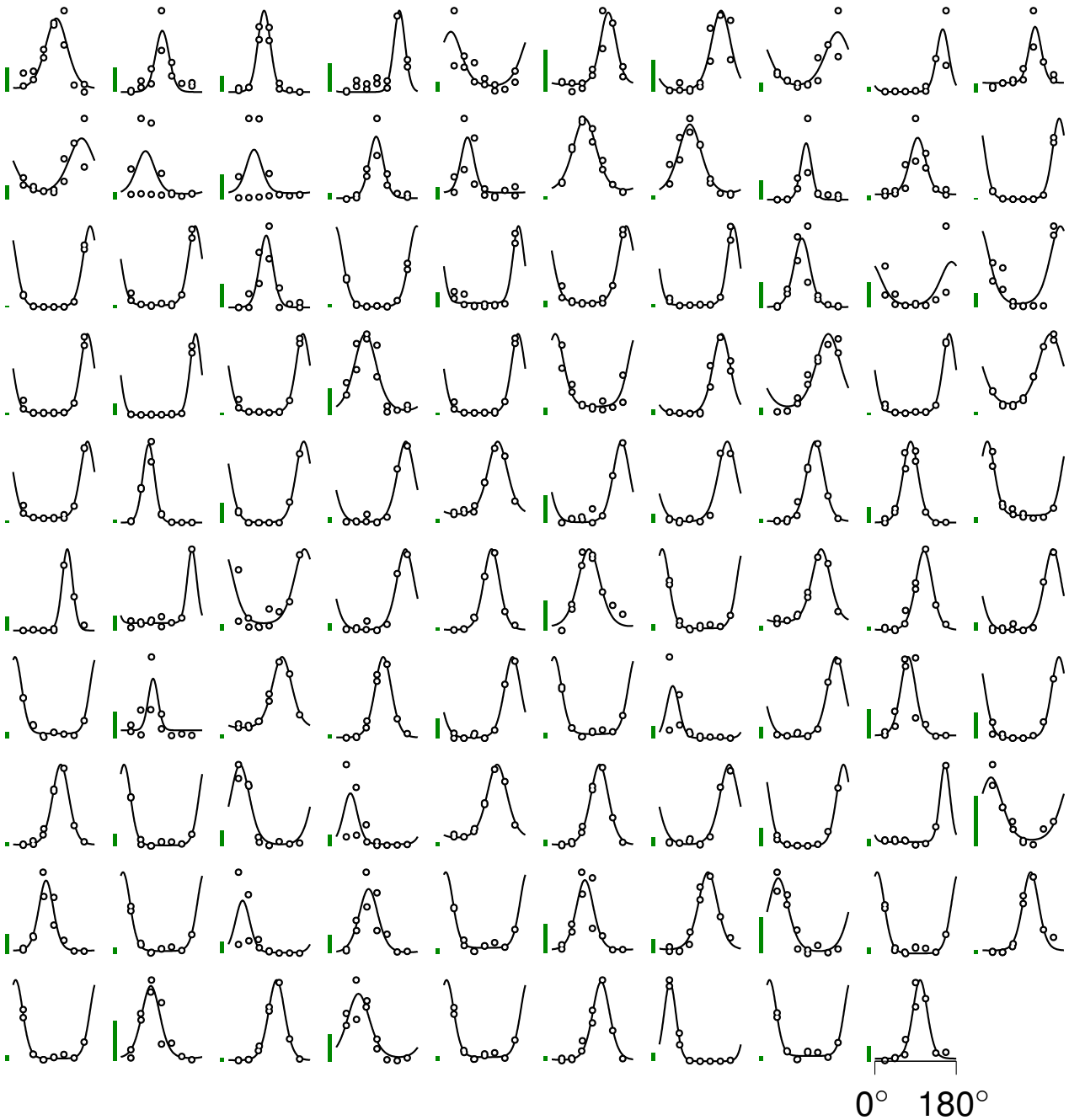
Orientation tuning curves

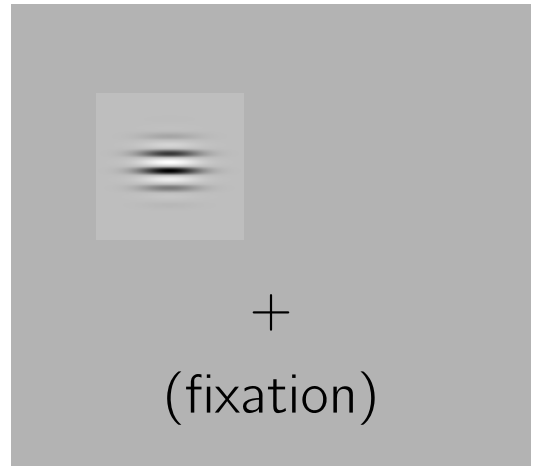




tuning curve:
firing rate (Hz)
as a function of
stimulus orientation (°)

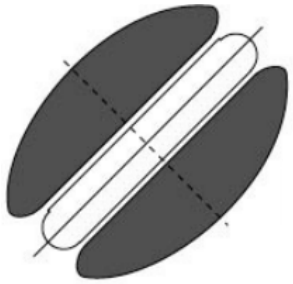
Orientation tuning curves



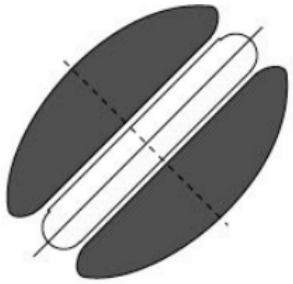


tuning curve:
firing rate (Hz)
as a function of
stimulus orientation (°)

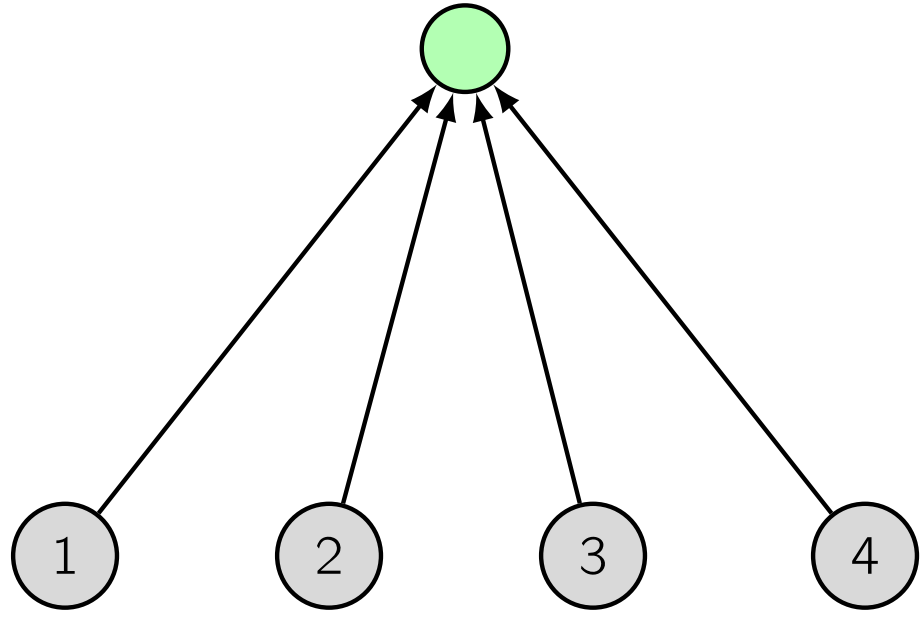
Hubel and Wiesel's "feedforward model"



Hubel and Wiesel's "feedforward model"

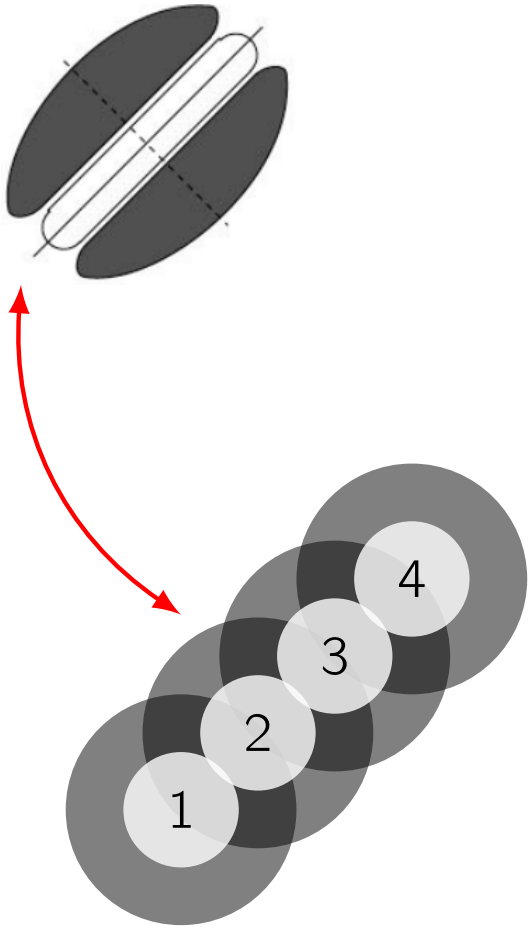


V1 neuron with elongated RF

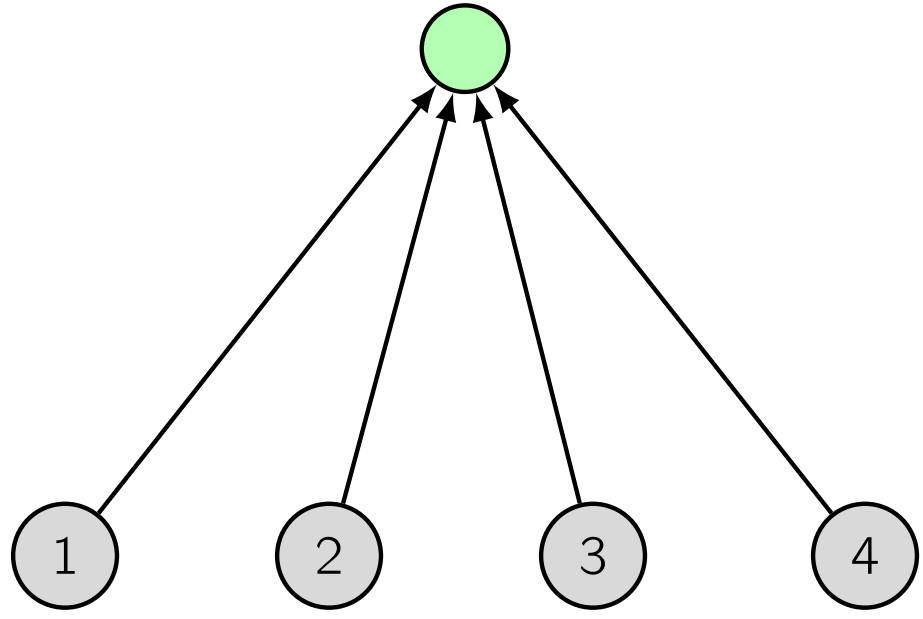


LGN neurons with circular center-surround RFs
which tile the visual field along a line

Hubel and Wiesel's "feedforward model"

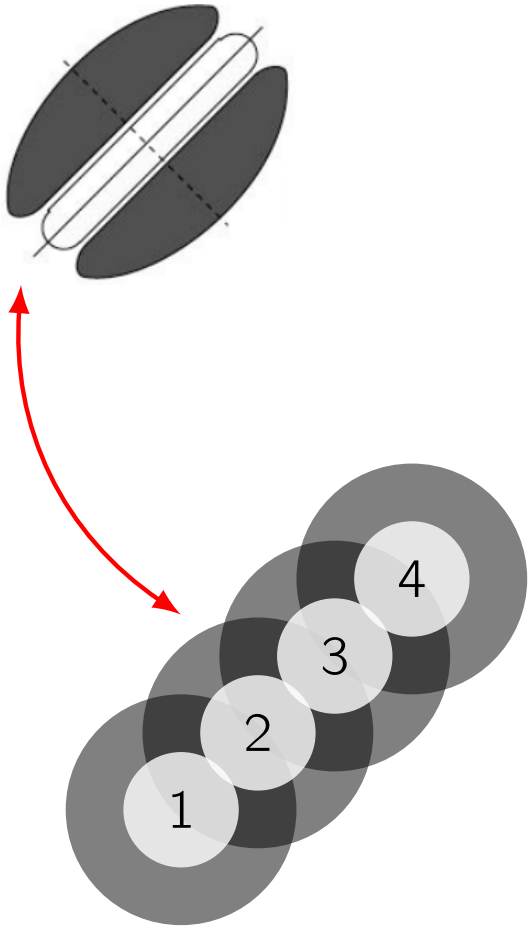


V1 neuron with elongated RF

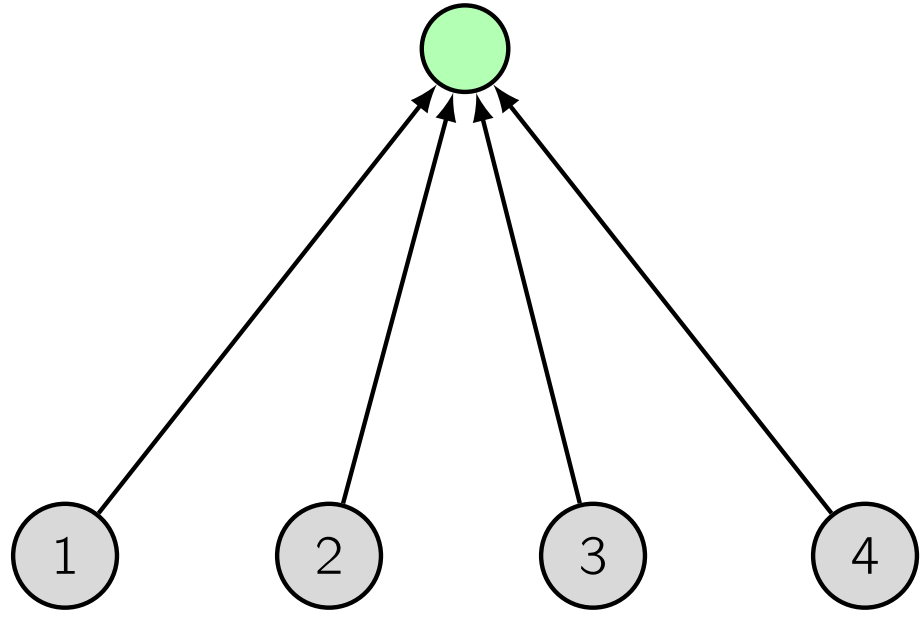


LGN neurons with circular center-surround RFs
which tile the visual field along a line

Hubel and Wiesel's "feedforward model"



V1 neuron with elongated RF



LGN neurons with circular center-surround RFs
which tile the visual field along a line

can be extended to account for different phases

(this model has some truth, but is highly simplistic)

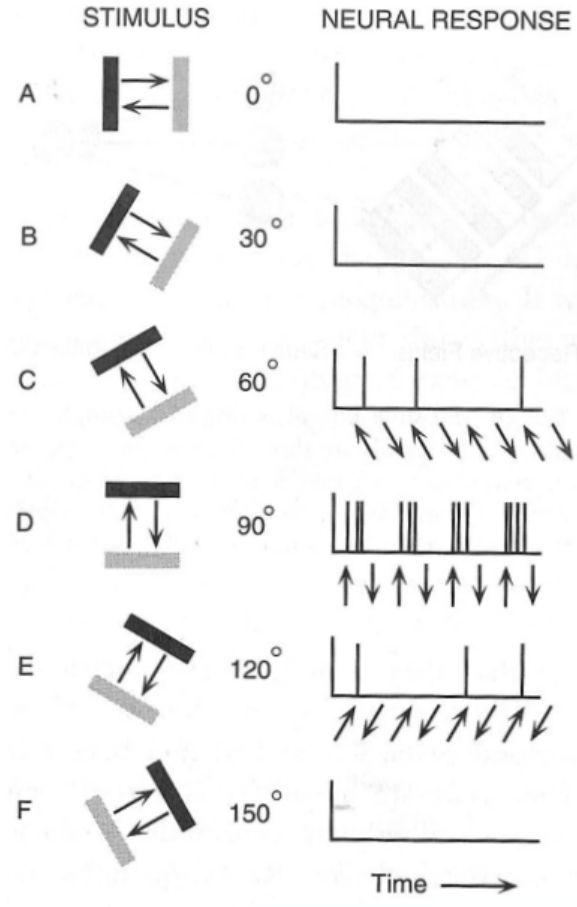
Receptive fields of V1 “complex cells”

(movie)

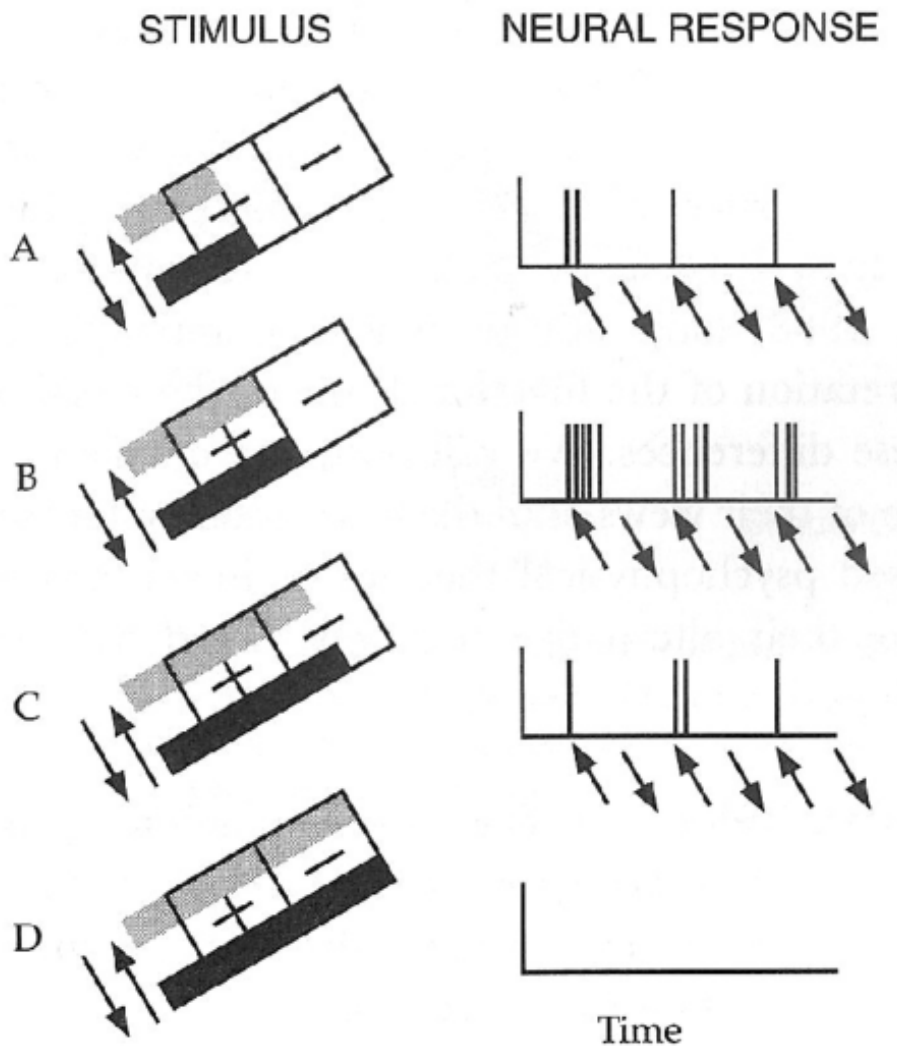
Receptive fields of V1 “complex cells”

elongated receptive fields (similar to simple cells), but:

- larger RF
- does not respond to single spot of light
- cannot be mapped using the same method as for simple cells (due to nonlinear summation)
- motion sensitive: responds to *moving lines*, often only in one motion direction
- less sensitive to exact retinal location (i.e. phase of a Gabor stimulus)

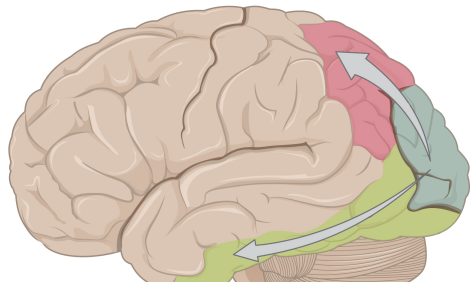


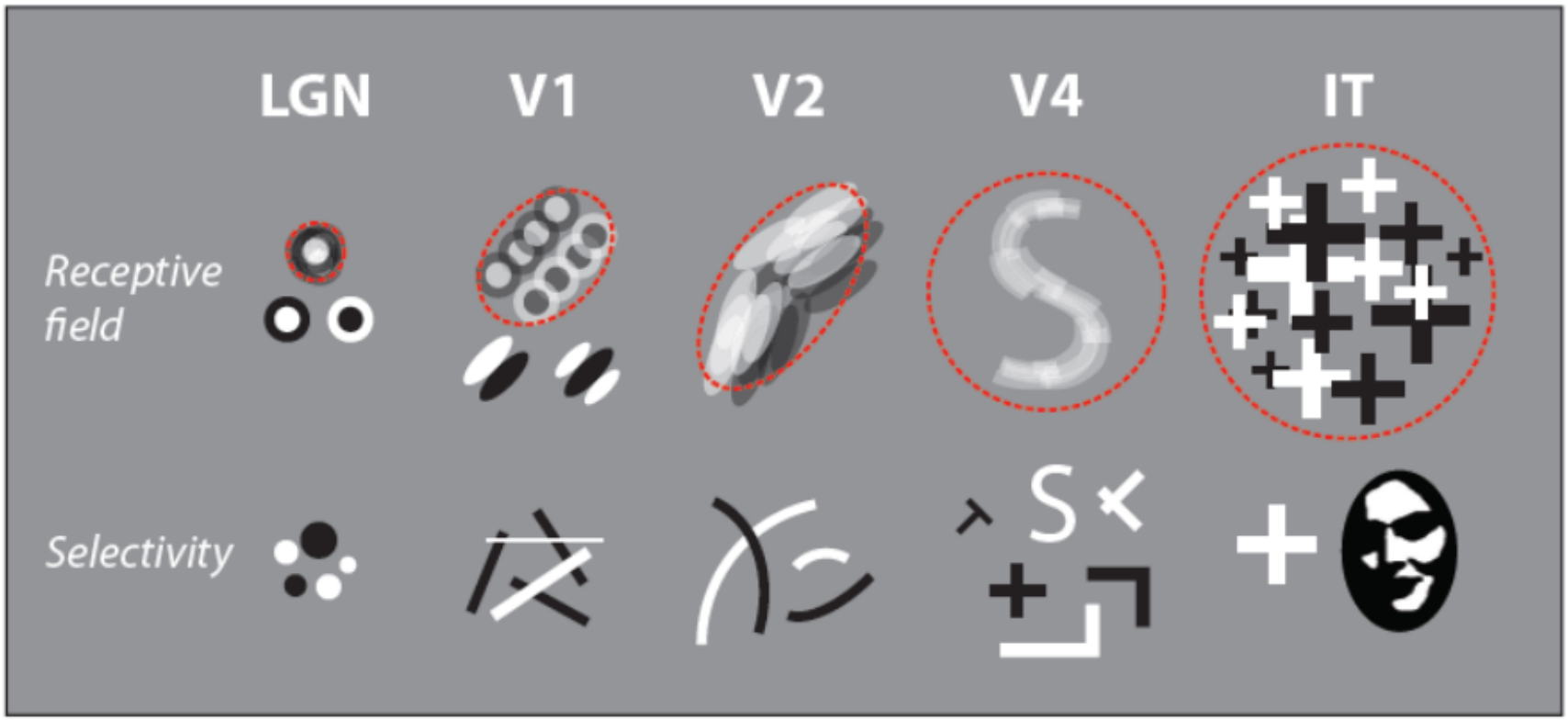
Receptive fields of V1 "hypercomplex cells"



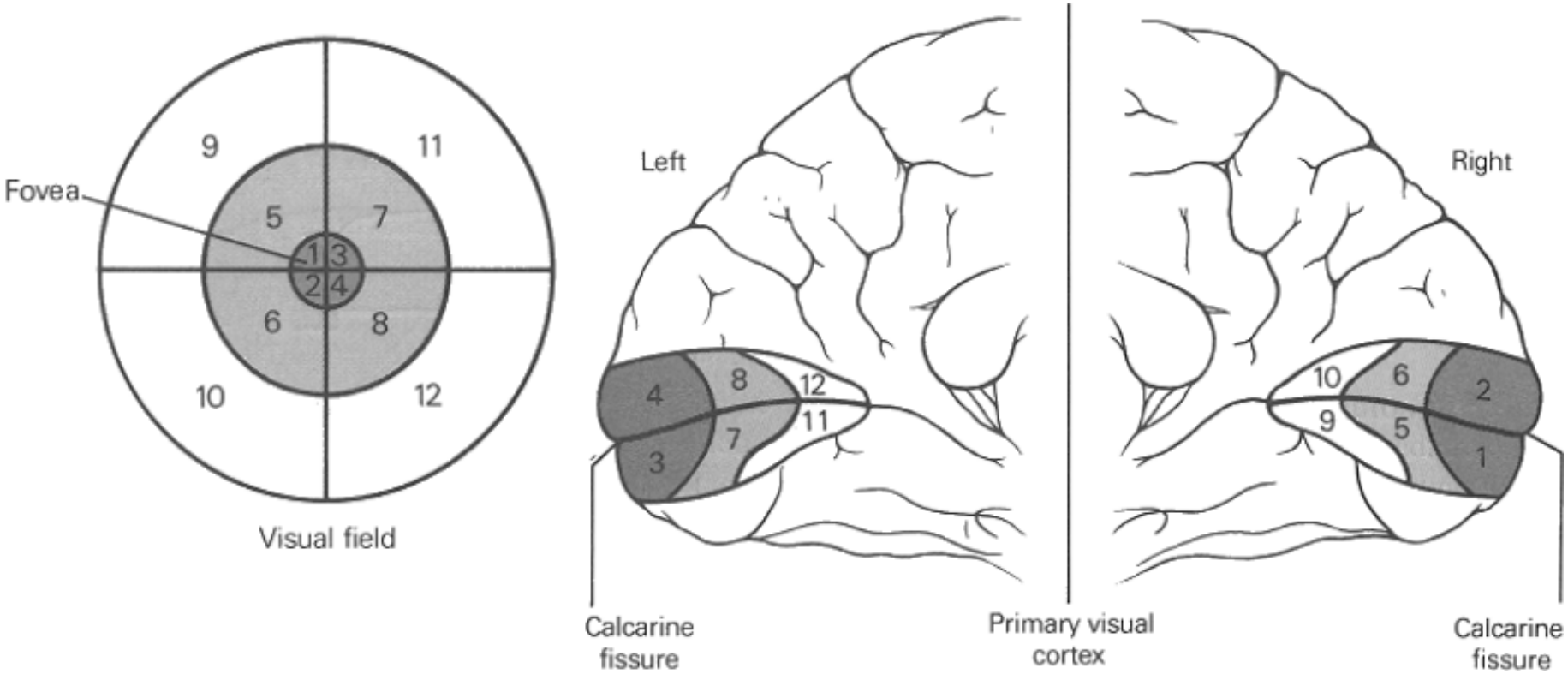
like complex cells, but so-called "end-stopped"

Receptive field hierarchy



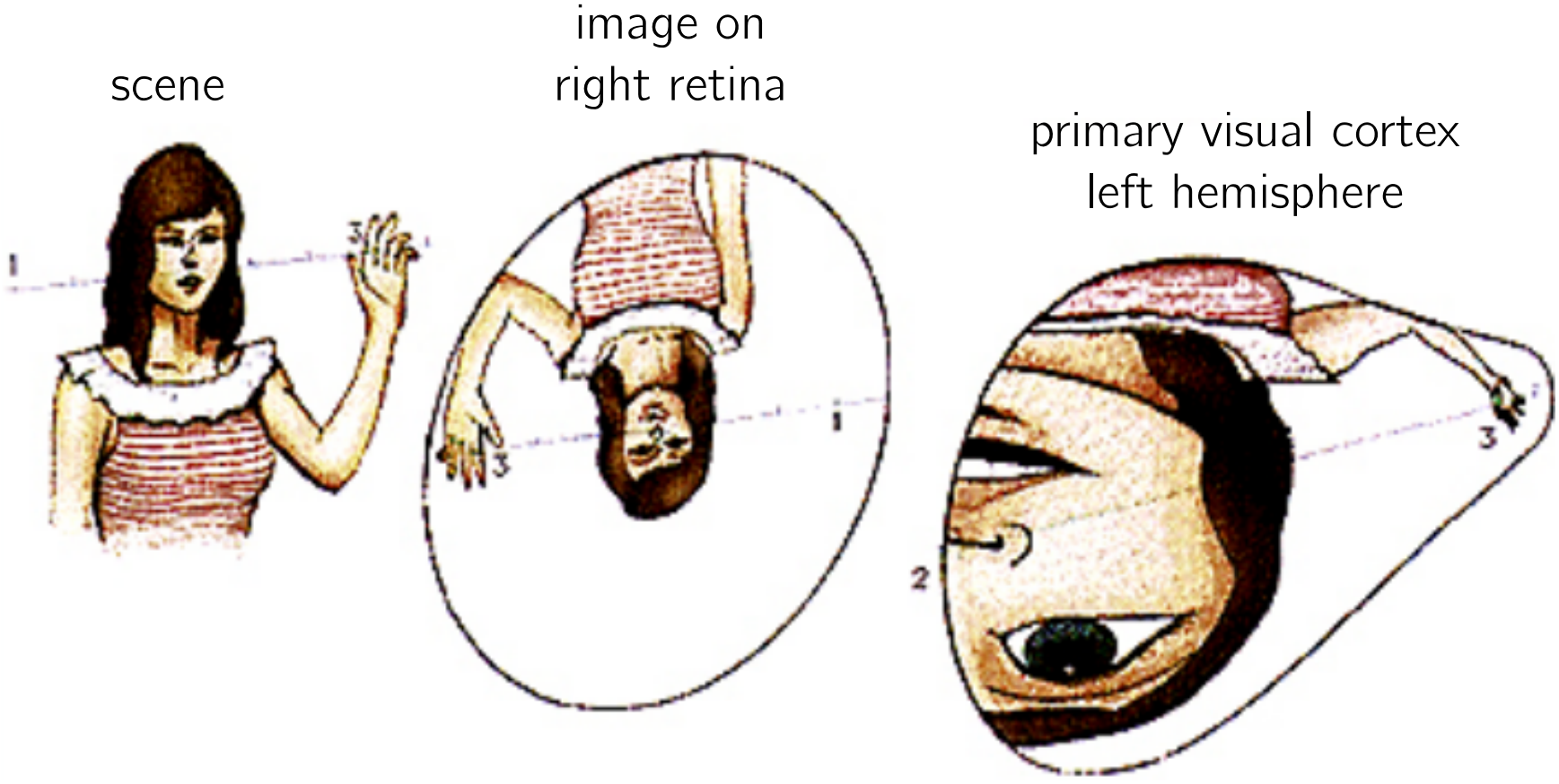


Spatial organisation of V1: retinotopy



- V1 has area $\approx 25\text{cm}^2$ in humans
- cortical map preserves retinal topography: neighbouring neurons have neighbouring RFs
- the map is distorted primarily due to cortical magnification of foveal vs. peripheral areas

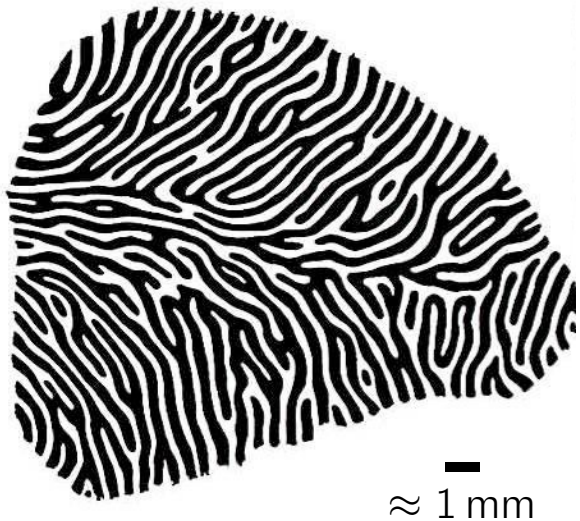
Spatial organisation of V1: retinotopy



- V1 has area $\approx 25\text{cm}^2$ in humans
- cortical map preserves retinal topography: neighbouring neurons have neighbouring RFs
- the map is distorted primarily due to cortical magnification of foveal vs. peripheral areas

Cortical maps

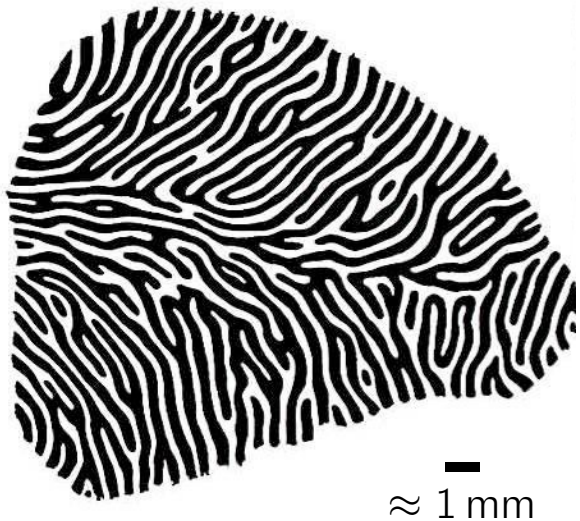
smooth map of
occular dominance:



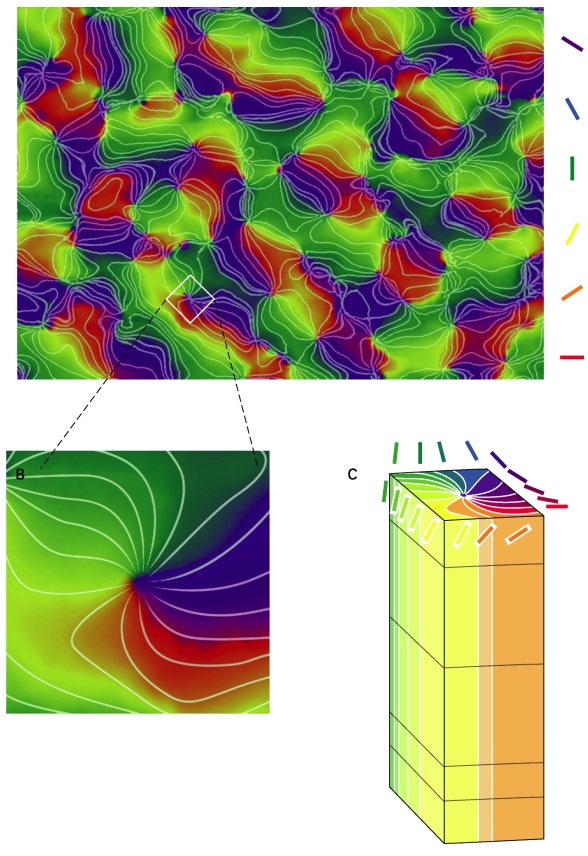
$\approx 1\,\mathrm{mm}$

Cortical maps

smooth map of
occular dominance:

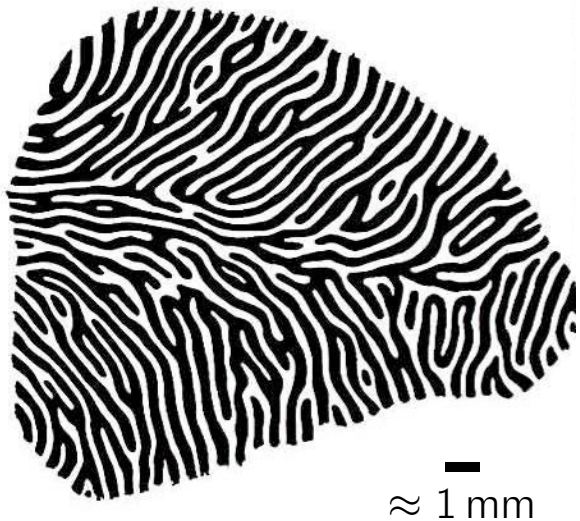


smooth map of
orientation preference

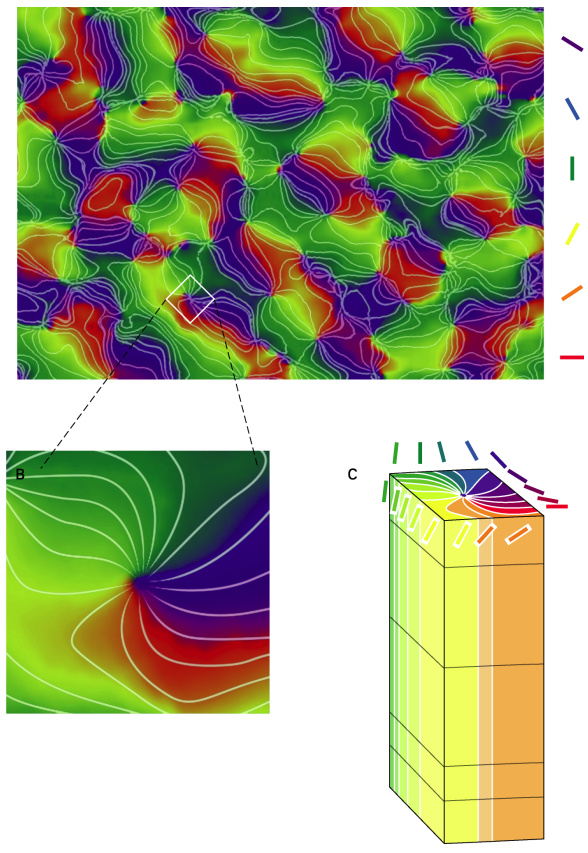


Cortical maps

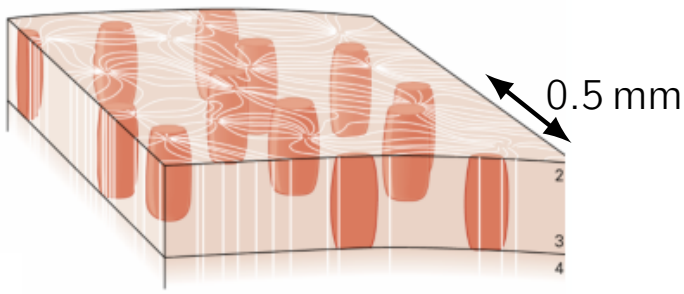
smooth map of
occular dominance:



smooth map of
orientation preference

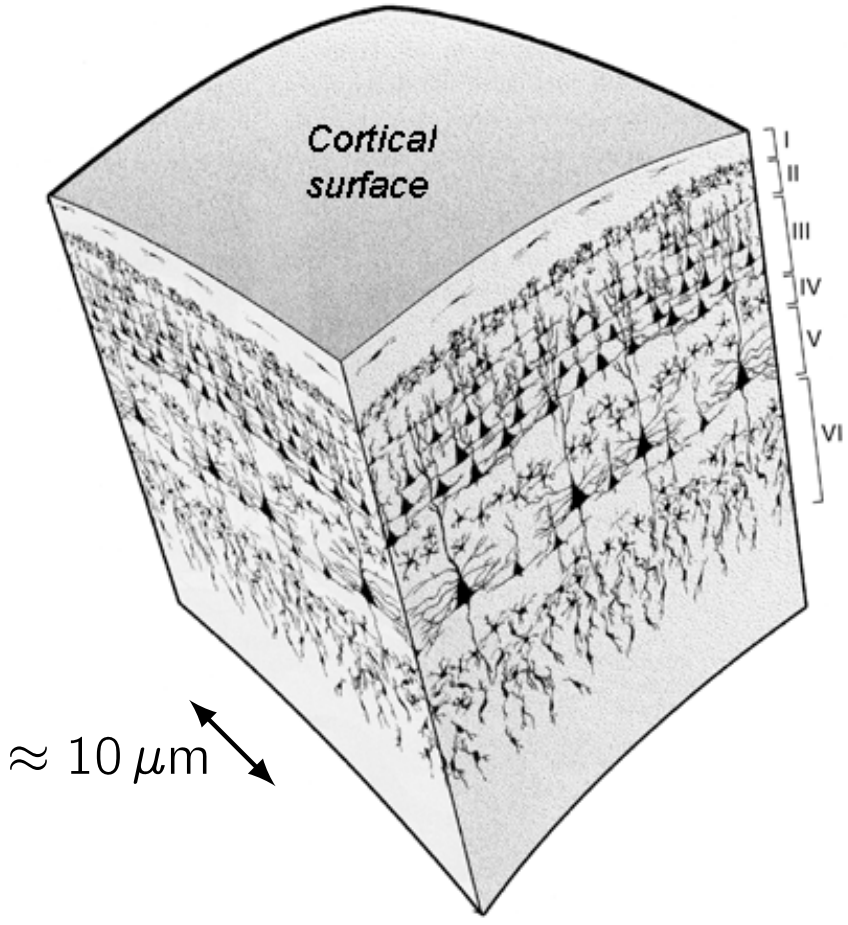


"blobs": cylinder-shaped with
no orientation preference
but color selectivity



The cortical column as organisation unit

V1 “column”

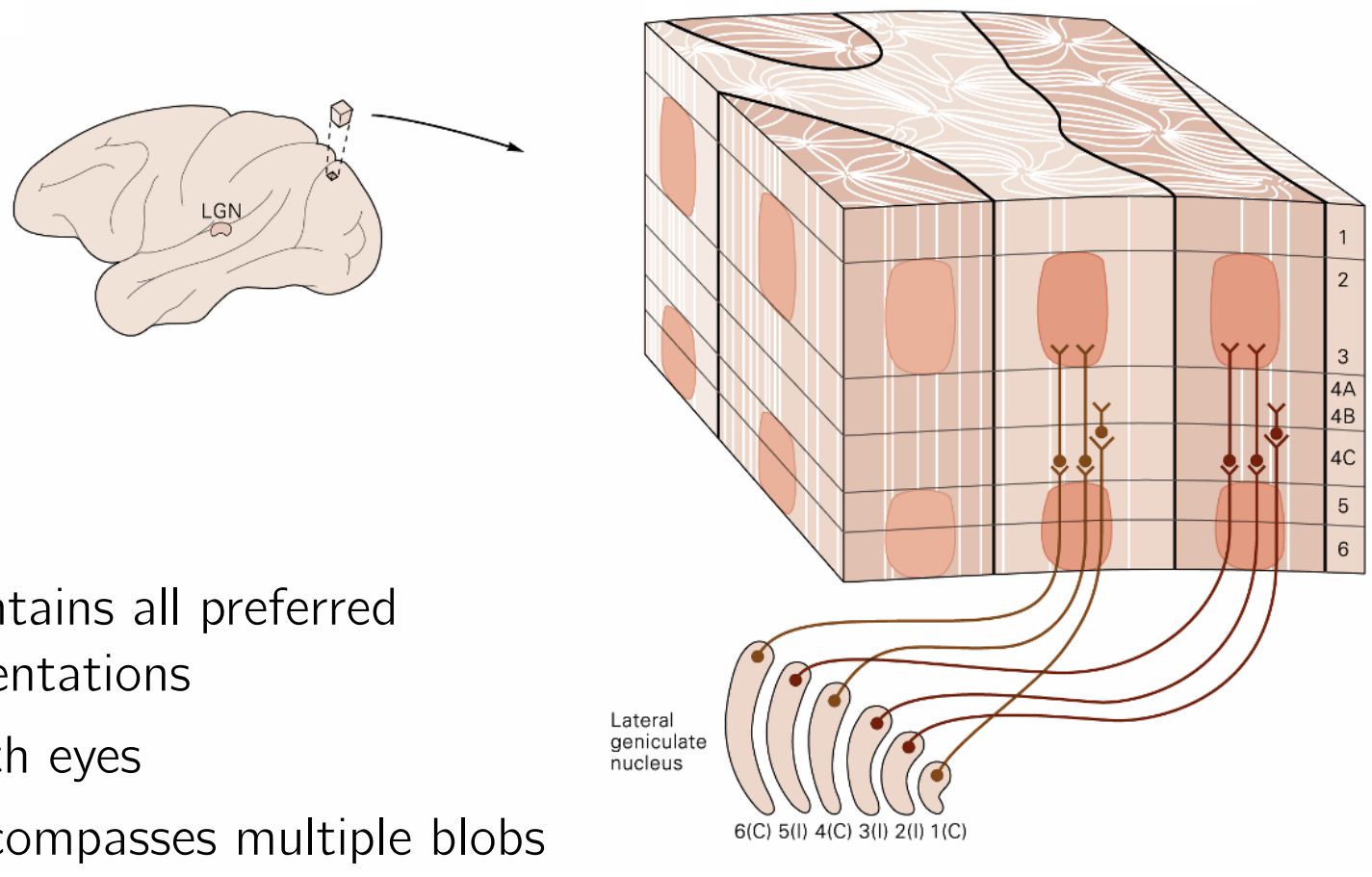


∼ 100 cells with similar tuning:

- sensitive to stimuli in the same location in the visual field
- prefer the same eye
- prefer the same orientation
- but range of spatial frequencies

Cortical hypercolumns

V1 “hypercolumn”

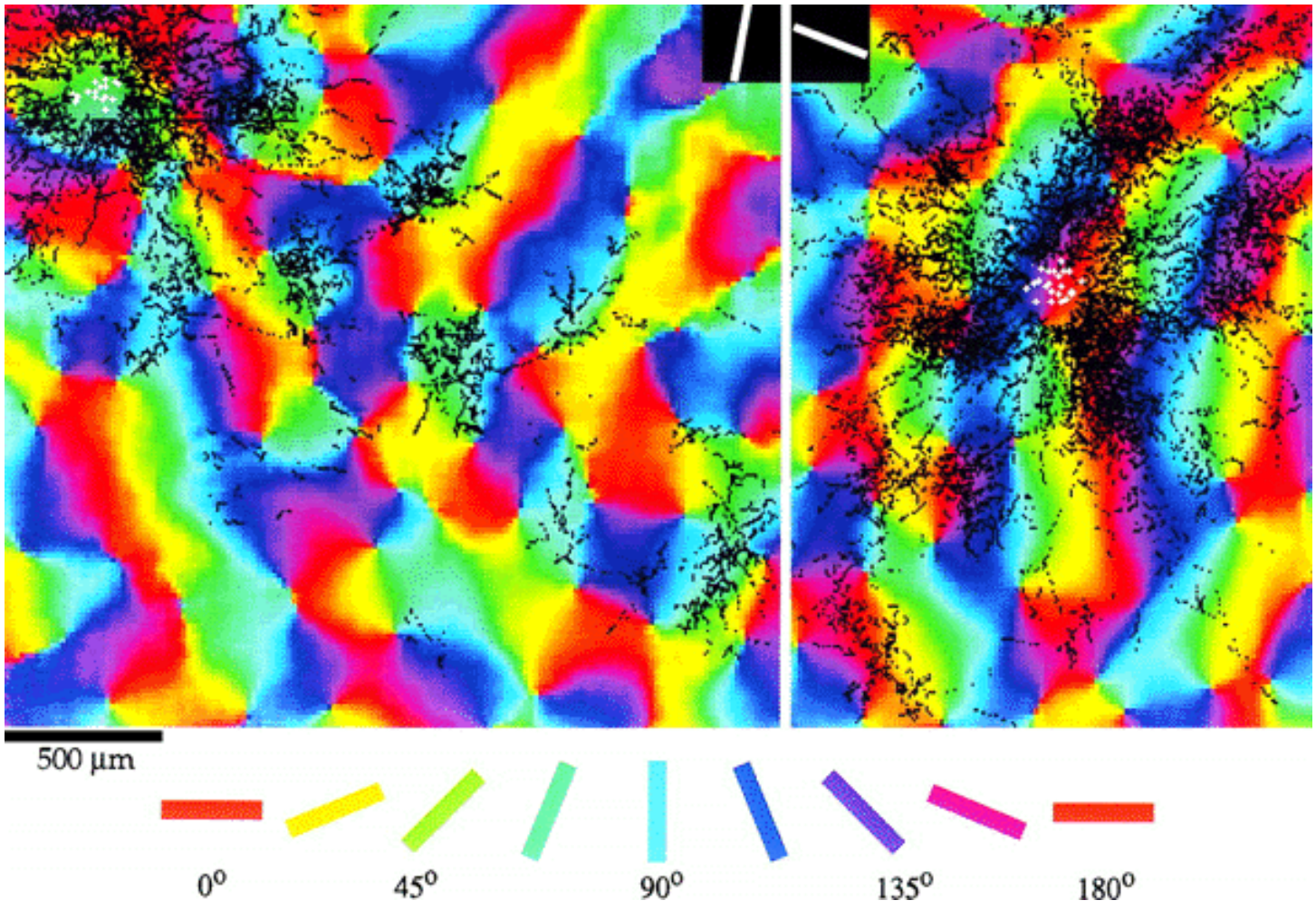


- contains all preferred orientations
- both eyes
- encompasses multiple blobs

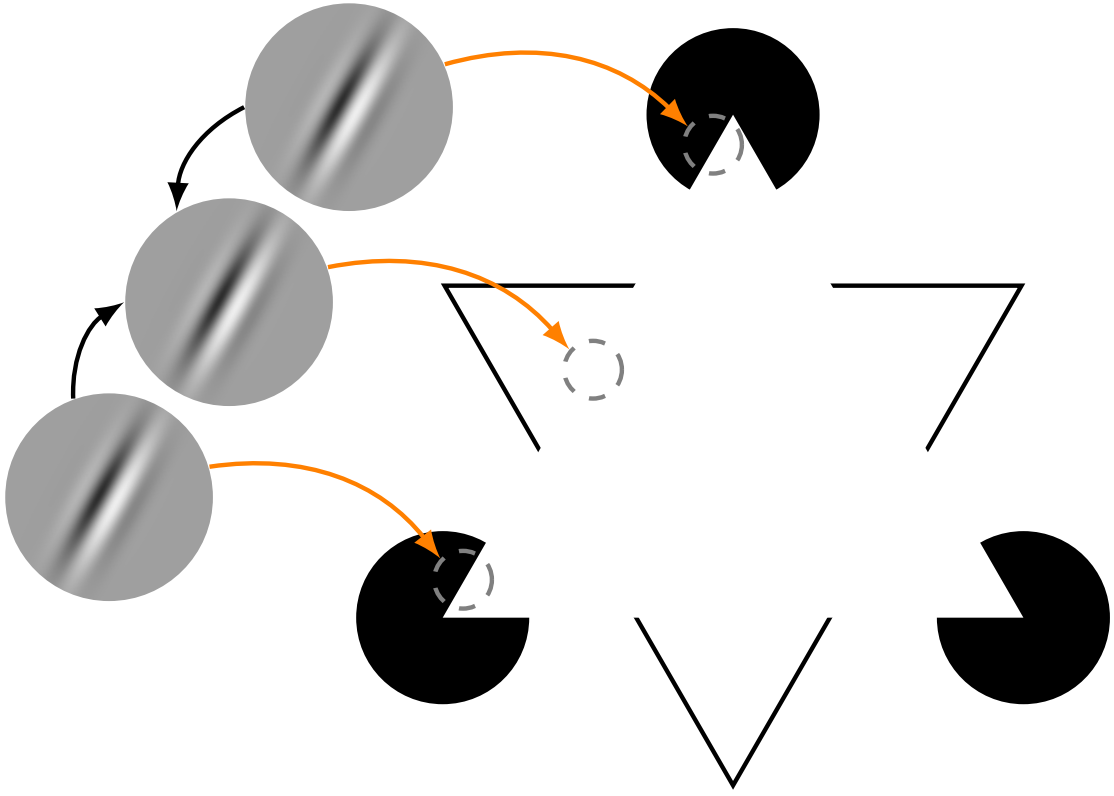
Cortical hypercolumns

V1 "hypercolumns" have long-range connections

(specifically organised such that neurons connect to other neurons with similar orientation preference)



Cortical hypercolumns



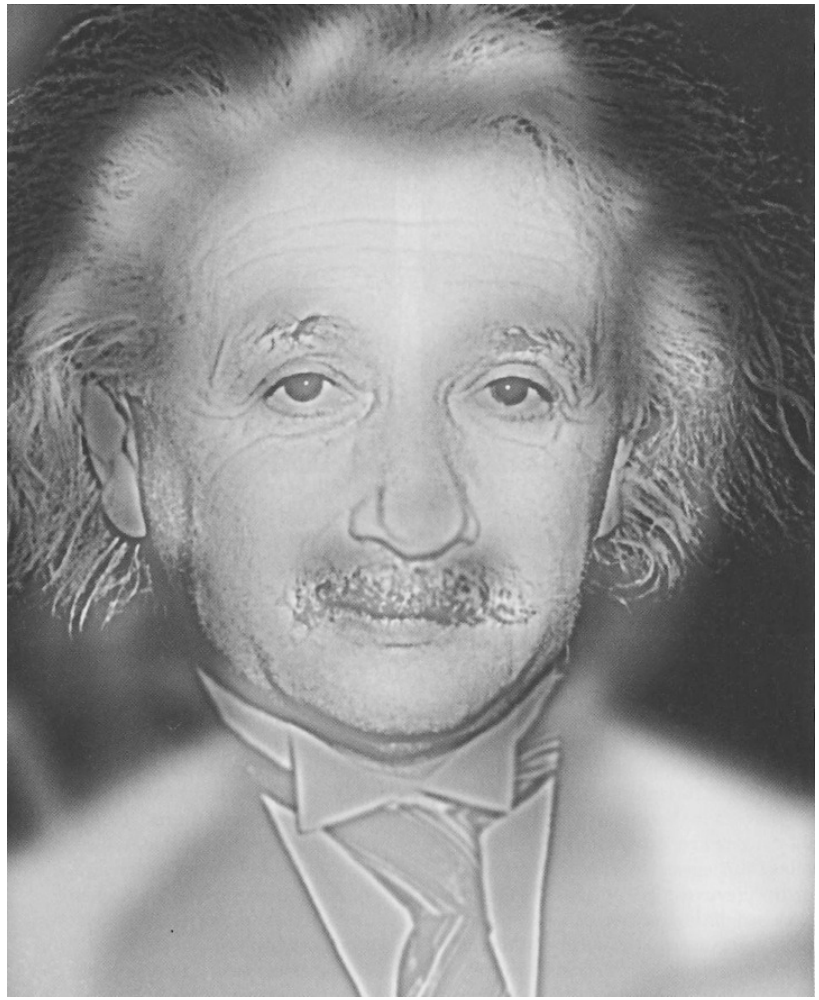
interactions between columns with similar orientation preference might account for fill-in effects

Channel theory

different features of the visual scene
(colour, orientation, spatial frequency, direction of motion, . . .)
are represented in independent channels (merged in later processing stages)

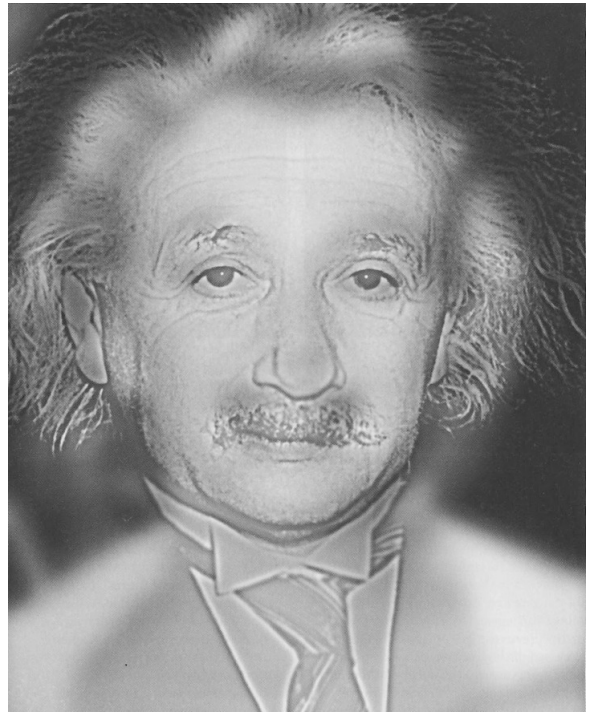
Channel theory

different features of the visual scene
(colour, orientation, spatial frequency, direction of motion, . . .)
are represented in independent channels (merged in later processing stages)



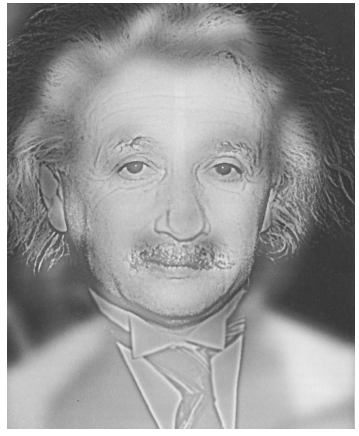
Channel theory

different features of the visual scene
(colour, orientation, spatial frequency, direction of motion, . . .)
are represented in independent channels (merged in later processing stages)



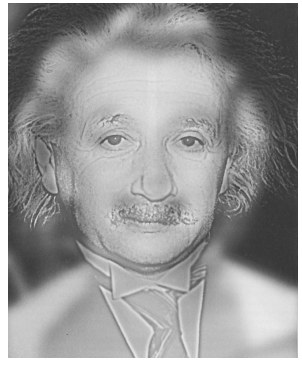
Channel theory

different features of the visual scene
(colour, orientation, spatial frequency, direction of motion, . . .)
are represented in independent channels (merged in later processing stages)



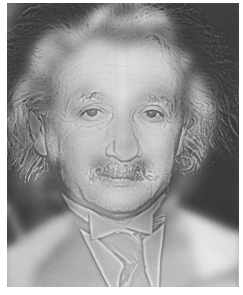
Channel theory

different features of the visual scene
(colour, orientation, spatial frequency, direction of motion, . . .)
are represented in independent channels (merged in later processing stages)



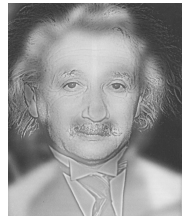
Channel theory

different features of the visual scene
(colour, orientation, spatial frequency, direction of motion, . . .)
are represented in independent channels (merged in later processing stages)



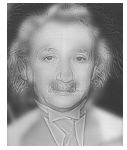
Channel theory

different features of the visual scene
(colour, orientation, spatial frequency, direction of motion, . . .)
are represented in independent channels (merged in later processing stages)

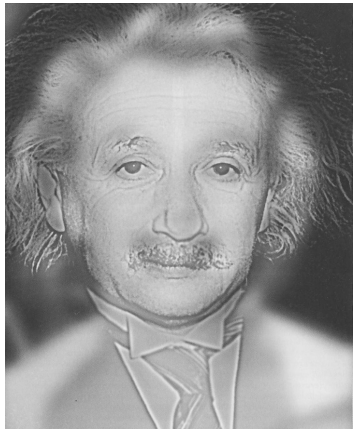


Channel theory

different features of the visual scene
(colour, orientation, spatial frequency, direction of motion, . . .)
are represented in independent channels (merged in later processing stages)

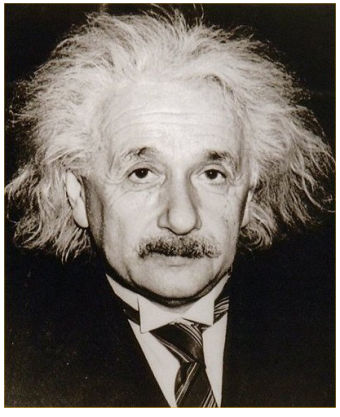


Hybrid images

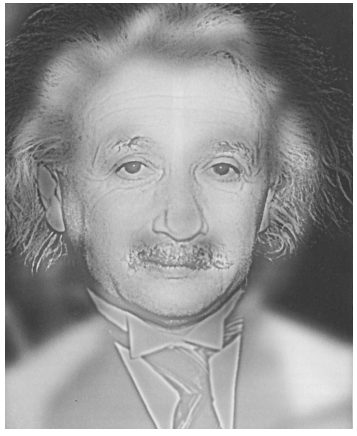


=

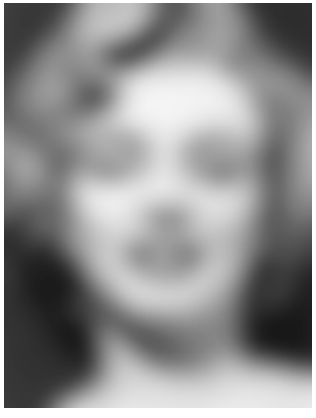
+



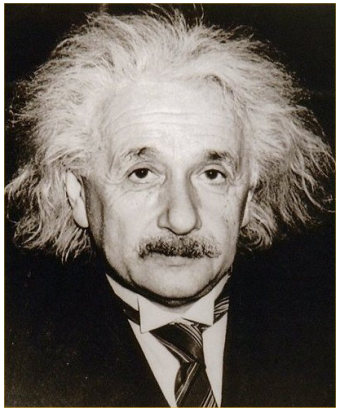
Hybrid images



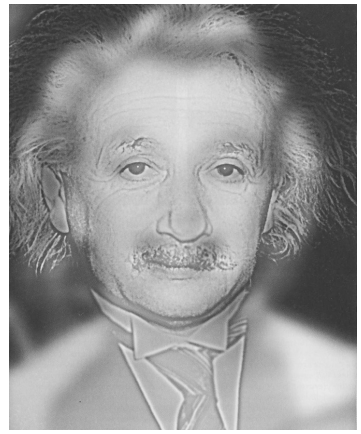
=



+

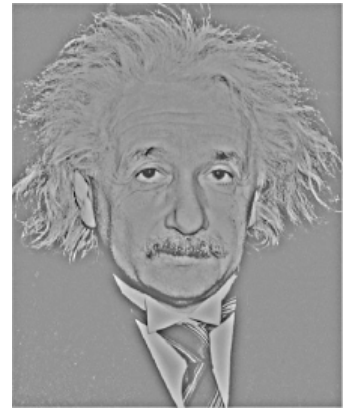


Hybrid images



=

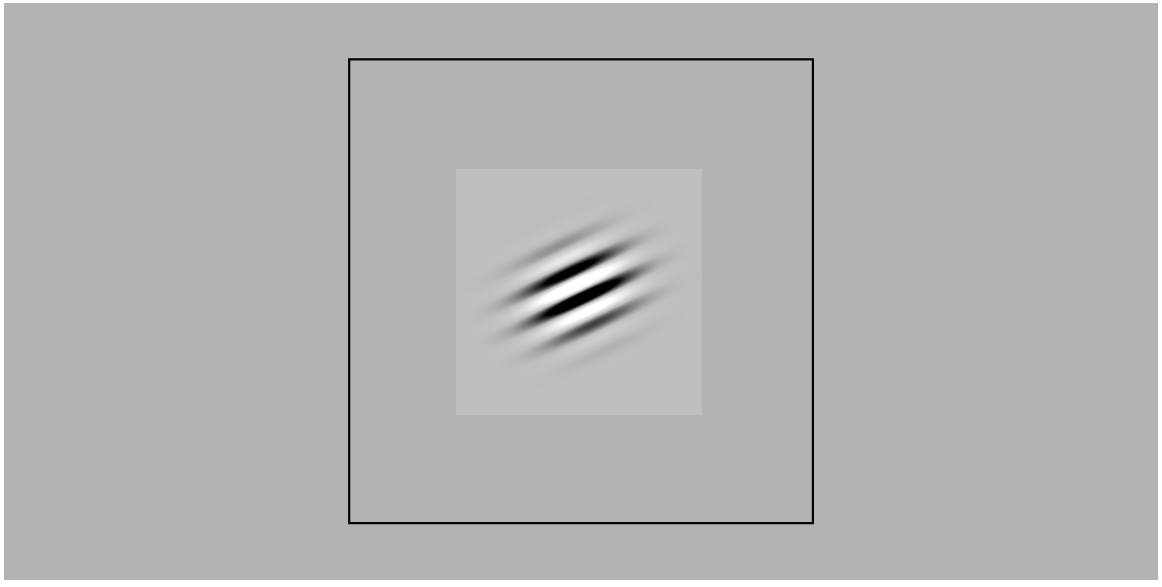
+



Perception of spatial frequency

two-alternative forced-choice task:
which of the two stimuli contained a grating?

Perception of spatial frequency

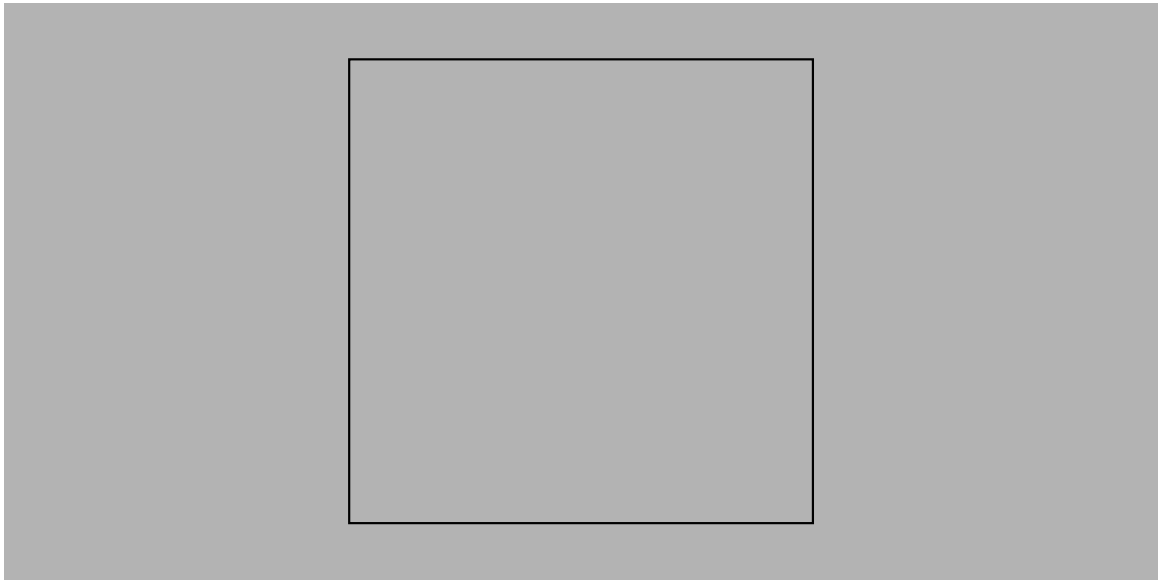


two-alternative forced-choice task:
which of the two stimuli contained a grating?

Perception of spatial frequency

two-alternative forced-choice task:
which of the two stimuli contained a grating?

Perception of spatial frequency

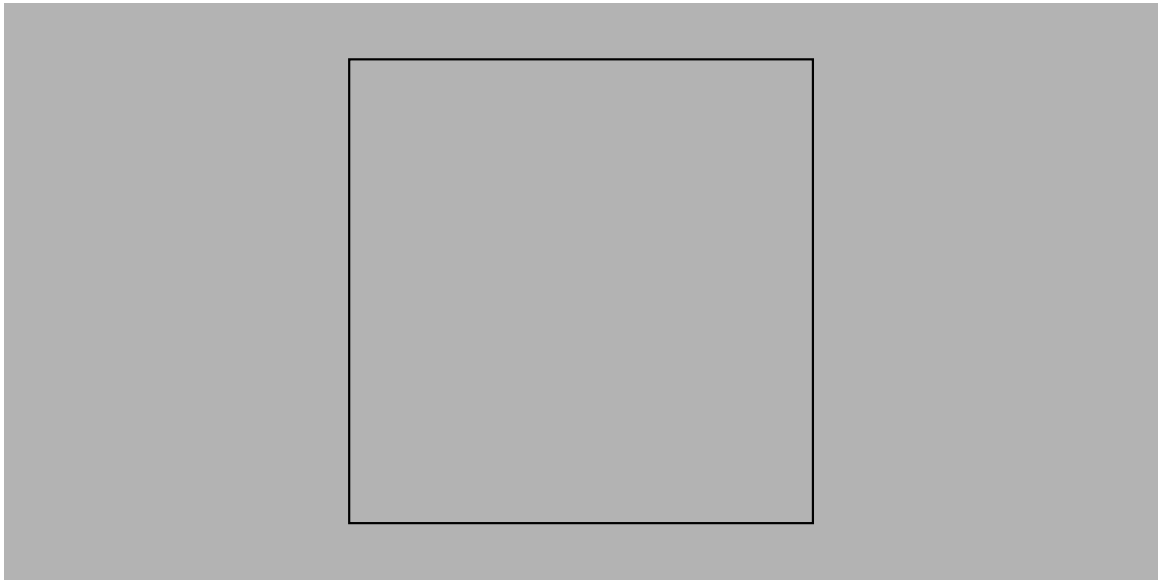


two-alternative forced-choice task:
which of the two stimuli contained a grating?

Perception of spatial frequency

two-alternative forced-choice task:
which of the two stimuli contained a grating?

Perception of spatial frequency

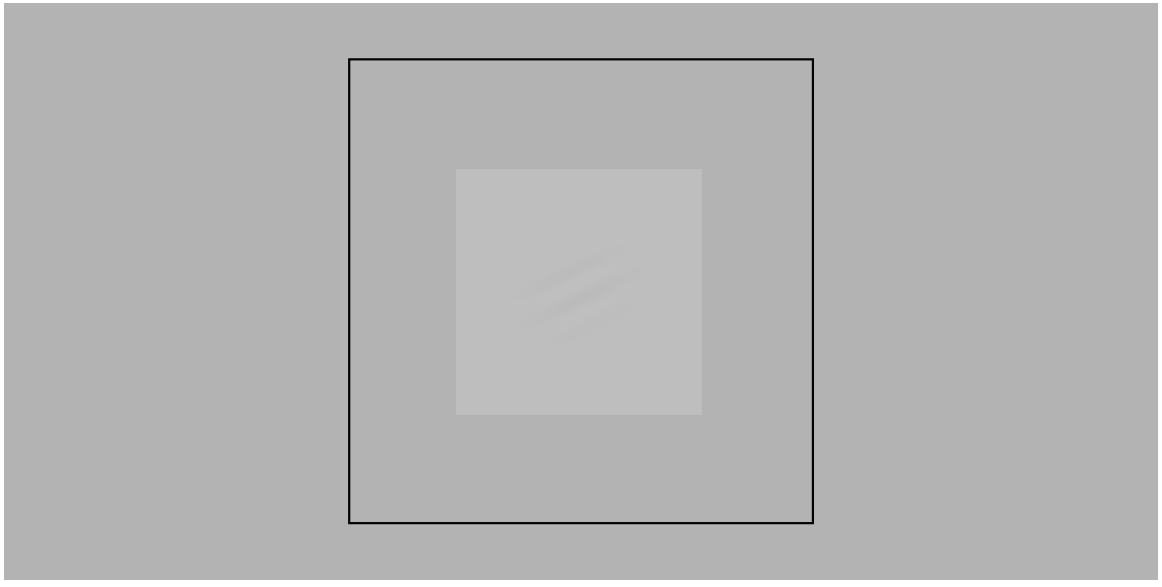


two-alternative forced-choice task:
which of the two stimuli contained a grating?

Perception of spatial frequency

two-alternative forced-choice task:
which of the two stimuli contained a grating?

Perception of spatial frequency

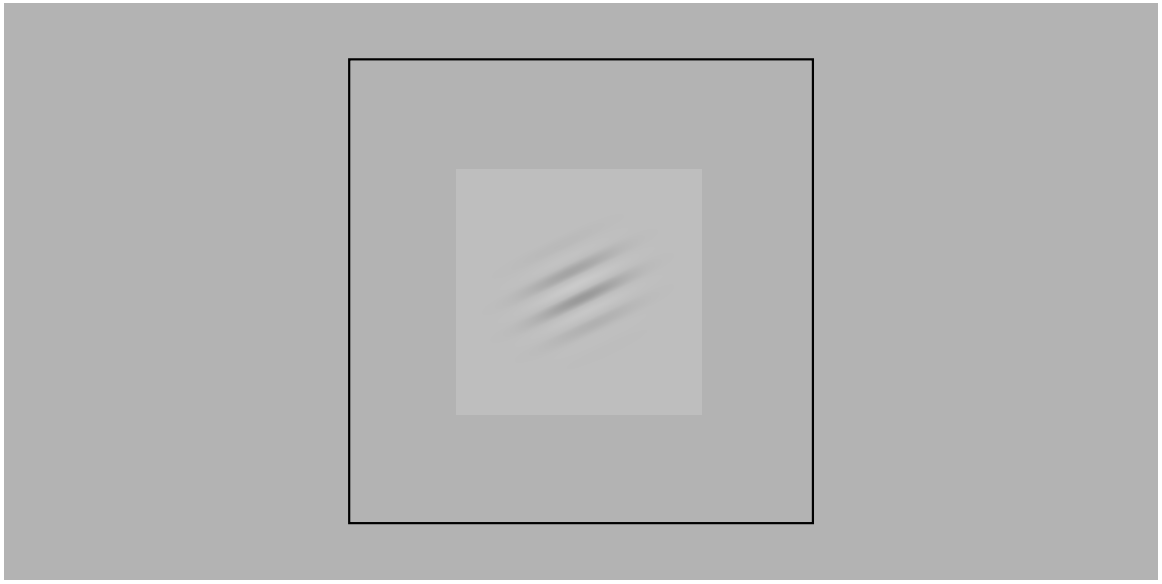


two-alternative forced-choice task:
which of the two stimuli contained a grating?

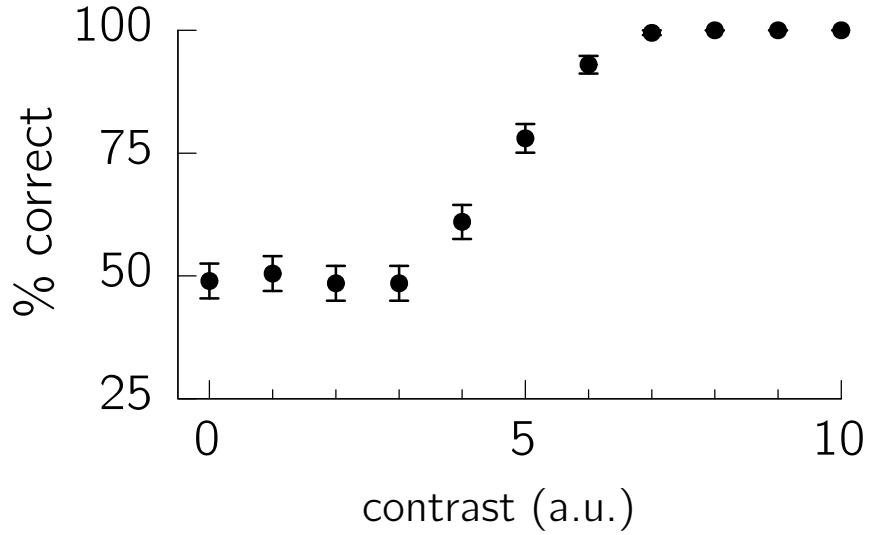
Perception of spatial frequency

two-alternative forced-choice task:
which of the two stimuli contained a grating?

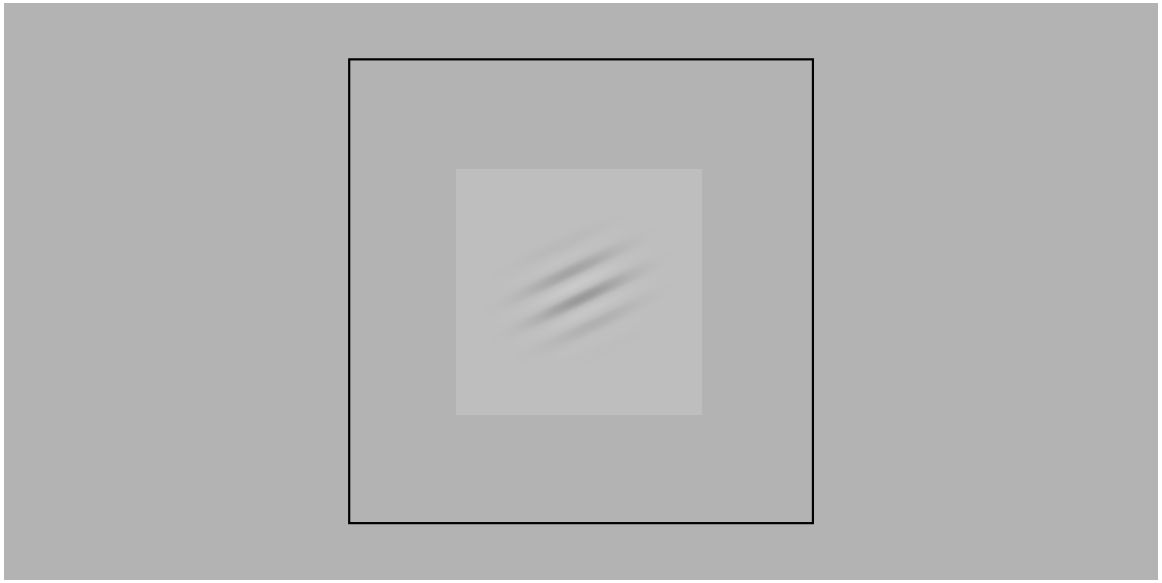
Perception of spatial frequency



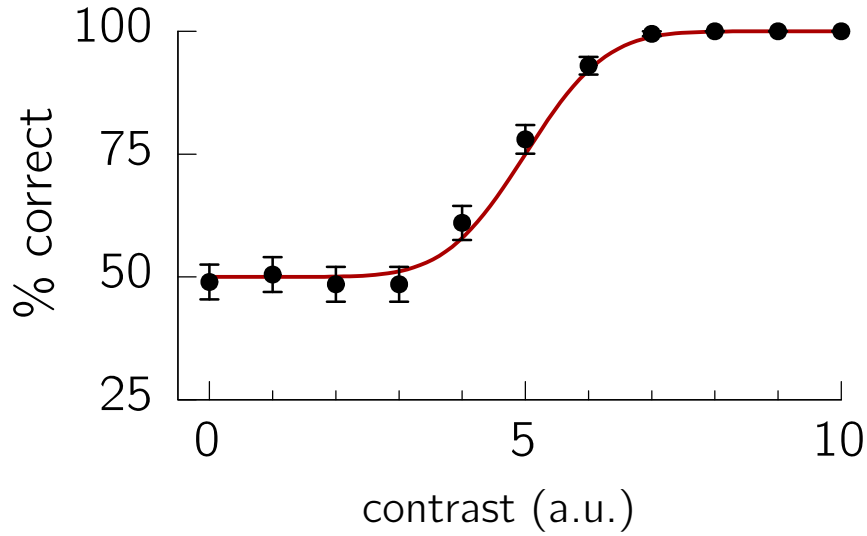
psychometric curve:



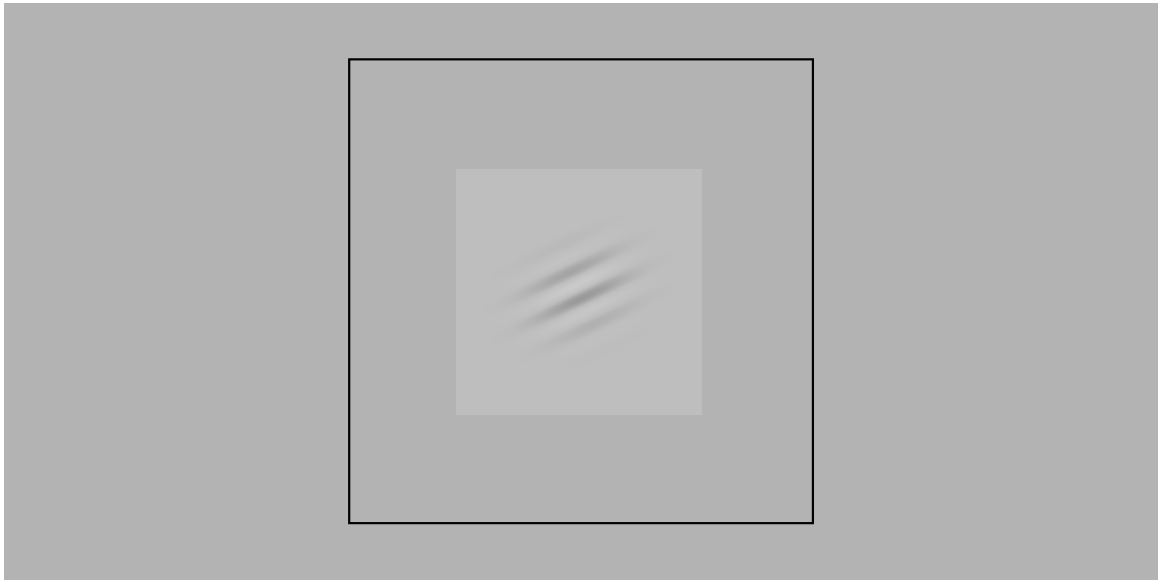
Perception of spatial frequency



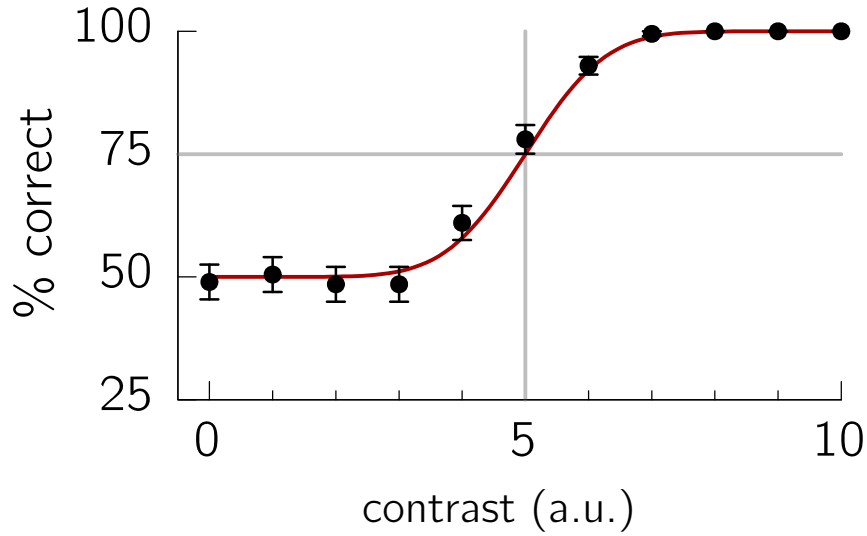
psychometric curve:



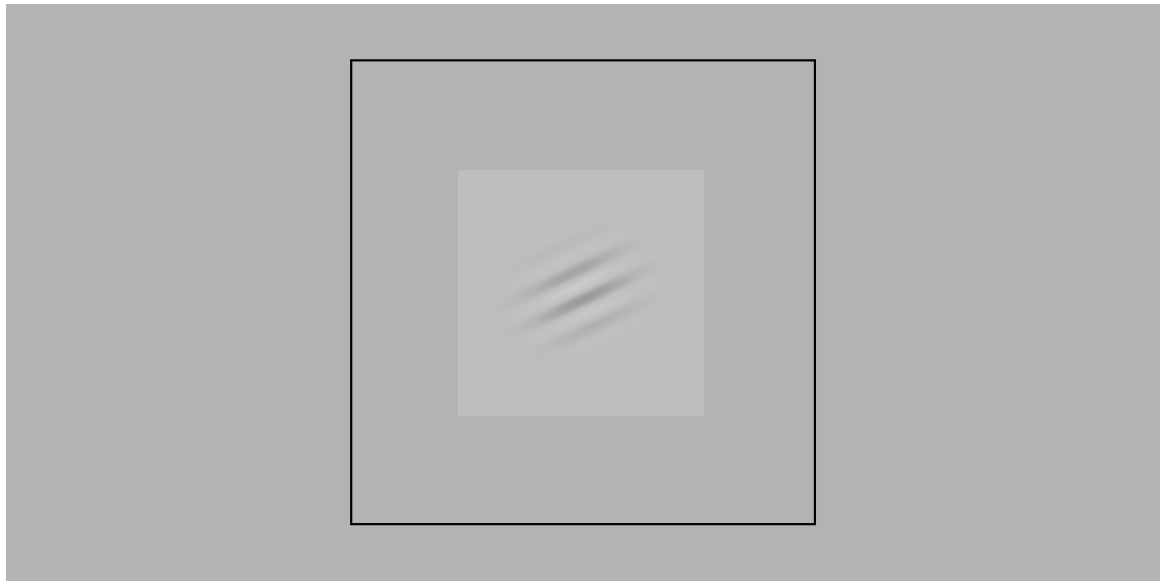
Perception of spatial frequency



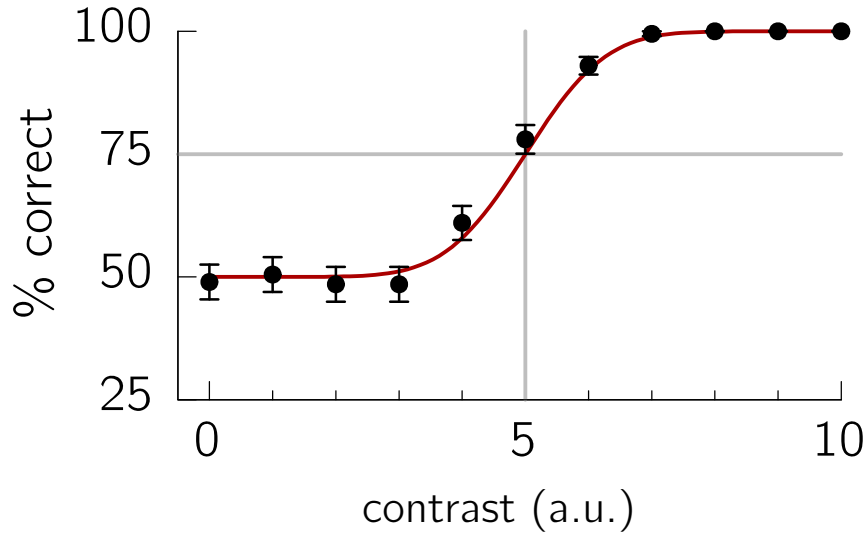
psychometric curve:



Perception of spatial frequency

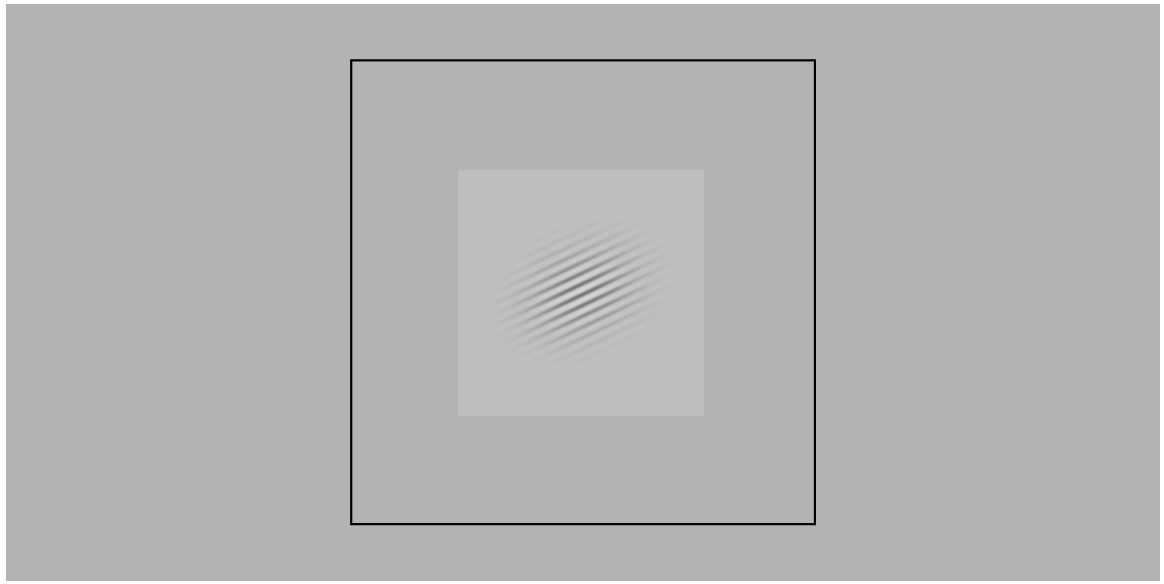


psychometric curve:

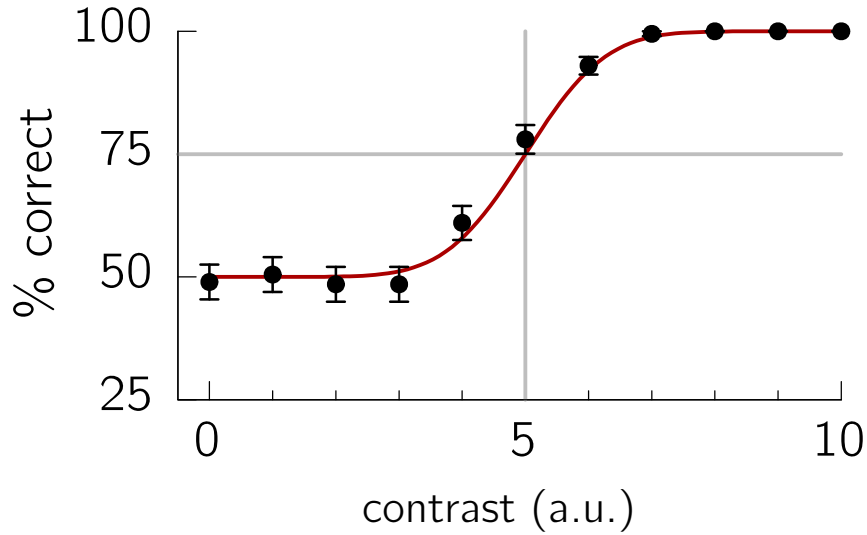


+ repeat experiment for a range of stimulus spatial frequencies

Perception of spatial frequency

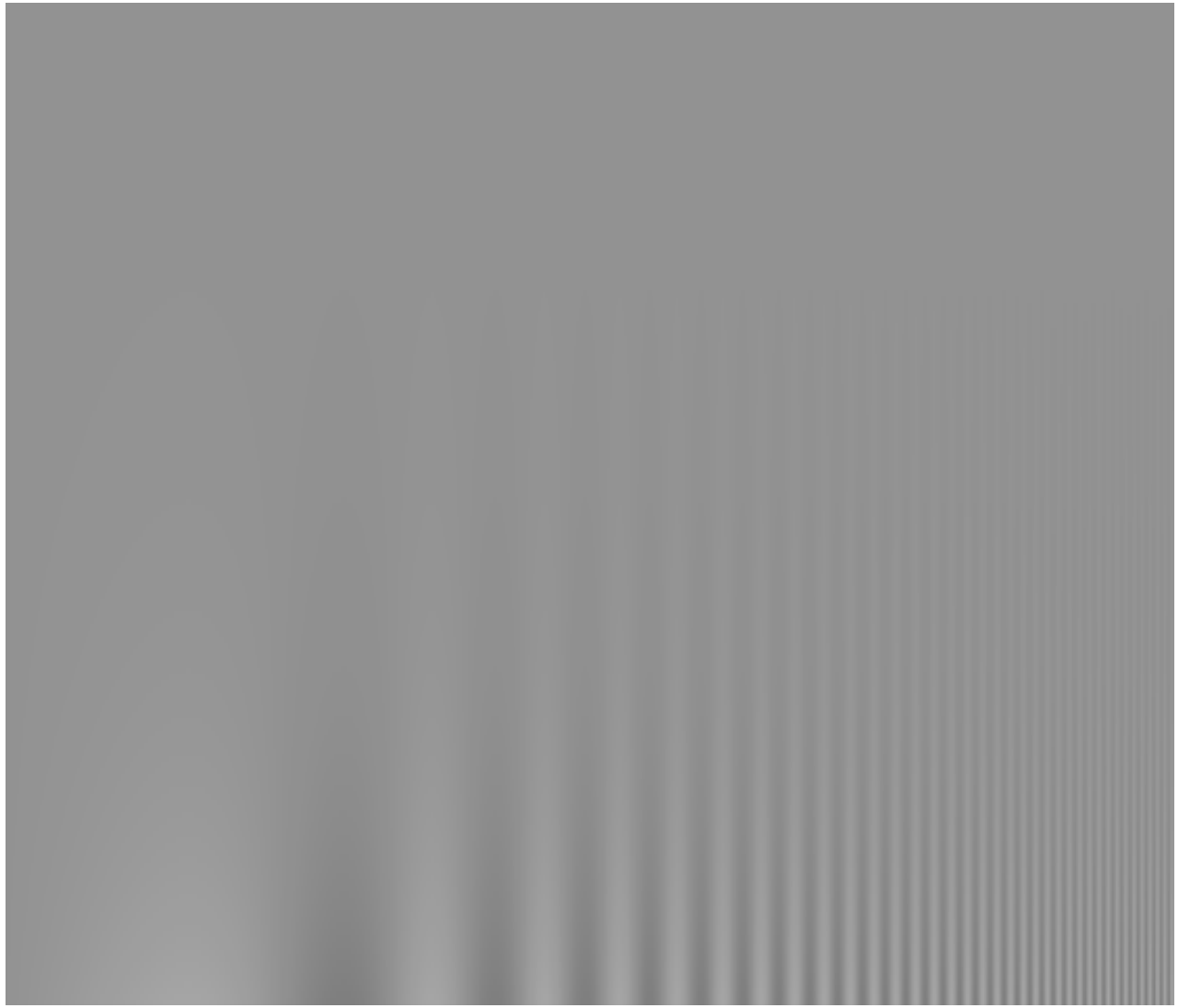


psychometric curve:



+ repeat experiment for a range of stimulus spatial frequencies

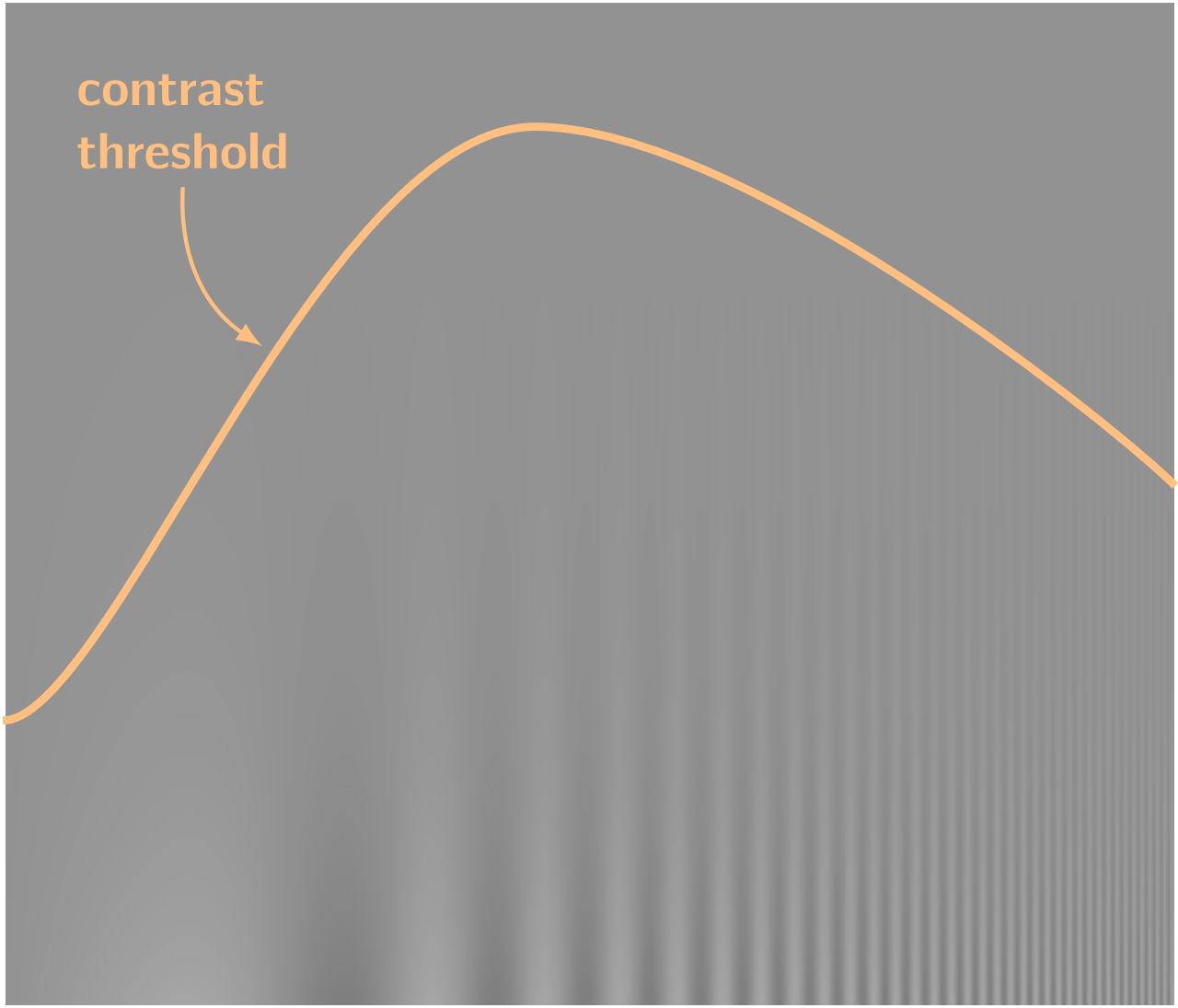
Contrast sensitivity function



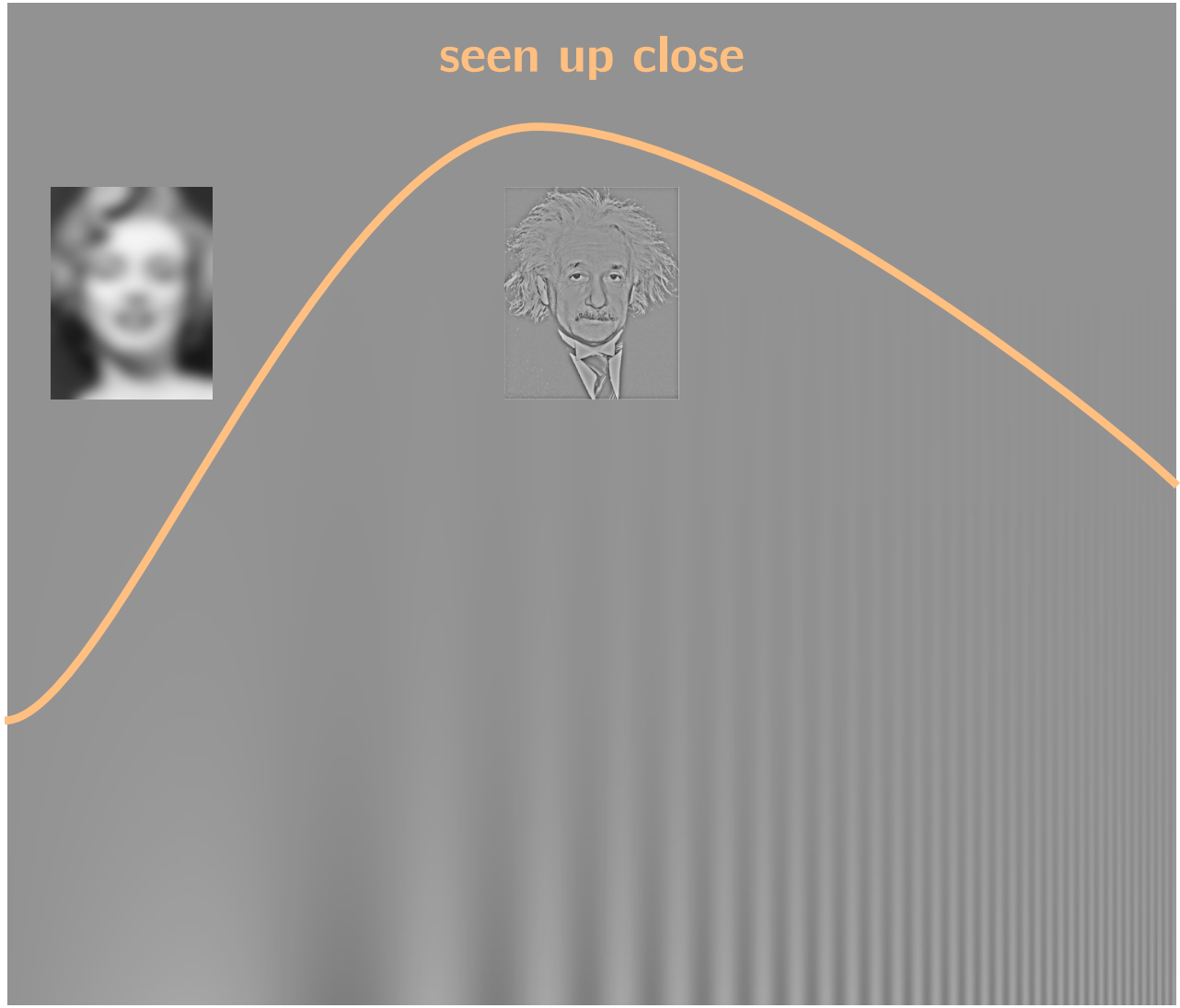
visual contrast

spatial frequency (cycles/degree)

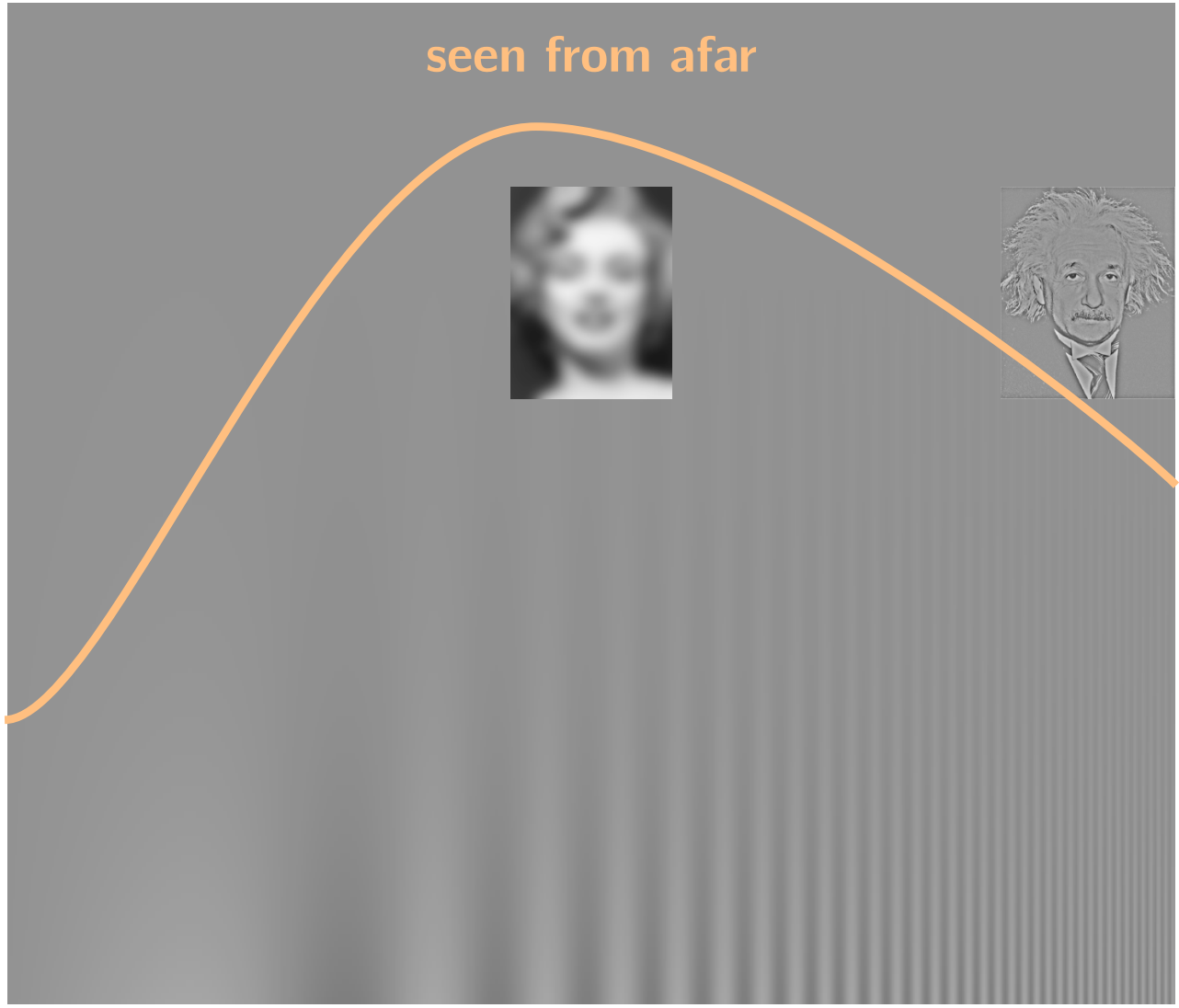
Contrast sensitivity function



Contrast sensitivity function

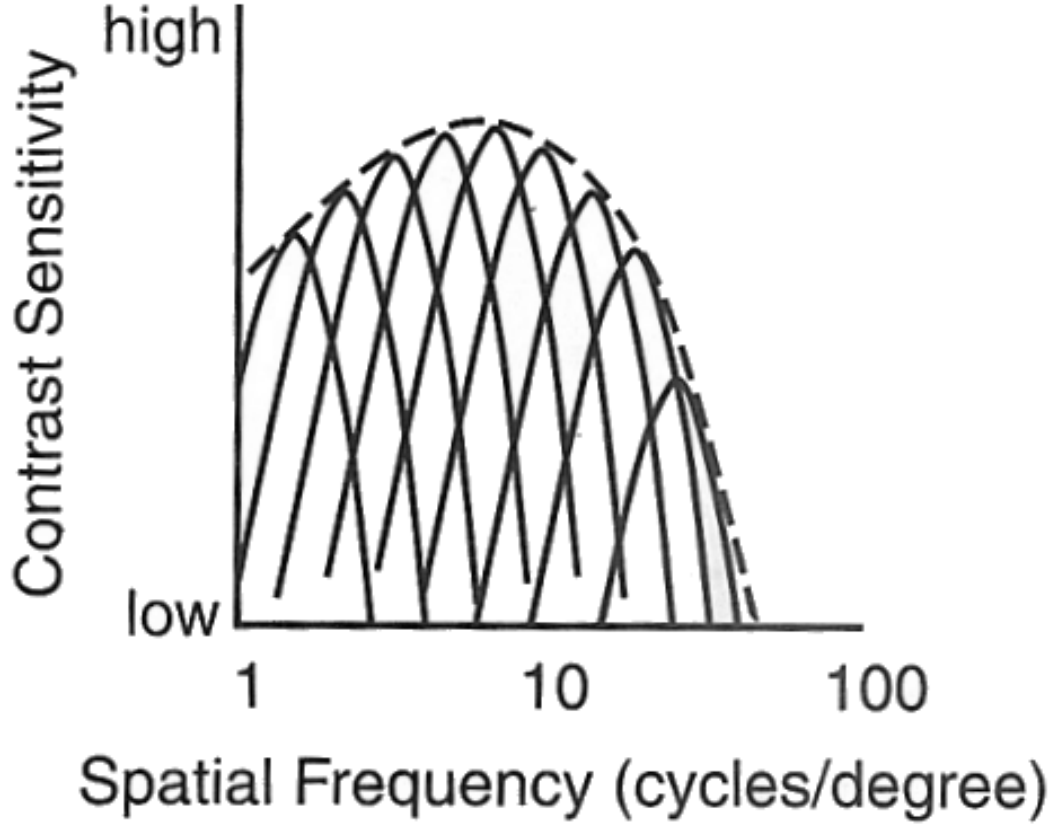


Contrast sensitivity function



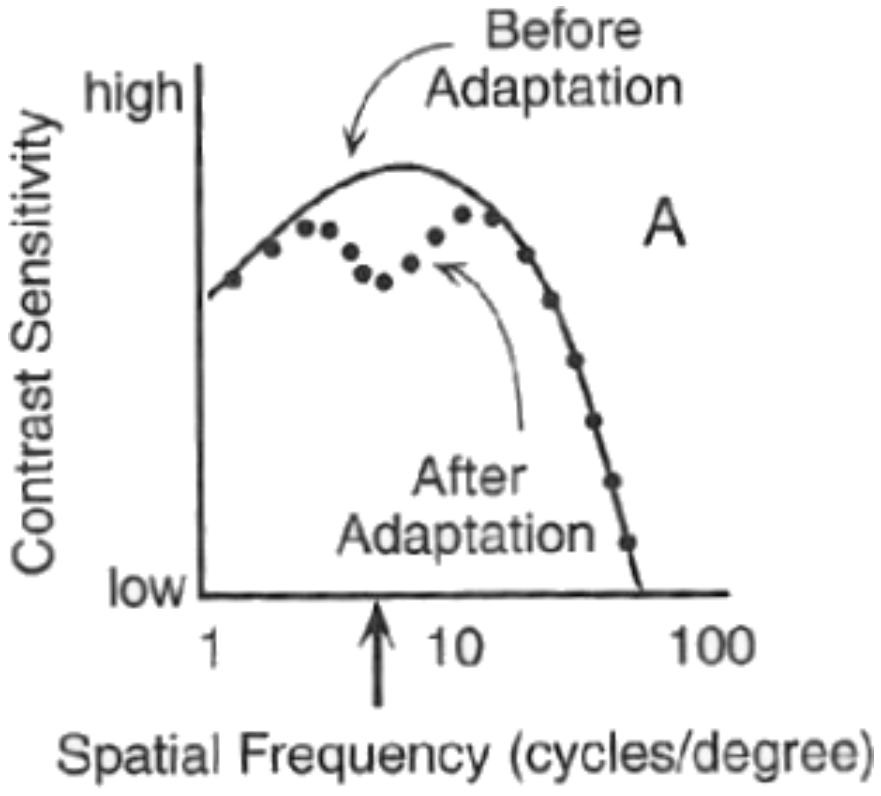
Origin of the contrast sensitivity function

hypothesis: a set of overlapping channels are used
to represent the whole range of spatial frequencies

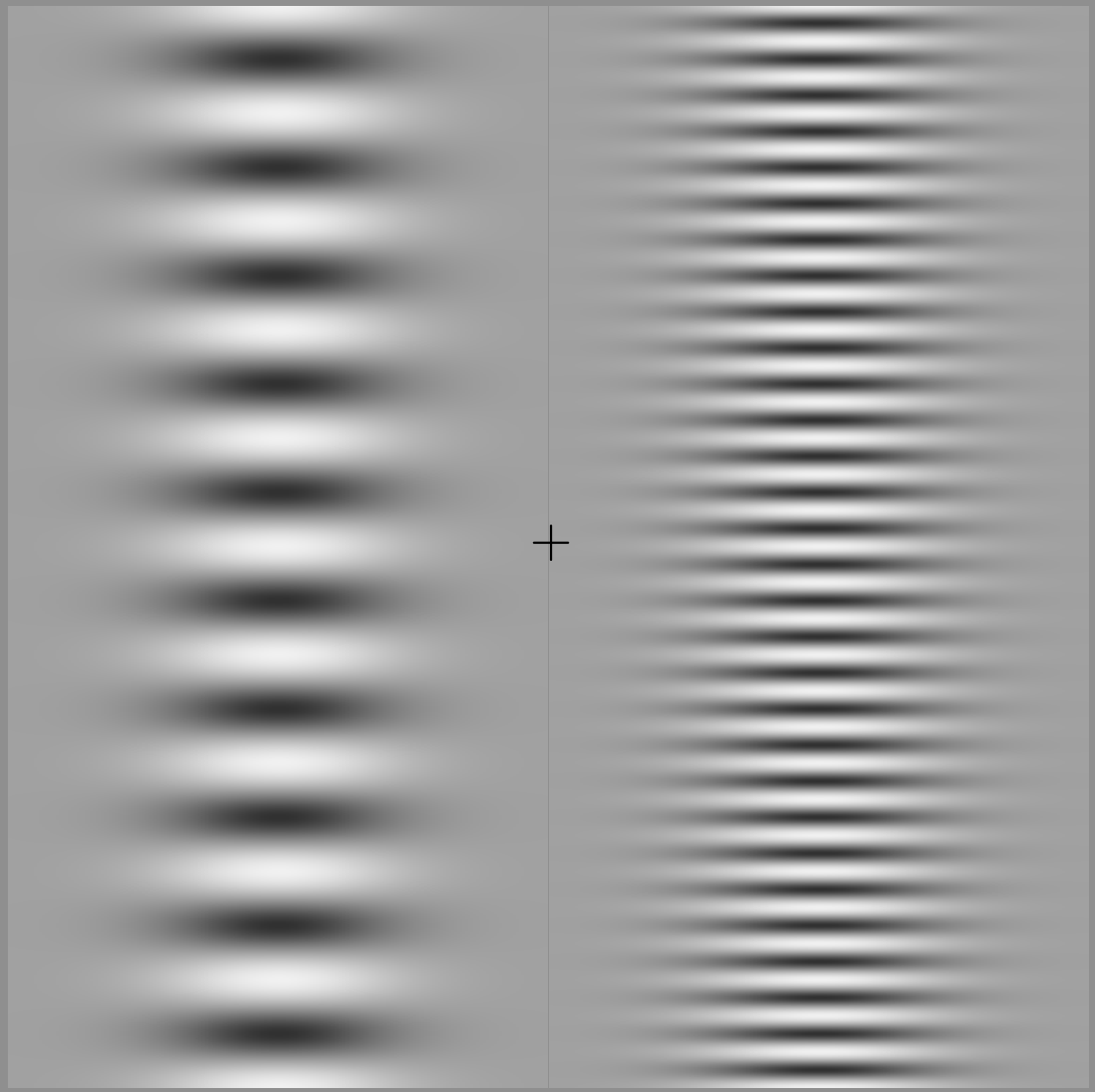


Neural fatigue and after-effects

prolonged exposure to a given frequency
decreases sensitivity around that frequency



Neural fatigue and after-effects



Neural fatigue and after-effects