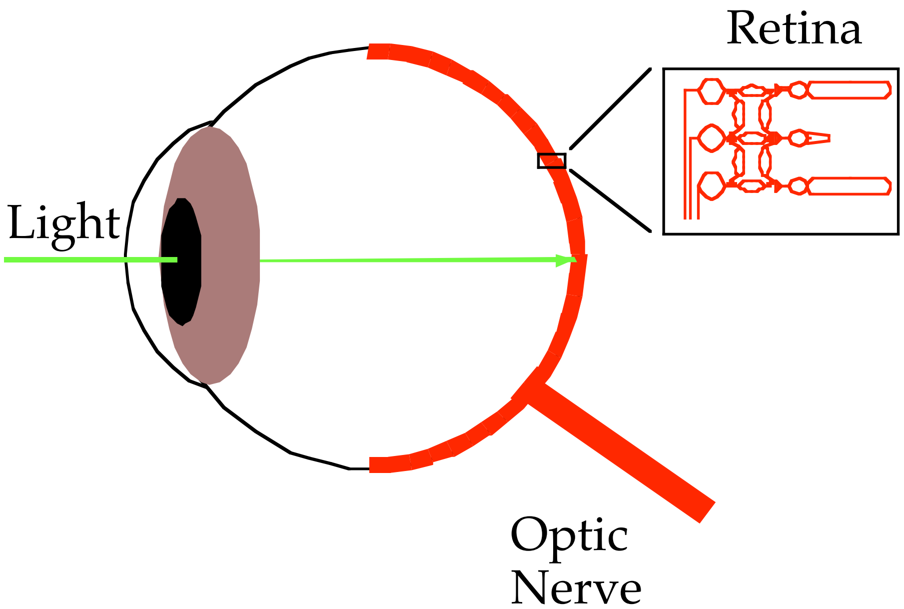
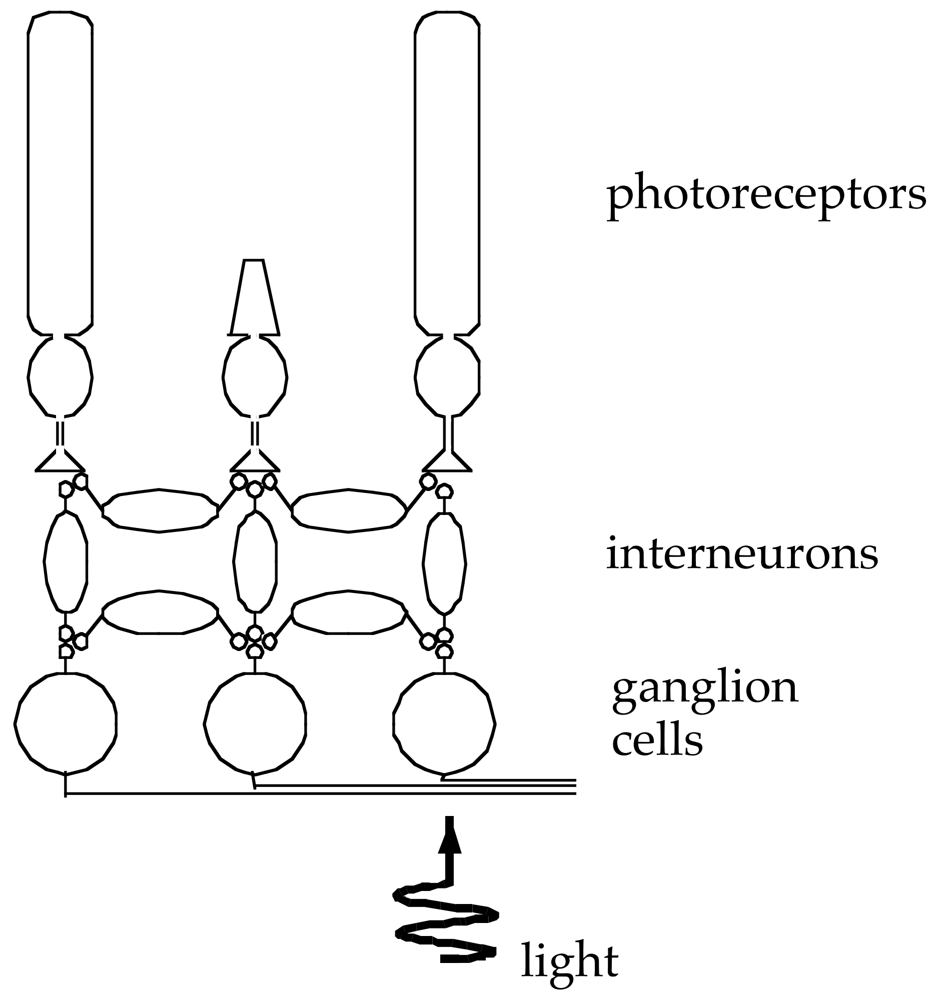
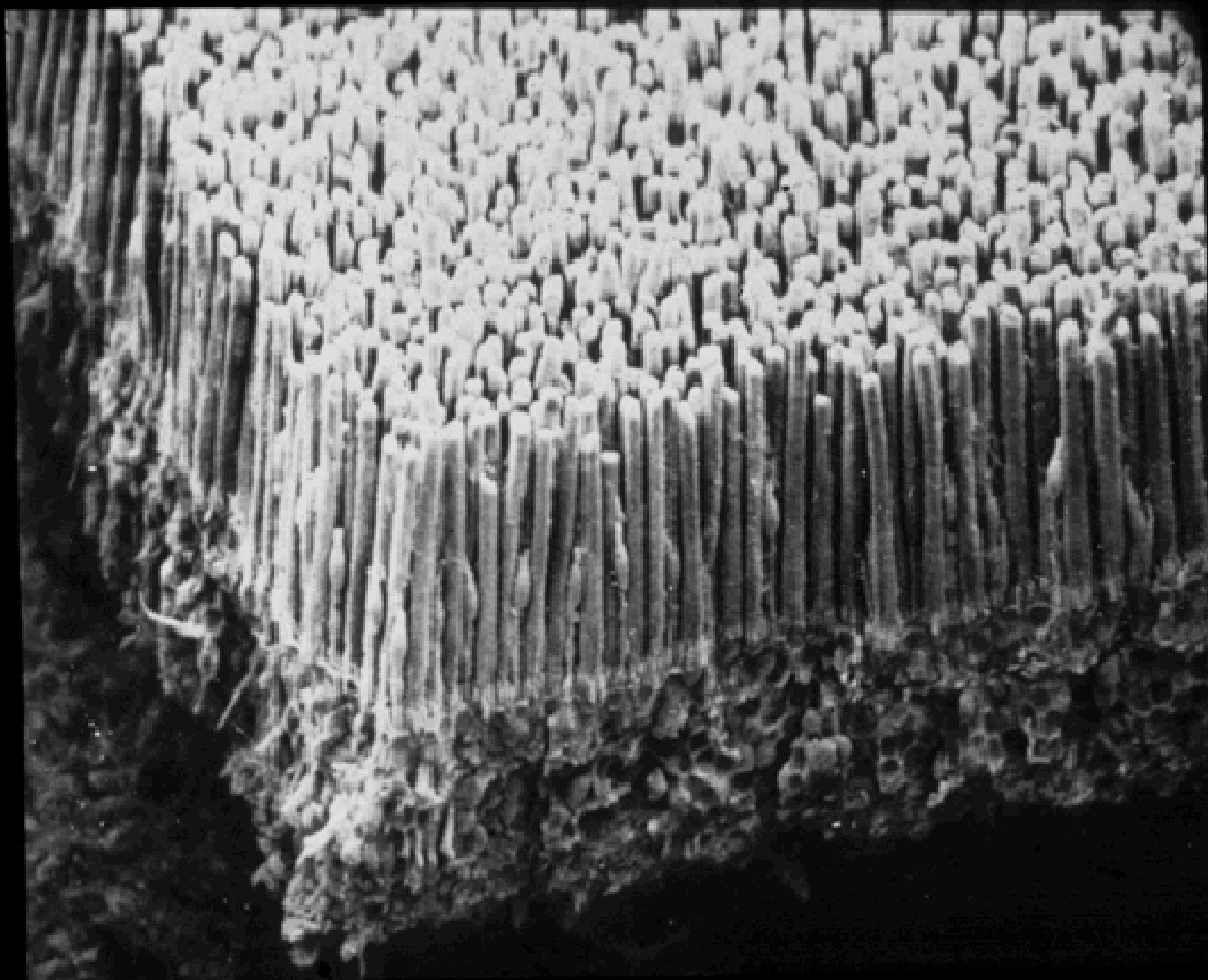
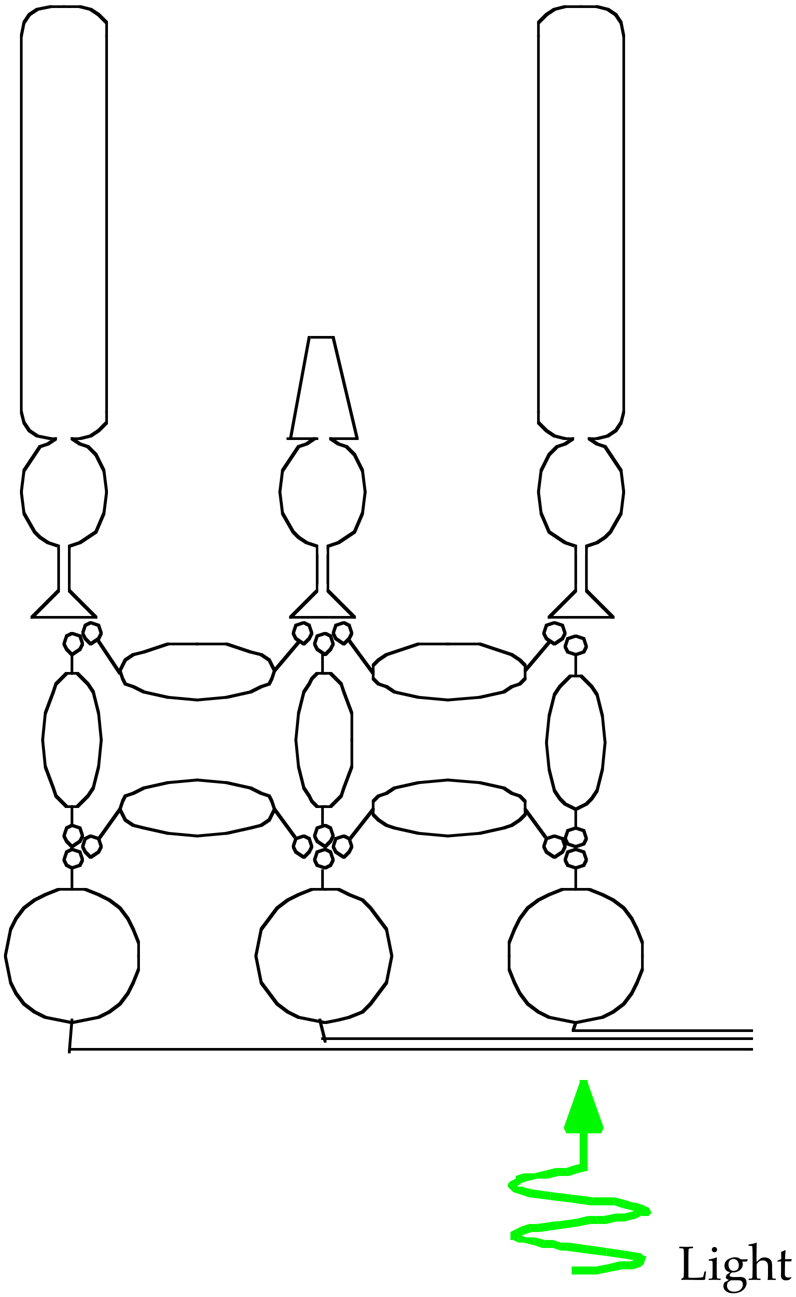




- Encoding and estimation
- Bottleneck and limits to visual fidelity





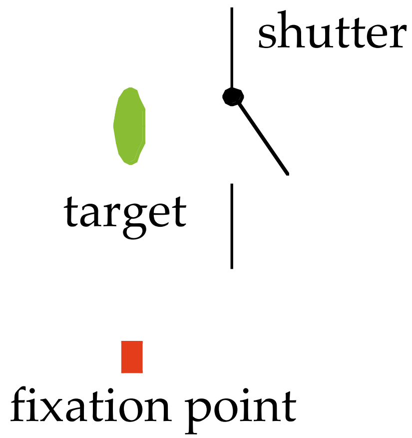
What constraints does behavioral sensitivity place on detection and processing in retina?

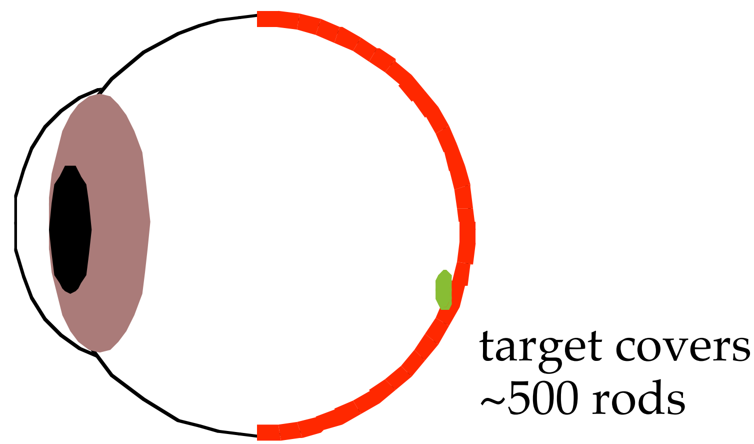
- what is absolute sensitivity of behavior?
- what are properties of noise limiting behavioral sensitivity?

What are properties of single photon responses in rod photoreceptors and how do they relate to behavior?

How are signals resulting from absorption of a few photons maintained through retina?

BEHAVIORAL EVIDENCE FOR SINGLE PHOTON DETECTION BY RODS





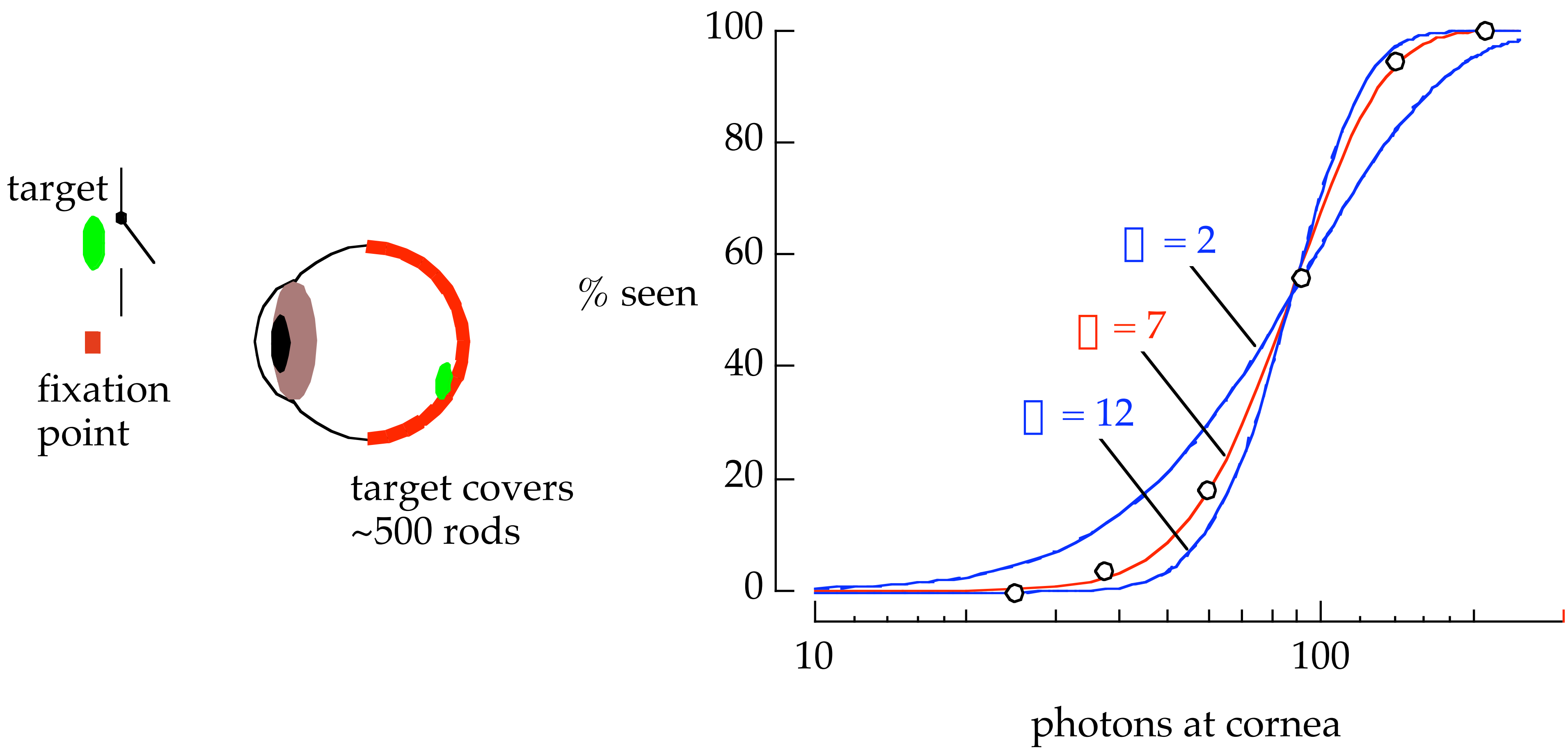
- just detectable flash about 100 photons at cornea
- 10-30% of photons at cornea absorbed by rods
  (quantum efficiency)

CONCLUSION: threshold ~10-30 absorbed photons,
spread over ~500 rods

PROBLEM: Quantum efficiency difficult to measure

FREQUENCY OF SEEING

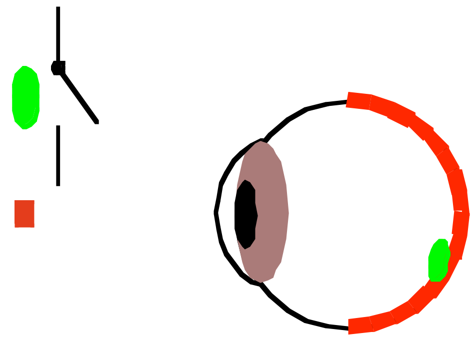
(Hecht, Shlaer and Pirenne, 1942)

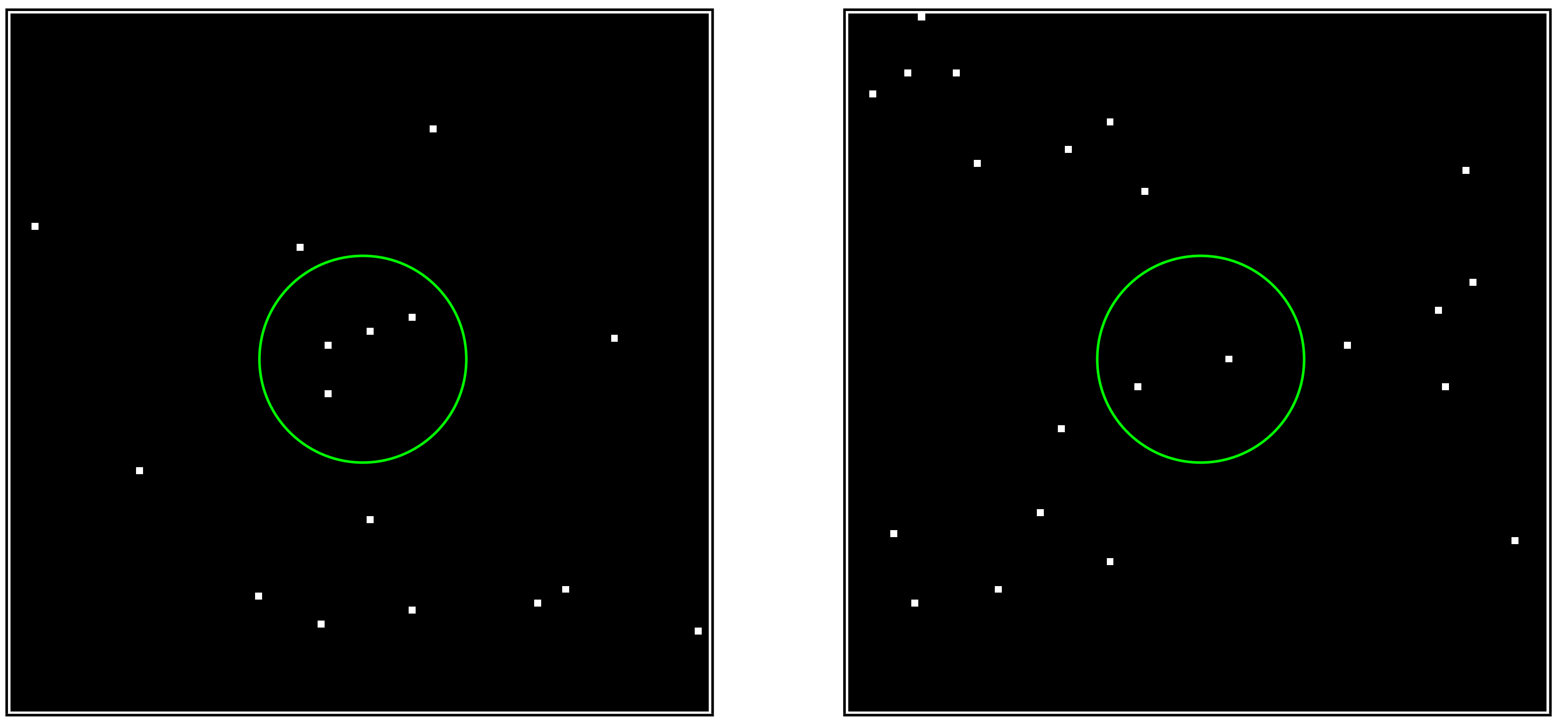


KEY: use variability in response to avoid unknown fraction absorbed
CONCLUSION: □ = 5-7 photons absorbed spread over 500 rods
PROBLEMS: (1) Estimated quantum efficiency low (~5%)
(2) No way to account for false positives (intrinsic noise)

"DARK LIGHT" AND VISUAL SENSITIVITY

(Barlow, 1956)

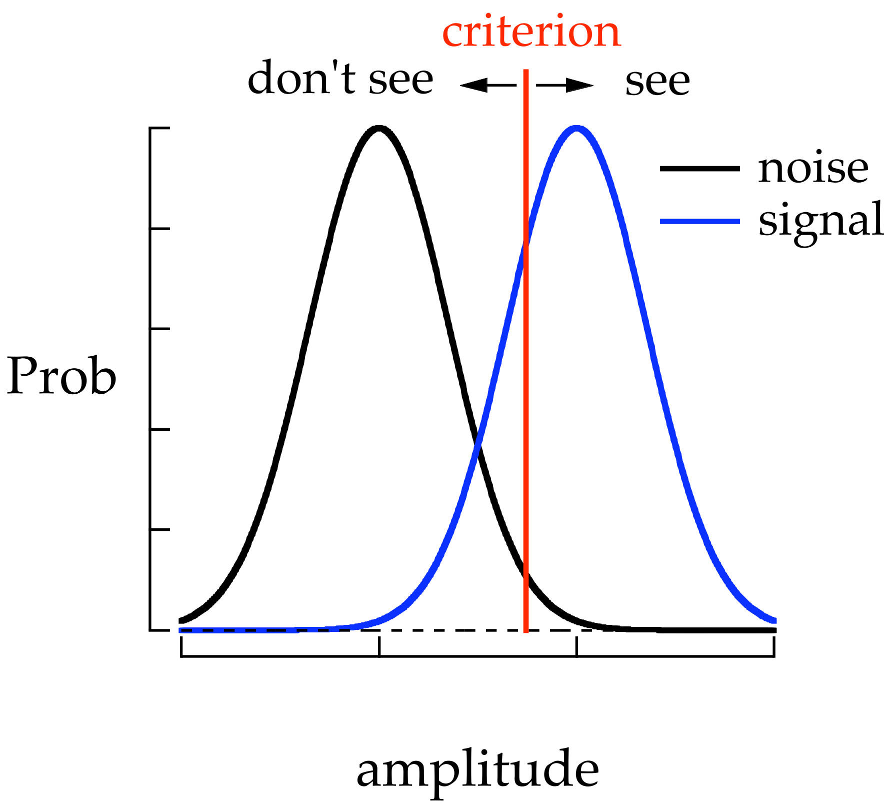


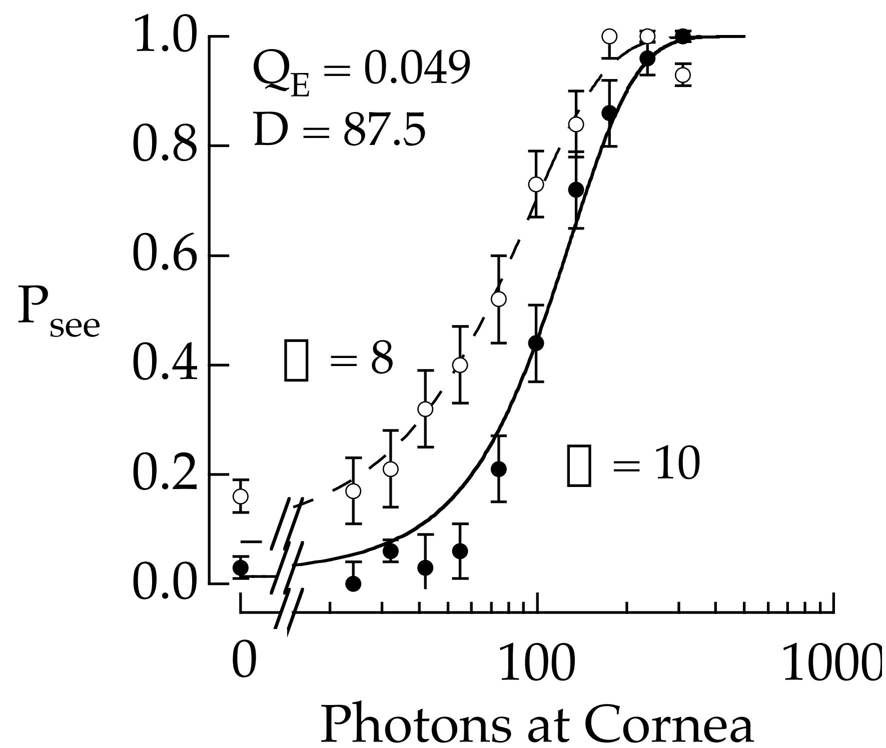


False positives: internal noise masquerading as light response.
Use false positive rate to estimate noise limiting absolute sensitivity.

THRESHOLD TRADES FOR FALSE POSITIVES

(Barlow, 1956; Teich et al., 1982)

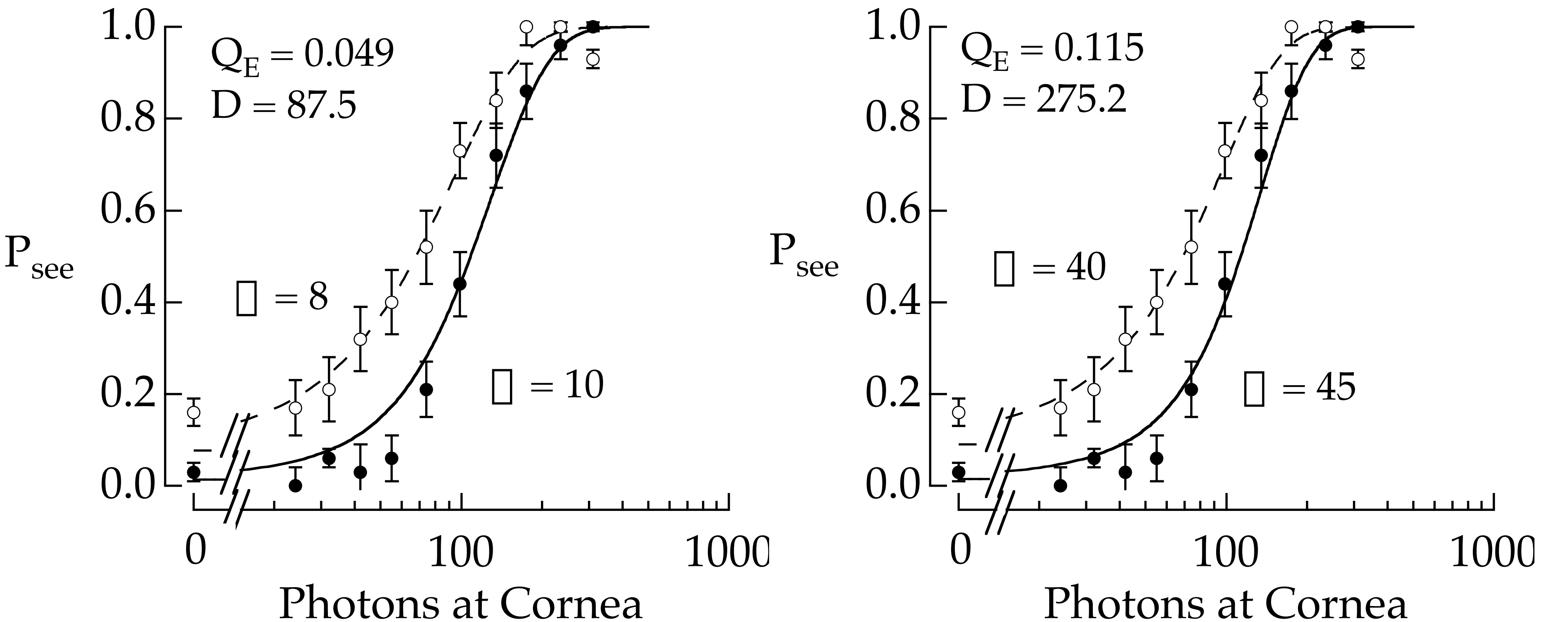




information from small # of photons available, but accessing it produces errors due to intrinsic noise

QUANTUM EFFICIENCY, DARK LIGHT AND THRESHOLD TRADE

(Barlow, 1956; Teich et al., 1982)

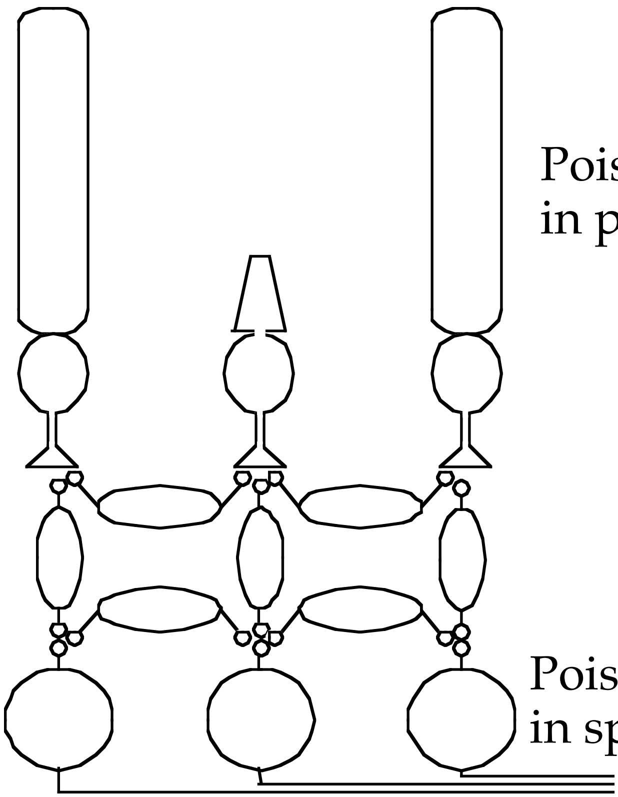


(1) Behavioral Q_E lower than absorptive Q_E, some single photon responses discarded

OR

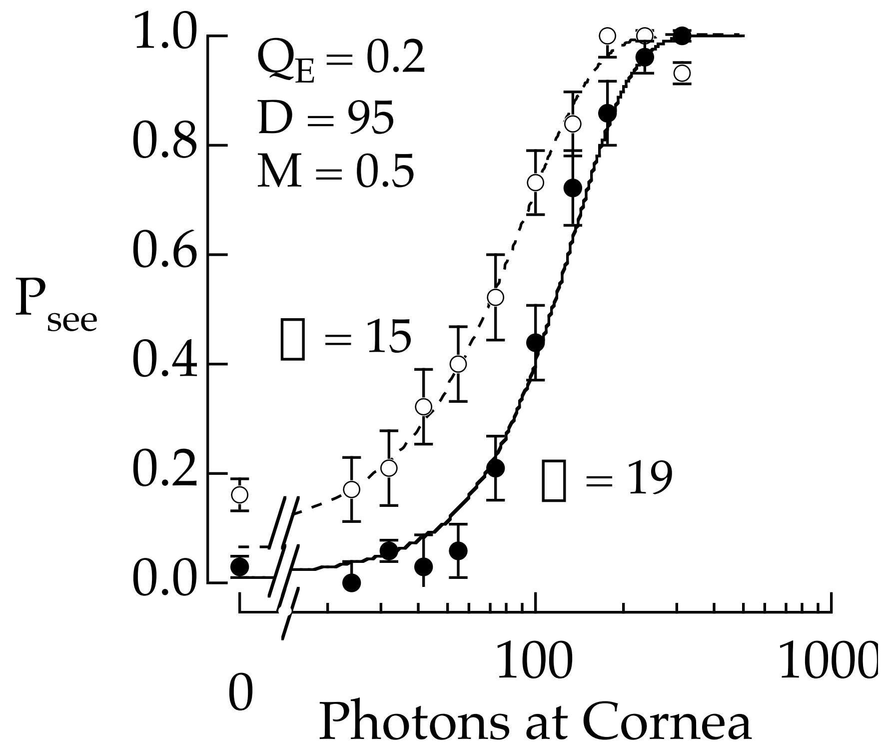
(2) Behavioral and absorptive Q_E similar, thresholds and dark noise elevated

WHAT IF NOISE IS NOT ALL ADDITIVE?

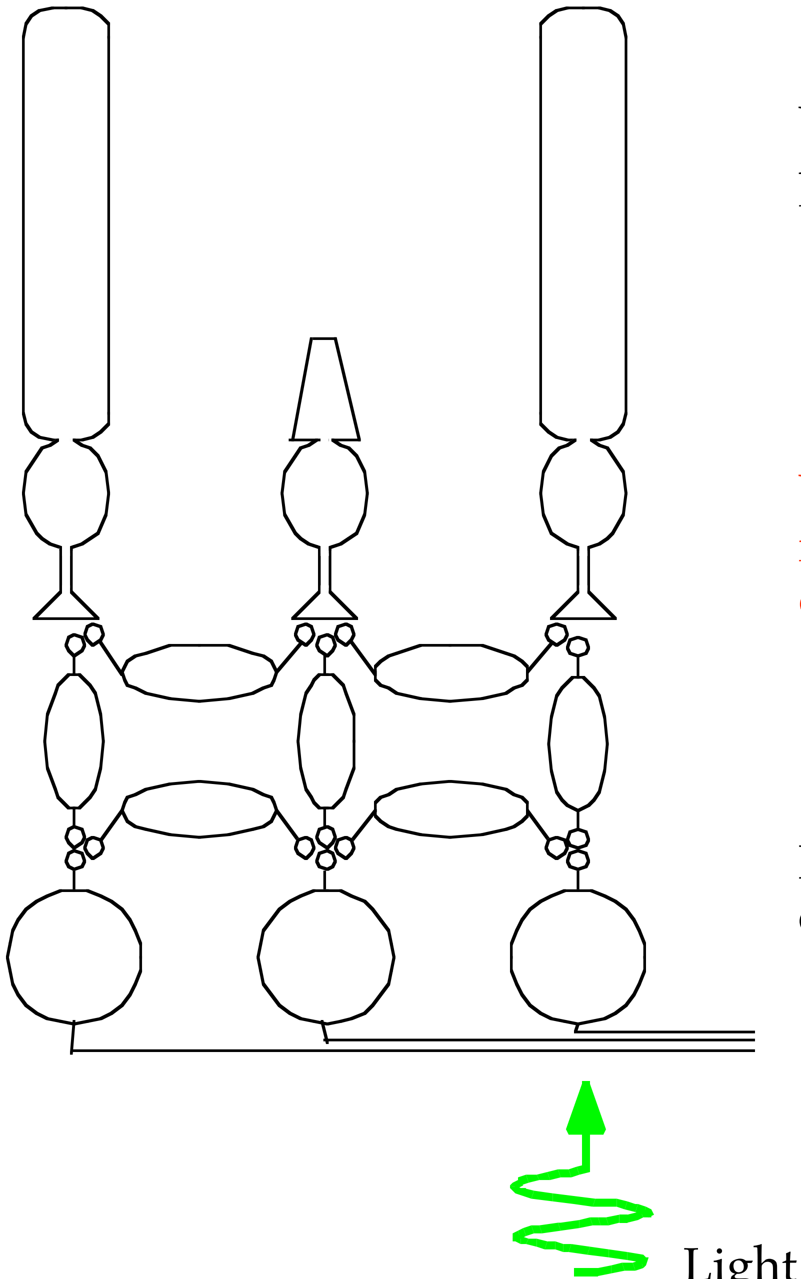


Poisson fluctuations in photon absorption

Poisson fluctuations in spike generation



Combination of additive and multiplicative noise permits high Q_E with low dark light and threshold



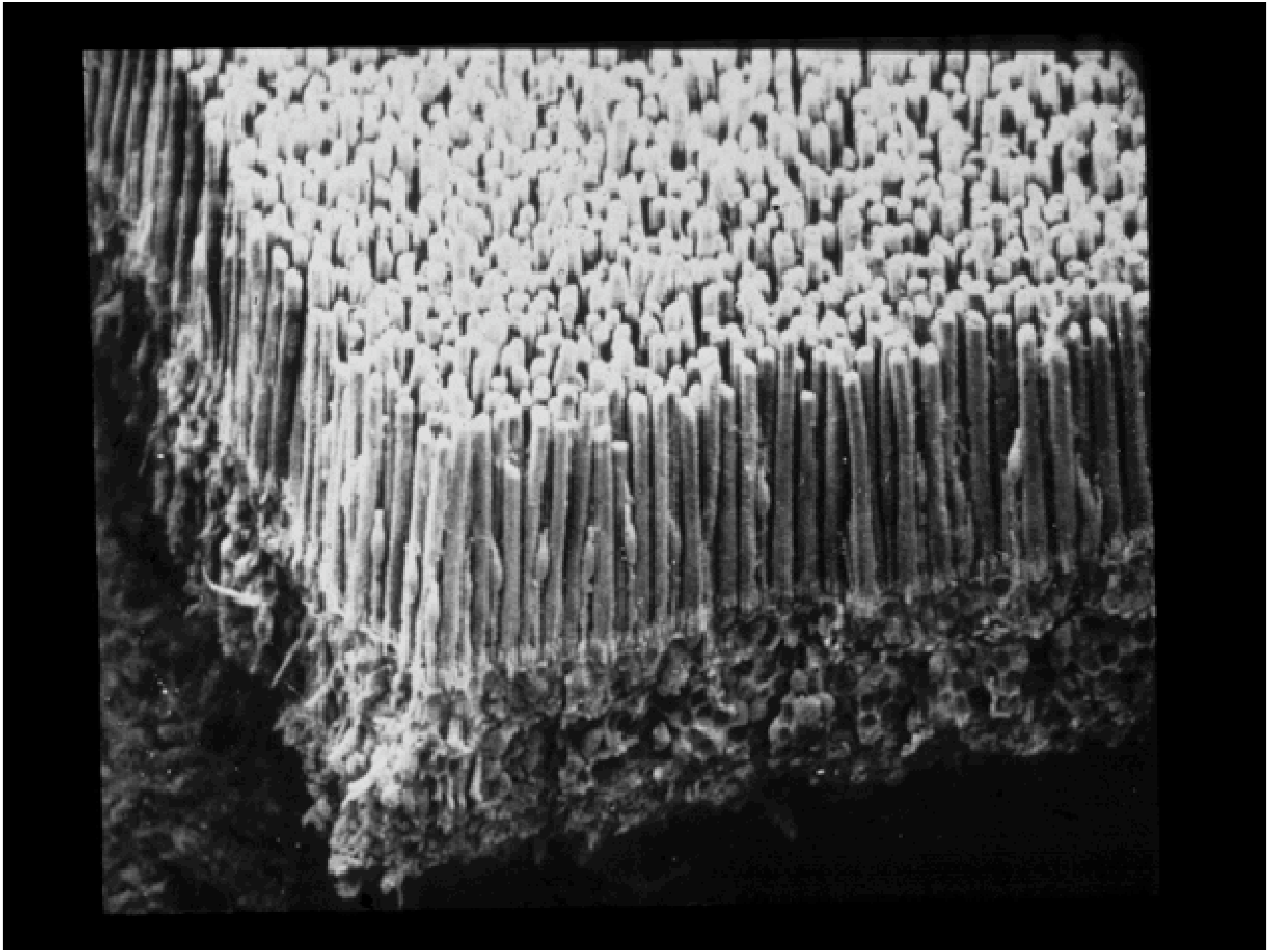
What constraints does behavioral sensitivity place on detection and processing in retina?

- perception influenced by a small number of photons, perhaps one
- noise limiting behavior ~0.01-0.03 photon like events/rod/sec

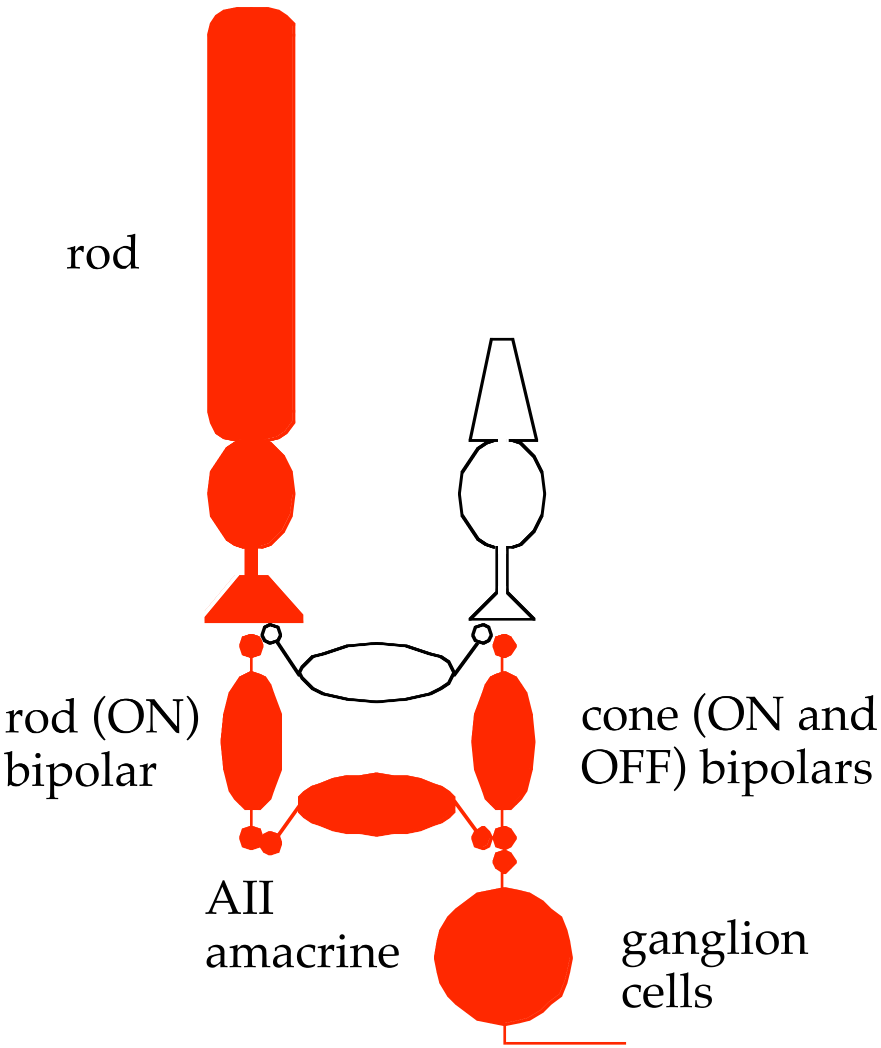
What are properties of single photon responses in rod photoreceptors and how do they relate to behavior?

- what are sources of noise in rod signals?
- how close does behavior come to limits imposed by rod noise?

How are signals resulting from absorption of a few photons maintained through retina?

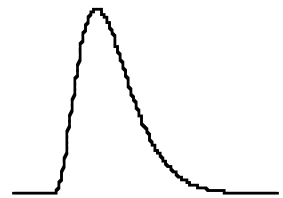


IMPLICATIONS OF BEHAVIORAL SENSITIVITY



(Dacheux and Raviola, 1986;
Sterling et al., 1988)

- phototransduction:
  - single photons reliably transduced



- synaptic transmission:
  - reliable transmission of single photon responses

- neural coding:
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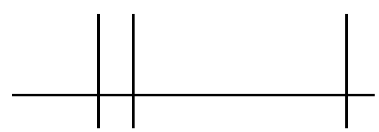
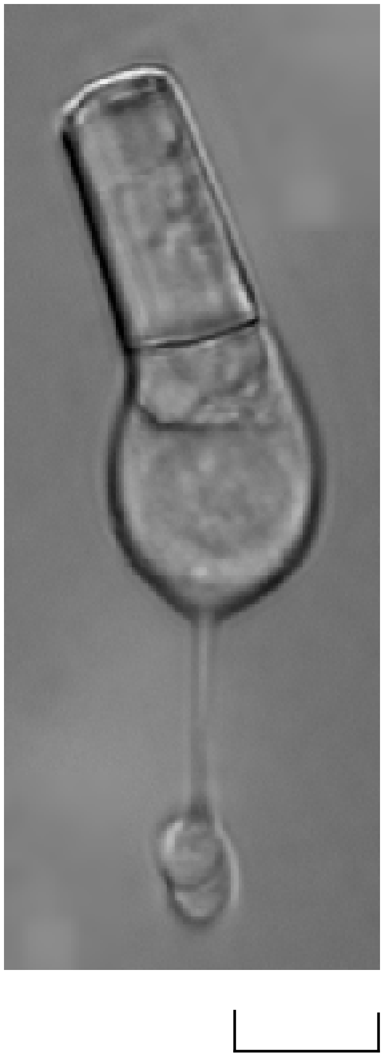


ROD DARK CURRENT

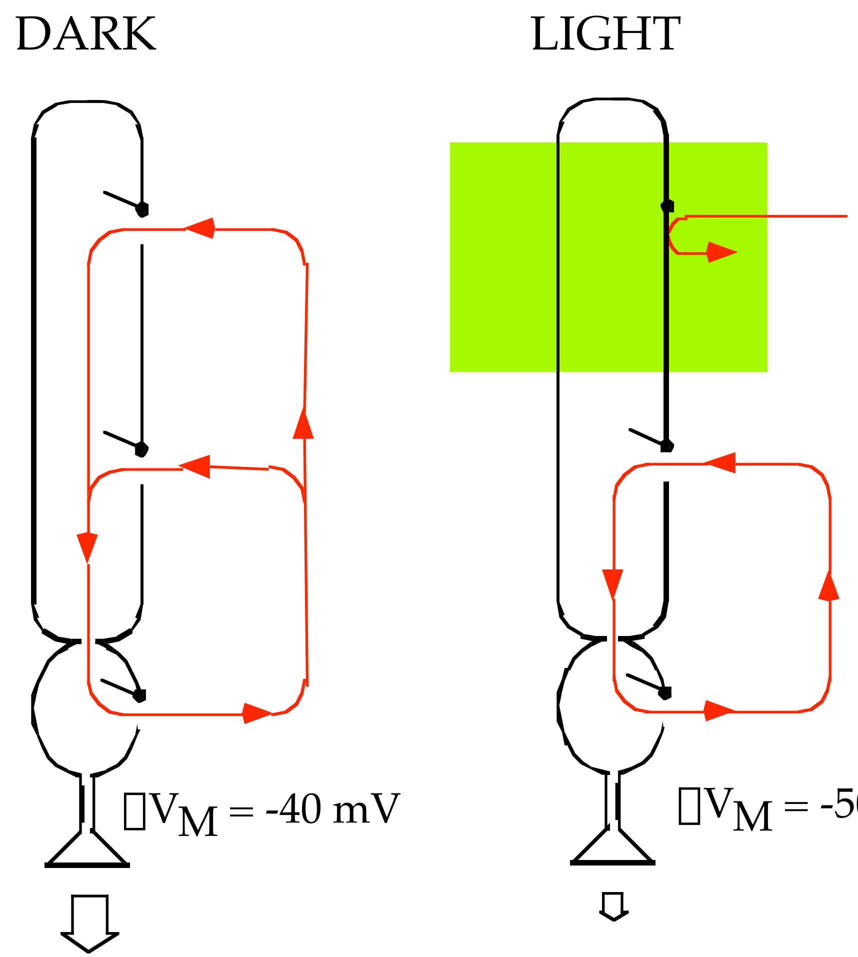


outer
segment

inner
segment

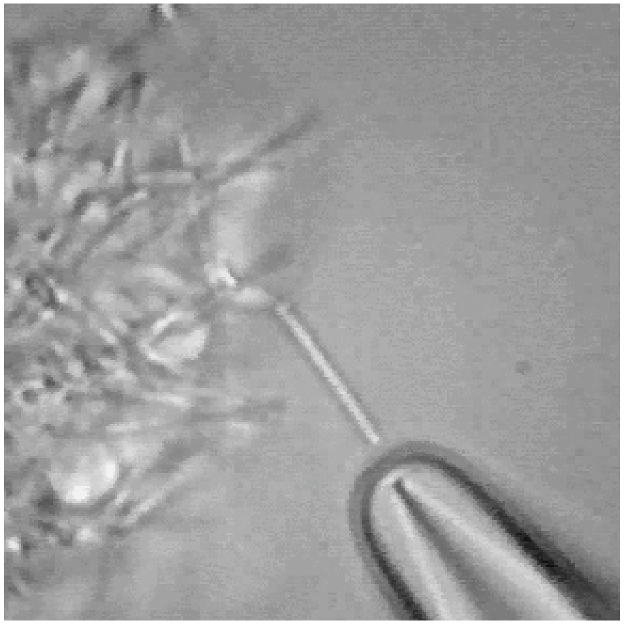
synaptic
terminal

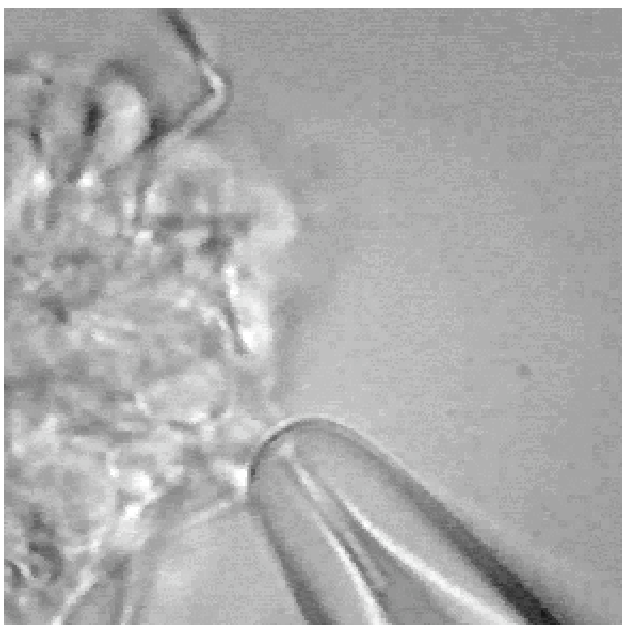
10 μm

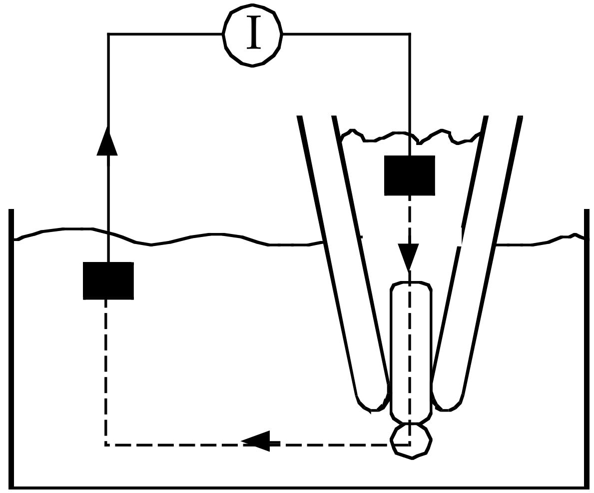


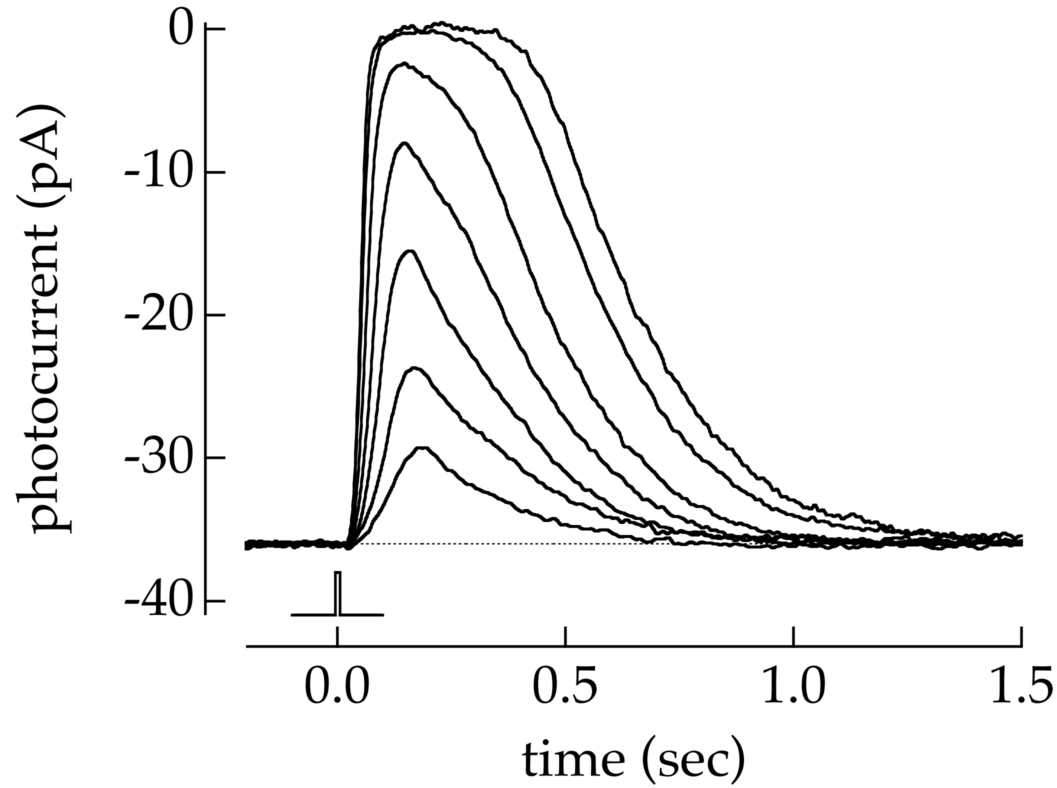
SUCTION ELECTRODE RECORDING

(Baylor et al., 1979)





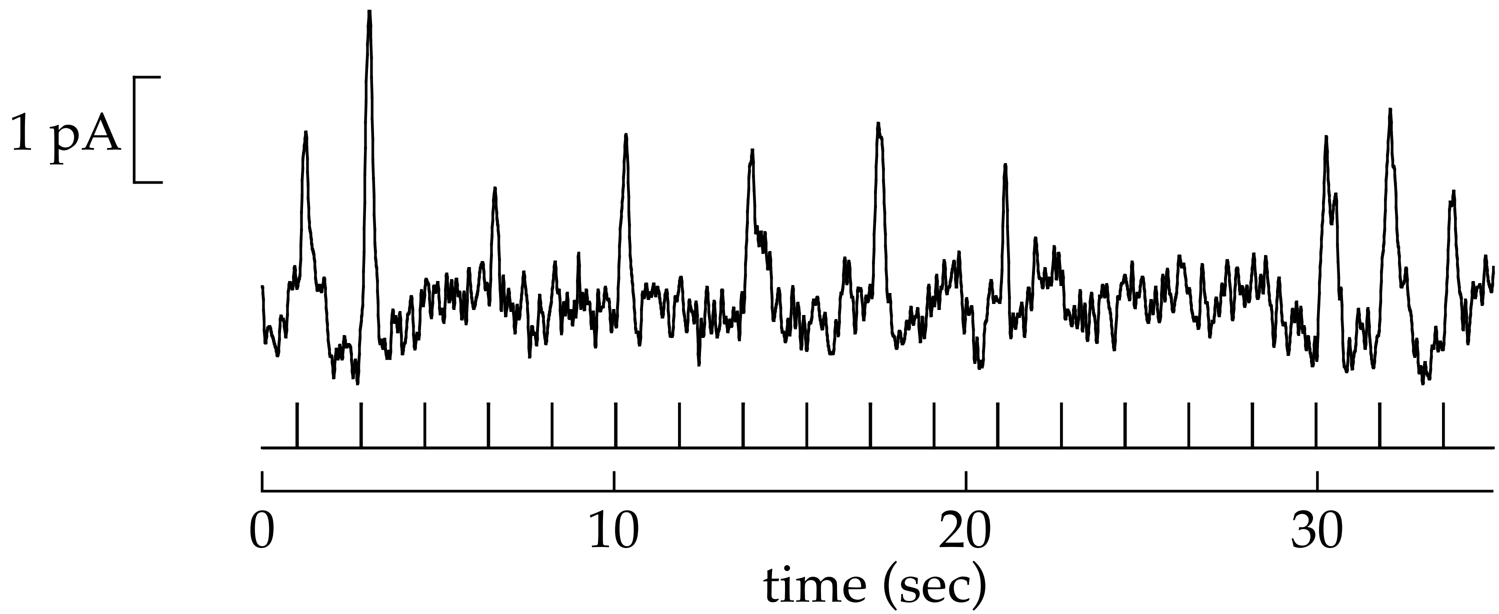




RODS RESPOND TO SINGLE PHOTONS

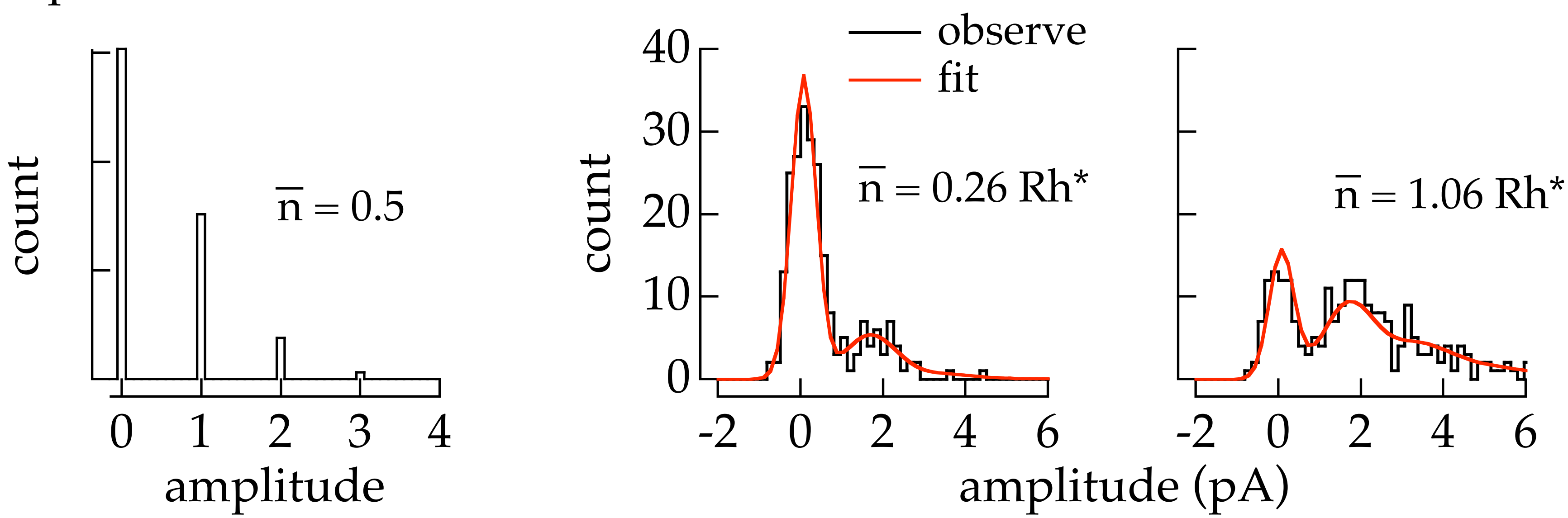
(Field and Rieke, 2002)

Responses to a repeated flash are quantized

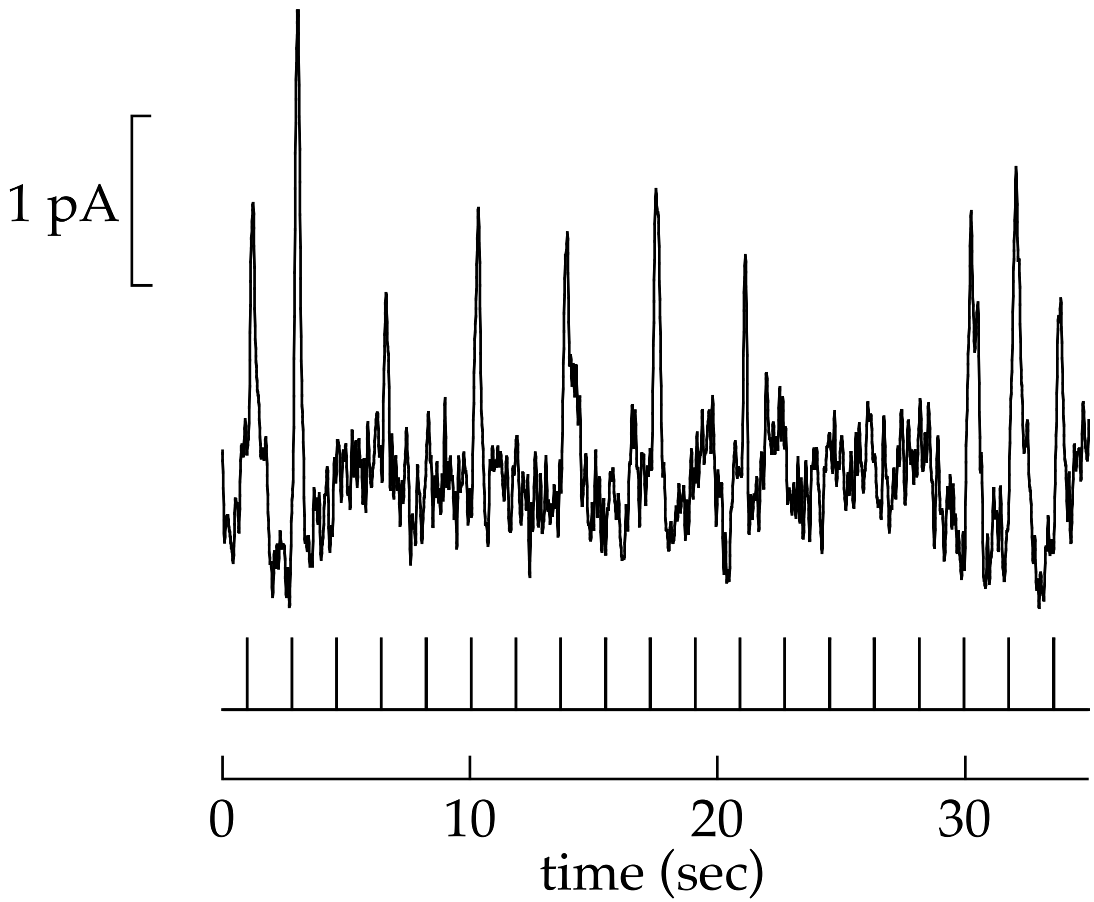


Exercise: fit!

Response statistics Poisson



FUNCTIONAL REQUIREMENTS OF PHOTON DETECTION



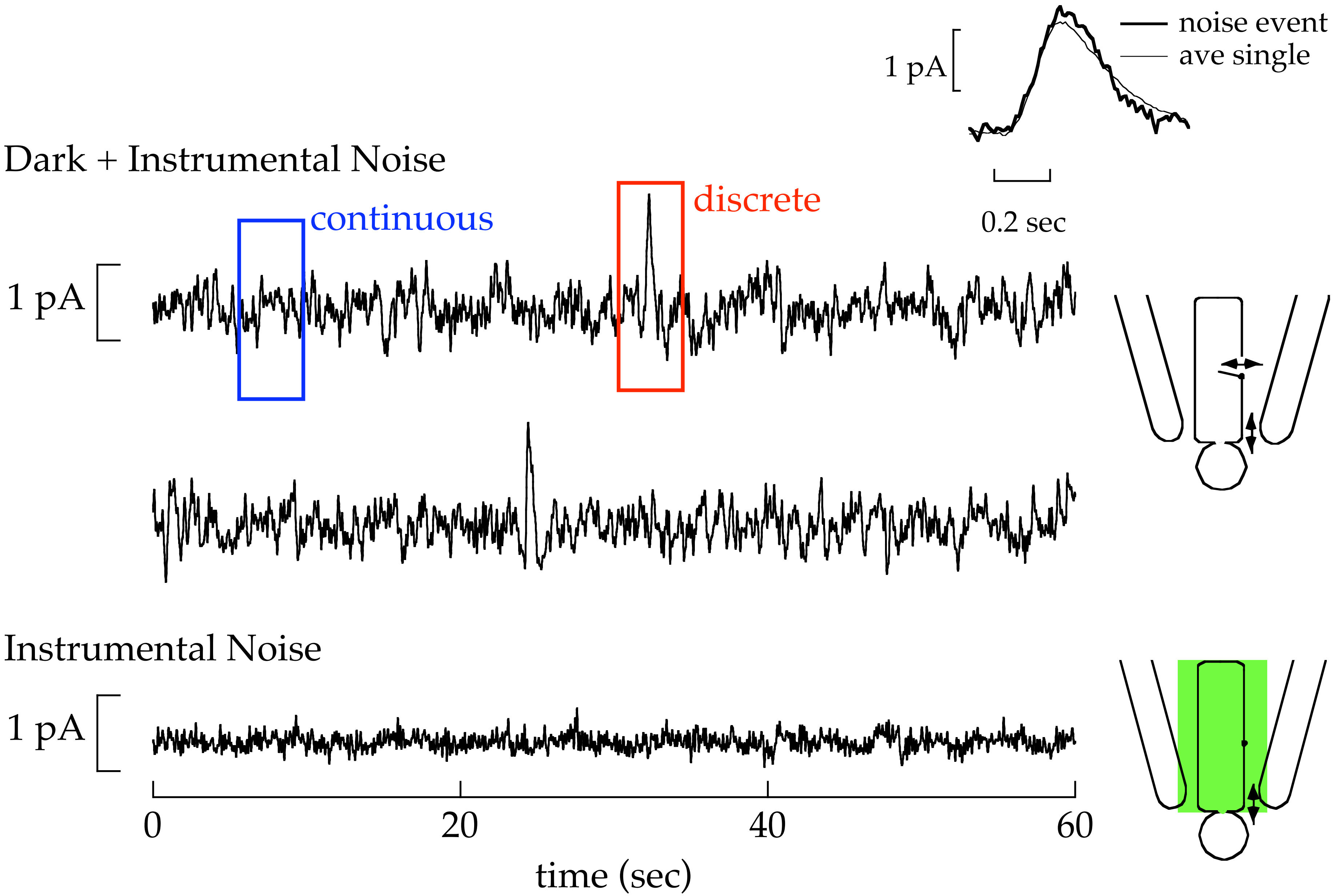
- AMPLIFICATION
  explained by known properties of phototransduction (Pugh and Lamb, 1993)

- LOW DARK NOISE
  - "dark light" ~ 0.01-0.03 Rh* from behavior
  - implications for retinal processing

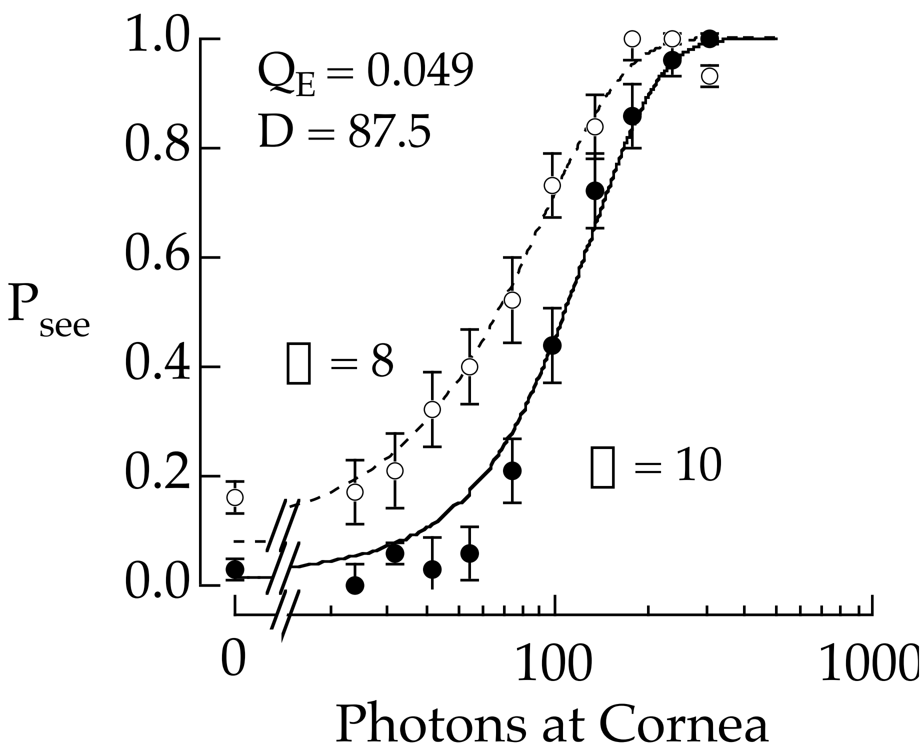
- REPRODUCIBLE SINGLE PHOTON RESPONSE
  - required for photon counting
  - temporal sensitivity (?)

DARK NOISE IN MAMMALIAN RODS

(Baylor et al., 1984)



BEHAVIORAL "DARK LIGHT" CLOSE TO THERMAL RATE IN RODS



BEHAVIOR:

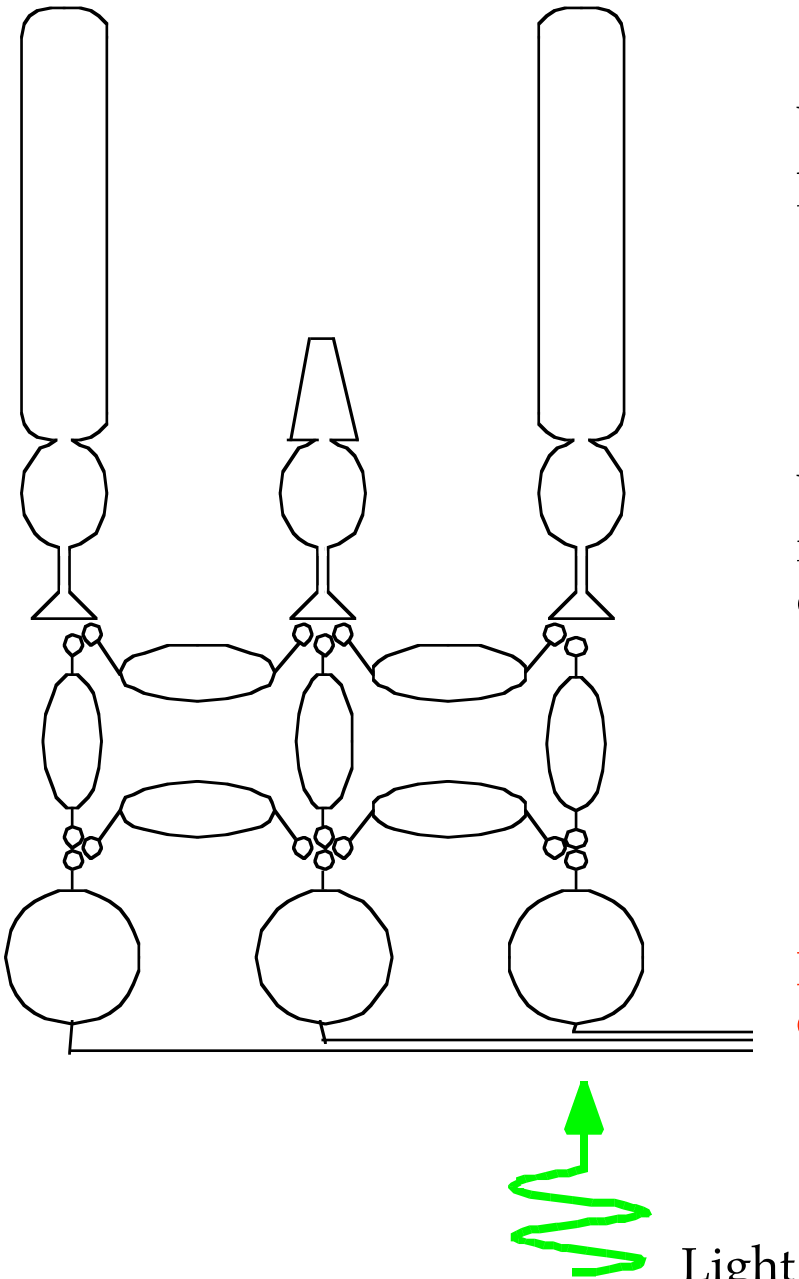
dark noise equivalent to ~0.01-0.03 photon-like noise events per sec per rod

DISCRETE ROD NOISE:

event rate ~0.005-0.01 per sec

TO THINK ABOUT:

what happened to continuous noise?



What constraints does behavioral sensitivity place on detection and processing in retina?

- perception influenced by a small number of photons, perhaps one
- noise limiting behavior ~0.01-0.03 photon like events per rod per sec

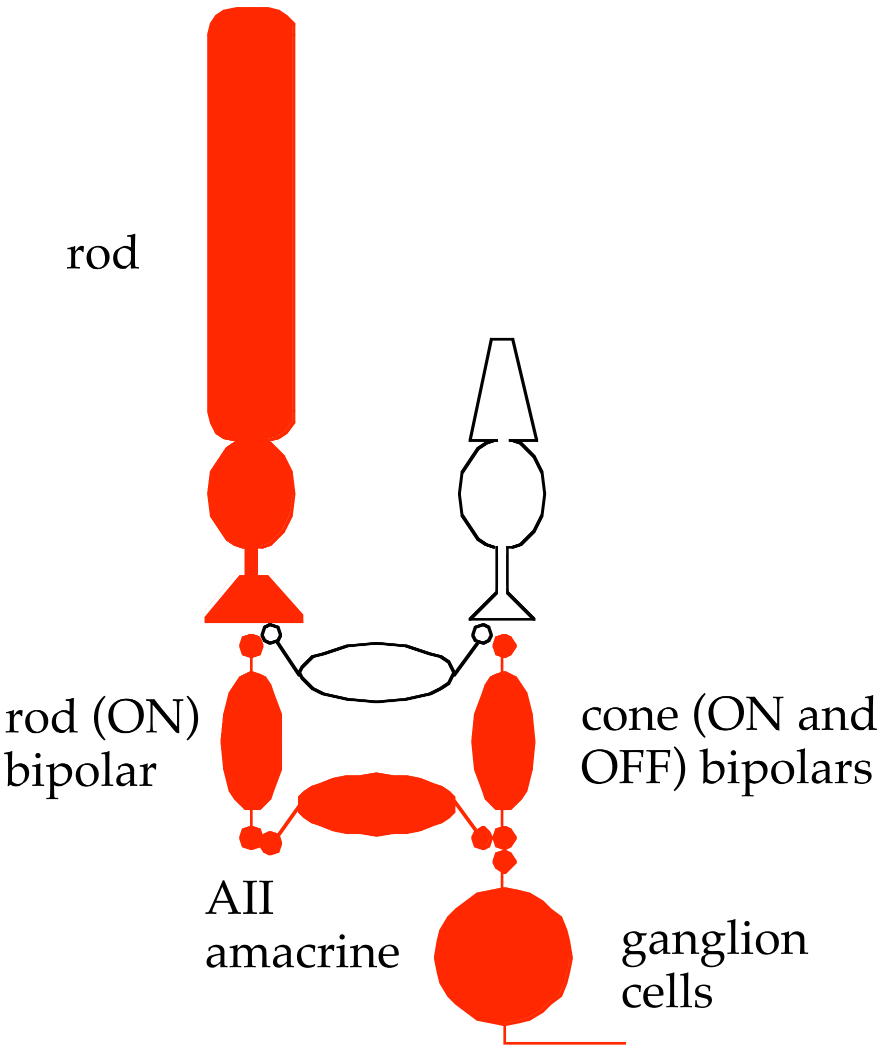
What are properties of single photon responses in rod photoreceptors and how do they relate to behavior?

- thermal activation of rhodopsin generates photon-like noise events at ~0.005 per sec
- reproducible responses to each absorbed photon preserve information about time of photon arrival

How are signals resulting from absorption of a few photons maintained through retina?

- how does rod-bipolar signal transfer influence sensitivity?

IMPLICATIONS OF BEHAVIORAL SENSITIVITY



(Dacheux and Raviola, 1986;
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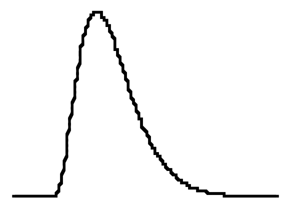
- phototransduction:
  - single photons reliably transduced



- synaptic transmission:
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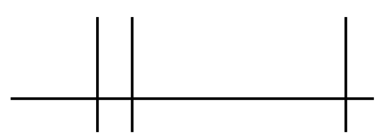
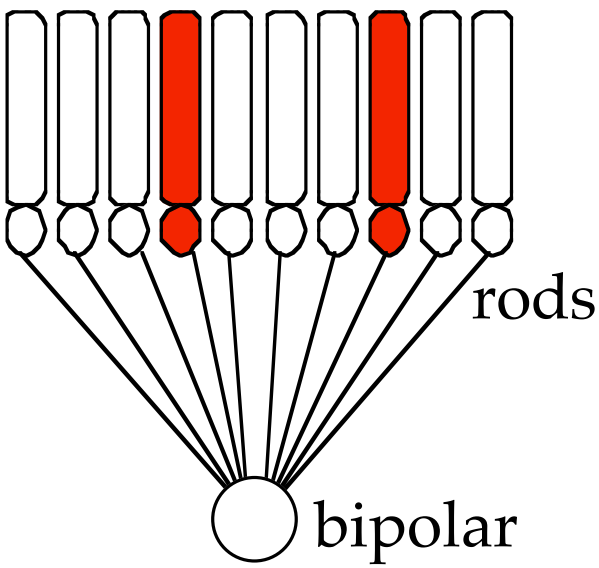


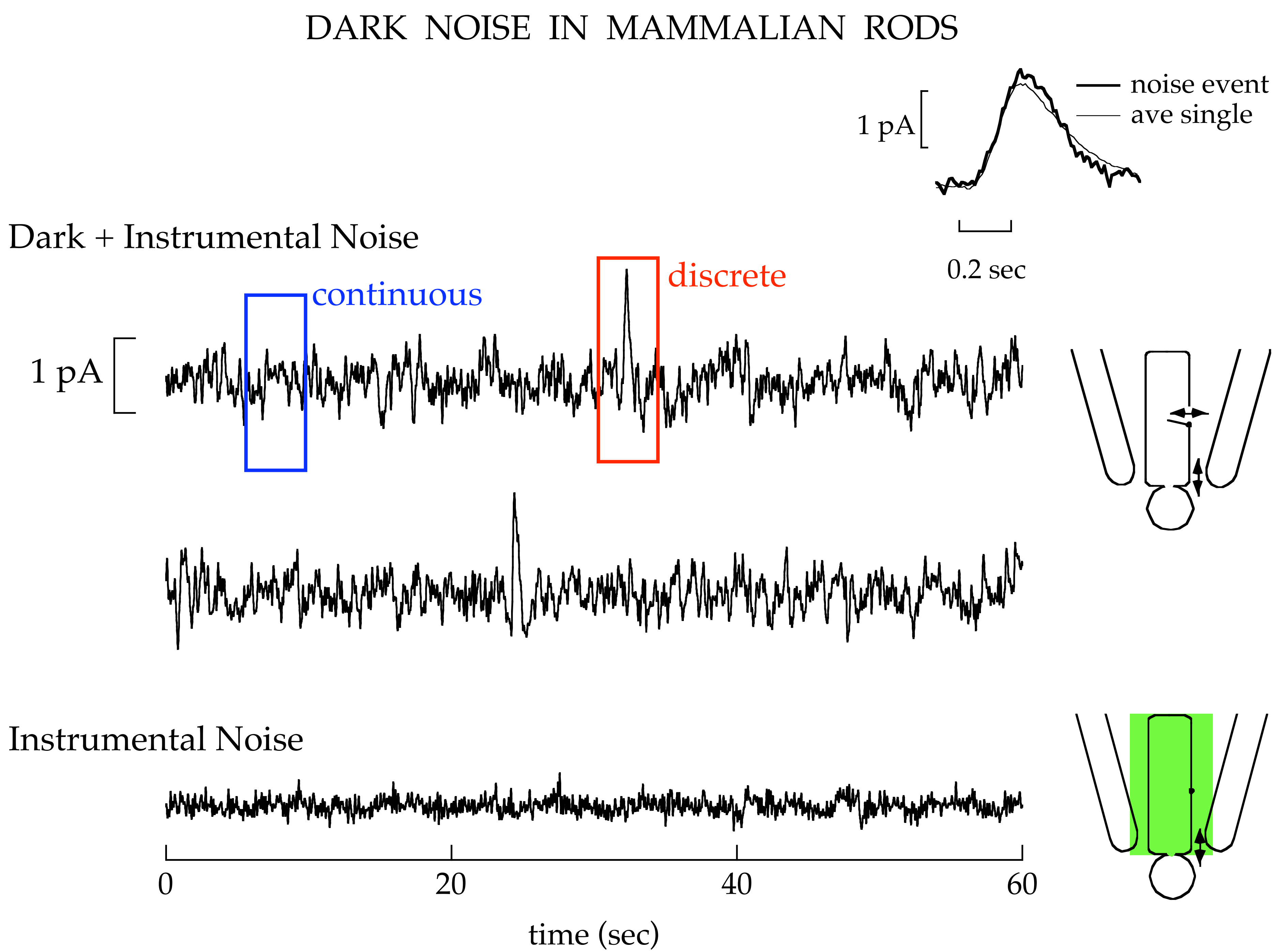
CONVERGENCE AND SPARSE SIGNALING IN MAMMALIAN RETINA



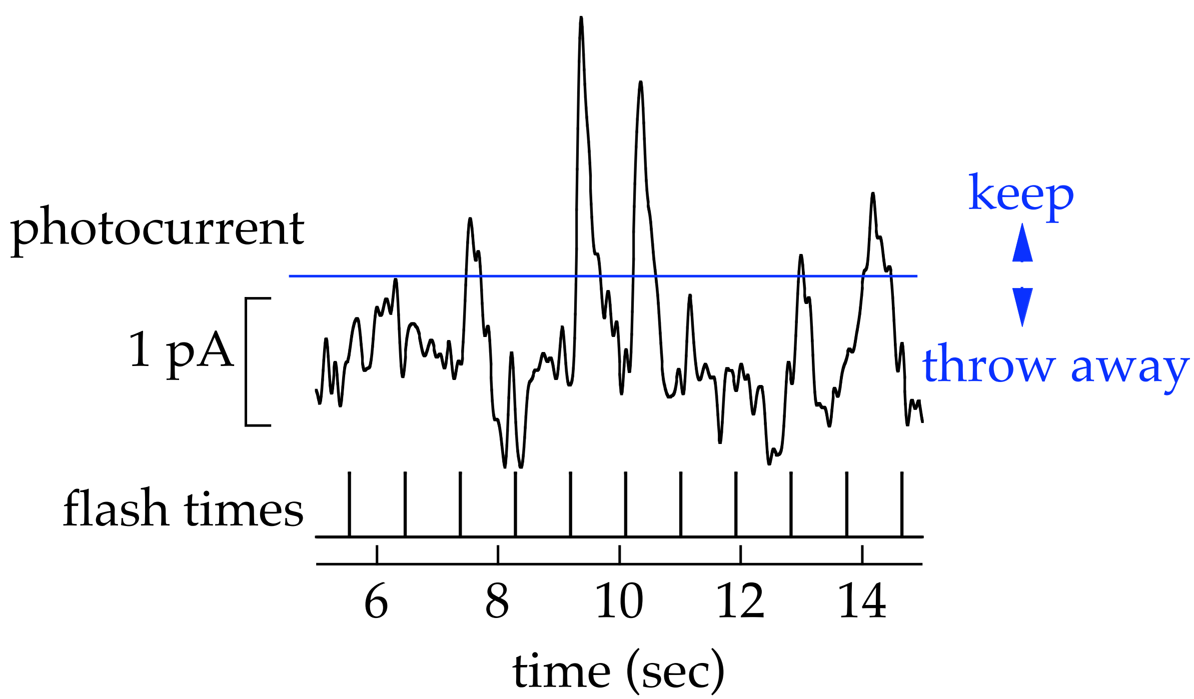
- At visual threshold photons small fraction of rods contribute to each independent visual image

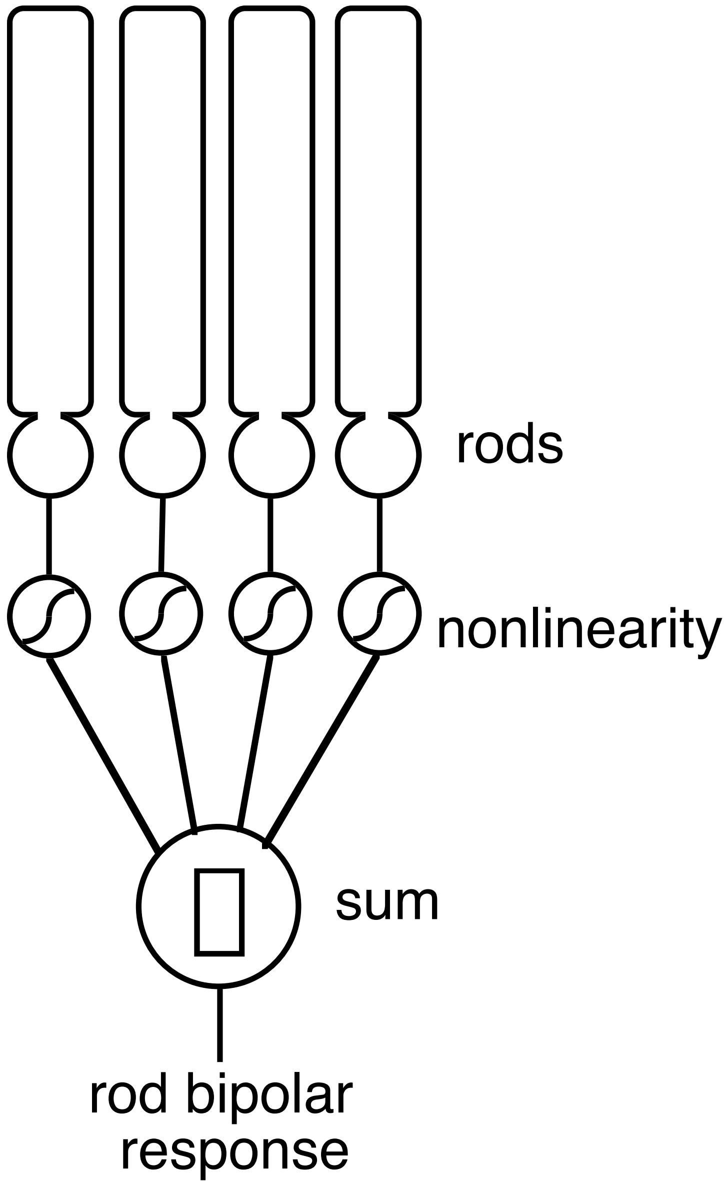
- Sensitivity can be substantially increased if signals from rods absorbing photons can be retained and others discarded - e.g. by thresholding

- General problem in nervous system!


DARK NOISE IN MAMMALIAN RODS
noise event
ave single
1 pA
0.2 sec
Dark + Instrumental Noise
continuous
discrete
1 pA
Instrumental Noise
0
20
40
60
time (sec)

SEPARATION OF ROD SIGNAL AND NOISE BY THRESHOLDING NONLINEARITY



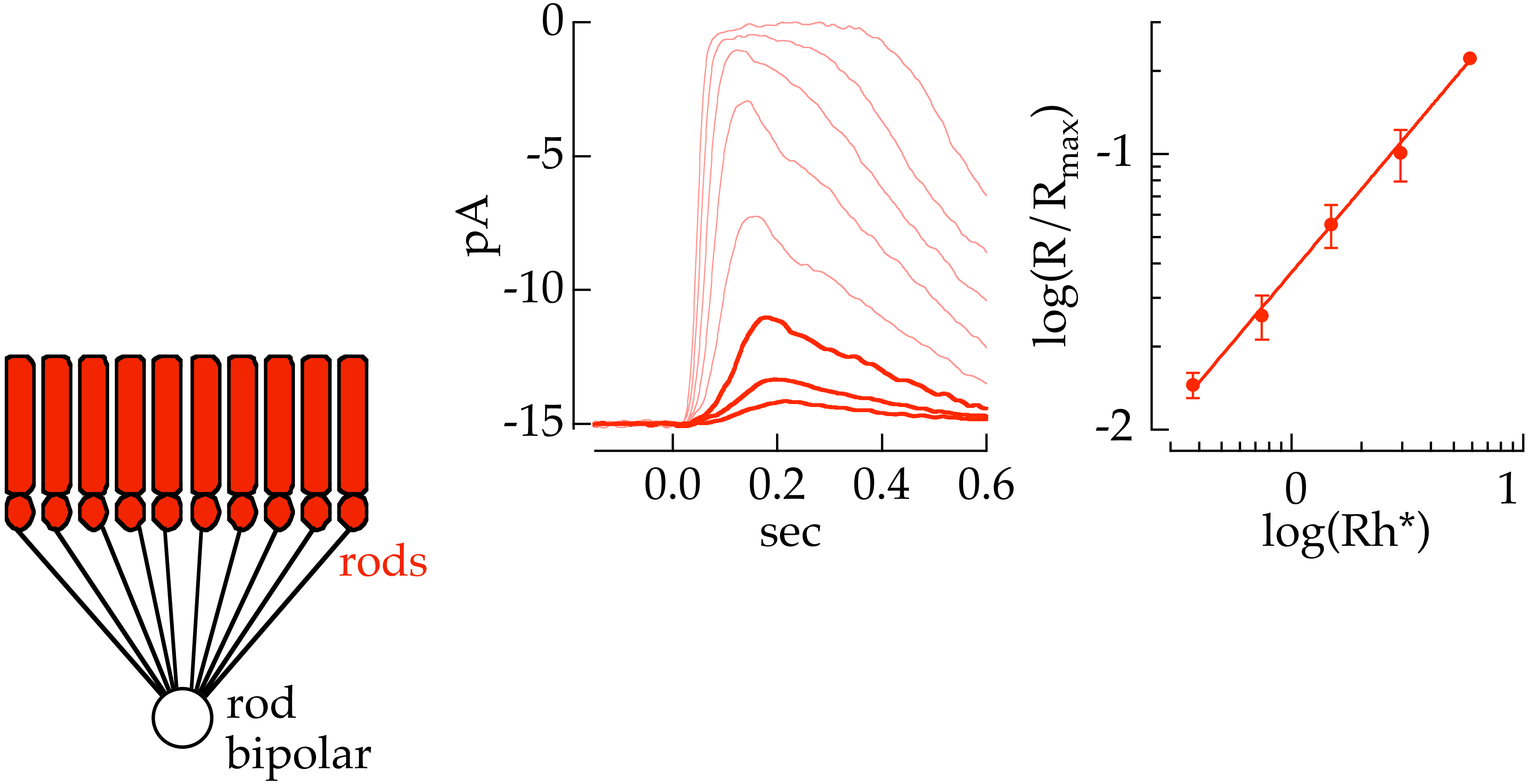


• Mouse rod-rod bipolar signal transfer is nonlinear.
- dependence of response on flash strength
- discreteness of dim flash response

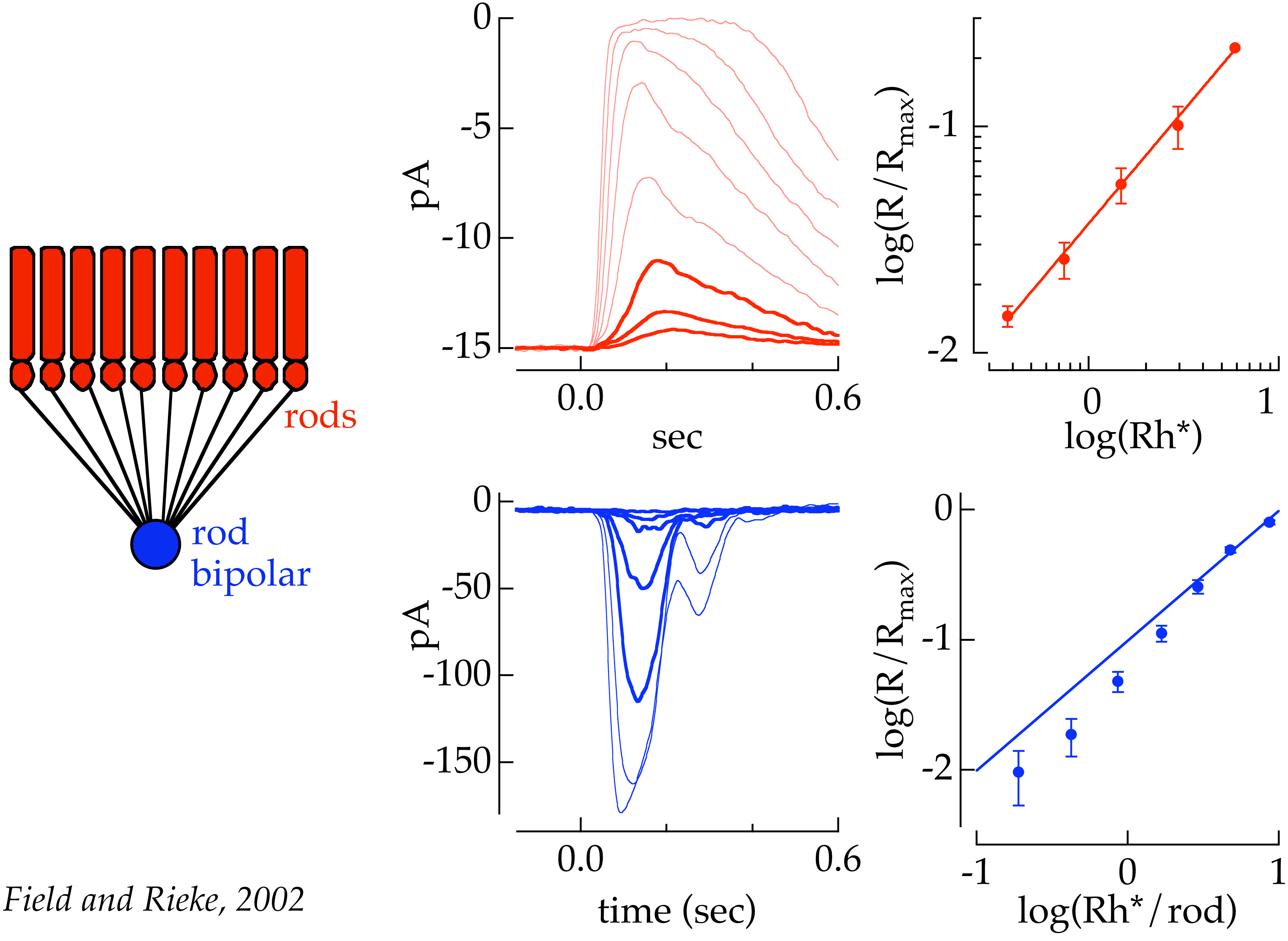
• Nonlinear signal transfer eliminates or severely attenuates majority of rod's single photon responses.

• Rejection of noise more than compensates loss of signal - thus rod bipolars provide near-optimal readout of rod signals near visual threshold.

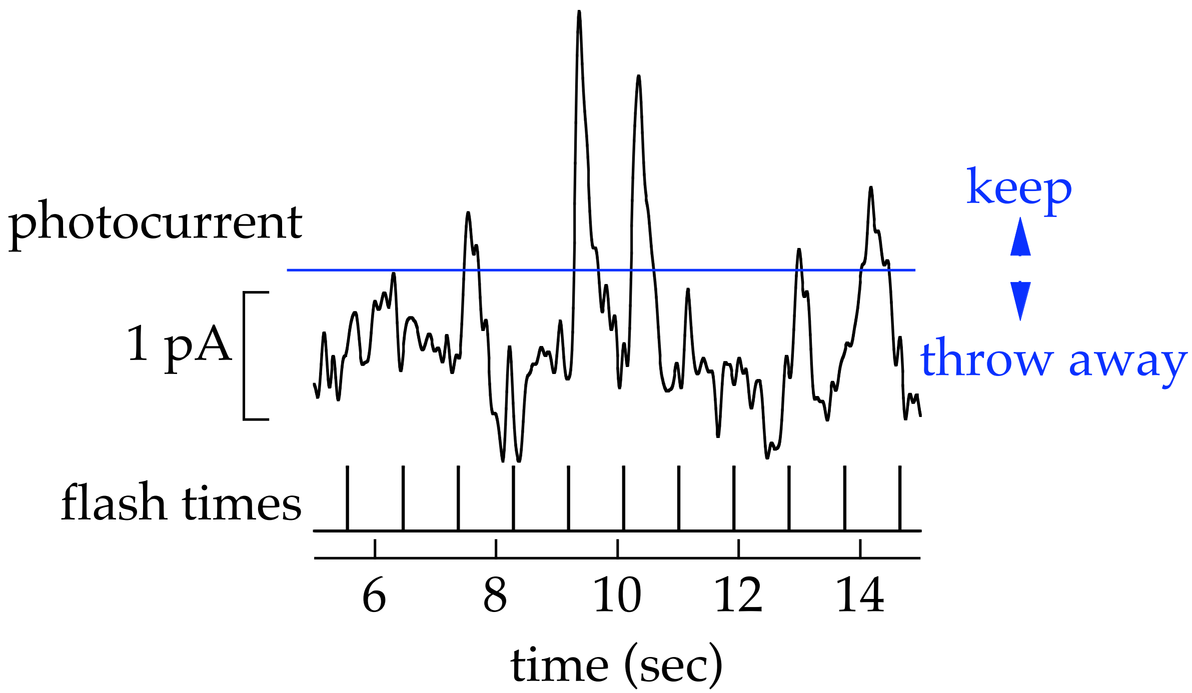
DIM FLASH RESPONSES OF RODS GROW LINEARLY WITH FLASH STRENGTH



RESPONSES OF ROD BIPOLARS BUT NOT RODS GROW SUPRALINEARLY WITH FLASH STRENGTH

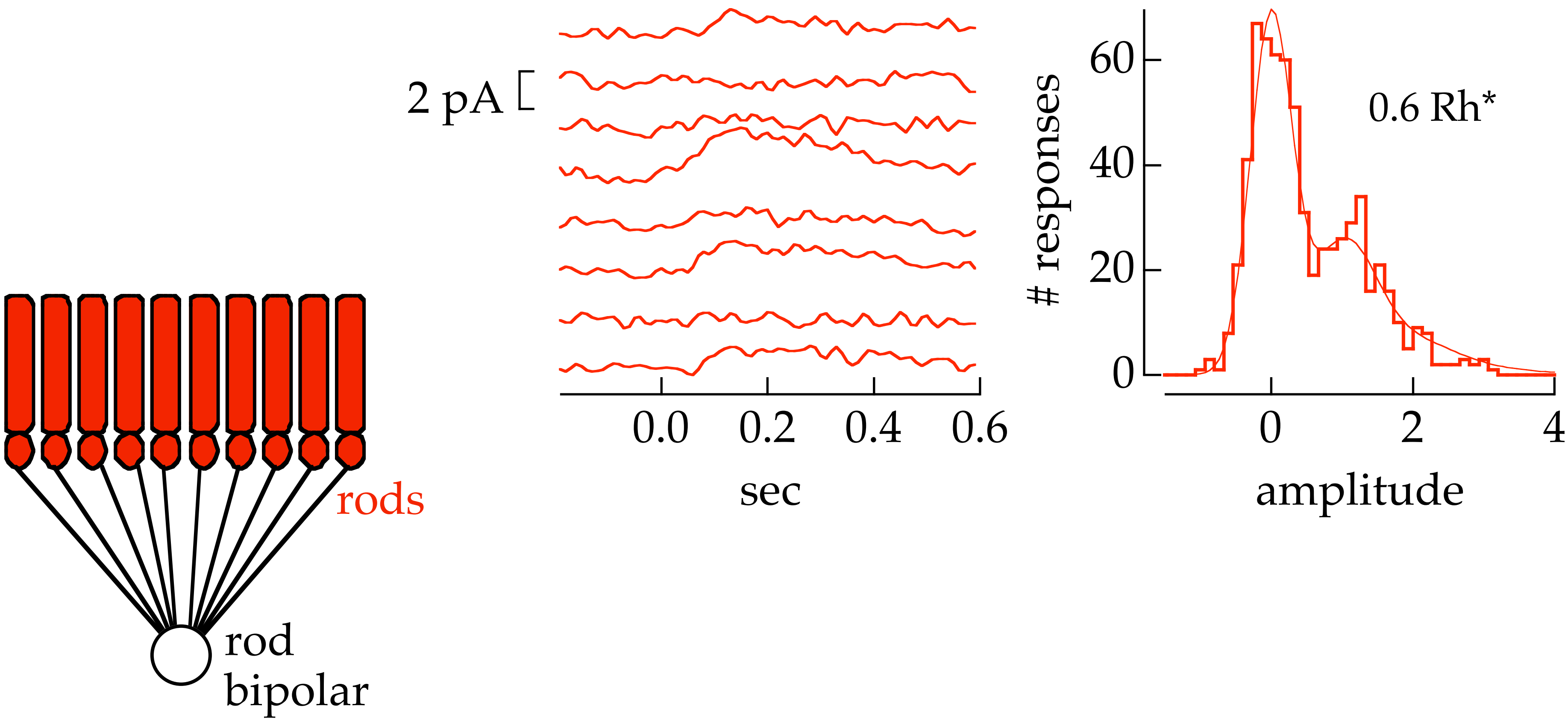


Field and Rieke, 2002

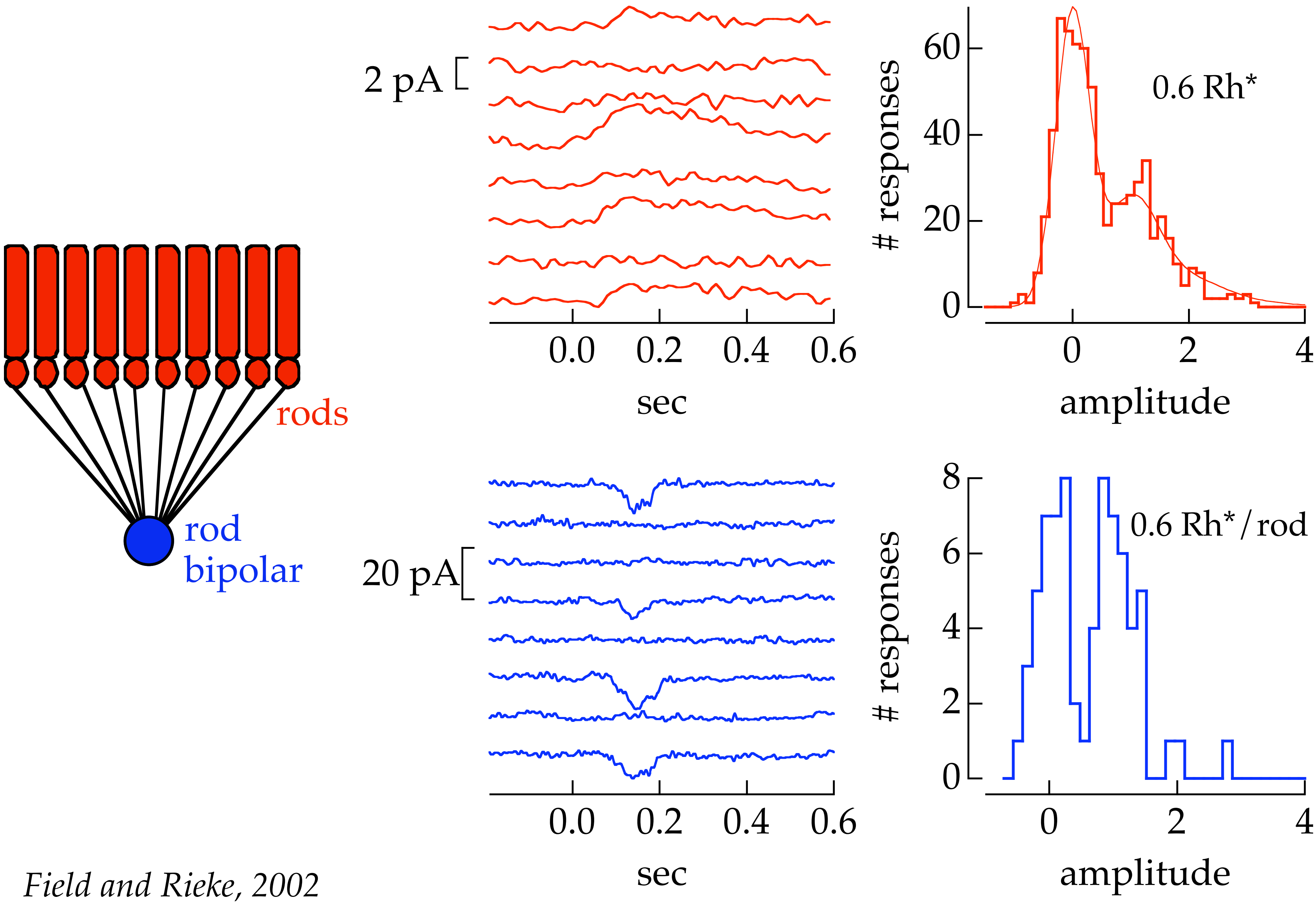


Does rod-rod bipolar signal transfer separate rod signal and noise?

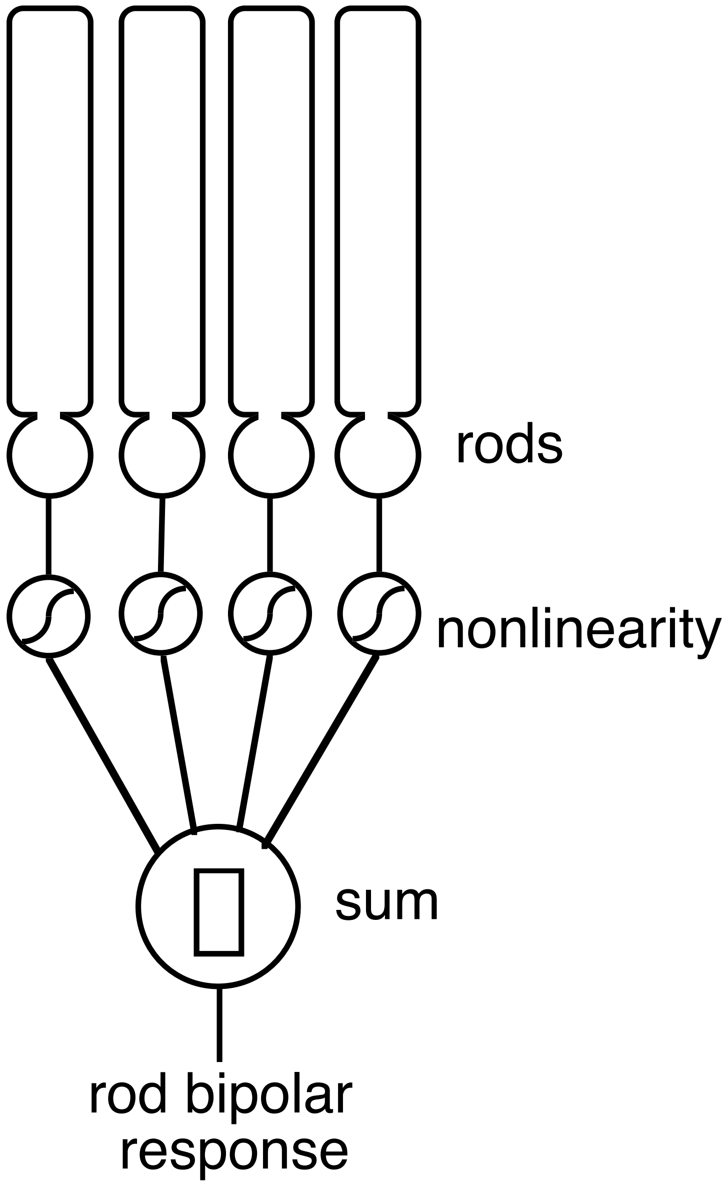
MOUSE ROD SINGLE PHOTON RESPONSES ARE PARTIALLY OBSCURED BY NOISE



ROD BIPOLARS GENERATE DISCRETE RESPONSES TO DIM FLASHES



Field and Rieke, 2002

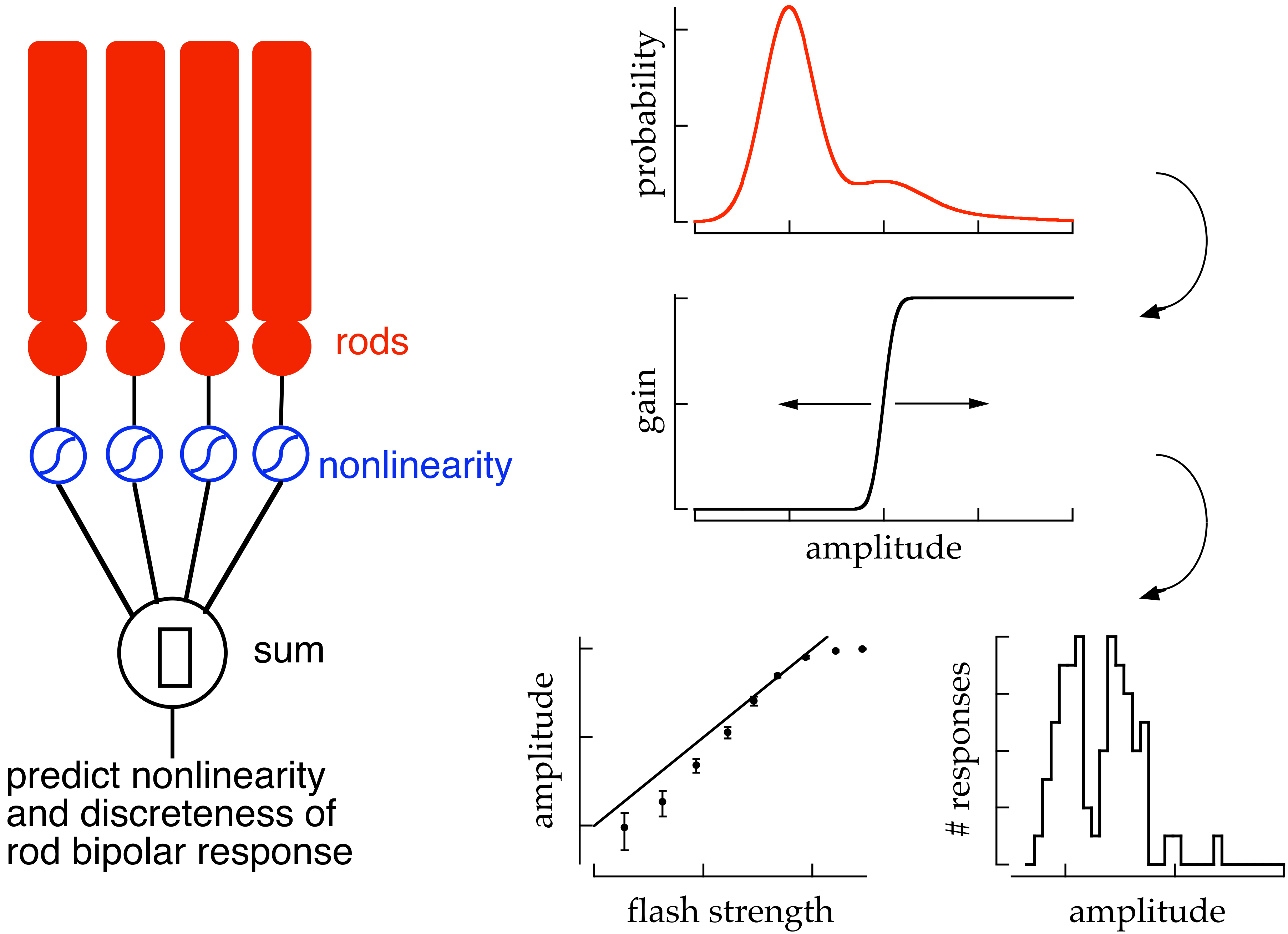


- Mouse rod-rod bipolar signal transfer is nonlinear.

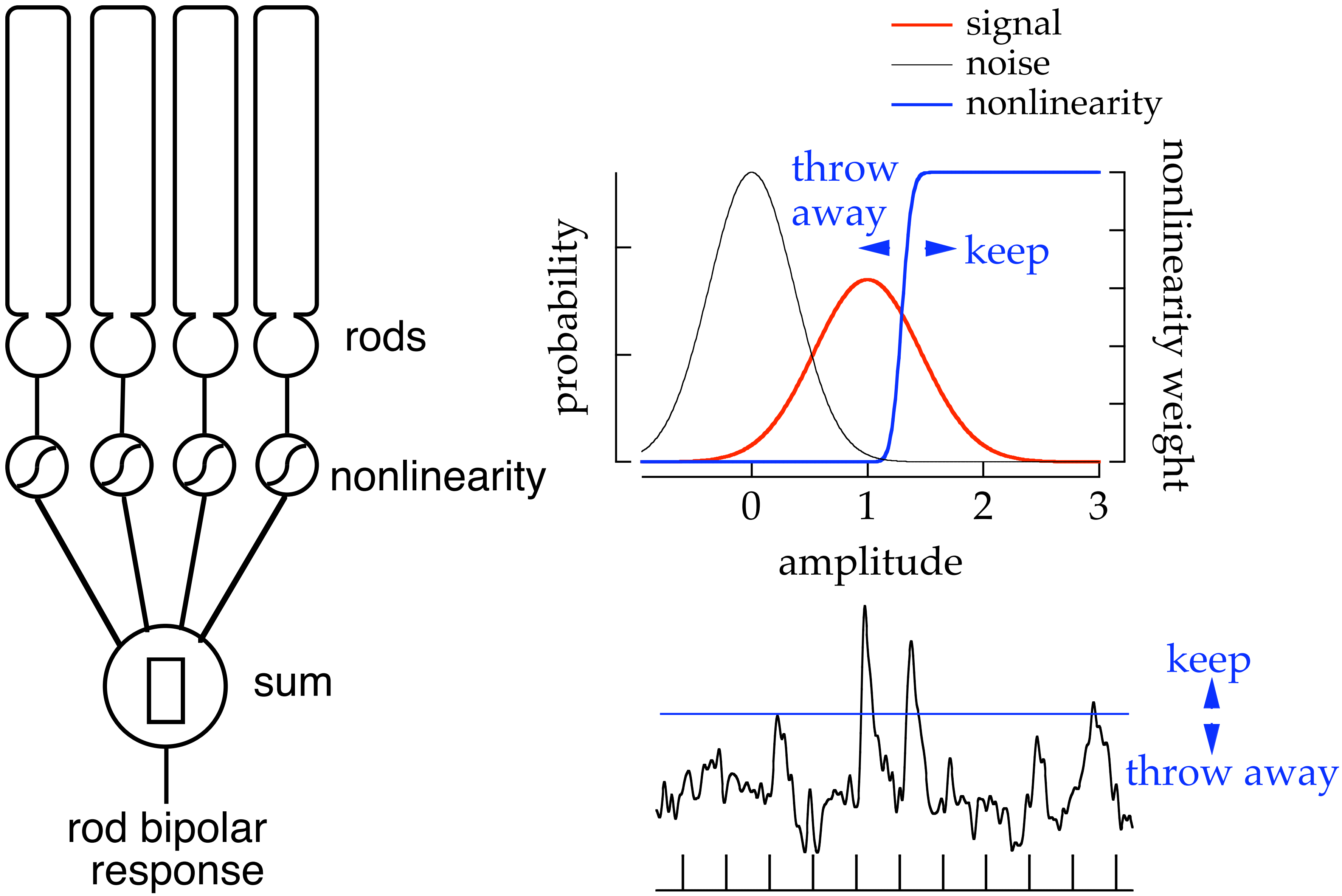
- Nonlinear signal transfer eliminates or severely attenuates majority of rod's single photon responses.

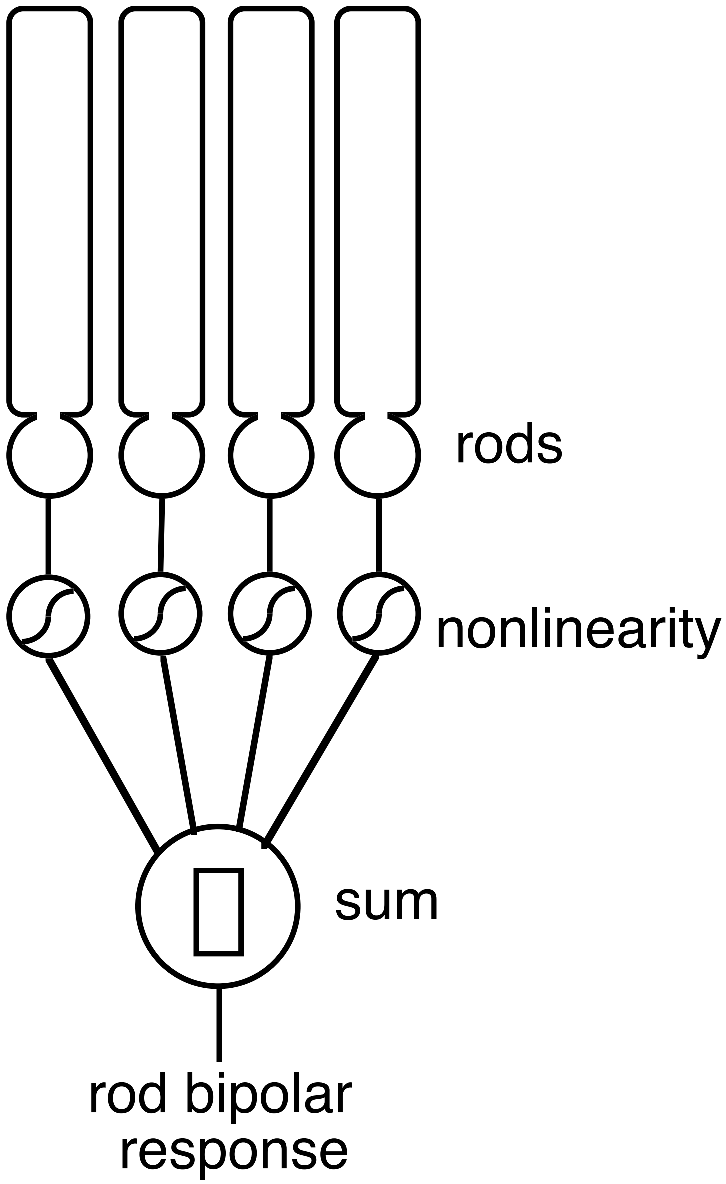
- Rejection of noise more than compensates loss of signal - thus rod bipolars provide near-optimal readout of rod signals near visual threshold.

MODEL FOR ROD-ROD BIPOLAR SIGNAL TRANSFER



MANY OF ROD'S SINGLE PHOTON RESPONSES ELIMINATED IN ROD-ROD BIPOLAR SIGNAL TRANSFER



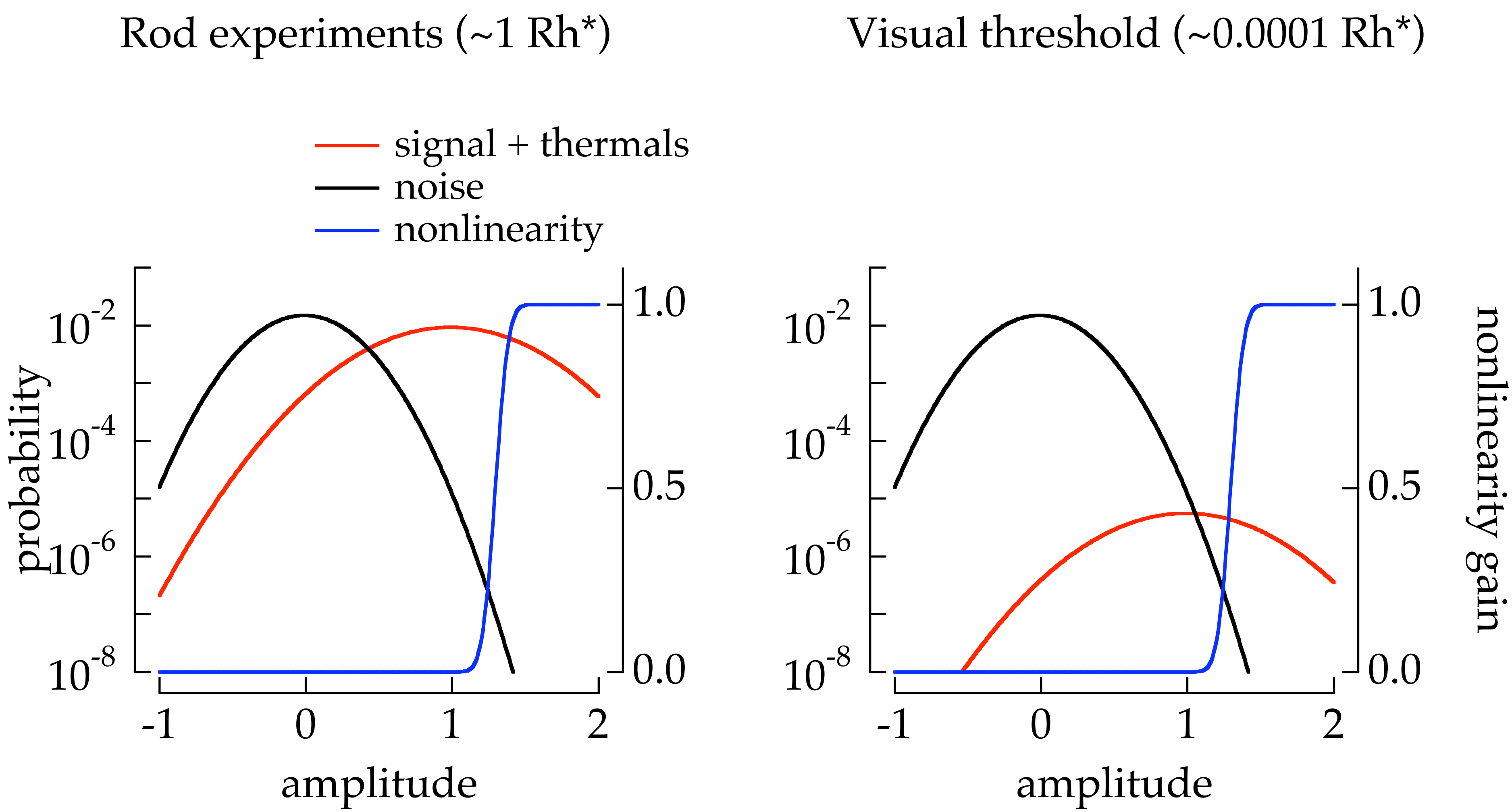


- Mouse rod-rod bipolar signal transfer is nonlinear.

- Nonlinear signal transfer eliminates or severely attenuates majority of rod's single photon responses.
- can this explain low Q_E from behavior?

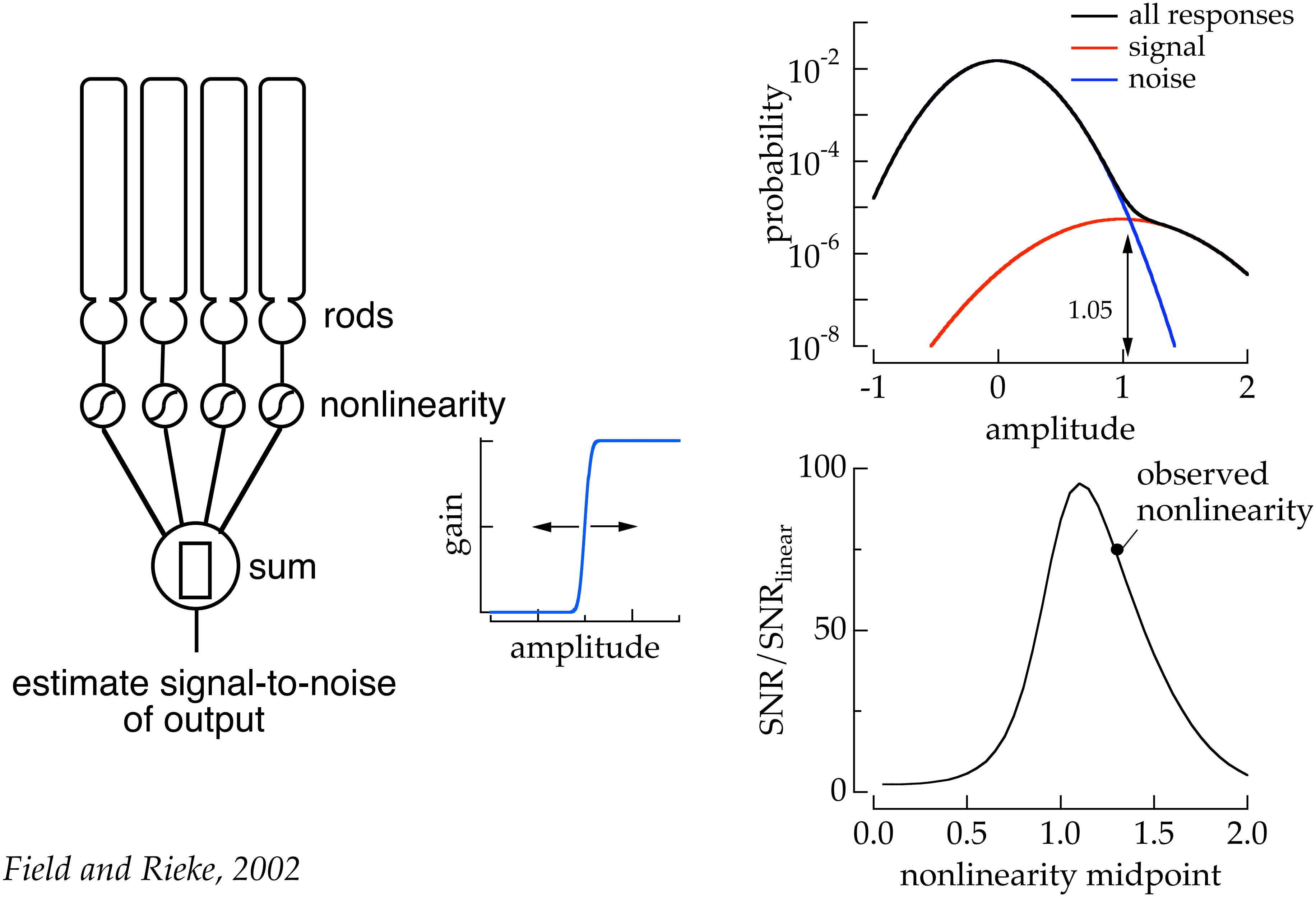
- Rejection of noise more than compensates loss of signal - thus rod bipolars provide near-optimal readout of rod signals near visual threshold.

DISTRIBUTION OF ROD RESPONSES AT VISUAL THRESHOLD



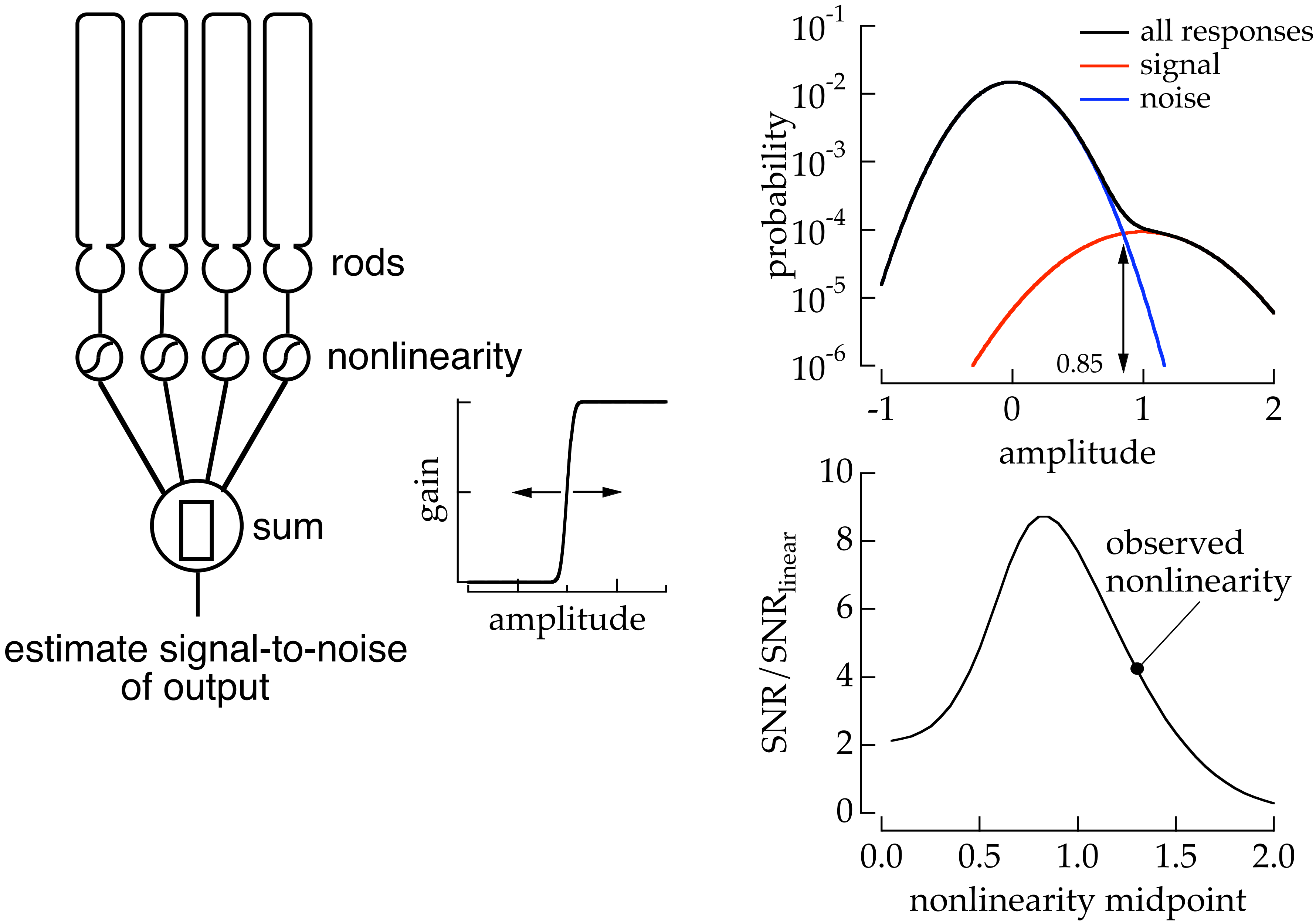
Prior probability of getting a photon very low!

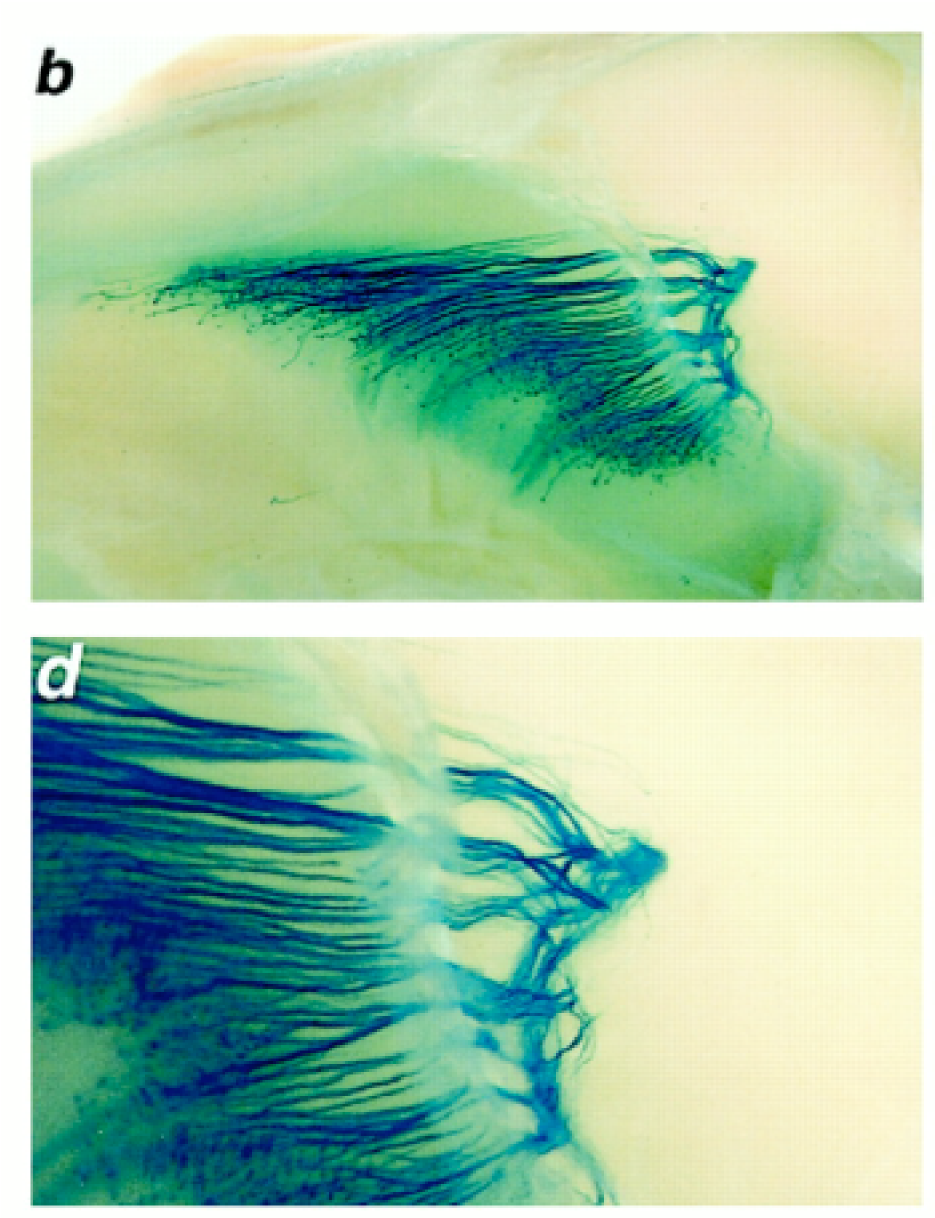
ROD BIPOLAR PROVIDES NEAR OPTIMAL READOUT OF ROD SIGNALS AT VISUAL THRESHOLD (0.0001 Rh*/rod/integration time)

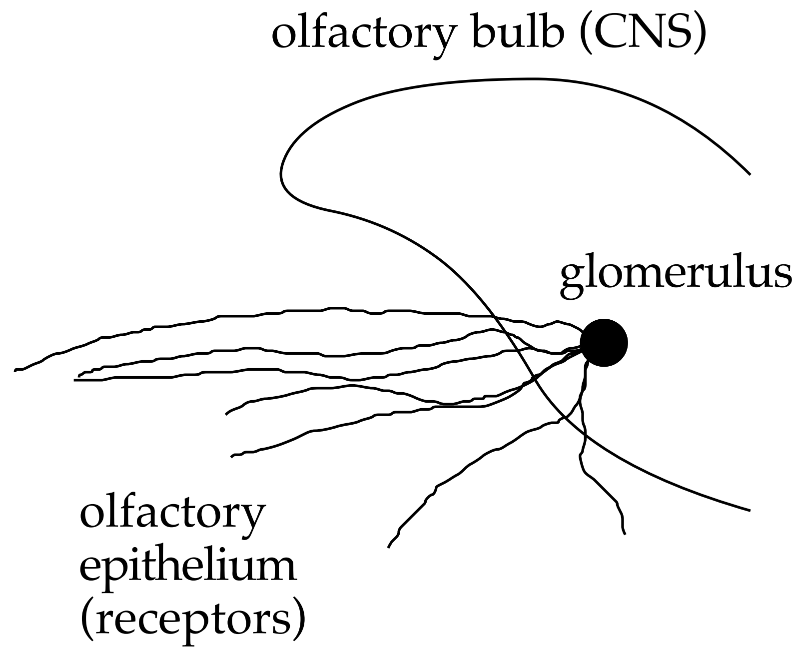


Field and Rieke, 2002

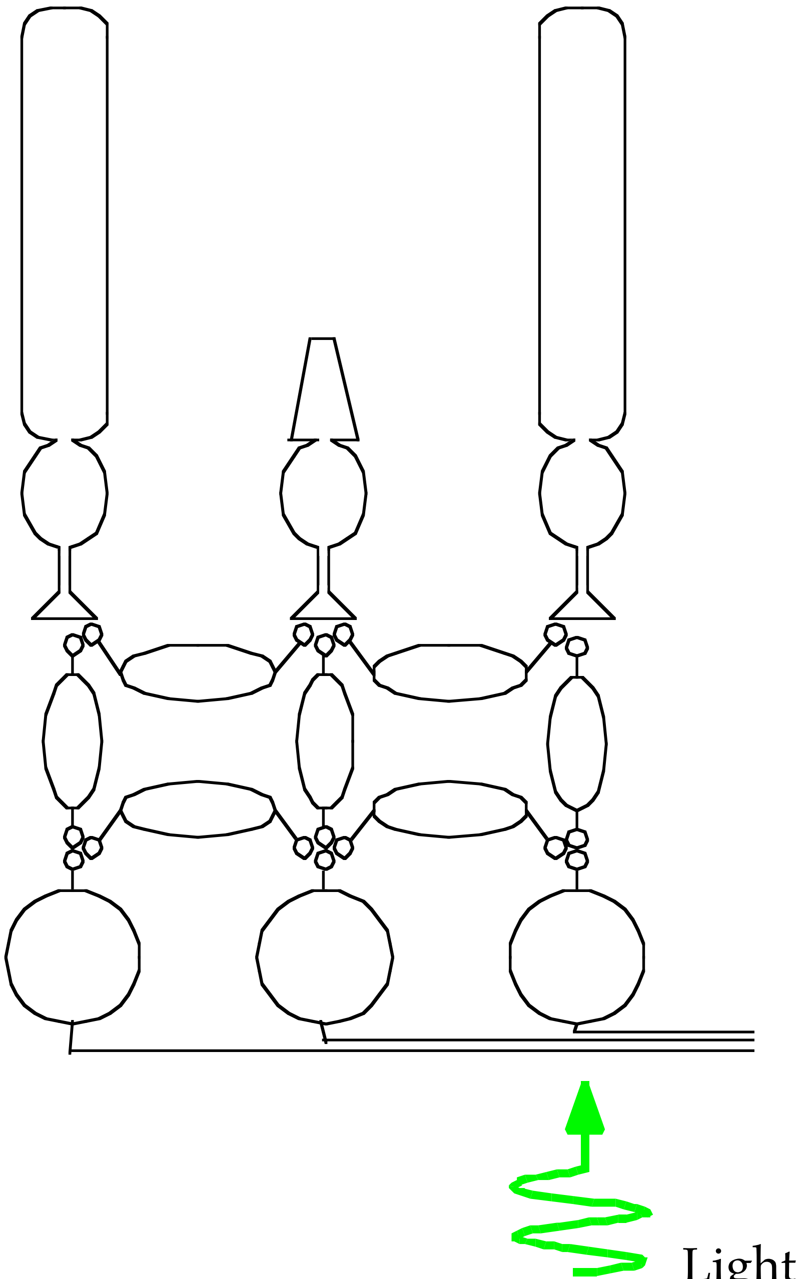
NONLINEAR SIGNAL TRANSFER LIMITS SENSITIVITY WELL ABOVE VISUAL THRESHOLD (0.01 Rh*/rod/integration time)







Mombaerts et al, 1996



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- noise limiting behavior ~0.01-0.03 photon like events per rod per sec

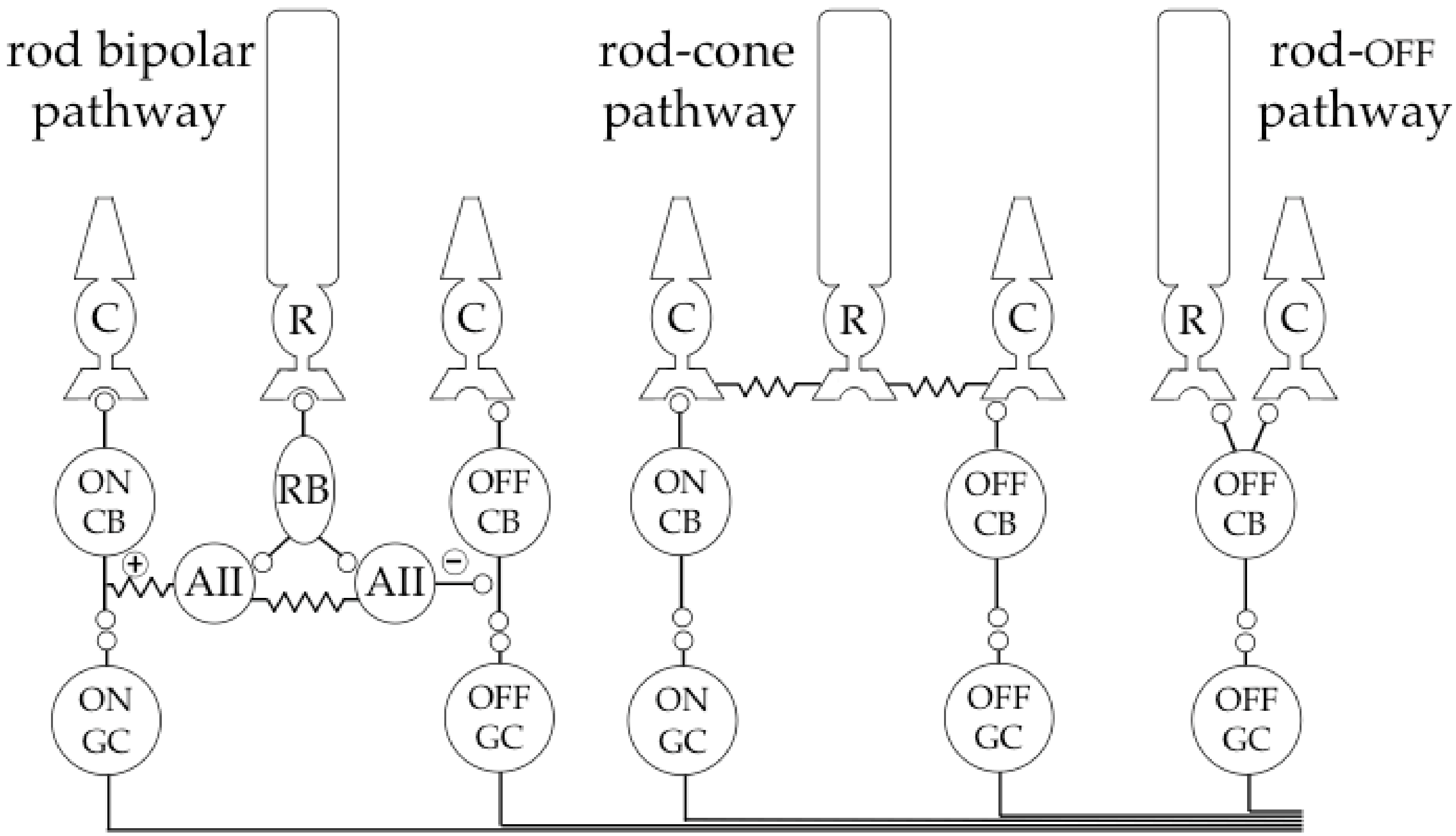
What are properties of single photon responses in rod photoreceptors and how do they relate to behavior?

- thermal activation of rhodopsin generates photon-like noise events at ~0.005 per sec
- reproducible responses to each absorbed photon preserve information about time of photon arrival

How are signals resulting from absorption of a few photons maintained through retina?

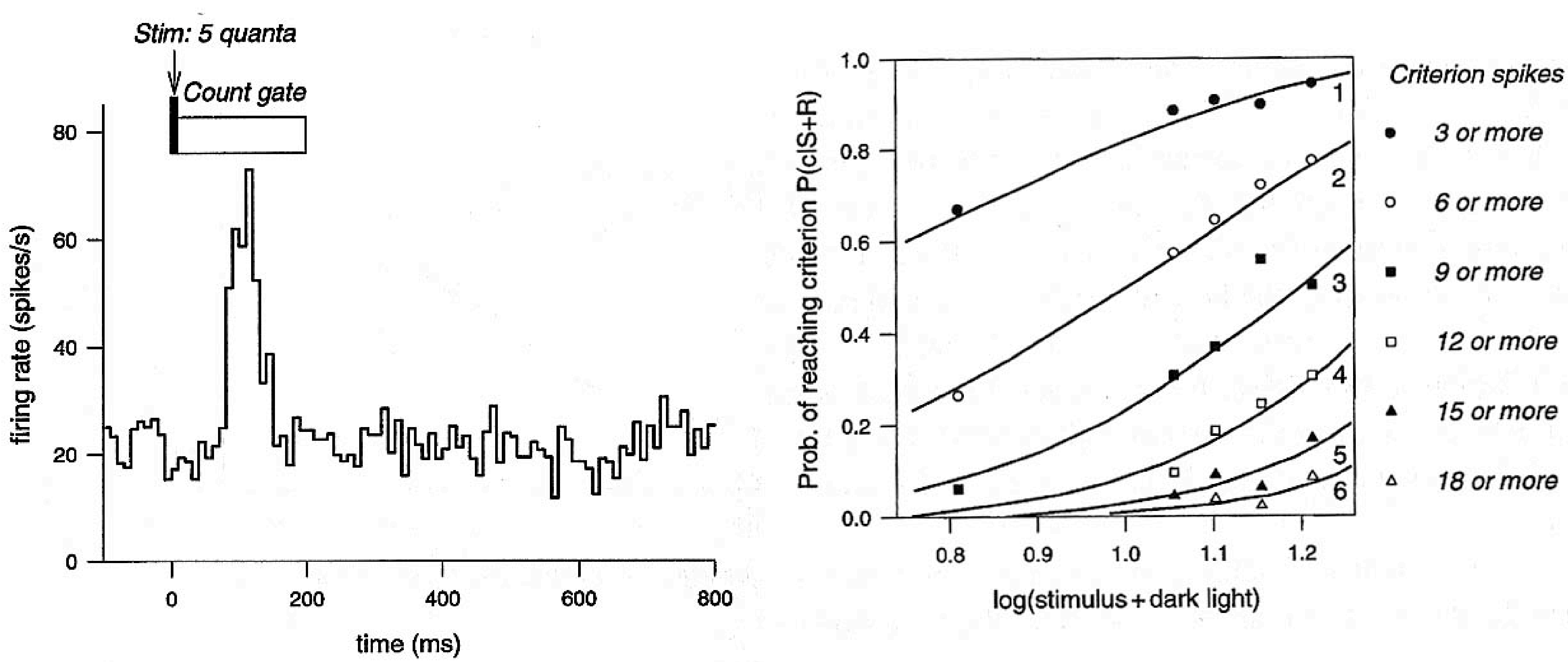
- thresholding nonlinearity at rod-to-rod bipolar synapse separates signal and noise

- Does rod bipolar-AII synapse remove noise intrinsic to bipolar?
- What is role of ‘alternate’ pathways?



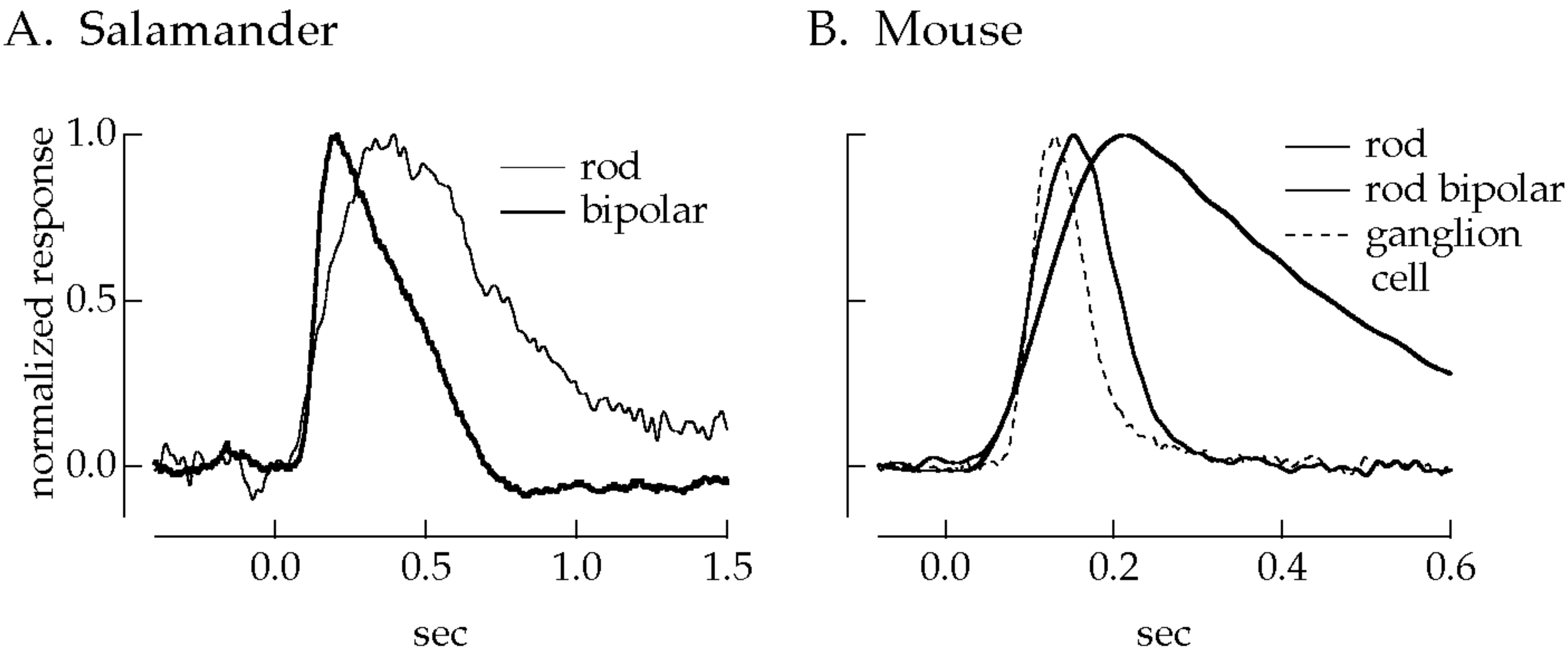
How sensitive are retinal ganglion cells?

(Barlow, Levick and Yoon, 1971)

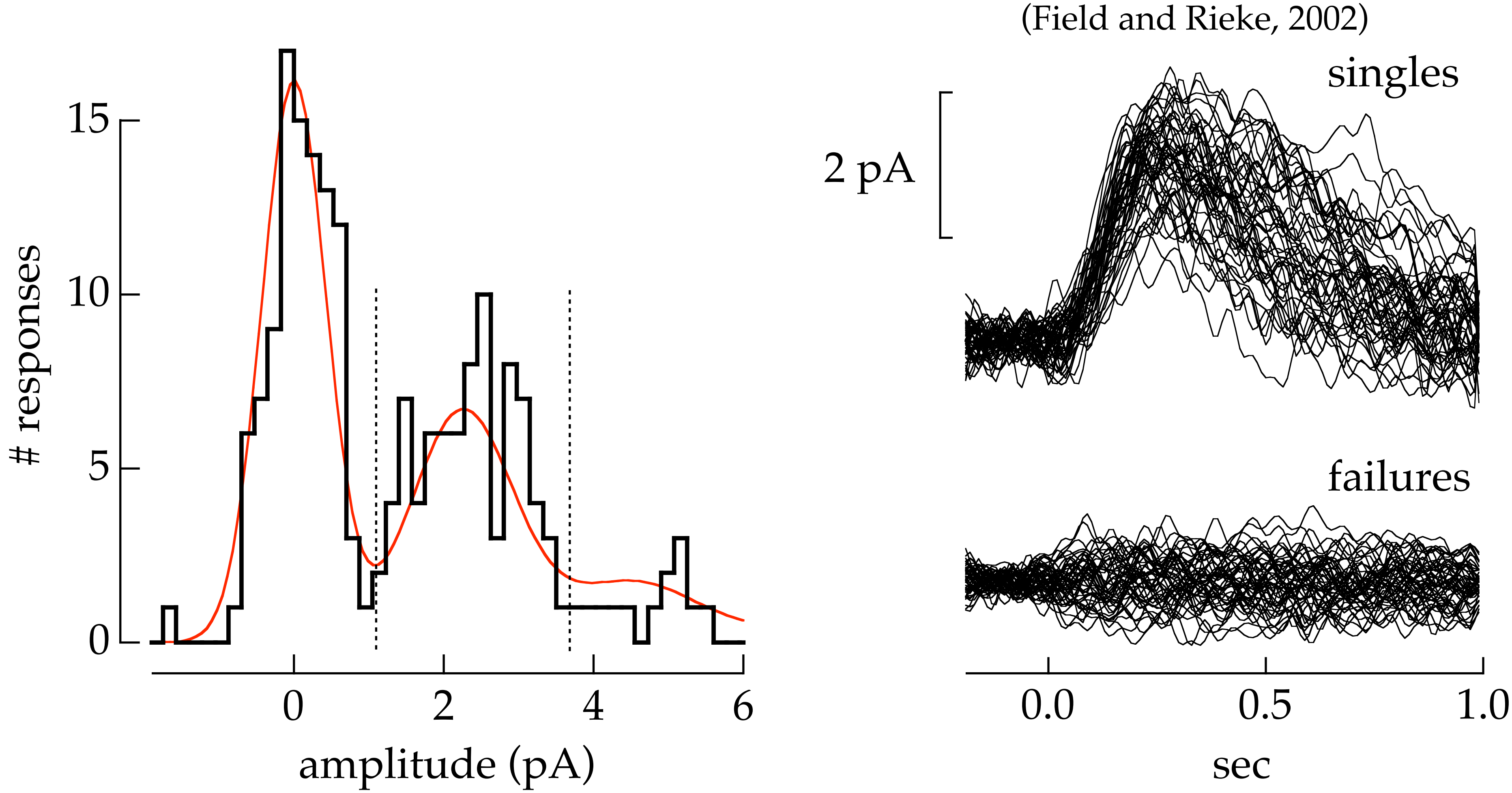


temporal and detection sensitivity (it’s not all about detecting the presence or absence of photons)

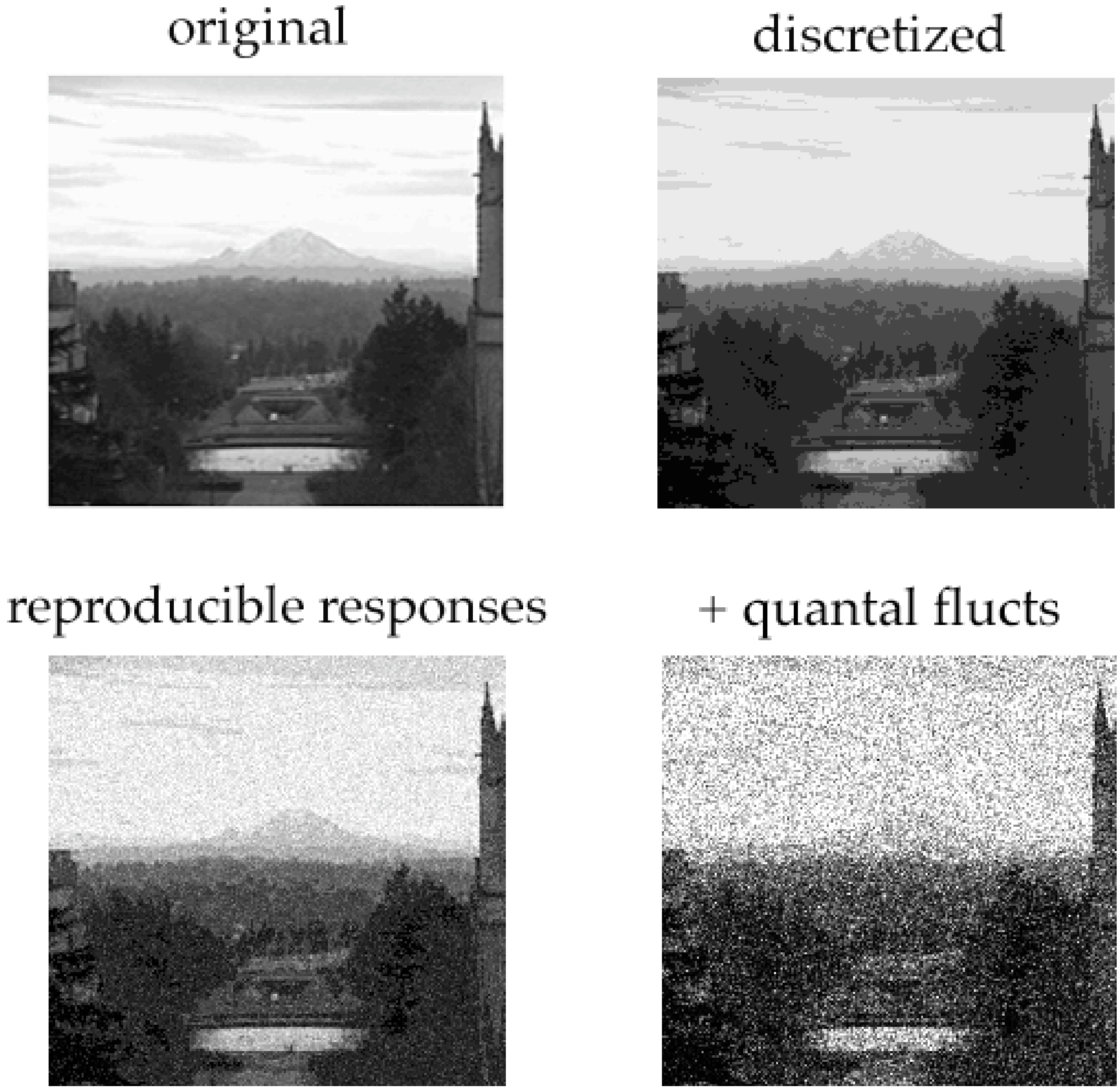
- Are kinetics of rod-bipolar synapse matched to rod signal and noise - i.e. does synapse cut off variable part of rod responses?
- What does this mean for temporal sensitivity?



EVIDENCE FOR REPRODUCIBILITY



CV_{area} = standard deviation / mean = 0.26 ± 0.06


original
discretized
reproducible responses
+ quantal flucts

Transduction and processing of single photon responses

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A.P. (Sam) Sampath
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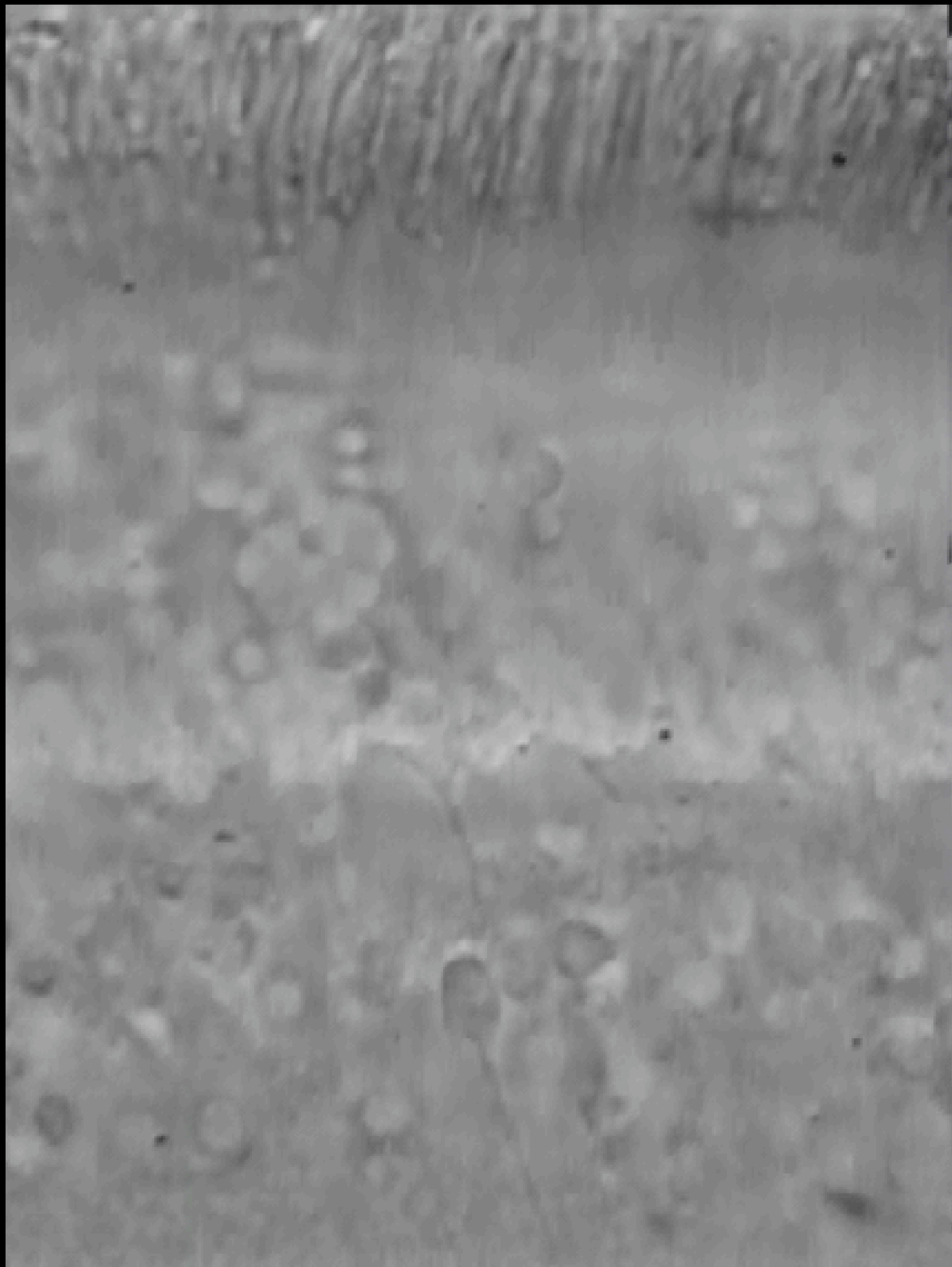
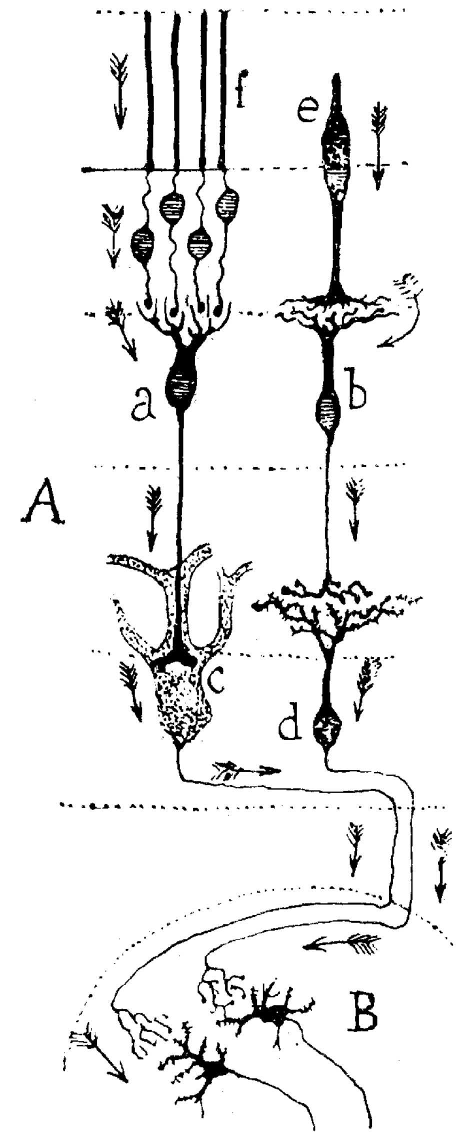
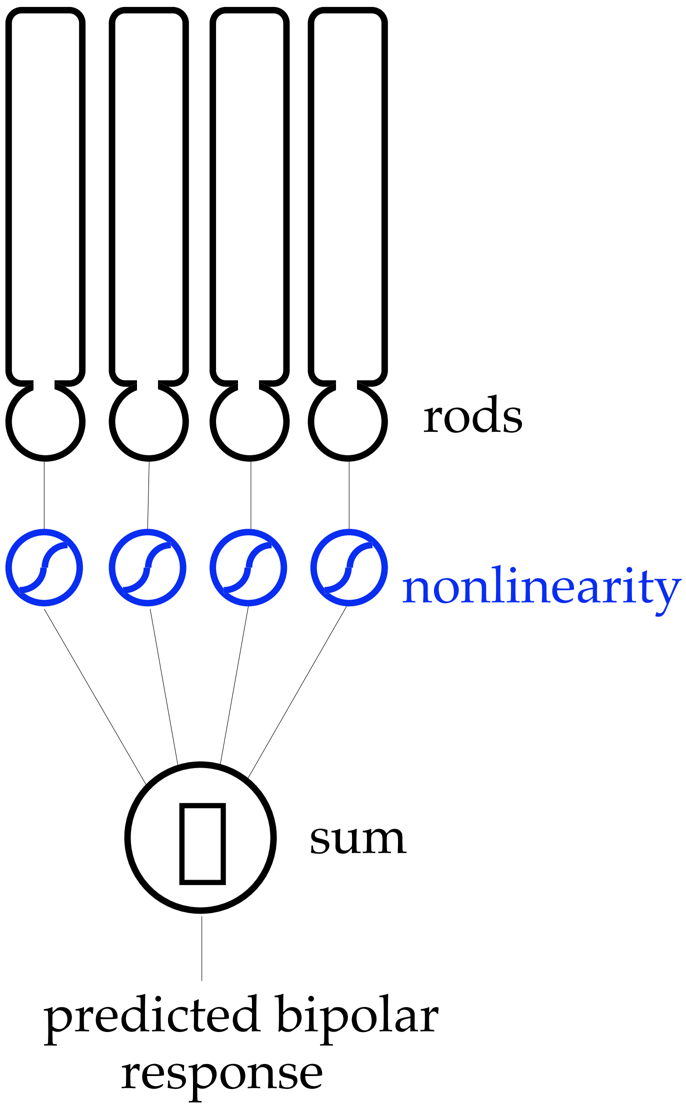


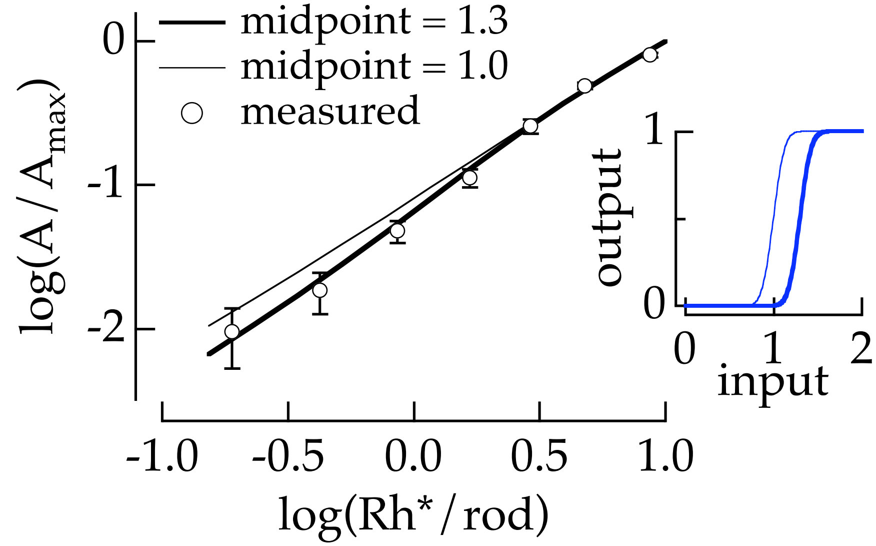


Cajal, 1909

ESTIMATING PROPERTIES OF ROD-ROD BIPOLAR SIGNAL TRANSFER



Nonlinear dependence on flash strength



Discreteness of response