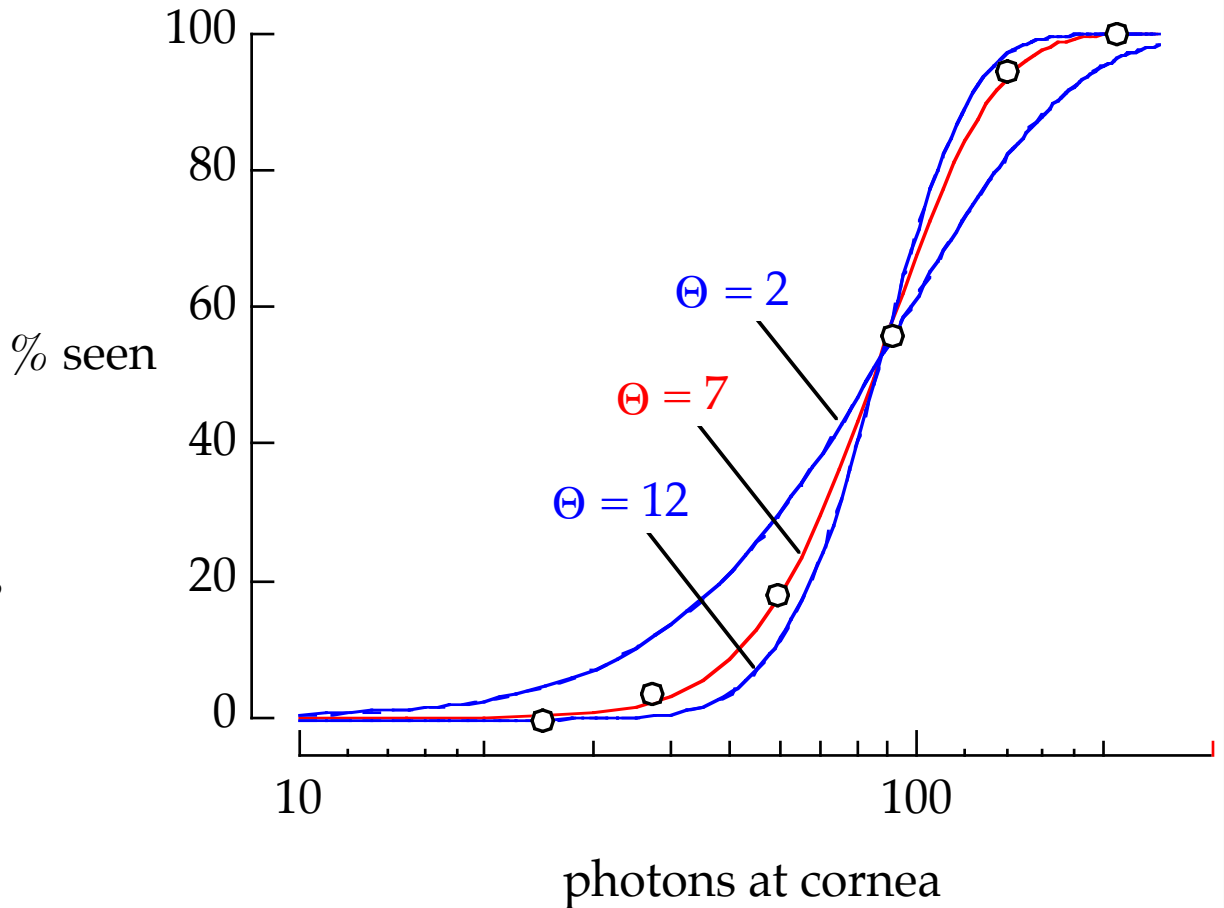
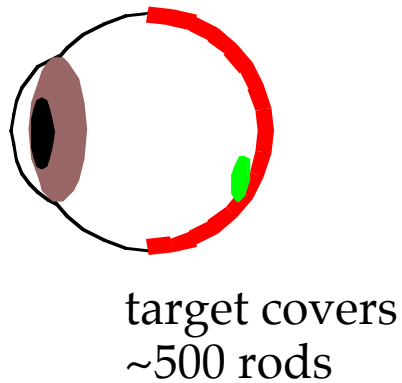
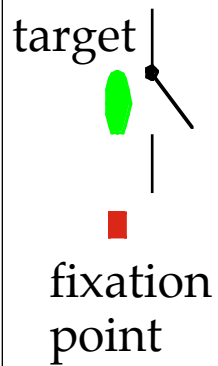


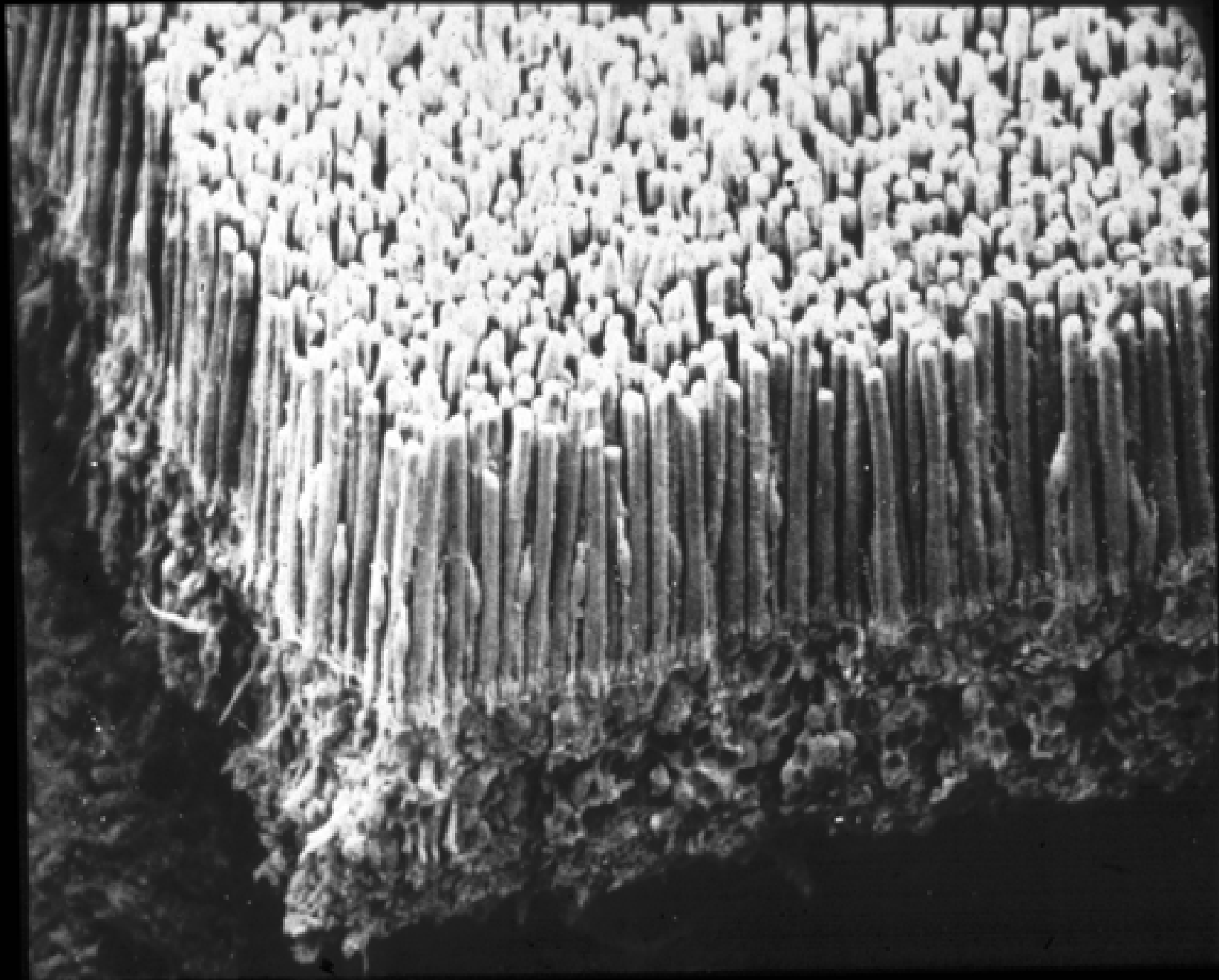
# FREQUENCY OF SEEING EXPERIMENTS (Hecht, Shlaer and Pirenne, 1942)



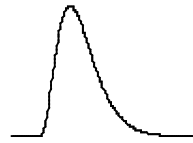
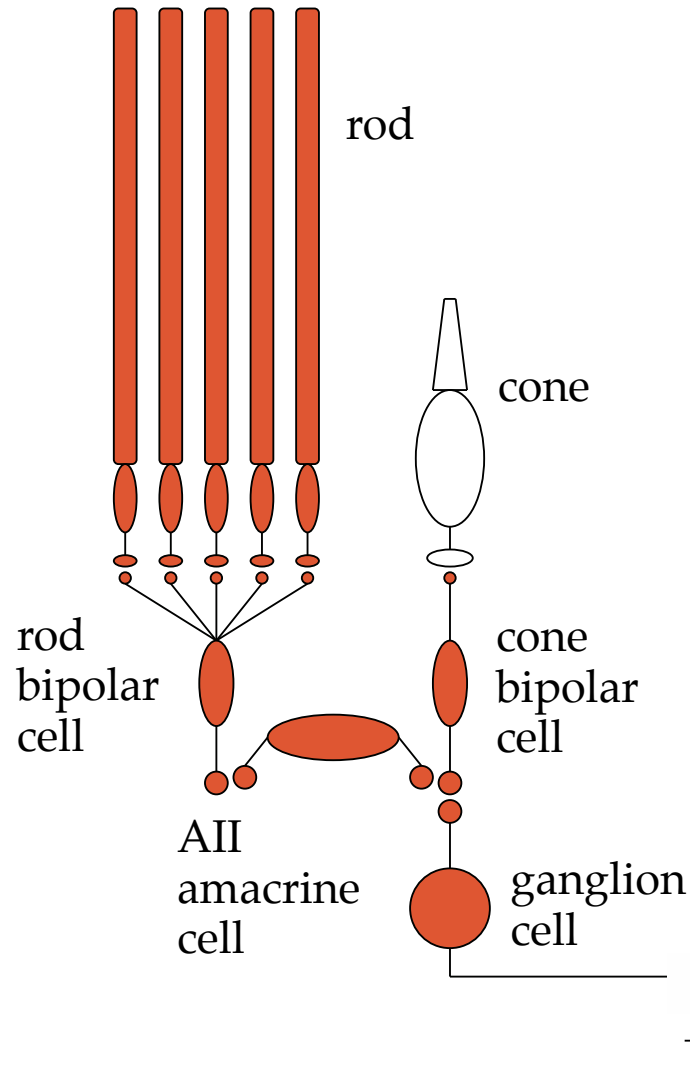
CONCLUSION:  $\Theta = 5-7$  photons absorbed spread over 500 rods

PROBLEM: No way to account for false positives (noise)

Signal and noise distributions  
and false positives (on board)



## IMPLICATIONS OF BEHAVIORAL SENSITIVITY



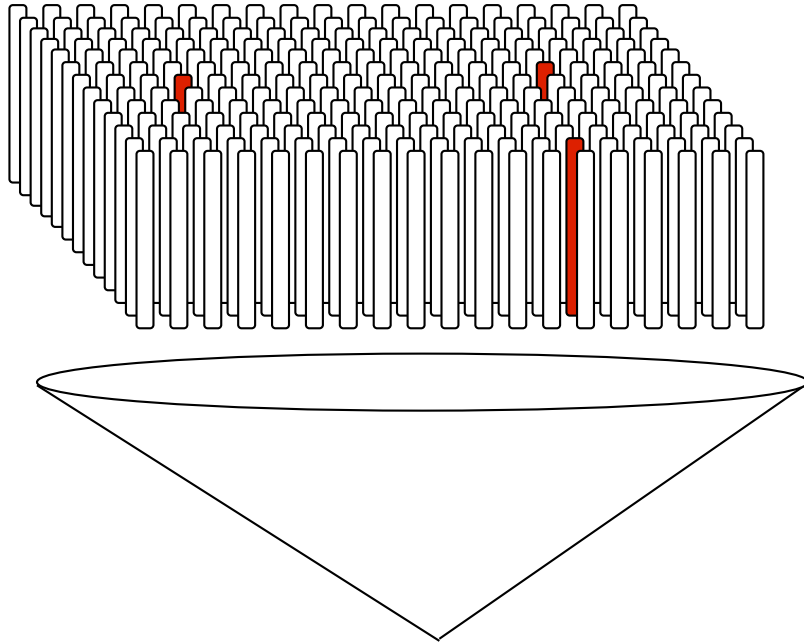
- **phototransduction**
  - single photons reliably transduced

- **synaptic transmission**
  - reliable transmission of single photon responses

- **neural coding**
  - absorption of a single photon alters optic nerve activity

But the task of the retina is in fact more challenging ...

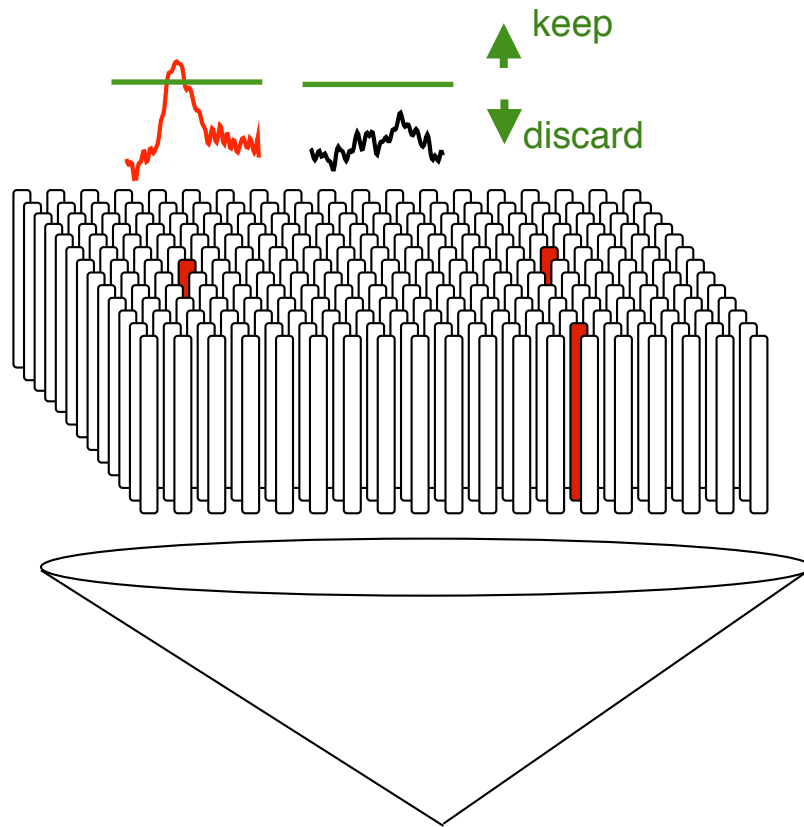
## CONVERGENCE AND SPARSE SIGNALING IN MAMMALIAN RETINA



- At visual threshold photons  $< 0.1\%$  of the rods contribute signals while all rods generate noise
- Under these conditions averaging is a disaster - instead requires separation of signal from noise
- General problem in nervous system

What is optimal readout of array of detectors when small fraction active?

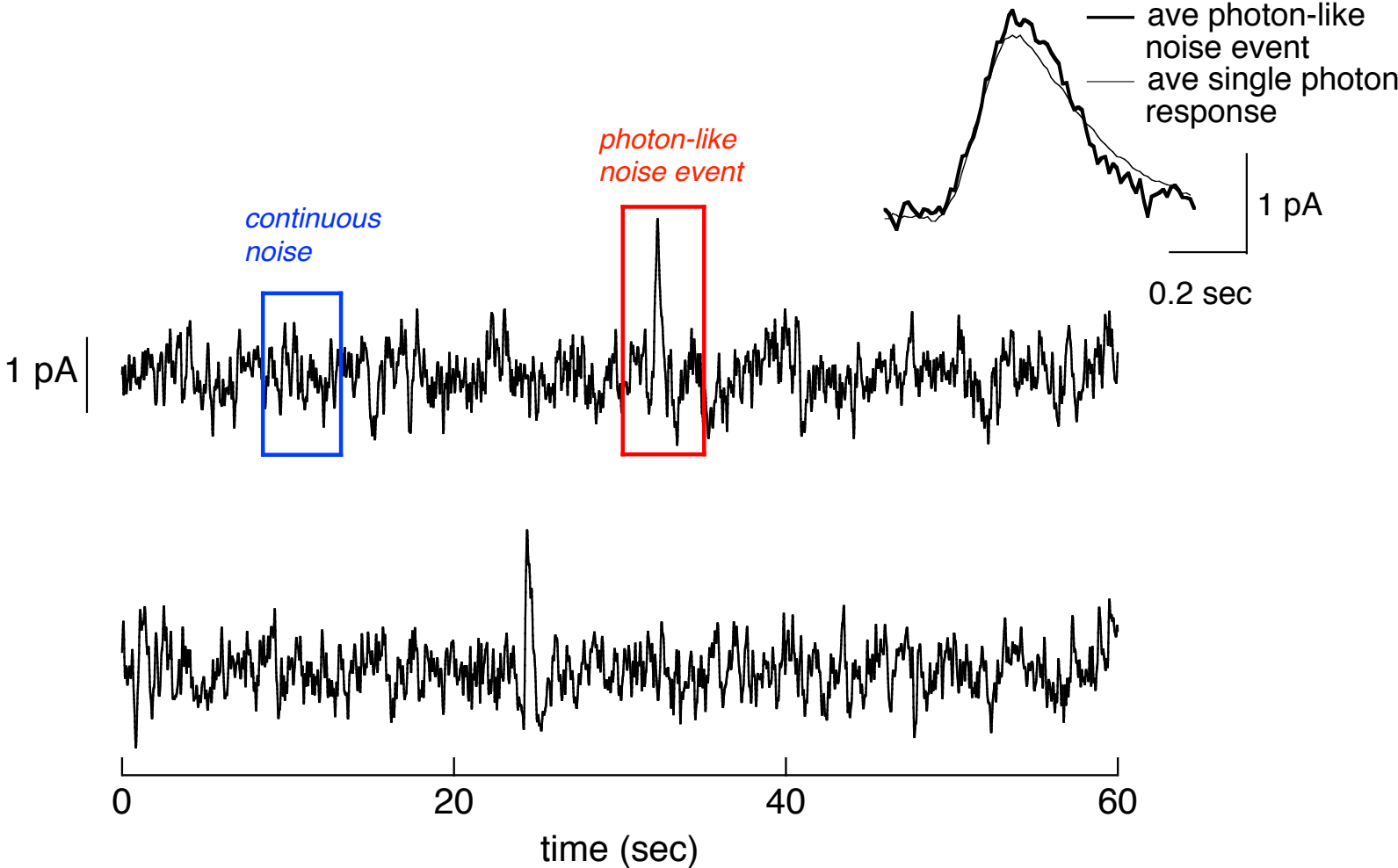
## CONVERGENCE AND SPARSE SIGNALING IN MAMMALIAN RETINA



- At visual threshold photons  $< 0.1\%$  of the rods contribute signals while all rods generate noise
- Under these conditions averaging is a disaster - instead requires separation of signal from noise
- General problem in nervous system
- Sizeable behavioral consequences for getting this right!

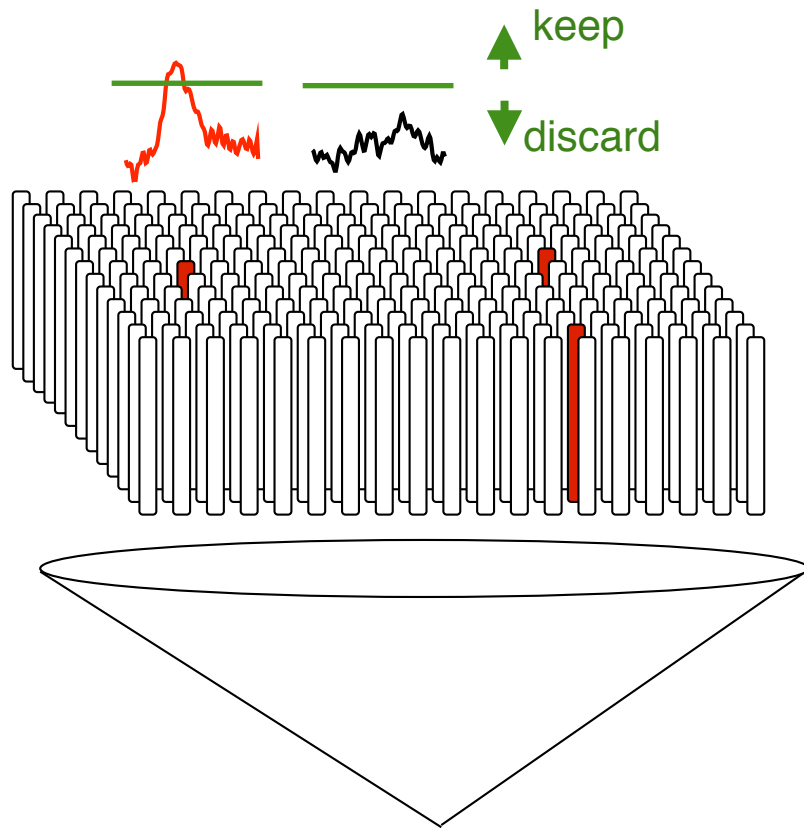
*Baylor et al., 1984*  
*van Rossum and Smith, 1998*  
*Field and Rieke, 2002*

# RODS GENERATE PHOTON-LIKE NOISE EVENTS AND CONTINUOUS NOISE



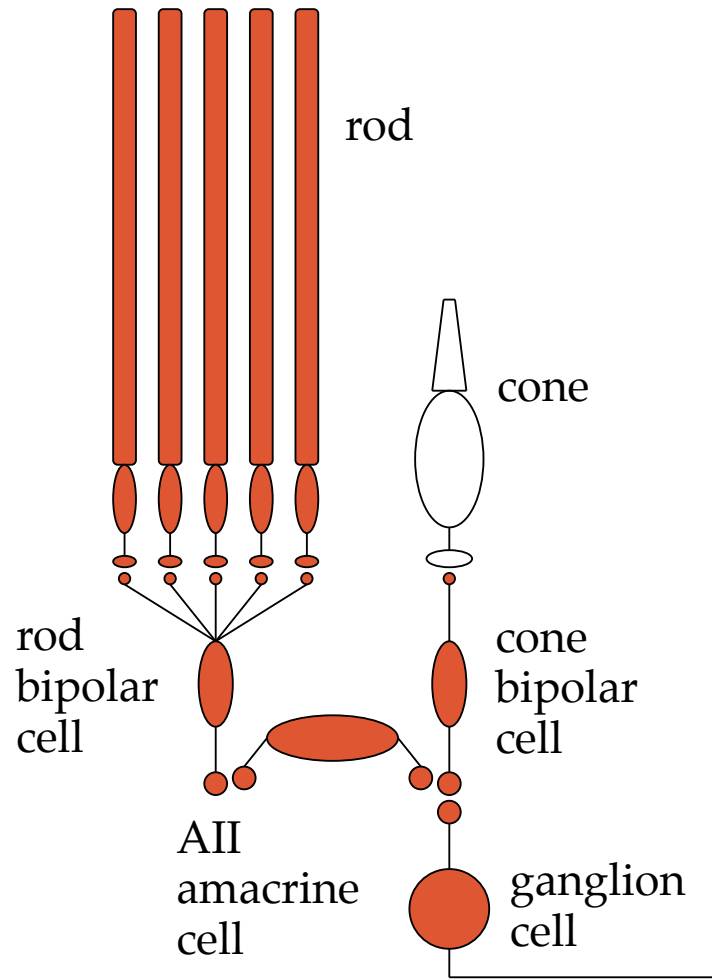
Baylor et al., 1984  
Greg Field



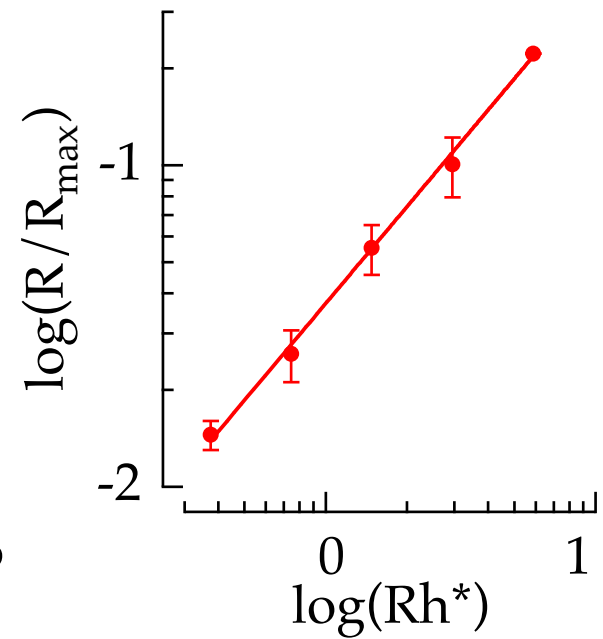
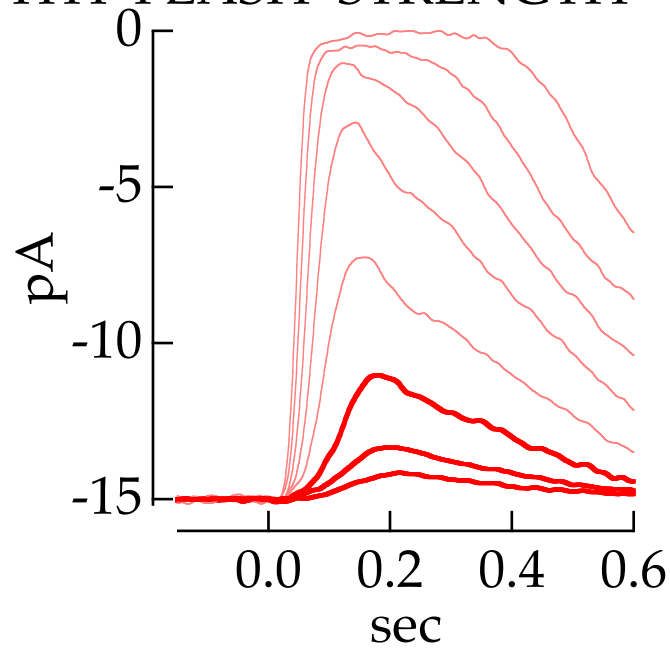
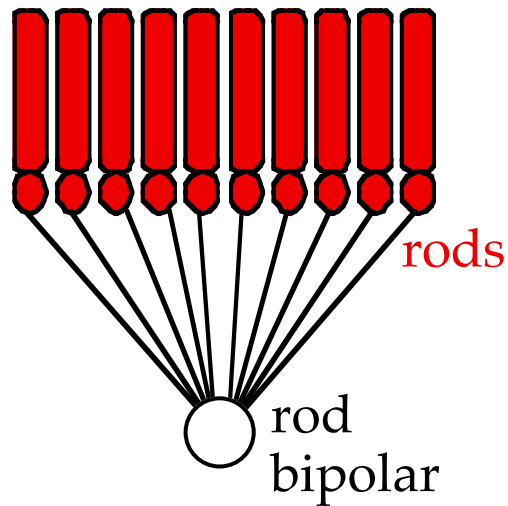


- Mouse rod-rod bipolar signal transfer is nonlinear.
  - dependence of response on flash strength
  - discreteness of dim flash response
- Nonlinear signal transfer eliminates or severely attenuates majority of rod's single photon responses.
- Rejection of noise more than compensates loss of signal - thus rod bipolars provide near-optimal readout of rod signals near visual threshold.

# THE ROD BIPOLAR PATHWAY

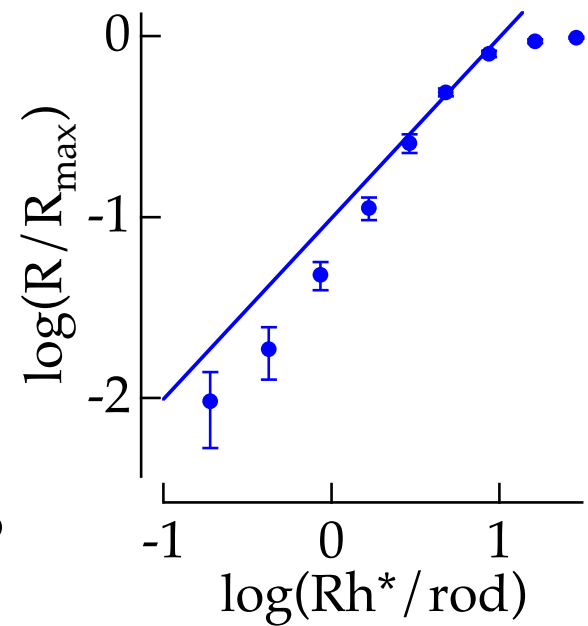
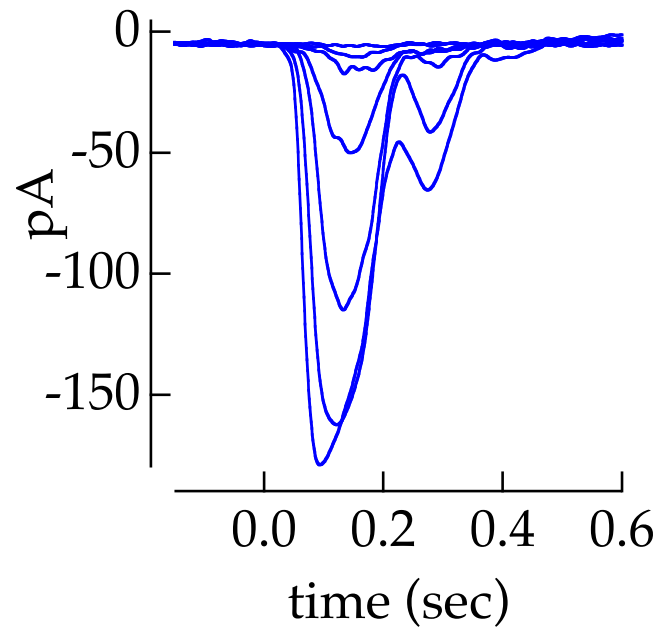
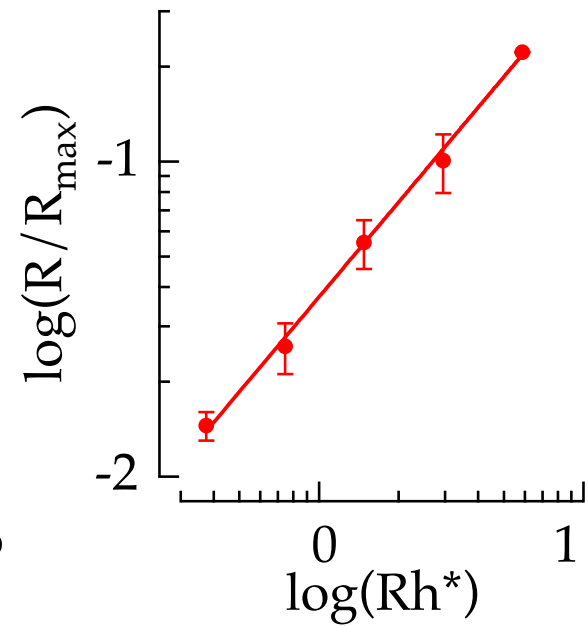
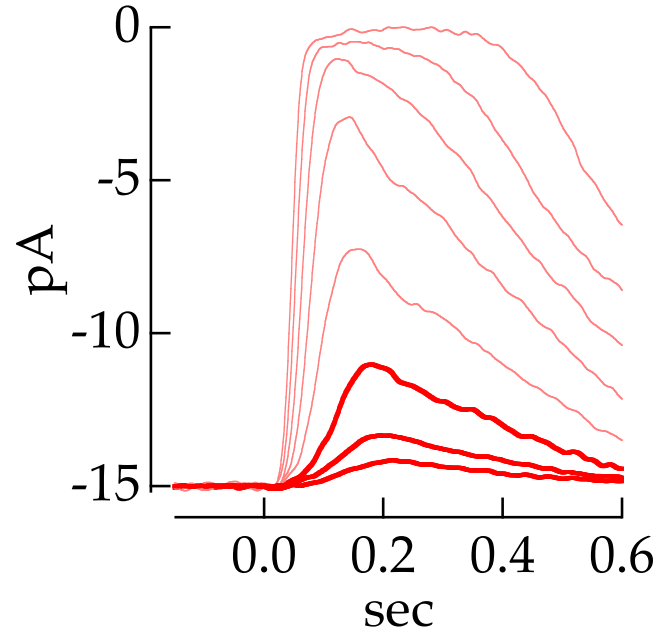
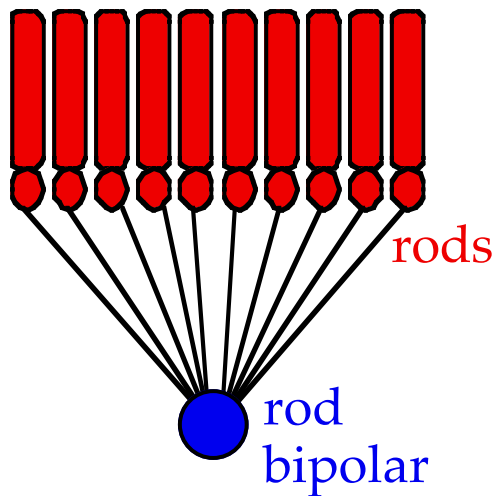


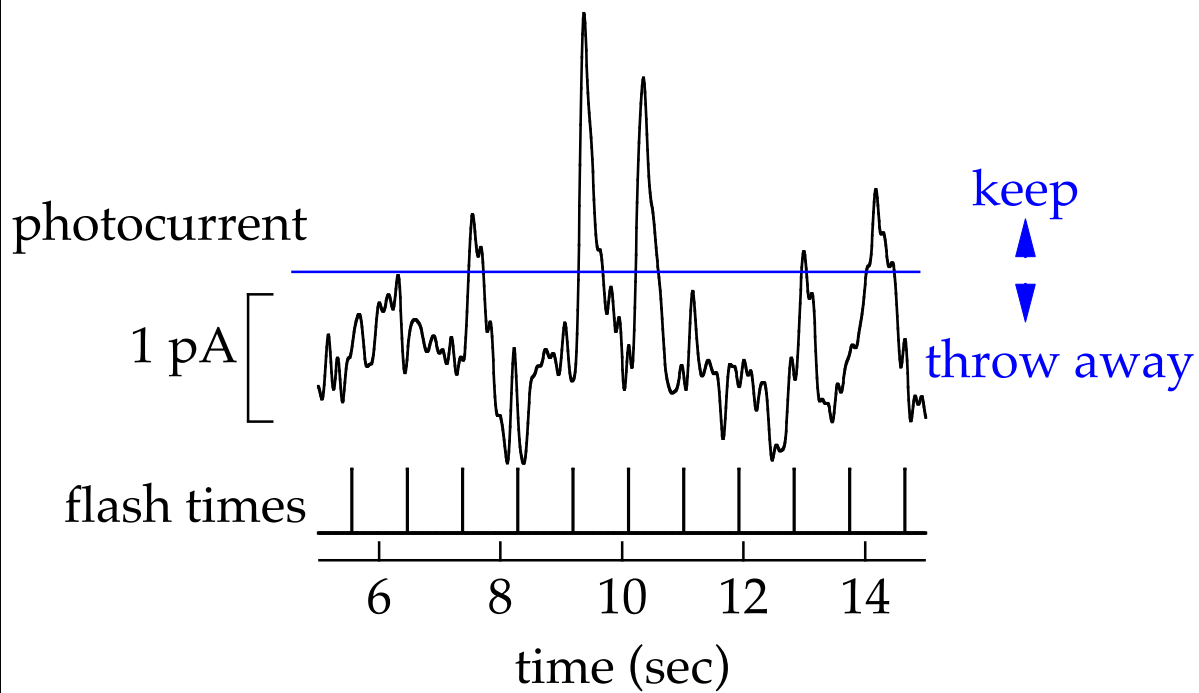
# DIM FLASH RESPONSES OF RODS GROW LINEARLY WITH FLASH STRENGTH



why log-log?

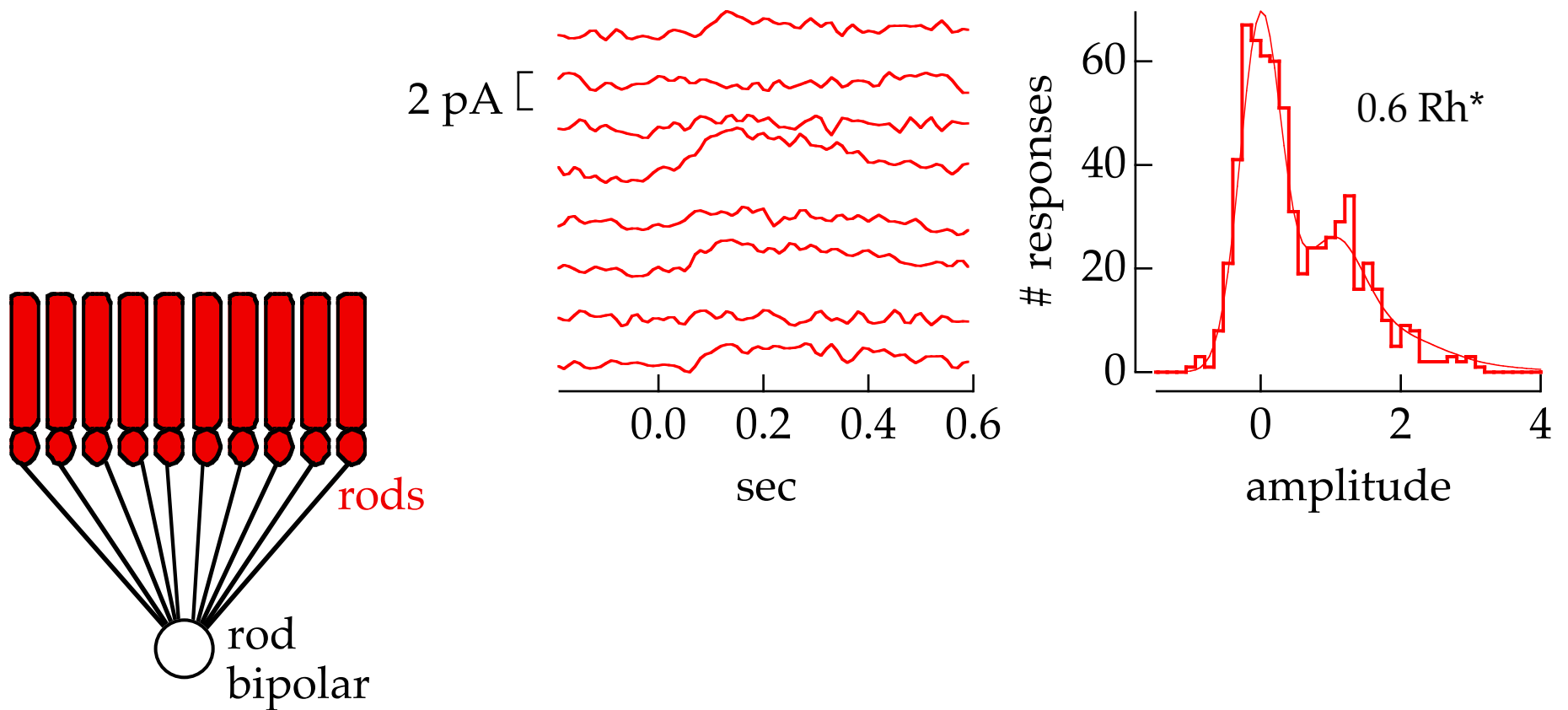
# RESPONSES OF ROD BIPOLARS BUT NOT RODS GROW SUPRALINEARLY WITH FLASH STRENGTH



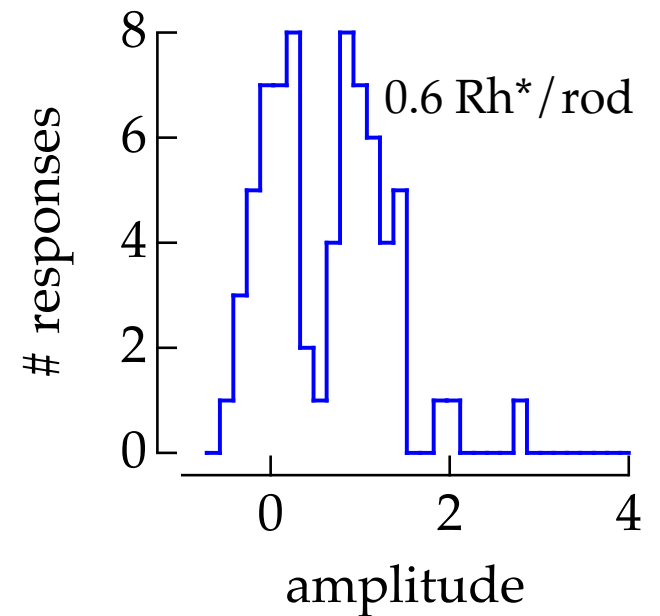
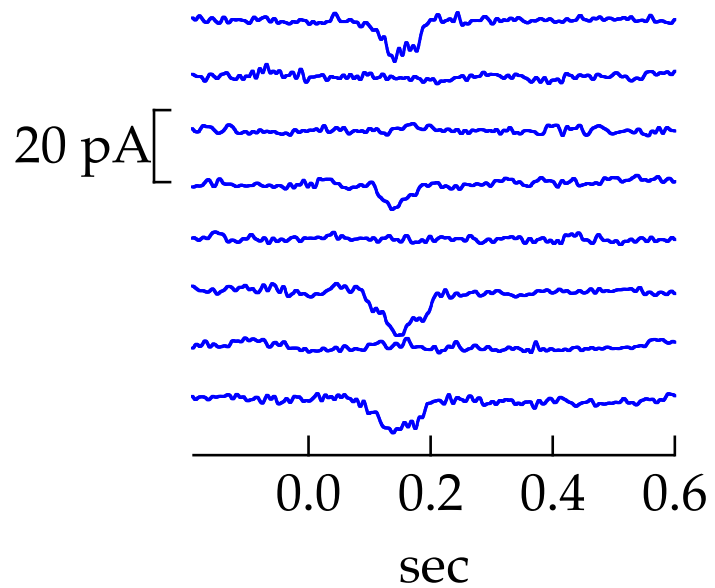
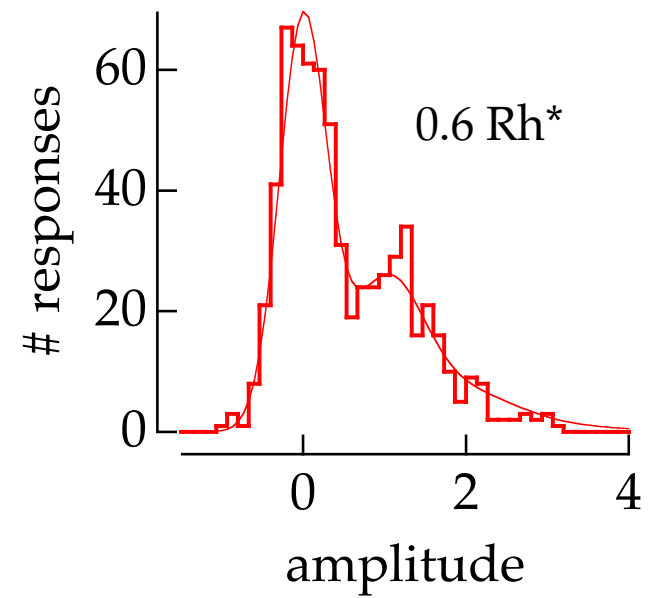
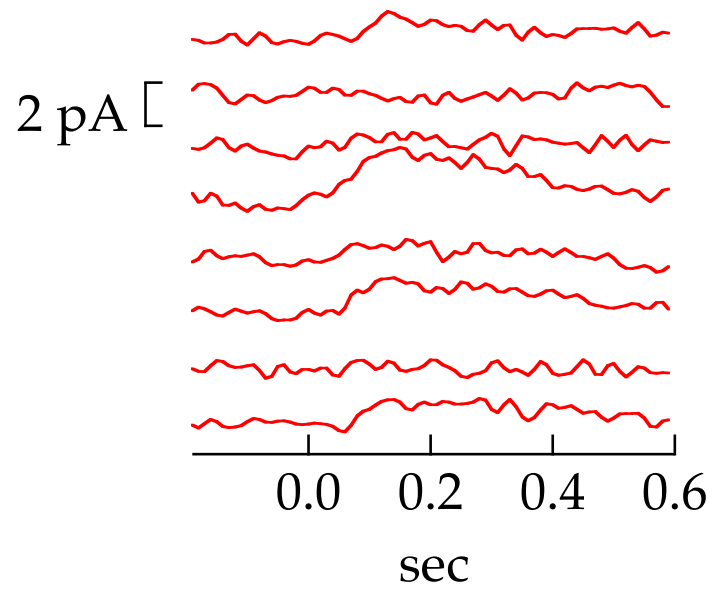
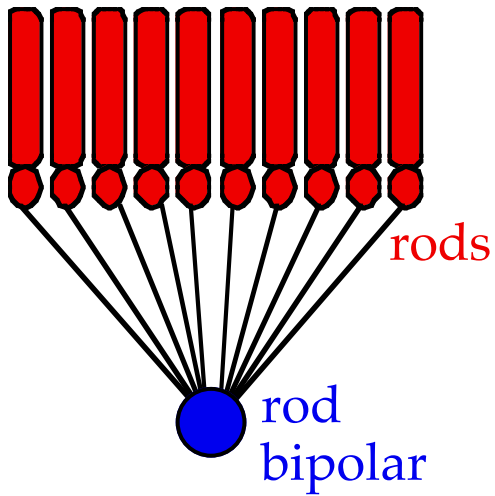


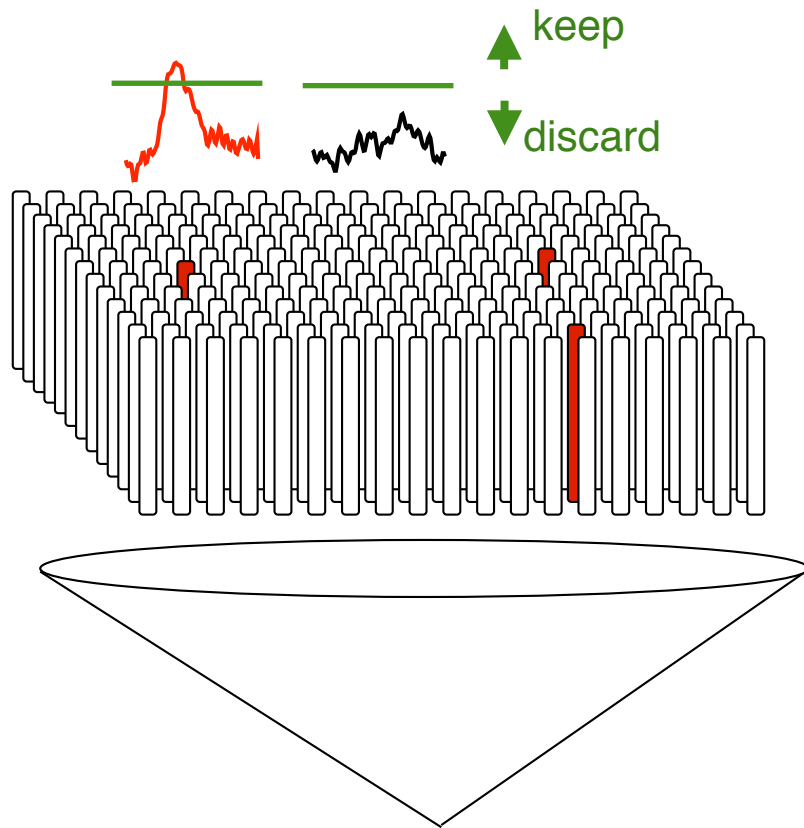
Does rod-rod bipolar  
signal transfer separate  
rod signal and noise?

# MOUSE ROD SINGLE PHOTON RESPONSES ARE PARTIALLY OBSCURED BY NOISE



# ROD BIPOLARS GENERATE DISCRETE RESPONSES TO DIM FLASHES

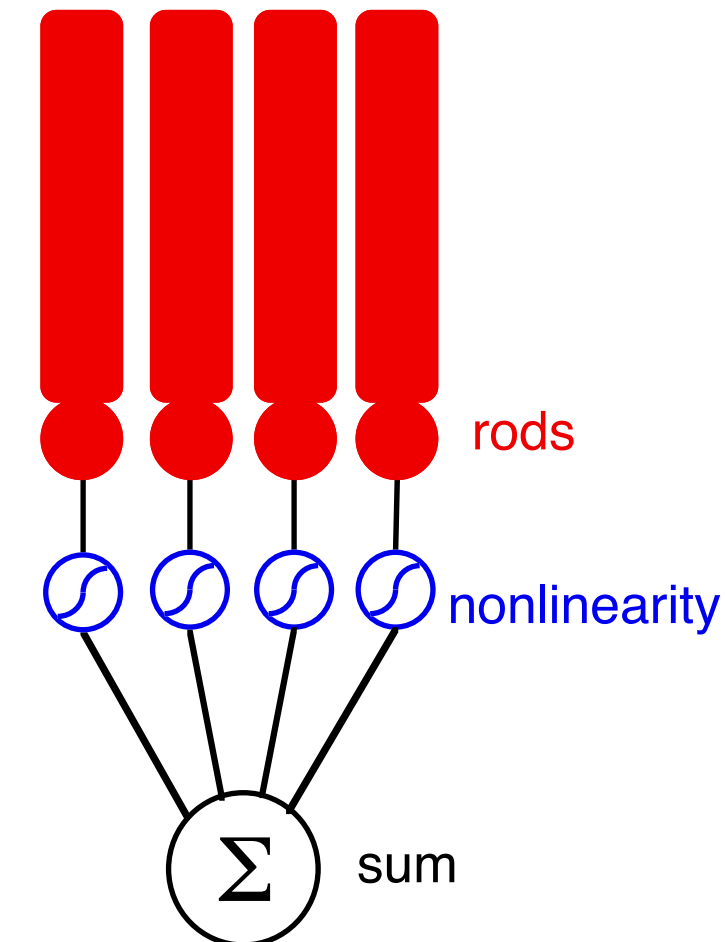




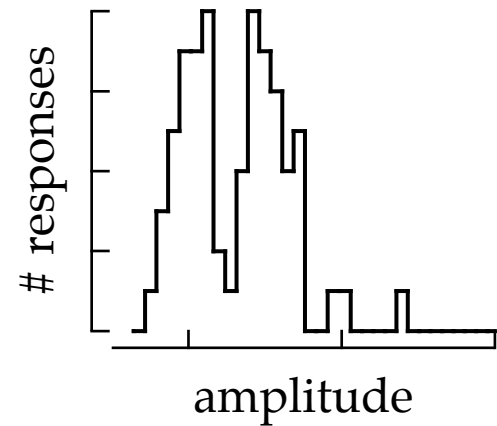
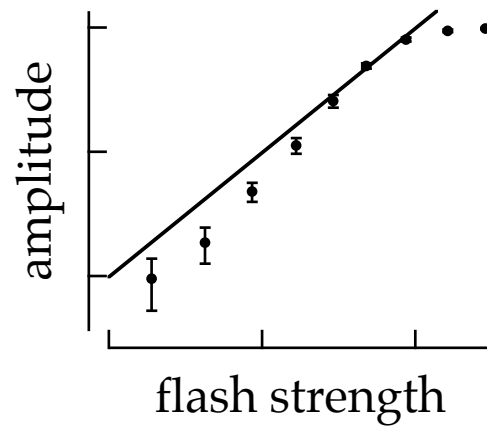
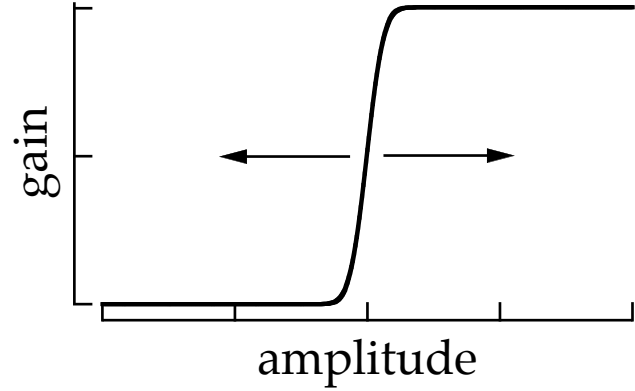
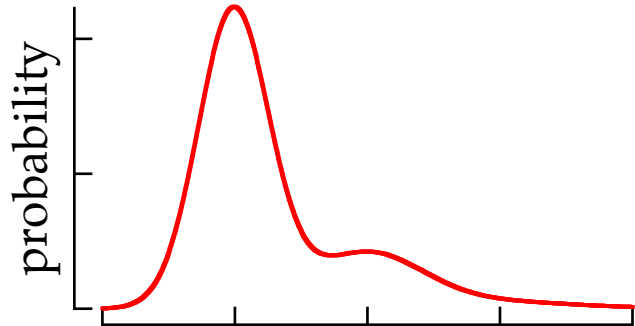
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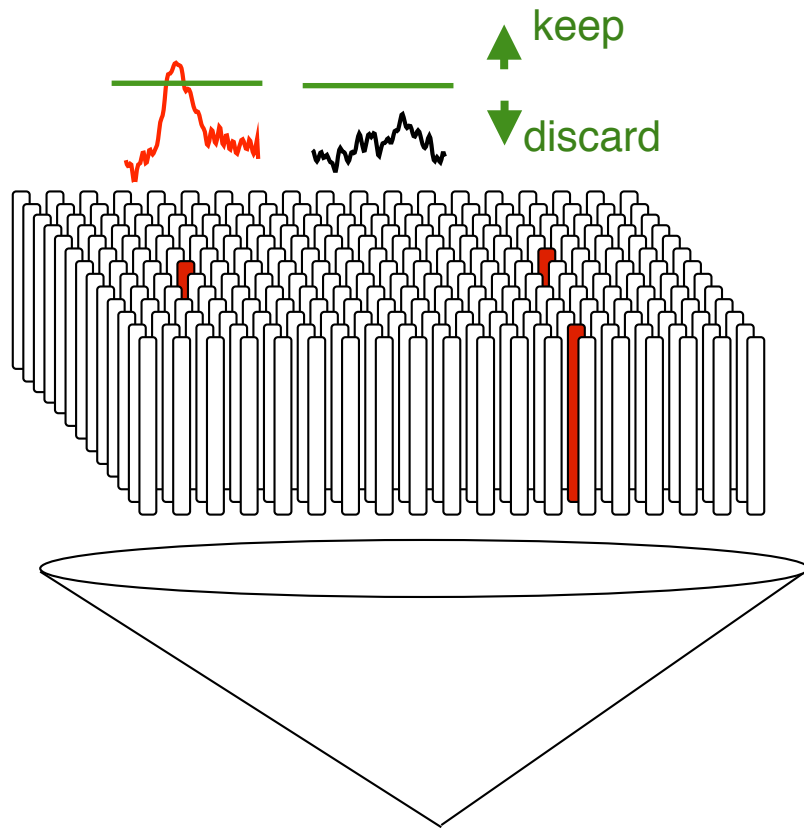
# MODEL FOR ROD-ROD BIPOLAR SIGNAL TRANSFER



predict nonlinearity  
and discreteness of  
rod bipolar response



Signal and noise distributions  
and discrimination (on board)



- 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.

# DISTRIBUTION OF ROD RESPONSES AT VISUAL THRESHOLD

Rod experiments ( $\sim 1 \text{ Rh}^*$ )

Visual threshold ( $0.0001 \text{ Rh}^*$ )

