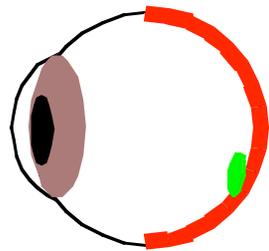
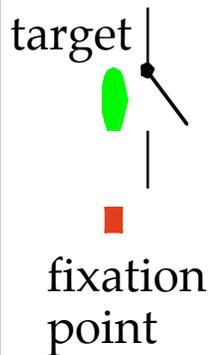
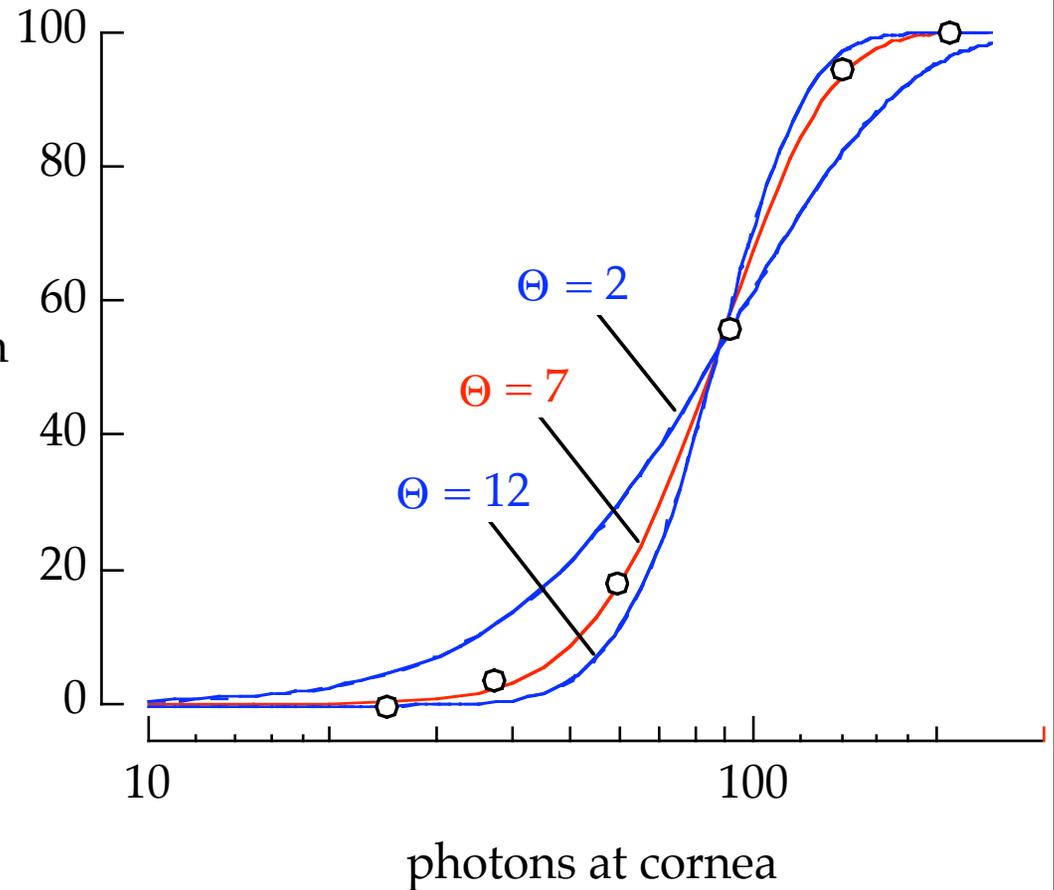


FREQUENCY OF SEEING EXPERIMENTS (Hecht, Schlaer and Pirenne, 1942)



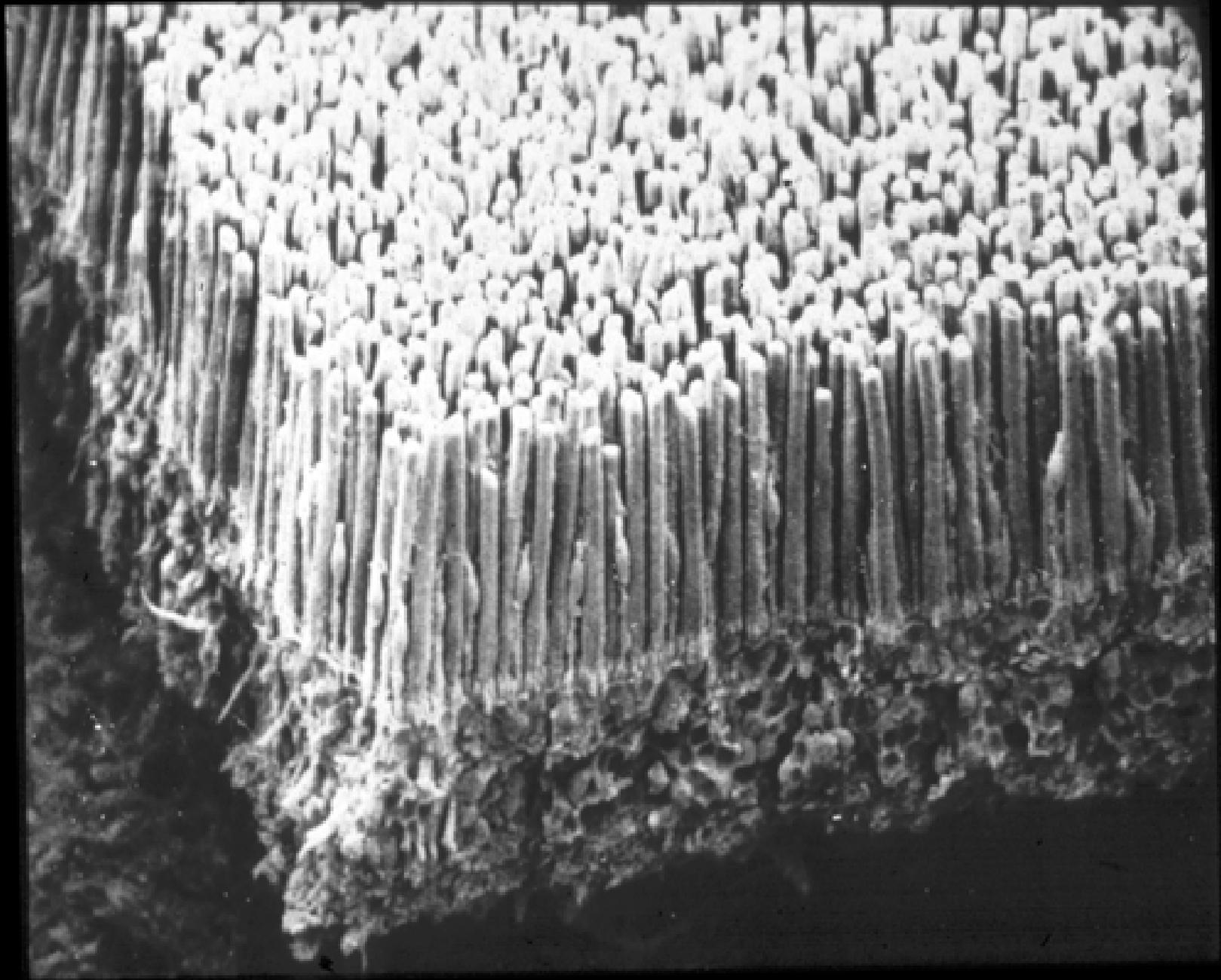
target covers
~500 rods

% seen

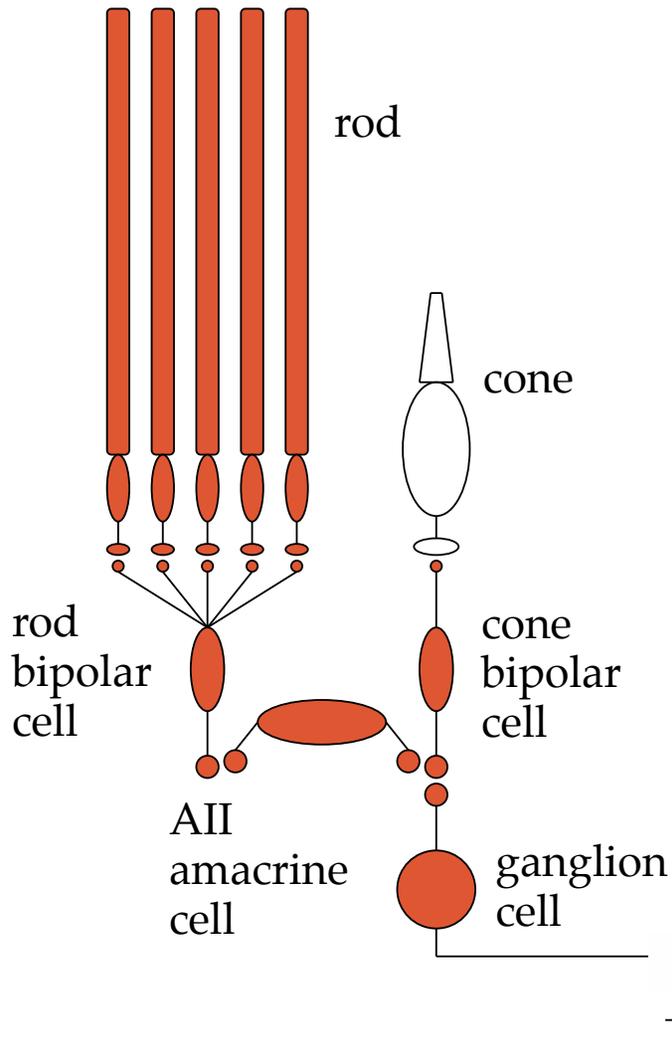


CONCLUSION: $\Theta = 5-7$ photons absorbed spread over 500 rods

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



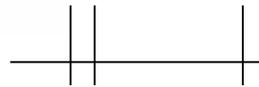
IMPLICATIONS OF BEHAVIORAL SENSITIVITY



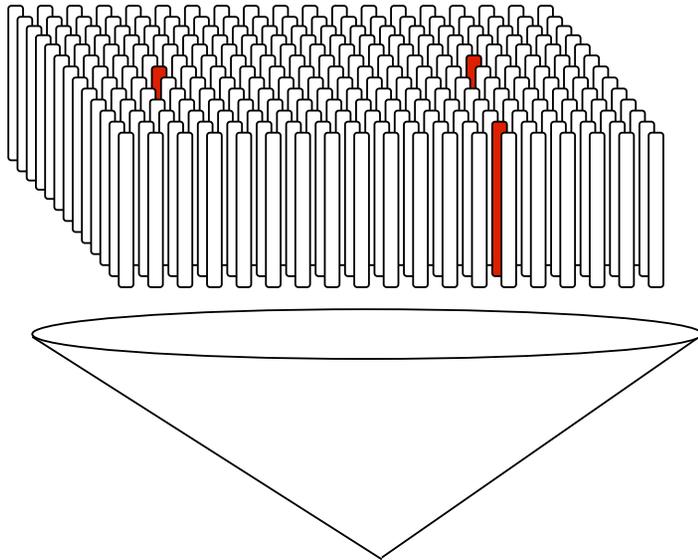
- **phototransduction**
 - single photons reliably transduced

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

- **neural coding**
 - absorption of a few photons produces change in optic nerve activity

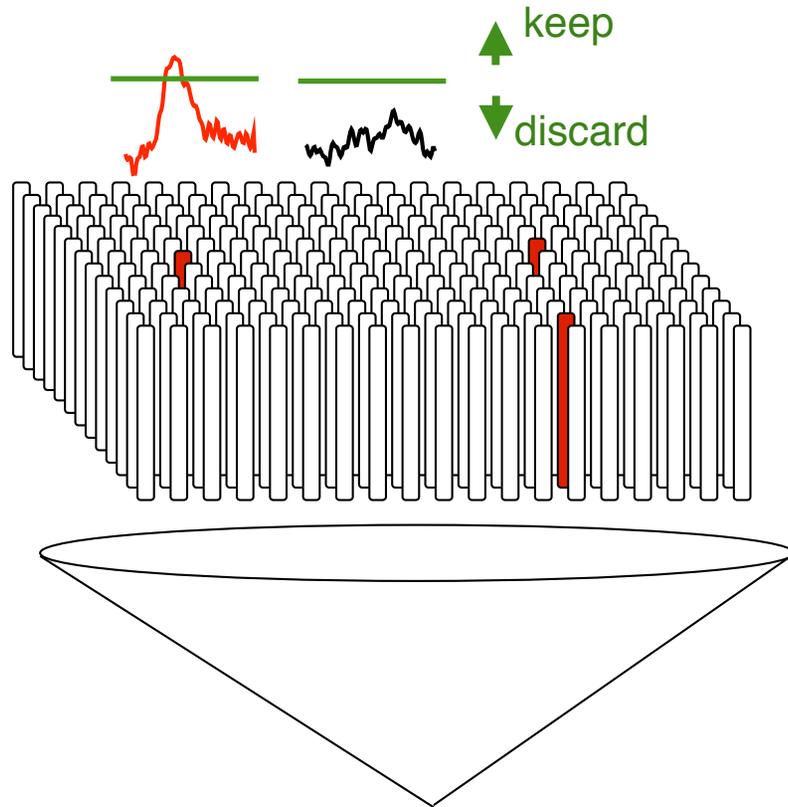


CONVERGENCE AND SPARSE SIGNALING IN MAMMALIAN RETINA



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

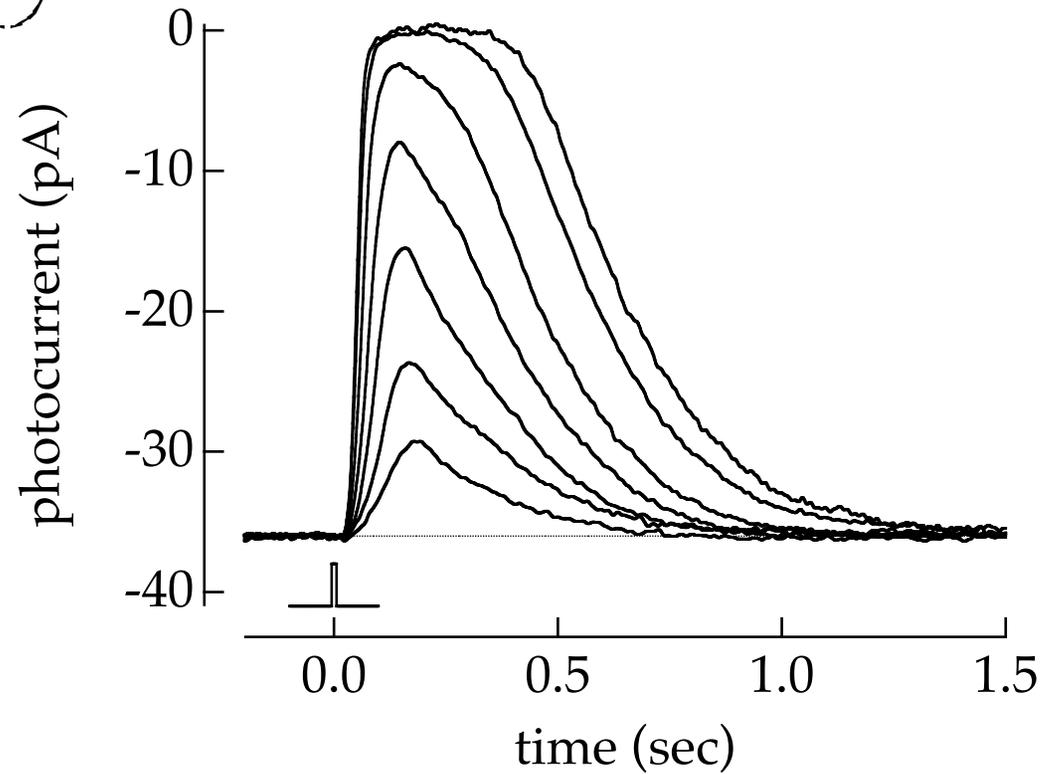
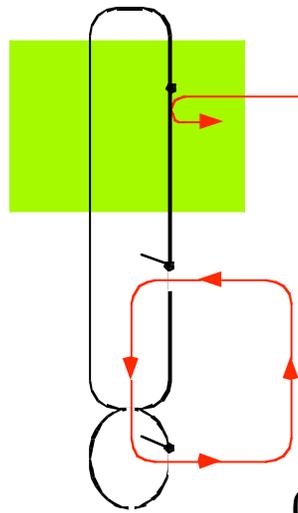
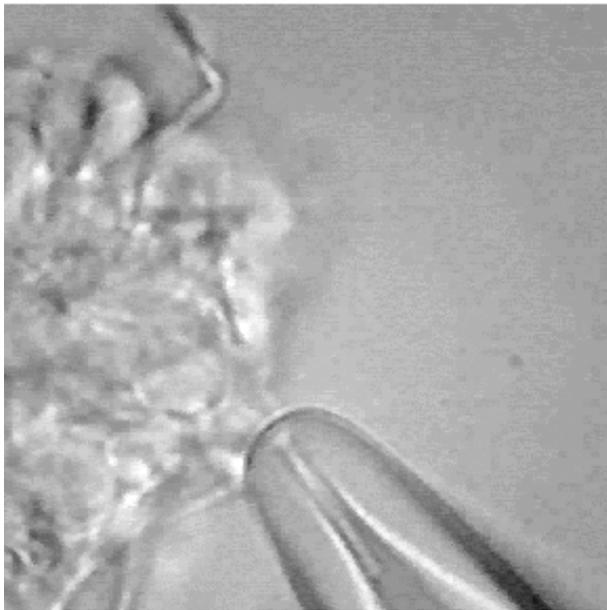
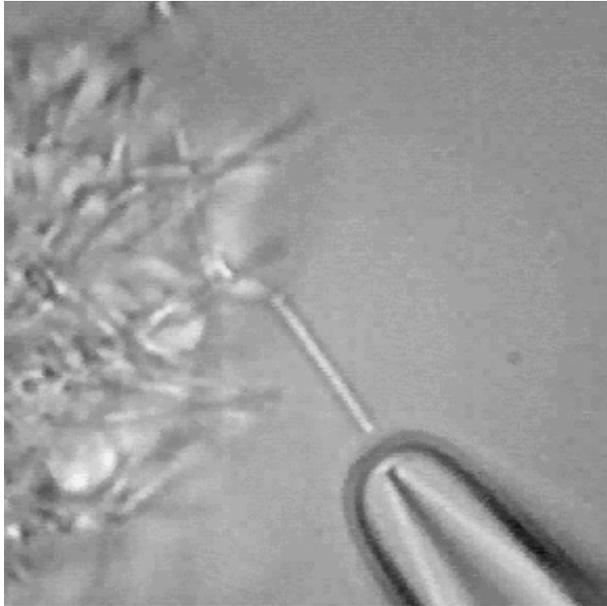
ROD-ROD BIPOLAR SIGNAL TRANSFER AND ABSOLUTE VISUAL SENSITIVITY



- 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.

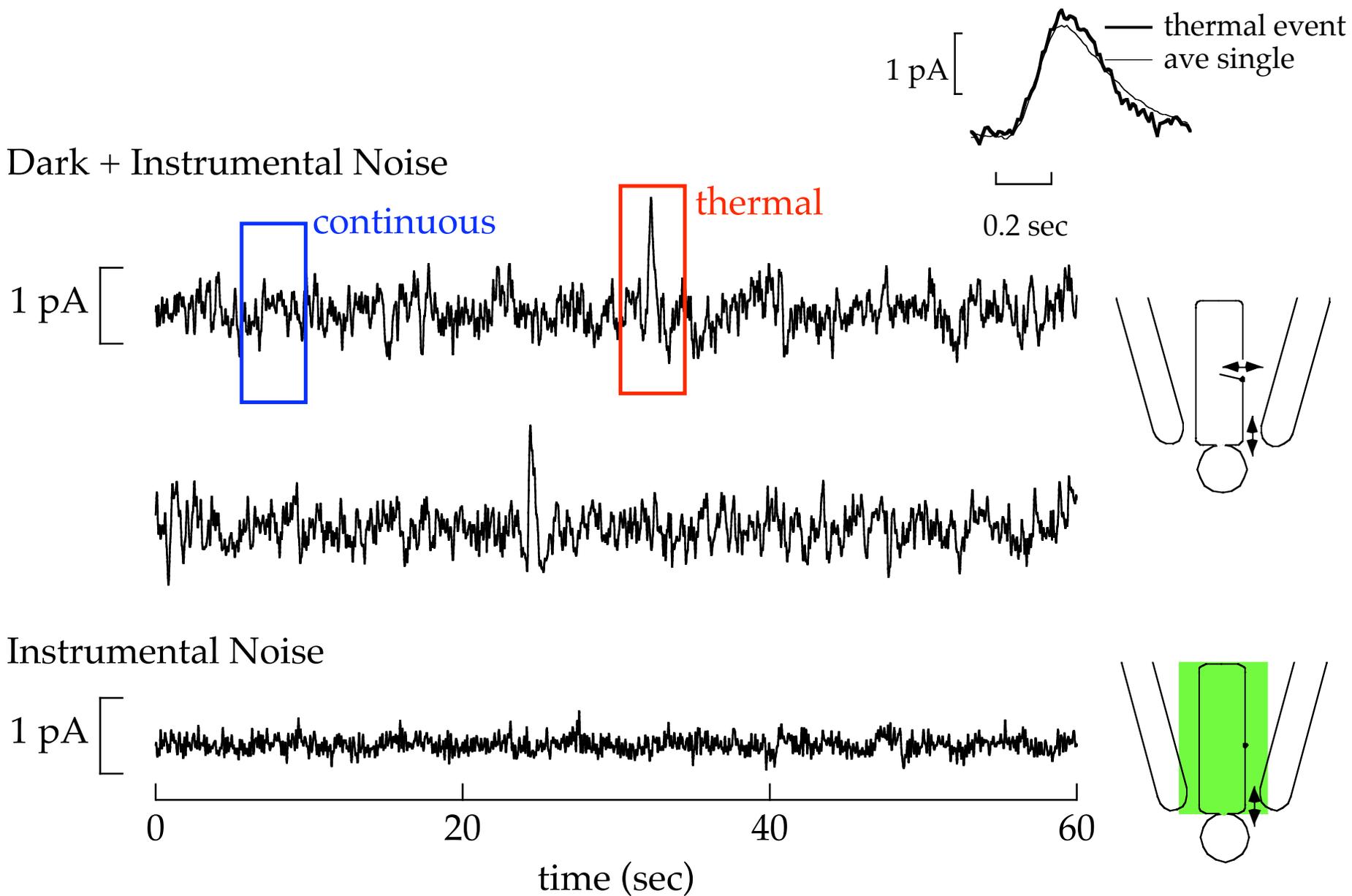
SUCTION ELECTRODE RECORDING

(Baylor et al., 1979)

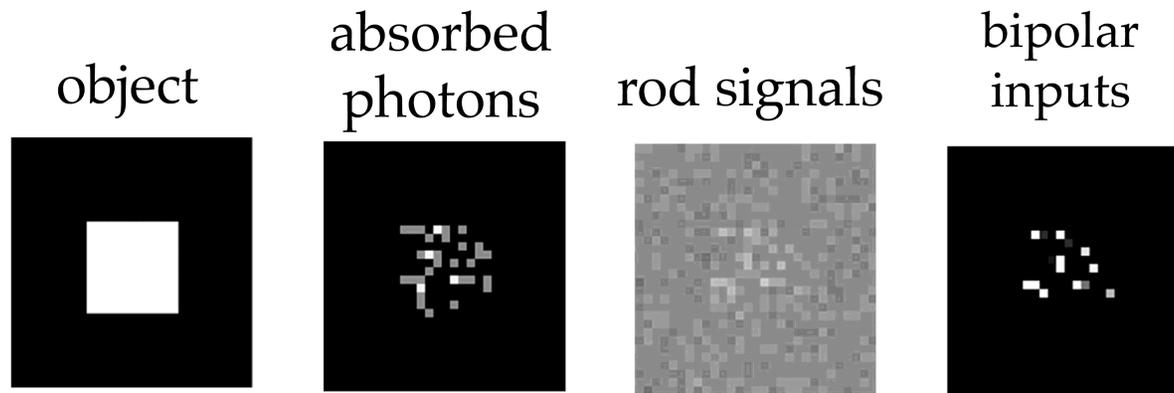
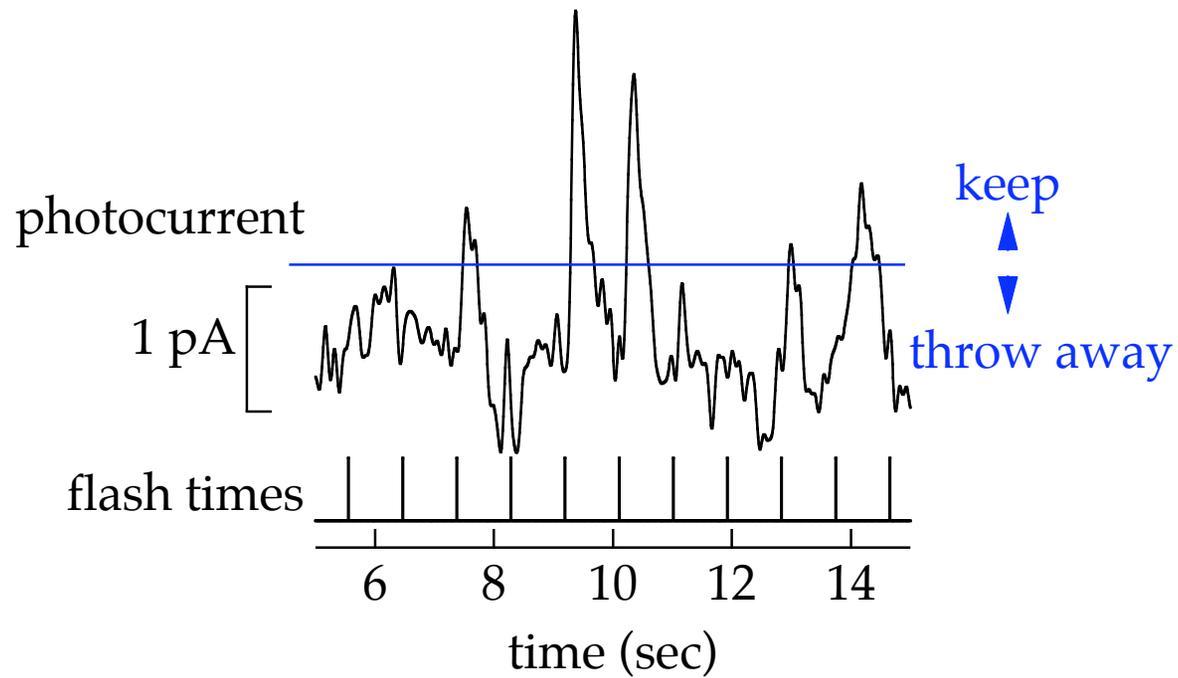


DARK NOISE IN MAMMALIAN RODS

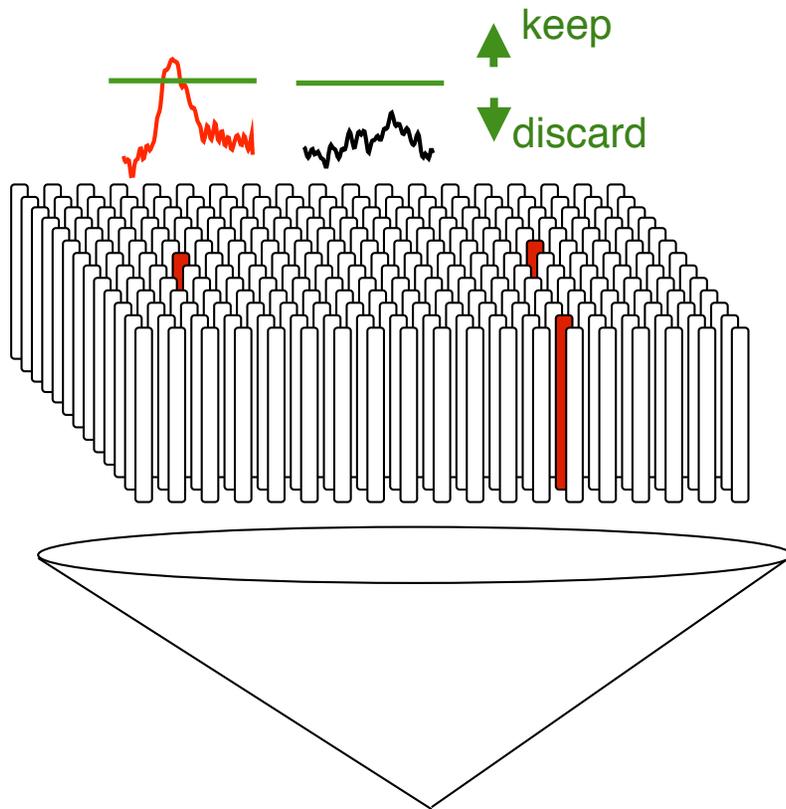
(Baylor et al., 1984)



SEPARATION OF ROD SIGNAL AND NOISE BY THRESHOLDING NONLINEARITY



(modified from Wilson, 2002)



- Mouse rod-rod bipolar signal transfer is nonlinear.

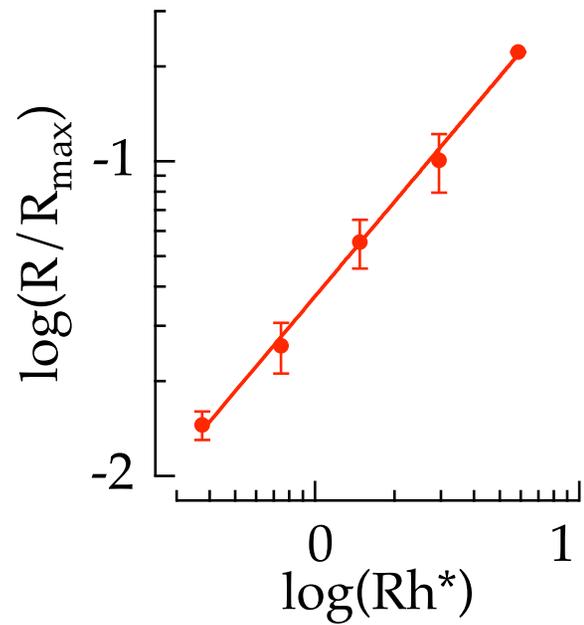
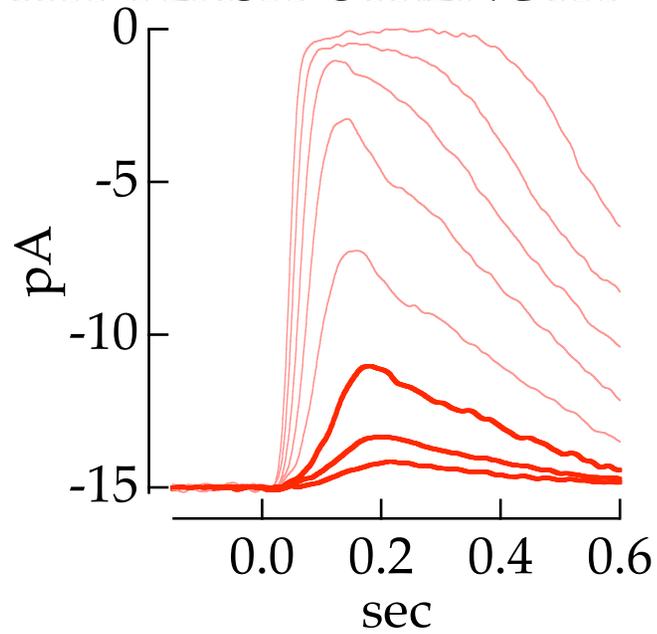
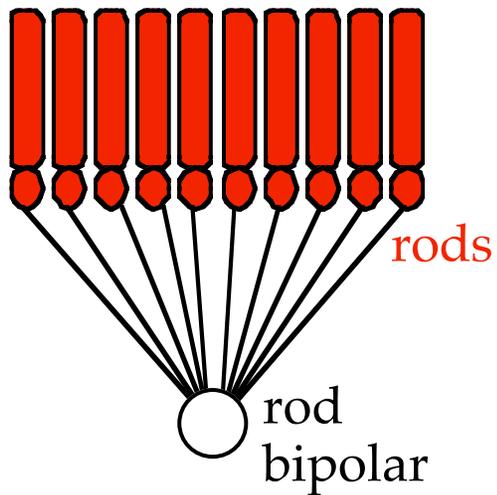
- dependence of response on flash strength

- discreteness of dim flash response

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

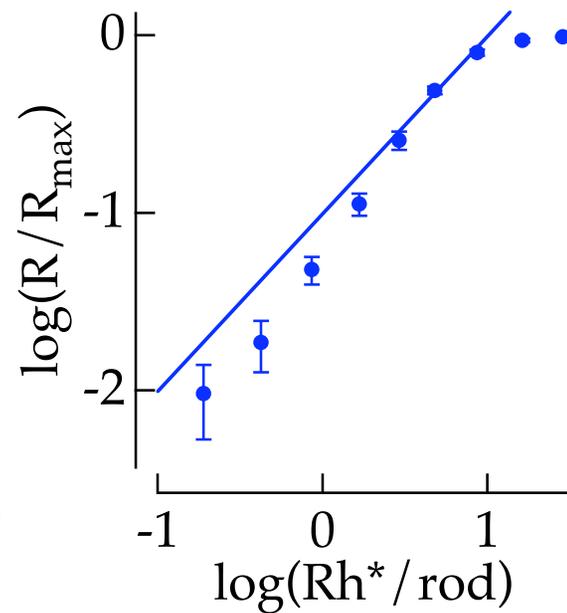
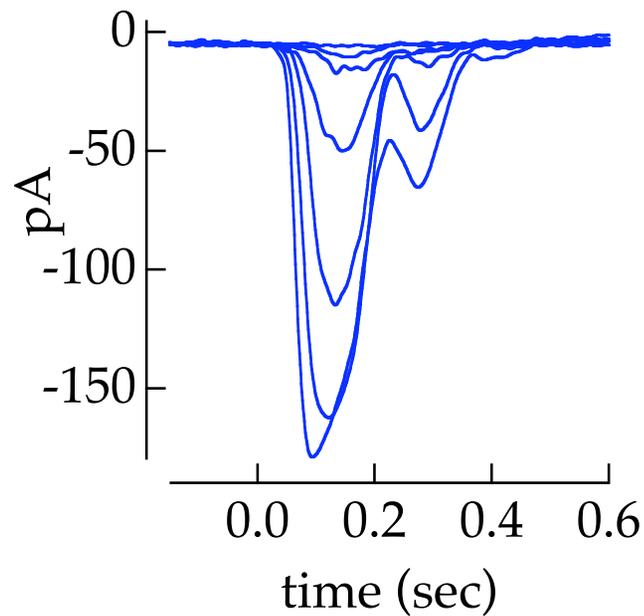
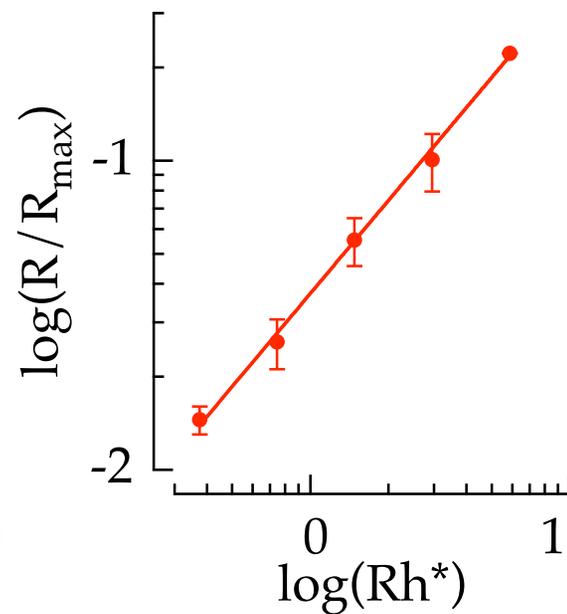
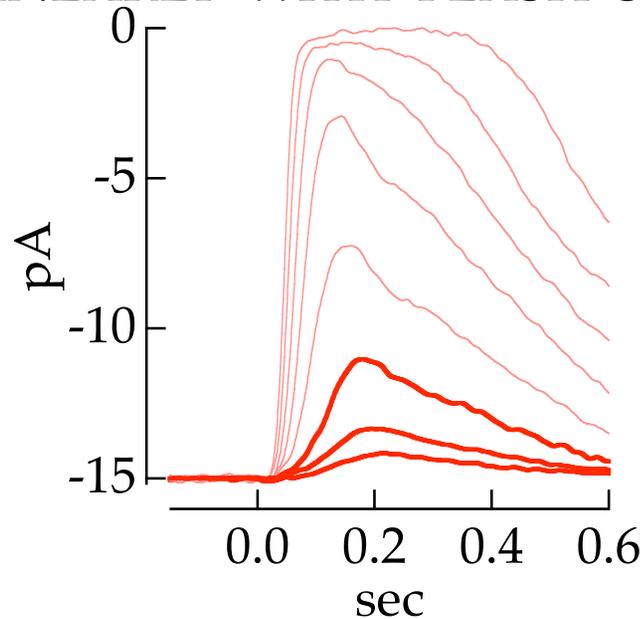
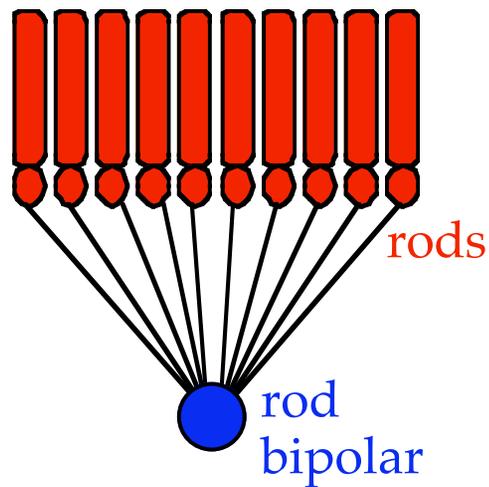
- Rejection of noise more than compensates loss of signal - thus rod bipolars provide near-optimal readout of rod signals near visual threshold.

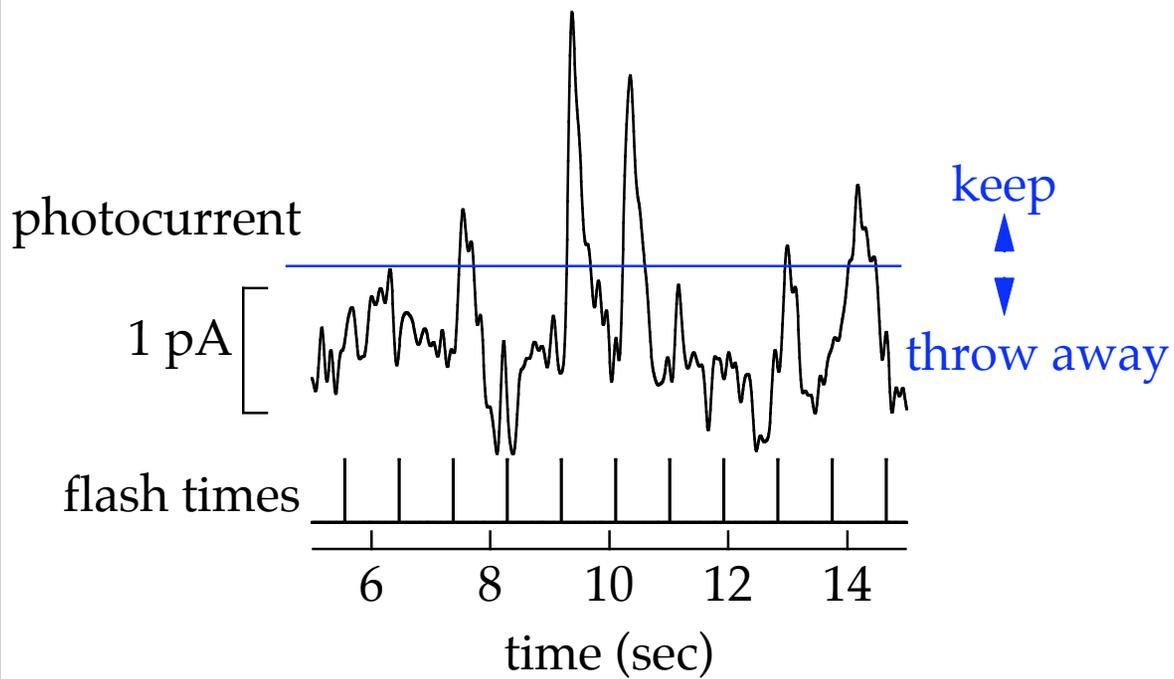
DIM FLASH RESPONSES OF RODS GROW LINEARLY WITH FLASH STRENGTH



why log-log?

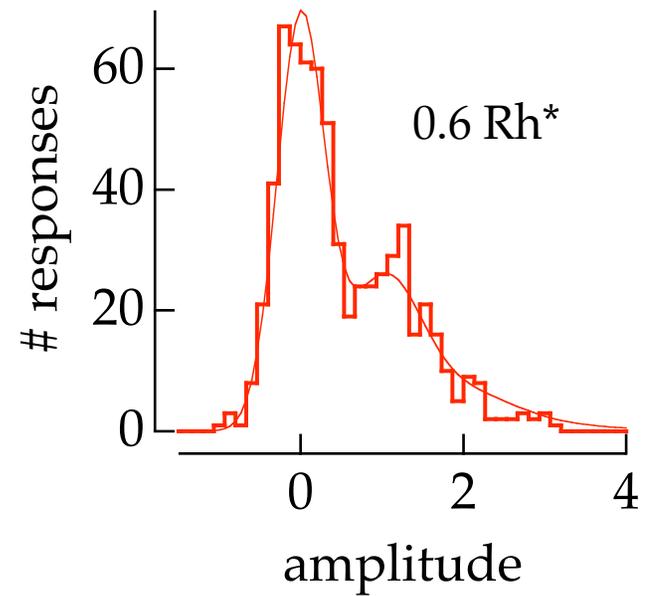
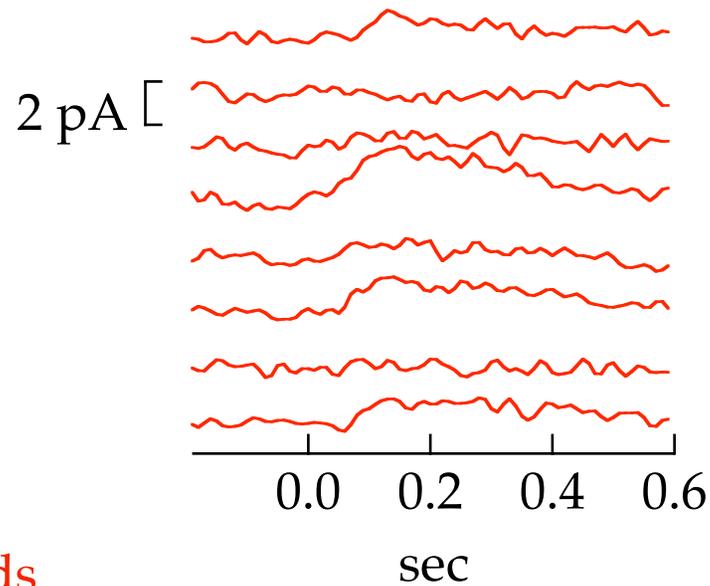
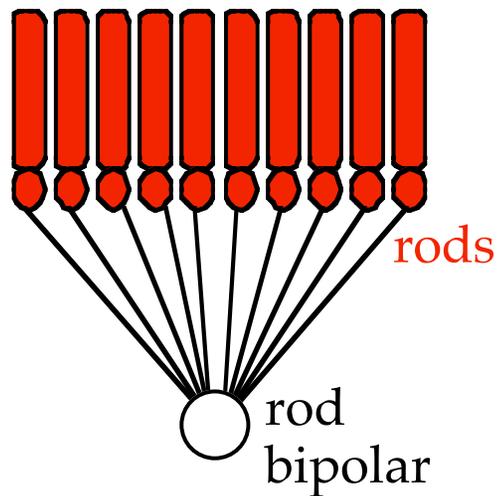
RESPONSES OF ROD BIPOLARS BUT NOT RODS GROW SUPRALINEARLY WITH FLASH STRENGTH



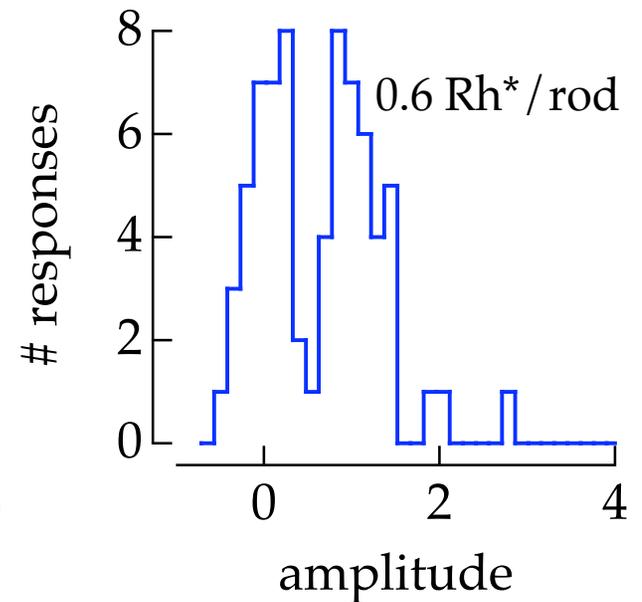
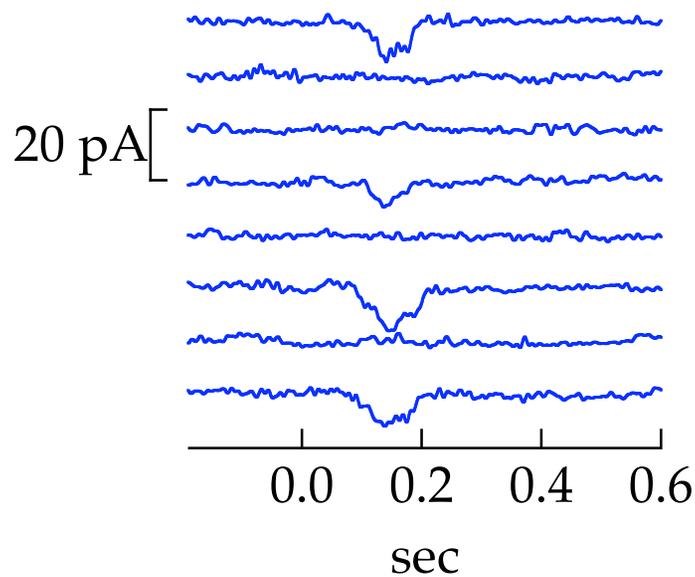
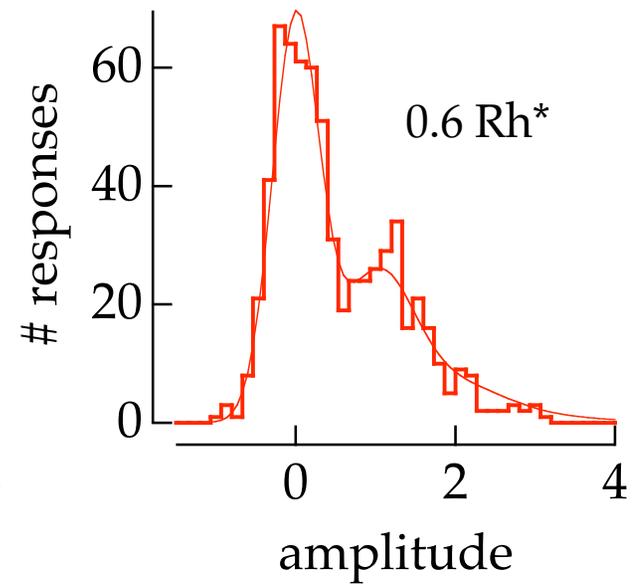
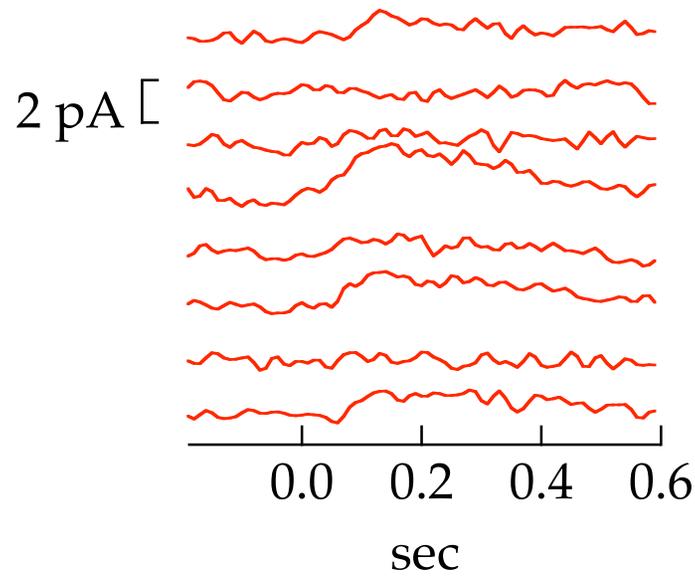
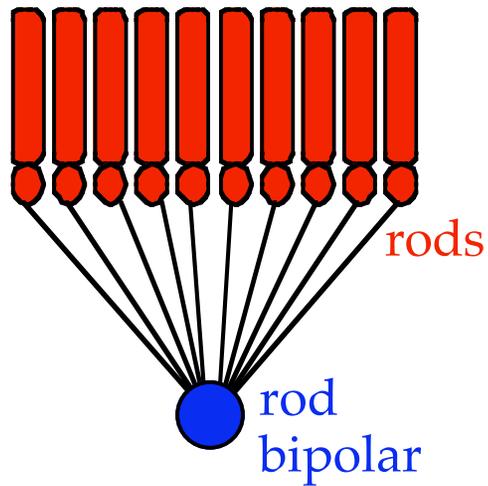


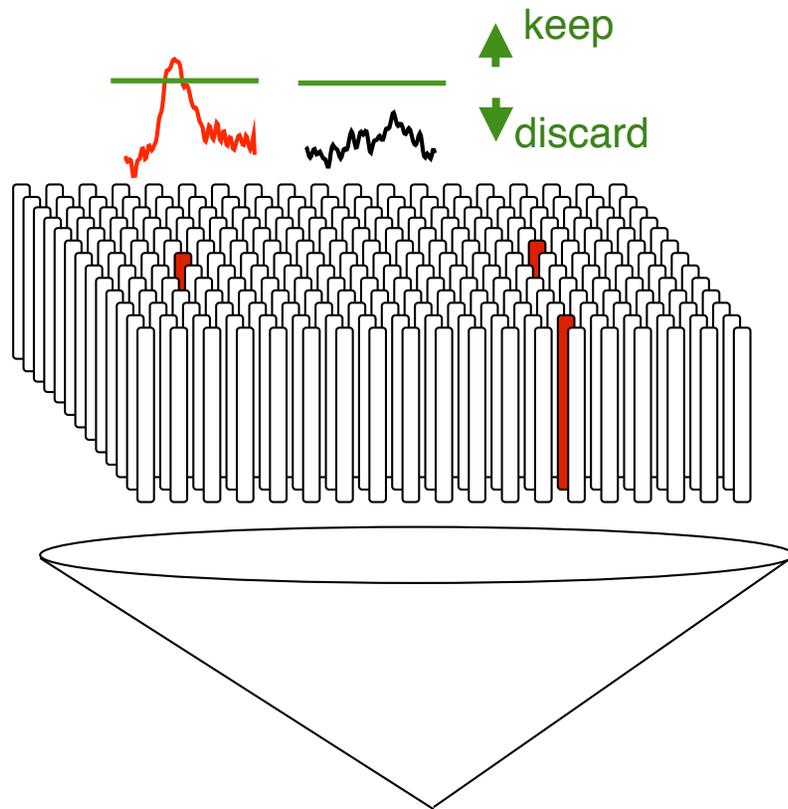
Does rod-rod bipolar
signal transfer separate
rod signal and noise?

MOUSE ROD SINGLE PHOTON RESPONSES ARE
PARTIALLY OBSCURED BY NOISE



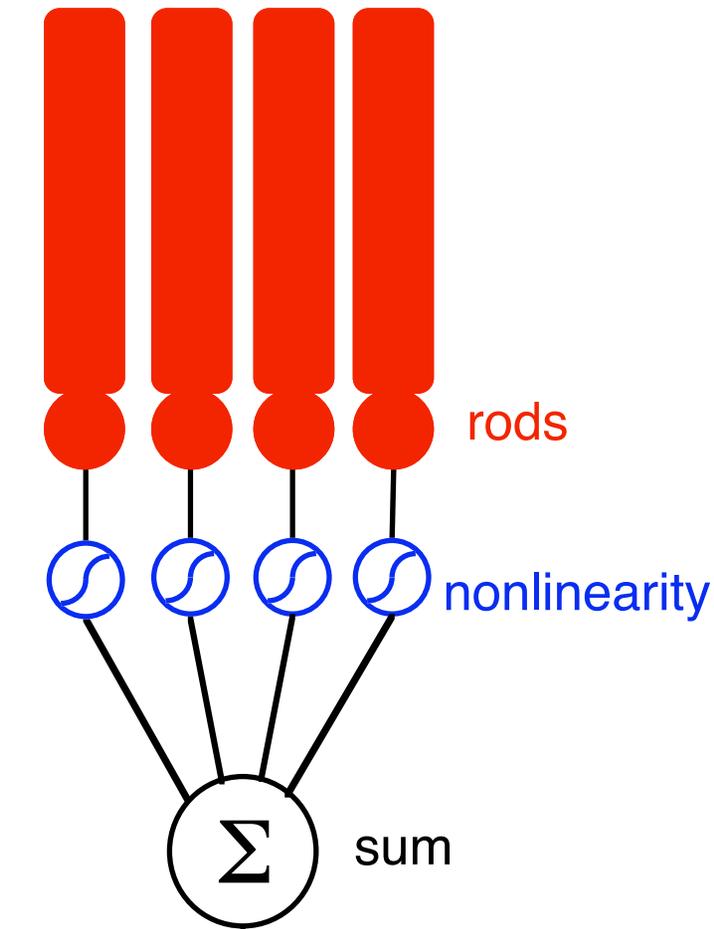
ROD BIPOLARS GENERATE DISCRETE RESPONSES TO DIM FLASHES



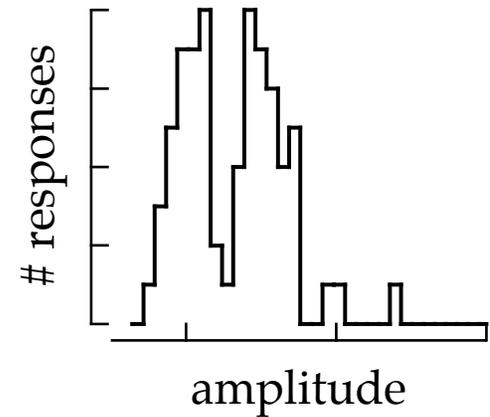
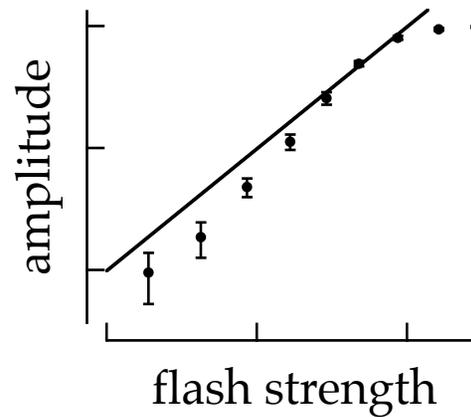
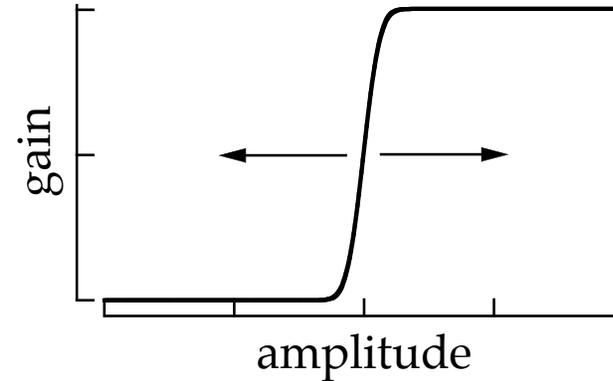
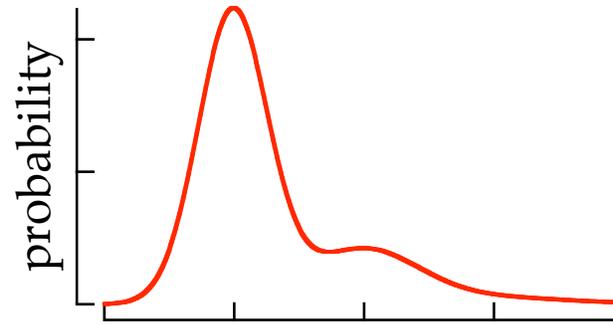


- Mouse rod-rod bipolar signal transfer is nonlinear.
- Nonlinear signal transfer eliminates or severely attenuates majority of rod's single photon responses.
- Rejection of noise more than compensates loss of signal - thus rod bipolars provide near-optimal readout of rod signals near visual threshold.

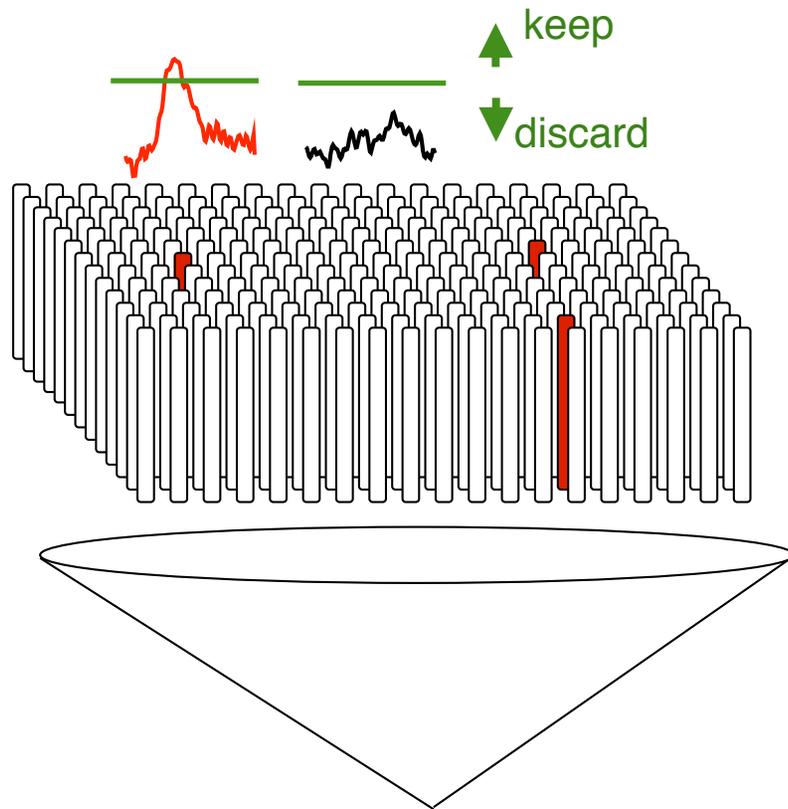
MODEL FOR ROD-ROD BIPOLAR SIGNAL TRANSFER



predict nonlinearity
and discreteness of
rod bipolar response



signal and noise distributions
and discrimination

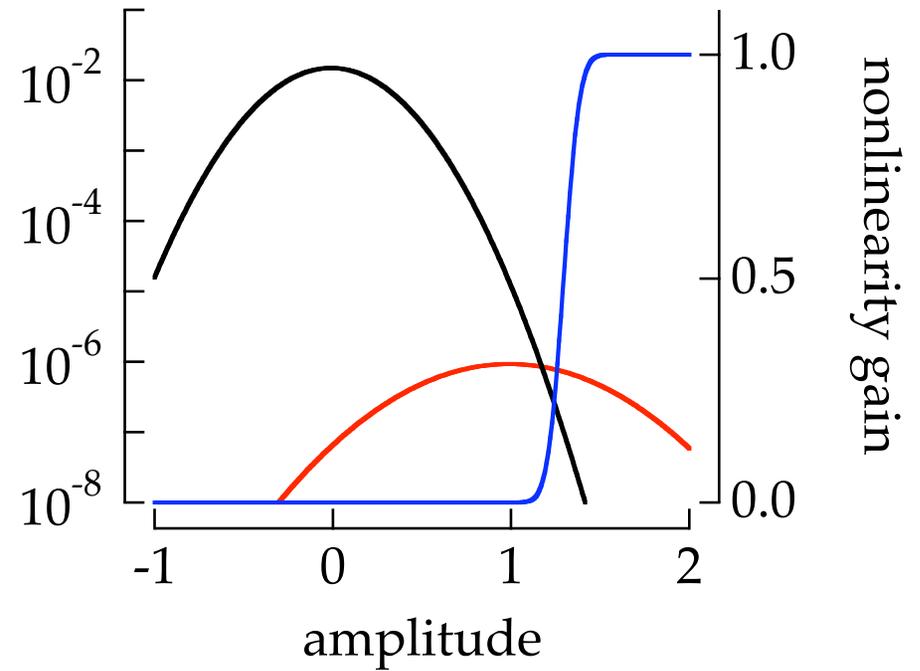
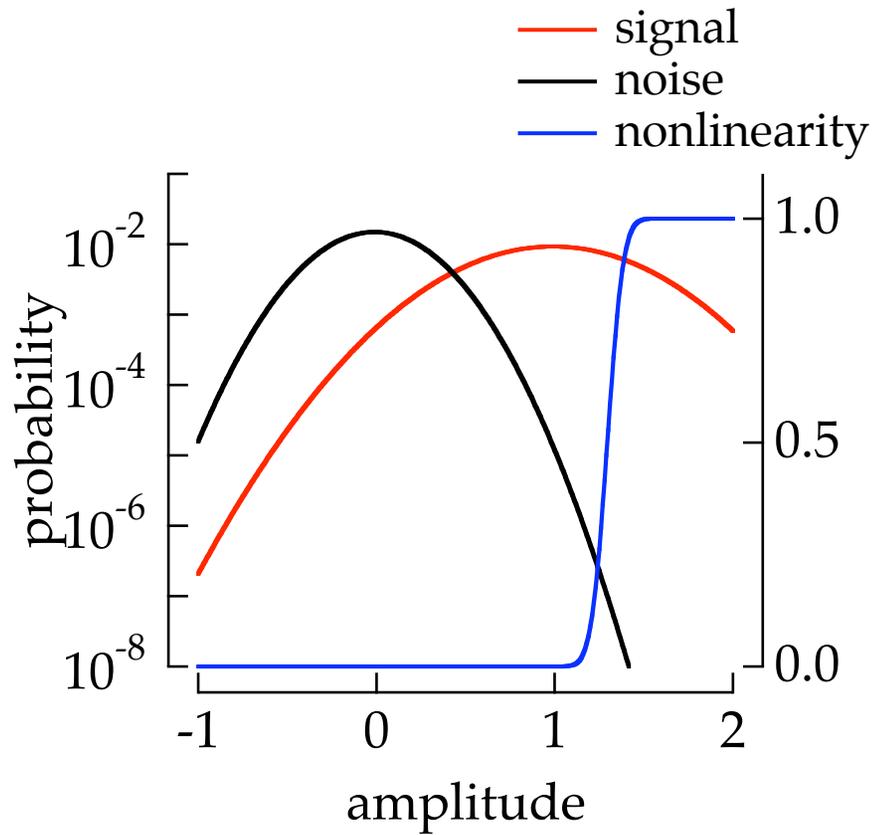


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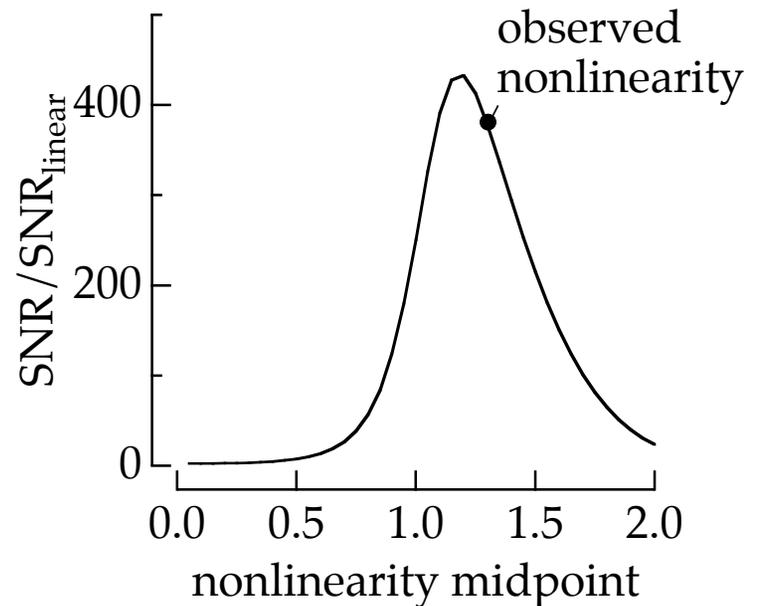
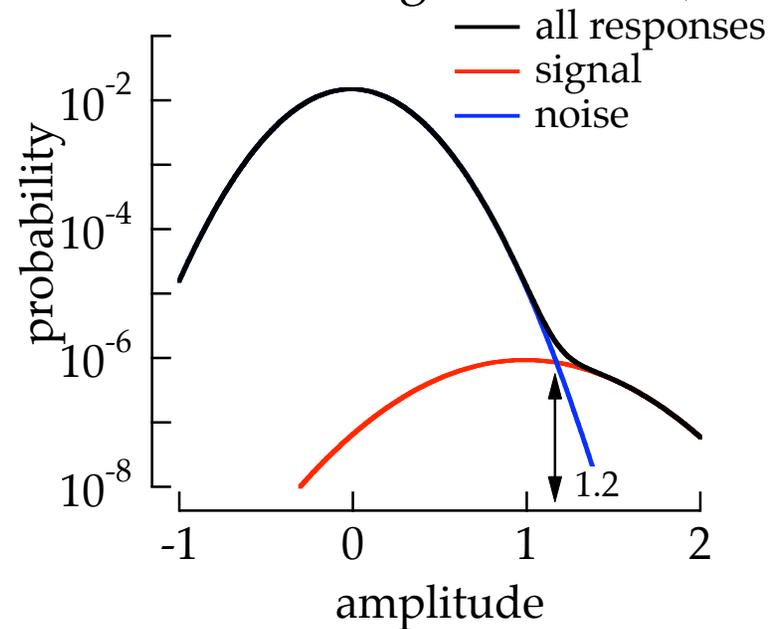
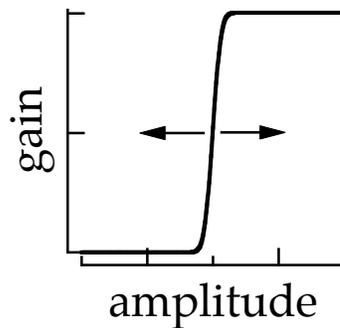
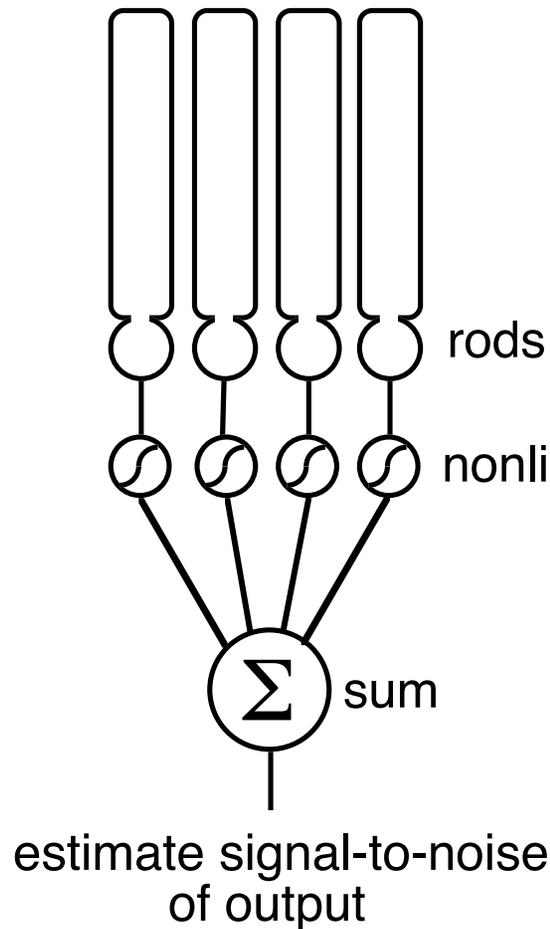
DISTRIBUTION OF ROD RESPONSES AT VISUAL THRESHOLD

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

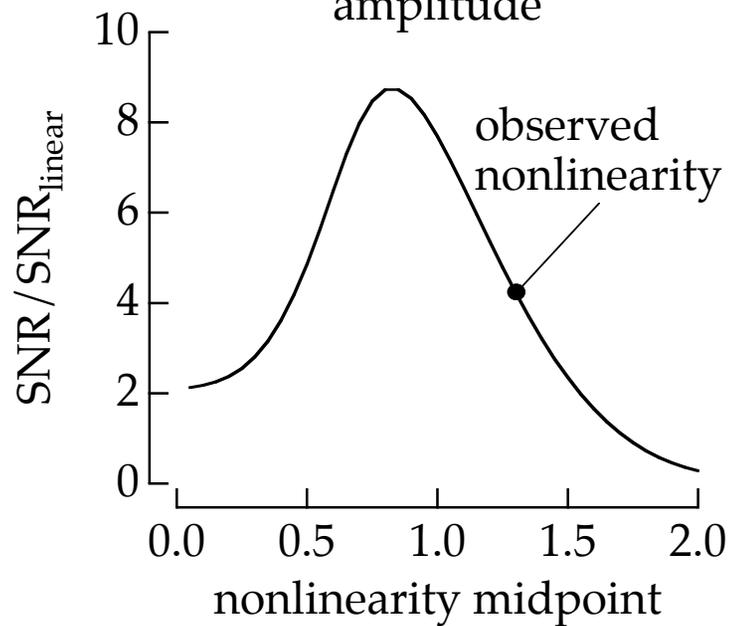
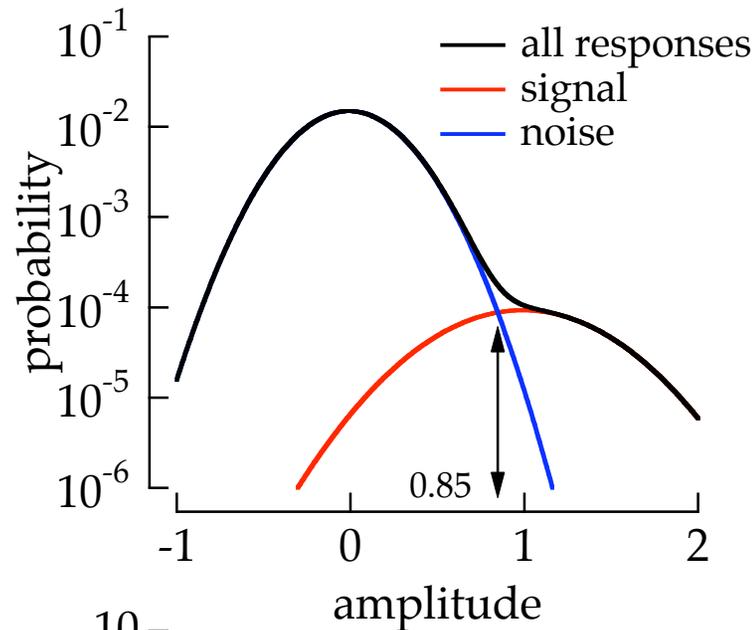
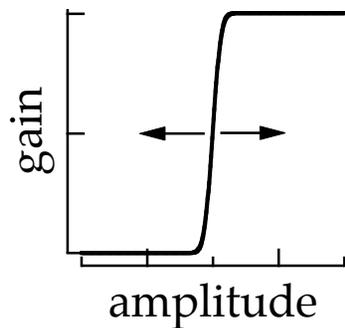
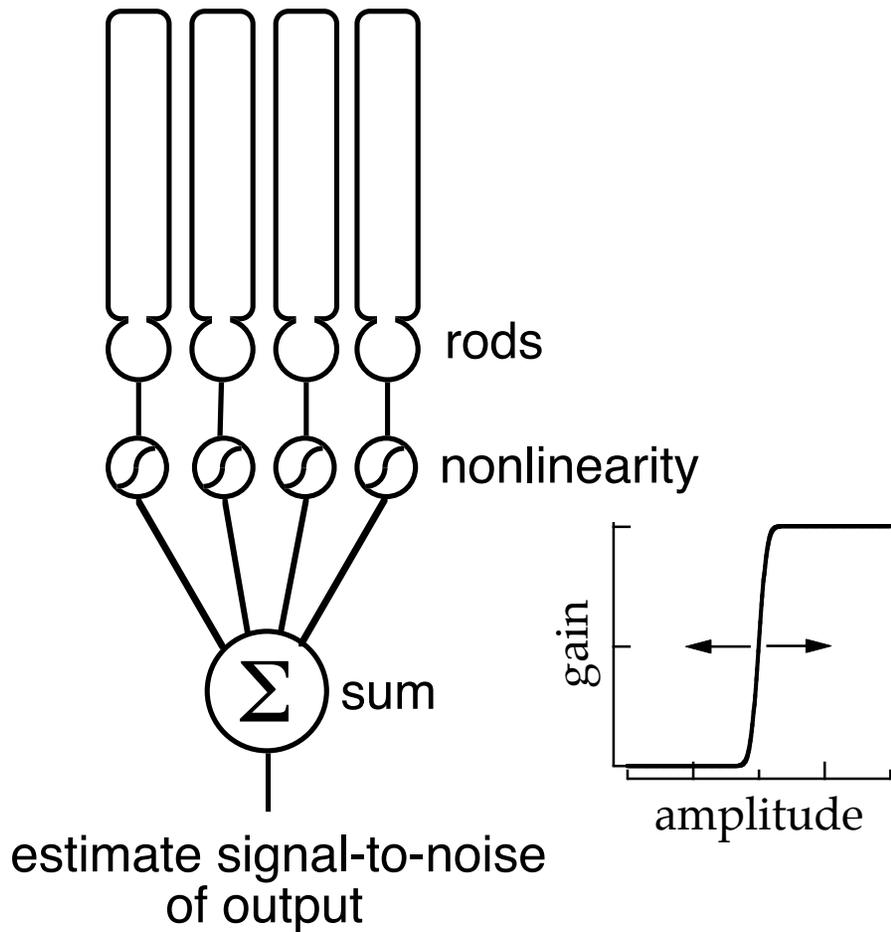
Visual threshold (0.0001 Rh^*)

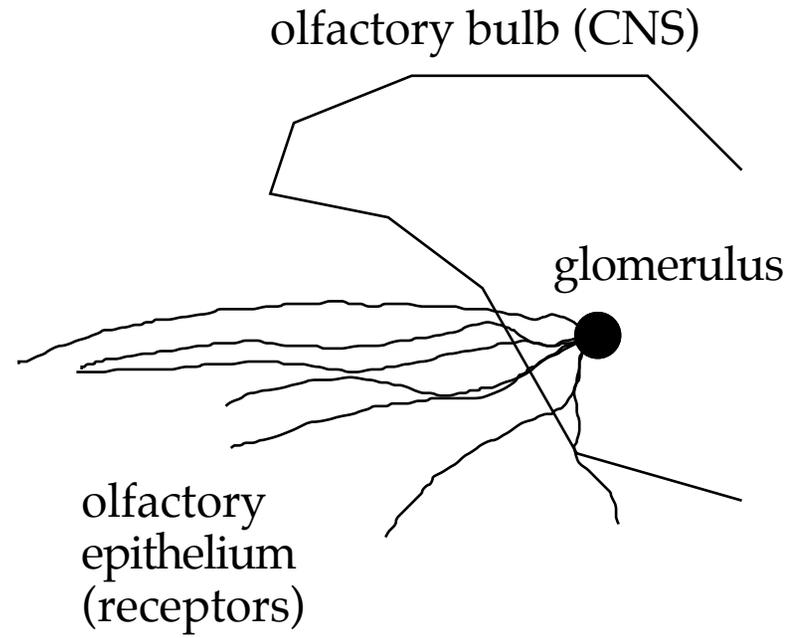
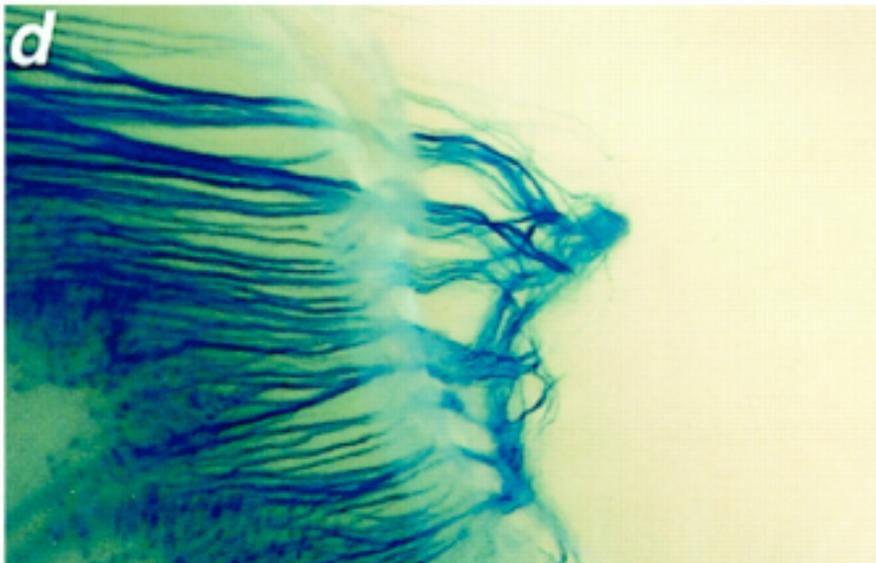
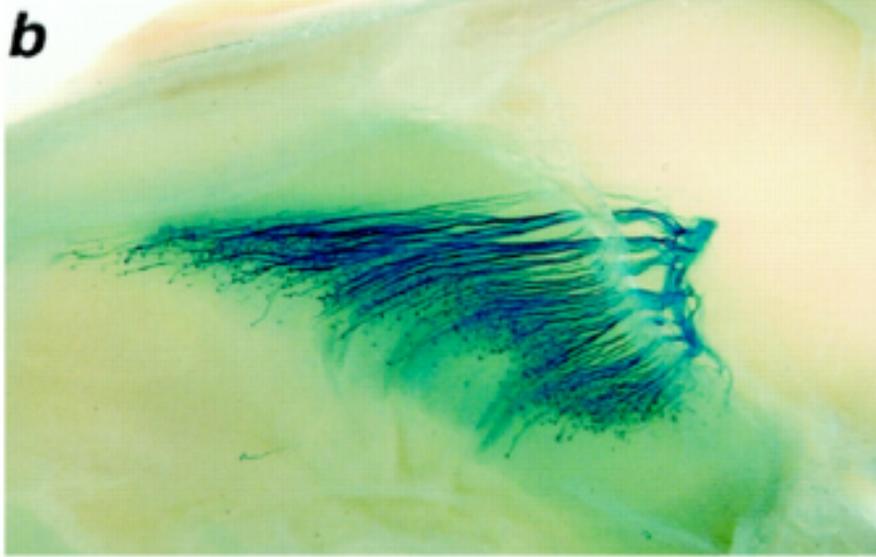


ROD BIPOLAR PROVIDES NEAR OPTIMAL READOUT OF ROD SIGNALS AT VISUAL THRESHOLD ($0.0001 \text{ Rh}^* / \text{rod} / \text{integration time}$)



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





Mombaerts et al, 1996