

# Lecture 6: How Do Photoreceptors Work?

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CSC 259/459, Fall 2024  
Computer Imaging & Graphics

# Logistics

Programming assignment 1 is due 9/25, 11:30 AM

- Can work in groups of 2.

Project proposal due 10/16 11:30 AM.

- I've put up a list of ideas. In the past, many choose to implement some concepts discussed in the class.
- Can work in groups of 2.

# The Roadmap

Theoretical Preliminaries

**Human Visual Systems**

Color in Nature, Arts, & Tech

(a.k.a., the birth, life, and death of light)

Digital Camera Imaging

Modeling and Rendering

Applications



Introduction and Overview

**Photoreceptors**

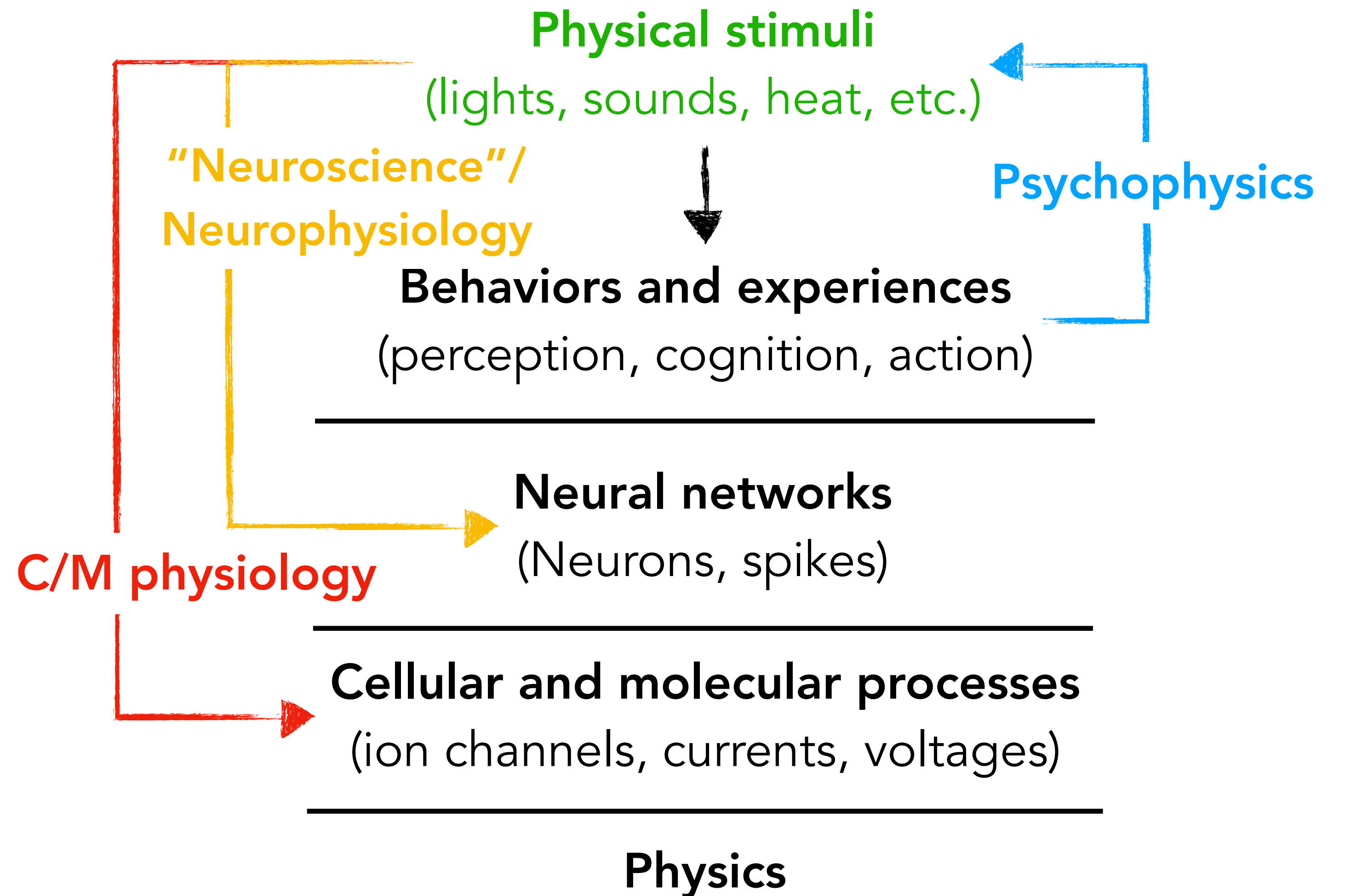
Retinal Representations

Light and Dark Adaptation

Color Vision and Colorimetry

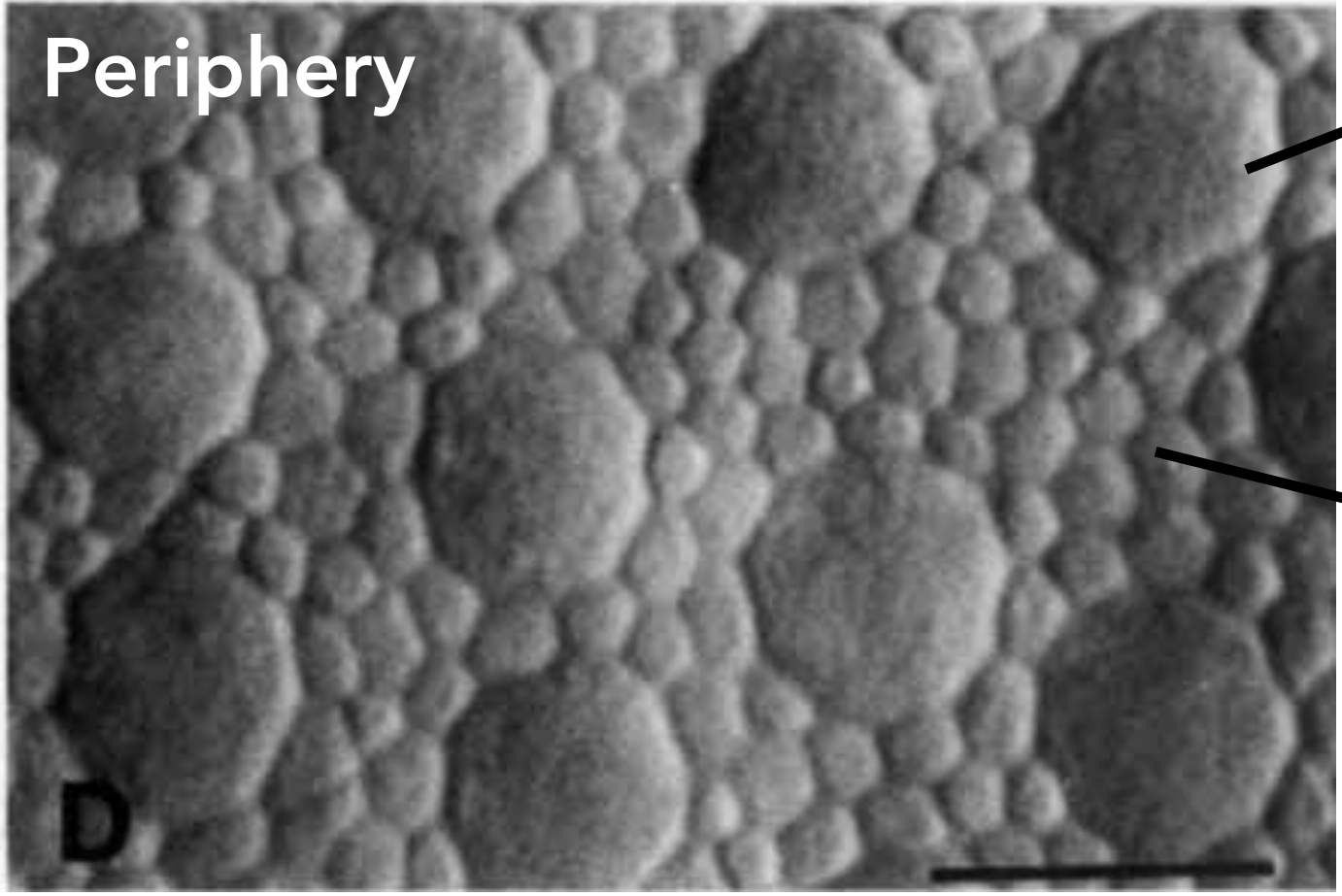
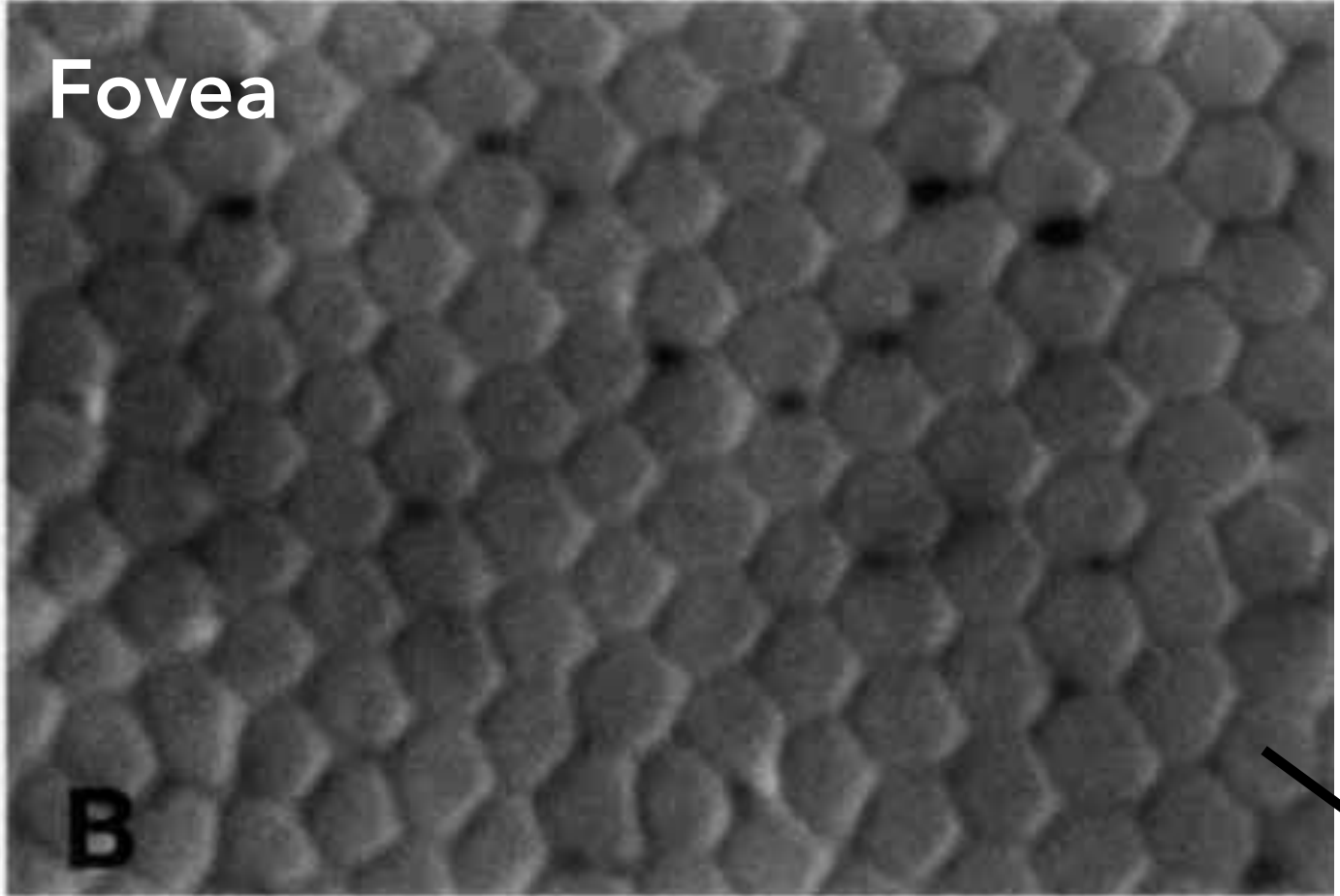
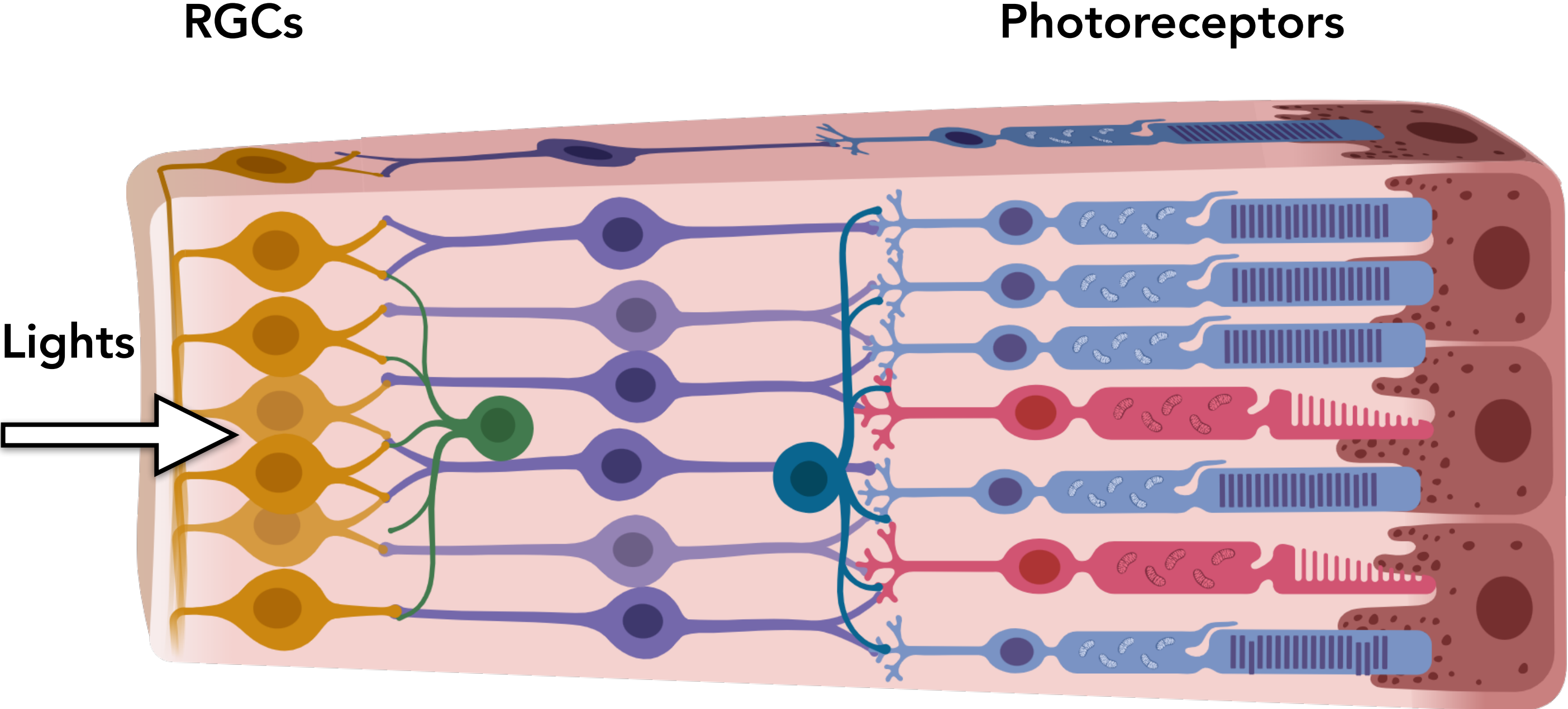
# Why Study Photoreceptors?

- First step in seeing; sets the limit of our vision.
- A great example of how different levels of abstraction are connected.
- Why and why don't certain physiological results match behavioral results?





# Recall: Photoreceptors on the Retina

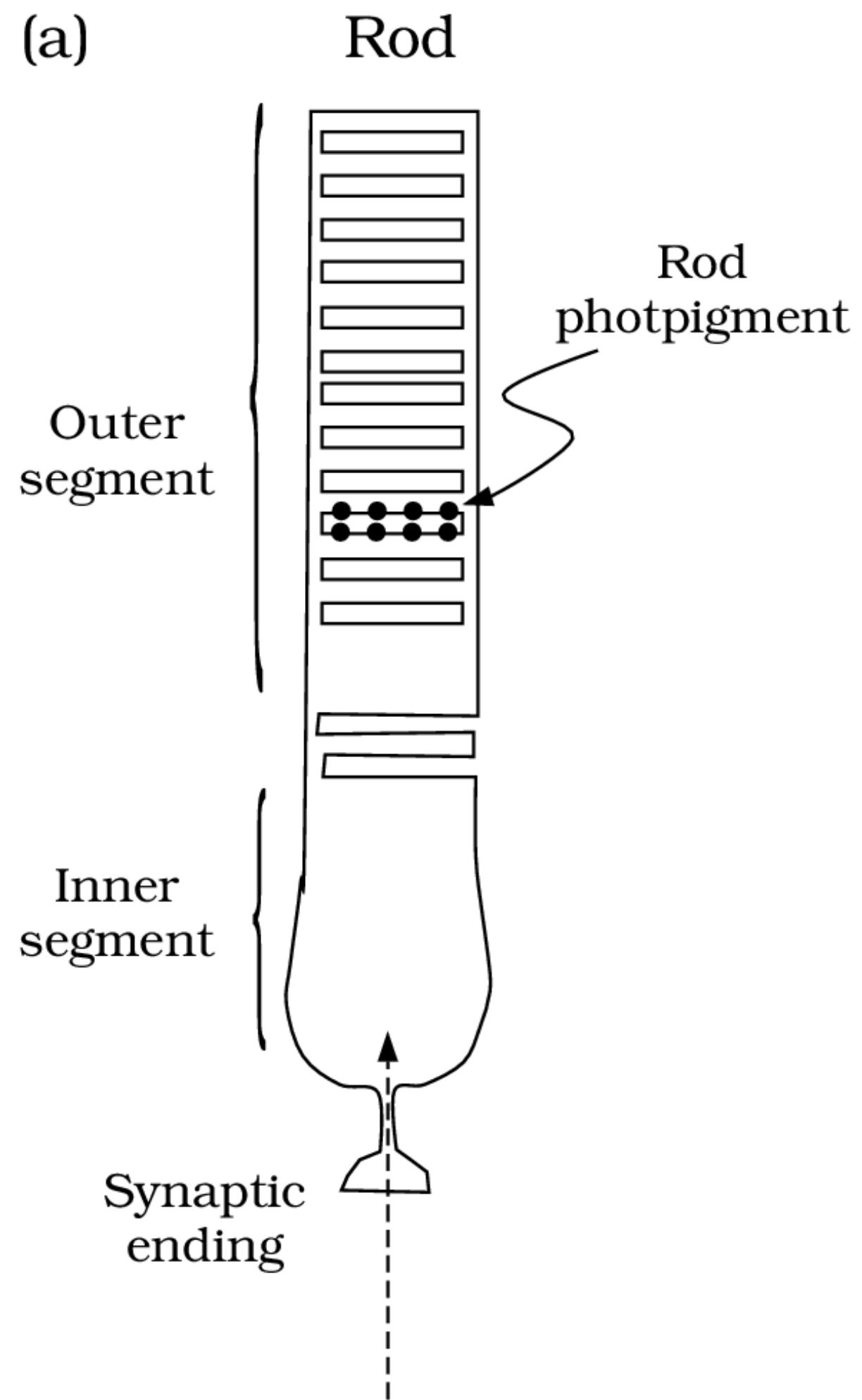


Cone

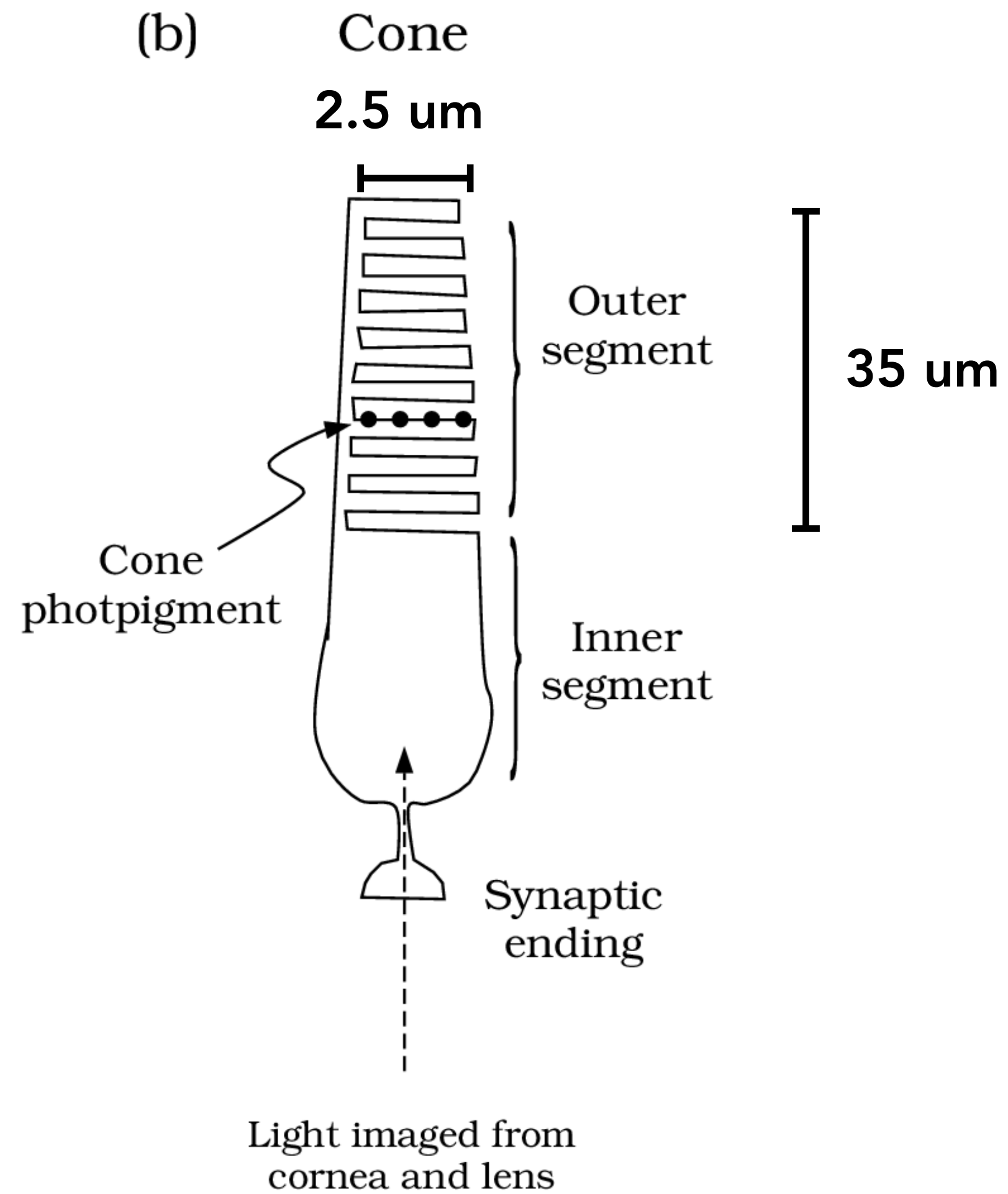
Rod

10 um

# Anatomical Structure



Light imaged from  
cornea and lens

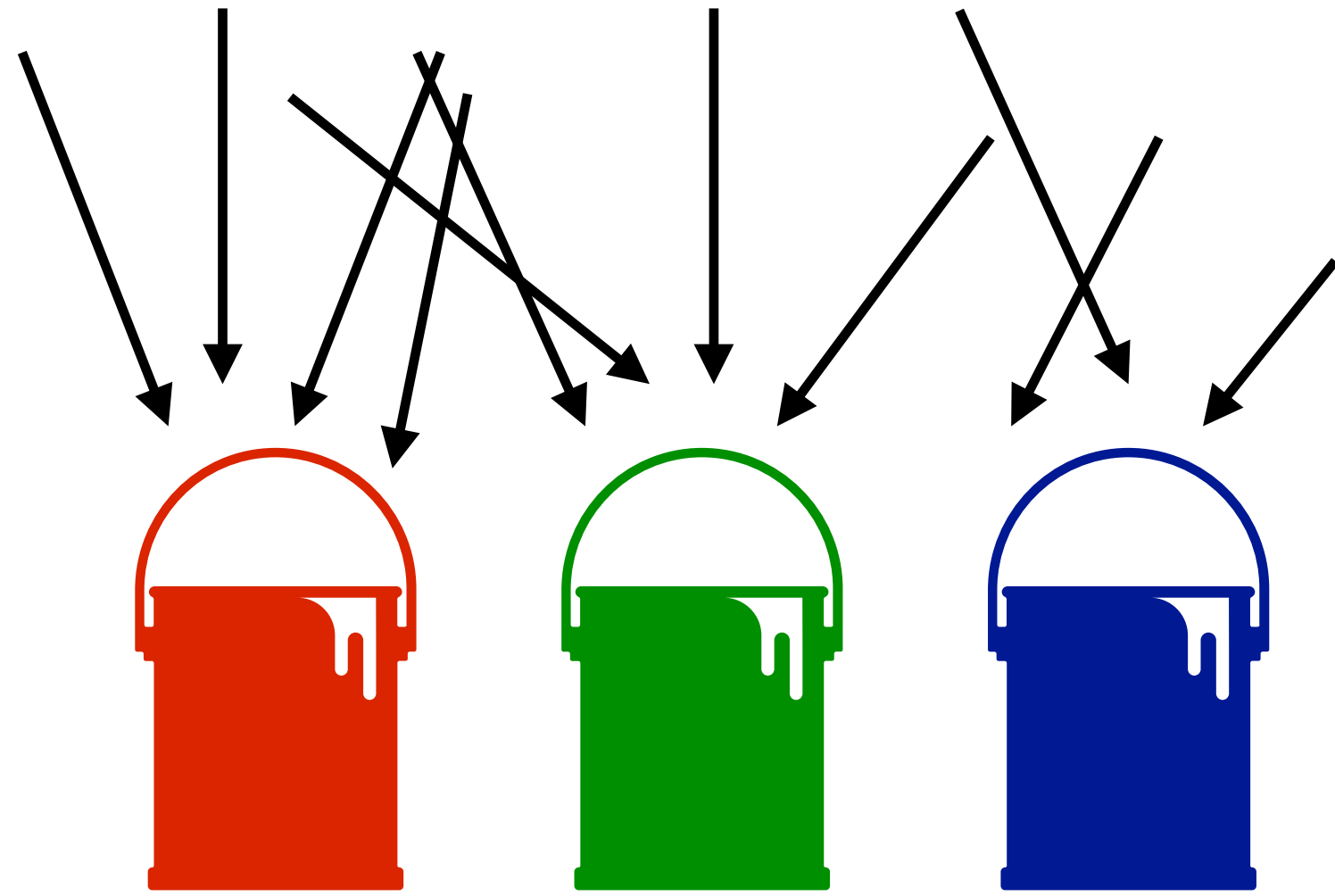


\* dimensions for a fovea cone; from Polyak 1941

# Counting Photons

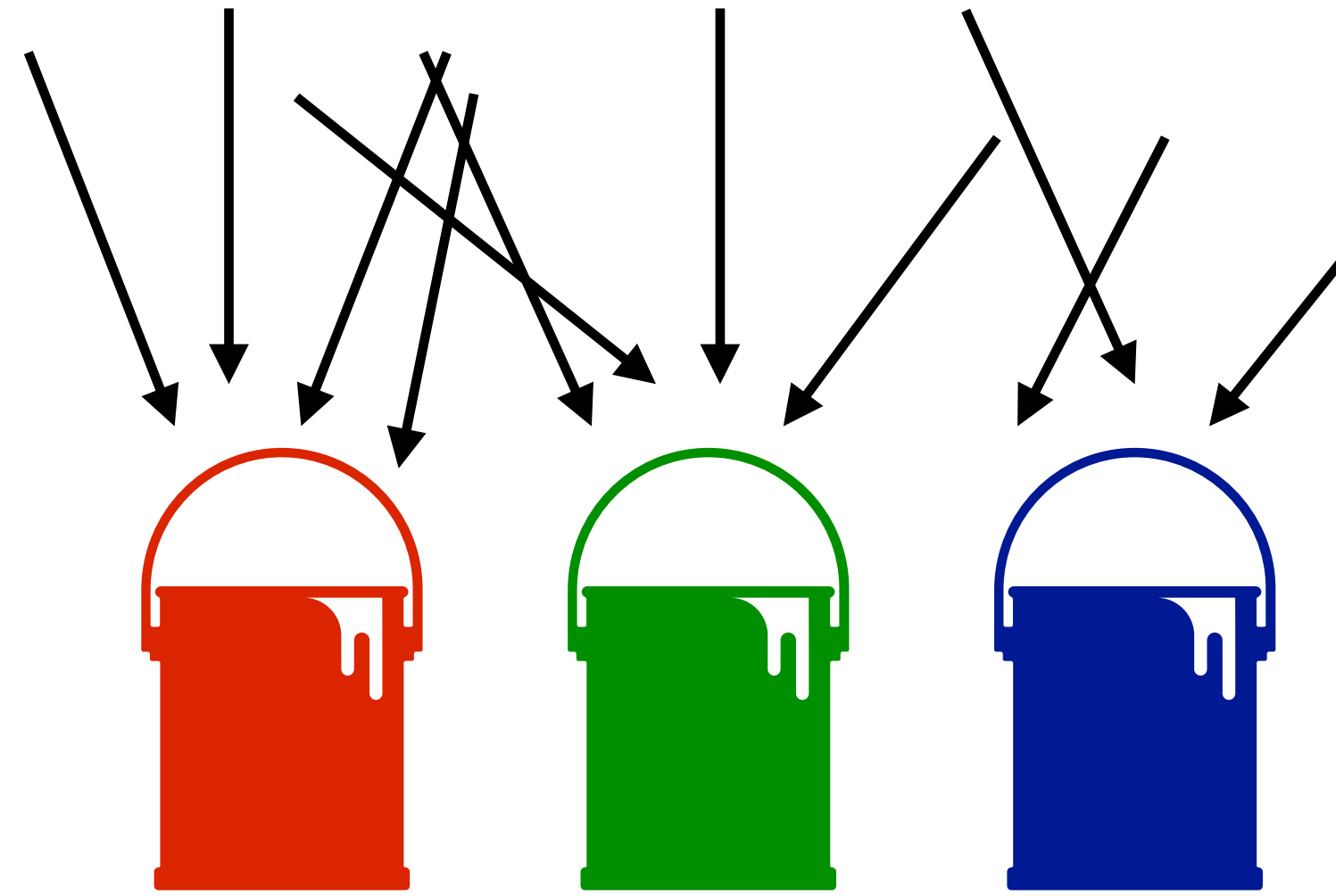
## (Principle of Univariance)

# A Simplified Functional View of Photoreceptors



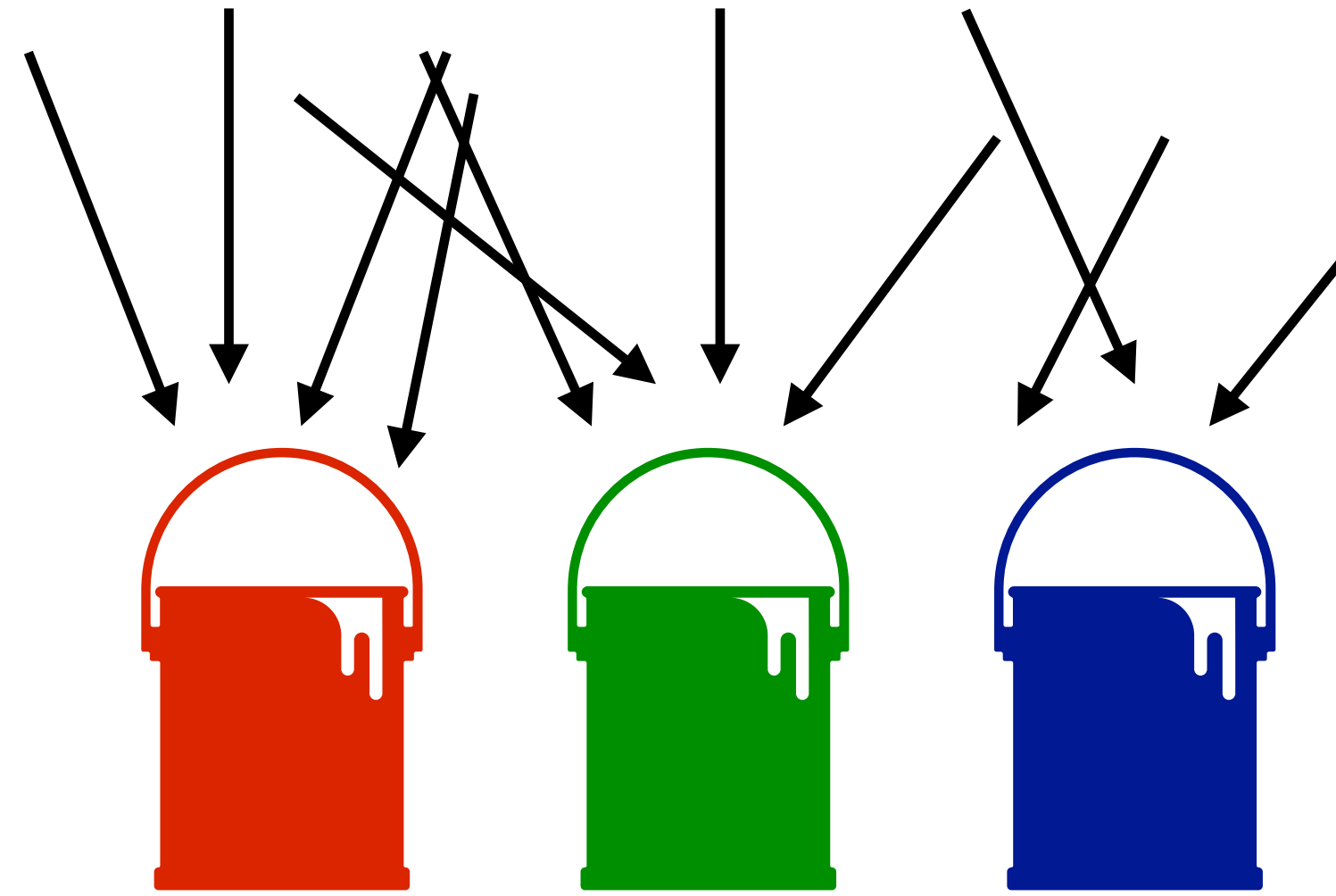
- Each photoreceptor is a bucket that collects photons.
- Many photons that enter the eye don't hit any bucket (absorbed by lens and macular pigments)
- Any photon that hits a bucket has a probability of being absorbed.
- The probability  $p(\lambda)$  is wavelength-specific and varies between photoreceptor types

# A Simplified Functional View of Photoreceptors



- Once a photon is absorbed, it has a probability of **exciting** the photoreceptor
- Excitation means generating an electrical response, also called isomerization or pigment bleach
- This probability is called the **Quantum Efficiency** of the photoreceptor ( $Q_e$ ), and is generally constant in the visible spectrum
- **Excitation probability of a single photon:**
  - $p(\lambda) Q_e$
  - Usually we ignore  $Q_e$  since it's a constant and just talk about absorption

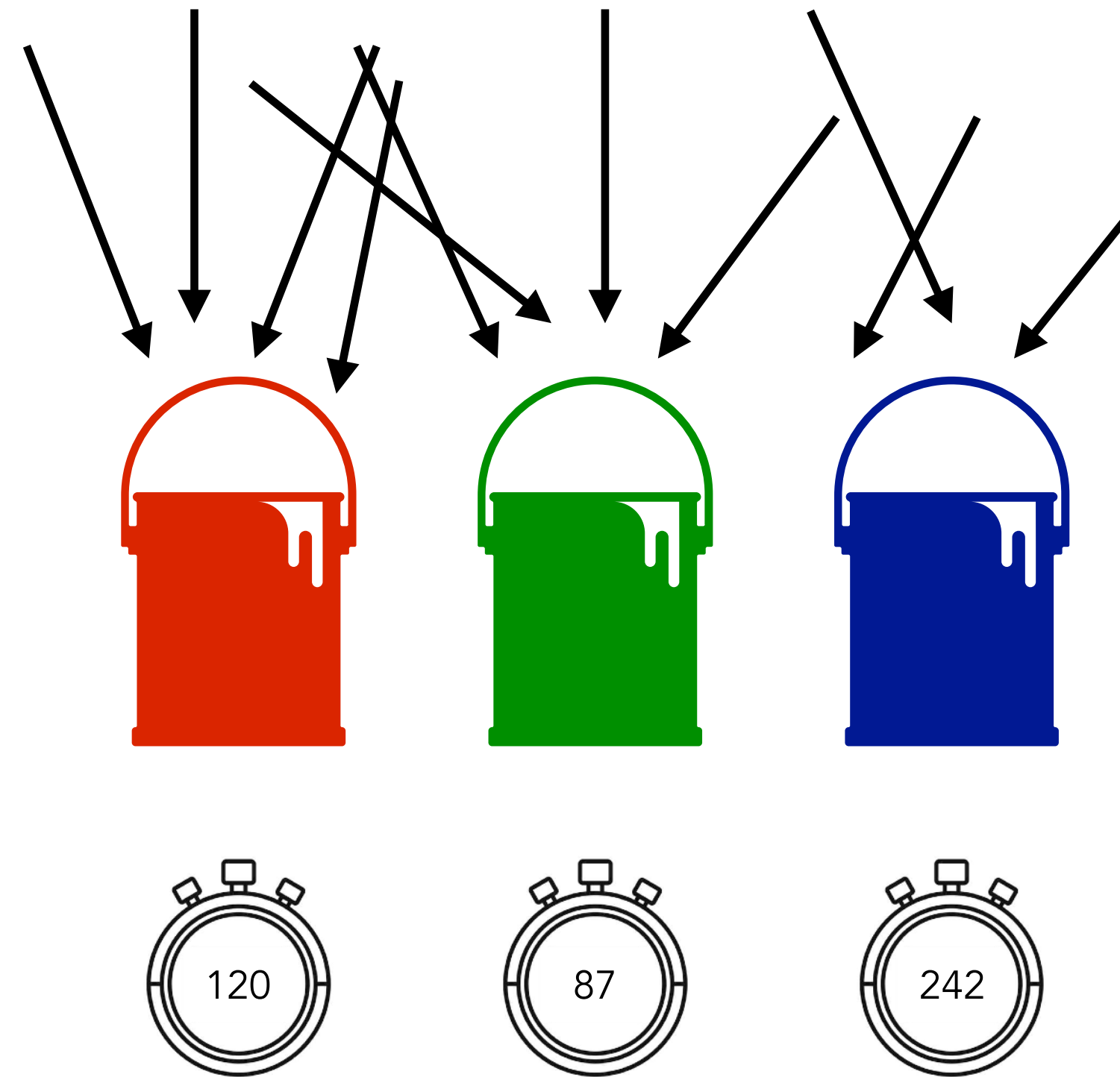
# Principle of Univariance



- For each photoreceptor type:
  - The electrical response caused by a pigment excitation is constant regardless of the photon's wavelength.
  - Each photon generating an electrical response has the same effect as any other photon that does so.
  - The only effect that wavelength has is to impact the probability a photon gets absorbed; after absorption the wavelength information is lost.



# Principle of Univariance



- As if each photoreceptor is counting excitations
- If two photoreceptors (of the same type) have the same "counter value", their electrical responses are the same.
- It does **not** mean the electrical response is proportional to the number of excitations; more later.

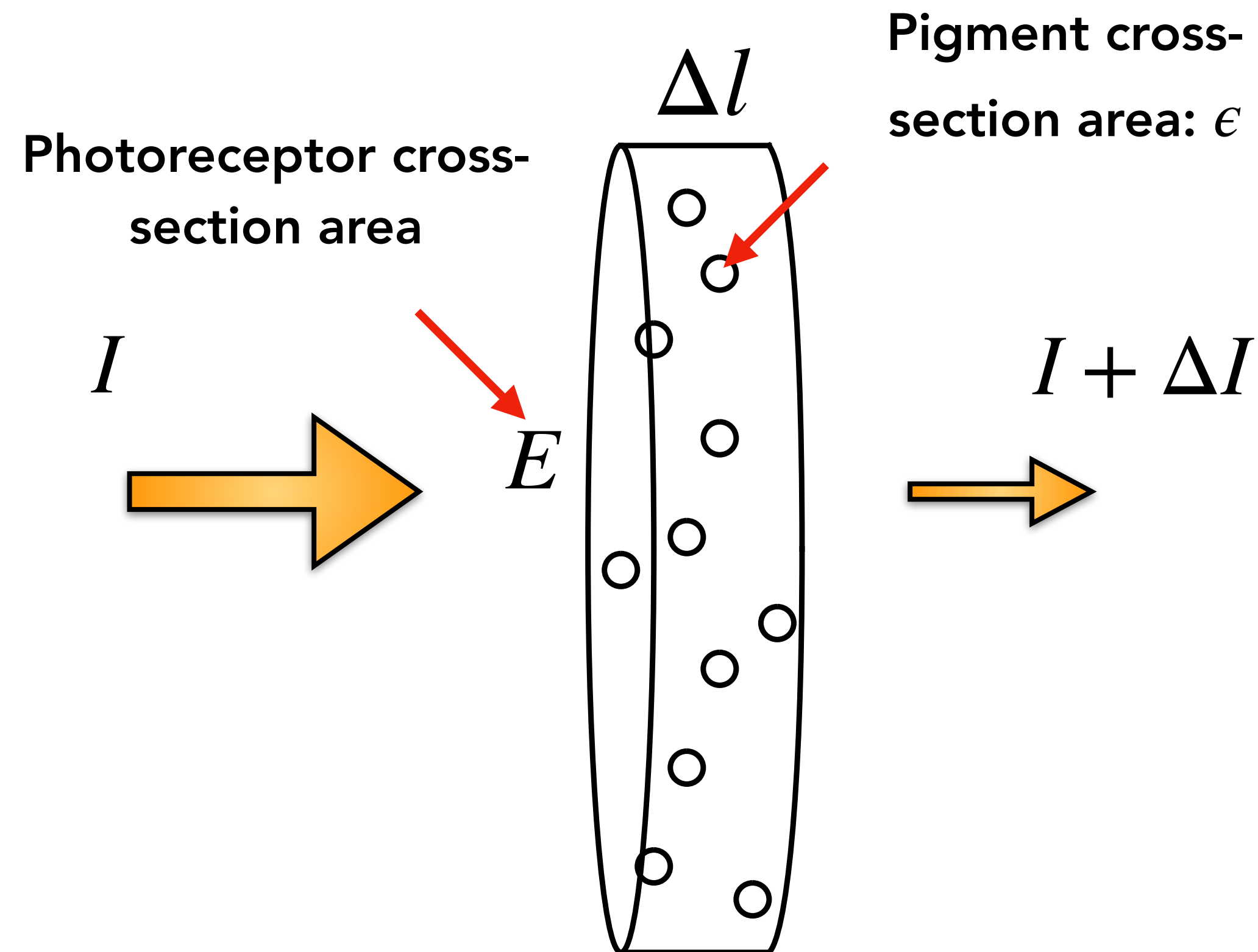
# Measuring Spectral Absorption

- Single photon absorption probability is the percentage of photons absorbed in a flux, which we can measure
- Two general methods, one direct and the other indirect
  - Direct: Microspectrophotometry
  - Indirect: Measuring electrical responses (using suction electrode)



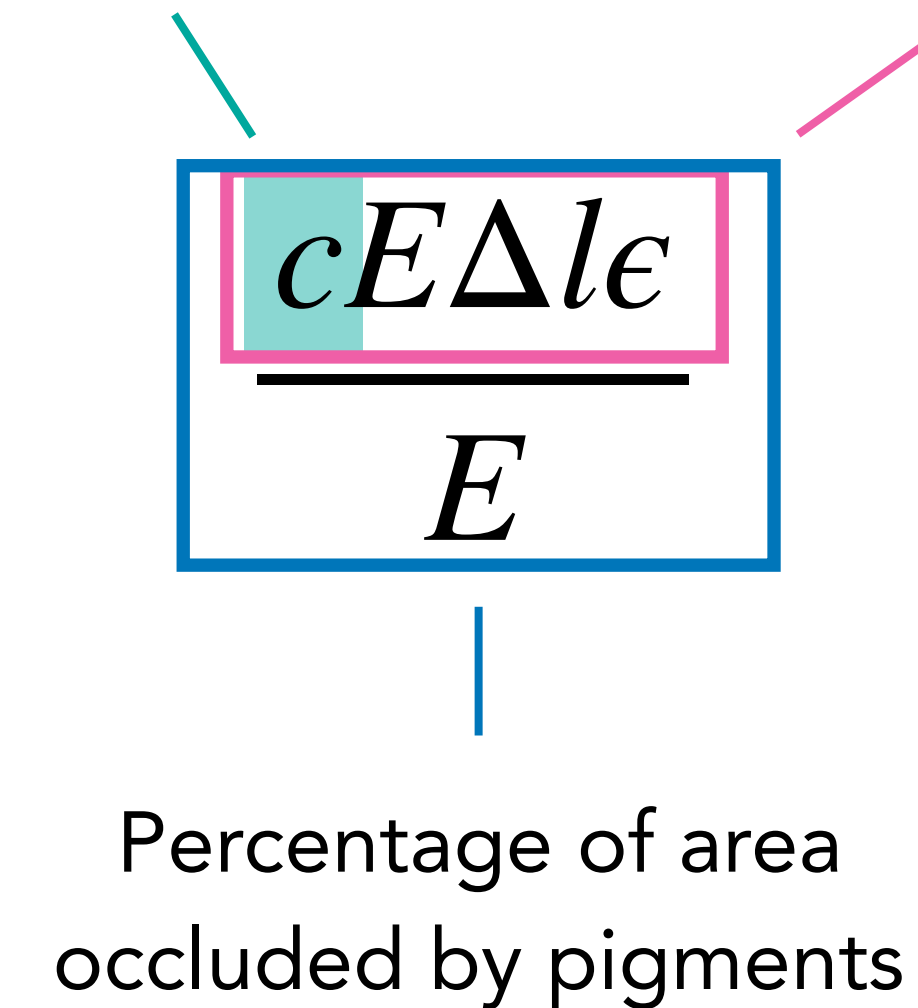
# Modeling Pure Absorption (Ignore Back Scattering)

Consider a very thin slice of a photoreceptor (so thin that no pigments are covering each other)



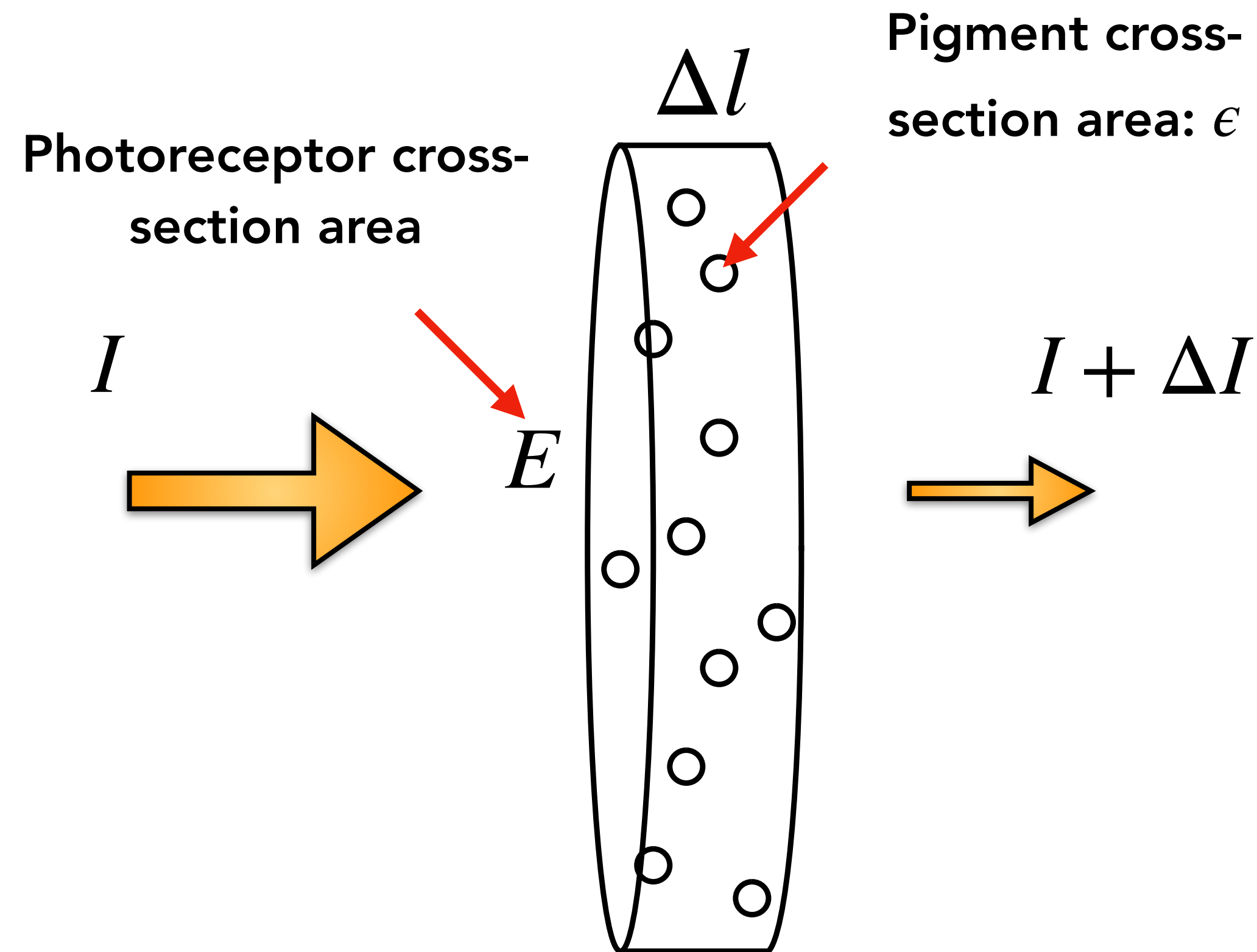
Concentration (# of pigments / unit volume)

Total area covered by the pigments



# Modeling Pure Absorption

Consider a very thin slice of a photoreceptor (so thin that no pigments are covering each other)

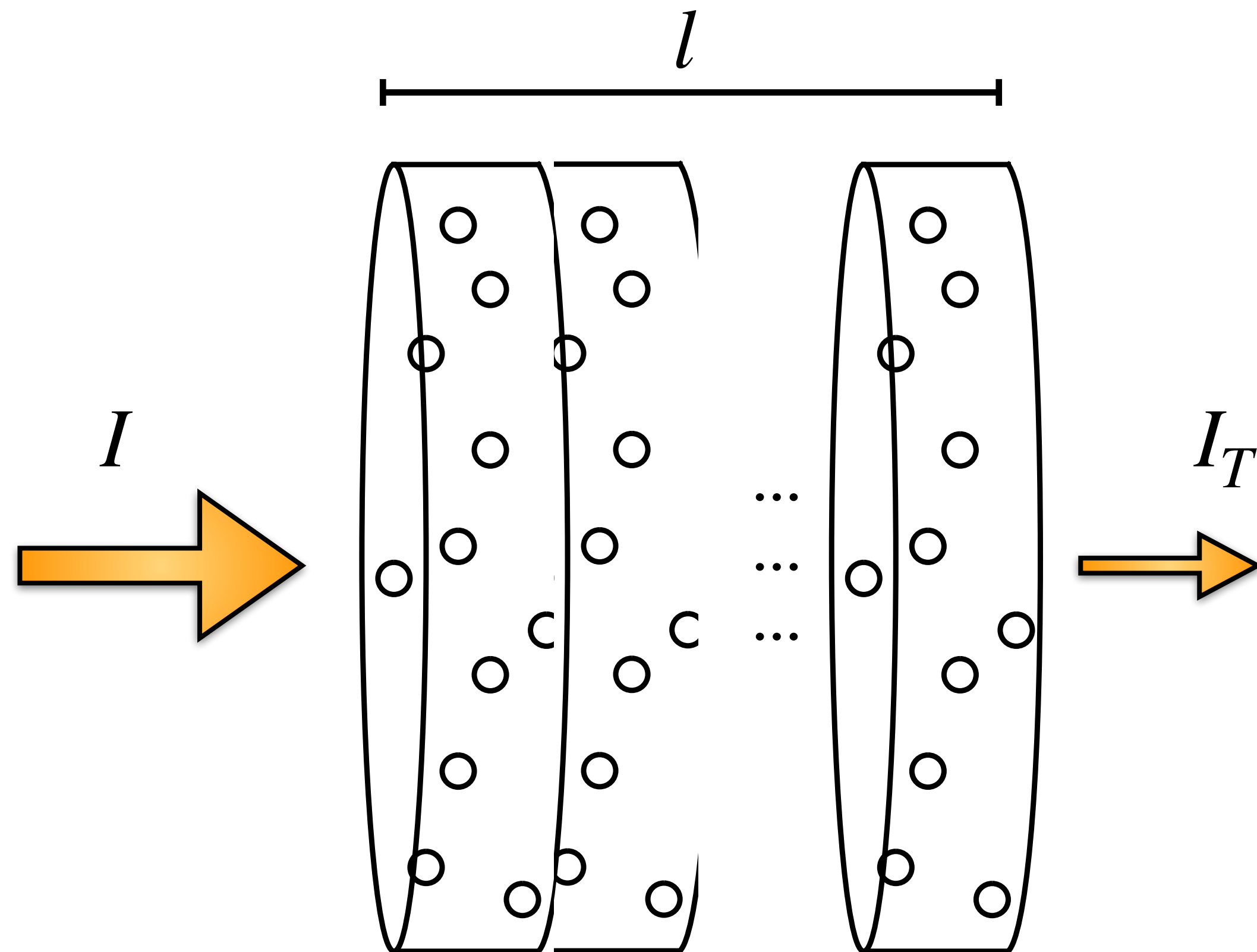


Percentage of absorbed photons

$$\frac{cE\Delta l\epsilon}{E} = \frac{\Delta I}{I}$$

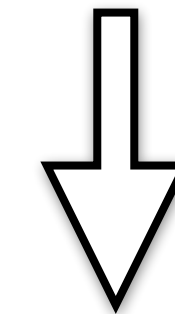
$$\frac{\Delta I}{\Delta l} = -cI\epsilon$$

# Beer-Lambert Law



As  $s$  increases (light travel farther), the intensity decreases **exponentially!**

$$\frac{dI}{dl} = -cI\epsilon$$



$$I_T = Ie^{-cle}$$

If density is uniform

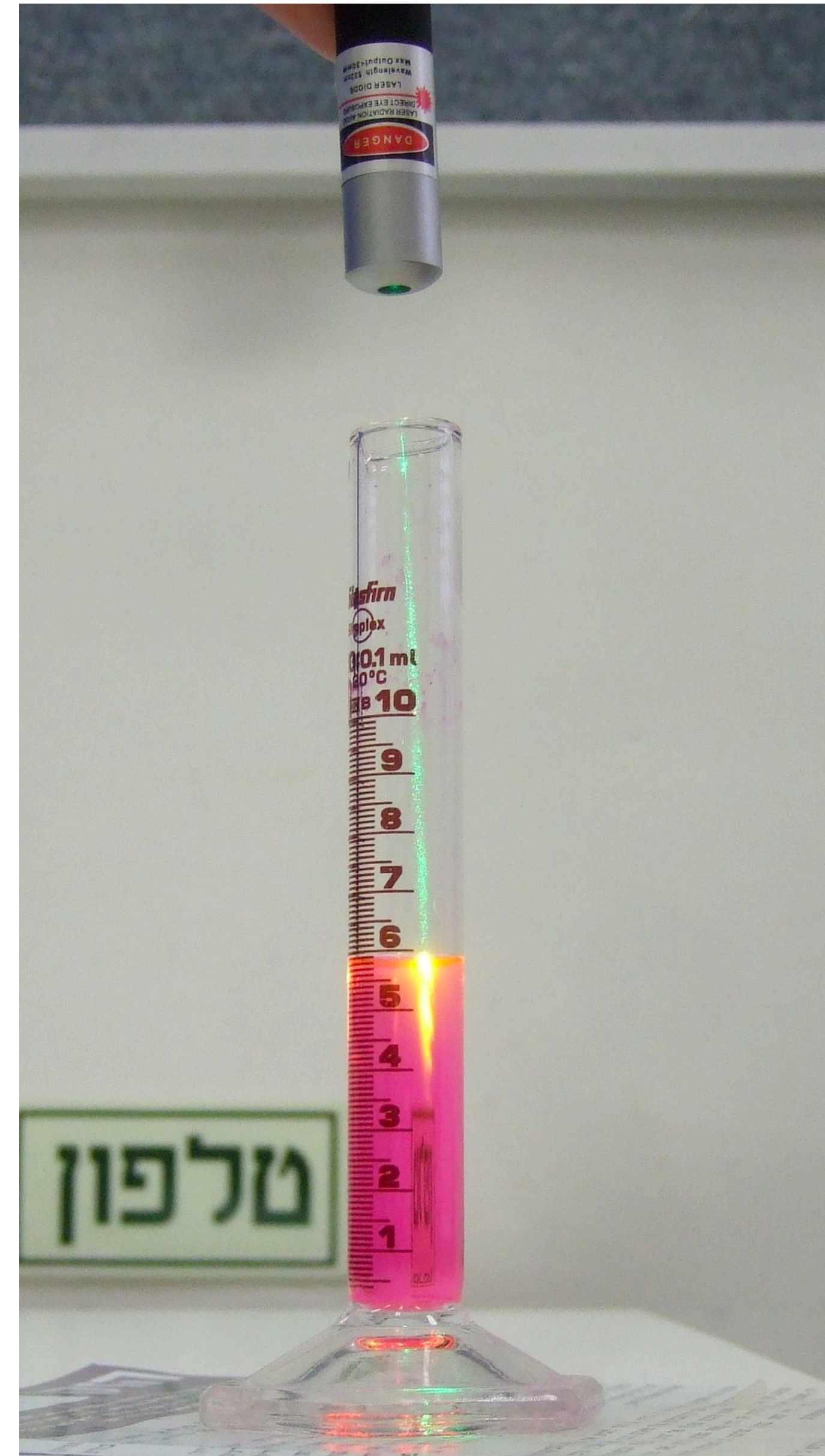
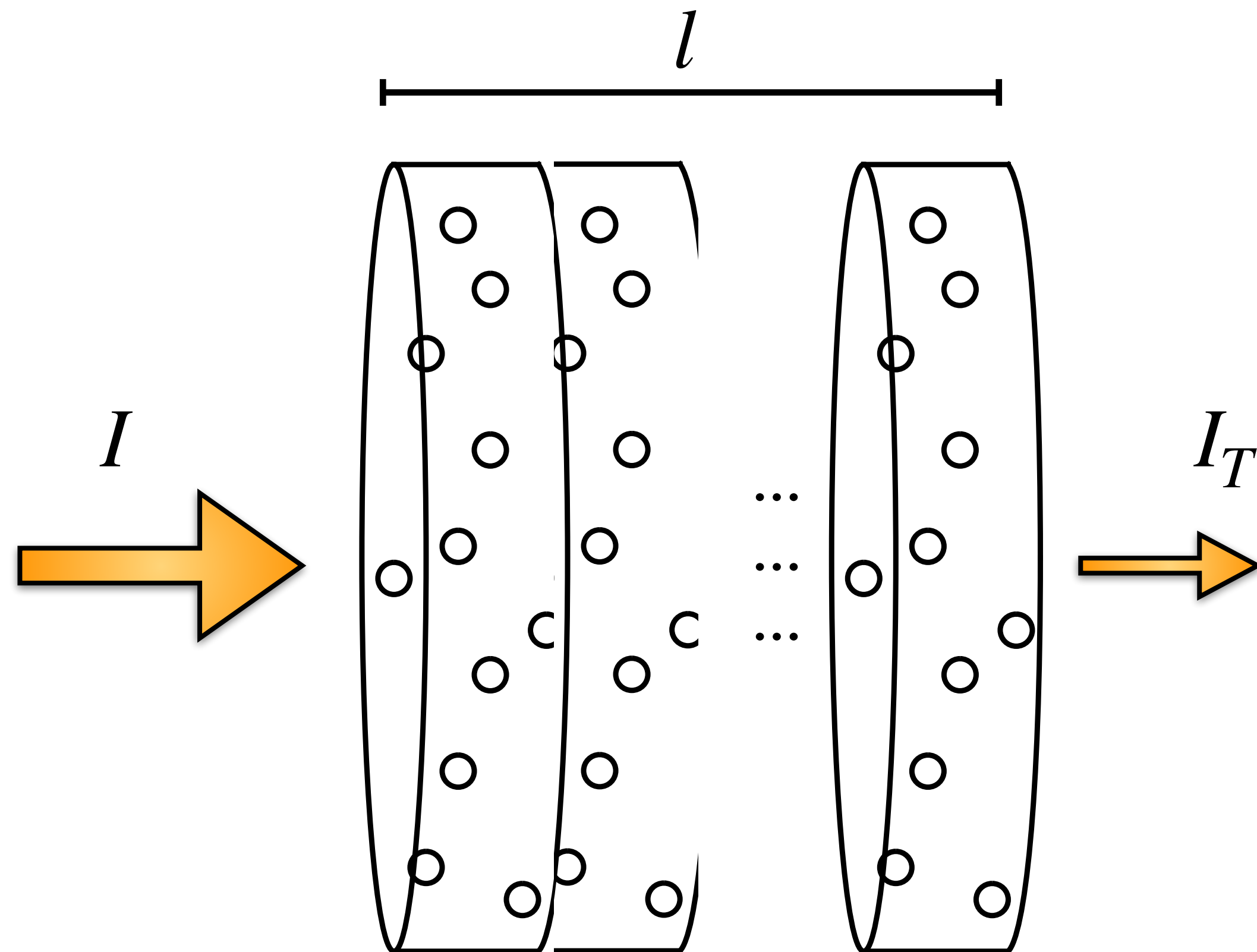
$$I_T = Ie^{-\int_0^l c(l)\epsilon}$$

If density is non-uniform

*"The person credited with a scientific law is almost certainly not the one who discovered it."*  
Bouguer was the first to discover this law.



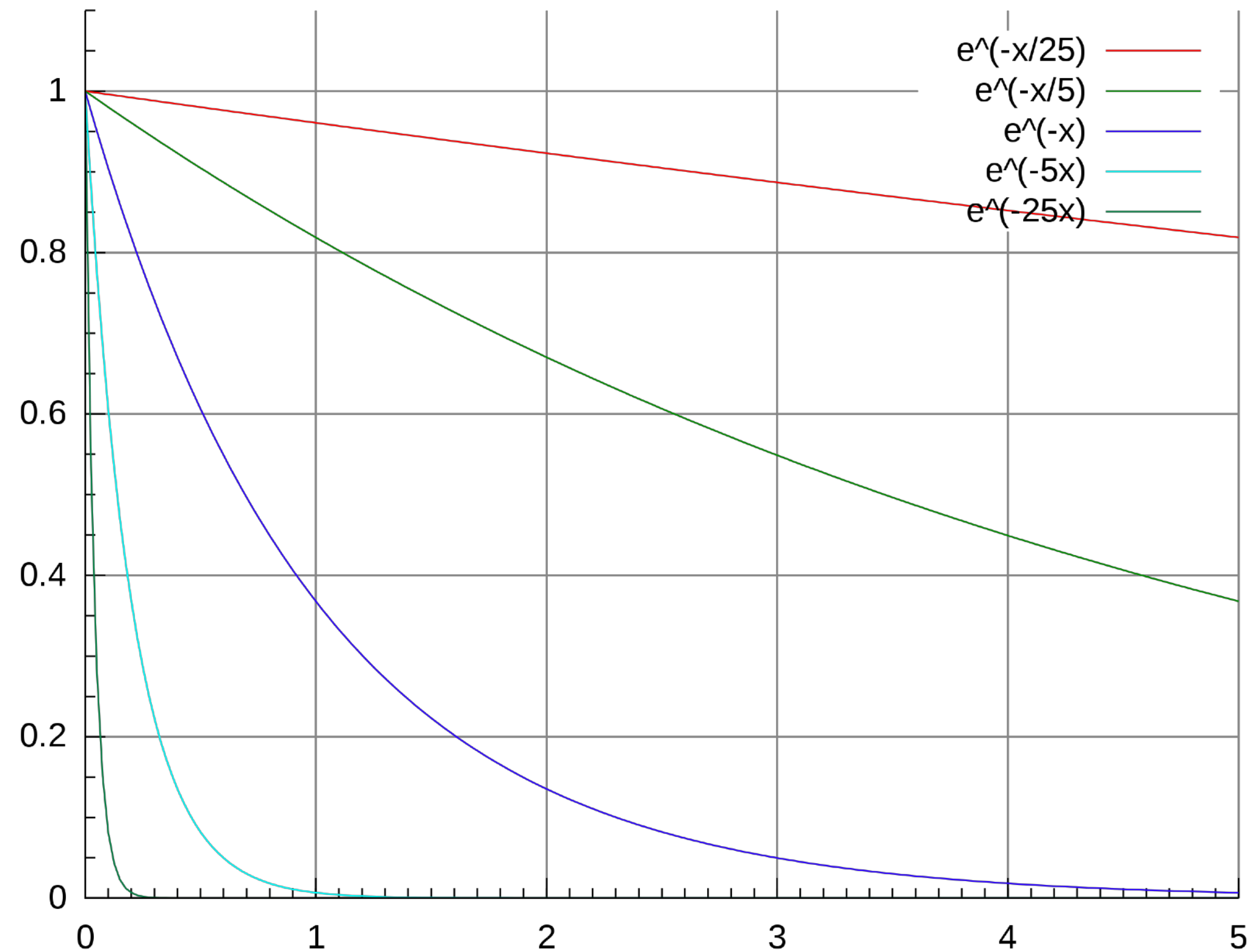
# Beer-Lambert Law





# Exponential Decay

$$I_T = Ie^{-cle}$$



Exponential decay happens when a quantity decreases at a rate proportional to its current value.

- Opposite of exponential growth.

Exponential decay means lights are hard to be completely absorbed.

- 10% of light @ 70 m deep under ocean, but you can still see lights at 850 m deep.

Many real-world scenarios exhibit exponential growth/decay.

# Transmittance, Absorptance, Absorbance

Concentration  
(Unit: 1/m<sup>3</sup>)

Proportional to cross-  
section area (Unit: m<sup>2</sup>)

$$I_T = I e^{-cl\epsilon}$$

Optical length (Unit: m)

**Transmittance**  
(fraction transmitted)

$$T = \frac{I_T}{I} = e^{-cl\epsilon}$$

**Absorptance**  
(fraction absorbed)

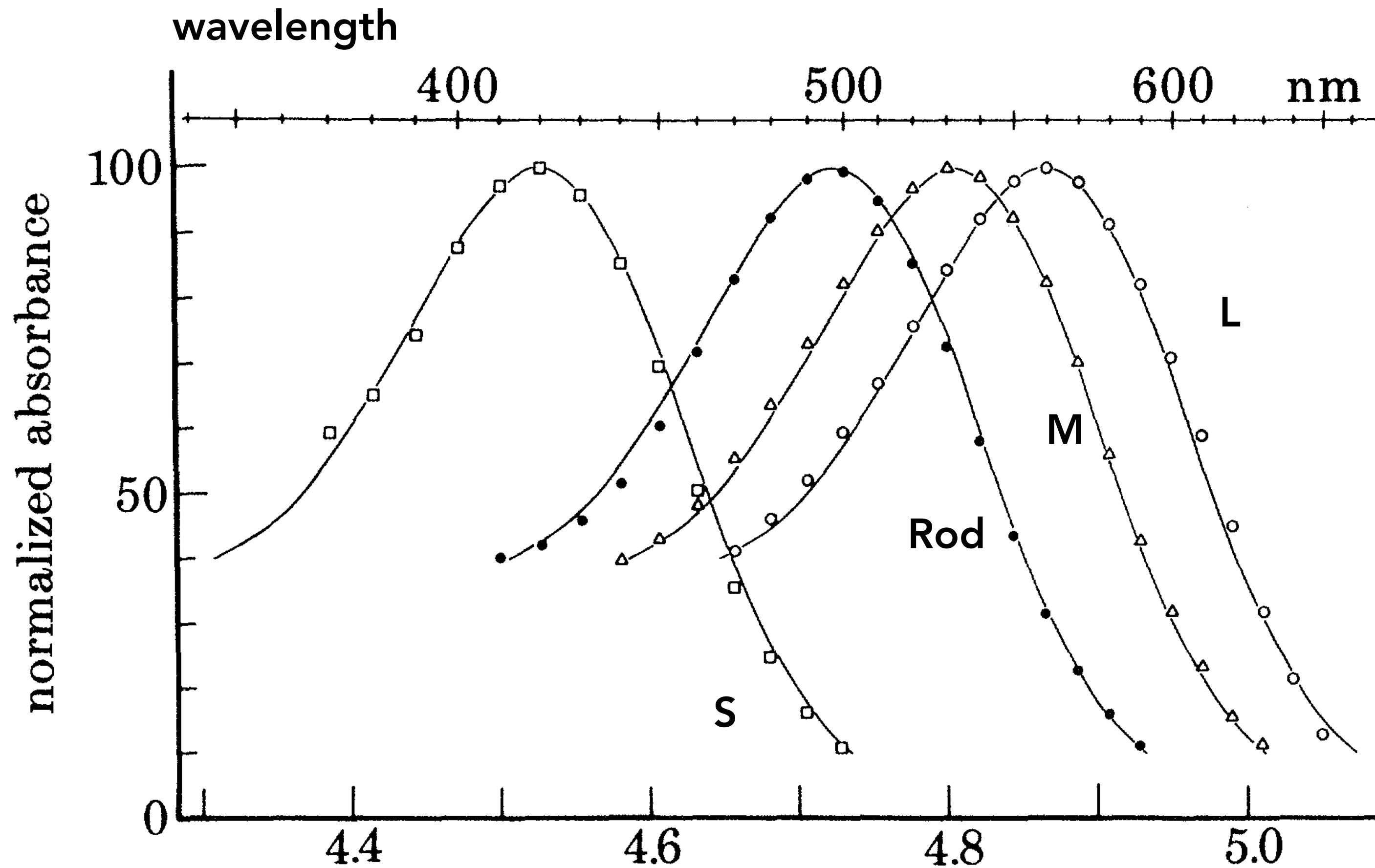
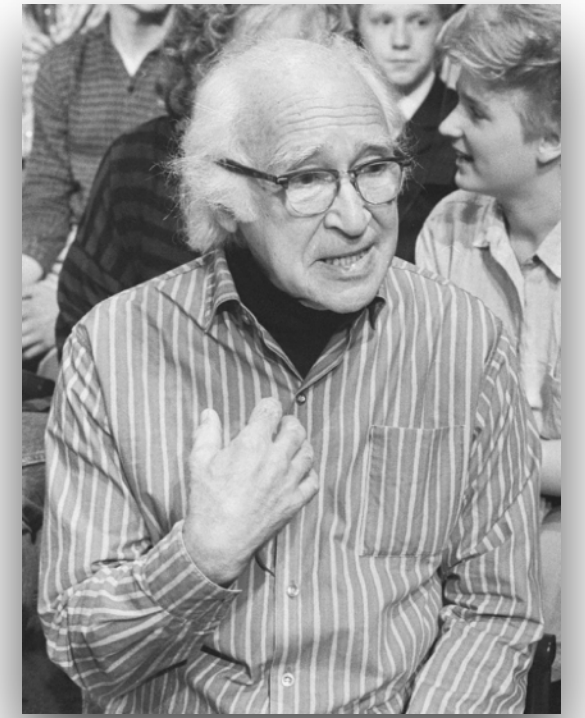
$$p = 1 - T = 1 - e^{-cl\epsilon}$$

**Absorbance**  
(Optical Density)

$$A = -\log(T) = cl\epsilon$$

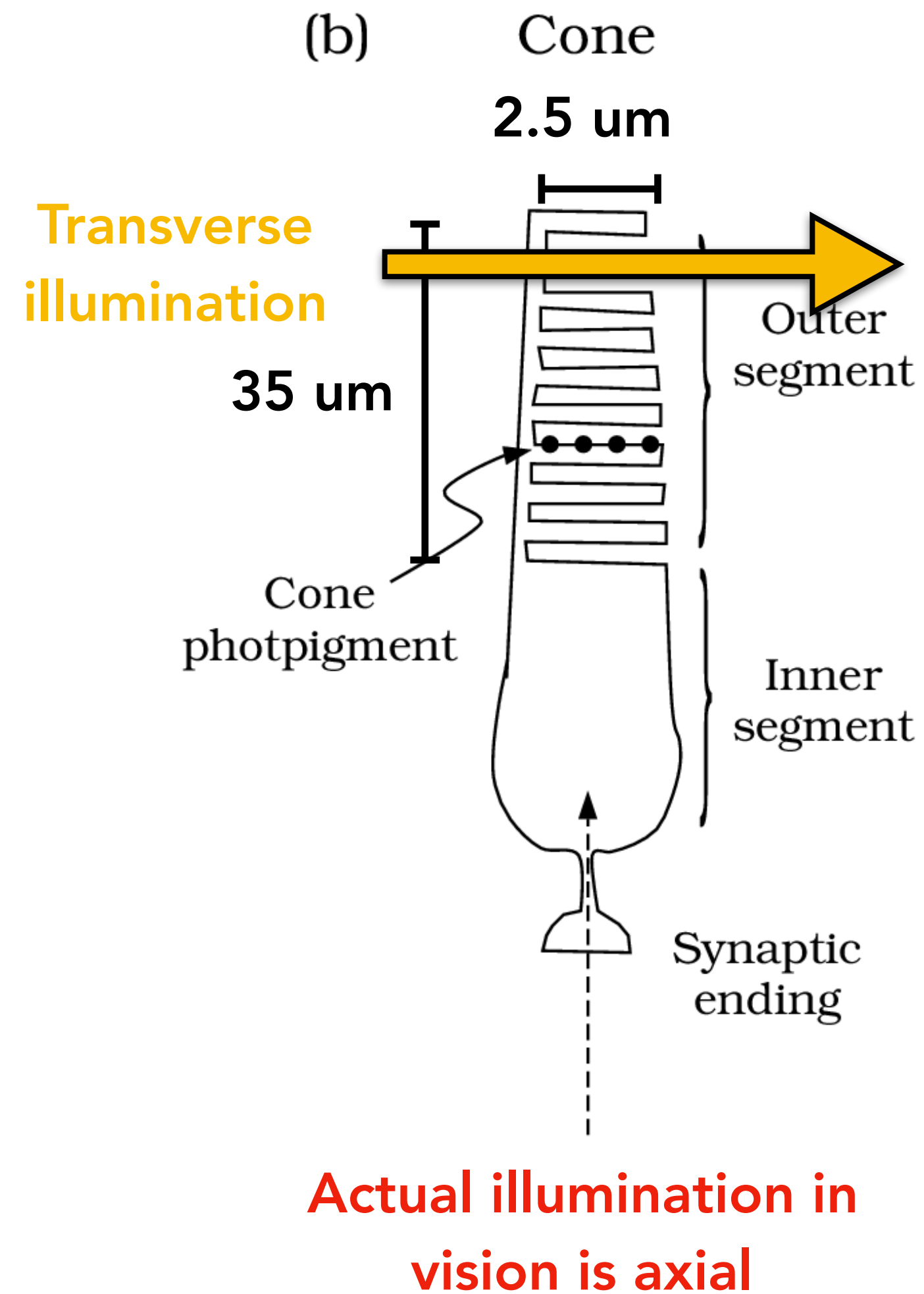
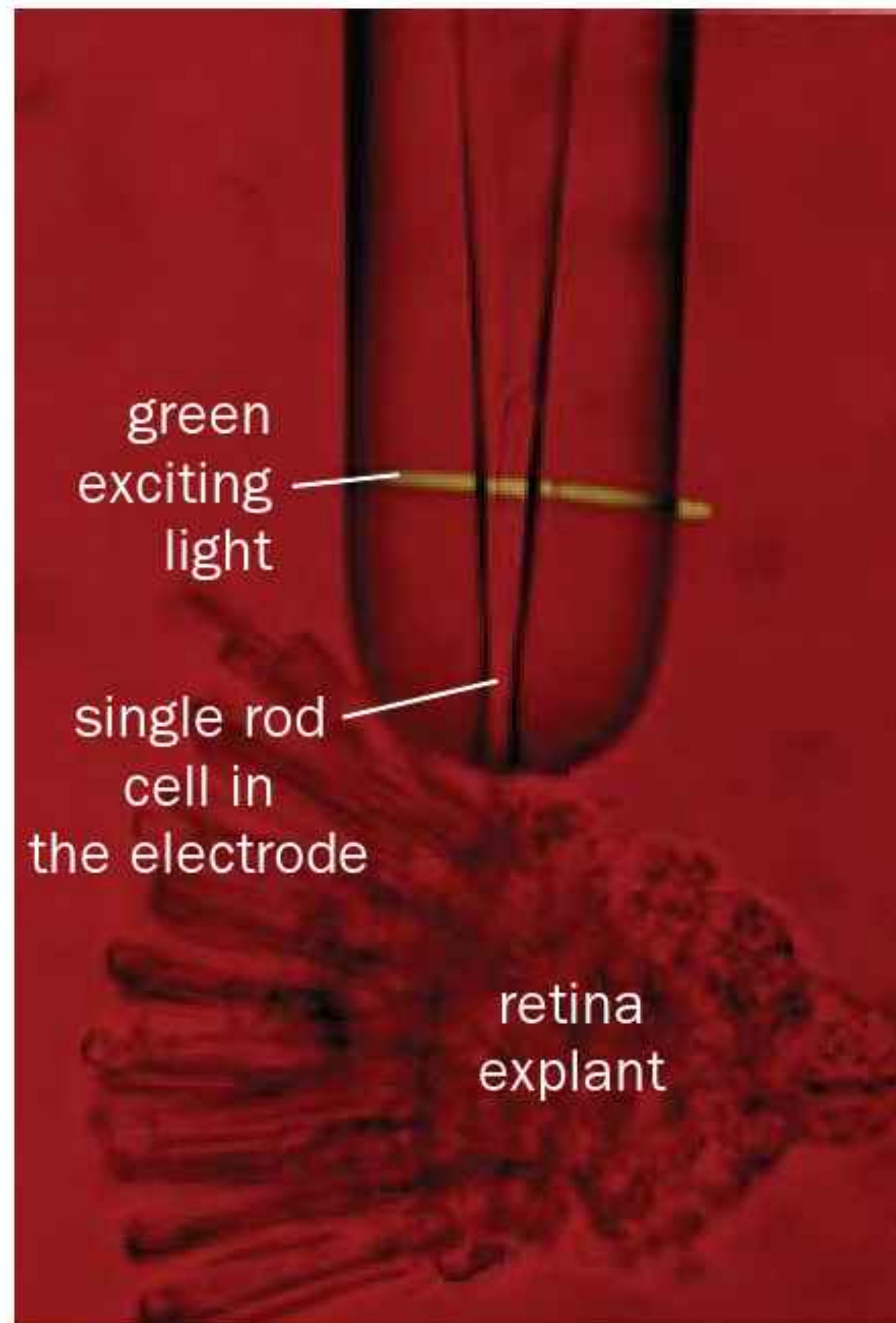
# (Normalized) Absorbance Spectra

George Wald  
(Nobel prize, 1967)



- Absorbance is usually normalized to peak at unity
- MSP results showed three distinct cone spectra, providing the first physiological evidence for the existence of three cones
- **L**(ong), **M**(edium), **S**(hort)

# Complication: Transverse vs. Axial Illumination



$$A_{\text{transverse}} = cl_{\text{transverse}}\epsilon$$

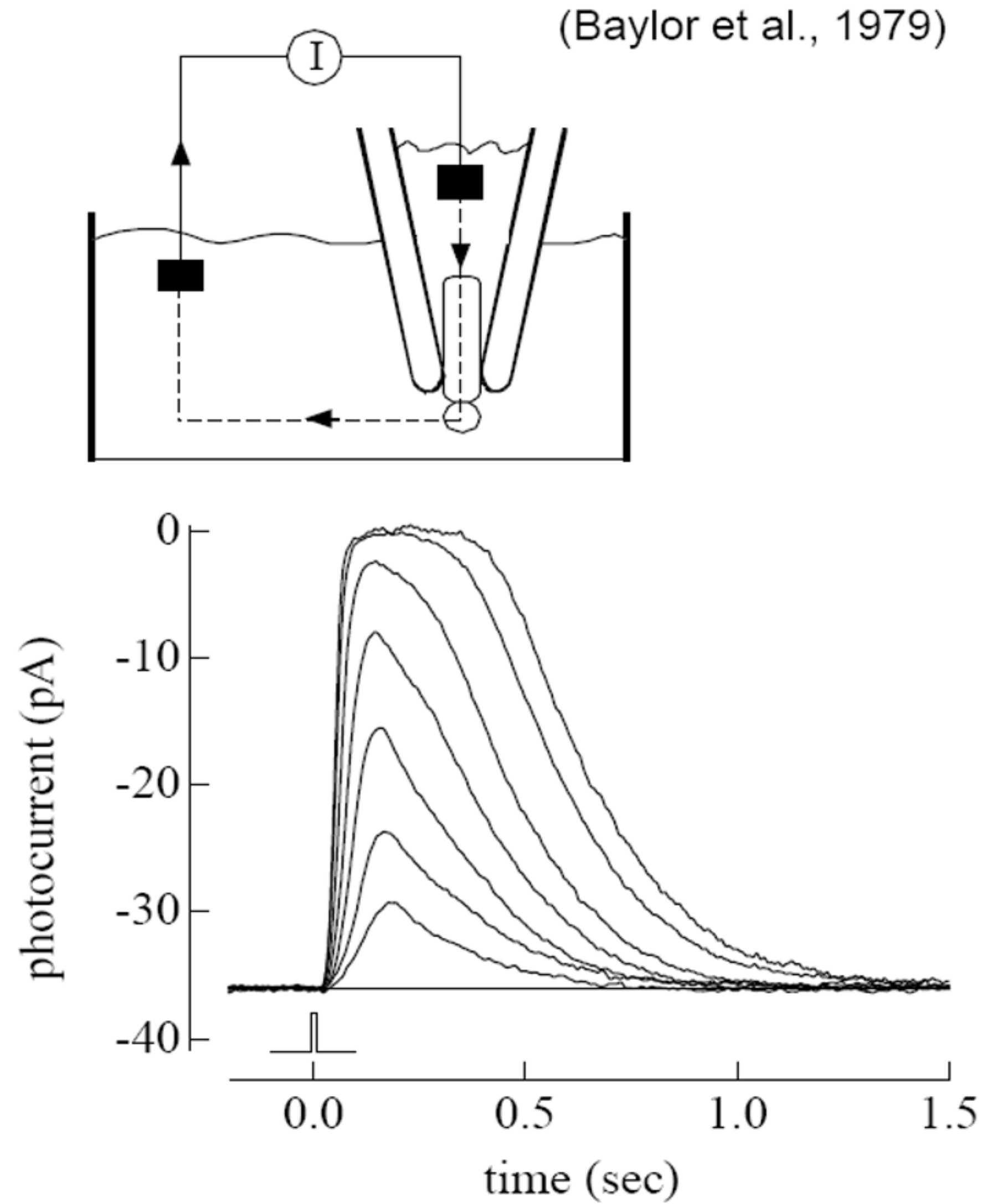
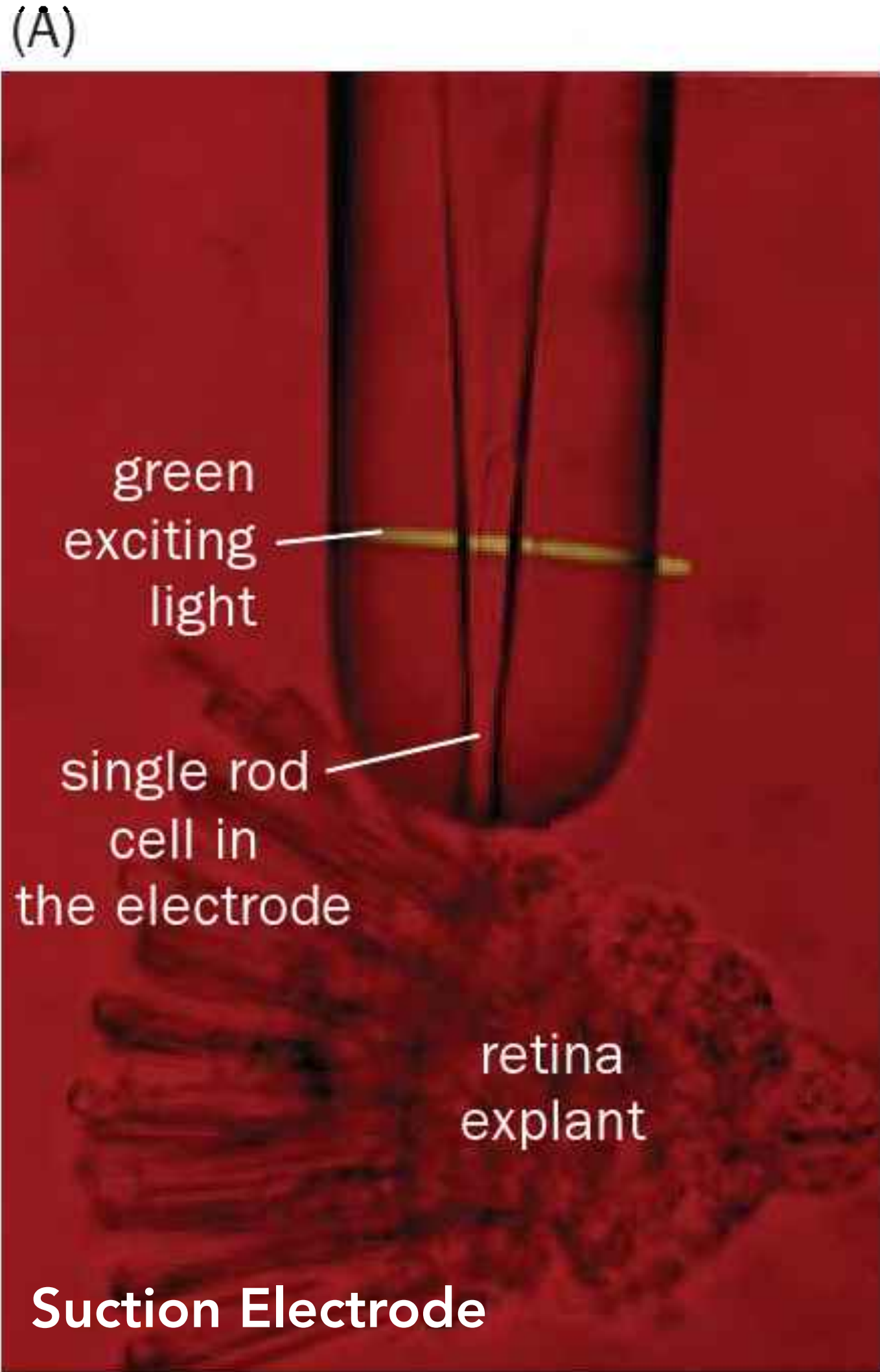
$$A_{\text{specific}} = c\epsilon$$

$$A_{\text{axial}} = cl_{\text{axial}}\epsilon$$

$$p_{\text{axial}} = 1 - e^{-A_{\text{axial}}}$$

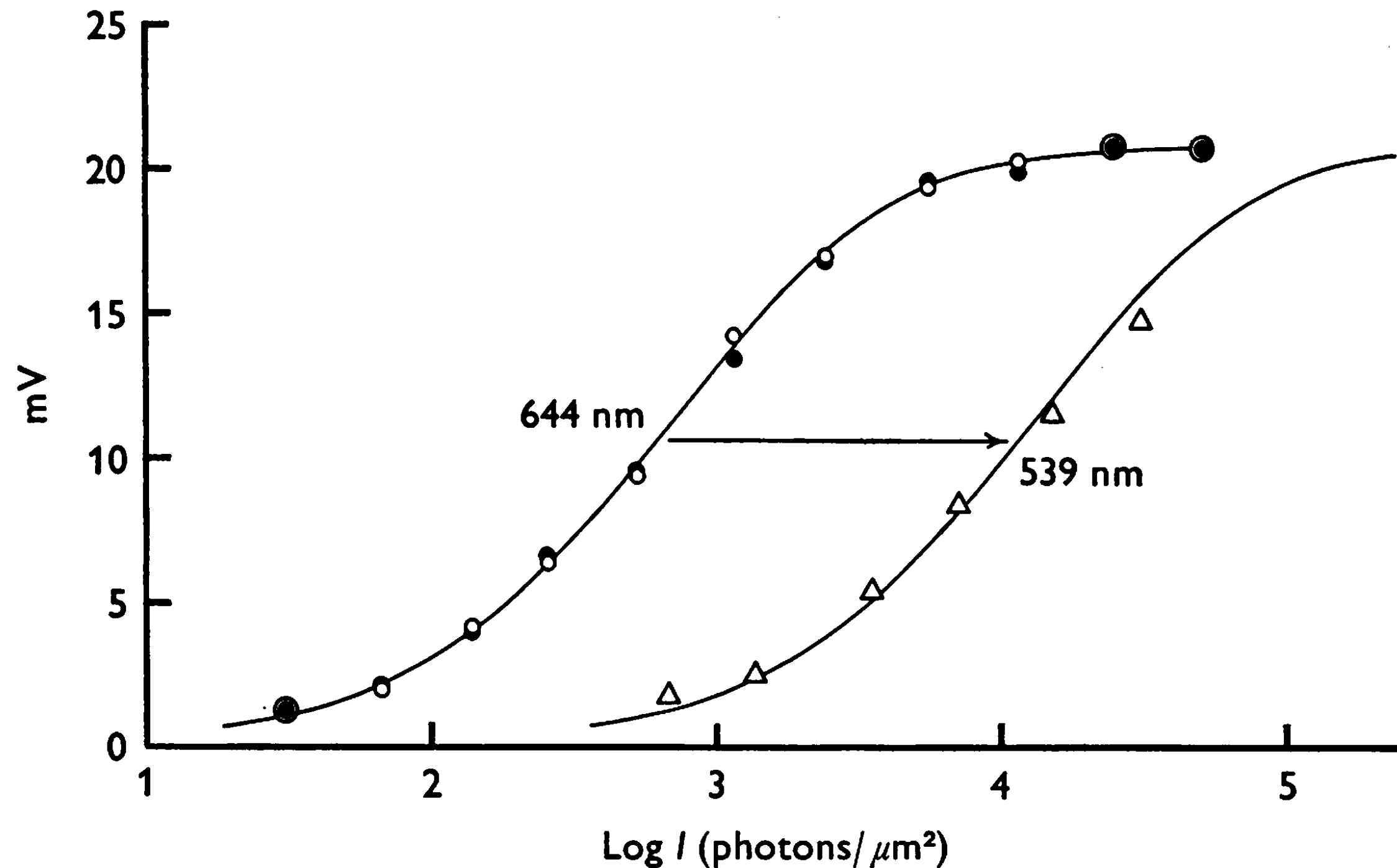


# Electrical Responses From Suction Electrode



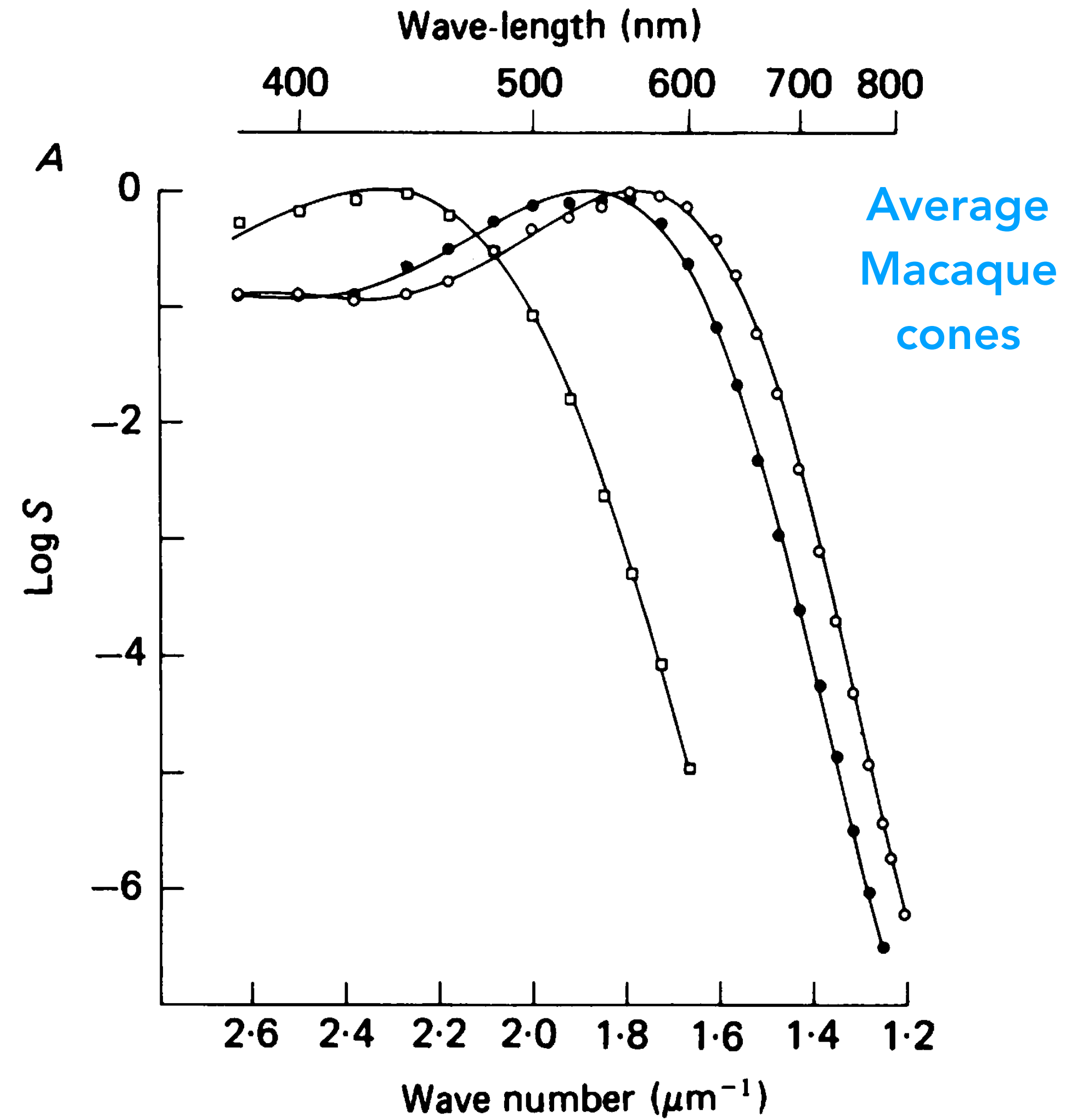
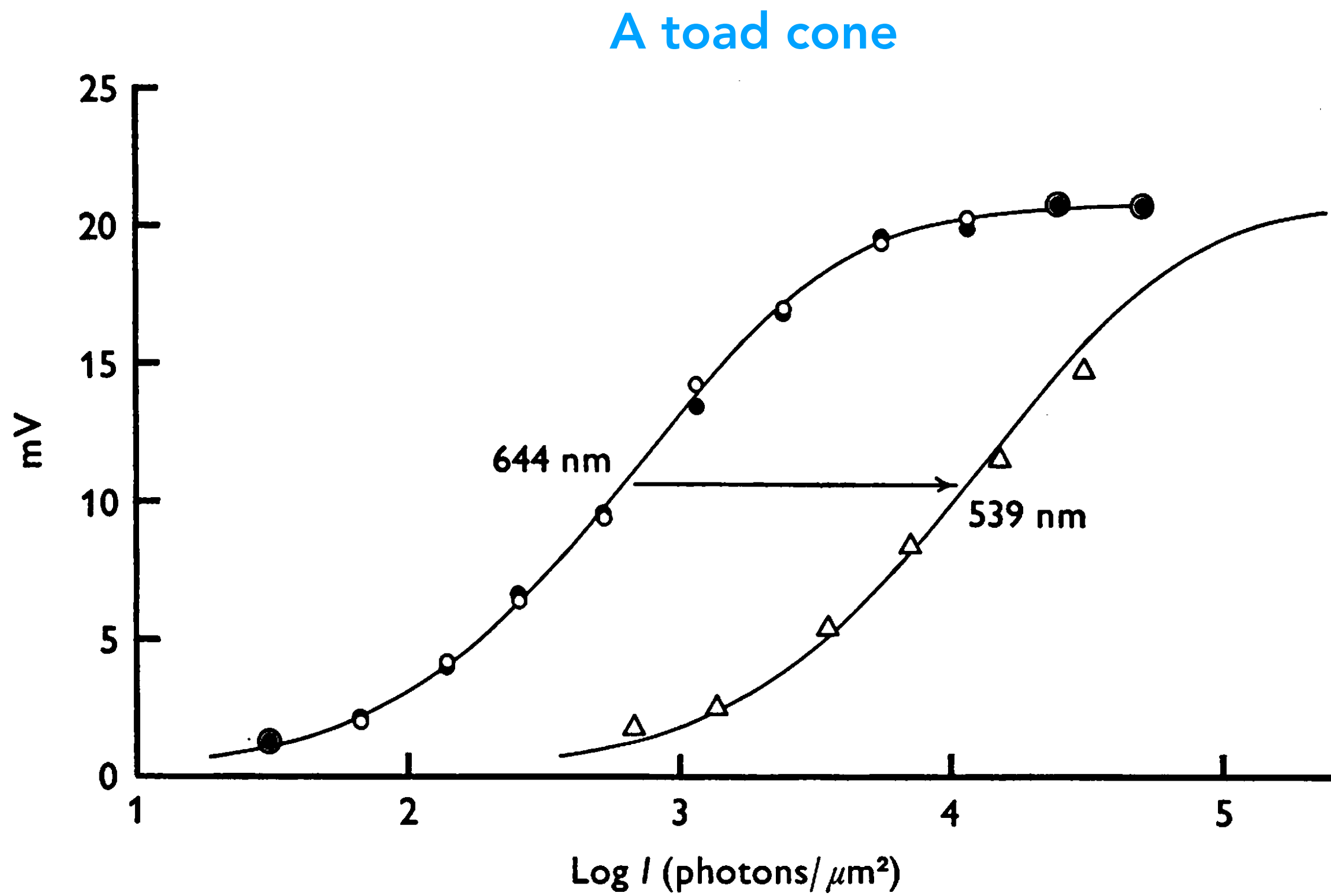
# Electrical Responses vs. Light Intensity

A toad cone



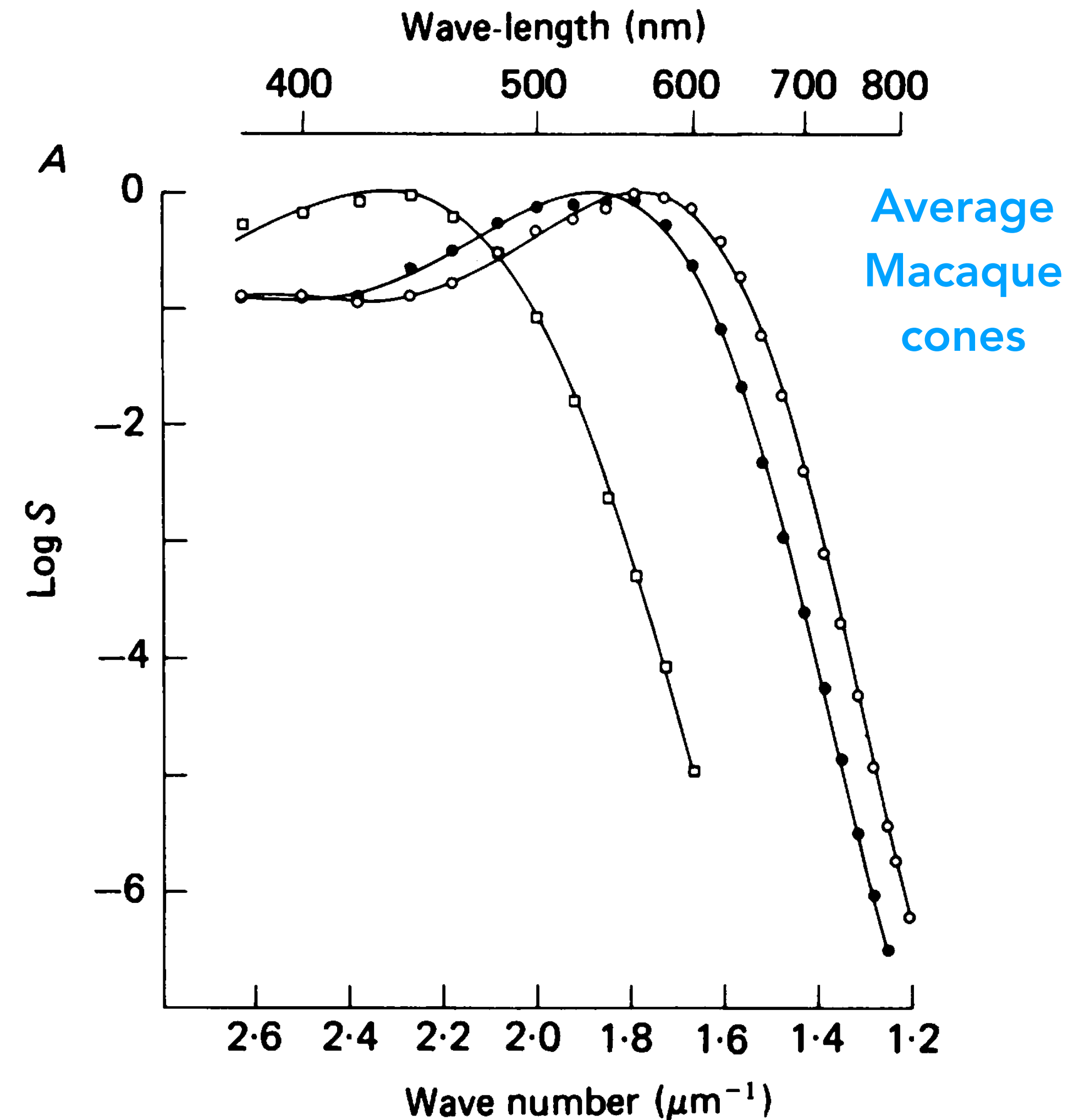
- Electrical response (photovoltage) vs. flash intensity at two wavelengths.
- The responses at 644 nm and 539 nm are the same, but the light intensity (# of photons) at 539 nm is 18.6 times higher than that at 644 nm.
- It must mean the absorptance at 539 nm is 5.3% (1/18.6) of that at 644 nm — according to the Principle of Univariance.

# Spectral Sensitivity From Electrical Responses



# Spectral Sensitivity From Electrical Responses

- The spectral sensitivities are relative
  - We can only tell absorptance of A nm is 5% of that of B nm, but we don't know absolute fraction absorbed at A/B.
  - So the results are equivalent to the *normalized* absorptance spectra measured from MSP, which can give us *absolute* absorptance.
  - $1 - e^{-A} \approx A$ , so normalized absorbance can be approximated by normalized absorptance.



# Cone Fundamentals

# Spectral Sensitivity Measured from Cornea

- So we have focused on absorption by just the photoreceptors
- But for a flux of photons enter the eye, they are absorbed by other media before reaching the retina
  - They are called pre-receptoral filters
- There are two main pre-receptoral filters, optics and macular pigments



# Absorption by Ocular Media

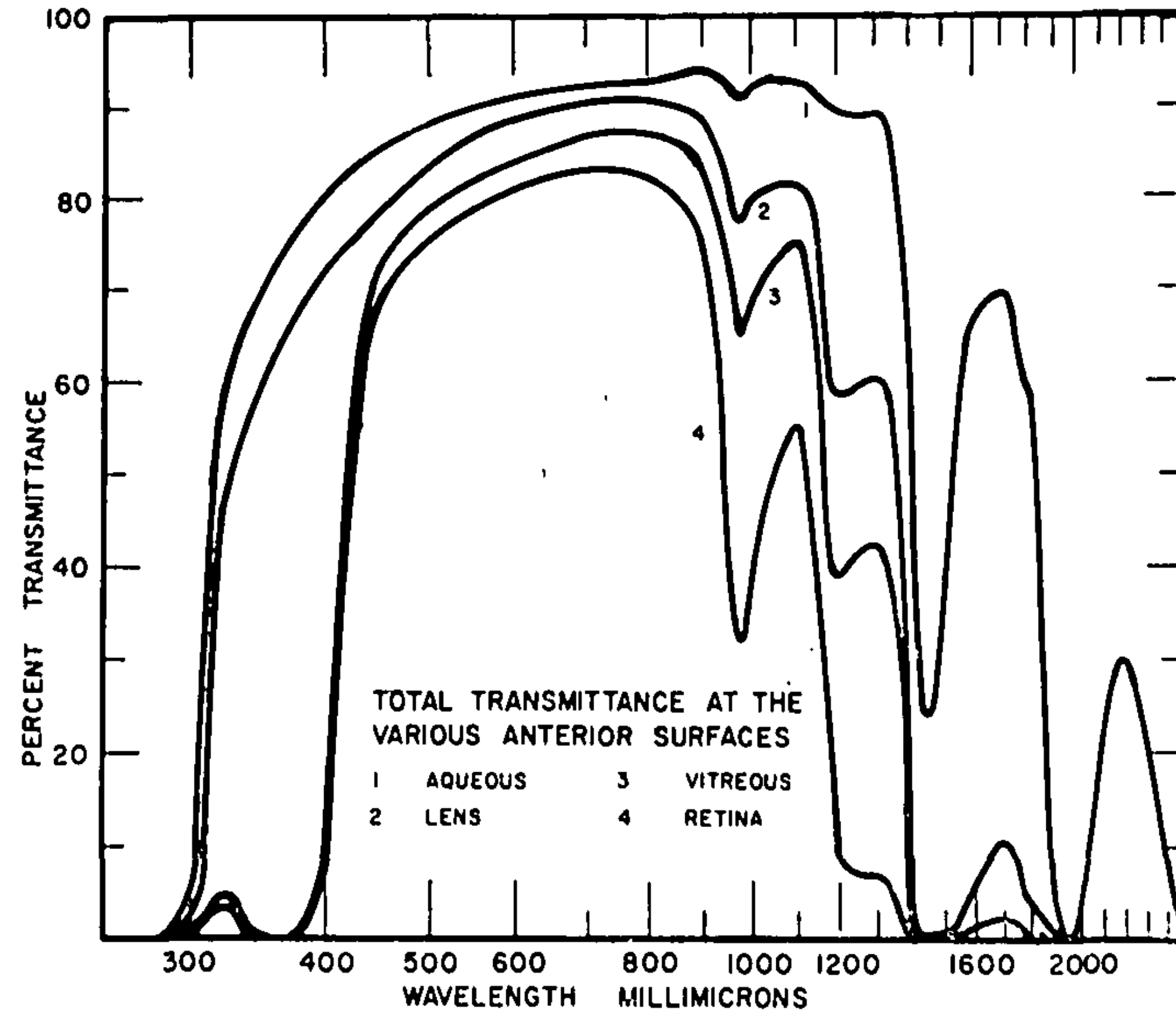
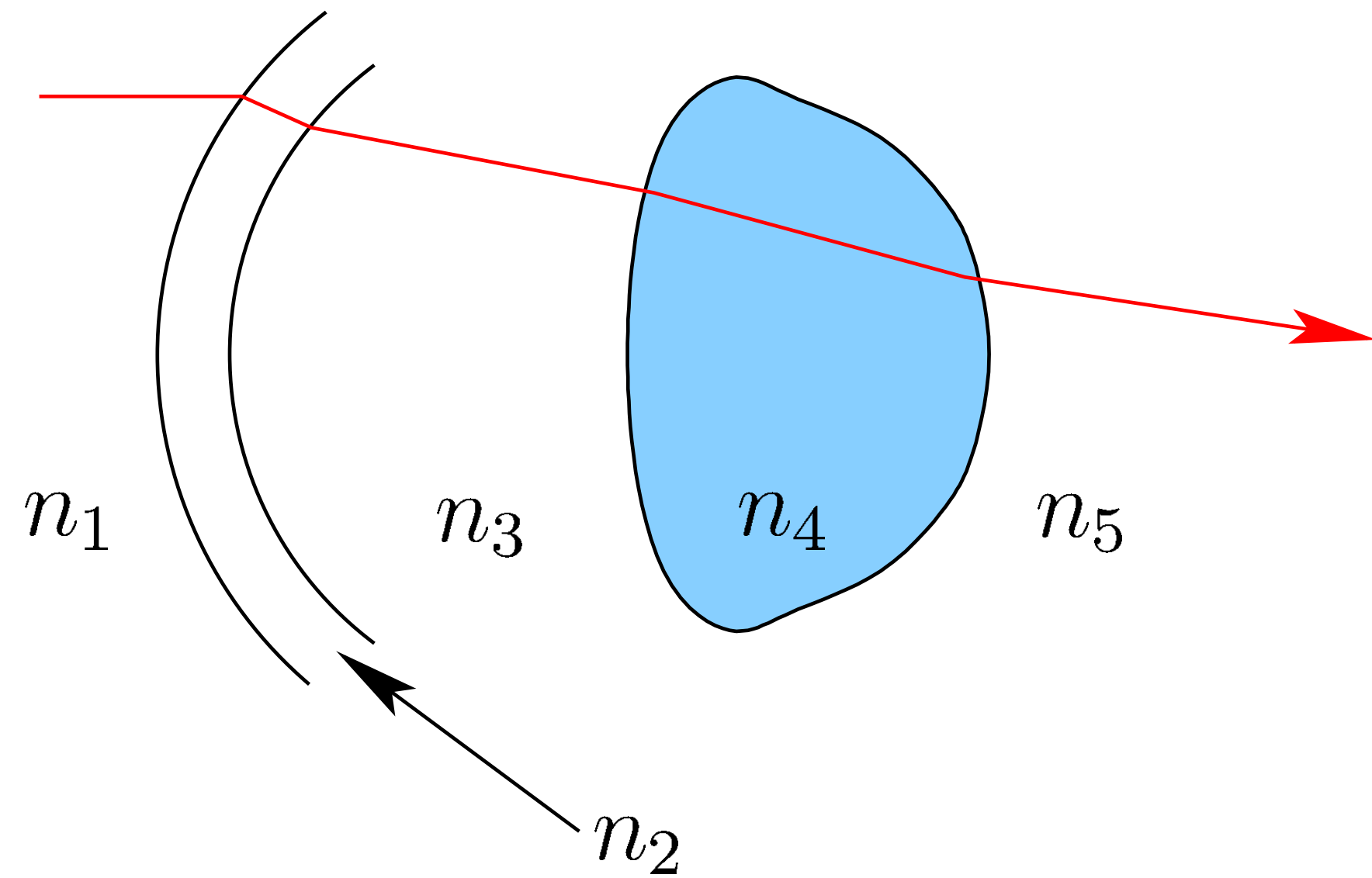
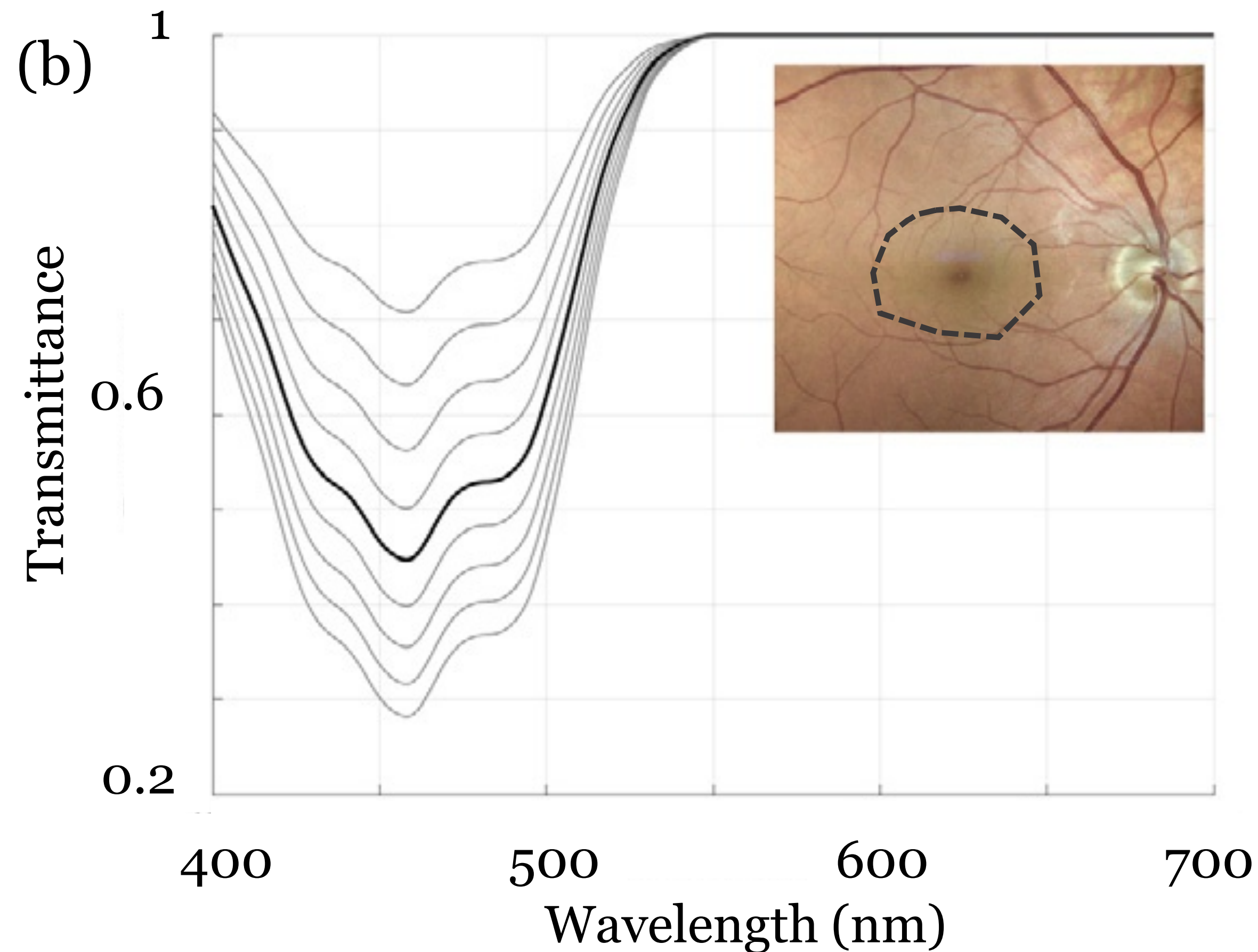


Fig. 7. Total transmittance through entire eye.

# Absorption by Macular Pigments



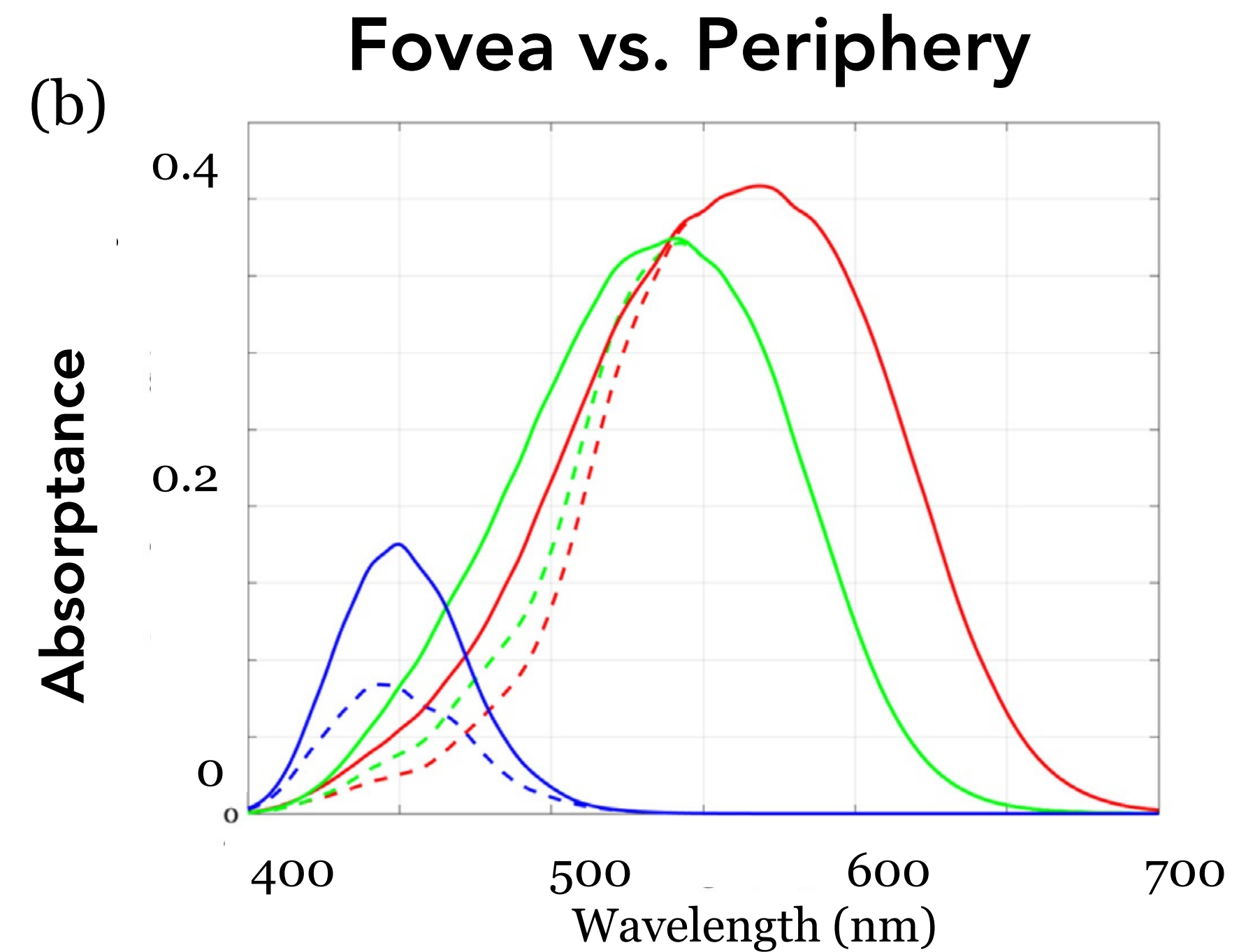
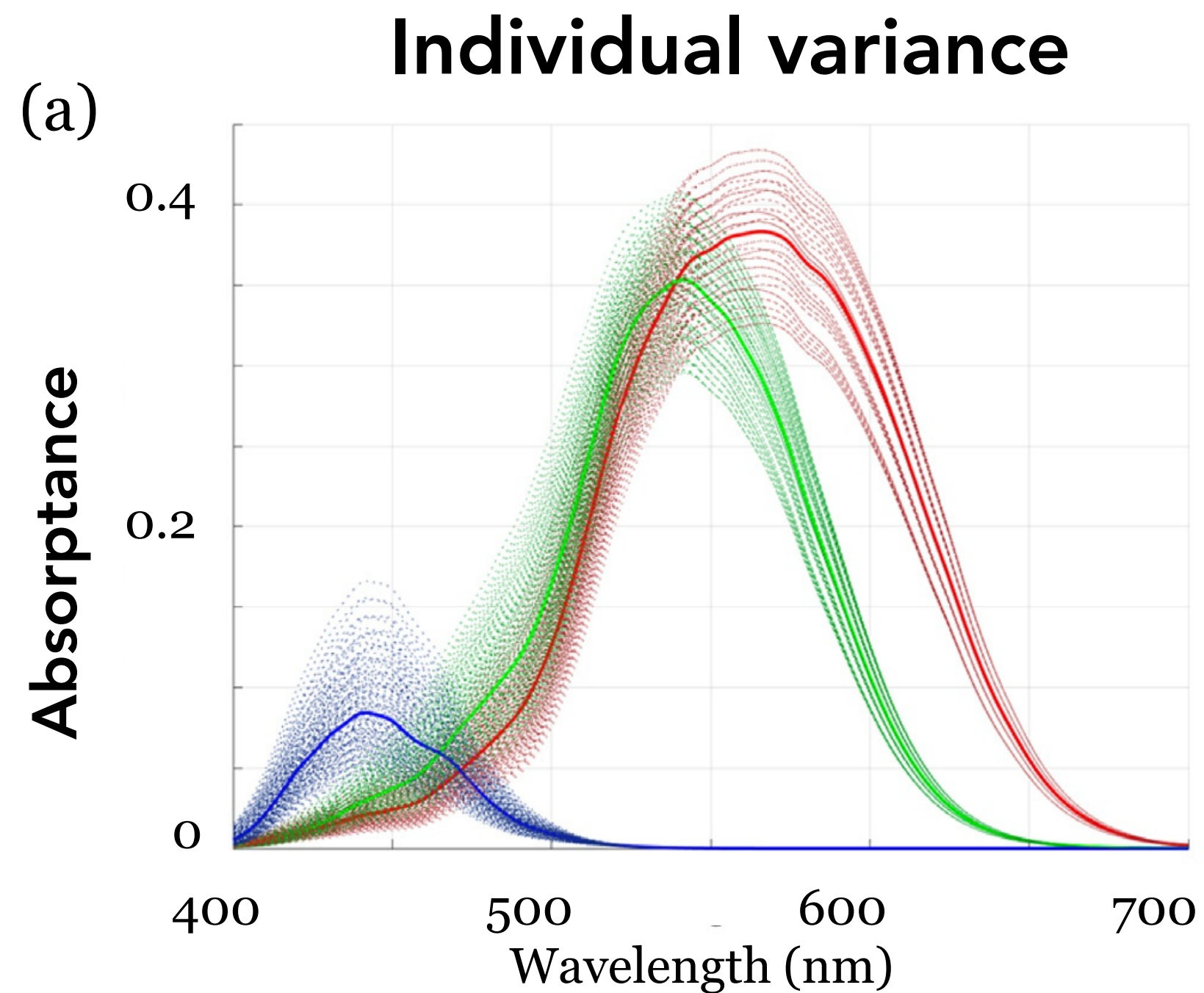
- **Macular pigments**
  - Concentrated in a small area inside the fovea (so don't affect rod vision much, and the results at periphery will be different)
  - Believe to exist to counter optical aberrations and protect retina from light damage



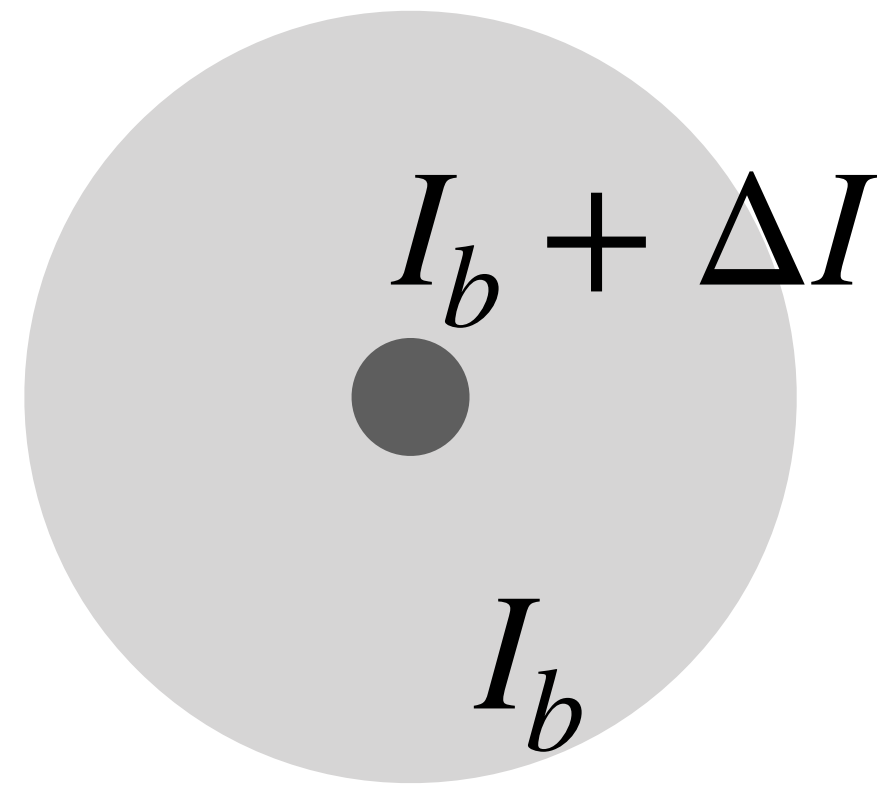
# Cone Fundamentals (Cornea-Referred Spectral Sensitivity)

$$E(\lambda) = l(\lambda)m(\lambda)p(\lambda)$$

Ocular transmittance      Macular transmittance      Photoreceptor absorptance

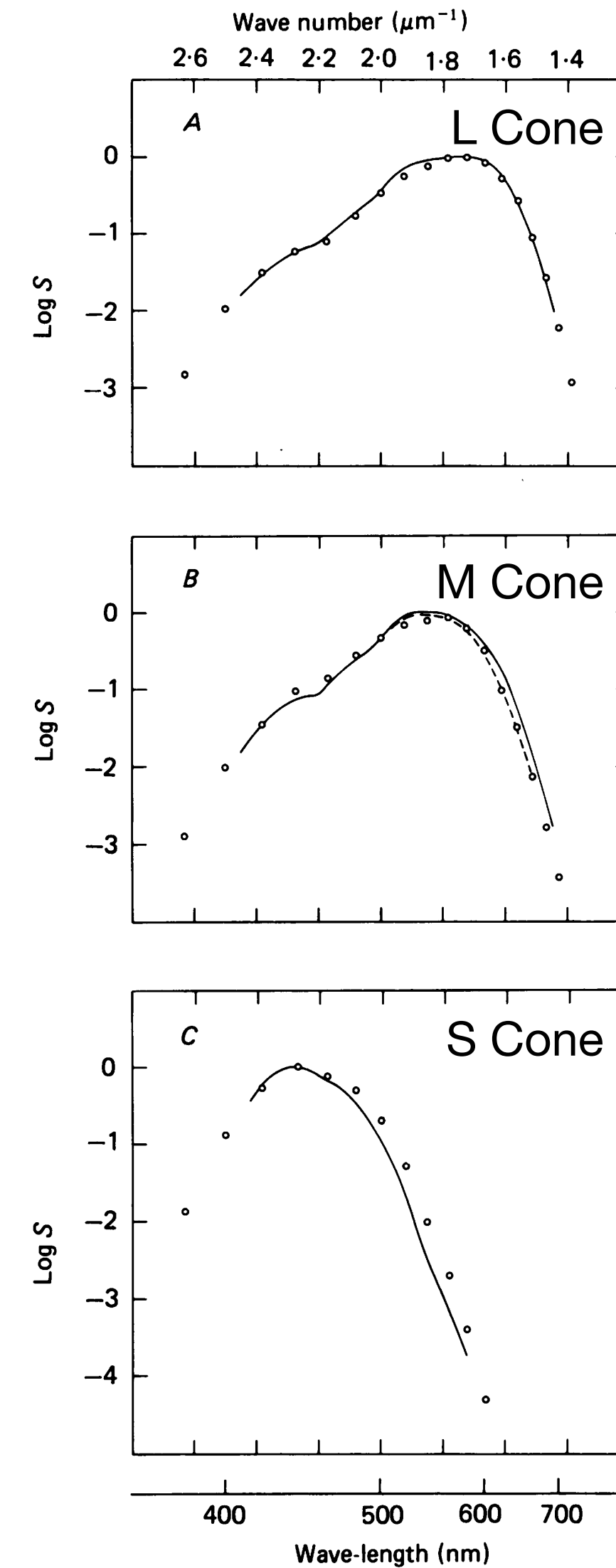
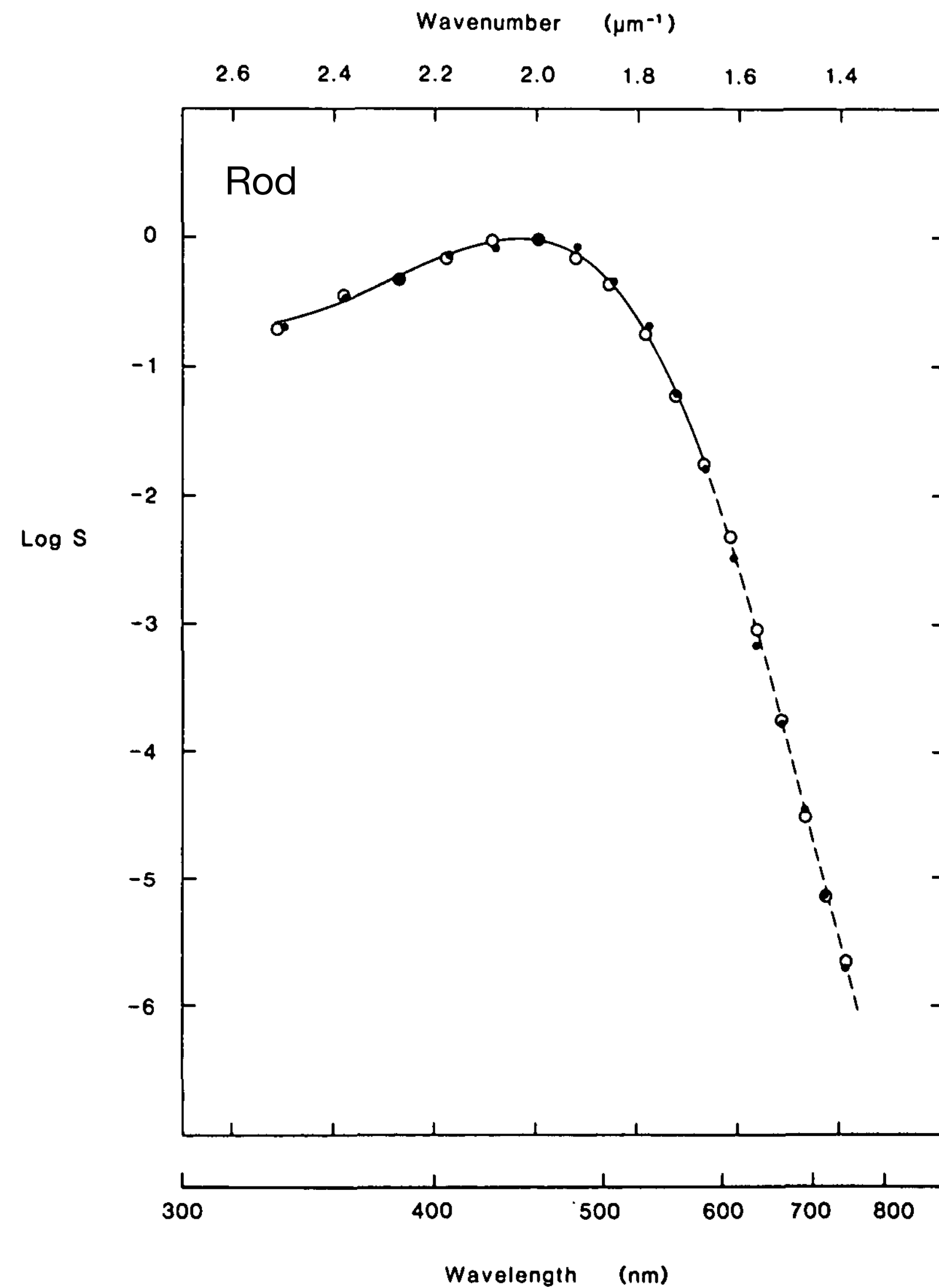


# Cone Fundamentals From Psychophysics

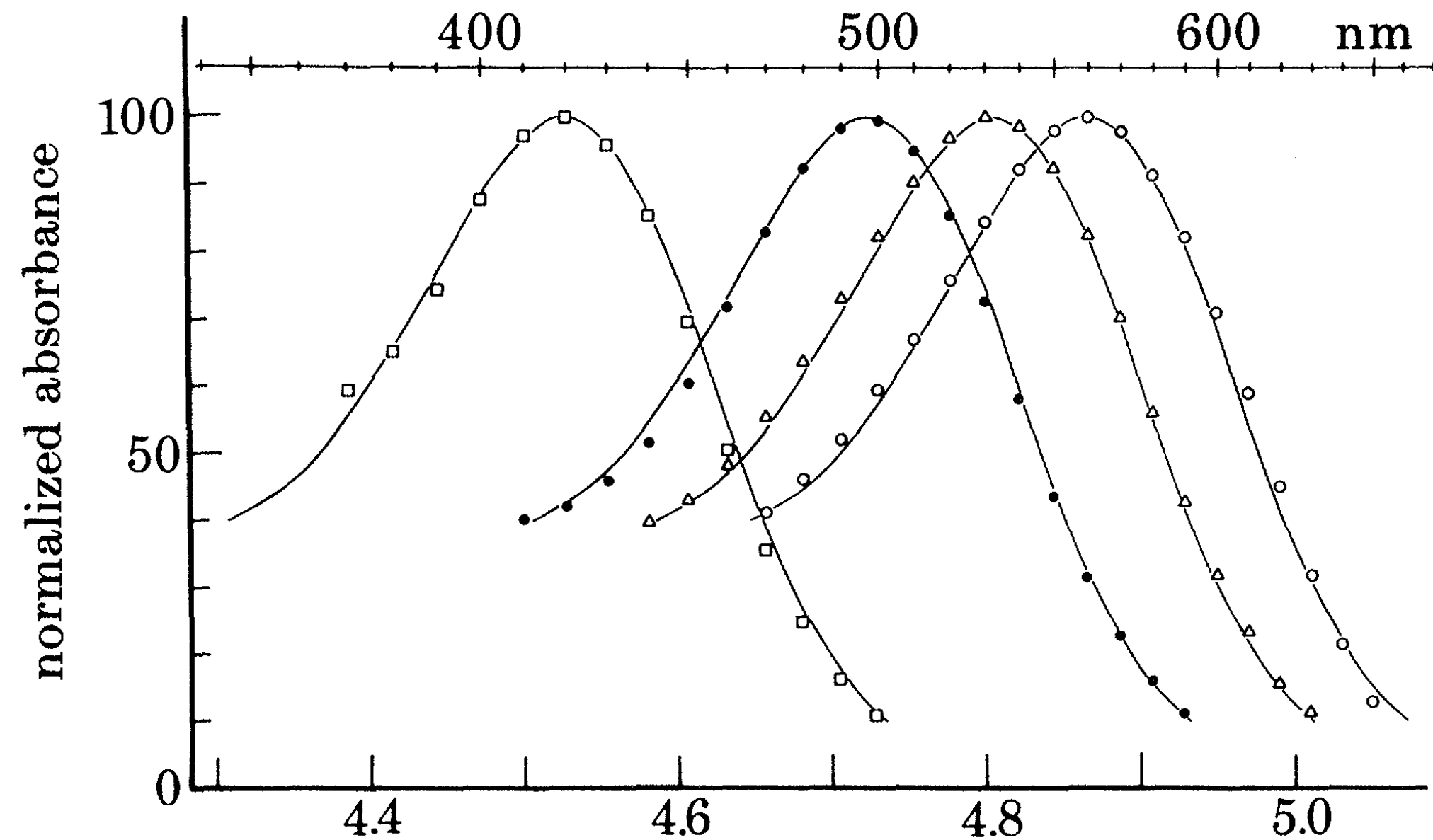


- For each photoreceptor type and frequency:
  - Adjust the intensity of the test light so that it's just noticeable from the background
  - The sensitivity at that frequency for that photoreceptor type is  $1/\text{threshold intensity}$
- Repeat this for each frequency and for each photoreceptor type
- Assumption is that the electrical response needed for "just noticeability" is constant.

# Data from Physiology and Psychophysics Match



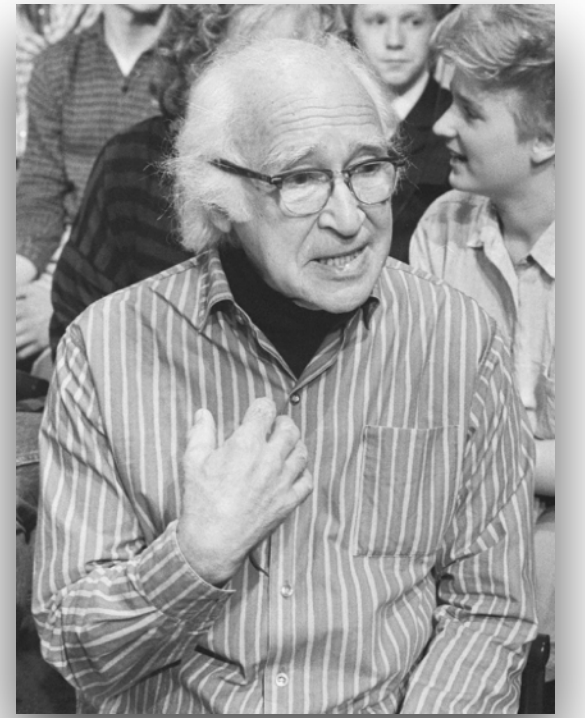
# Photoreceptor Isolation in Psychophysics



**Sensitivities overlap substantially, so in psychophysics how do we measure the responses from just one type?**

- Isolate rods vs. cones
  - Adjust light intensity to bleach rods
  - Measure from rod monochromats
- Isolate S cones by measuring from S-cone monochromats
- Isolating M cones from Deuteranopes, who have only M and S cones
  - Use high spatial/temporal frequency lights, to which S cones are insensitive.
  - Isolating L cones from Protanopes

**George Wald**  
(Nobel prize, 1967)



# Beyond Photon Counting:

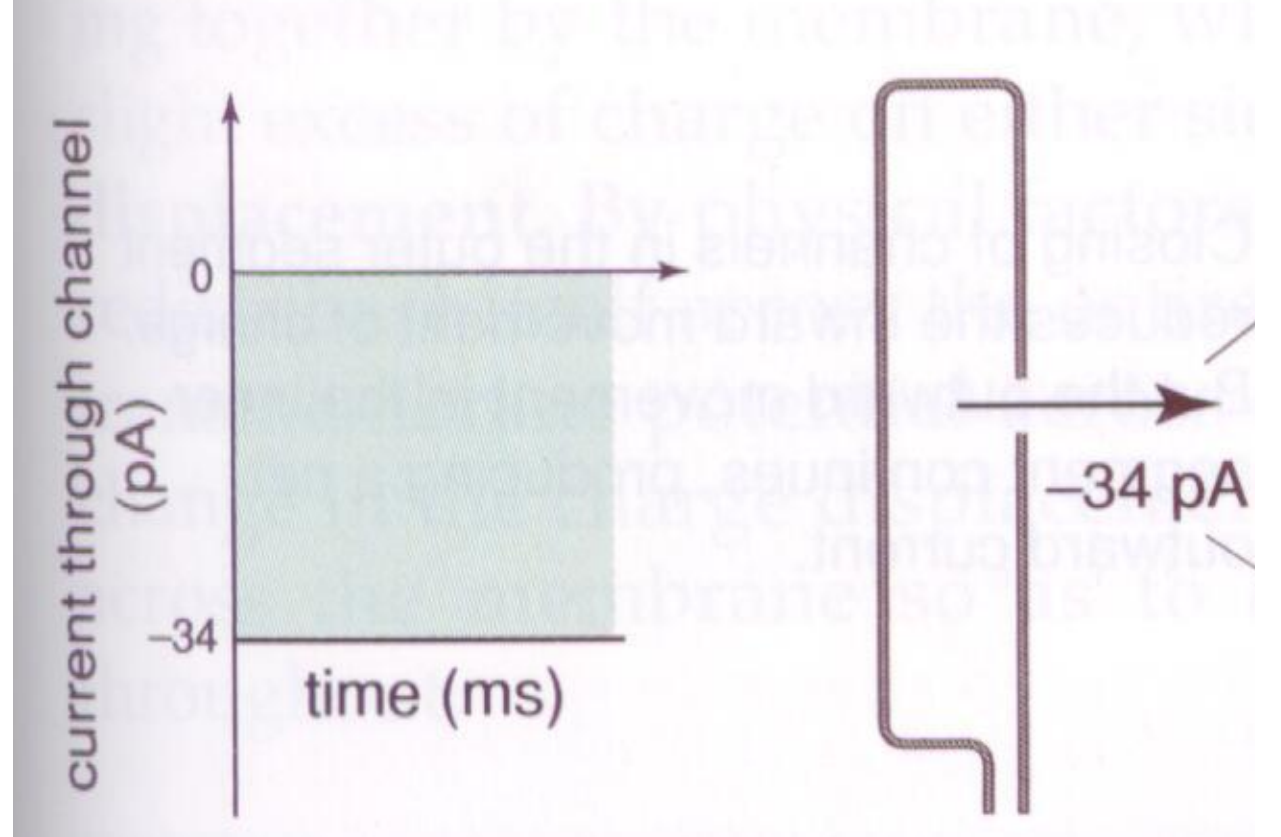
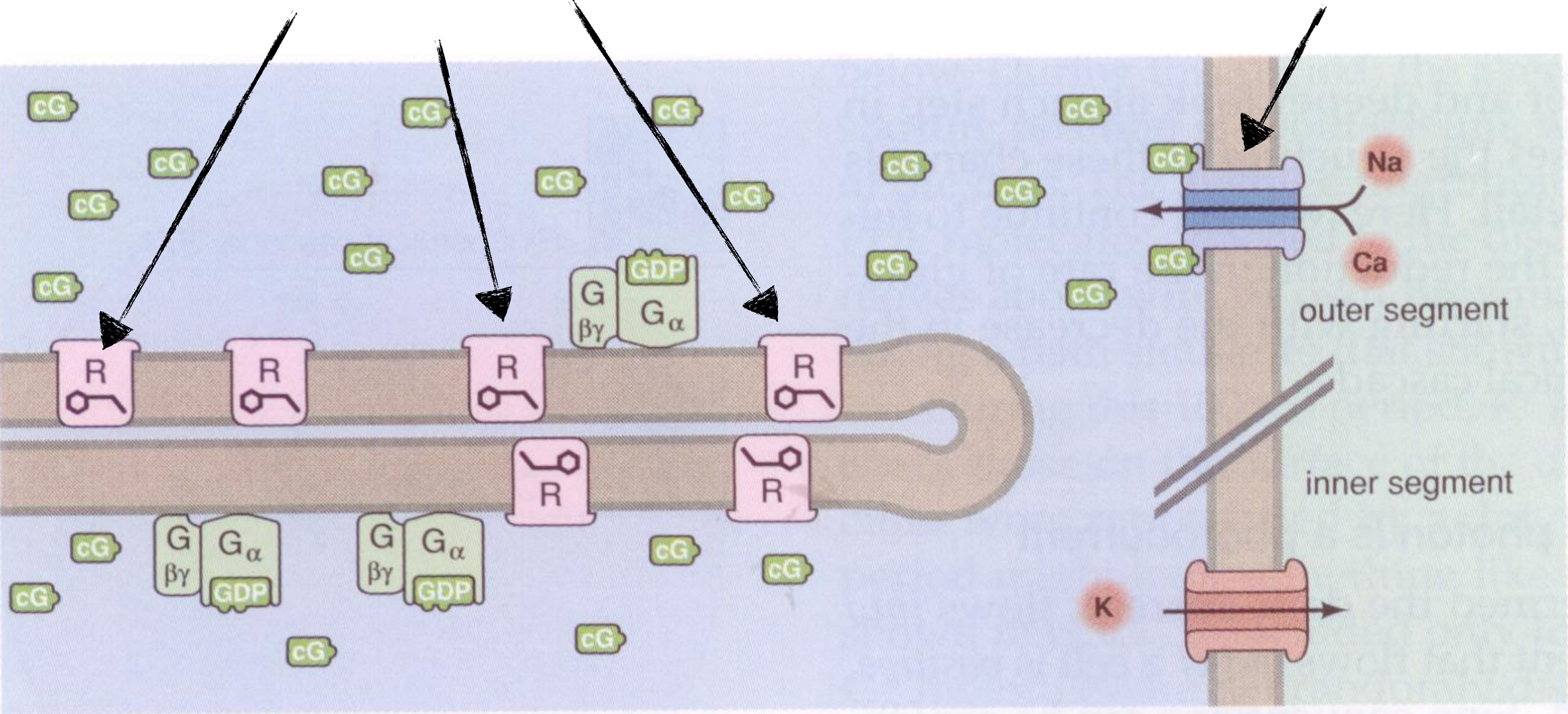
- Phototransduction
- Deactivation and Pigment Regeneration



# Dark Current of a Photoreceptor

Unexcited photopigments

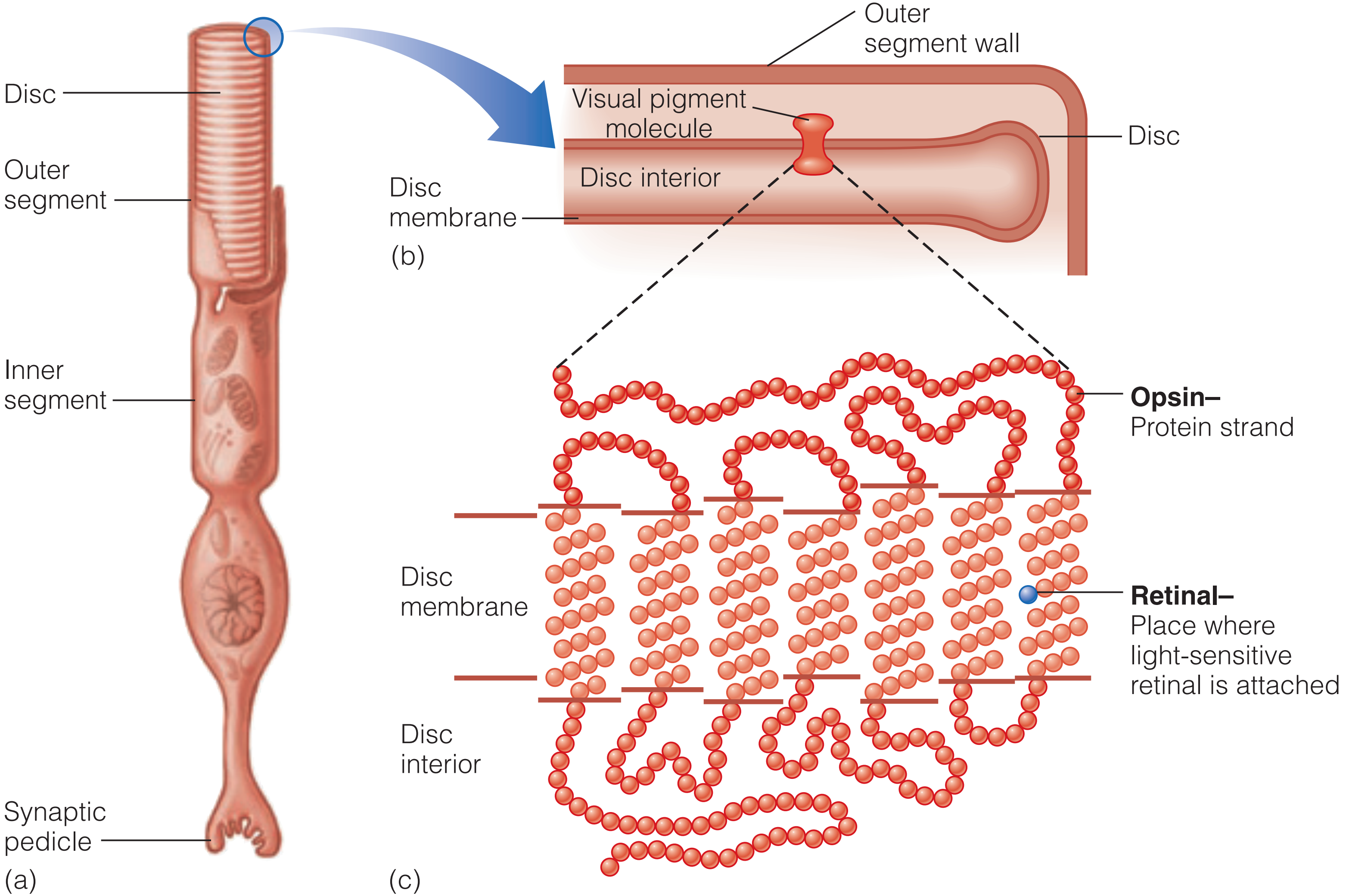
cG-gated ion Channel



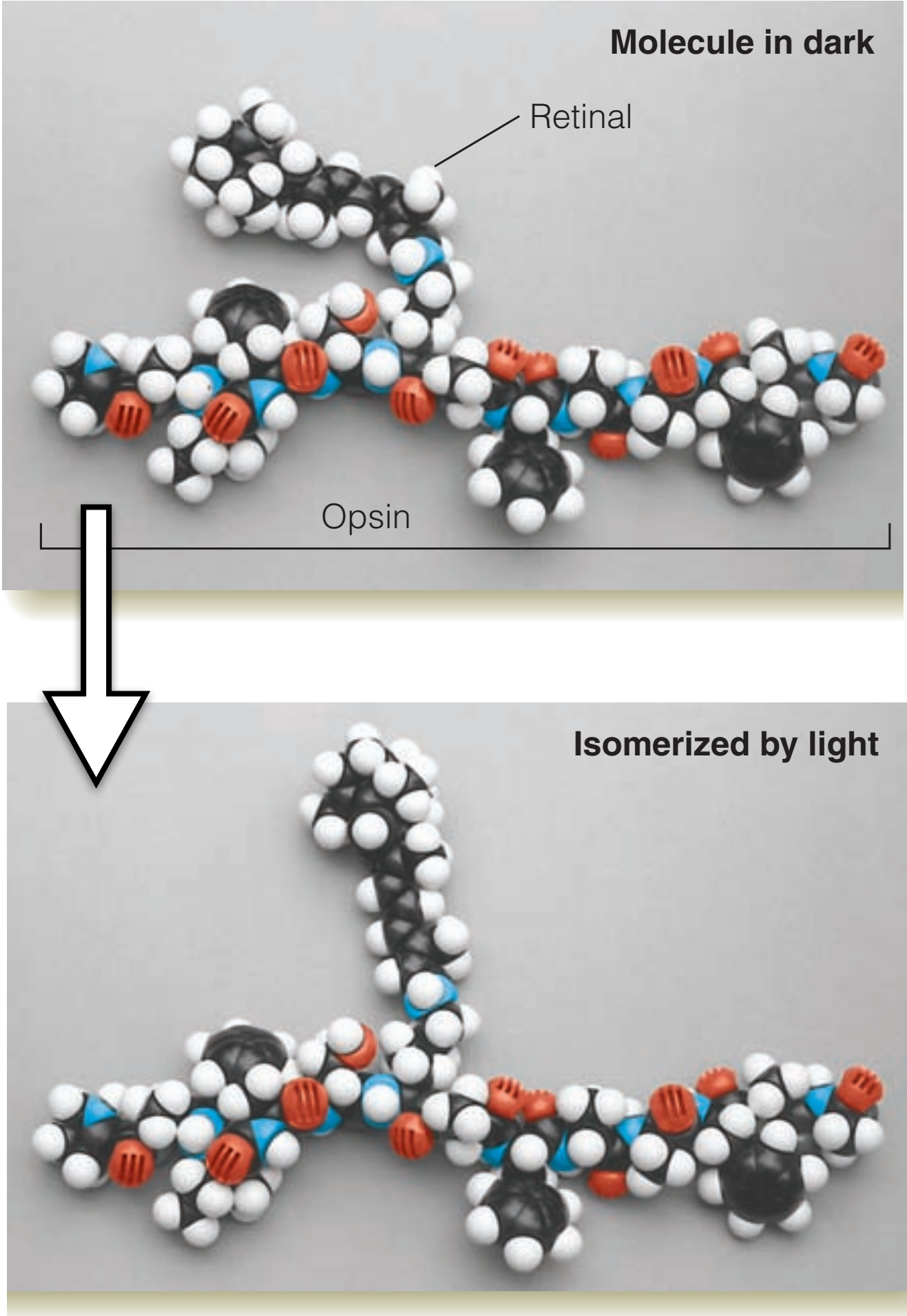
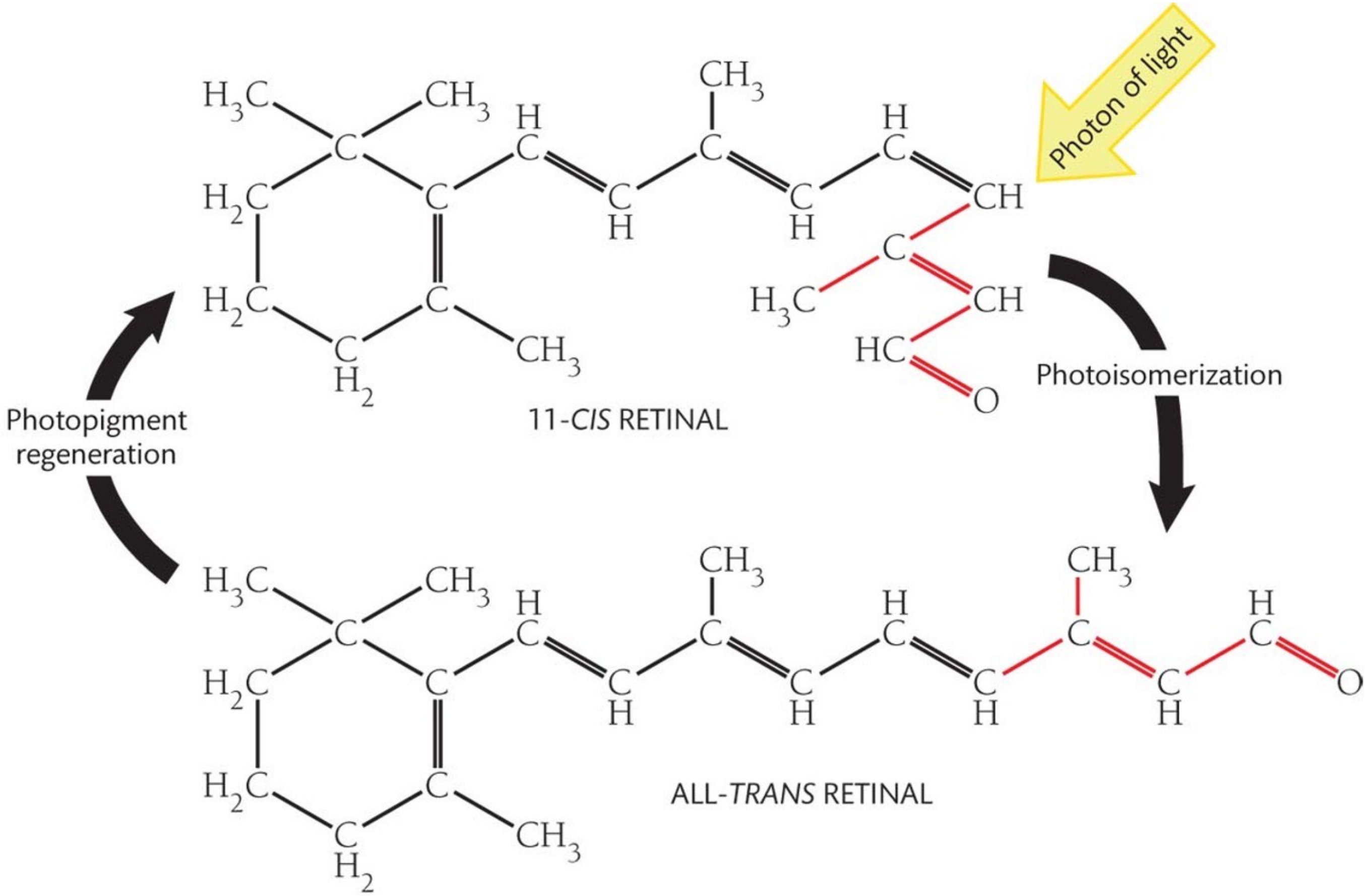
Because currents and voltages are conventionally measured from the interior of the cell to the extracellular fluid, a current is positive if it passes out of the cell and thus negative if it passes into the cell. Hence the dark current has a negative value.



# Pigment = a Long Opsin + a Small Retinal



# Pigment Isomerizes Upon Photon Absorption



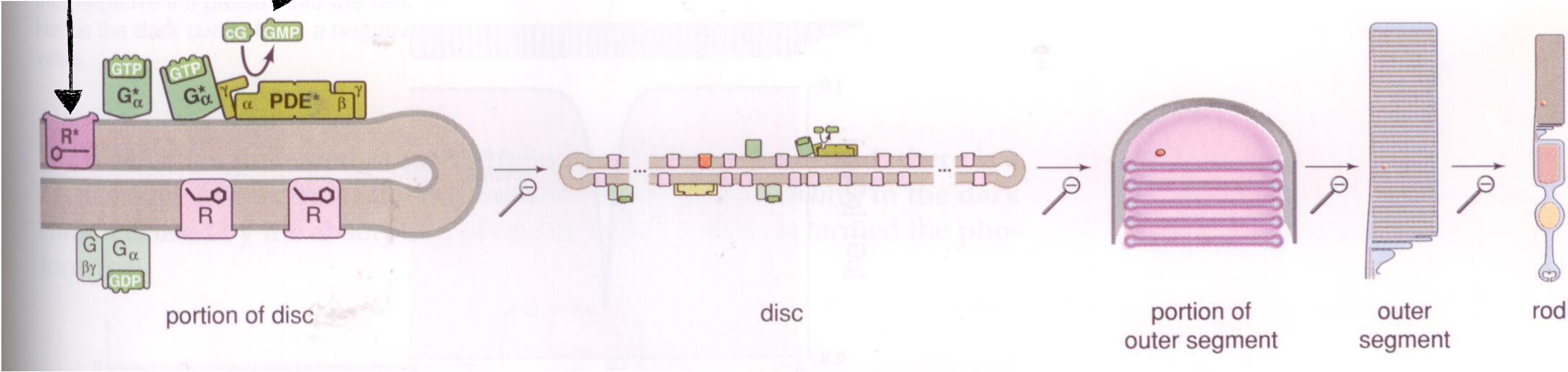


# Phototransduction

After a pigment is excited, it roams about and causes a cascade of biochemical reactions that reduce the cG concentration.

A single excited pigment removes thousands of cG molecules

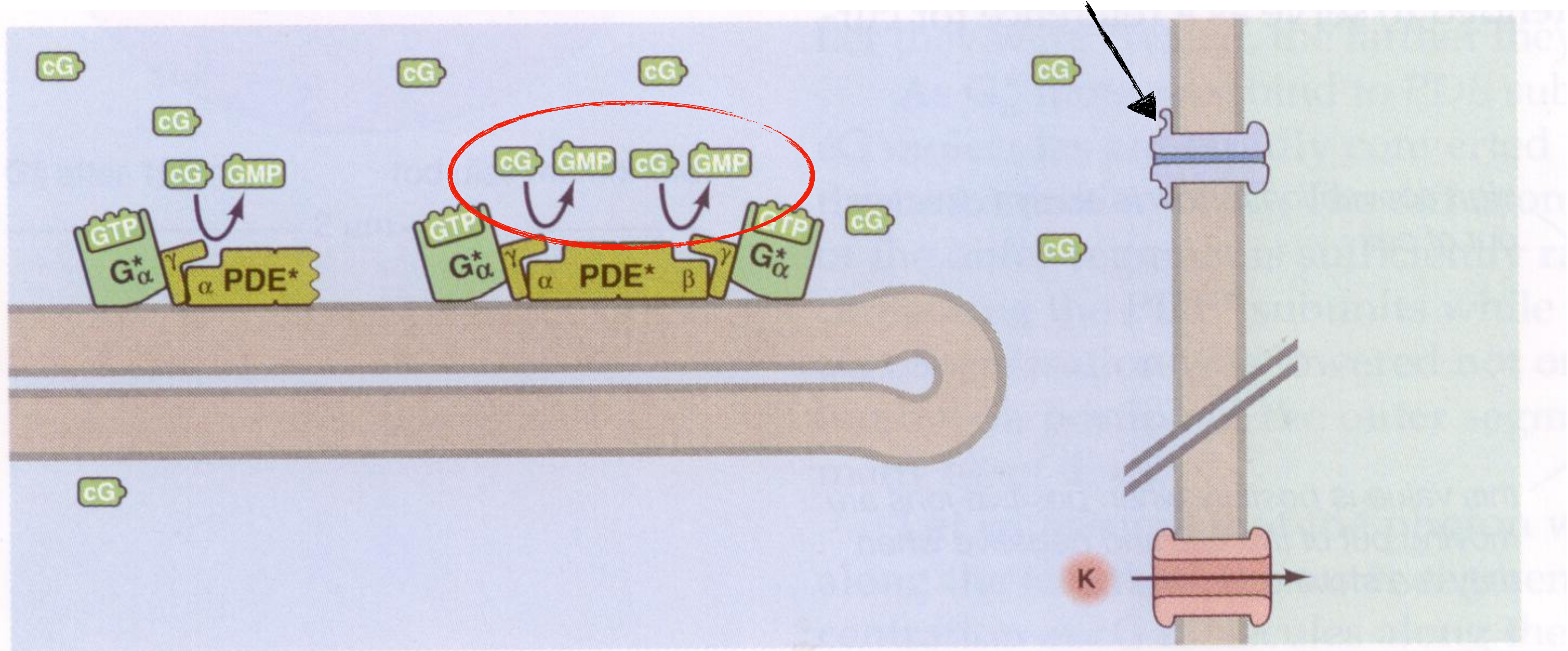
An activated/excited pigment





# cG-Gated Ion Channels Close

a single rod pigment excitation reduces about 1,400  
cG channels (2% reduction in dark current)



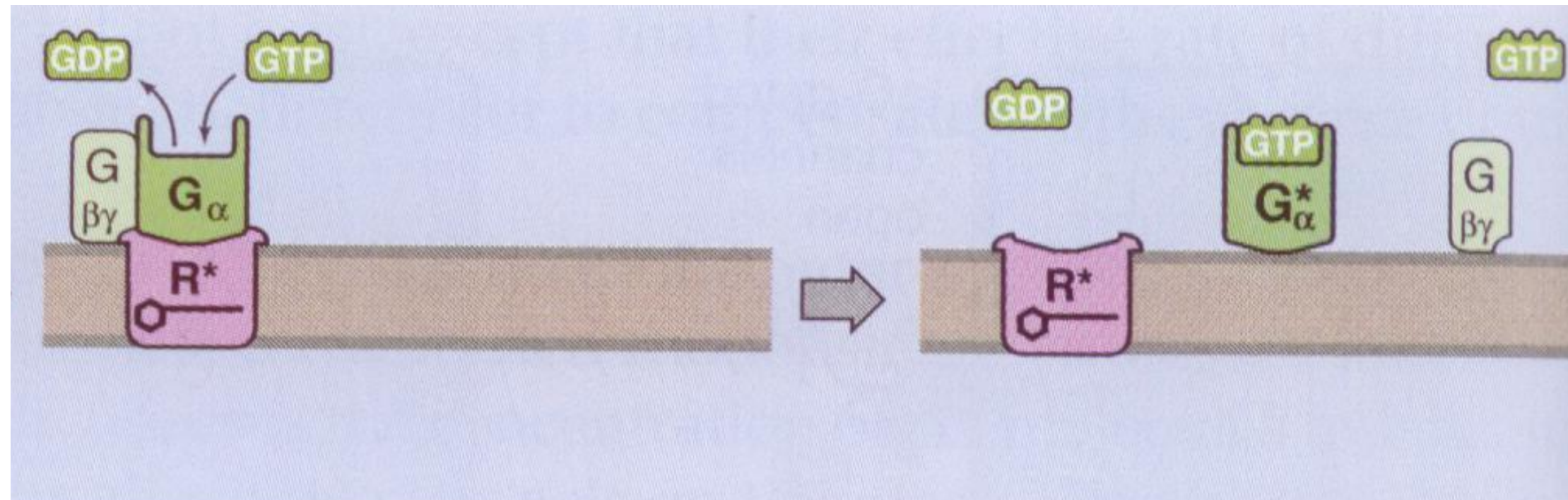






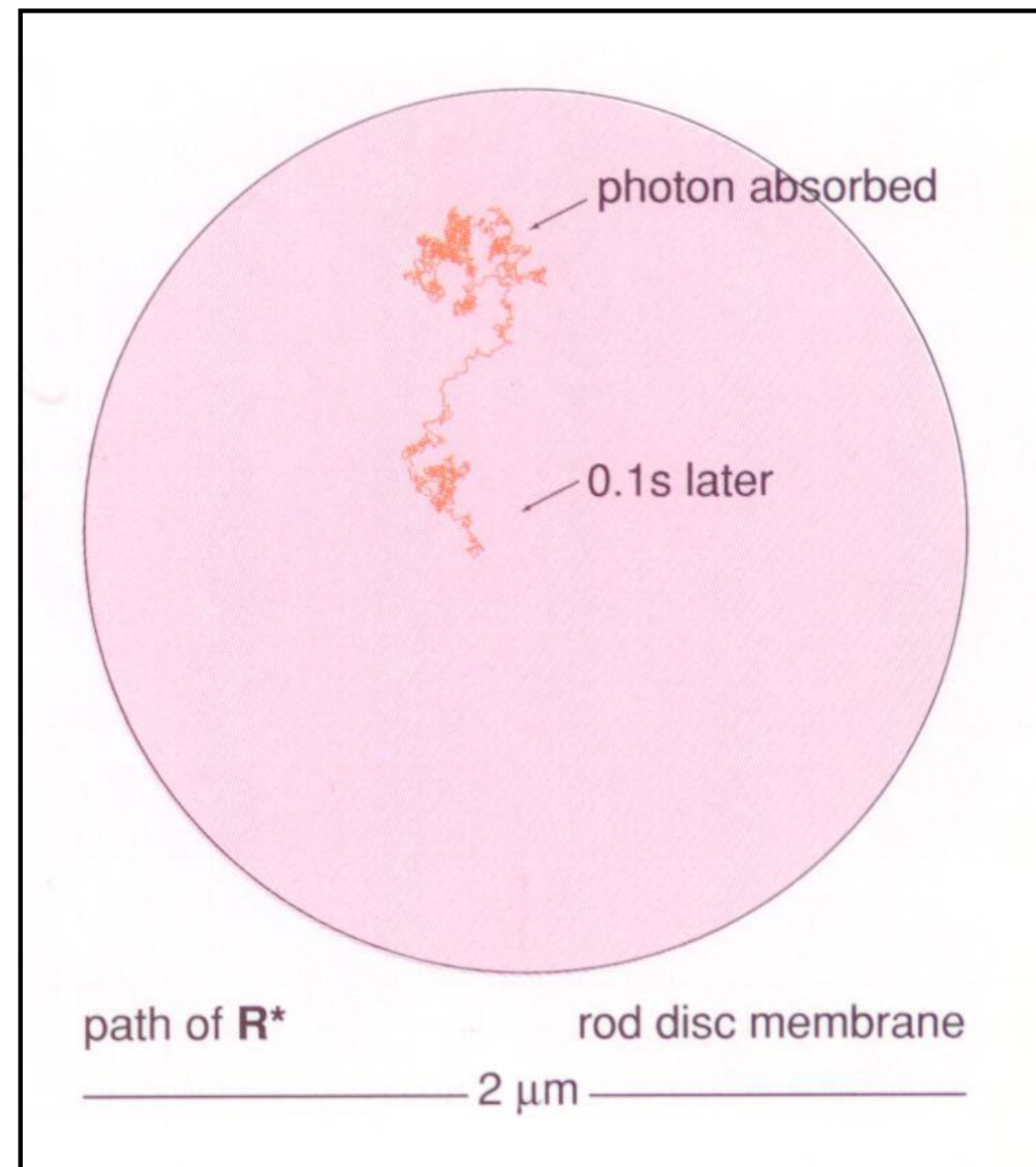
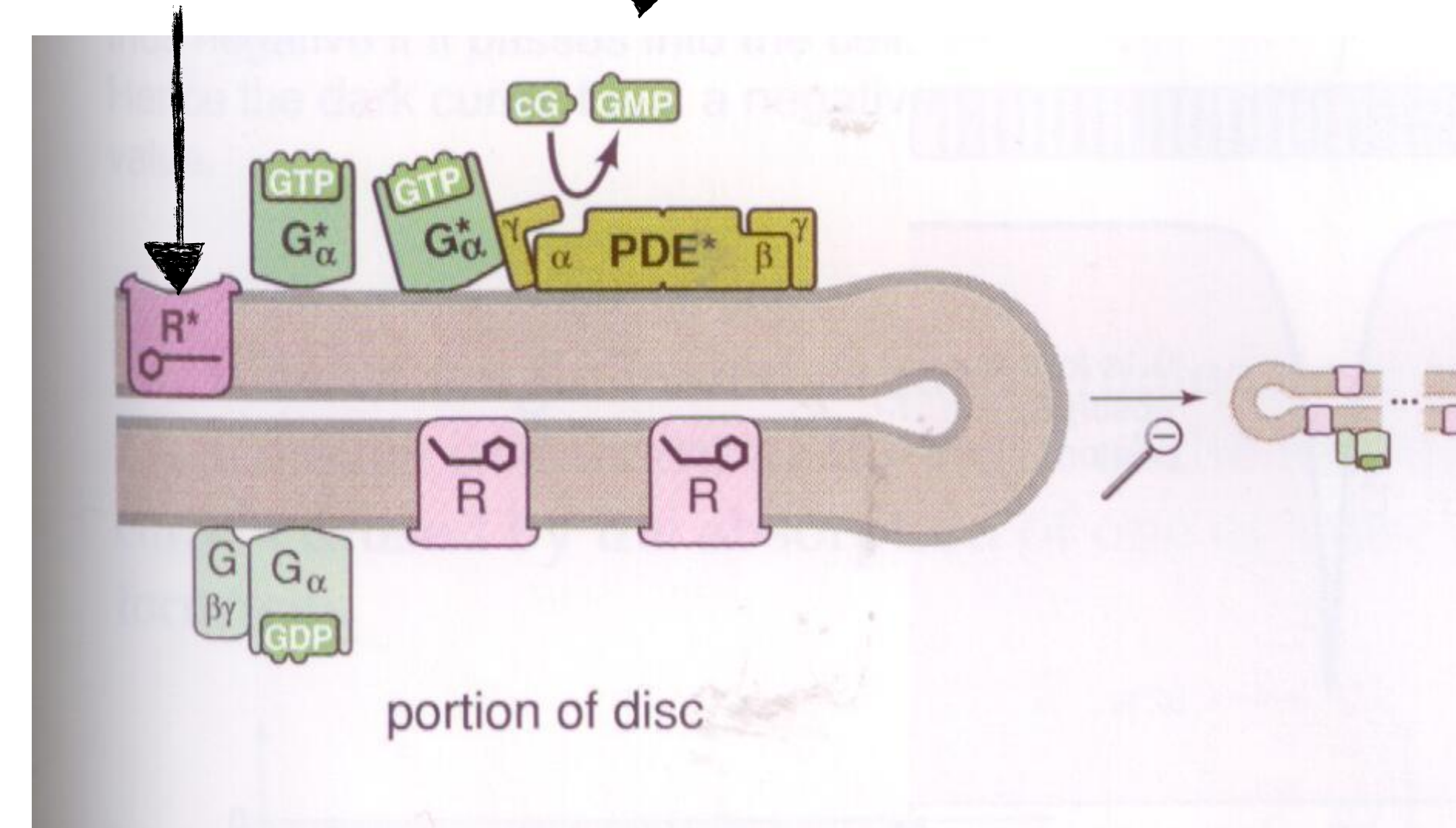
# Steps in Phototransduction

1



A single excited pigment removes thousands of cG molecules

An activated/ excited pigment

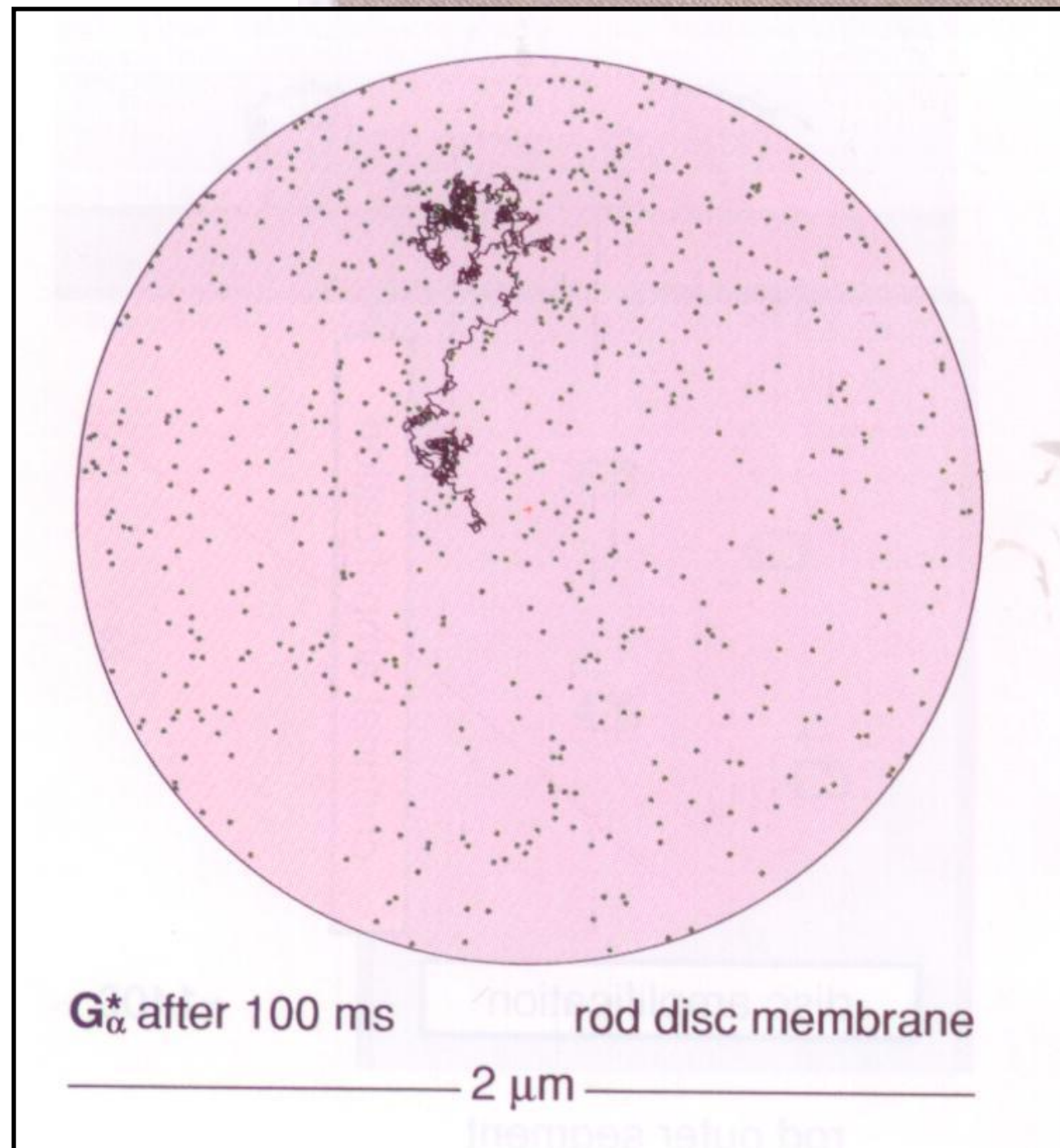
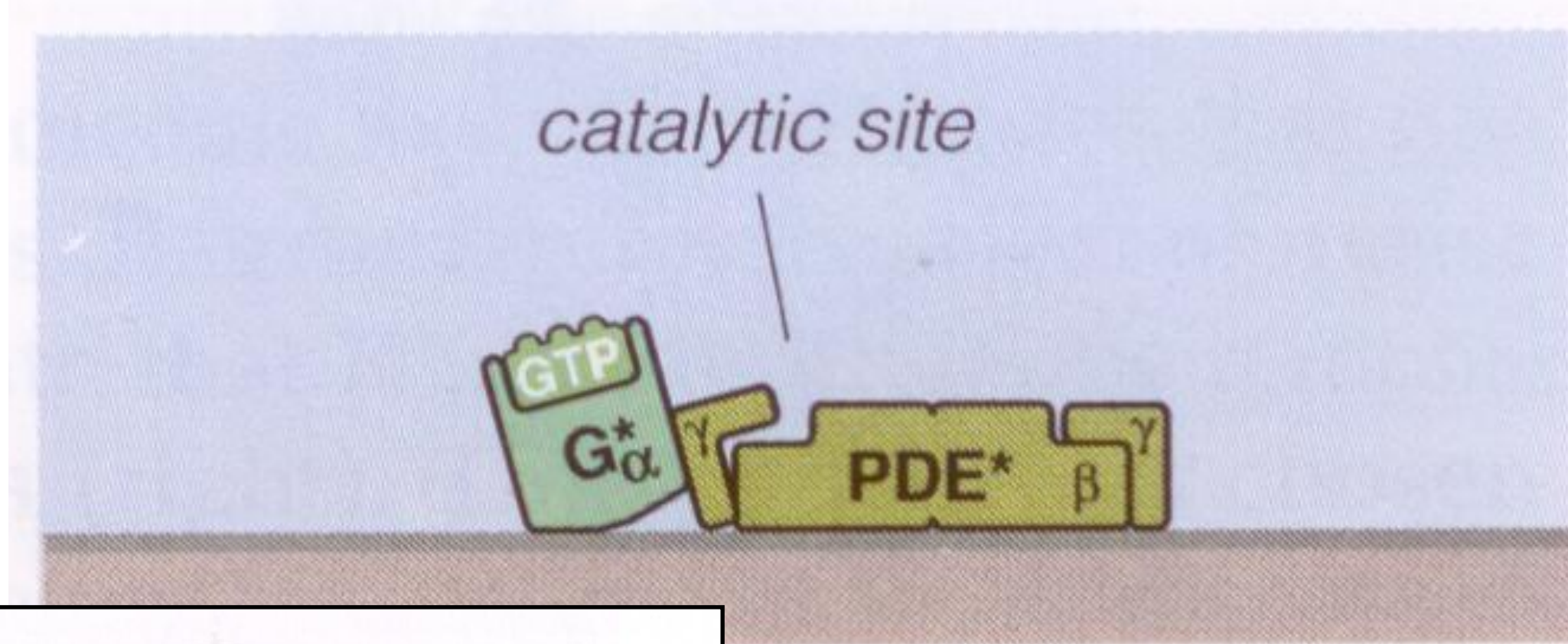


An activated **pigment** roams about and can activate many (~700) **G proteins** by replacing the GDP with GTP



# Steps in Phototransduction

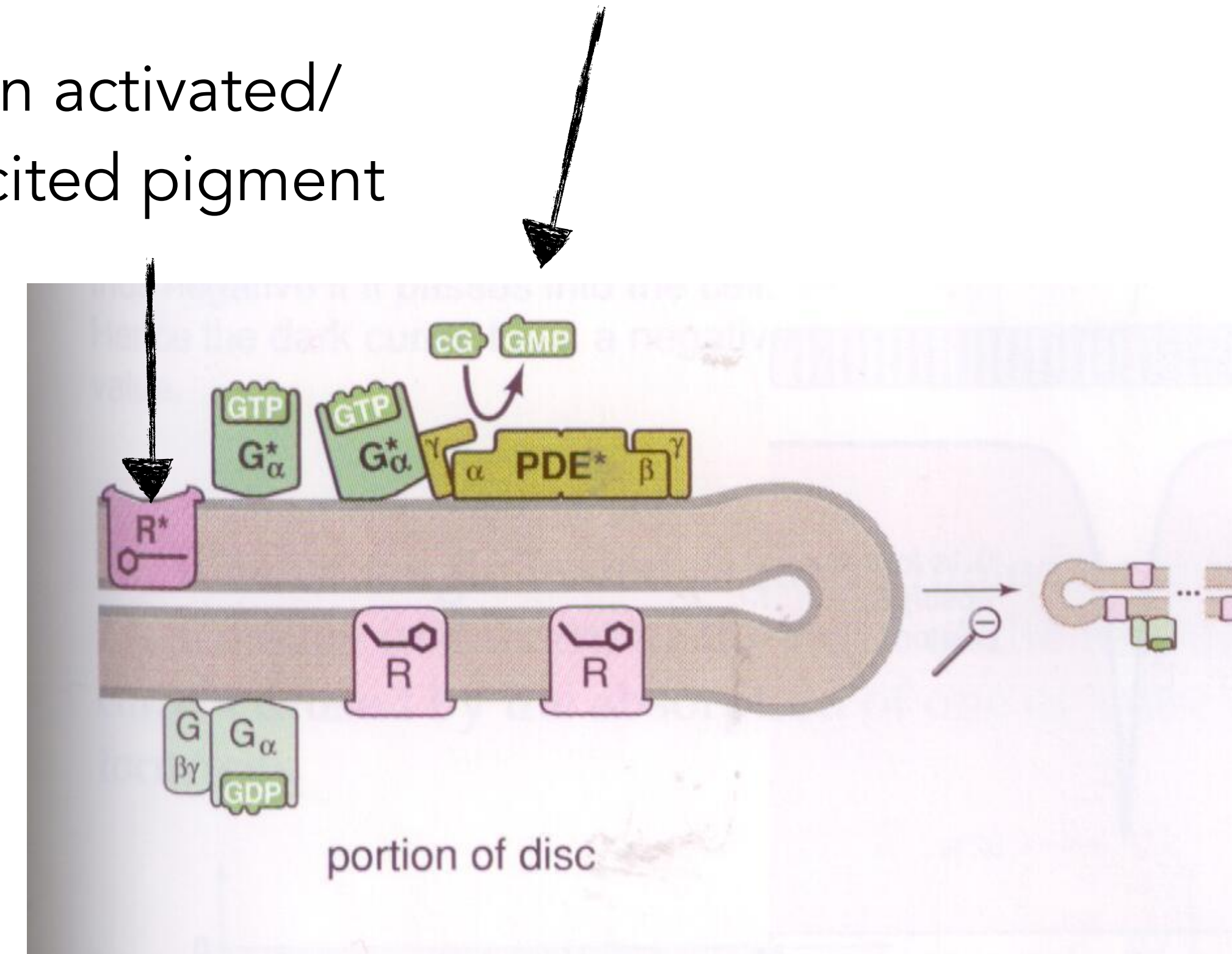
2



An activated **G protein** roams about and binds to a phosphodiesterase (**PDE**) and activates it.

A single excited pigment removes thousands of cG molecules

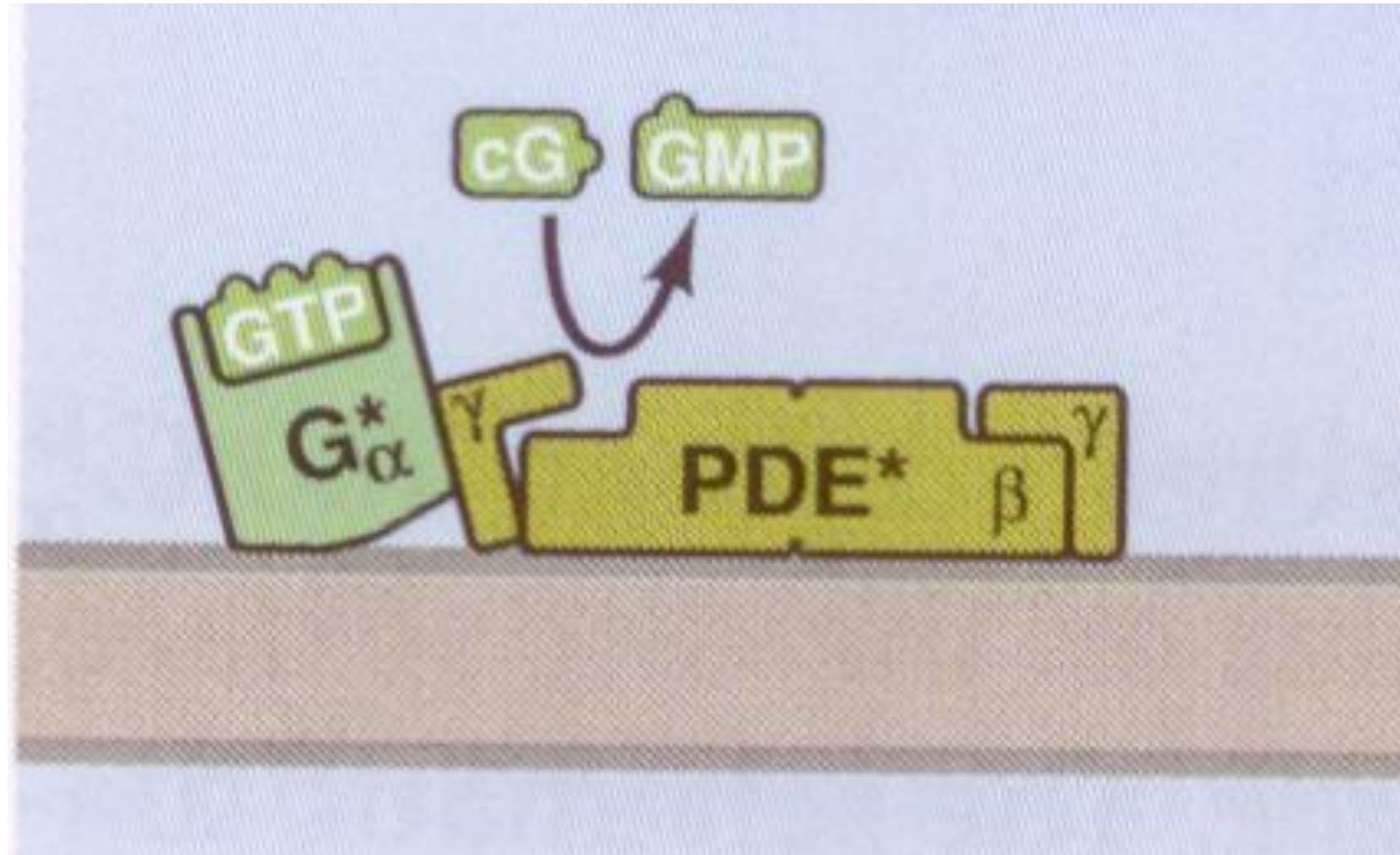
An activated/ excited pigment





# Steps in Phototransduction

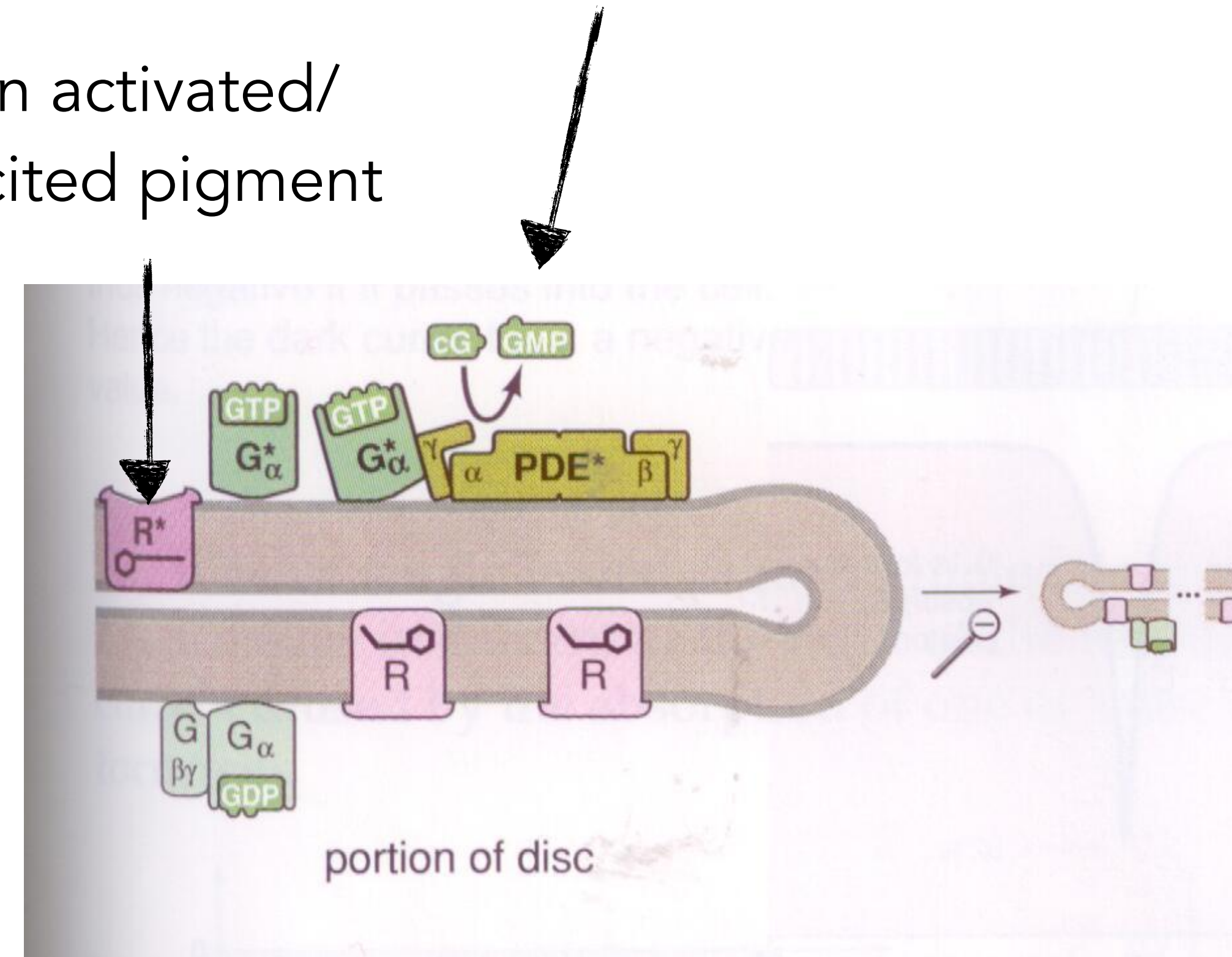
3



An activated **PDE** roams about and hydrolyzes multiple cG molecules.

A single excited pigment removes thousands of cG molecules

An activated/  
excited pigment

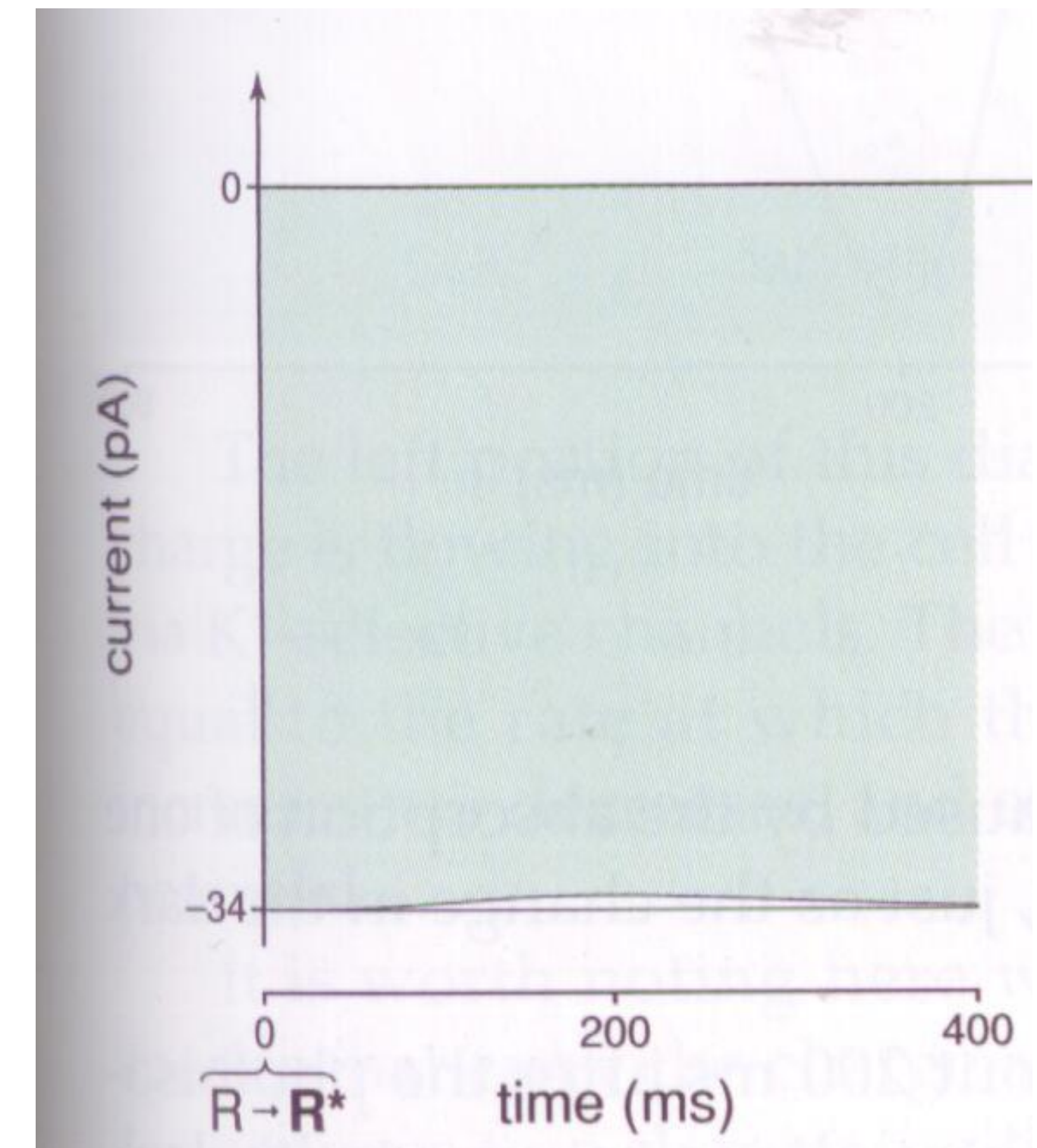


# Beyond Photon Counting:

- Phototransduction
- Deactivation and Pigment Regeneration

# Phototransduction Deactivation

- There are a finite number of pigments (in fact all the materials involved in phototransduction) and cG-gated ion channels.
- When all the biomaterials are consumed or all the channels are closed, transmembrane current will be 0 and there will no further response — saturation.
- Why aren't our photoreceptors constantly saturated?!

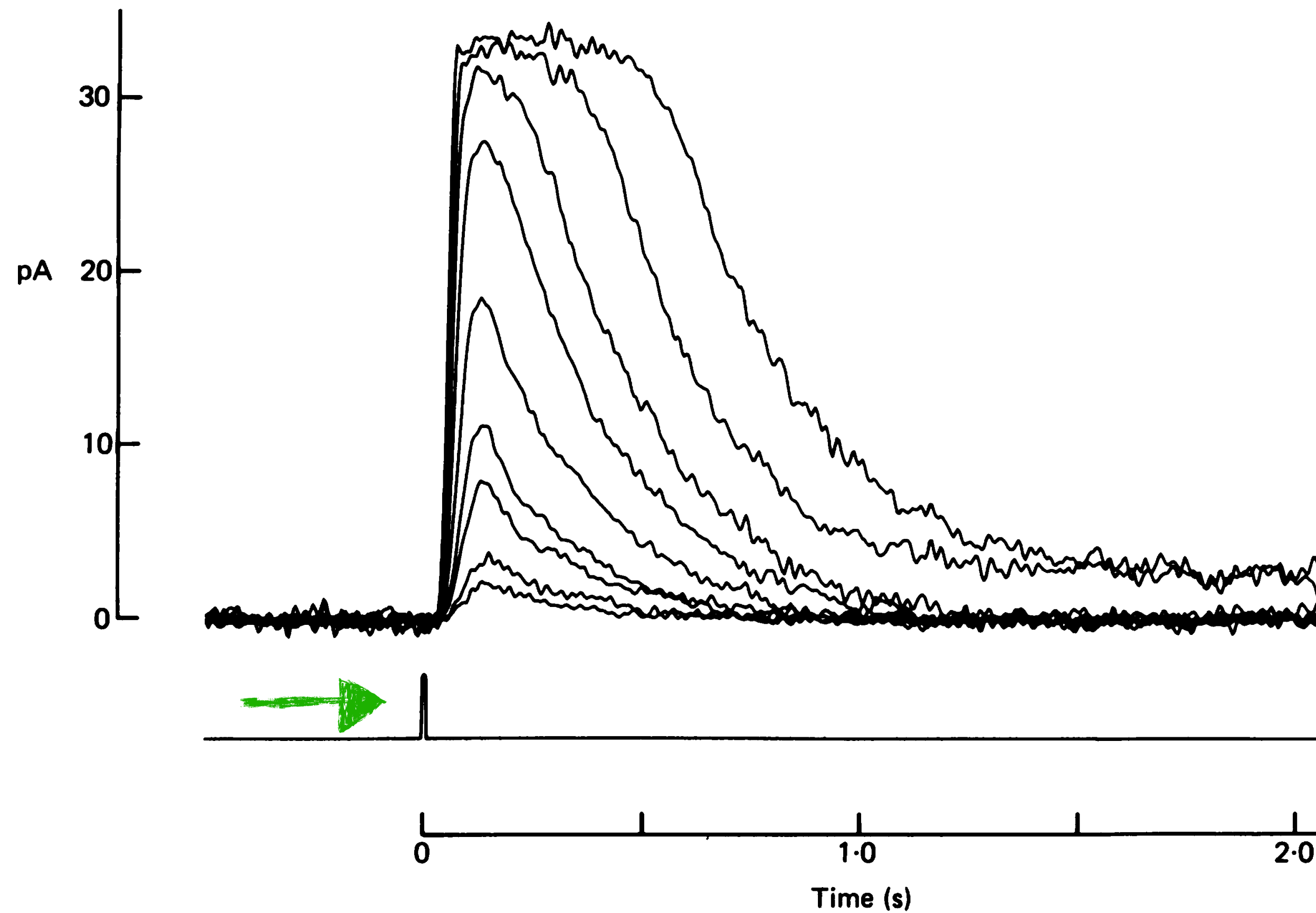




# "Counteracting Forces"

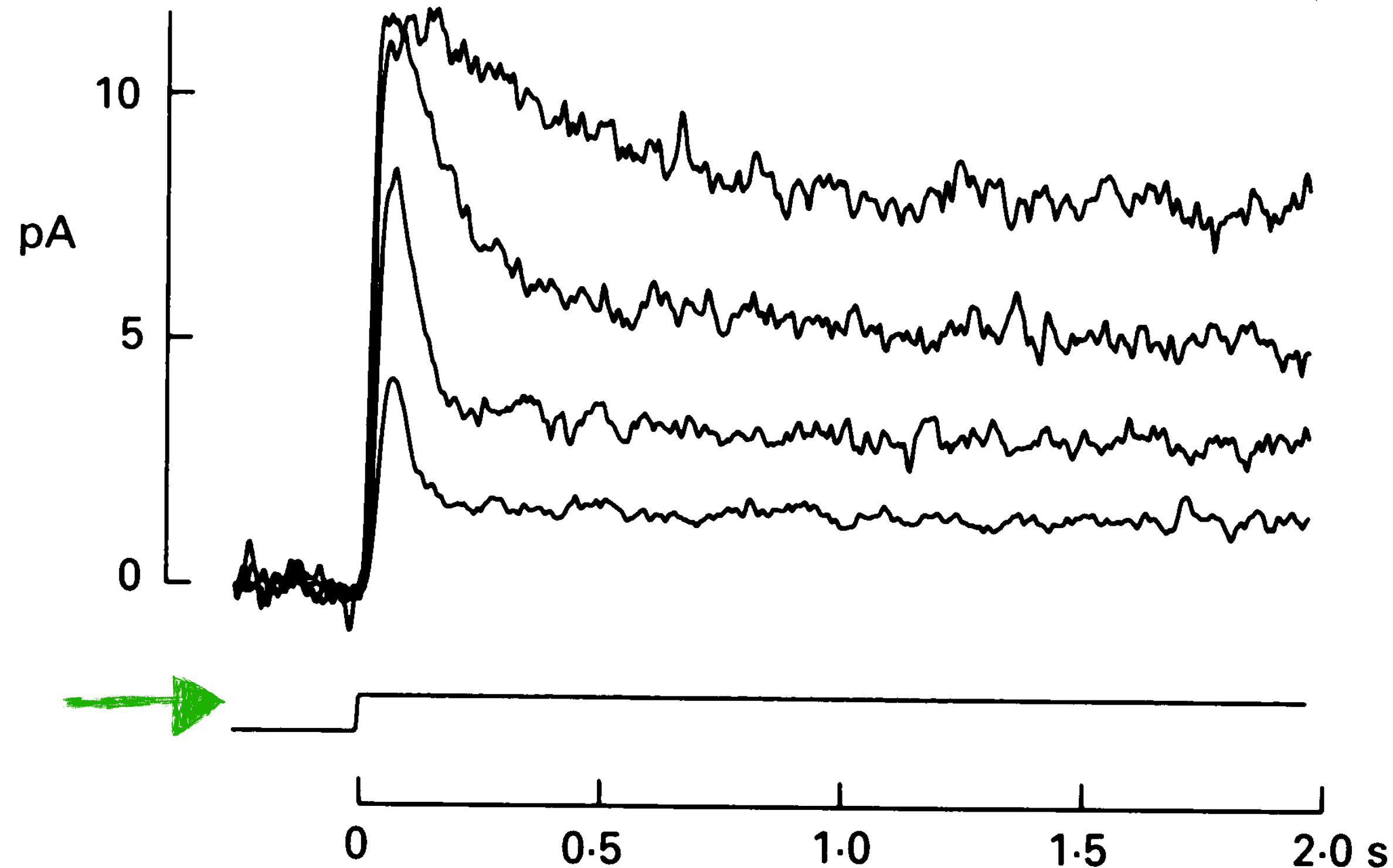
- For a photoreceptor to be able to continue responding to lights, two things must happen.
- Deactivation/termination of phototransduction and re-open ion channels.
  - When the closed ion channels are re-opened, we have restored the dark current and those open channels are available for being closing again
- Continuously regenerate pigments (retinoid cycle or visual cycle)
  - Re-generated pigments are re-available for isomerization
- Both are constantly at work to "counter" the affect of phototransduction.
  - Usually the countering forces and the activation reach an equilibrium and we enjoy a steady vision; otherwise our vision is saturated (no responses to further lights).

# Proof that Deactivation is Constantly at Work



- After a brief flash of light (i.e., a fixed amount of photons are delivered), the response first rises and then falls.
- The response rises because more ion channels are being open, and it falls because the closed ion channels are being re-opened, i.e., deactivation.
- Without deactivation the response would have fell.

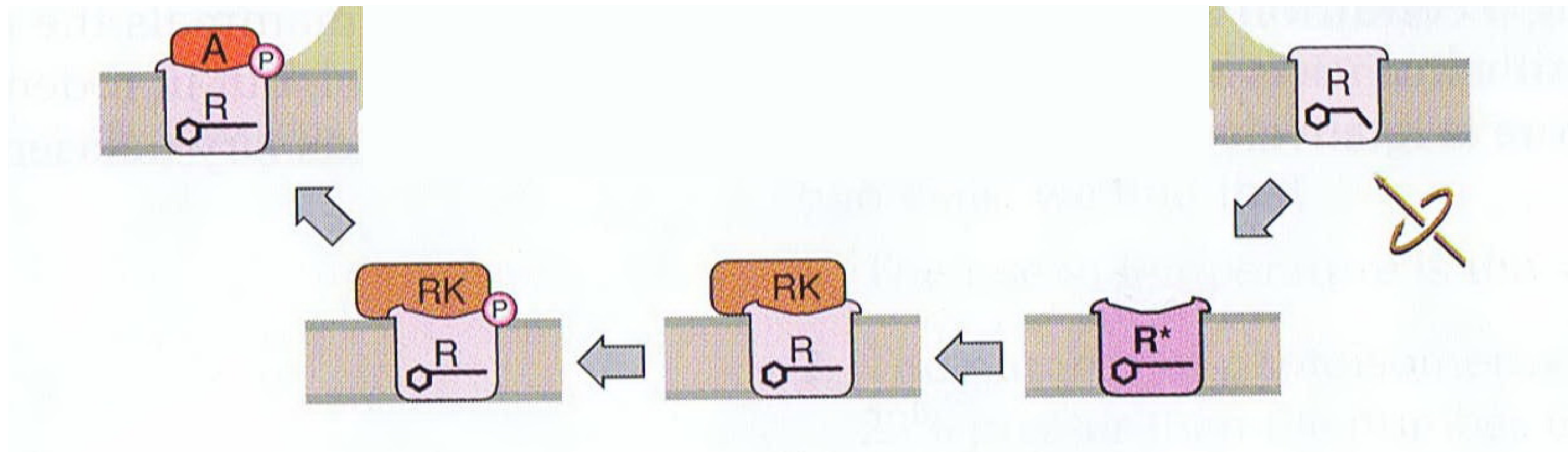
# Proof that Deactivation is Constantly at Work



- With a steady light (called step light), the response eventually reaches an equilibrium.
- Steady light means new photons are constantly being delivered to the photoreceptor, so new ion channels are constantly being closed.
- But the response reaches equilibrium, which means the ion channel closing rate matches that of the re-opening rate.

# Deactivation Mechanisms

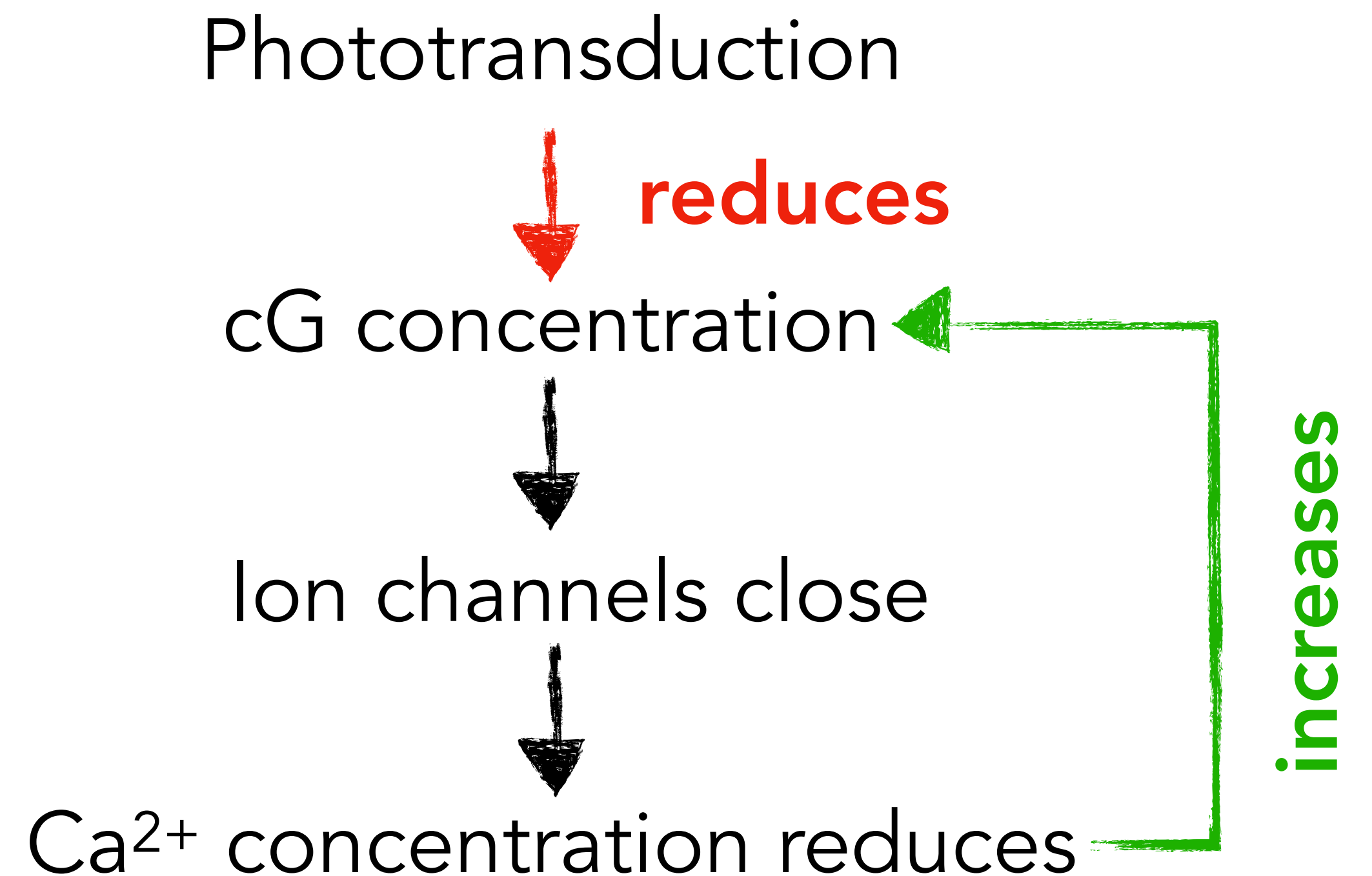
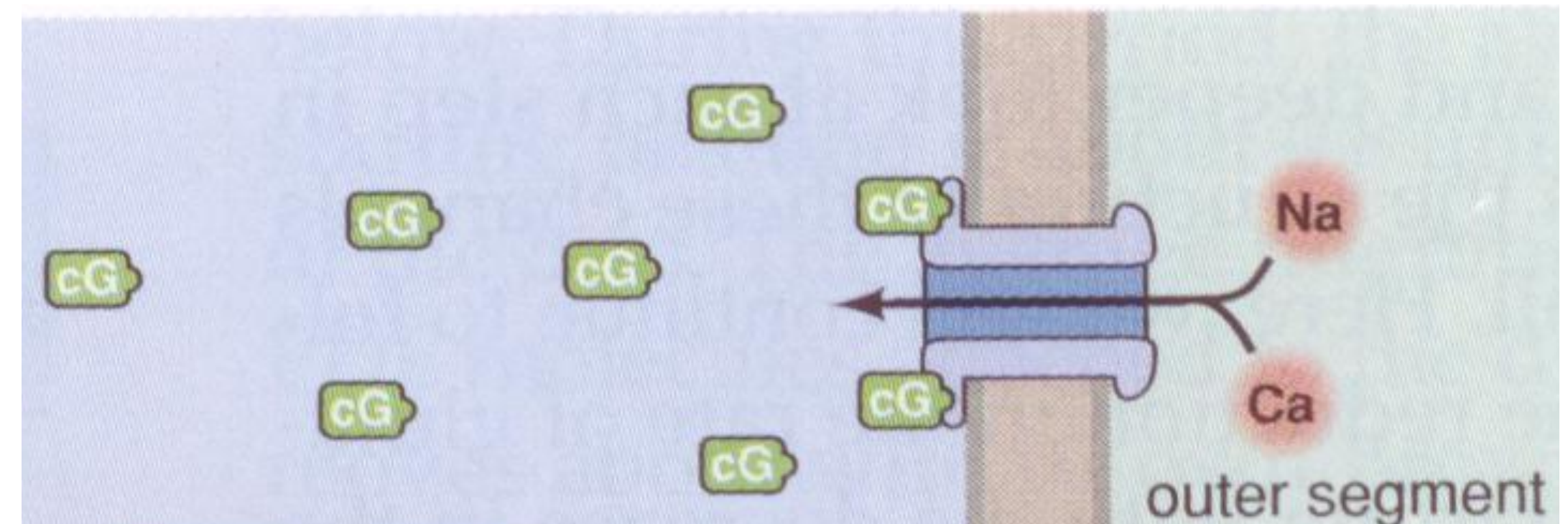
- Just like the activation of the phototransduction, deactivation also involves a set of biochemical reactions.
- Just to give you a flavor, here is how excited pigments are deactivated.
  - An enzyme, rhodopsin kinase (RK) binds to and phosphorylates an activated pigment
  - Another protein called *arrestin* (A) then binds to phosphorylated pigment, which inhibits the pigment to activate G proteins, essentially deactivating the pigment.



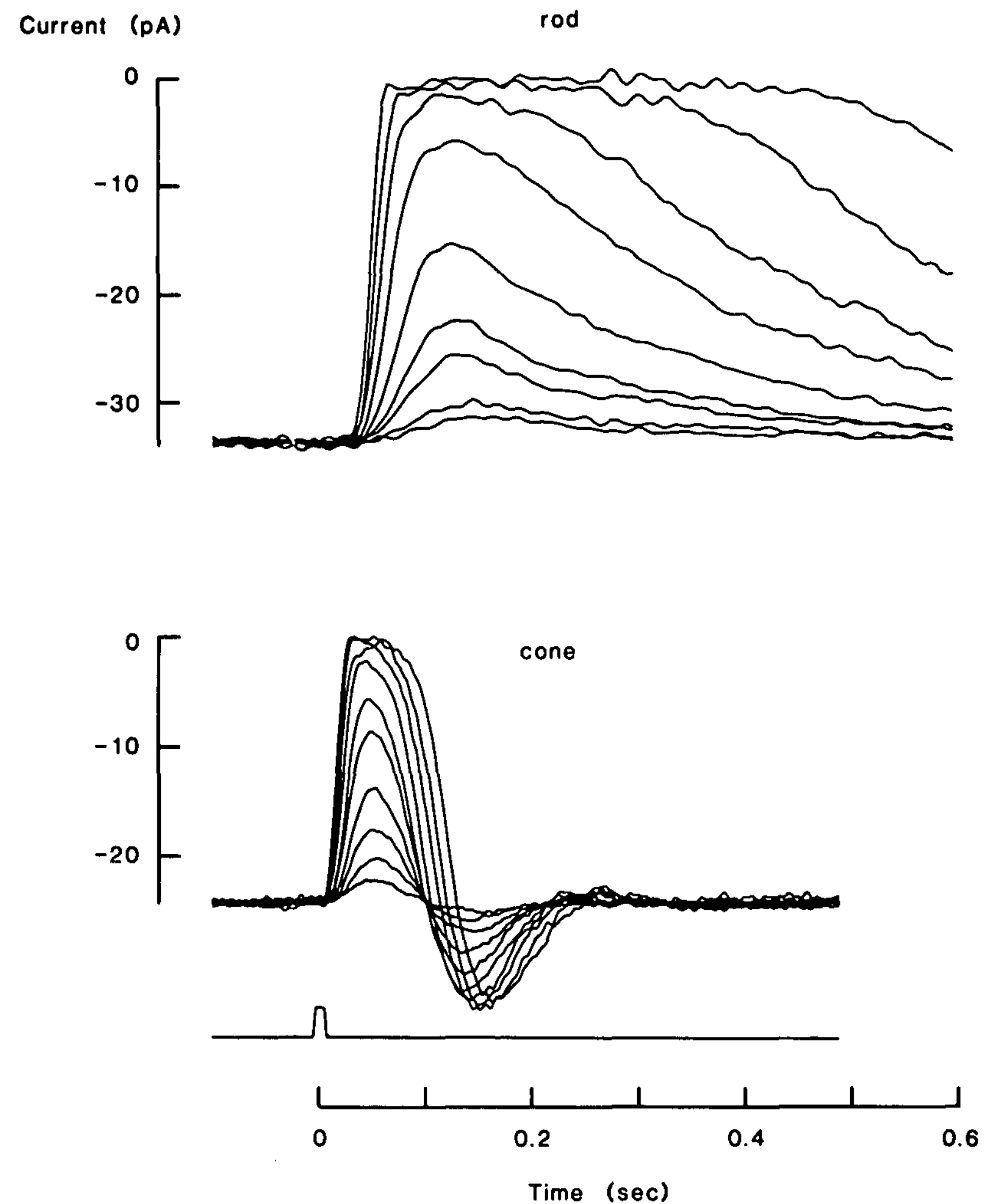


# Accelerating Deactivation via Negative Feedback

- Two opposing forces:
  - Activated pigments **reduce** cG concentration, which closes ion channels and reduces  $\text{Ca}^{2+}$  concentration
  - $\text{Ca}^{2+}$  inhibits guanylate cyclases (GCs), which synthesize cG.
  - So reduction in  $\text{Ca}^{2+}$  **increases** the cG synthesis rate.
- This is a classic **negative** feedback in a dynamical system, which accelerates the time to equilibrium.



# Undershoots in Cone Kinetics



- Biphasic response in cones
- There is an undershoot in the kinetics
- The negative feedback in cones is so strong that it causes a temporary overproduction of cG molecules, which open more ion channels than there are even in dark



# Retinal Falls Off from the Pigment after Deactivation

Illustration of the three states of a single pigment

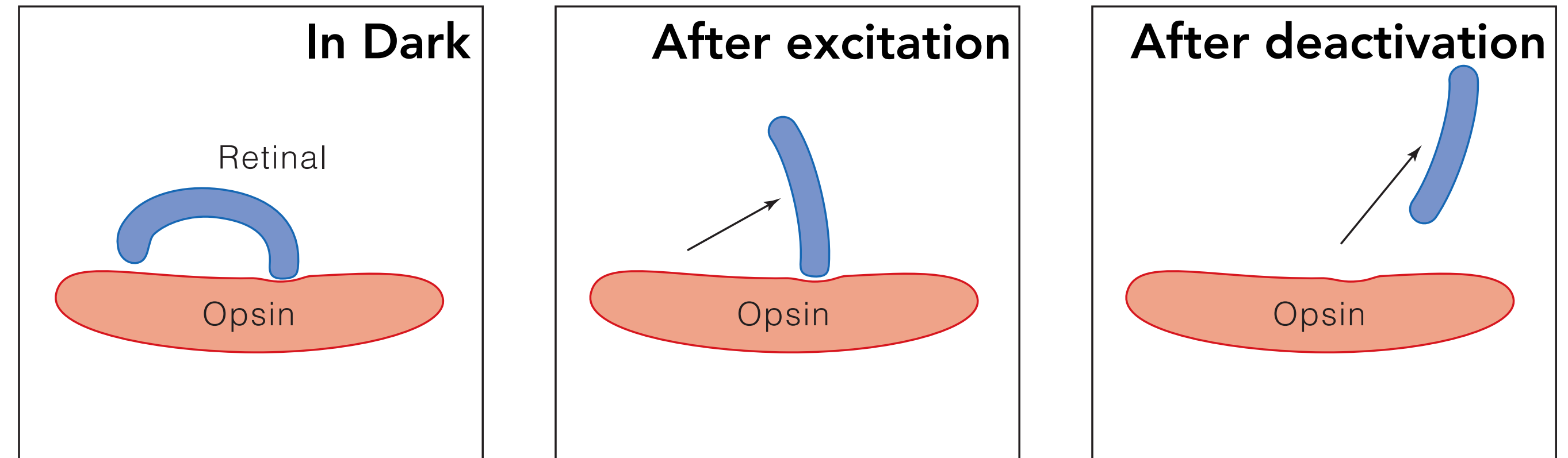
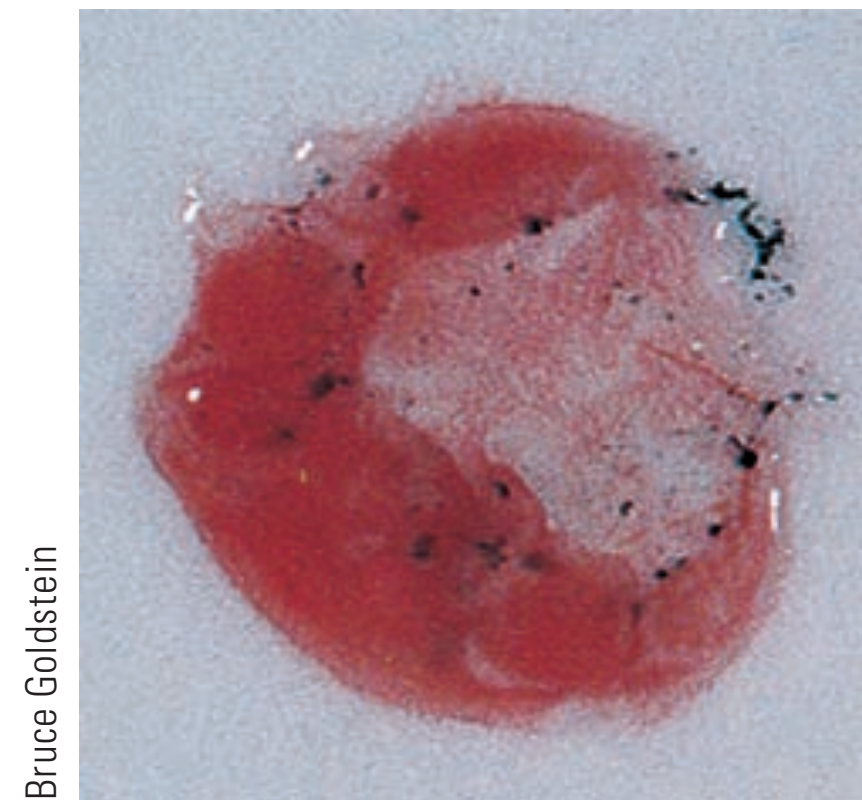
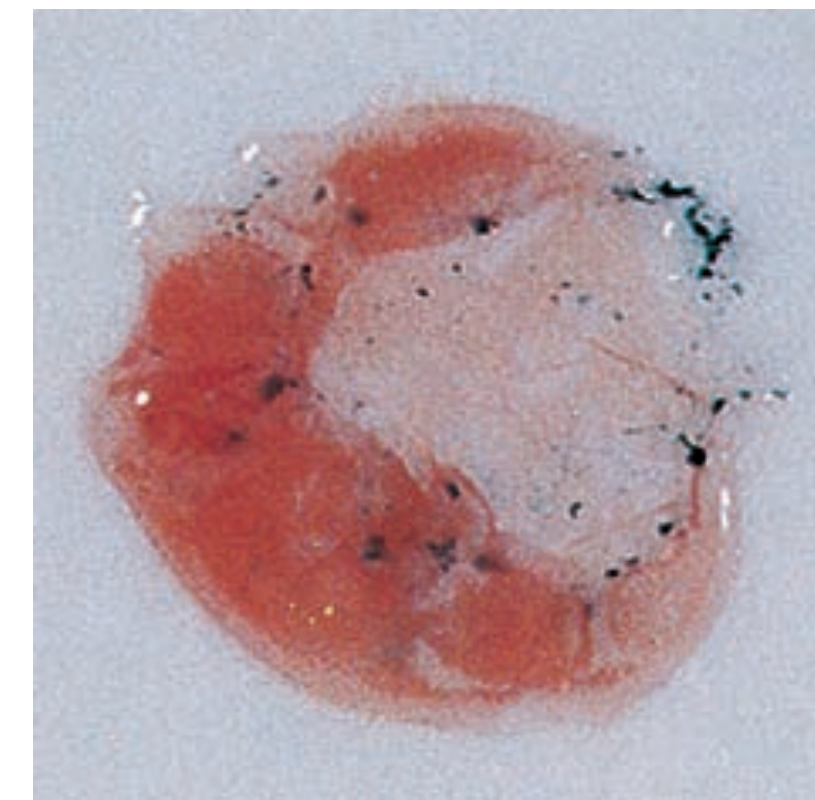


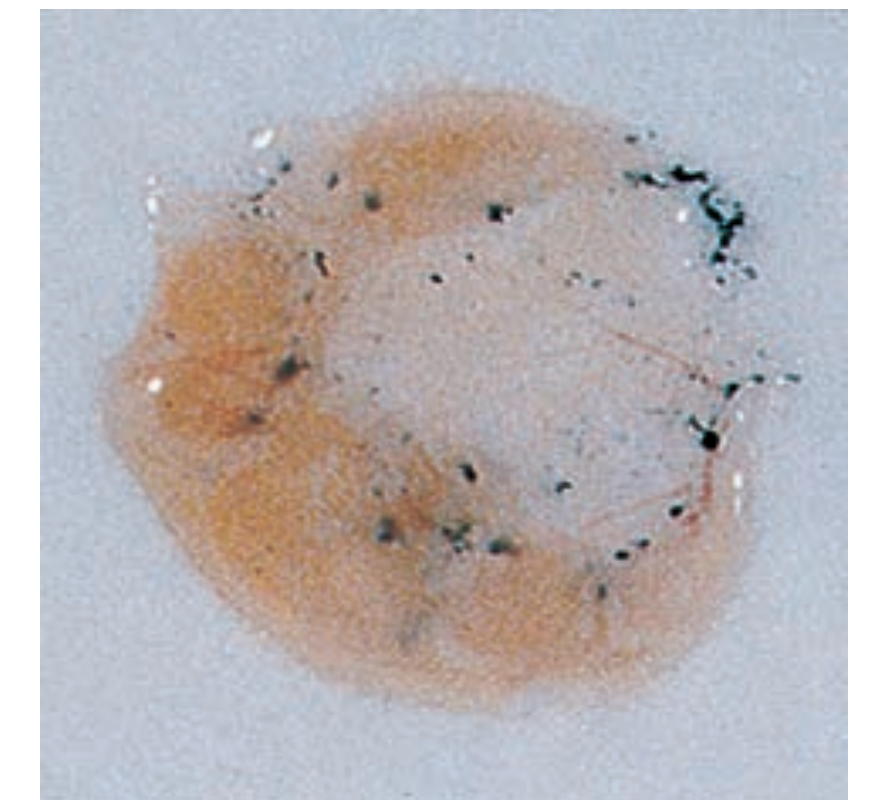
Image of a dissected frog retina; when more pigments are excited/activated/bleached, the photoreceptor becomes more transparent, since fewer pigments are absorbing lights



(a)



(b)

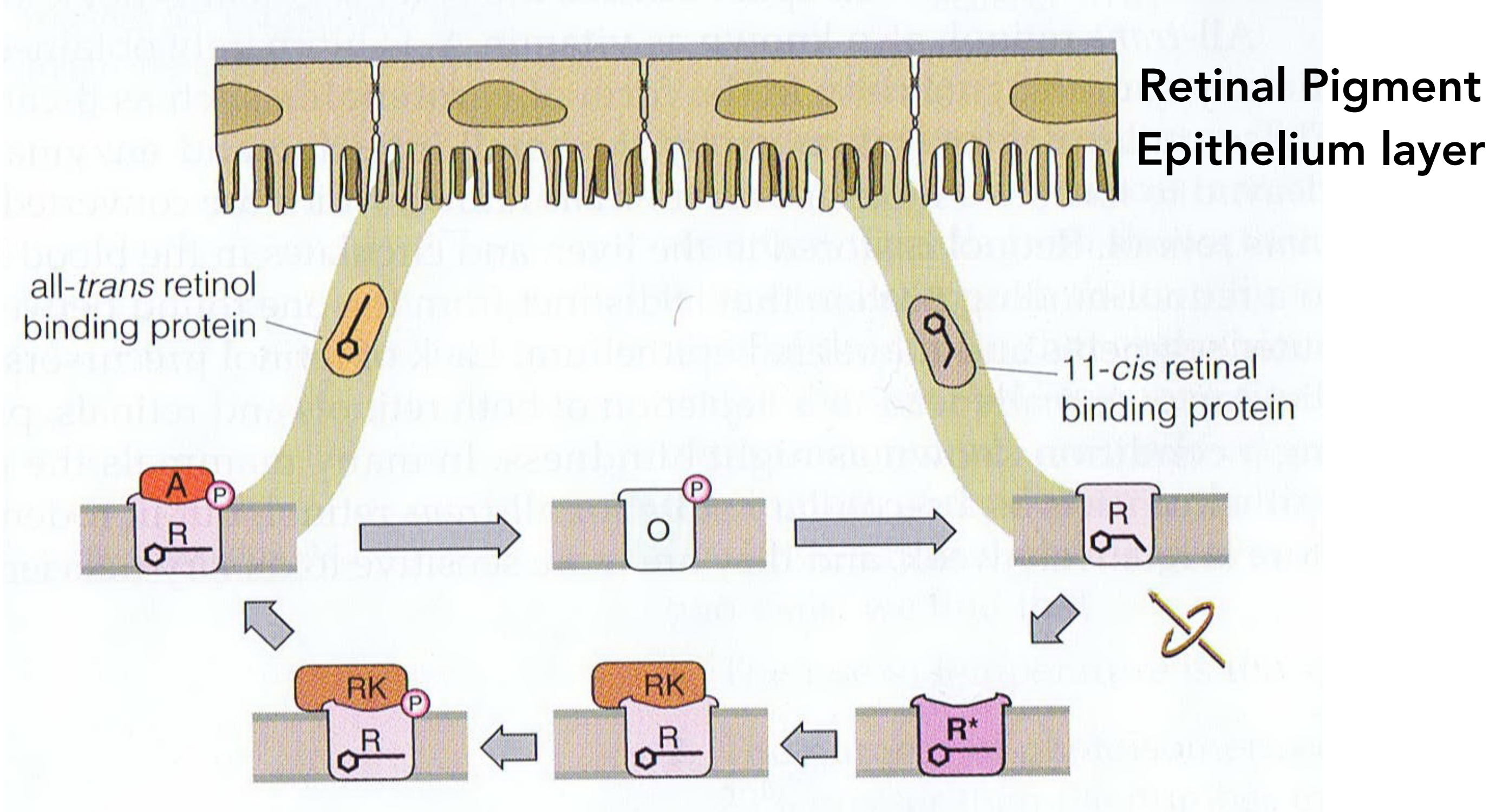
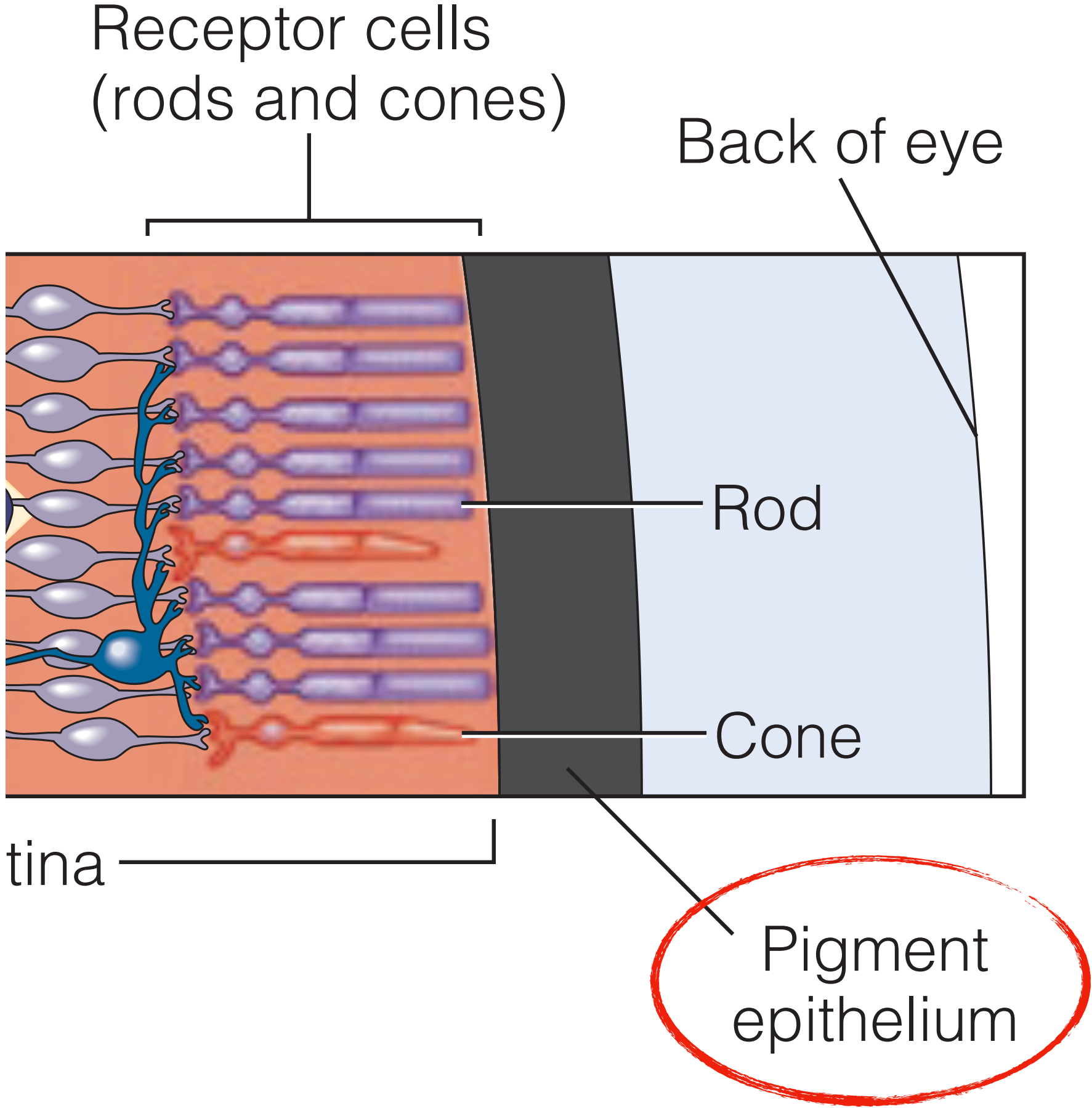


(c)

Bruce Goldstein



# Pigment Regeneration in RPE

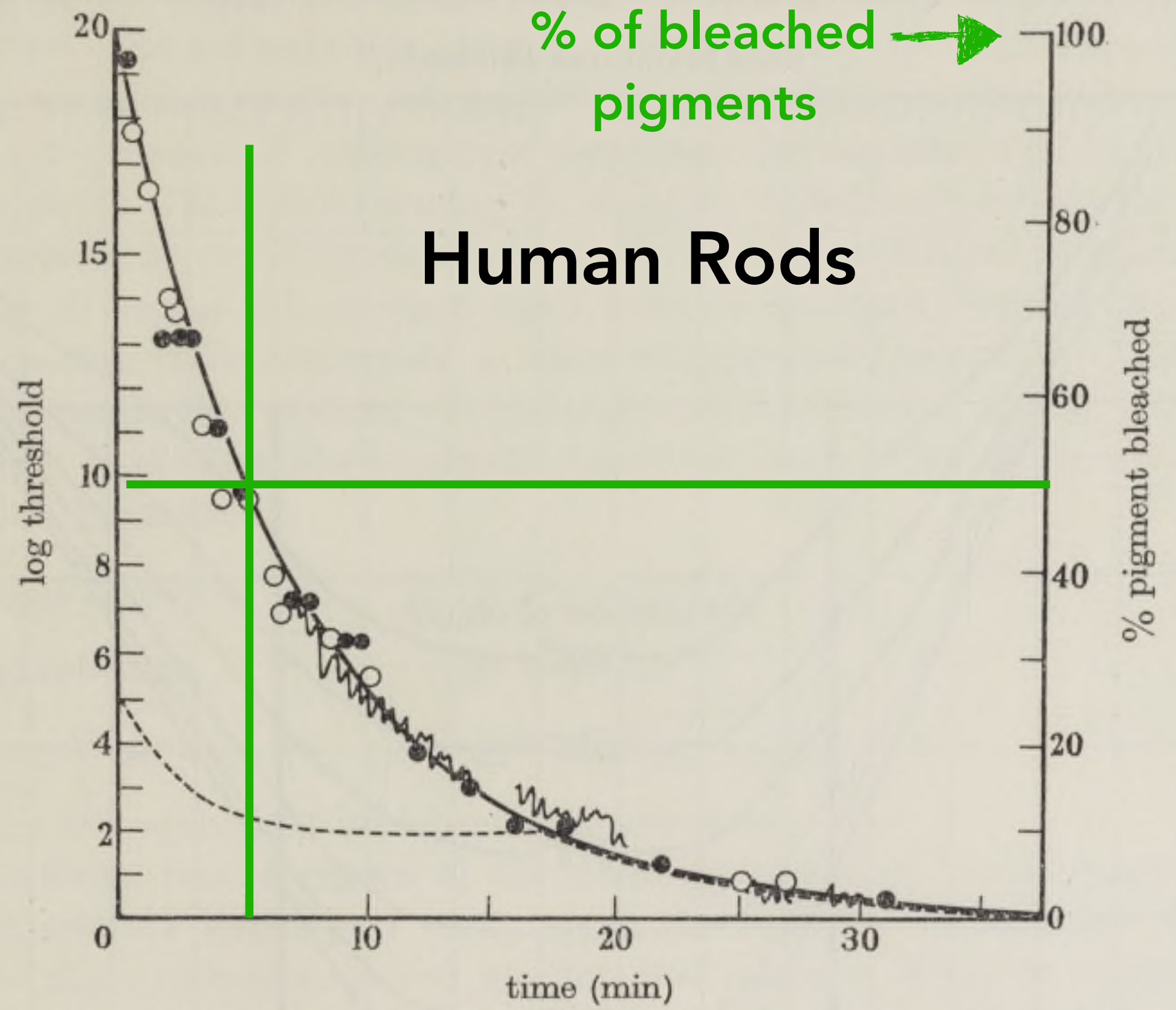
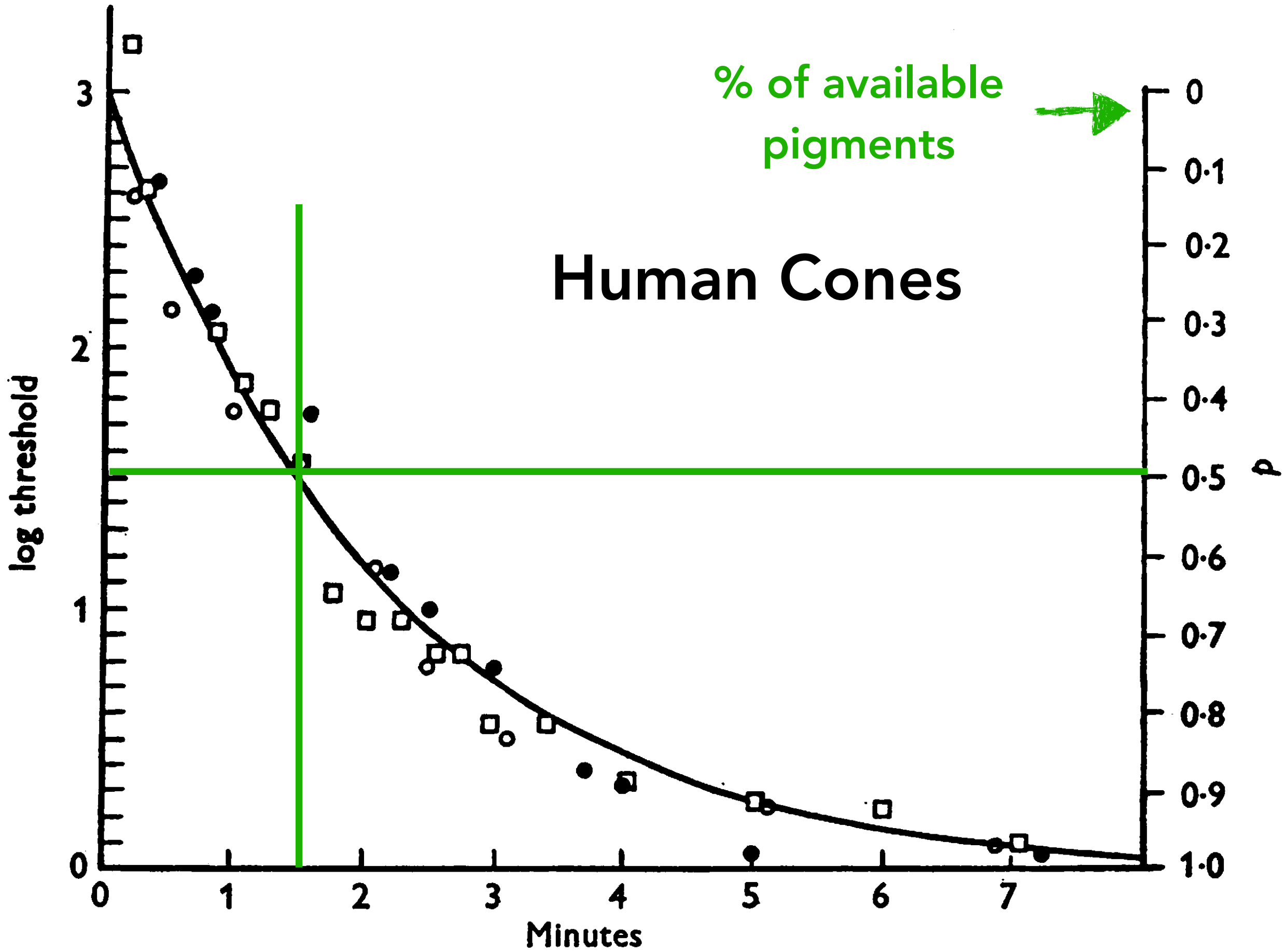


All-trans retinal, after fallen off, is transported to the REP layer, where it is transformed back to 11-cis retinal



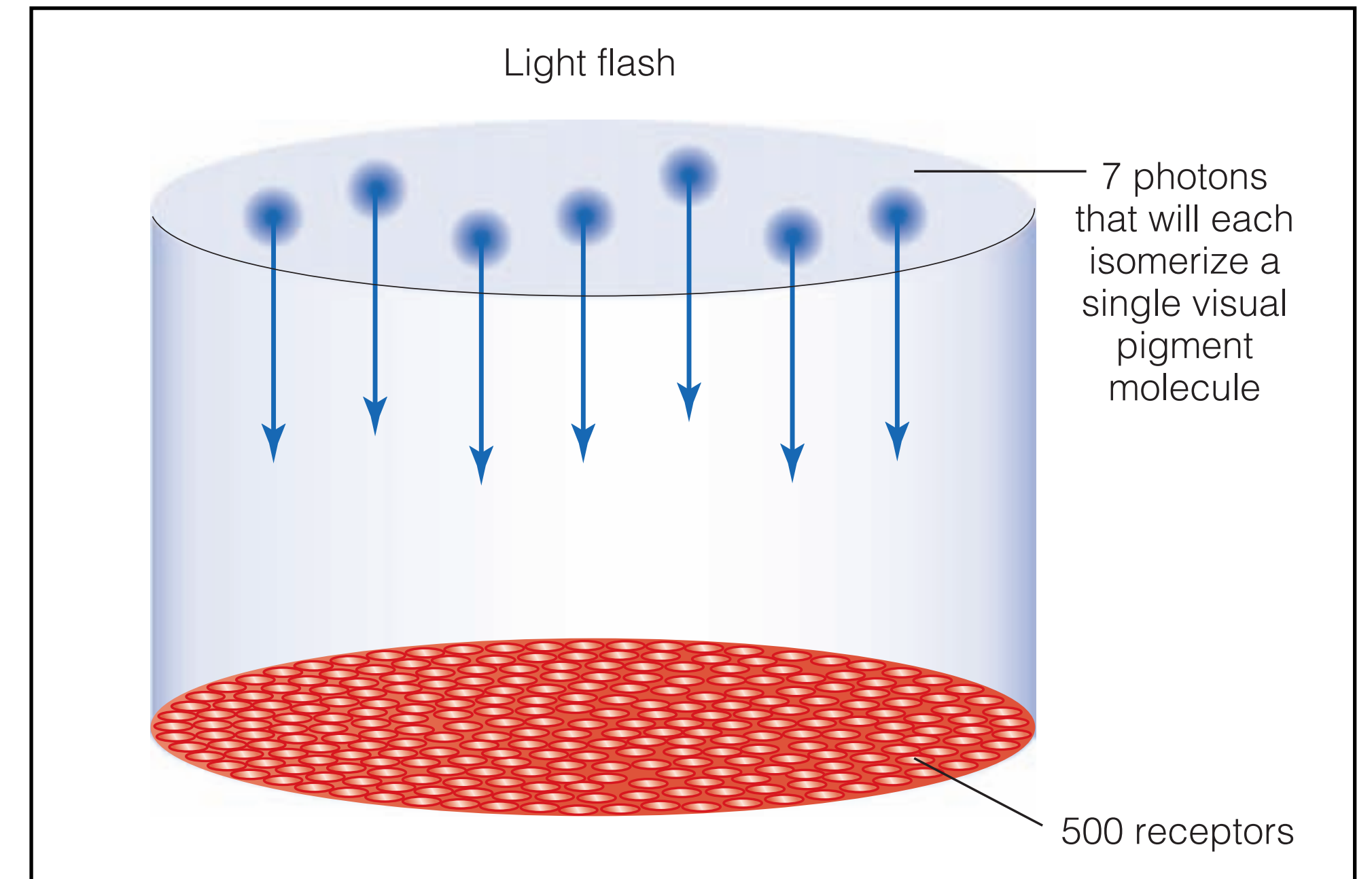
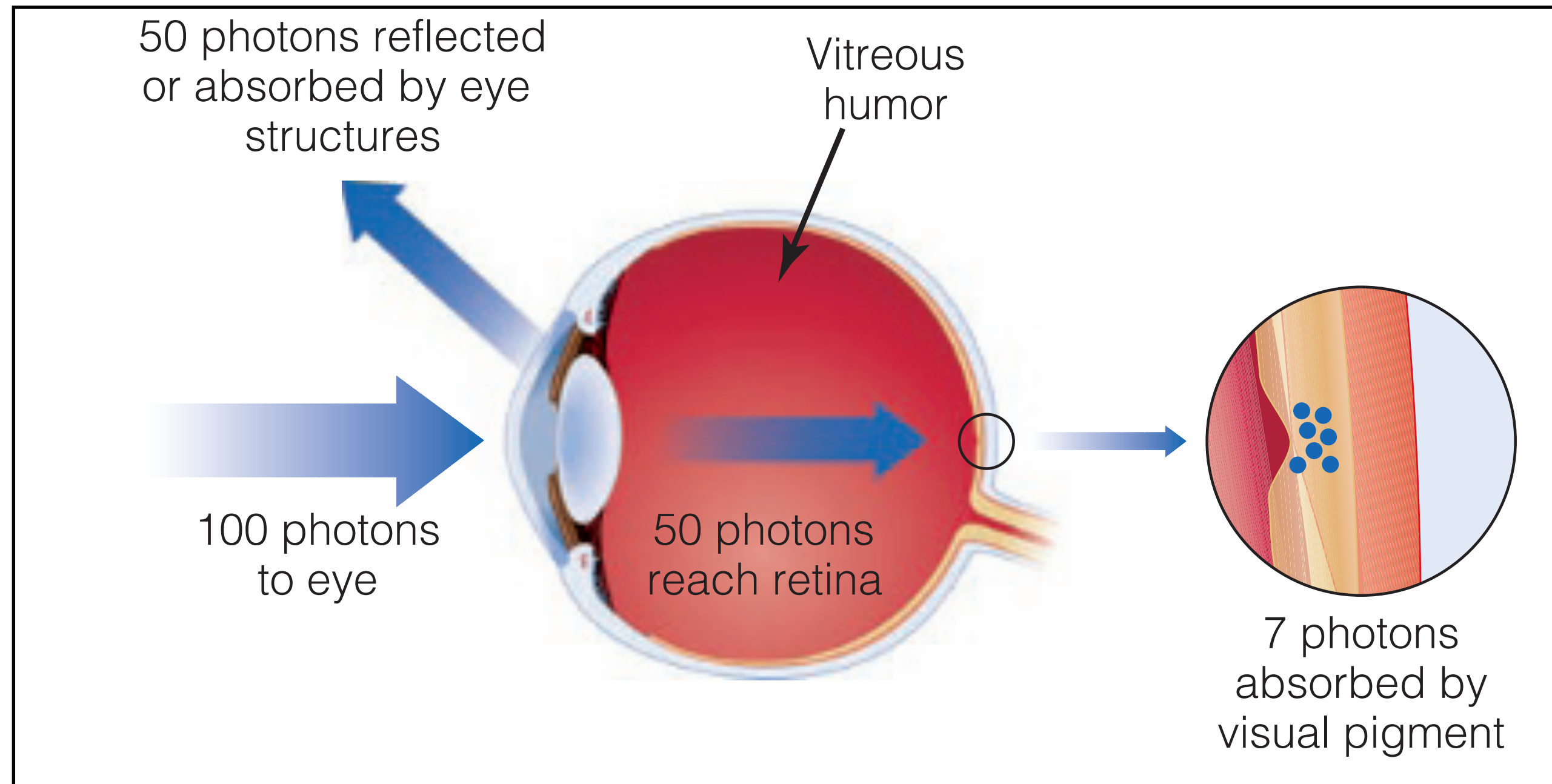
# Pigment Regeneration Kinetics

Bleach all pigments using intense light, then remove light, and measure % of pigments vs. time. Pigment regeneration in cones is faster than in rods — half time 3X faster (ignore left y-axes).



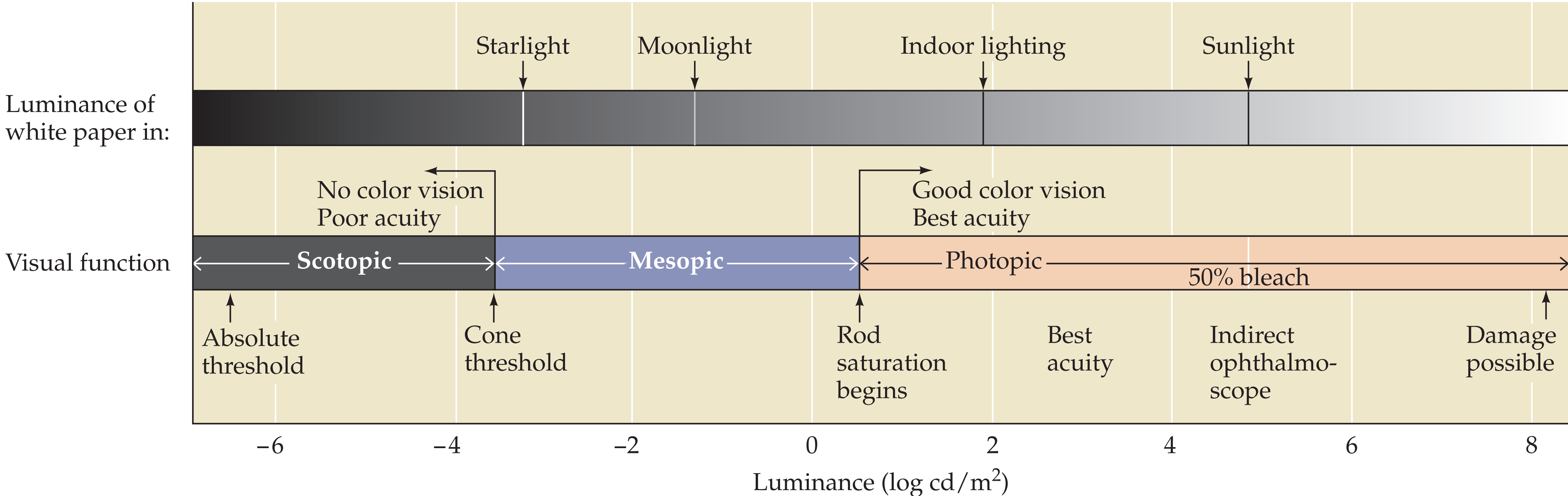
# **Rods vs. Cones: Absolute Sensitivity and Saturation**

# Rod Vision is More Sensitive than Cone Vision



- Human can reliably detect a flash when only about 5 to 7 pigments are excited in about 500 rods; in contrast, it takes about 5 pigment excitations per cone in a pool of about 10 cones for humans to signal a flash.

# Rod Vision is More Sensitive than Cone Vision



**FIGURE 11.11** The range of luminance values over which the visual system operates. At the lowest levels of illumination, only rods are activated. Cones begin to contrib-

ute to perception at about the level of starlight and are the only receptors that function under relatively bright conditions.



# Why?

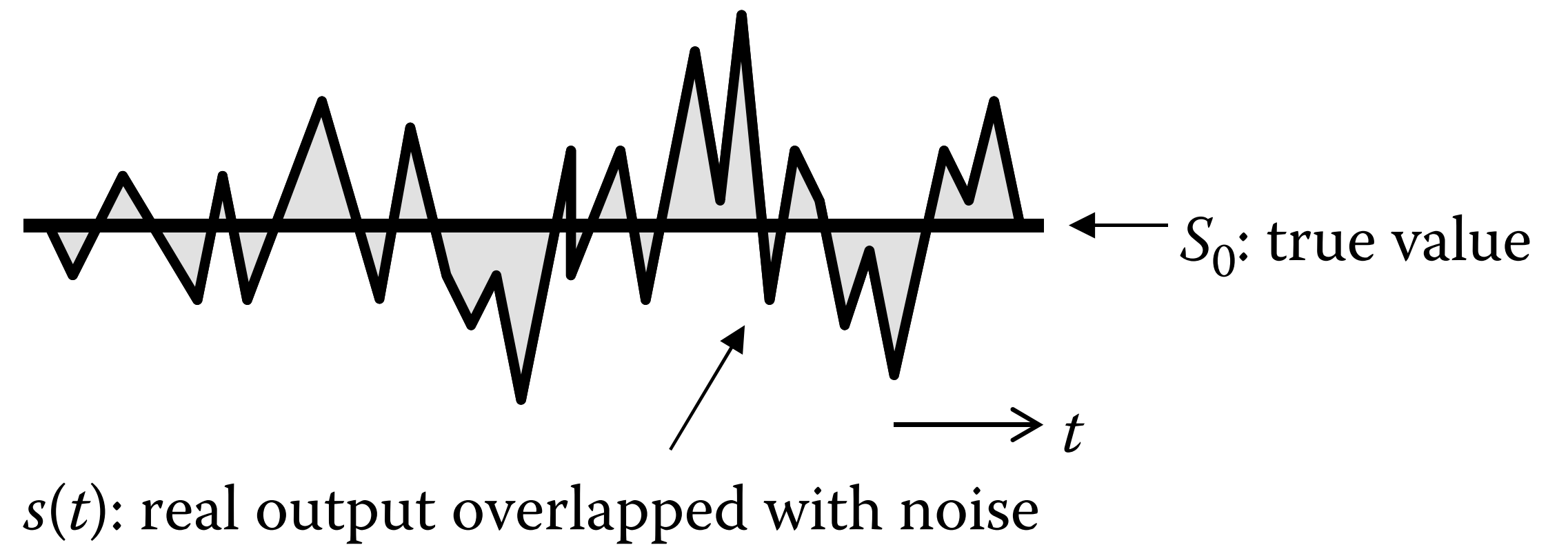
- A single rod has a higher signal-to-noise ratio (SNR) than a cone
  - Higher single photon response in rod
  - Lower noise in rod
- A single rod's response kinetics is longer, which increases the effective signal integration time
- Rods have a higher degree of convergence (to RGCs)

# Signal to Noise Ratio (SNR)

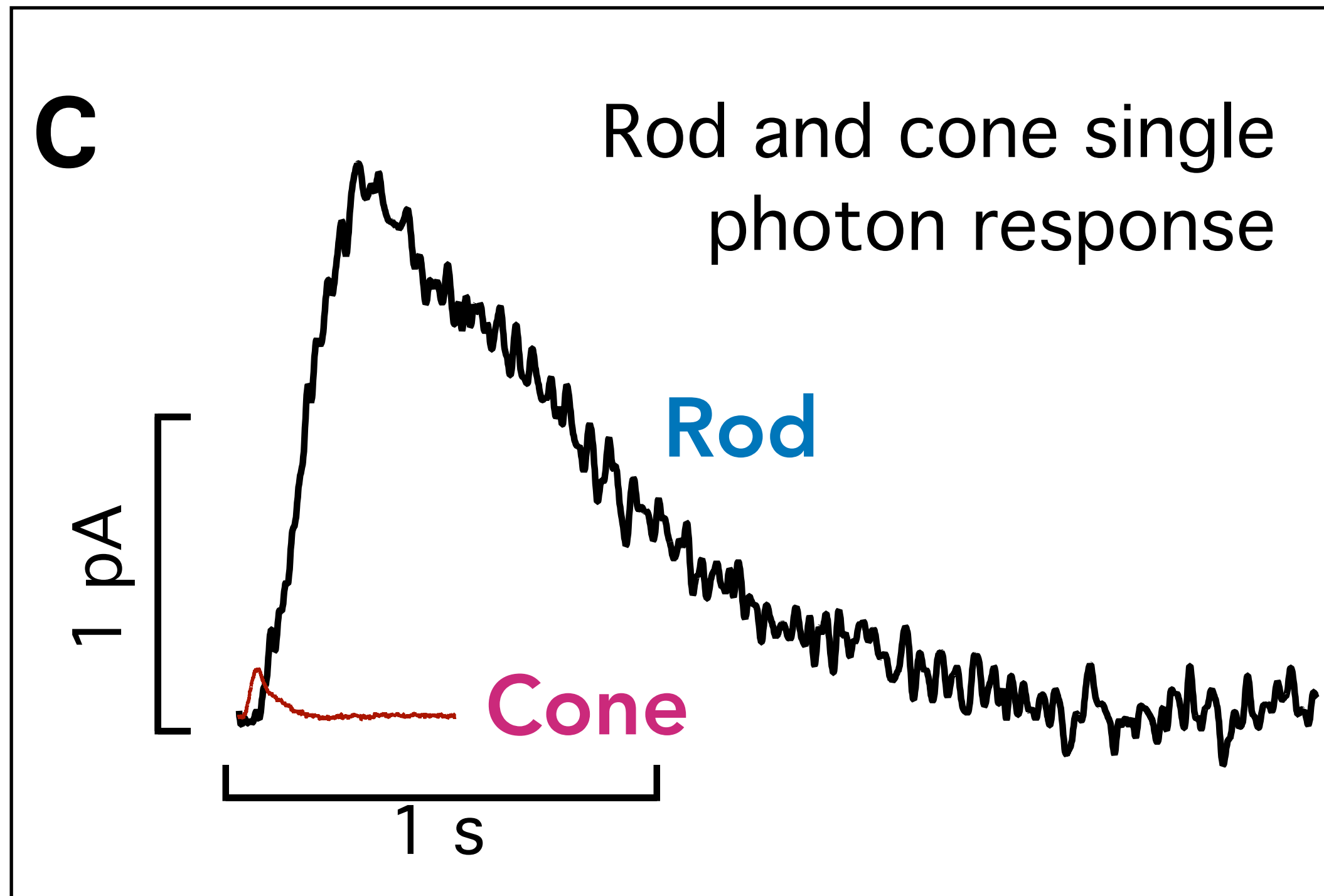
**Signal:** mean value

**Noise:** Std. of value

**SNR** = Signal / Noise

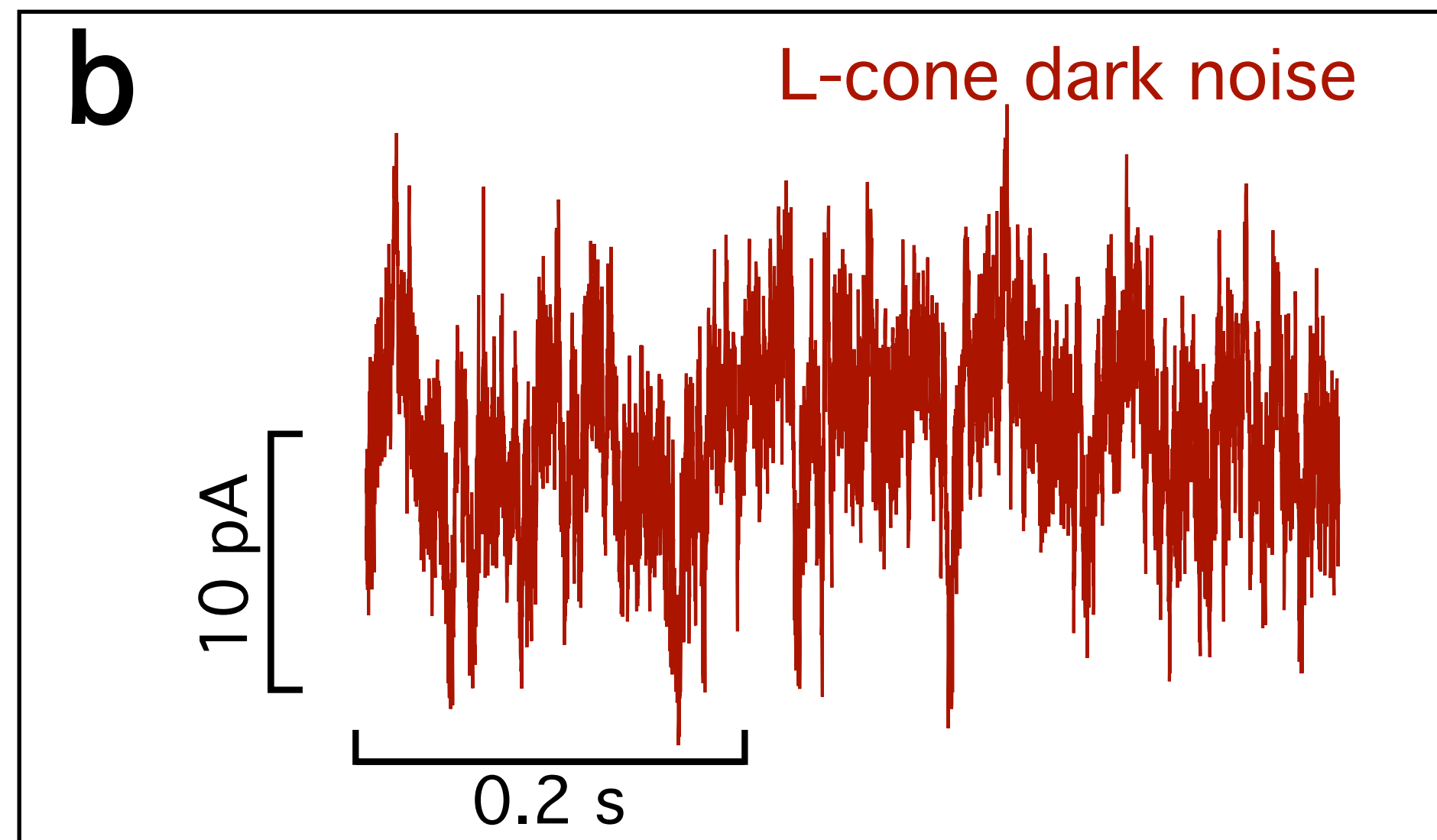
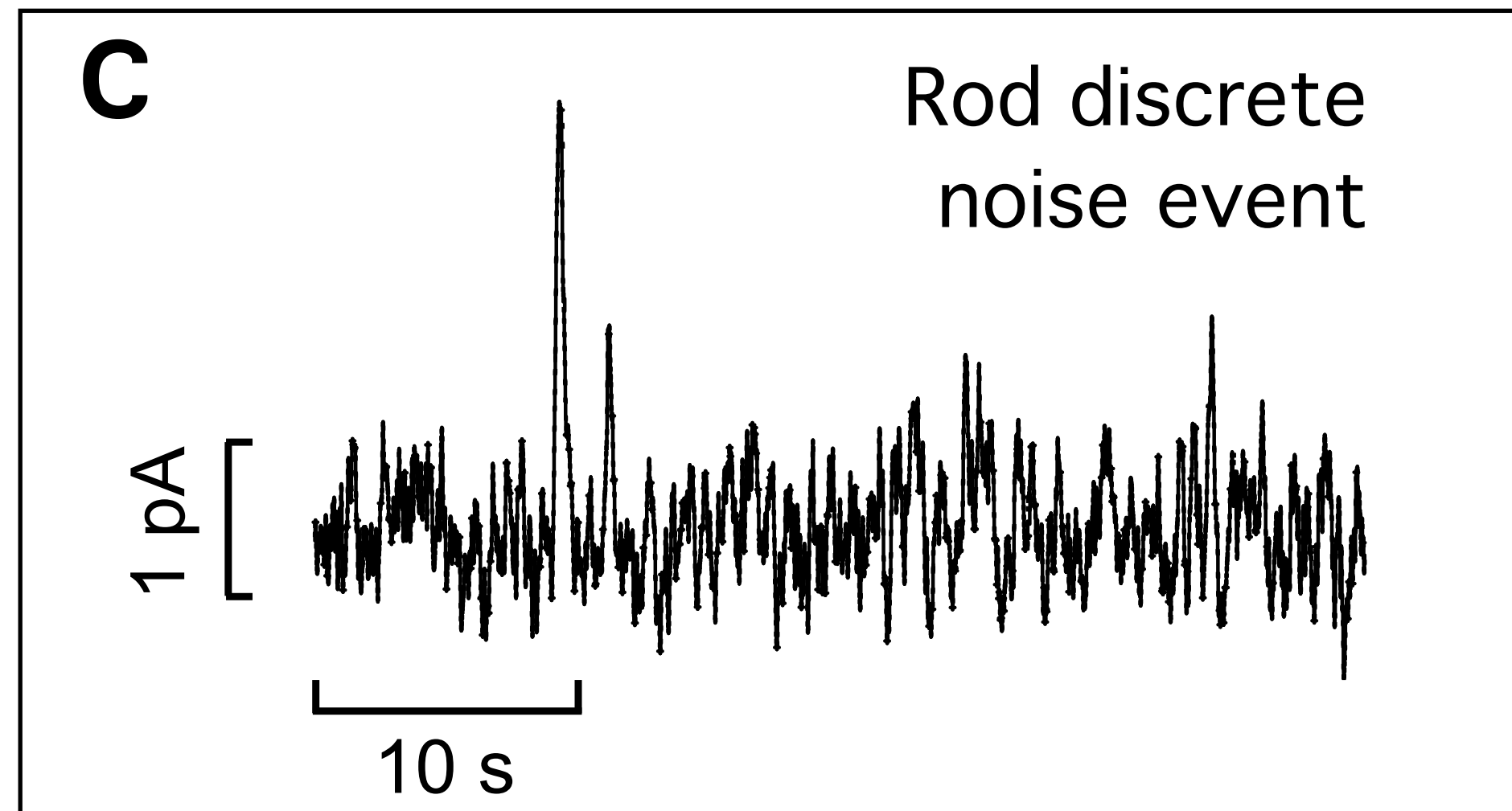


# Single Photon Response



- Single photon response
  - Rod is ~20x higher than cone
- ~30 pigment excitations closes half of the ion channels in a rod. It requires about 650 excitations in a cone to do SO (Baylor et al., 1984; Schnapf et al., 1990).
- Why? Phototransduction in rods is much more rapid.
  - So more ion channels have already been closed before counteracting forces kick in

# Dark Noise in Photoreceptors

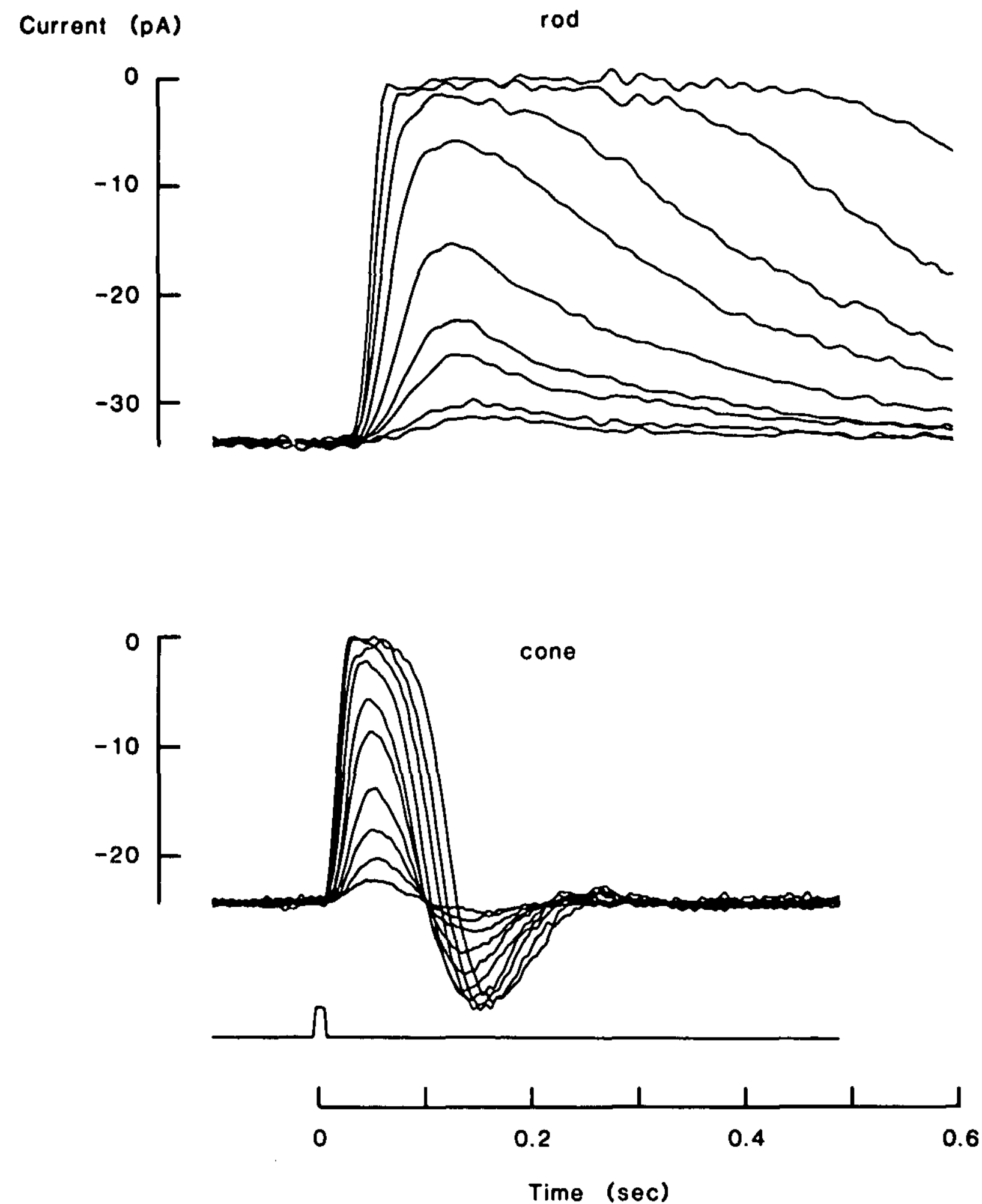


- Photocurrent should be 0 in dark, but it's not. Photocurrent in dark is called dark noise.
- Two components of dark noise:
  - Discrete: spontaneous thermal excitation of pigments
  - Continuous PDE activations
- Dark noise is much higher in cones than in rods.



# Kinetics of Responses in Rods and Cones

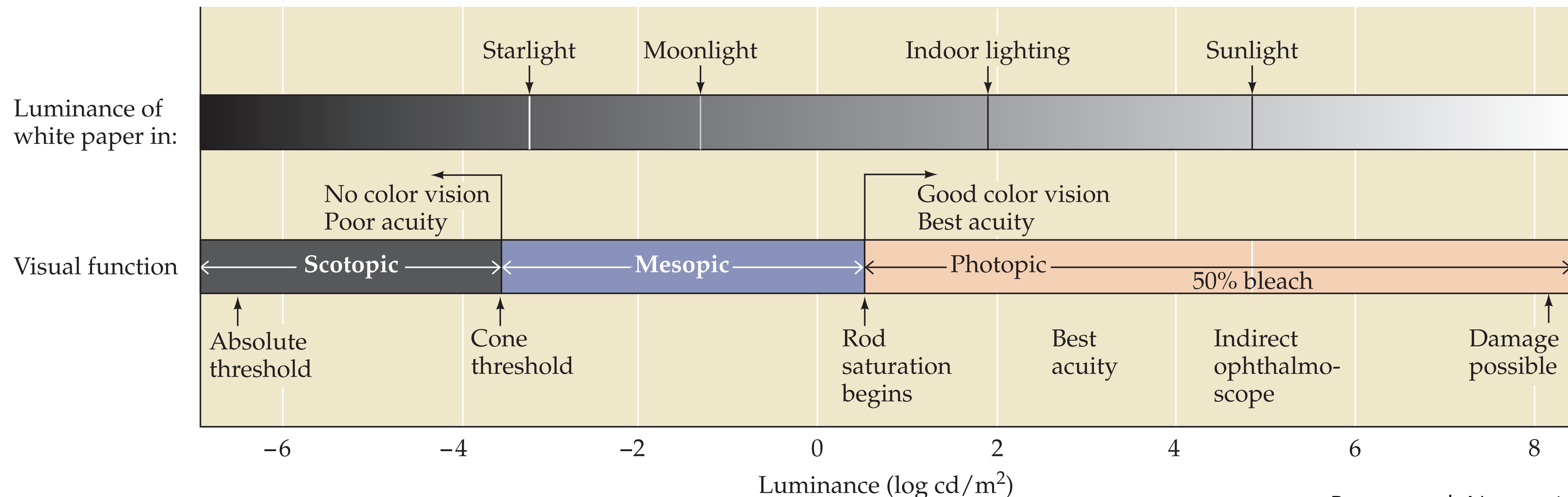
\* from macaque rod and L cone



- Cone response decays much faster than does rod.
- Because deactivation force is stronger in cones
- A longer duration integrates responses of more incoming photons.
- If the time durations of two excitations overlap, the total electrical response is greater than that of one excitation.

# Rod Vision Saturates Much More Easily

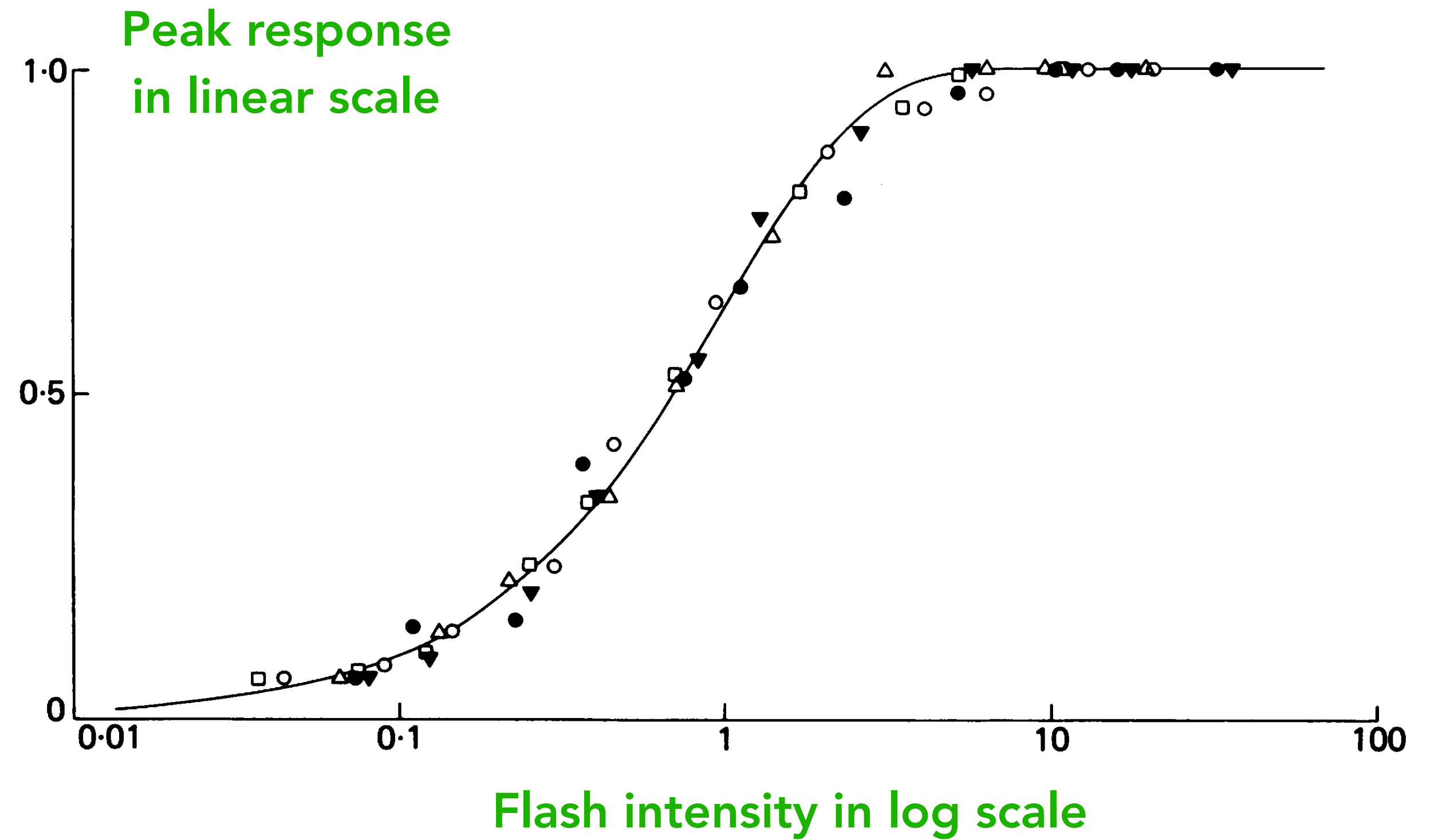
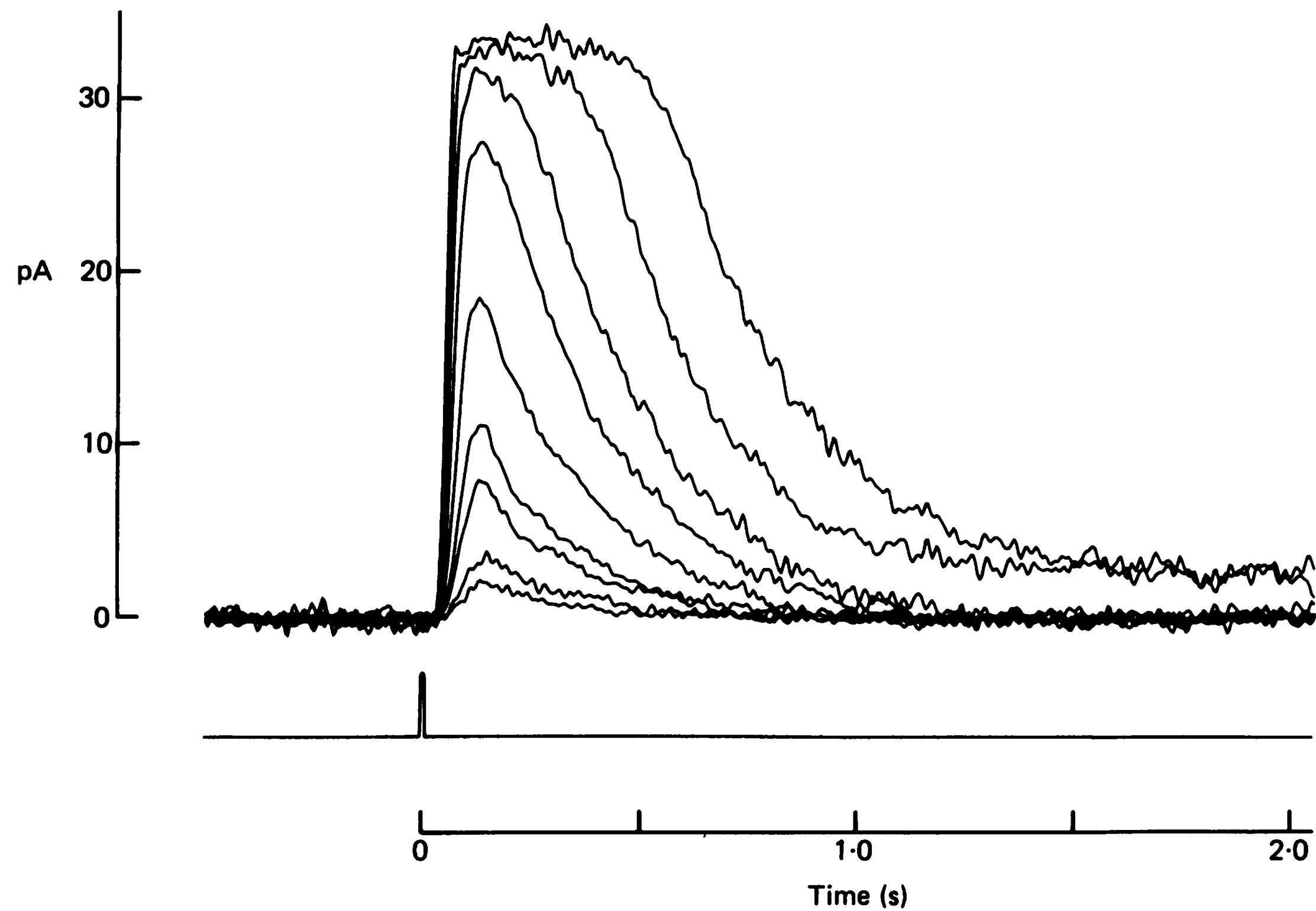
- Downside of being more sensitive. Saturation difference is unlikely affected by differences in the speed of pigment regeneration.
- Tens of millions of pigments in a photoreceptor, but a rod saturates after a few hundred pigment excitations.



# Response vs. Intensity

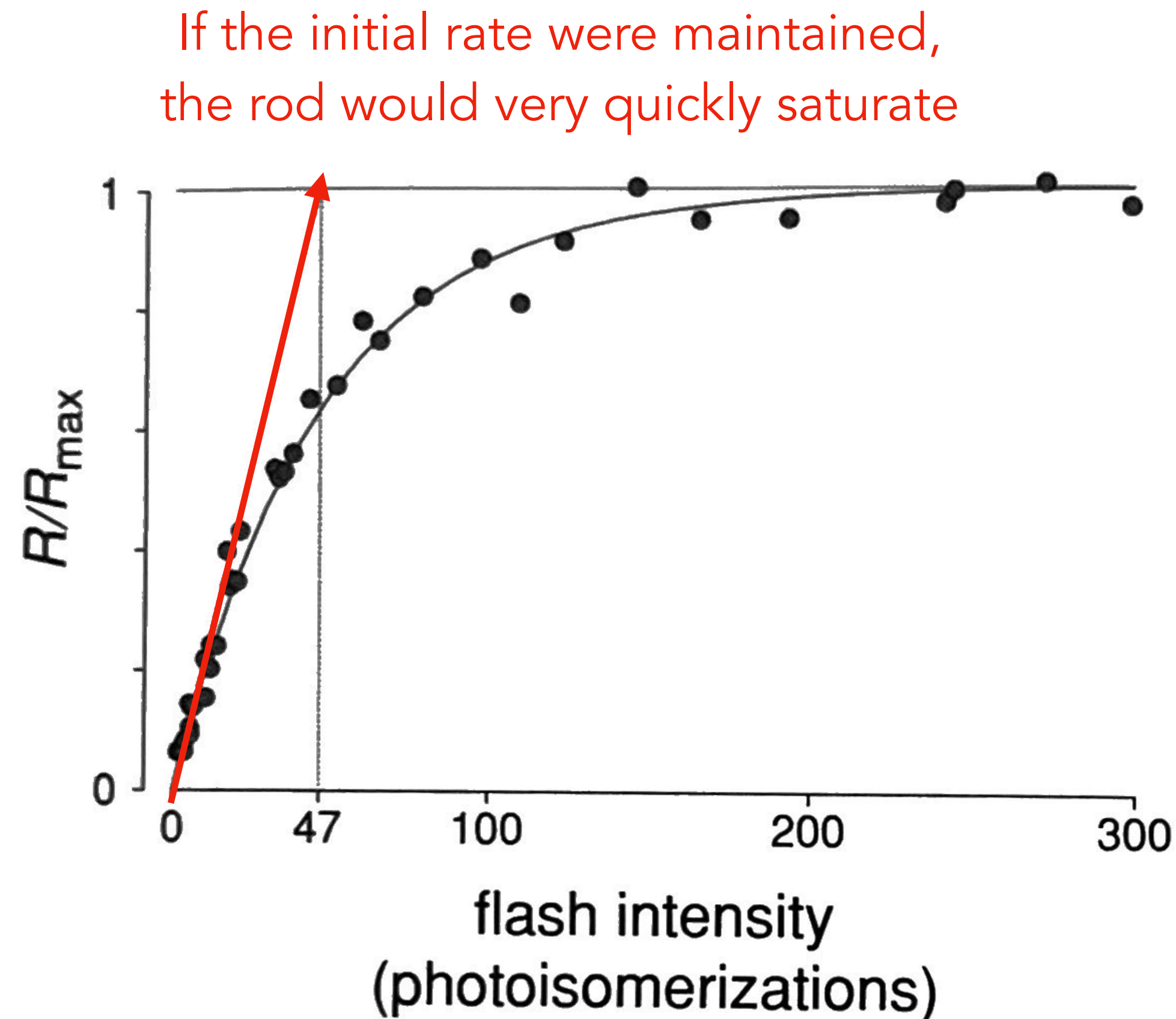
# (Peak) Response vs. Light Intensity

\* Macaque rods





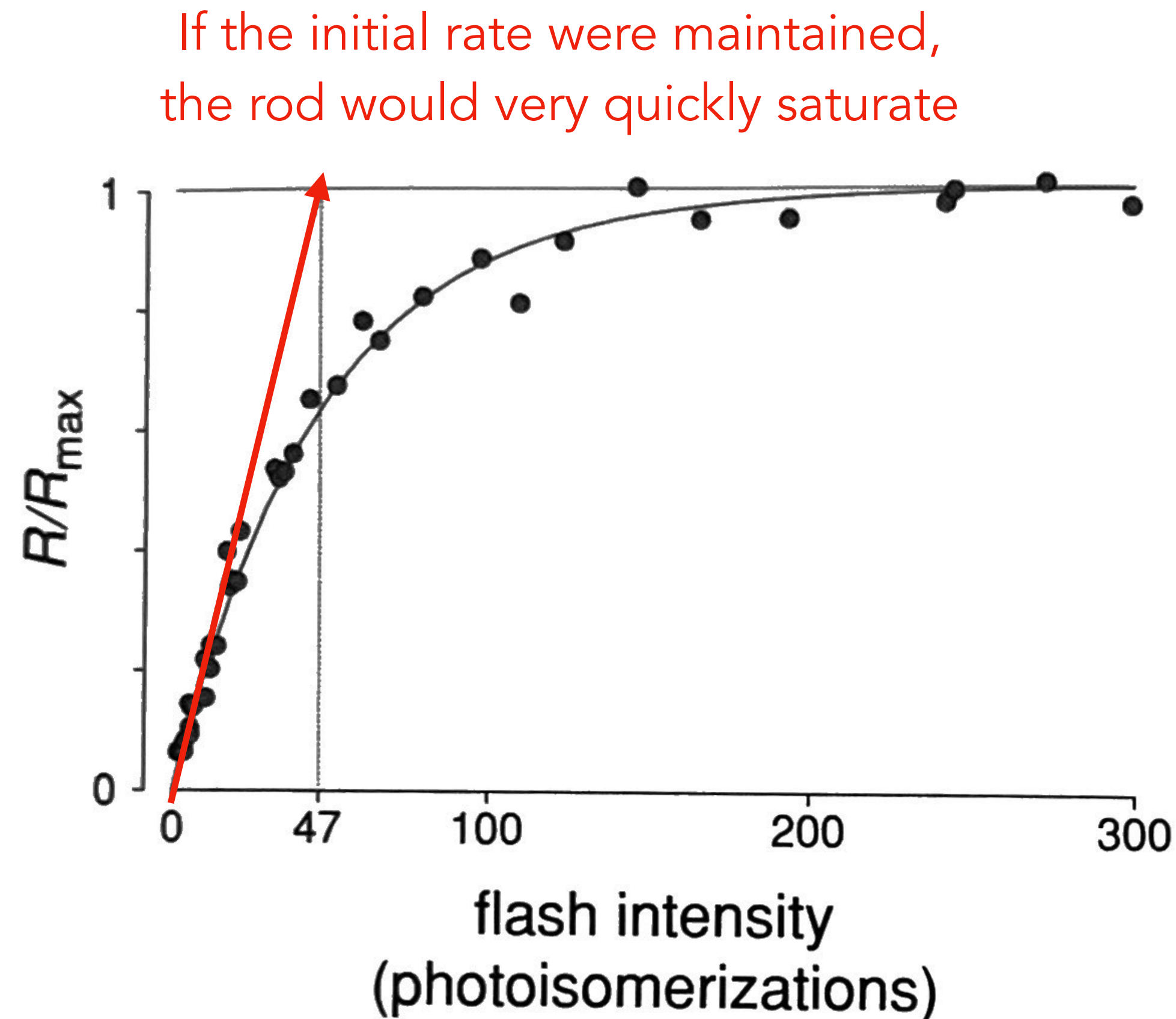
# (Peak) Response vs. Light Intensity



Same data but both in linear scale

- Electrical response vs. light intensity is not linear!
  - ~exponential saturation
  - as if the photoreceptor becomes less sensitive when light becomes more intensity: **desensitization**
  - essential for **adaptation**; more later.
  - This doesn't contradict the Principle of Univariance!
- Why do photoreceptors desensitize? What benefit?

# (Peak) Response vs. Light Intensity



Same data but both in linear scale

- Why not linear?
  - Think of what produces the responses
- ~Linear when the light is dim
  - That's how people estimate single photon response (assuming this limited linearity)
- This is also why perceived brightness is not linear w.r.t. light power/intensity

# Brightness Encoding

Linearly increase light power/intensity



Allocate more bits to  
encode this range



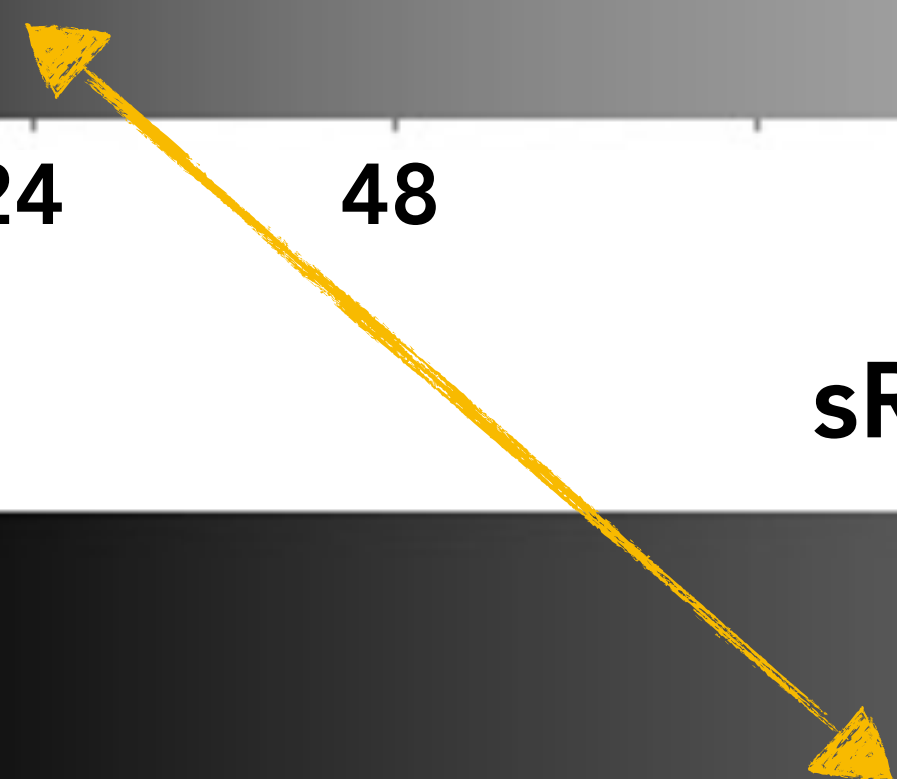
Allocate fewer bits to  
encode this range

# Brightness Encoding

Linearly increase light power/intensity



sRGB encoding of brightness





# Key Things to Take Away

- Principle of univariance:
  - Electrical response is independent of wavelength
  - Implication: if two lights cause the same amount of pigment excitation, they are seen as the same light.
- Overall photoreceptor sensitivity = ocular transmittance x macular transmittance x photoreceptor absorptance
- Phototransduction is a cascade of biochemical reactions caused by a single pigment excitation closing ion channels and producing photocurrents.

# Key Things to Take Away

- Two countering forces that prevent our vision from constant saturation
  - Pigment regeneration
  - Deactivation of phototransduction
  - Former happens in *minute*-scale and latter in *ms*-scale
- Rod vision is more sensitive than cone vision and is more easily saturated
- Photoreceptor response vs. light intensity is not linear, and that's why your perceived brightness is not linear w.r.t. light intensity