Dark and light adaptation: a job that is accomplished mainly in the retina

Dark adaptation: recovery in darkness … of sensitivity and photoreceptor pigment.

Light adaptation: “The ability of the visual system to adjust its performance to the ambient level of illumination”

Lamb (Chapter 20, 2011) Adler

Range of Visual Sensitivity: Scotopic, Mesopic, Photopic

Figure 3.5. Scotopic, mesopic and photopic ranges for the macaque retina. (R. G. Smith, personal communication).
Rod and cone sensitivity: During dark adaptation and recovery from bleaching of photopigment, cones recover sensitivity more quickly than rods.


Effect of pre-adapting light on dark adaptation


Figure 3: Dark adaptation curves following different durations of a pre-adapting luminance. Wald and Clark's data are from Bartlett (10).
Effect of retinal location on dark adaptation

Wavelength of the stimulus affects dark adaptation due to spectral sensitivity of rods and cones
Factors that contribute to dark and light adaptation in the retina

- Pupil area (about 1 log unit)
- Molecular mechanisms in rods and cones controlling sensitivity, saturation, pigment depletion and regeneration
- Gain control: Neural adaptation occurs in stages in the retinal circuits
  - IpRGCs may play a role
- Saturation of circuits, switching circuitry

Image forming “pattern” vision mediated by rods and cones, and non image forming vision (NIF) mediated by ipRGCs when environment light is a regulator of physiology and behavior
Intrinsically photosensitive RGCs

A subpopulation of RGCs are intrinsically photosensitive (ipRGCs)

- Identified through retrograde labeling from SCN
- Responses are very slow and sustained

Berson et al., 2002

IpRGCs project predominantly but not exclusively to 'non-visual' brain regions such as the SCN and the OPN (pupil light reflex)

Berson, 2003
Pupillary light reflex

Pupil control: role of classical photoreceptors (rod and cone opsins) vs melanopsin in the retina ganglion cells that project to the midbrain

Diminished Pupillary Light Reflex at High Irradiances in Melanopsin-Knockout Mice vs. Rodless-Coneless Mice

Lucas et al., 2003
Macaque: Blockade of all postreceptoral rod and cone-driven responses shifts (reduces) sensitivity of pupilloconstriction

Gamlin et al, 2007

Rod and cone photoreceptors

- Relative sensitivities
- Saturation
- Calcium feedback
- Pigment depletion
Rod and cone sensitivity: During dark adaptation and recovery from bleaching of photopigment, cones recover sensitivity more quickly than rods.

Rod and cone sensitivity: During dark adaptation and recovery from bleaching of photopigment, cones recover sensitivity more quickly than rods.


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Figure 2. Scotopic (rods) and photopic (cones) spectral sensitivity functions. Welch data from Davson, H. Physiology of the Eye, 5th ed. London: Macmillan Academic and Professional Ltd. 1990.

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Figure 4. Scotopic (rods) and photopic (cones) spectral sensitivity functions. Welch data from Davson, H. Physiology of the Eye, 5th ed. London: Macmillan Academic and Professional Ltd. 1990.

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Rod and cone sensitivity: During dark adaptation and recovery from bleaching of photopigment, cones recover sensitivity more quickly than rods.

Figure 5. Scotopic (rods) and photopic (cones) spectral sensitivity functions. Welch data from Davson, H. Physiology of the Eye, 5th ed. London: Macmillan Academic and Professional Ltd. 1990.

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Rod and cone sensitivity: During dark adaptation and recovery from bleaching of photopigment, cones recover sensitivity more quickly than rods.

Figure 6. Scotopic (rods) and photopic (cones) spectral sensitivity functions. Welch data from Davson, H. Physiology of the Eye, 5th ed. London: Macmillan Academic and Professional Ltd. 1990.

Rod and cone sensitivity: During dark adaptation and recovery from bleaching of photopigment, cones recover sensitivity more quickly than rods.

Rod and cone sensitivity: During dark adaptation and recovery from bleaching of photopigment, cones recover sensitivity more quickly than rods.

Figure 7. Scotopic (rods) and photopic (cones) spectral sensitivity functions. Welch data from Davson, H. Physiology of the Eye, 5th ed. London: Macmillan Academic and Professional Ltd. 1990.

Rod and cone sensitivity: During dark adaptation and recovery from bleaching of photopigment, cones recover sensitivity more quickly than rods.

Rod and cone sensitivity: During dark adaptation and recovery from bleaching of photopigment, cones recover sensitivity more quickly than rods.

Figure 8. Scotopic (rods) and photopic (cones) spectral sensitivity functions. Welch data from Davson, H. Physiology of the Eye, 5th ed. London: Macmillan Academic and Professional Ltd. 1990.

Rod and cone sensitivity: During dark adaptation and recovery from bleaching of photopigment, cones recover sensitivity more quickly than rods.

Rod and cone sensitivity: During dark adaptation and recovery from bleaching of photopigment, cones recover sensitivity more quickly than rods.

Figure 9. Scotopic (rods) and photopic (cones) spectral sensitivity functions. Welch data from Davson, H. Physiology of the Eye, 5th ed. London: Macmillan Academic and Professional Ltd. 1990.

Rod and cone sensitivity: During dark adaptation and recovery from bleaching of photopigment, cones recover sensitivity more quickly than rods.

Rod and cone sensitivity: During dark adaptation and recovery from bleaching of photopigment, cones recover sensitivity more quickly than rods.

Figure 10. Scotopic (rods) and photopic (cones) spectral sensitivity functions. Welch data from Davson, H. Physiology of the Eye, 5th ed. London: Macmillan Academic and Professional Ltd. 1990.
- Rods signals saturate: even when only about 1% of pigment is bleached
- Cone signals avoid saturation even during bleaching
- Shut off mechanisms: shut off time constants for each step of the phototransduction cascade are 20 times shorter in cones than in rods
- Cones regenerate pigment more quickly than rods
- Cone visual cycle includes Mueller cells which are closer to the cells than RPE which are essential for rod visual cycle

**Pigment regeneration, requires RPE for rods, not cones**

*Isolated retina*

**Fig. 3.** Primates and human retina promote cone pigment regeneration. (A) Primates rods and cones ERG responses from retina dark-adapted to maxcap after excitation. Exposure to bright light abolishes the rod component (slow, high sensitivity), whereas the cone component (fast, low sensitivity) recovers substantially. (B) Primates cone ERG responses from retina isolated immediately after excitation from the RPE. No rod response is observed if the retina is dark-adapted in the absence of RPE (left). Following subsequent bleach and 1-h dark incubation (right), cone response amplitude and sensitivity recover substantially. (C) Only cone responses are observed in human retina, isolated under surgical light from the RPE prior to dark adaptation (left). Significant cone recovery is observed following subsequent bleach and 1-h dark incubation (right). (D) Human cone sensitivity and amplitude recovery following bleach is blocked by preillumination of the retina in Müller cell inhibition (middle). The effect of L-6-AAA was reversed by megesterol 51-cis RPE (right). (E) Full range of photoreceptor responses to 16,500 photons μm−2 1600 μs (k-c); and to 160,500 photons μm−2 1,600 μs (k). Adapted from Wang and Kefalov (2008).
Pigment regeneration, requires RPE for rods. Cone visual cycle includes Mueller cells.

**Rod**
- Pigment regeneration
- Requires RPE for rods
- Cone visual cycle includes Mueller cells

**Cone**
- Calcium dependent mechanisms
- Feedback in photoreceptors
- Extends the sensitivity of the response
- Via GC and cGMP→ channels open

Wang and Ketalov 2010 PRER The Cone-specific visual cycle

Calcium dependent mechanisms: feedback in photoreceptors: extends the sensitivity of the response; via GC and cGMP→ channels open.
Primate rod outer segments – adjustment of sensitivity

Compression prediction

Tamara et al. 1991

Saturation of responses

Hyperbolic vs exponential

Derived P3 (μV)

Log normalised flash energy
Compression – the photoreceptor has a fixed response range. If a steady background uses up some of the range, only the remaining portion will contribute to a flash response.

Light adaptation of the whole visual pathway (mainly in the retina)

- Increment threshold - rod pathways incremental sensitivity
  threshold vs intensity (TVI) curve
Increment threshold: rod & cone, vs rod only

Parafoveal: small stimuli: 1 deg dia, 60 ms, yellow-green flash (580 nm) on green background

Peripheral: larger stimuli - 9 deg dia, 200 ms, green flash on red background

Primary rod pathway – post receptoral mechanisms

Convergence

Fig. 16. Convergence of rods, rod bipolar and all amacrine cells to alpha and beta cells of cat retina.
Light adaptation of an achromat (Norby)– no cone vision (rod monochromat)

Night vision (Hess, Sharpe & Norby)

Rod-vision: loss of sensitivity prior to saturation is not due to photoreceptors

Rod photoreceptor
Compression occurs
Near saturation of the Increment sensitivity function

Walraven et al. 1990
Effect of light adaptation on cat retinal ganglion cell activity

Sakmann & Creutzfeldt, 1969

Automatic gain control

Rod monochromat Weber region of TVI curve

Adaptation occurs in stages

Rat retina recordings

Green & Powers, 1982
Dark-adapted ERG

The ERG has several distinct waves:

a-wave primarily from photoreceptors

b-wave primarily from bipolar cells

scotopic threshold response (STR) from inner retinal amacrine and ganglion cells

Adaptation occurs in stages in the retina. This can be seen by examining adaptation of waves of the ERG from different stages or retinal processing.

Cat ERG: Rod-driven (data points)

Human rod monochromat (thick solid line)
Controlling the gain of rod mediated signals in the mammalian retina – single cell records

A. Rod bipolar pathway

- 10,000 rod photoreceptors
- ~500 rod bipolars
- ~20 All amacrines
- 1 ganglion cell

B. Mouse Retinal slice

Gain control in rod pathway

Convergence based on macaque peripheral parasol cell

<table>
<thead>
<tr>
<th>Location</th>
<th>Convergence</th>
<th>Known gain control?</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rod</td>
<td>1</td>
<td>yes (phototransduction)</td>
</tr>
<tr>
<td>Rod bipolar cell</td>
<td>~20</td>
<td>yes (synapse with All amacrine)</td>
</tr>
<tr>
<td>All amacrine cell</td>
<td>~200</td>
<td>no</td>
</tr>
<tr>
<td>On parasol ganglion cell</td>
<td>~2000</td>
<td>no</td>
</tr>
</tbody>
</table>

Schwartz & Rieke, 2014

Dunn et al., 2006
Light adaptation in cone vision involves switching between receptor and post-receptoral sites

Dunn et al., 2007: (Nature)

CX36 Between rods and cones
CX36 Between All amacrine cells
CX36 Between All amacrine cells and On cone bipolar cells
*CX45 on bipolar cell side
Not shown, CX36 between off alpha ganglion cells
### Three rod pathways - switching circuits

<table>
<thead>
<tr>
<th>Pathway</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>ON1</td>
<td>Primary – Rod – RBC – All – CB - GC</td>
</tr>
<tr>
<td>ON2</td>
<td>Secondary – Rod – Cone – CB - GC</td>
</tr>
<tr>
<td>OFF1</td>
<td>Tertiary – Rod - Off CB - GC</td>
</tr>
</tbody>
</table>

**Mills & Massey, 1995** - CX36 coupling in the IPL: All to All (Cx36-36) and All to On cone bipolar cells (Cx36 – 45)
Dopamine (DA) uncouples gap junctions between AII (A2) amacrine cells

All (A2) Coupling is removed in CX36 -/-) mice
Cx36 (KO) On ganglion cells

Rod signals cannot reach On ganglion cells because of loss of gap junctions between AII amacrine cells and on cone bipolar cells in the inner retina, and between rods and cones in the outer retina.

Deans et al., 2002

Convergence and segregation of the multiple rod pathways in mammalian retina.

Top
Off ganglion cells fed by the sensitive rod circuit have reduced sensitivity maybe because AII amacrine cells are no longer coupled.

Bottom
AP4 (APB) eliminates signals in On (rod) bipolar cells and the sensitive rod circuit mediated by RBCs

(Volgyi et al., J. Neurosci. 2004 Dec 8;24(49):11182-92)
Overview of retinal circuits
Parallel pathways through the retina
- Midget, On and Off (70% rgcs)
- Parasol, On and Off (10% rgcs)
- SMS pathway (On-OFF) (8% rgcs); S – Off-On

Average contrast gain of M and P cells, using optimal spatial stimuli, P cells have less rod input than M-cell
Scotopic spatial resolution is set by P-cells even though M-cells are more sensitive.