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).
Factors that contribute to dark and light adaptation in the retina

- Contribution of the 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
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
Blockade of all postreceptoral (On and Off 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 photocurrents: prolonged
Cone photocurrents: brief
Rods are 70-100 times more sensitive than cones

Figure 6: Scotopic (rod) and photopic (cone) spectral sensitivity functions. Wilkins data from Davson, H. Physiology of the Eye, 5th ed. London: Macmillan Academic and Professional Ltd; 1950.
Saturation of responses

Hyperbolic vs exponential

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.
- 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.
Cone visual cycle includes Mueller cells

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

Tamara et al. 1991 Primate rods – adjustment of sensitivity

Compression prediction
- Light adaptation

- Increment threshold - rod pathways alone

**Primary rod pathway**
Night vision (Hess, Sharpe & Norby) – an achromat – no cone vision (rod monochromat)

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

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

Automatic gain control

Rod monochromat

Sakmann & Creutzfeldt, 1969

Adaptation occurs in stages

Rat retina:
Green & Powers, 1982
Dark-adapted ERG

The ERG has several distinct potentials:

- 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.
Dunn et al., 2006, J. Neurosci. Controlling the gain of rod mediated signals in the mammalian retina

A
Rod bipolar pathway

B
Mouse Retinal slice

Gain control in rod pathway

Convergence based
On macaque peripheral parasol cell

Schwartz & Rieke, 2014
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

Dunn et al., 2007: (Nature) Light adaptation in cone vision involves switching between receptor and post-receptoral sites
CX36, 45 in the retina

Between rods and cones
Between All amacrine cells
Between All amacrine cells and On cone bipolar cells
*CX 45 on bipolar cell side
Not shown, between off alpha ganglion cells

Rod Pathways - switching circuits

<table>
<thead>
<tr>
<th>ON1</th>
<th>ON2</th>
<th>OFF1</th>
<th>OFF2</th>
<th>OFF3</th>
</tr>
</thead>
<tbody>
<tr>
<td>PRL</td>
<td>OPL</td>
<td>INL</td>
<td>IPL</td>
<td>GCL</td>
</tr>
</tbody>
</table>

- mgluR
- igluR

Primary – Rod – RBC – All – CB - GC
Secondary – Rod – Cone – CB - GC
Tertiary – Rod - Off CB - GC
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 All amacrine cells: Hampson et al., 1992
Deans et al., 2002 All Coupling is removed in CX36 -/-) mice

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

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 do not have very much rod input, but it is more than suggested by this figure.

Kaplan & Shapley

Lennie & Fairchild, 1994
Scotopic spatial resolution is set by P-cells even though M-cells are more sensitive.