B.3 Membranes, Dichroism and Receptor Sensitivity

SIMON B. LAUGHLIN, RANDOLF MENZEL, and ALLAN W. SNYDER

Contents

1.	Introduction	237
2.	The Vertebrate Photoreceptor Membrane	238
2.1	The Binding of Rhodopsin	238
2.2	Chromophore Orientation	240
2.3	The Motion of Rhodopsin Molecules	241
3.	The Dichroism of Membranes and Membrane Arrays	242
3.1	The Vertebrate Rod Outer Segment (ROS)	242
3.1.1	The Single Disc - Intrinsic Dichroism	242
3.1.2	A Stack of Discs - Form and Intrinsic Dichroism	243
3.2	Microvilli and Rhabdomeres	244
3.2.1	The Single Microvillus - Intrinsic Dichroism	245
3.2.2	Rhabdomeres - Form and Intrinsic Dichroism	245
3.2.3	Application of Theory - Estimating Rhabdomeric Dichroism	246
3.2.4	The Model Microvillus and PS	249
3.2.5	A Fluid Membrane Model for Dipole Alignment	250
4.	Dipoles Orientated for Maximal Absorption	254
4.1	The Vertebrate Rod Outer Segment (ROS)	255
4.2	The Rhabdomere of the Fly (Unfused Rhabdom)	257
4.3	The Fused Rhabdom	257
	References	258

1. Introduction

Photoreceptors are specialised cells evolved for high sensitivity to light. The light absorbing molecule is a dipole embedded in a protein molecule. This chromophore-protein complex, the rhodopsin molecule, is part of the cell membrane, where it is free to undergo lateral and rotational diffusion. The high quantum capture property of highly evolved photoreceptors is the result of several molecular, fine and gross structural mechanisms: (1) The concentration of rhodopsin molecules within the membrane is extremely high; (2) The membranes holding the rhodopsin molecules are organised in closely packed stacks of discs (vertebrate photoreceptors) or dense packages of tubes (rhabdomeric invertebrate photoreceptors); (3) Light is contained within the light absorbing structure as the result of the high optical density of these membrane stacks (light guide).

Besides these facts the quantum capture property of the whole light absorbing structure of a photoreceptor is very sensitive to the orientation of the dipole molecule relative to the light path. In general, the dipole absorber molecule must be perpendicular to the light path for highest absorption. This is indeed found in the membrane stacks of the vertebrate rod outer segment (ROS). However, the dipoles need not be randomly orientated in the plane perpendicular to the light path for maximal absorption of unpolarised light. The concept derived

A. W. Snyder et al. (eds.), *Photoreceptor Optics*

here shows that the organisation of the whole light guiding and light absorbing structure determines how the chromophore dipoles should be arranged for maximal absorption of unpolarised light. In essence we come to the same conclusion as in a previous paper (SNYDER et al., 1973): that the arrangement of the light absorbing molecules is primarily an evolutionary adaptation for optimal absorption of unpolarised light, and that dichroic absorption of single visual cells in arthropods is a by-product of this general mechanism.

This paper has three principal objectives:
1) We review briefly contemporary knowledge of photoreceptor (fluid) membrane with special emphasis on the factors that contribute to its dichroism (Section 2).
2) We derive theoretical expressions for the dichroism of vertebrate outer segment disc membrane and rhabdomeric membrane (Section 3). It is shown that the dipoles are orientated in the membrane to provide three diverse photoreceptor types with maximum sensitivity to unpolarised light (Section 4). The theory follows that of SNYDER and LAUGHLIN (1975) but here we provide a more physical or intuitive derivation of their results.
3) We develop a unified photoreceptor membrane theory applicable to all highly developed photoreceptors both vertebrate and invertebrate. The unifying concept is that membranes have evolved to provide photoreceptors with the maximum absolute sensitivity to unpolarised light. This theory explains the mechanism for dipole alignment in some rhabdomeric membrane (Section 3.2.5).

2. The Vertebrate Photoreceptor Membrane

In order to understand how dichroic chromophores can be incorporated into a membranous organelle so as to produce a dichroic structure we need to make several assumptions about the manner in which the chromophore is incorporated into the membrane. Our knowledge of the retinal-opsin bond (DE GRIP et al., 1973) and the dynamic state of rhodopsin in the membrane has advanced recently through the study of vertebrate rod outer segments (CONE, 1972; POO and CONE, 1974). Unfortunately there is at present little understanding of the equivalent properties of invertebrate rhabdomeric membranes (rev. ABRAHAMSON and FAGER, 1973; HAMDORF and SCHWEMER, this vol.). However it will be shown below that the behaviour of rhodopsin in rod outer segment (ROS) disc membranes conforms exactly with the general model proposed by NICHOLSON and SINGER (1972). It is for this reason that we will discuss the vertebrate membrane in some detail and use it as the basis of an invertebrate polarisation analyser.

2.1 The Binding of Rhodopsin

Direct microspectrophotometric (MSP) measurements show that rhodopsin and its associated photoproducts are localised within the outer segments of rods (rev. LIEBMAN, 1972). Electron microscopy demonstrates that each outer segment is a stack of membrane discs. Each disc consists of a single contiguous membrane enclosing a broad flattened intracellular vacuole (Fig. 1). Rhodopsin is essentially a membrane lipo-protein (WALD, 1973); it can only be extracted using detergents and it requires a proportion of bound lipids to show its normal activ-