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Introduction

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Nature makes use of the propensity of retinal for light-dependent double-bond isomerization in a number of systems and in a variety of ways. The common theme for light receptors based on this kind of chemistry is that (1) the retinal is bound in most cases to a small membrane protein via a protonated lysine-retinal Schiff base, (2) the absorption maximum in the visible is tuned to a suitable wavelength largely by electrostatic interaction with polar protein residues, and (3) the light-induced bond rotations and strains in the retinal set off reaction chains during which at least part of the excess free energy acquired is transferred to the protein and causes pK shifts of acidic residues and/or backbone conformational changes. The physiological consequence of the process initiated by absorption of light is either the activation of an information transfer chain (sensory and visual rhodopsins) or energy transduction which drives the electrogenic movement of ions across the membrane (ion-motive rhodopsins). Rhodopsins with these functions occur in bacteria and in higher organisms; from an evolutionary standpoint they are not related to one another. Nevertheless, all of these proteins are remarkably similar and form a distinct family.

This volume is intended to reflect an evolving dialogue between investigators concerned with retinal proteins as information-transducing and as energy-transducing devices. Initially this dialogue came about because of shared methodology. NMR, FTIR, and resonance Raman spectroscopy are particularly suited for studies of retinal bond motions, and the intense absorption of rhodopsins in the visible allows defining the reaction sequences through measurements of light-induced changes in optical properties. FTIR reveals, in addition, changes in the protonation states of residues and in hydrogen bonding. Because the reactions of rhodopsins are initiated by light, single turnover experiments using short laser pulses simplify the kinetic studies. The latter approach has led to the development of instrumentation for the measurement of transient changes in the visible, as well as in the infrared. All of this technology has been shared, virtually without any modifications, between the two communities. In the last years, however, the recognition has taken hold that important and deep-seated analogies exist in the structure and mechanism of rhodopsins with sensory and energy-transducing roles, and these persist regardless of whether they are in bacteria or eukaryotic organisms.

Because bacteriorhodopsin is (1) a simpler and sturdier protein than the others, (2) occurs in a two-dimensional crystalline lattice, and (3) more abundantly available, much more is known about this system. An atomic resolution model for its seven-helical transmembrane structure, based on electron cryo-microscopy, has stimulated much thought on the mechanism of function in this protein, light-driven proton transport, as do the consequences of single residue replacements. The present model, discussed from various points of view in this volume, links the retinal bond movements to internal proton transfers and the release and subsequent uptake of protons at the surface, as well as to a switch reaction which confers direction on the overall process. Significant residue and protein conformational changes are seen by a variety of methods. Although the nature of all of these is not yet clear, the possible rationales for them in the transport process are beginning to emerge. In halorhodopsin the transported ion is chloride. While binding this anion clearly requires somewhat different rules than binding protons, the general principles for driving the transport by the light-induced transient retinal isomerization appear to be the same.

The bacterial sensory rhodopsins and the visual rhodopsins, which serve information processing func-

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tions, undergo very similar reaction sequences after absorption of light as the ion-motive rhodopsins, but they have no demonstrable transport functions. Instead, they appear to couple the retinal isomerization to a protein conformational change which causes altering of their interactions with another membrane protein, a G-protein, in the first step of the ensuing signal transfer and amplifieation chain. More information about the nature of the conformational changes in the sensory and transport rhodopsins will reveal if these motions of the proteins are always coupled to internal proton transfers or in some of the cases only to motions of the retinal, deciding thereby whether or not they have a common structural basis.

On the one hand, the visual and sensory rhodopsins are related to bacteriorhodopsin and halorhodopsin in their retinal-based photoreactions, but on the other hand also to G-protein linked receptors of chemical signals in their structures and functions. The rhodopsins are thus at a focal point of modern biology, where essential regulatory and energy-coupling membrane functions come together. Their study has excited much interest in the past, and raises many intriguing questions for the coming years.