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Progress in Phototransduction*

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Introduction

"The nature of the coupling mechanism between light absorption on the lamellar membrane – the photocurrent generated by the outer-segment plasma membrane – is one of the most important unsolved problems of retinal physiology". This quote from Rodieck (1973, p 328) is still valid but we may feel fortunate with the knowledge that crucial pieces of the puzzle have been discovered in the last decade. Various aspects of the phototransduction mechanism have been highlighted during the Vth International Congress of Eye Research, held in Veldhoven, the Netherlands (from 5–8 October 1982). The correspondences and differences of phototransduction in both vertebrate and invertrebrate photoreceptor cells have been extensively discussed, and this issue of Biophysics of Structure and Mechanism is a selection of the presentations in symposia at this meeting.

The diagram in Fig. 1 is an attempt to summarize the main elements of the phototransduction mechanism. Here we will only briefly review the present views. The numbers between square brackets following in the text refer to the various processes in Fig. 1.

The Visual Pigment

Vision starts with light absorption by rhodopsin [1]. The fact that the peptide sequence of bovine rhodopsin has been resolved (expect for minor details) and that its secondary structure has been predicted (Ovchinnikov et al. 1982; Hargrave et al. 1983 – this issue) may be called this year's most exciting (and perhaps also most painstaking) step forward in visual pigment research (Dratz and Hargrave 1983).

* Based on material presented at the Fifth International Congress of Eye Research, Eindhoven, October 1982

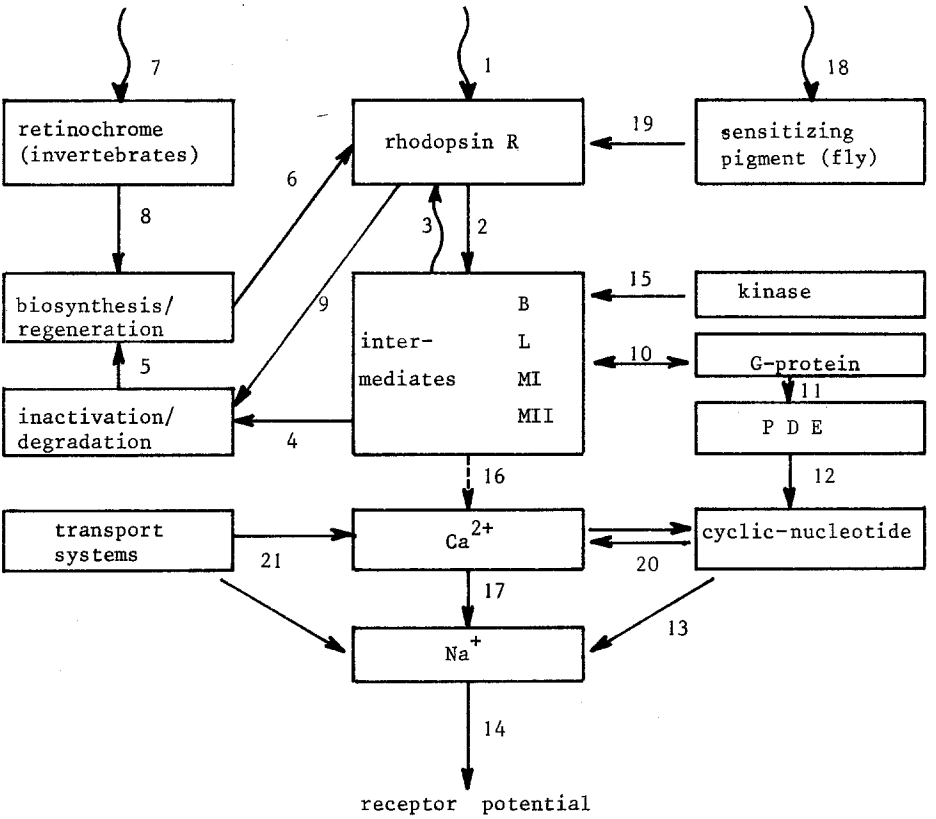

Fig. 1. Schematic presentation of the main pathways in the phototransduction mechanism. The various processes are discussed in the text where they are indicated by numbers between square brackets

The thermochemical changes [2] occurring in the visual molecule after light absorption go through a series of stages. The stages, extensively studied by low-temperature spectroscopy, were traced at room temperature by flash photolysis and laser methods in extracts or excised retinae from e. g. cattle and squid (review Yoshizawa and Shichida 1982). A corresponding series of stages was found for fly in the first in vivo laser analysis of a visual pigment (Kruizinga et al. 1983 – this issue). The intermediates, notably the metarhodopsins, can be photoconverted [3] into rhodopsin (e. g., cattle, Williams 1974; octopus, Schwemer 1969). Up to recently invertebrate metarhodopsins have been considered thermostable and hence photoregeneration was hypothesized to be the pathway for maintaining a high rhodopsin content in the photoreceptor cells of invertebrates (Hamdorf 1979). However, recent studies have shown that invertebrate metarhodopsins can decay rather rapidly, and furthermore that rhodopsin is regenerated (through a slower route) in the dark (fly, Schwemer 1979, 1983 – this issue; butterfly, Bernard 1983 – this issue 1983).

A hydrolysis of photoconverted visual molecules into opsin and all-trans retinal [4] and a subsequent regeneration in the dark [5] is wellknown for vertebrates (e. g., Rodieck 1973). The 11-cis retinal required for the functional restoration of rhodopsin is produced through esterification of the all-trans retinal, isomerization of the ester, hydrolysis into 11-cis retinol, and oxidation (frog, Bridges 1976).

An essential role in retinoid movement between vertebrate photoreceptor and pigment epithelial cells is performed by various binding proteins [5] (Chader 1982). In invertebrates a quite direct isomerization of all-trans retinal into the 11-cis form is realized by a very specific retinal-binding protein, namely the light driven [7] isomerase retinochrome [8] (e. g., Hara and Hara 1982, squid; see also Pepe et al. 1982, bee). The necessity of 11-cis retinal for rhodopsin regeneration is described by Schwemer (fly, 1983 – this issue).

We note that a turnover of visual membrane [9] discovered in vertebrates (e. g., Young 1970) is clearly an omnipresent process also in invertebrates (spider, Blest 1978; fly, Schwemer 1979; review Autrum 1981).

Enzymatic Activities

Photoconversion of vertebrate rhodopsin triggers a number of enzymatic processes leading to a change in the cyclic GMP concentration, which affects the photoreceptor potential. Biochemical studies in the last few years have greatly advanced understanding of rhodopsin-activated enzymes; reviewed in Miller (1981), Uhl and Abrahamson (1981), Stryer et al. (1981), Fein and Szuts (1982). The following steps are visualized in the contribution by Kühn and Chabre (1983 – this issue). First [10], metarhodopsin II is coupled to a GTP-binding protein (G-protein, Bennett et al. 1982, Emeis et al. 1982; transducin, Stryer et al. 1981; see Kühn et al. 1981). The activated form of the GTP-binding protein [11] then activates the phosphodiesterase (PDE) (Liebman and Pugh 1981; Stryer et al. 1981; Bennett 1982; Yoshizawa and Fukuda 1983 – this issue) which [12] lowers the cyclic GMP level. The plasma membrane Na^+-conductance is lowered, altering the receptor potential [14] (Miller 1981; Miller and Laughlin 1983 – this issue). Feedback control is provided among other mechanisms by phosphorylation of intermediates in the photochemical cyclic (Yamamoto and Shichi 1983 – this issue), by a specific kinase [15] (Kühn 1981) and by modulation of PDE-activity by a protein inhibitor (Liebman and Evanczuk 1982; Hurley 1982).

Receptor Potential

The receptor potential, i.e., the light-induced change in transmembrane potential, is hyperpolarising in vertebrates and depolarising in invertebrates (see Fain and Lisman 1981 and Fein and Szuts 1982, for reviews). This difference is often associated with the quite different structural organization of the light-absorbing organelles. Vertebrate rods and cones consist of a stack of discs

and invertebrate rhabdomeres consist of microvilli. Although the structural and electrophysiological differences are quite prominent it may well be that the phototransduction machinery in the two receptor types is basically the same. For instance, the variation in molecular weight of the rhodopsins is smaller than thought before (rev. Stavenga and Schwemer 1983) and also the lipid and fatty acid composition of the visual membrane is very similar (Paulsen et al. 1983). Furthermore, for invertebrate photoreceptors it has been shown that calcium flux is light dependent [16] and that calcium is an important agent in controlling membrane conductance [17] (see Stieve 1981). Pharmacological agents activating adenylate cyclase injected in *Limulus* photoreceptors induced depolarizations similar to light induced changes in membrane potential (Fein and Corson 1981; see also Fein and Szuts 1982). Invertebrate rhodopsin can activate bovine PDE (Ebrey et al. 1980) and a native GTPase (Calhoon et al. 1980, Vandenberg and Montal 1982). G-protein isolated in a crude soluble fraction from cephalopod retina is closely related to bovine G-protein (Saibil and Michel-Villaz, in preparation). Also for vertebrates both calcium and cyclic nucleotides are considered to play a central role in phototransduction (for ample discussions see Miller 1981).

Spectral sensitivity measurements of fly photoreceptors have revealed a novel aspect, namely that a sensitizing pigment can transfer absorbed light energy [18] to rhodopsin [19]. Further evidence for this new element in phototransduction is presented by Vogt and Kirschfeld (1983 – this issue).

The ultimate effector responsible for the receptor potential has, however, not yet been established. Experimental analyses directed to this question are clearly complicated by the interactions between calcium and cGMP [20].

An important factor to account for in future electrophysiological studies in photoreceptors is the presence of various ion transport systems [21], of which the Na^+/K^+-pump and the Na^+-Ca^{2+} exchange system have been well documented (Schnetkamp 1980; Fain and Lisman 1981; Armon and Minke 1983 – this issue). Quantification of their activities is difficult, but essential for a valid interpretation of electrophysiological data.

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