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Rapid Photopigment Conversions in Blowfly Visual Sense Cells Consequences for Receptor Potential and Pupillary Response*

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Abstract. Combined optical and electrophysiological experiments on the kinetics of visual pigment conversions in blowfly and the resulting pupillary response and late receptor potential are described. The photometrically detectable conversions of rhodopsin and metarhodopsin in the living wild type fly are completed within 0.5 ms. Prolonged pupillary responses and receptor potentials occur upon intense blue flashes. Subsequent intense red flashes abolish the prolonged responses in the case of both membrane potential and the pupil. The interrelation of potential and pupil is discussed.

Key words: Fly photoreceptor cells — Visual pigment — Receptor potential — Pupillary response.

Introduction

In the analysis of the phototransduction process the bistability of invertebrate visual pigments is an important quality. Recent research has clearly established that the two visual pigment states R (rhodopsin) and M (metarhodopsin) are expressed in the electrically measurable cell responses (review Hamdorf, 1979). The present consensus is that rhodopsin photosensitivity is the only determinant for the spectral sensitivity of the dark adapted cell at low light intensities (Goldsmith, 1972; Atzmon et al., 1978; Strong and Lisman, 1978). High light intensities of a selected wavelength range eliciting a high rhodopsin conversion rate versus little metarhodopsin conversion result in prolonged depolarizing afterpotentials (PDA); wavelengths inducing a high metarhodopsin conversion rate annihilate the PDA (barnacle: Hochstein et al., 1973; blowfly: Hamdorf and Razmjoo, 1977; Muijser et al., 1975; dronefly: Tsukahara et al., 1977; *Limulus:* Nolte and Brown, 1972; Minke et al., 1973). Related electrophysiological phenomena expressing visual pigment conversions are the fast photovoltages or early receptor potentials (ERP; barnacle: Hillman et al., 1973;

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Minke et al., 1973, 1974, 1978; *Limulus:* Lisman and Sheline, 1976; Lisman and Bering, 1977; fly: Pak and Lidington, 1974; Kirschfeld et al., 1977; Stark et al., 1977).

A distinctly different (optical) means to analyse the phototransducer process is provided by the pupil mechanism. This is the system of pigment granules situated in many invertebrate visual receptor cells, which function is the control of light flux (review Franceschini and Kirschfeld, 1976; Stavenga, 1979). In this paper we investigate the time courses of visual pigment conversions induced by monochromatic light flashes and the resulting late receptor potential and pupillary responses in the wild type blowfly *Calliphora erythrocephala.* The two photointerconvertible visual pigment states in this case are given by R495 and M580 (Hamdorf et al., 1973; Hamdorf and Rosner, 1973; Stavenga et al., 1973; Razmjoo and Hamdorf, 1976; Stavenga, 1976). Due to the bathochromically shifted metarhodopsin a virtually 100% rhodopsin population can be established by long wavelength irradiation. As was demonstrated in the mutant chalky a subsequent blue flash can create at least within approximately 30 ms a photoequilibrium with a large metarhodopsin fraction (Stavenga, 1976). Since fast photovoltages measured in flies called M-potentials (Pak and Lidington, 1974; Kirschfeld et al., 1977; Stark et al., 1977) last in the order of a few milliseconds the underlying molecular processes in principle could reflect the decay of thermolabile intermediate visual pigment states as was concluded from ERP measurements in barnacle (Minke et al., 1974, 1978). Direct microspectrophotometry was undertaken to elucidate this hypothesis. Furthermore, these photochemical experiments were essential for the interpretation of measured receptor potential and pupillary responses induced by double flashes.

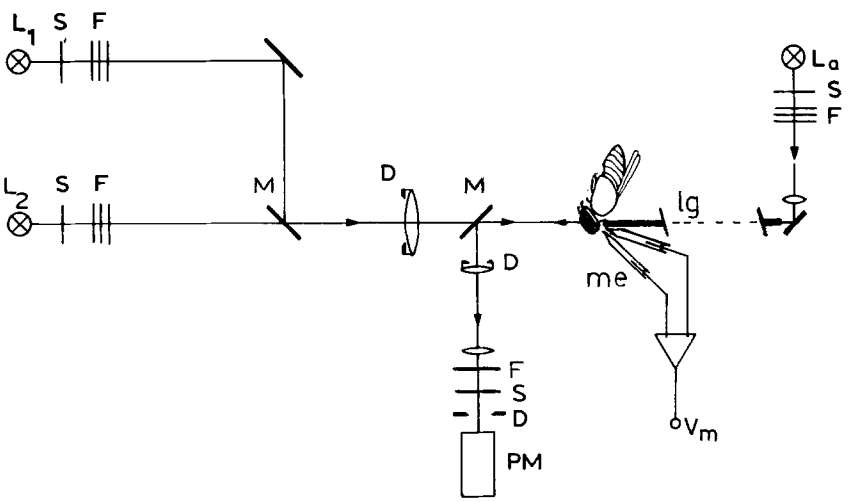

Fig. 1. *Experimental set-up.* L_1, L_2, and L_a are light sources controlled by filters F and shutters S. L_1 and L_2 are brought together in the half-mirror M and focussed on the eye of the fly. The light of L_a is sent antidromically through the rhabdomeres by means of the light guide (lg). The photomultiplier PM (with its shutter S, filter F and diaphragm D) detects the antidromic transmission. The microelectrodes (me) are brought into the eye to measure the membrane potential of the visual sense cells

Methods

The experiments were carried out on the fly *Calliphora erythrocephala* M. (wild type, wild captured). A light guide and a pair of glass microelectrodes were put in the back of the head after removing the chitin as shown in Figure 1.

The light guide, photomultiplier and optics were arranged so that the spectral transmission variations of the rhabdomeres could be detected; for further detail, see Stavenga et al. (1973). The method allows the measurement of both the action of the pupil and the state of the visual pigment.

The two glass microelectrodes were inserted into the fly to measure the membrane potential of the sense cells. Further details are described elsewhere (Muijser, 1979). Recordings were accepted whenever they had saturating peak potentials in the range 55–70 mV. A 450 W Xenon arc lamp, a 150 W Iodine lamp, a 300 Ws Xenon flash with a small arc and an ordinary photographic Xenon flash were available in the positions of L_1 and L_2 (Fig. 1).

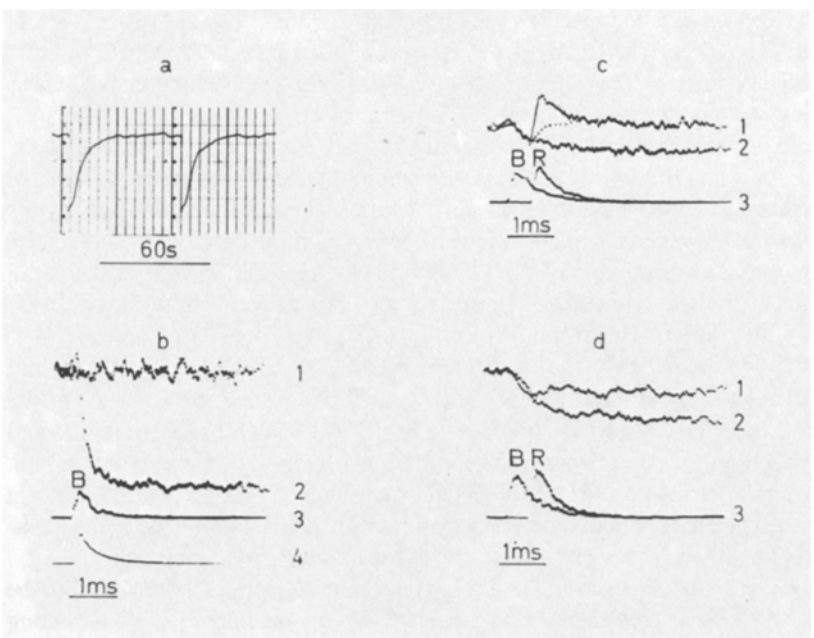

Fig. 2. a and b Time dependence of the antidromic transmission at 588 nm after single blue flashes. In **a** two blue flashes are given and the abrupt transmission drop indicates photochemical conversion of rhodopsin to metarhodopsin. The transmission rises again by means of the intense antidromic light that reconverts metarhodopsin back to rhodopsin. In **b** trace 2 shows how fast the conversion takes place, trace 4 represents the stimulus, trace 3 the stimulus artifact (due to fluorescense) in the rhabdomeres and trace 1 is the control experiment where no stimulus flash was given. **c** and **d** Double flash experiments. Trace 2 is the control experiment, the response of the transmission to a single blue flash B. It shows incomplete conversion due to the use of a less powerful flashlight (also there is no artifact). In the experiment represented by trace 1 after a blue flash B a subsequent red flash R reconverts completely the pigment, but leads to an artifact which has been used to represent the red flash R in the stimulus (trace 3). Also the artifact has been subtracted from trace 1 (dotted line). **d** is without an artifact due to the use of a RG 630 low pass filter instead of a RG 610 at the expense of complete reconversion

Results

Time Course of Photoconversion of Blowfly Visual Pigment

The kinetics of fly visual pigment was measured in a living virtually intact blowfly *Calliphora erythrocephala*. The test wavelength $\lambda_t = 588$ nm was selected for its position near to the maximum of the difference spectrum (Hamdorf et al., 1973; Stavenga et al., 1973). The continuous test light was applied antidromically and the light transmitted by all receptor types was measured from the deep pseudopupil by a photomultiplier fitted with an interference filter with peak transmission at 588 nm.

The changes in transmission in the yellow (588 nm) caused by intense flashes applied orthodromically are presented in Figure 2, on a slow time scale in Figure 2a and much faster in Figure 2b–d. Because of the quite bright yellow test beam the visual pigment is put into a steady state with virtually all molecules in the rhodopsin state initially (Stavenga et al., 1973; Stavenga, 1976). A subsequent blue flash appears to be sufficiently intense to shift within 0.5 ms (Fig. 2b) the photo-steady state towards the side of metarhodopsin, as is evidenced by a large drop in transmission at 588 nm (Fig. 2a and b). The test beam restores the original high rhodopsin population within a minute (Fig. 2a). Figure 2a also shows that subsequent blue flashes have identical results.

The rapid shift in photo steady state indicates that not only rhodopsin to metarhodopsin conversion but also the opposite photochemical process is completed within the short time scale of 0.5 ms. [For, a photochromic substance with two photointerconvertible states reaches the new wavelength dependent photo-steady state exponentially as a function of time under steady illumination with in the exponent the sum of the rate constants of both states (Hamdorf and Schwemer, 1975; Goldsmith, 1978; Hochstein et al., 1978).]

With blue light the conversion of rhodopsin and that of metarhodopsin cannot be separated due to substantial photosensitivity of both states in the blue. On the other hand in the yellow and red photosensitivity of rhodopsin becomes minor and therefore metarhodopsin can be studied separately with long wavelength irradiation. This can be demonstrated by the double flash experiment of Figure 2c and d. First a blue flash was given to create metarhodopsin and 0.5 ms later a red flash was presented to the fly to reconvert the metarhodopsin back to rhodopsin.

To induce complete reconversion the strongest available flashlight had to be used with a RG610 low pass filter. Unfortunately, this arrangement leads to a strong stimulus artifact due to a substantial fraction of light reflected from the eye into the photomultiplier after leaking through the 588 nm interference filter. Therefore the wavelength of the antidromic light was changed to 566 nm. Figure 2c (trace 1) shows that for this wavelength the artifact is tolerable. The stimulus artifact is shown as the second, red flash in trace 3. By subtraction the pure photochemical process can be obtained (dotted line). (The first flash in trace 3 represents the blue flash.) Trace 2 is the control single blue flash experiment.

Figure 2d is without a stimulus artifact due to the use of a RG630 low pass filter but at the expense of complete reconversion. Figures 2c and 2d clearly establish that metarhodopsin conversion occurs rapidly, i.e., at least within 0.5 ms, thus confirming the conclusion stated above.

The physiological processes following double flashes as applied in Figures 2c and d are described next.

Flash Induced Pupillary Responses

Irradiation of fly photoreceptor cells induces migration of pigment granules inside the cell soma (Kirschfeld and Franceschini, 1969). The optically detectable effect is a drop in transmission of the rhabdomeres and an increase in reflection from the eye (Franceschini, 1975; Stavenga, 1979). Transmission changes following coloured light flashes measured from blowfly are presented in Figure 3. The procedure here was as follows. First a red flash (indicated by 1 and 3 in Fig. 3) was applied to the eye to ensure a virtually pure rhodopsin population of the visual pigment molecules. Then two intense light flashes were delivered: a blue flash followed by a red flash (indicated by 4 in Fig. 3); the time interval between the flashes was varied.

It appears that the pupillary response to the two flashes increases when the flashes become increasingly separated in time (Figs. 3 and 4). The explanation of this feature in terms of photopigment conversions is evident. Comparison of the response to a single blue flash (2 in Fig. 3) and the response to two flashes spaced 5 ms apart (4 in Fig. 4), clearly shows that pupil closure following rhodopsin conversion by a blue flash is partially inhibited by the reconversion caused by the red flash. From the

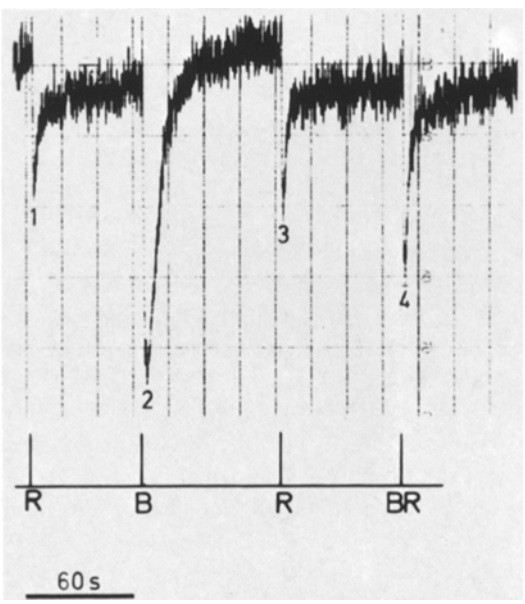

Fig. 3. Pen recording of the transmission at 511 nm trough the rhabdomeres. Due to the absorption coefficients of rhodopsin and metarhodopsin being equal at 511 nm (isosbestic wavelength), the transmission is influenced by pupillary responses only. Traces 1 and 3 are responses to red flashes, trace 2 is the response to a single blue flash, and trace 4 is the response to a blue flash of the same intensity followed by a red flash 5 ms later

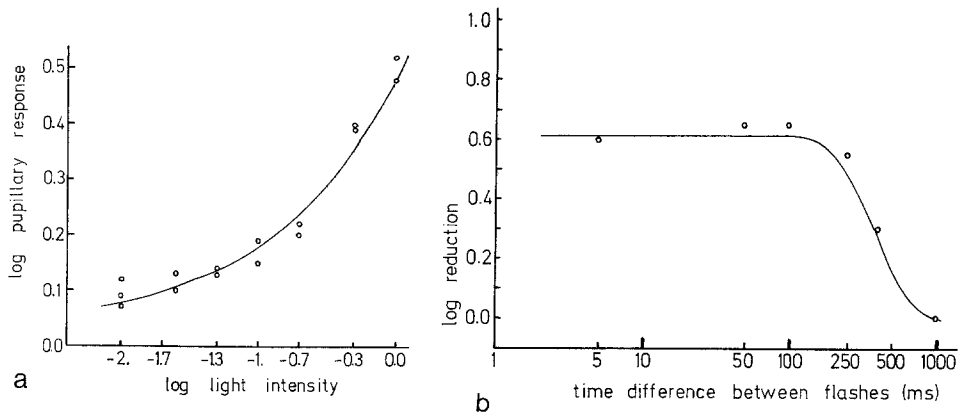

Fig. 4. a Pupillary response as a function of the intensity of the flash light (log-log scale). **b** A blue flash closely followed by a red flash is less effective in stimulating the pupil compared to a single blue flash. In the figure the reduction is given in terms of the light stimulus reduction needed to obtain an equal response to a single blue flash as a function of the time delay between the blue and red flashes in ms

log pupil response versus log flash light intensity curve (Fig. 4a) the attenuation needed to match the response of a single blue flash to the response to a double flash was assessed. This attenuation is plotted as a function of the time difference between the blue and red flash (Fig. 4b). Figure 4b demonstrates that the pupillary response induced by a rhodopsin converting blue flash can be partially called off by a reconverting red flash following within about 200 ms.

Closely related phenomena observed in membrane potential responses are described in the next section.

Flash Induced Electrical Responses

Fly visual sense cells respond to flashes with a depolarizing, pulse shaped receptor potential. For moderately intense flashes the depolarizing pulse reaches saturation and an AHP (after-hyperpolarization, e.g., Tsukahara et al., 1977) appears. The response to flashes which substantially convert rhodopsin is clearly elongated with a PDA (prolonged depolarizing potential), as shown in Figure 5f. The height and deviation of the PDA depends on the extent of change in the pigment state. The blue flashes B in Figure 5 convert about 30% rhodopsin to metarhodopsin (determined spectrophotometrically). The procedure in the electrophysiological experiments of Figure 5 was identical to that in the optical experiments of the previous section, Figures 3 and 4.

First a red flash R was given to ensure that the photo-steady state was nearly 100% rhodopsin. Then, after 25 s of dark adaptation a double flash (blue light first and after a variable delay red light) was presented. In trace f a single blue flash is presented to show the PDA. The PDA was depressed by a red flash 25 s later. Trace b is included to demonstrate that a longer dark adaptation time (180 s) has not much influence.

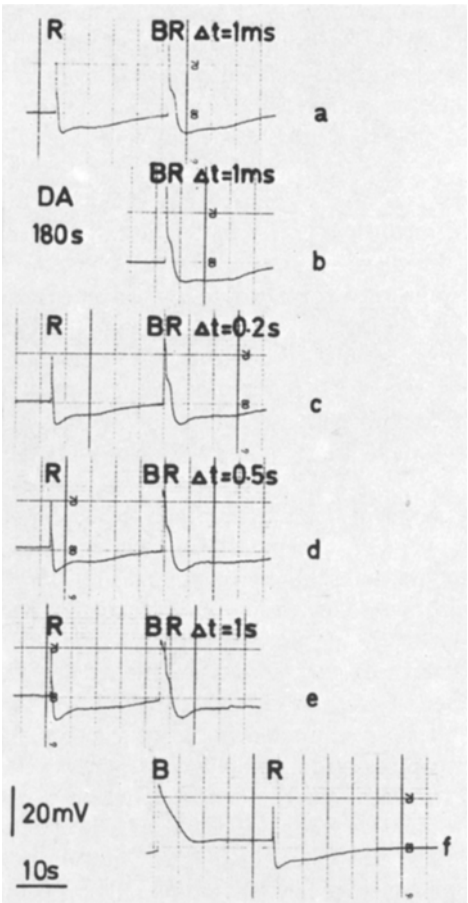

Fig. 5. Responses of the membrane potential to red flashes R, blue flashes B and double flashes BR (Δt indicates the time separation). See text for further detail

Figure 5 demonstrates that the PDA induced by a blue flash is inhibited by a visual pigment reconverting red flash; there remains an AHP as if only a single red flash had been presented. The implications of these results are discussed below.

Discussion

Photoconversion of the thermostable[1] states of blowfly visual pigment occurs rapidly. Rhodopsin into metarhodopsin conversion and vice versa is complete within 0.5 ms. Intermediates with lifetimes up to 100 ms were demonstrated photometri-

[1] Strictly speaking neither rhodopsin nor metarhodopsin is stable. Thermal isomerization of rhodopsin occurs at an extremely low rate, i.e., half-time is several years, as follows from bumps (see Lisman and Bering, 1977) and metarhodopsin is converted in the dark by an unknown, probably metabolic process, with half-time in the order of ½ h or longer (Pak and Lidington, 1974; Stavenga, 1975; Bruno et al., 1977).

cally for the visual pigments of *Limulus* (Fein and Cone, 1973; see also Lisman and Sheline, 1976) and butterflies (Stavenga et al., 1977). [It may be not accidental that the visual pigments in these cases have a hypsochromic shifted metarhodopsin; see also barnacle visual pigment for which a number of thermolabile intermediate states have been concluded from early receptor potential measurements (Minke et al., 1973, 1974).]

Not a hint of an intermediate was observed in the milliseconds range for the visual pigment of blowfly in which case the metarhodopsin is bathochromic shifted. It is obvious to hypothesize generally that fly visual pigment conversions have time courses of much less than 1 ms as was presumed for *Drosophila* (Lo and Pak, 1978[2]). It is not straight-forward, however, to reconcile this claim with the fast photovoltages (ERP; M-potentials) measured for flies, the blowfly *Calliphora* included. The biphasic M-potential has a negative and a positive phase peaking at 1 and 4 ms respectively in *Drosophila,* with slightly varying values for *Musca* and *Calliphora* (Pak and Lidington, 1974; Kirschfeld et al., 1977; Stark et al., 1977).

Recently it has become clear, however, that only the first, negative phase is a genuine early receptor potential (originating in the receptors) and that the later, positive phase is the lamina response to the first phase (Stephenson and Pak, 1978; Minke and Kirschfeld, personal communication). Thus the problem is reduced to relating the rapid photopigment conversion to the deduced ERP.

Blue flashes following red light and subsequent dark adaptation induce late receptor potentials living much longer than those evoked by red flashes. Moreover, red flashes abolish the blue flash induced prolonged membrane depolarizations (Fig. 5). It was found that corresponding effects are expressed in the pupillary responses. The migration of intracellular pigment granules towards the rhabdomeres, which starts rapidly upon illumination (delay < 0.1 s; Stavenga, unpublished), results in a substantial transmission decrease after a blue flash only when the following red flash is delivered after more than 0.5 s, the time for an average pigment granule to approach the rhabdomere boundary. Apparently at shorter intervals pigment migration is effectively inhibited. Comparing the electrophysiological and optical measurements, which were performed in the same set-up under identical conditions it may be concluded that pigment migration is directly dependent on the existence of a membrane depolarization, when maintained for a sufficiently long time. Electrophoresis as the physical cause of retinular cell pigment migration was proposed by Stavenga (1971; see also Stavenga et al., 1975) but questioned by Miller and Cawthon (1974) (see Miller, 1975; Olivo and Larsen, 1978). The physical forces underlying pigment migration clearly deserve further investigation. It was shown in this paper that a fruitful approach will employ heterochromatic flashes.

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[2] In this paper a blue-induced decrease in transmittance of *Drosophila* rhabdomeres was reported and it was argued that no metarhodopsin absorption is involved. On the basis of the scantily described experimental details this explanation cannot be accepted without serious dissatisfaction (see further Stark et al., this volume).

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