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Visual Pigment Processes and Prolonged Pupillary Responses in Insect Photoreceptor Cells*

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Abstract. The visual pigment in the peripheral retinular cells of the hoverfly *Syrphus balteatus* was investigated by absorbance difference measurements. Different visual pigments were found in the dorsal versus the ventral part of the eye in the male, but not in the female. In the male in the dorsal part of the eye the visual pigment has an isosbestic point at 513 nm; in the ventral part this value is 490 nm. The latter value is found in the female in both parts of the eye.

Prolonged pupillary responses were studied in the male *Syrphus* and appeared to be most marked in the ventral part of the eye. In both hoverfly and blowfly prolonged pupillary responses are induced by short wavelength light only; i.e., by light which excessively can convert rhodopsin into metarhodopsin. By contrast, in butterflies red light (and a long dark adaptation time) is necessary to evoke a prolonged pupillary response. It was demonstrated in both hoverfly and blowfly that long wavelength light, which reconverts metarhodopsin into rhodopsin, inhibits a prolonged pupillary response; or, accelerates pupil opening.

Key words: Insect photoreceptors – Visual pigment – Pupil mechanism.

Introduction

Insect photoreceptor cells generally contain numerous tiny pigmented granules which migrate in response to a change in illumination. Due to their strong light absorbing and scattering properties the pigment granules can effectively influence the light flux in the lightguiding and visual pigment containing structures of the photoreceptors, i.e., the rhabdomeres of flies or the rhabdoms of bees, thus executing a light control or pupil function (review Kirschfeld and Franceschini, 1969; Goldsmith and Bernard, 1974; Franceschini, 1975; Franceschini and Kirschfeld, 1976; Stavenga, 1979).

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Although the physico-chemical basis of the pigment migration is still far from a complete understanding the initial step of the chain is clear. Light absorption by the visual pigment molecules is the trigger as is evidenced for several species from different insect orders by the following lines of evidence. Firstly the action spectrum of the pupillary response in photoreceptor cells R1–6 determined from transmission measurements in the fruitfly (Franceschini, 1972a, b) is very similar to the sensitivity spectrum obtained by electrophysiological methods (Minke et al., 1975; Harris et al., 1976), and to the absorption spectrum of the rhodopsin (Ostroy et al., 1974). Furthermore, chromatic adaptation experiments, in which the extent of pigment migration in the retinular cells was measured by histology in cockroach (Butler, 1971), ant (Menzel, 1972), bee (Kolb and Autrum, 1974) and cabbage butterfly (Ribi, 1978), also provided strong evidence that pigment migration is driven via rhodopsin absorption. Finally, Bernard and Stavenga (1977, 1978), using the pupillary scattering, obtained action spectra for the pupillary response in various flies and bumblebees similar to photoreceptor spectra reported with independent techniques.

Hence, the intimate connection of visual pigment processes and pupillary responses initiates a two-sided approach to studying the pupil mechanisms. (a) when the visual pigment photochemistry has been studied in detail, as is the case for instance in the blowfly and fruitfly, one can analyse the physiological processes induced by visual pigment conversions via the pupillary response, and (b) pupil measurements can disclose the visual pigment's spectral properties. Both these aspects will be highlighted in the present paper. That the pupil mechanism is inside photoreceptor cells offers a unique non-invasive means of studying the physiological process of phototransduction at the cellular level. The hoverfly *Syrphus balteatus* was chosen as a special case to study the relation between visual pigment and pupil mechanism, since pupil action spectra measured previously from another *Syrphus* species had revealed that the eye is globally non-uniform (Bernard and Stavenga, 1977). Previously, on the basis of microspectrophotometric measurements performed on another hoverfly, namely the dronefly *Eristalis tenax,* as well as on the blowfly *Calliphora erythrocephala,* it was concluded that fly visual pigment can have distinctly different absorption spectra; the two states (rhodopsin and metarhodopsin) of blowfly visual pigment were found to be R495 and M580 and those of dronefly visual pigment R460 and M550 (Stavenga, 1976). Curiously enough the action spectra of the pupil obtained in *Syrphus* peaked in the dorsal part of the eye at 490–500 nm and in the ventral part of the eye at 450–460 nm (Bernard and Stavenga, 1977, and in preparation). It thus seemed that dorsally a blowfly-like visual pigment was located. This question was further investigated by absorbance difference measurements and considered in relation with features of the pupil.

Materials and Methods

The animals were prepared and mounted on a goniometer as described before (Stavenga, 1975a, 1976). Orthodromic light, i.e., incident in the natural way, was from a 450 W Xe-lamp or a 150 W Iodine lamp. A small window was cut in the back of the head of the flies to admit antidromic light which originated also from the 450 Xe-source and propagated through a flexible light guide. The antidromic transmission of

the photoreceptor was measured by a photomultiplier EMI 9558B or 9559QB which was coupled to a microscope. In the case of butterflies the light reflected from the eye was measured.

Results

Visual Pigment of the Hoverfly Syrphus balteatus

The spectral properties of the peripheral retinular cells in the hoverfly *Syrphus balteatus* can be visually investigated with normal orthodromic illumination owing to the reflecting pupillary granules, most clearly visible in the deep pseudopupil (Franceschini, 1972a, b, 1975). That syrphid eyes are globally non-uniform (Bernard and Stavenga, 1977) is easily demonstrated by using steep-band pass optical filters, e.g., from the Schott OG-series. Whereas one observes with an OG 590 filter in front of the Iodine lamp a brightly reflecting set of peripheral retinular cells R1–6 in the dorsal part of the eye, ventrally a dull non-reflecting pseudopupil is seen.

Changing the locus of observation gradually from the dorsal to the ventral part of the eye the granular pupil reflection suddenly vanishes, either when passing the equator or at a few ommatidial rows ventrally of the equator, depending on the specimen. Possible explanations, for instance that ventrally the pupillary granules are absent or that they scatter little ventrally are inadequate because upon inserting an OG 570 filter one can quickly evoke an evenly bright shining pseudopupil as the one observed dorsally. Also, the action spectra difference (Bernard and Stavenga, 1977) gives a clear proof of the change in photoreceptor properties. Difference spectra calculated from antidromic transmission measurements confirmed this conclusion (Fig. 1a). The dorsal visual pigment of the male has an isosbestic point $\lambda_{iso} \approx 513$ nm; ventrally $\lambda_{iso} \approx 490$ nm. Very similar values were obtained in blowfly and dronefly respectively (Hamdorf et al., 1973; Stavenga et al., 1973; Razmjoo and Hamdorf, 1976; Stavenga, 1976). Moreover the photo-equilibrium spectra were very similar as obtained in the respective cases (Fig. 1b). The maximum of the difference spectrum derived ventrally is shifted to 575 nm which is rather shifted towards longer wavelenghts in respect of the 550 nm found in dronefly (Fig. 1a).

No complete difference spectra were determined for females but both dorsally and ventrally the isosbestic point is approximately 490 nm.

Pupil Mechanisms and Visual Pigment Conversions in Syrphus balteatus

Another means for characterizing the properties of a photoreceptor cell is offered by the pupil mechanism. Figure 2a demonstrates that ventrally in the male *Syrphus balteatus* a prolonged pupillary response is evoked by a violet flash ($\lambda = 419$ nm; 0.5 s duration). The reopening proceeds sluggishly but a ready speeding-up (Fig. 2b) is induced by a subsequent yellow flash (0.5 s of $\lambda = 588$ nm). Dorsally (Fig. 2c), the same violet flash ($\lambda = 419$ nm) as applied ventrally does slow down pupil opening, but the time course of recovery is considerably faster (Fig. 2a). A more bluish flash ($\lambda = 456$ nm, a wavelenght most effective in rhodopsin-metarhodopsin conversion) induces just a little stronger prolonged pupillary response. More research is

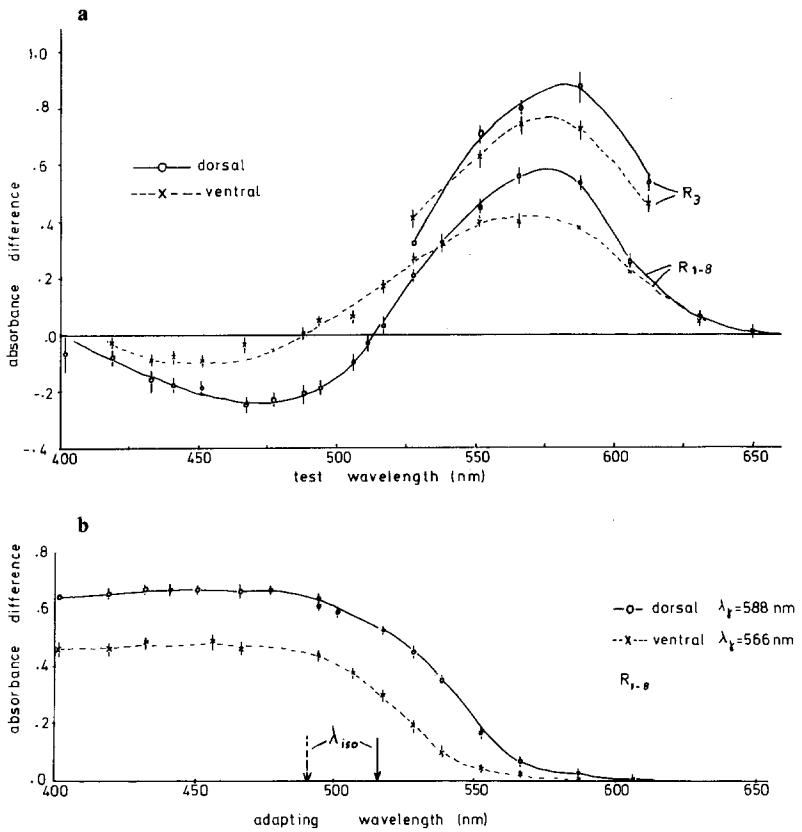

Fig. 1a and b. Difference spectra and metarhodopsin fraction spectra from the visual pigments of the peripheral retinular cells in dorsal and ventral part of the compound eye of the hoverfly *Syrphus balteatus*. Antidromic transmission was measured at a variety of test wavelengths in two photoequilibria established by adapting lights of wavelength $\lambda = 451$ nm and $\lambda > 630$ nm respectively. The absorbance difference was calculated from transmission measurements performed on the whole deep pseudopupil in order to minimize influences by retinular movement. This procedure contains a methodological error because a constant background from the central rhabdomeres is involved. A few measurements from retinular cell type R3 exclusively accordingly yield a higher absorbance difference but the shape of the difference spectra is not substantially changed (**a**). Measurement of the antidromic transmission at one and the same test wavelength at photoequilibria established by a variety of monochromatic illuminations yielded the curves of **b**. The absorbance difference is proportional to the metarhodopsin fraction created by the adapting wavelength (Stavenga, 1976)

needed to clarify the receptor dependence of the pupillary response, but it is clear that the male *Syrphus* provides an attractive preparation for a comparative study.

A discomforting property of the *Syrphus* pupils is the meagre influence on light transmission; the drop in transmission is 0.3—0.8 log units. A much better light control action is executed by the pupil of blowfly retinular cells lowering transmission to 2.5 log units; (see Stavenga, 1975a). Prolonged pupillary responses in this fly species are described below.

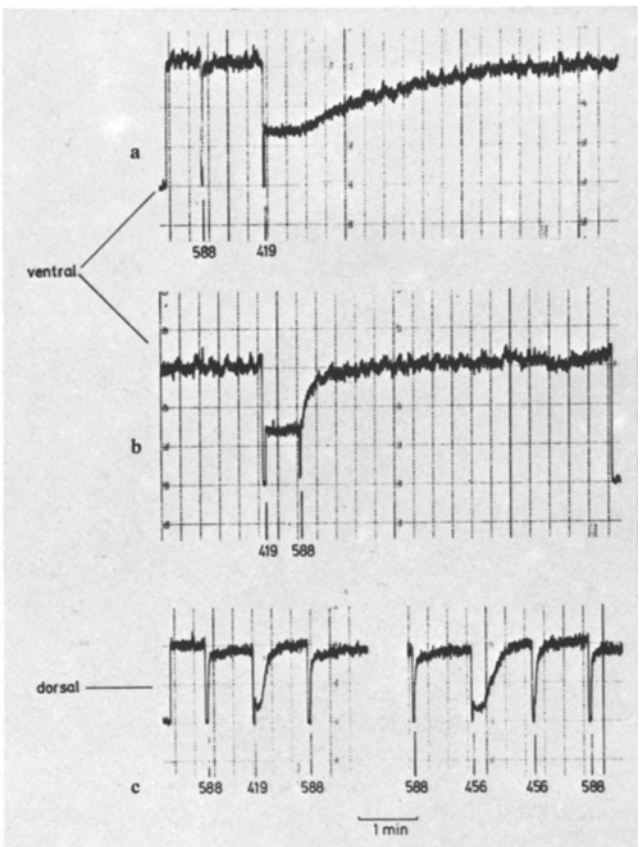

Fig. 2. Prolonged pupillary responses in the hoverfly *Syrphus balteatus*. In **a** and **b** the antidromic transmission at wavelength 488 nm was measured in the ventral part of the eye. The pupillary response to a 0.5 s flash of 588 nm light induced a slight drop in transmission during a few seconds. A 0.5 s flash of 419 nm, sufficiently to fully reach the photo-steady state, induced a prolonged pupillary response (**a**), which, however, is inhibited by the 0.5 s 588 nm flash when delivered after the 419 nm illumination (**b**). Dorsally antidromic transmission was measured at 508 nm, which wavelength still is shorter than the isosbestic point (**c**). The 419 nm flash here is considerably less effective in inducing a pupillary response. A more bluish 456 nm flash slows down pupil opening only a little more. A second blue flash is much less effective than the former one indicating that induction of a prolonged pupillary response needs a substantial conversion of rhodopsin molecules into the metarhodopsin state. During illumination the photomultiplier was protected

Prolonged Pupillary Responses in the Blowfly Calliphora

The characteristics of the process of pupil opening after illumination were investigated in a blowfly. Important parameters are light intensity and wavelength. In the experiment of Figure 3 (see the inset) a flash of 3 s duration closes the pupil to an extent which increases monotonically with light intensity. After light-off the pupil reopens with a varying time course. The time needed to let the pupil relax so that the transmission is halfway from the light adapted to the dark adapted value is called t_k.

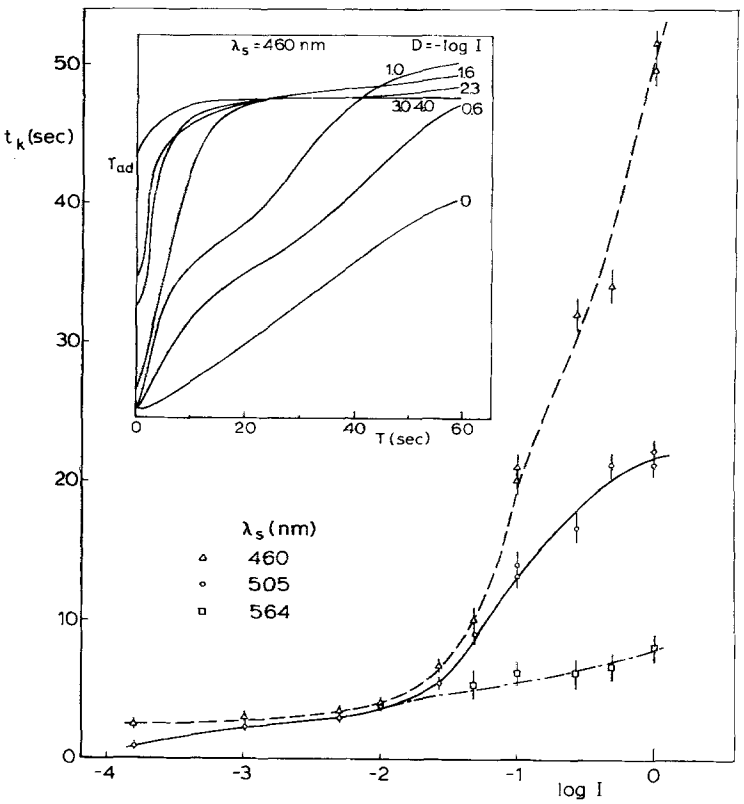

Fig. 3. Dependence of pupil opening on intensity of the previous illumination in the blowfly *Calliphora*. In the inset the time course of the antidromic transmission is shown after 3 s of illumination, which is preceded by a red illumination (603 nm) and 2 min in darkness. The halftime t_k of the transmission recovery curves is presented as a function of log intensity for three illumination wavelengths $\lambda_s = 460$, 505, and 564 nm respectively. (The intensity of the respective illuminations was approximately equal)

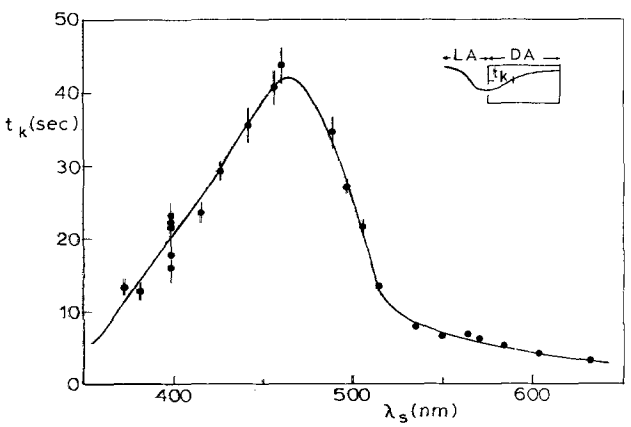

Fig. 4. Pupil recovery as a function of the wavelength of the illumination. Procedures as in Figure 3

This half-opening time appears to be fairly constant at low intensities, but it increases after more intense flashes, particularly when flash wavelength is in the blue (Figs. 3 and 4). This feature and the possibility to induce a rapid opening with red light (Fig. 2b; see also Stavenga et al., 1975) clearly indicates that prolonged pupillary responses occur when a substantial number of visual pigment molecules is put into the metarhodopsin state. A similar conclusion can be derived in the case of butterflies, although visual pigment properties are quite different there.

A Prolonged Pupillary Response in the Butterfly Inachis io

Owing to the existence of a reflecting tapetum in the compound eye of butterflies (Miller and Bernard, 1968) light which has propagated through the fused rhabdom and is reflected at the tapetum can be measured in the so-called luminous pseudopupil (review Stavenga, 1979). Illumination of a 1 min dark-adapted eye with red light, 606 nm, induces a prompt drop in reflection (Fig. 5a) due to the action of migration pigment granules inside the retinular cells (Stavenga, 1975c; Stavenga et al., 1977; Ribi, 1978). Subsequent illumination of the eye with 4 log units weaker (but still above threshold, Fig. 5b) light demonstrates the process of pupil opening, lasting about ½ min. A following slight and slow decrease of reflection presumably is due to a dark recovery process. Repeating the experiment but now after a 12 h dark adaptation time yields a strongly hampered opening of the pupil (Fig. 5c). In this relation it must be borne in mind that during several hours of dark adaptation the visual pigments of butterflies are fully regenerated into their active (rhodopsin) state (Stavenga, 1975b, c; Bernard, 1979). With red light both the red and the green visual pigments are effectively converted towards the hypsochromic shifted metarhodopsin state; thus red light induces in butterflies a similar shift in photoequilibrium as is induced in flies by blue light, and consequently a prolonged pupillary response results.

Discussion

Prolonged pupillary responses in insect photoreceptor cells reflect the spectral properties of the visual pigments. The analogy with the case of prolonged depolarizing afterpotentials (PDA) recorded with intracellular electrodes (e.g., Hochstein et al., 1973; Hamdorf and Razmjoo, 1977) is obvious (Stavenga et al., 1975). Unsatisfactory in the analysis of the prolonged pupillary responses is the variability of the time course of the phenomenon among specimens as was also observed for the PDA in barnacle (Lantz et al., 1977). Startling however is the difference of the pupillary responses in the upper and lower eye halves of individual male hoverflies *Syrphus balteatus*. This difference may be correlated to the difference in visual pigments. However, the pupil in the blowfly-like upper half of *Syrphus* is a poor competitor for the pupil in *Calliphora* (Figs. 2 and 3). It might be that the control of light flux is a more important function of the pupil in *Calliphora,* while the pupil in *Syrphus* is more directed to effectuate the control of the visual sense cell's acceptance angle (Hardie, 1978; Beersma, 1979).

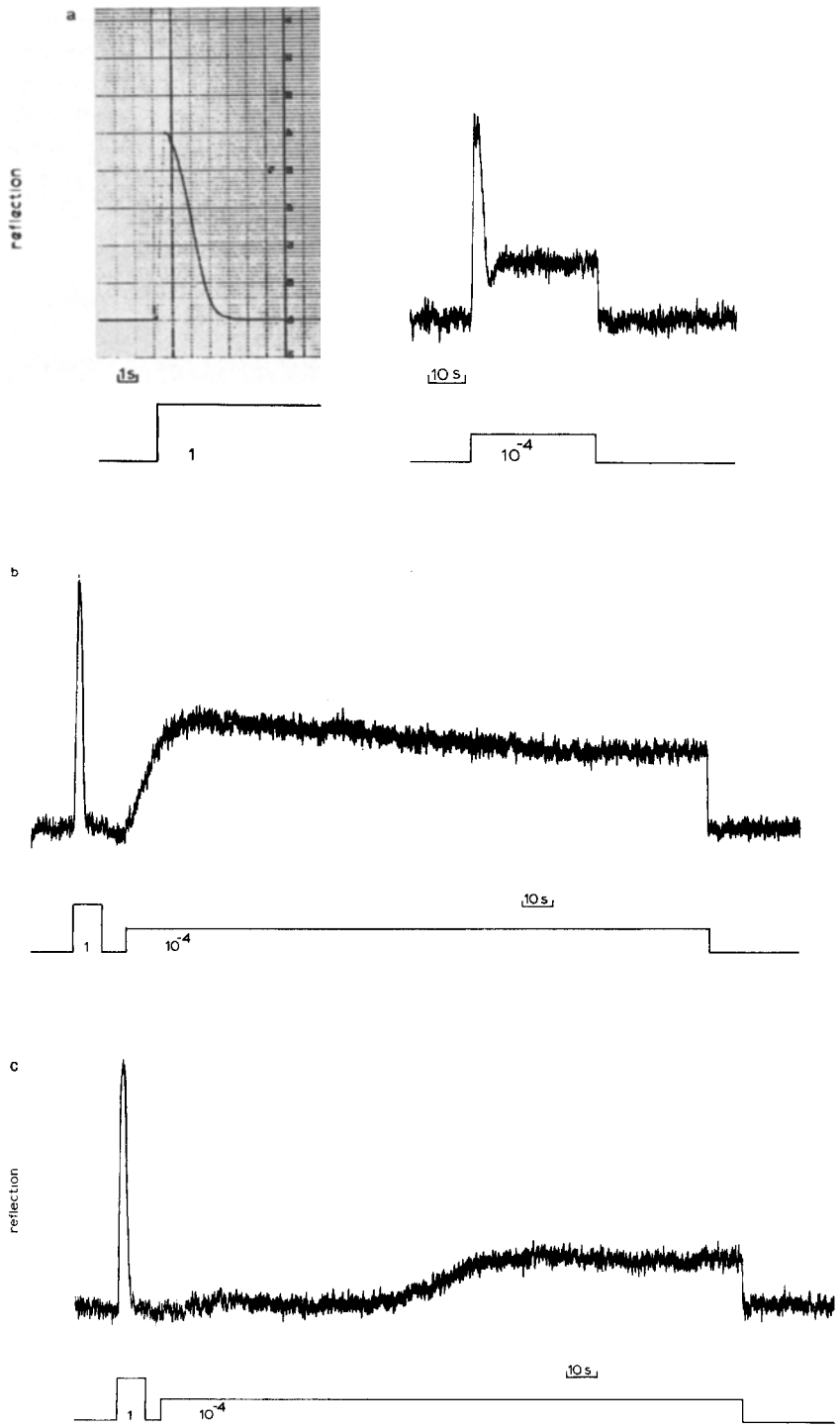

Fig. 5. (Legend see page 183)

The sexual difference in the dorsal part of the eye of *Syrphus* concerning the visual pigments creates another problem for interpretation. The hoverfly *Eristalis* has a rhodopsin with absorption spectra peaking at 450–460 nm (Horridge et al., 1975; Stavenga, 1976; Tsukahara et al., 1977). Males of *Syrphus* have a 490–500 nm peaking rhodopsin dorsally only. Hence, the male *Syrphus* has a subdivided eye, which is a sexual characteristic of several fly families as documented extensively by Dietrich (1909). In fact, Dietrich lists a number of male hoverflies with subdivided eyes including *Syrphus* and *Syritta* on the basis of dorsally larger facets, longer ommatidia and (somewhat) less abundant but brighter pigment compared to ventrally. For *Syritta* it was beautifully analysed how males chase females specifically with their dorsal fovea (Collett and Land, 1975). A related study was performed by Kirschfeld and Wenk (1976) on simuliid flies. However, in the latter family the dorsal eye of males contain screening pigment translucent for longer-wavelength light, whereas the ventral eye has a dense dark red-brown screening pigment. It thus was argued that shorter wavelength receptors were present in the dorsal eye of simuliids, so that screening pigment and visual pigment are tuned (Kirschfeld and Wenk, 1976) similarly as was clarified for the blowfly (Stavenga et al., 1973, 1975). Yet, it is now convincingly demonstrated that dorsally instead of a shorter wavelength receptor a longer wavelength receptor exists in the eyes of male syrphids. Presumably the dorsal receptors of males are for better spotting the yellow coloured females. This may be questionable since detection of yellow light with a rhodopsin having $\lambda_{max} \approx 500$ nm is not the best. But, perhaps a shift to 500 nm of λ_{max} is the optimum indeed. Rhodopsins studied so far, which have extreme absorption at a longer wavelength than the latter value invariably have a hypsochromic shifted metarhodopsin (Goldsmith, 1972). In view of the principle of rapid dark adaptation due to photoregeneration by light leaking through the red screening pigments a bathochromic shifted metarhodopsin is very advantageous (Stavenga et al., 1973, 1975; Stark, 1975; Cosens, 1979).

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Fig. 5. Prolonged pupillary responses in the eye of the butterfly *Inachis io*. The reflection was measured from the luminous pseudopupil. Complete extinction of the eyeshine is caused by an intense red illumination (606 nm) due to the action of retinular cell pigment granules, which execute a pupillary function (**a**, left). A 4 log units weaker light only partially induces pupil closure (**a**, right). The time course of pupil opening was recorded in **b** as follows. First the maximal intensity red light was delivered to the eye and the reflection drop was measured while a 4 log unit (10^{-4}) neutral density filter was put in front of the photomultiplier. The illumination was shut off after 10 s and the 4 log unit filter was removed and placed in the illumination beam. Then the shutter was reopened and thus the weak red light was exposed to the eye. It appears that the reflection rises and subsequently levels off into the state adapted to the weak light. Repetition of this procedure after an overnight dark adaptation time results in a prolonged closure of the pupil (**c**), lasting well over 1 min

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