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The Function of Photostable Pigments in Fly Photoreceptors*

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Abstract. The photoreceptors in the fly's ommatidia contain a bistable visual pigment, which can be shifted back and forth by means of light of appropriate wavelengths. The situation is complicated, however, by the presence of photostable pigments. One of them (located in rhabdomeres no. 1–6) absorbs in the UV, another one (in rhabdomeres no. 7y) in the blue spectral range. Such pigments act as (dichroic) colour filters that modify the spectral and polarisation sensitivity of the photoreceptors by means of *absorption*. It could be shown furthermore that such pigments can also act as sensitizing pigments that modify spectral sensitivities due to *sensitization*.

Key words: Photoreceptors, visual – Bistable – Photostable pigments.

Introduction

The primary process in photoreceptors takes place at the membrane bound visual pigment. Hence properties such as spectral or polarisation sensitivity are determined primarily by the properties of the visual pigment. It is shown in the following review that the properties of photoreceptors can be modified considerably by the additional presence of photostable pigments.

Pale and Yellow Rhabdomeres No. 7

If we inspect individual rhabdomeres of dipteran ommatidia we find a striking inhomogeneity of the centrally located rhabdomeres, called no. 7: whereas several of them (roughly $\frac{1}{3}$) transmit blue light without substantial attenuation, most of them heavily absorb this light whereby they appear dark (Fig. 1). If illuminated with white light the two kinds are pale (7p) or yellow (7y) respectively (Kirschfeld and Franceschini, 1977; Kirschfeld et al., 1978).

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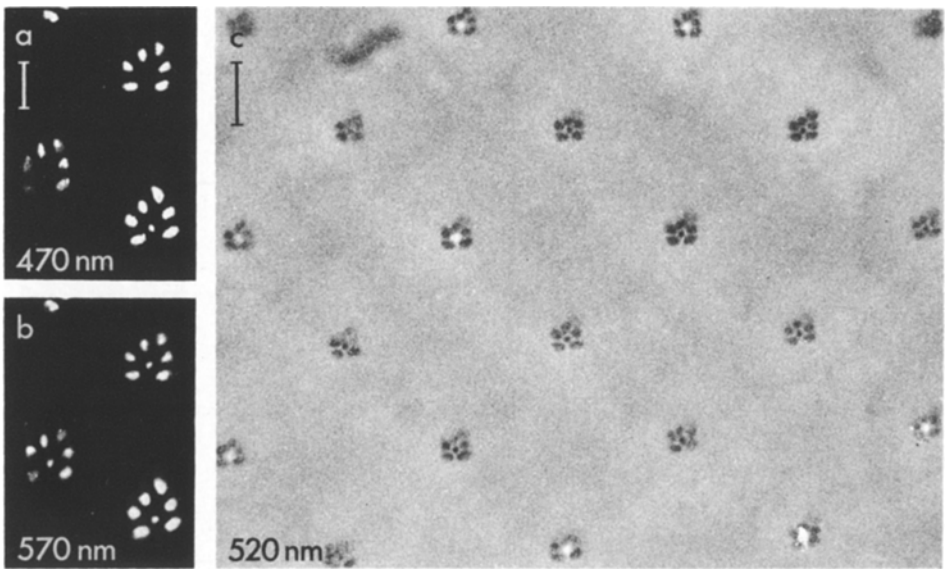

Fig1. a, b Rhabdomeres of three ommatidia of an eye-cup preparation (*Musca* ♀, white-eyed mutant) as seen in the microspectrophotometer. The ommatidia were cut down in length so that in the center only rhabdomere no. 7 is still present. When illuminated with blue light (470 nm) most of the rhabdomeres no. 7 appear dark (7y), the rest are bright (7p). In yellow light all rhabdomeres no. 7 are bright. **c** With a special technique ("antidromic illumination", Franceschini and Kirschfeld, 1971), pale and yellow rhabdomeres can easily be observed also at intact animals. Rhabdomeres no. 1—6 are dark due to the absorption of the mixture of rhodopsin and metarhodopsin created by the light of wavelength of 520 nm (from Kirschfeld et al., 1978)

If we measure with a microspectrophotometer the extinction spectrum of the 7y rhabdomeres, we find a spectrum very similar to that of a carotene, with a maximum close to 460 nm (Fig. 2). The pigment cannot be bleached away or shifted into a different spectral region. Furthermore, the pigment shows dichroism, with maximal extinction perpendicular to the direction of the microvilli. This is unusual insofar, as all known visual pigments in microvillar receptors exhibit maximal extinction parallel to the microvilli (see several reviews in Photoreceptor Optics, Snyder and Menzel, 1975).

Besides this *photostable* pigment there is also a *photoisomerisable* pigment present in these receptors, which is bistable and can be shifted back and forth with, e.g., blue and UV light (Harris et al., 1976). The combination of an isomerisable pigment, which obviously is the visual pigment, with a photostable pigment also accounts for a further paradox of these rhabdomeres: dichroic extinction increases with time, when monitored with blue light after UV-preadaptation. This is due to the fact that the isomerisable pigment is dichroic with stronger absorption parallel to the microvilli and, when in the blue absorbing state, partly compensates for the dichroic absorption of the photostable pigment. When the isomerisable pigment is shifted away from the blue absorbing state, this compensatory effect disappears and hence the measured dichroic absorption increases (Kirschfeld et al., 1978; McIntyre and Kirschfeld, in preparation).

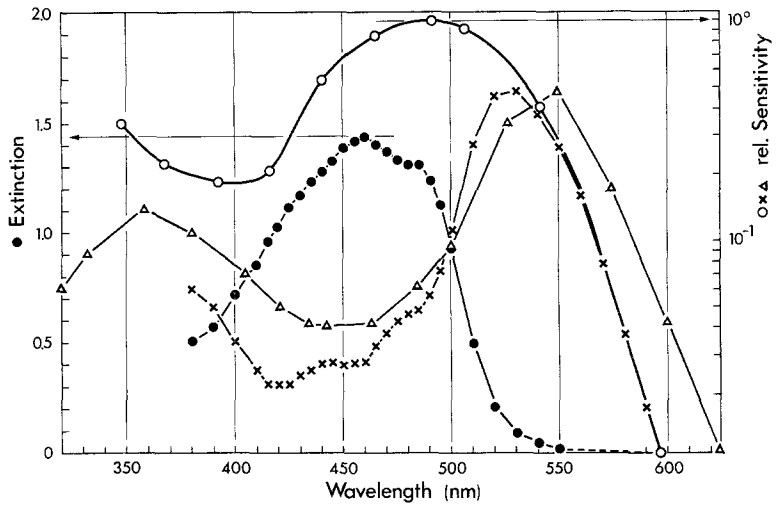

Fig. 2. The effect of the photostable pigment ("carotene") in rhabdomeres no. 7y (as measured in *Musca*) onto the spectral sensitivity of receptors no. 8. Open circles represent spectral sensitivity of receptors no. 8 as measured (in *Drosophila*) without the influence of the screening effect of the photostable pigment (Harris et al., 1976). Dots represent the extinction spectrum of the "carotene" in rhabdomeres 7y. Crosses represent the predicted spectral sensitivity of receptors 8 if the screening effect of the "carotene" is taken into account: the sensitivity maximum is shifted considerably to longer wavelengths. For comparison, the spectral sensitivity of identified receptors 8 from *Calliphora* (wild type), illuminated along the optical axis is also drawn (triangles) (Hardie, 1977) (from Kirschfeld et al., 1978)

The Role of Photostable Pigments in Photoreceptors

Since the extinction of the photostable pigment is considerable (optical density at 460 nm of whole rhabdomeres 7y: 1.5–2), there is one necessary and trivial consequence: it must act as a *colour-selective attenuator* for light. Hence spectral as well as dichroic sensitivity of the receptors will be modified by such a photostable pigment. This must be true for receptor no. 7y itself, but in the fly also for photoreceptor no. 8, which is located proximal to receptor no. 7. Figure 2 shows that the effect on receptors no. 8, located behind no. 7y is considerable in theory, and also that the predicted effect is in general agreement with electrophysiological results of Hardie (1977). (The slight discrepancy between both spectra might be due to the fact that they have been taken from different dipteran species, or due just to the fact that they have been measured in three different laboratories.)

Besides this trivial effect one might imagine that photostable pigments, fitted into a photoreceptors membrane, might *modify properties* of this *membrane* like their fluidity. As a further possible role of the stable pigment in rhabdomere 7y, one could also consider that it acts as a *store* for the visual pigment *chromophore* since carotene is a precursor of retinal.

A more interesting effect of a photostable pigment, however, might be a *sensitizing function*. Photostable pigments like, e.g., β-carotene are well known to act as "antenna"-pigments in photosynthesis. Such pigments absorb light and transfer the

energy to an effector pigment like chlorophyll a. The question is whether a sensitizing function of photostable pigments can be demonstrated in photoreceptors.

Evidence for a Sensitizing Pigment

We have tried to demonstrate a sensitizing function of the "carotene" in 7y rhabdomeres but we do not yet have a conclusive answer. There are, however, still six other receptors in the flies ommatidia (R 1—6) in which a sensitizing function of a photostable pigment could be demonstrated (Kirschfeld et al., 1977).

If spectral sensitivity is measured in these receptors, one finds two maxima, one close to 500 nm, the other in the near ultraviolet, at 360 nm (Burkhardt, 1962; McCann and Arnett, 1972; Dörrscheidt-Käfer, 1972; Horridge and Mimura, 1975). Dual peak sensitivity of this type cannot be explained on the basis of extinction spectra of known rhodopsins: these pigments have only a small peak at shorter wavelengths, of some 25% of the maximum (β-peak) (see e.g., Morton, 1972). This dual peak spectral sensitivity was always a matter of debate.

Possible explanations are inter alia: two different visual pigments in one and the same photoreceptor (Horridge and Mimura, 1975; Rosner, 1975), waveguide effects that selectively can enhance short wavelength extinction of light (Snyder and Pask, 1973), or a sensitizing function of a photostable pigment as mentioned above. The waveguide concept as an explanation (together with a selfscreening effect as it has also been discussed) actually has been eliminated already by older experiments, in which spectral sensitivity of white eye mutants has been determined by means of the ERG (e.g., Goldsmith and Fernandez, 1968; Minke et al., 1975; Stark, 1975; Harris et al., 1976). These spectral sensitivities also exhibit a pronounced UV-peak. Since in these mutants and with the kind of illumination chosen rhabdomeres are stimulated primarily with stray light crossing the rhabdomeres obliquely, waveguide effects and selfscreening are considerably reduced and hence cannot explain the high UV-sensitivity.

Experiments with selective chromatic adaptation have shown that the spectral shape of the sensitivity of these cells cannot be modified by these means (Burkhardt, 1962; Tsukahara and Horridge, 1977; Stark et al., 1977). This favours the view that there should be only one visual pigment. The argument has to be used with care, however; since even in the case of the presence of two visual pigments selective adaptation not necessarily needs to modify the shape of the spectral sensitivity function substancially after selective chromatic adaptation. This is due to the fact that the main contribution to the adaptation process, that is to the loss in sensitivity, e.g., in the fly receptors no. 1—6 after illumination, is due not to a reduced rhodopsin concentration, but to membrane processes. This can be concluded from the fact that sensitivity can easily be reduced by two or three orders of magnitude by means of selective chromatic adaptation (see e.g., Stark et al., 1977). It is known, at the other hand, that by means of selective chromatic adaptation the rhodopsin concentration can only be reduced to some 20% at the most (Hamdorf et al., 1973; Stavenga et al., 1973), and that sensitivity due to this rhodopsin concentration is also reduced only to this same fraction (Razmjoo and Hamdorf, 1976). That is, the contribution of the reduced rhodopsin concentration to the whole loss in sensitivity is only some

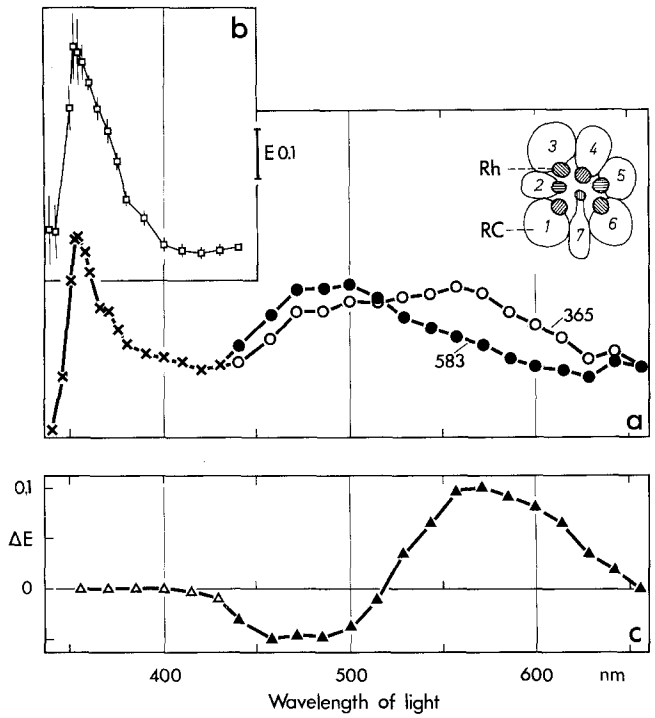

Fig. 3. a Extinction spectrum of rhabdomeres type 1–6 (*Musca*), measured either by adapting the preparation to light of 365 nm (○) or to light of 583 nm (●). In the UV both spectra overlap (×). **b** Mean extinction spectrum in the UV as measured at five more ommatidia. **c** Difference spectrum as derived from **a.** Inset: cross section through one ommatidium indicating the rhabdomeres Rh and receptor cells RC (after Kirschfeld et al., 1977)

1–10%. But if the sensitivity loss is primarily due to membrane processes, than it should affect signals induced by both presumed visual pigments to the same degree, at least if we make the plausible assumption that both visual pigments are acting onto the same membrane sites. And in this case no substantial modification of the sensitivity spectra is expected, even if there were two visual pigments present.

Microspectrophotometrically it can be shown that UV light creates the same metarhodopsin as blue light. There is, however, no decrease in extinction in the UV at the same time. Furthermore, in the absolute extinction spectrum there can be demonstrated an extinction maximum in the UV that is not affected by illumination (Fig. 3). Both observations fit to the concept of a photostable, UV absorbing sensitizing pigment, but they are not sufficient to proof it (Kirschfeld et al., 1977).

The sensitizing pigment hypothesis can be formulated as follows:

$$X + h\nu \rightarrow X^*, \tag{1}$$

$$X^* + R \rightarrow R^* + X, \tag{2}$$

$$R^* \rightarrow M. \tag{3}$$

Or, in words, due to the absorption of a light quantum, the unspecified, photostable molecule X is converted into the excited state X^* (Eq. 1). In a secondary process it then may interact with a rhodopsin molecule R, converting it into an excited state R^* (Eq. 2), which finally leads to metarhodopsin M (Eq. 3). Alternatively, the molecule X^* may loose the extra energy by fluorescing:

$$X^* \rightarrow X + h\nu' , \tag{4}$$

or by suffering deactivating collisions with other molecules. In the latter case the energy is dissipated as heat.

If the energy transfer occurs by means of the well known dipole-dipole interaction according to Förster's (1951) theory, the distance between the molecules, that is actually their concentration, determines (besides other parameters) whether the secondary process occurs according to Eqs. (2) and (3) or according to Eq. (4), assuming that the lifetimes of the excited state is sufficiently short.

This predicted, concentration-dependent efficiency of energy transfer was used in order to test the sensitizing-pigment hypothesis: In flies with reduced rhodopsin concentration within the rhabdomeres the efficiency in shifting rhodopsin into metarhodopsin is selectively reduced in ultraviolet light compared with blue light. That is, relatively more UV quanta are needed when rhabdomeres are used that contain an artificially reduced concentration of rhodopsin (Kirschfeld et al., 1977). This results fits to the finding, that flies, grown on vitamin A deficient media, exhibit a selectively reduced UV-sensitivity in receptors R 1–6 (Goldsmith et al., 1964; Stark et al., 1976). Stark et al. (1977) also interpret the vitamin A dependent UV-peak of the receptors 1–6 as well as some observations on fluorescence of rhabdomeres 1–6 as an indication that there should be an energy-transfer mechanism from a stable pigment to visual pigment.

In flies with reduced rhodopsin concentration not only is the efficiency selectively reduced for shifting rhodopsin into metarhodopsin, but in many cases the decay in rhodopsin concentration is no longer exponential. This finding can be interpreted as a consequence of a concentration – and hence distance between the molecules – dependent energy transfer from the photostable to the visual pigment. It fits also, however, to another model as discussed below, in which the UV-sensitivity is interpreted as being due to a second, photostable chromophore of the visual pigment that transfers the energy to the isomerisable pigment (Kirschfeld et al., 1977; Minke and Kirschfeld, 1979).

Insofar the sensitizing-pigment hypothesis is strongly supported by the mentioned results. There is still a second prediction, following from the sensitizing-pigment hypothesis, that we are able to test.

Besides the rhodopsin there is usually also metarhodopsin present in the rhabdomeres of R 1–6. If there is energy transfer of the sensitizing pigment onto *rhodopsin,* the following discussion shows that we expect an energy transfer also onto *metarhodopsin;* that is, photosensitivity not only of rhodopsin but also that of metarhodopsin should have *a second maximum* in the UV. Förster-type of energy transfer depends – besides of other parameters like relative orientation of molecules and their distance – primarily on the amount of overlap between the *fluorescence spectrum* of the (photostable) *donor* (= sensitizing) molecule and the *absorption spec-*

trum of the visual pigment *acceptor*. If there is sufficient overlap of the rhodopsin with the donor fluorescent spectrum, there should also be some overlap at least with the metarhodopsin absorption spectrum, and hence an energy transfer. This is because the absorption spectra of rhodopsin and metarhodopsin in the visible spectral range considerably overlap (Fig. 4). Based on a method developed by Hochstein et al. (1978) we determined (Minke and Kirschfeld, 1979) the photosensitivity spectrum of the R 1–6 rhodopsin and metarhodopsin (Fig. 4). As can be seen, not only the rhodopsin has a pronounced second peak in UV-photosensitivity, but the same is true for the metarhodopsin. Obviously, also a further necessary condition following from the sensitizing pigment concept is fulfilled: the photosensitivity spectra in the UV of rhodopsin as well as of metarhodopsin closely coincide. This would not have been expected if the absorption in the UV had been due, e.g., to a somehow in-

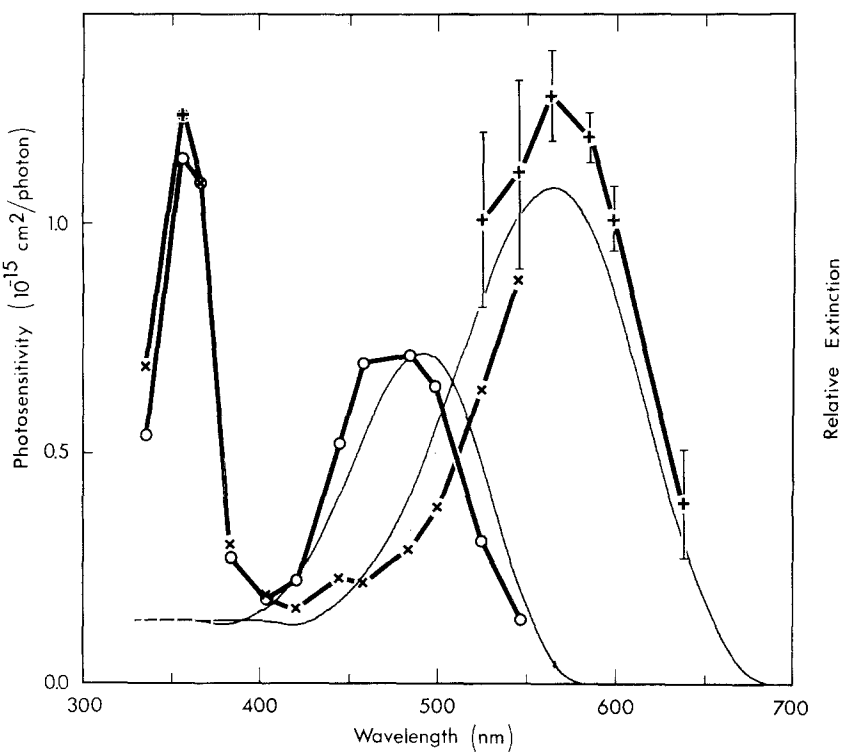

Fig. 4. Photosensitivity spectra of fly (*Calliphora*) rhodopsin (O) and metarhodopsin (×, +). The methods used to derive the spectra measure the efficiency with which rhodopsin and metarhodopsin are converted into each other, depending upon the wavelength and intensity of light. Therefore instead of absorption spectra *photosensitivity spectra* are derived, which enclose effects of sensitizing pigments. For the spectrum of metarhodopsin two different methods had to be applied, depending upon whether there is a spectral overlap between R and M (×) or not (+). This explains the somewhat differing result at wavelengths from 520–540 nm. Thin lines: extinction spectra of rhodopsin and metarhodopsin (Hamdorf, Schlecht and Täuber, pers. comm.) as derived from a difference spectrum of *Calliphora* compound eye receptors no. 1–6 by assuming a Dartnall-nomogram shape (with an additional shoulder at short wavelengths) for rhodopsin as well as for metarhodopsin (from Minke and Kirschfeld, 1979)

creased β-peak: then a β-shoulder (as the visible peak) of metarhodopsin might be expected to be shifted to longer wavelengths. This coincidence is necessary, however, if both UV-peaks are due to one and the same photostable pigment. Stark et al. (1977) with more indirect methods also found a sensitivity peak of metarhodopsin in the UV. They also interpret it as being due to an energy transfer from a UV-absorbing, photostable pigment. Possible explanations for the considerable quantitative discrepancies between their results and the metarhodopsin spectrum as shown in Figure 4 are discussed elsewhere (Minke and Kirschfeld, 1979).

With a different approach, based on a method to determine photochromic pigment absorption spectra developed by Stavenga (1975), Tsukahara and Horridge (1977) determined visual pigment spectra from the dronefly. They did not find a UV-peak. The method they used in principle gives no information on the spectra in those spectral region's where the difference spectrum is zero, and hence it is not valid to demonstrate the presence of a sensitizing pigment: Sensitizing pigments, since photostable, give a null difference spectrum. Therefore these results, as the authors point out, are not against our sensitizing-pigment concept.

Different Models of Energy Transfer

We discussed the results of R 1–6 on the basis of an energy-transfer model, in which the sensitizing-pigment molecules must be close to the acceptor molecules, but not necessarily chemically bound to it: energy transfer in this case is by means of electromagnetic waves and not by electrical charges. We cannot exclude the possibility, however, that what we measure as photostable extinction is due to a second chromophore, chemically bound to the rhodopsin molecule. In this case energy transfer was not restricted to electromagnetic waves but also electrical charges could be transferred. The experiments with receptors R 1–6 of vitamin A deprived flies, which have been shown to have less UV-sensitivity, then are explained by assuming that in these flies most of the rhodopsin molecules lack the second (more loosly bound) chromophore. We have not yet been able to distinguish between the two different models.

With respect to R 7p and y the question arises, whether both have the same visual pigment, which then in the case of R 7y is modified by the additional presence of the "carotene", or whether both visual pigments are different from the beginning.

It is known that receptors R7 are basically UV-receptors with a sensitivity peak close to 360 nm (Harris et al., 1976; Eckert et al., 1976). A detailed analysis by Hardie et al. (1979) indicates that there is in R 7y receptors, in addition to the UV-peak, a "tail" in the blue spectral range. According to these results, the dual peak spectral sensitivity (UV and blue) as also reported for R7 (Smola and Meffert, 1976) is due to off-axis stimulation of these receptors.

From these facts one might expect that the visual pigments could be the same in both kinds of receptors, whereby the tail in 7y might be created by the blue absorbing "carotene". This, however, is not the case. Difference spectra (measured so far in the visible range) clearly show that the isosbestic point as well as the extinction peak in receptors 7y are shifted considerable (40–50 nm) towards longer wavelengths

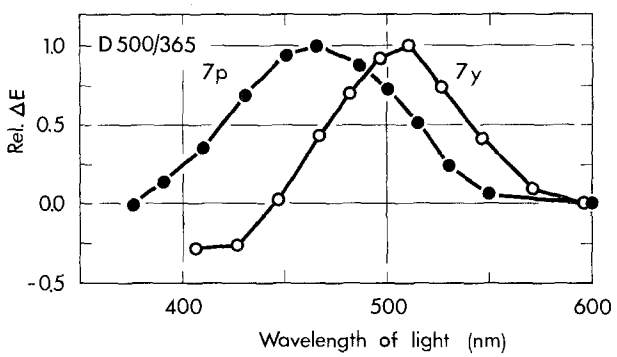

Fig. 5. Representative difference spectra of rhabdomeres no. 7p (●) and 7y (○), respectively, as measured at one individual rhabdomere each. The rhabdomeres have been adapted first to light of wavelength of 500 nm, than to UV light (365 nm)

with respect to the data for R 7p (Fig. 5). This difference can be explained at least in two possible ways: either the two opsins are different in 7p and y *from the beginning,* thus resulting in the different spectra, whether there is an additional photostable pigment in 7y or not. Or, a photostable chromophore acts – besides the first chromophore retinal – as a second chromophore, which is attached so closely to the first one that an interaction is possible between both: then a *bathochromic shift* would be created as seen in the spectrum of 7y (Fig. 5). An equivalent intra-molecular interaction apparently does not exist in R 1–6. This follows from the observation that if in these receptors the UV-peak is selectively reduced due to vitamin A-deprivation, the visible peak remains close to 500 nm (Stark et al., 1976, 1977). Hence, if the UV-peak in R 1–6 is created by a second, chemically to the visual pigment bound chromophore, this must be so far from the first one that no direct interaction between both chromophores is taking place.

In this context it is worthwile to note that whereas, as mentioned above, in rhabdomeres no. 7y the blue absorbing photostable pigment absorbs dichroically, no dichroism can be observed in the photostable UV absorption of rhabdomeres no. 1–6 (Kirschfeld, in preparation). This indicates that in rhabdomeres 1–6 the photostable chromophore dipoles are not fixed in the microvillar membrane in a systematic way similar to that of the isomerisable chromophores of the visual pigment.

Speculation

When we measured the spectra of rhabdomeres 7p and 7y we found besides the different locations on the wavelength scale, a second difference between the two rhodopsins: whereas the visual pigment in rhabdomeres 7y was quite stable, in rhabdomeres 7p during the measurement there was a continuous loss of visual pigment concentration, in the data of Figure 5 to some 25%. This loss has been corrected for in the spectrum as shown in Figure 5. It is known that in photosynthesis carotenes serve two different functions. They act at the one hand as sensitizers for

chlorophyll a; at the other hand they have also a protective function against photooxidation of chlorophyll, by taking over surplus energy. Since rhodopsin in 7y receptors is more stable than that in 7p receptors that lack the "carotene", we might consider that the analogy between photostable pigments in photosynthesis and visual pigments might concern not only a sensitizing function but also a *protecting function.* Hence photostable pigments possibly might also help to explain the difference between vertebrate visual pigments which decompose into opsin and the chromophore after absorption of light and that of microvillar photoreceptors, which usually are *bistable* systems.

We finally might ask why there are at all two different kinds of photoreceptors 7 in the fly compound eye, if both finally are predominantly UV-sensitive. We do not have a conclusive answer to this question. But since it is known that adaptation in vertebrates is also mediated by decomposition of rhodopsin in retinal and opsin, it might well be that both kinds of receptors 7 behave differently as far as light adaptation is concerned. And then both types of receptors 7 together could in principle be used as a means to determine absolute light intensities.

Conclusion

Photostable pigments within the membranes of photoreceptors in the fly have several types of significant functional consequences. We do not yet know, whether or not such photostable pigments are widespread in invertebrate photoreceptor membranes and if they are, what their function will be in every case. Apart from flies there are only a few examples in which their existence has been demonstrated: in the crayfish rhabdom (Wilms and Stieve, 1976), in receptors of some *Balanus* species (Minke and Kirschfeld, 1978), as well as in a membrane fraction of photoreceptors of lateral eyes of *Limulus* (Benolken, 1976).

Photostable pigments in vertebrates are well known from the oil-droplets of sauropsids. Since these oil-droplets are located in the inner segments they can have a significant screening function; a sensitizing function, by means of radiationless energy transfer, however, due to the distance to the visual pigments in the outer segments, is excluded. Nevertheless we might wonder whether sensitizing pigments are restricted to invertebrates; it seems worthwhile to check whether they might also be present at least in some vertebrate visual sense cells.

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