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SPECTRAL SENSITIVITY OF BLOWFLY PHOTORECEPTORS: DEPENDENCE ON WAVEGUIDE EFFECTS AND PIGMENT CONCENTRATION

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Abstract—Spectral and polarization sensitivities of blowfly R1–6 photoreceptor cells were measured by intracellular recordings in cells which differed in visual pigment content. The spectral sensitivity in the visible wavelength range can be quantitatively explained from the absorption spectrum of blowfly visual pigment when the waveguide properties of the rhabdomere are taken into account. The peak wavelengths of absorption and sensitivity spectrum are 490 and 487 nm respectively. At low visual pigment content a sensitizing pigment can enhance the relative U.V. sensitivity from 0.3 to 2.0. In flies with a high visual pigment content selfscreening substantially broadens the visible band of the spectral sensitivity and lowers the relative U.V. sensitivity. The gain of the electrical response appears to be independent of the visual pigment content.

Spectral sensitivity   Blowfly   Photoreceptor   Waveguide optics   Visual pigment   Sensitizing pigment

INTRODUCTION

The dominant factor determining the spectral sensitivity of a visual sense cell is the absorption spectrum of the visual pigment. However, a number of effects can modify a spectral sensitivity curve, as there are selfscreening, waveguide properties of photoreceptor and spectral filtering by photostable pigments (reviews: Hamdorf, 1979; Gribakin, 1979; Stavenga and Schwemer, 1984). In the present study we investigate the various influences affecting the spectral properties of the peripheral R1–6 photoreceptors of blowflies as a function of visual pigment content.

From the previous analyses of e.g. Burkhardt (1962), Stark *et al.* (1977), Hardie (1979) and Guo (1980a) we know that the spectral sensitivity profile of R1–6 photoreceptors exhibits two peaks, in the U.V. and blue–green range, respectively. The interpretation of these peaks has a long history (see e.g. Vogt and Kirschfeld, 1983), but recently convincing evidence has accumulated for the view that the blue–green peak represents the principal absorption band of the fly's visual pigment, which is now called xanthopsin (Vogt, 1983; Vogt and Kirschfeld, 1984), and that the U.V. peak mainly orginates from a sensitizing pigment, transferring absorbed light energy to the visual pigment

(Kirschfeld *et al.*, 1977, 1983). The chromophores of the visual pigment and the sensitizing pigment, being 3-hydroxy-retinal and 3-hydroxy-retinol, respectively thus are intimately related (Vogt and Kirschfeld, 1984).

As shown by Guo (1980a), in vitamin A deprived flies, the height of the U.V. peak in the spectral sensitivity curve relative to that of the blue–green peak increases substantially with age. Concomittantly with this increase in relative U.V. sensitivity, the polarization sensitivity in the U.V. decreases (Guo, 1980b). Vogt and Kirschfeld (1983) could quantitatively explain these phenomena from their sensitizing pigment hypothesis. Our spectral and polarization measurements closely agree with their conclusions. By including waveguide and selfscreening effects we find that spectral sensitivity curves of fly photoreceptors can now be interpreted in great detail.

MATERIAL AND METHODS

Animals

All experiments were performed on female blowflies *Calliphora erythrocephala*. The visual pigment content of the photoreceptors was varied by rearing the flies (wild type as well as the white eyed mutant *chalky*) under different light conditions. When flies reared on a vitamin A

rich diet are kept under normal daylight conditions, the photoreceptors maintain a high visual pigment content. Deprivation of blue light causes a low visual pigment content (see Schwemer, 1979, 1984). Dr J. Schwemer kindly provided *chalky* mutants, reared on a vitamin A deprived diet and kept under illumination conditions with no blue light.

Preparation and recording

Flies were prepared for intracellular recordings as described in Smakman *et al.* (1984). In brief, a tiny piece of the cornea in the dorsal part of the right eye was removed with a fragment of a razor blade. The opening was immediately covered with a small drop of vacuum grease. Subsequently the fly was mounted in the centre of a goniometer platform and a glass microelectrode was lowered vertically through the hole in the cornea. The electrodes, filled with 3 M KAc had 150–200 MΩ resistance in Ringer's solution. The reference electrode consisted of a sharpened silver wire and was placed in an unstimulated ventral part of the investigated eye. Only cells with -60 ± 1 mV resting potential were accepted.

Spectral sensitivity measurements

After successful penetration of a cell the goniometer platform with fly and intracellular microelectrode was adjusted with respect to a point light source for maximum response. This point light source was a flexible quartz lightguide with a diameter of 3 mm which was placed 20 mm in front of the fly's eye. Light of a Xenon arc with a quartz condensor was projected onto the lightguide by a quartz lens. Monochromatic illumination was obtained by using interference filters (DAL narrow band filters, Schott).

The intracellularly recorded light response of the cell was adjusted to a constant value (6 mV) by an analog–digital feedback system, in which a density wedge automatically controlled the intensity of the stimulating beam (Smakman and Pijpker, 1983). The position of the density wedge was measured at each wavelength, and subsequently the number of photons delivered at the respective wavelengths was calculated.

Polarization sensitivity measurements

A polarization filter (Polaroid, type HNP'B) was placed between the point light source and the fly's eye. With the analog–digital feedback system the response of the cell was adjusted to a constant value of 6 mV. The position of the density wedge was plotted against the polarization angle, yielding the polarization sensitivity.

Calibration

The calibration of the transmission of grey filters and the density wedge was performed at the various wavelengths using an EG&G radiometer (type 550-1), or a photodiode (type HUV1000B). The density of the wedge and grey filters varied slightly with wavelength. For determining the spectral sensitivity of each cell the measured values at each wavelength were corrected for these deviations.

Theoretical analysis

Assuming that no sensitizing pigment is present, the relative spectral sensitivity of a visual sense cell is given by (Hamdorf, 1979; Stavenga and Schwemer, 1984)

$$S(\lambda) = [1 - 10^{-E_X(\lambda)}]/[1 - 10^{-E_X(\lambda_{max})}] \quad (1)$$

were $E_X(\lambda)$ is the total extinction by the visual pigment (xanthopsin) at wavelength λ: the spectral sensitivity is normalized at the peak wavelength λ_{max}, and thus equals the normalized absorptance (see e.g. Cornwall *et al.*, 1984). In blowflies the visual pigment is contained in a rhabdomere, which acts as an optical waveguide. Then $E_X = 0.43 \, \eta_a \, \alpha_X(\lambda) \kappa L$ with η_a the average fraction of light power propagated within the boundary of the waveguide (Snyder and Pask, 1973), $\alpha_X(\lambda)$ the normalized spectral absorption coefficient of the visual pigment $[\alpha_X(\lambda_{max}) = 1]$, κ the extinction coefficient (extinction per unit length) of the rhabdomere at peak wavelength, and L the length of the rhabdomere. η_a depends on the wavelength λ and the rhabdomere diameter through the waveguide number V. We assumed that the tapering of the rhabdomere (Boschek, 1971; Smola and Wunderer, 1981) is linear, so that the diameter at the proximal end is reduced to half the distal value. Furthermore, because spectral sensitivities were always measured with the light source aligned with the cell, i.e. positioned at the peak of the angular sensitivity, we took for granted that only the first order mode propagates. The appropriate values of $\eta(V)$, kindly provided by Drs J. H. van Hateren, were approximated by $\eta(V) = a - b \exp(-cV)$, with $a = 0.96$, $b = 2.82$ and $c = 1.27$. Then $\eta_a = a - b \exp(-2d)[\exp(d) - 1]/d$, with $d = cV_0/2$ and V_0 the value of the waveguide number at the distal end of the rhabdomere, which was taken

as $V_0 = 3.6$ at $\lambda = 350$ nm, i.e. the average of the V-values derived in our angular sensitivity study (Smakman et al., 1984).

Using the absorption spectrum for fly visual pigment of Schwemer (1979, Fig. 1.6) we calculated spectral sensitivities with equation (1), resulting in satisfactory fits in the visible wavelength range (Figs 3 and 4). Distinct deviations between the theoretical curves and the experimental data are obvious in the ultraviolet, which are clearly due to the sensitizing pigment. When the rhabdomere contains a sensitizing pigment in addition to the visual pigment, the expression for the relative spectral sensitivity [equation (1)] is slightly modified. When E_S is the extinction by the sensitizing pigment and when $E_S(\lambda_{max}) = 0$, the spectral sensitivity becomes (Vogt and Kirschfeld, 1983)

$$S(\lambda) = \frac{E_X(\lambda) + \gamma_S E_S(\lambda)}{E_X(\lambda) + E_S(\lambda)} \cdot \frac{1 - 10^{-[E_X(\lambda) + E_S(\lambda)]}}{1 - 10^{-E_X(\lambda_{max})}} \quad (2)$$

where γ_S is the transfer efficiency from sensitizing pigment to visual pigment.

RESULTS

The spectral sensitivities of the peripheral photoreceptors R1–6 were measured from cells in the frontal part of the right eye of female blowflies. Before starting the measurements the cells were illuminated with intense red light to convert all the visual pigment into the xanthopsin state. After 10 min dark adaptation a criterion depolarization was established and the corresponding position of the grey wedge was monitored. Light of wavelengths 349, 373, 402, 442, 497, 537 and 588 nm was sequentially applied.

The spectral sensitivities of the exemplary cells presented in Fig. 1 vary in absolute height and in shape. The upper set of curves (Fig. 1) are spectral sensitivities obtained from a fly reared on a vitamin A rich diet and held under normal daylight conditions. The lower set of curves is from a fly held under light conditions with no blue light present. Schwemer (1984) showed that this procedure reduces the visual pigment content. Measuring the fluorescence of the visual pigment in vivo (cf. Stavenga, 1983) we also found that in the blue-light deprived flies visual pigment content is low. Thus, Fig. 1 is in agreement with the general notion that the absolute sensitivity of a cell is proportional to the visual pigment content.

Apart from the absolute height, the shape

of the sets of curves in the visible range differ. With increasing absolute sensitivity the curves broaden. Furthermore, in the U.V. range a large difference in relative sensitivity is apparent. The three parameters mentioned above, absolute sensitivity, shape of the curve in the visible range, and variability in the relative U.V. sensitivity, which all appear to depend on the pigment content of the photoreceptors, will be separately treated below.

Absolute sensitivity

The absolute sensitivity in Fig. 1 is taken as a measure of the visual pigment content of the photoreceptor. An assumption is then that at a given, constant criterion level of the electrical response, its gain is constant, irrespective of the visual pigment content of the photoreceptor. This assumption is put to the test in Fig. 2, where the absolute sensitivity, measured at 497 nm, is plotted against the relative sensitivity at 537 nm [here defined as $S(537)/S(497)$, see equation (1), methods]. The continuous curve in Fig. 2 was calculated from equation (1) by varying the value of κL, or, the visual pigment content. The measured sensitivities fall reason-
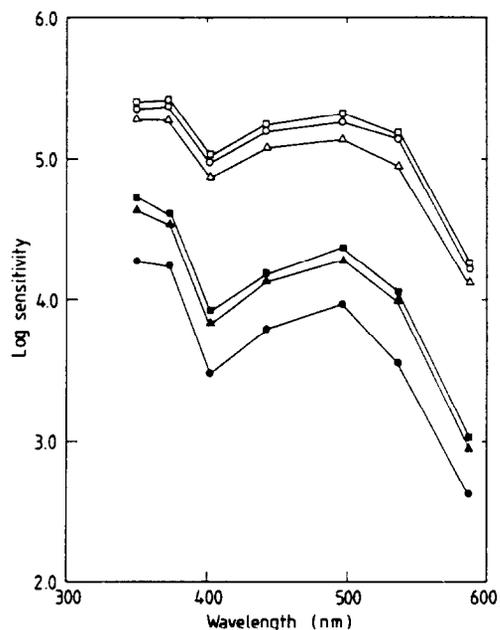

Fig. 1. Two sets of spectral sensitivity curves; wild type blowflies. Each set of curves is obtained from visual sense cells of one fly. The upper set of curves are measured from cells of a visual pigment rich fly (vitamin A rich diet and normal daylight). The lower set of curves are measured from cells of a visual pigment poor fly (vitamin A rich diet and held under light conditions with no blue light). Note the differences in absolute sensitivity, in broadening of the curve in the visible band and in relative U.V. sensitivity.
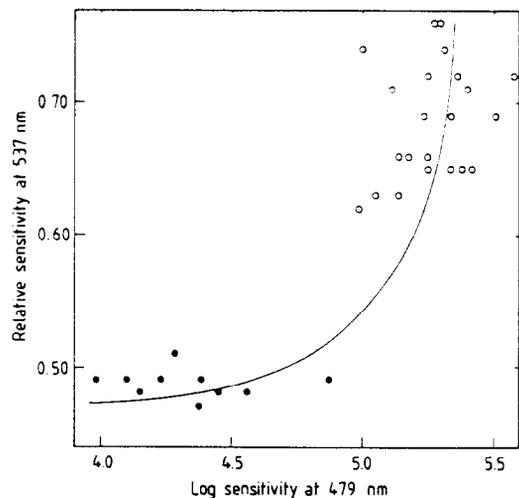
Fig. 2. The relation between the absolute sensitivity, measured at 497 nm, and the relative sensitivity at 537 nm in wild type flies, reared under conditions with no blue light (solid circles) and under normal daylight (open circles), respectively. The continuous curve was calculated from equation (1) (Methods) by varying κL (the visual pigment content).

ably well around the theoretical curve, suggesting that the gain of the electrical response of the photoreceptor cell indeed is independent of the visual pigment content.

It follows from Fig. 2 that with little visual pigment its concentration can be estimated from absolute sensitivity; at high sensitivities the width of the visual pigment curve provides a useful measure.

Selfscreening in the visible light range

A quantitative treatment of the broadening of the visual pigment curve is attempted in the following section. We determined the mean spectral sensitivities for three groups of cells. One group had a high visual pigment content, as they were from wild type flies reared on a vitamin A rich diet and were kept under blue light. The absolute sensitivity of these cells measured at 497 nm varied between 5.0 and 5.6 (according to the log scale of Fig. 2), with a mean value of 5.3 ($n = 22$). Another group of cells were from wild type flies which were also reared on a high vitamin A diet, but the visual pigment content of these cells was reduced, because they were held under light conditions with no blue light [the mean absolute log sensitivity of these cells at 497 nm was 4.4 (range 4.0–4.5), $n = 11$]. A third group of cells were from chalkies, which were reared on a vitamin A deprived diet and were also held under light

conditions with no blue light [the mean absolute log sensitivity at 497 nm was 4.3 (range 3.4–4.5), $n = 10$]. In Fig. 3 the mean spectral sensitivity curve of this last group of cells is compared with the normalized absorption spectrum of blowfly visual pigment (as determined from extracts by Schwemer, 1979). The experimental data were compared with a family of theoretical curves, belonging to various κL values. These theoretical curves were calculated as described in the methods. The best fit to the measured values is also shown in Fig. 3. The obtained curve is slightly shifted towards shorter wavelengths due to waveguide effects. No significant broadening of the curve occurs because of the low amount of visual pigment.

In Fig. 4 the mean measured values with the best fits are presented for the two groups of cells from wild type flies which were reared on a vitamin A rich diet. One group was held under light conditions with blue light, and thus had a high visual pigment content, and another group received no blue light, yielding a low visual pigment content. There is a large difference between the two groups of cells in the width of the curves in the visible range. The best fit of the spectral sensitivity of the cells with a high pigment content was obtained with $\kappa L = 2.8$. The best fit for the low visual pigment group yielded $\kappa L = 0.2$. Accordingly, the photoreceptors with little visual pigment contained 7% of the amount of visual pigment which existed in the rich cells. The different amounts of visual pigment of the two groups should
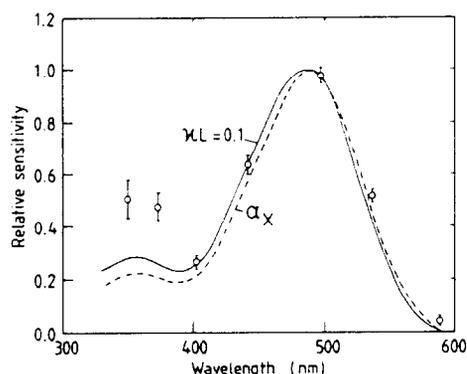

Fig. 3. The mean spectral sensitivity of visual pigment poor R1–6 photoreceptor cells of chalkies, reared on a vitamin A deprived diet and kept under light conditions with no blue light. The dotted curve is the normalized absorption spectrum of blowfly visual pigment (Schwemer, 1979). The continuous curve is the best fit of the mean spectral sensitivity, calculated from equation (1) of the Methods. The mean sensitivity in the U.V. differs from the calculated fit, presumably because some sensitizing pigment is present.
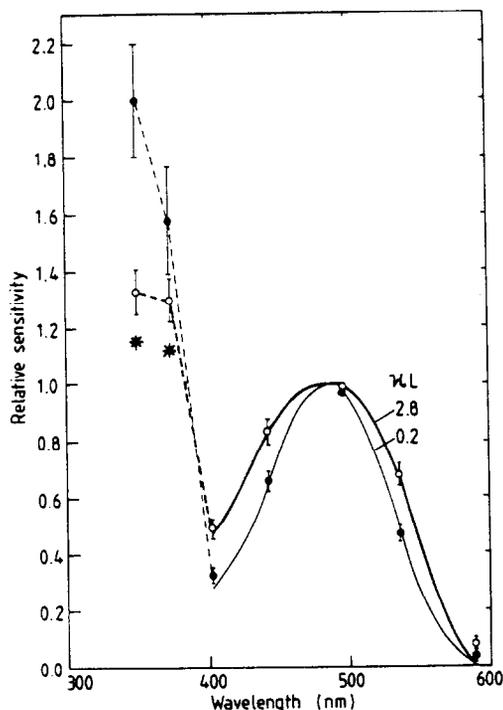
Fig. 4. The mean spectral sensitivity of R1–6 photoreceptors of wild type blowflies. All flies were reared on a vitamin A rich diet. One group of flies was reared under light conditions with no blue light (dots); the other group with blue light (open circles). The best fits in the visible band, calculated from equation (1) (Methods) are also shown (continuous lines). Note the difference in broadening of the curves in the visible band, which is due to selfscreening. Assuming that in both cases the ratio sensitizing pigment/visual pigment is maximal the relative U.V. sensitivity in the visual pigment rich cells has been calculated from the values of the pigment poor cells using equation (2) (Methods) and assuming $\gamma_s = 1$ (asterisks). The measured relative U.V. sensitivities of the visual pigment rich flies differ only slightly from the calculated values.

result in different sensitivities. Indeed, the difference in absorption, being 0.82 log units, corresponds well with the measured difference in absolute sensitivity, being 0.9 log units.

Sensitivity in the ultraviolet

The β-band, i.e. the absorption band in the U.V. of fly visual pigment is much lower than the α-band, the main band in the blue–green, as the ratio of the peaks is about 0.22 (see Schwemer, 1979; Paulsen and Schwemer, 1979; Vogt and Kirschfeld, 1983). The waveguide properties of the rhabdomere enhance the relative sensitivity in the U.V. to about 0.28 (Fig. 3). The experimental values, however, are significantly higher, even in the least pronounced case of the low vitamin A reared

chalkies (Fig. 3), where we measured sensitivities closely corresponding to those of Kirschfeld *et al.* (1983). The conclusion of these authors, namely that in these flies a low concentration of sensitizing pigment is present, agrees with the finding that the polarization sensitivity in the U.V. is slightly lower than that in the visible range [PS(349) = 1.4, PS(497) = 1.7 and PS(588) = 1.7].

The U.V. sensitivity of other groups of cells with low visual pigment (vitamin A, no blue light) is shown in Fig. 4. In these cells a high concentration of sensitizing pigment is maintained, as can also be seen from the polarization sensitivities: PS(349) = 1.1, PS(497) = 1.7 and PS(588) = 1.8. This is in good agreement with the results of Vogt and Kirschfeld (1983) and Hardie (1979). The relative U.V. sensitivity in these cells is extremely high. A part of this U.V. sensitivity is due to the absorption by the β-band of the xanthopsin, but the major part is due to the sensitizing pigment. From Fig. 4 we read that $S(349) = 2$. This sensitivity follows from equation (2) of the methods with $V(349) = 3.6$ and $\alpha_x + \alpha_s = 1.75$, when we assume that $\gamma_s = 1$. At 379 nm we calculate: $\alpha_x + \alpha_s = 1.38$. With the values derived for the case of the low visual pigment content, and taking into account the effect of selfscreening, we can estimate the spectral sensitivity of the pigment rich flies in the U.V. As is mentioned before, the mean spectral sensitivity of the visual pigment rich flies could be fitted with $\kappa L = 2.8$, which is also used to calculate the effect of selfscreening in the U.V. Assuming that the visual pigment molecules in rich and poor cells are identical in structure, and that in both cases of Fig. 4 the ratio of sensitizing pigment to visual pigment is the same, the relative U.V. sensitivity of the rich flies was calculated to be 1.15 at 349 nm and 1.12 at 373 nm (asterisks in Fig. 4).

We note that, as a consequence of the high pigment content, virtually all ultraviolet photons that are focussed on the rhabdomere will be absorbed. A high relative sensitivity in the U.V. can then only be achieved when the transfer of energy from sensitizing pigment to visual pigment is very efficient. For this reason we assumed above $\gamma_s = 1$; the slight deviation of experimental and calculated values increases progressively when we take $\gamma_s < 1$. When for example, $\gamma_s = 0.8$, we have to assume $\alpha_x + \alpha_s = 2.2$ to achieve $S(349) = 2$ in the case of the visual pigment poor cells. Using the same

values in the visual pigment rich flies we then calculate from equation (2) that $S(349) = 0.96$, a value which significantly deviates from 1.33, the measured relative sensitivity at 349 nm.

DISCUSSION

The shape of the spectral sensitivity curve in the visible range

The shape of the spectral sensitivity curve in the visible range differs from that of the visual pigment (Schwemer, 1979) due to at least two factors. First, waveguide effects enhance the short wavelengths with respect to the long wavelengths. Variation of the V-number hardly affects the width of the band in the visible range; only a slight shift in peak wavelength occurs (cf. Snyder and Miller, 1972; Stavenga and van Barneveld, 1975). With $V = 3.6 \pm 0.8$ the range of the predicted spectral sensitivities was within that of the experimental error limits. The second factor affecting the shape of the band in the visible range is selfscreening. Selfscreening broadens the curve at higher visual pigment contents (Hamdorf, 1979; Gribakin, 1979; Stowe, 1980; Cornwall et al., 1984; Hardie, 1985).

By taking into account both aspects, waveguide optics and selfscreening, the experimentally obtained spectral sensitivities could be satisfactorily fitted. At the highest visual pigment content the best fit was obtained with $\kappa L = 2.8$, with $V = 2.57$ at 490 nm (i.e. $V = 3.6$ at 349 nm). It then follows that η_a (λ_{max}) $\kappa L = 1.9$ and $E_x = 0.82$. So at λ_{max}, 85% of the photons that enter the rhabdomere are absorbed, a value only slightly lower than that estimated by Stavenga (1976).

Sensitivity in the ultraviolet range

In the ultraviolet, waveguide effects induce a distinct enhancement of the relative height of the U.V. peak (see Fig. 3). Of course, the enhancement is insufficient to explain the very high relative sensitivity in the U.V. found in the low visual pigment flies, which were reared on a high vitamin A diet and held under light conditions where blue light was absent (Fig. 4). Thus a high concentration of sensitizing pigment has to be assumed.

In the case of the cells with a high visual pigment content we concluded that the absorptance was 0.85 at λ_{max}. Consequently, nowhere relative sensitivity can be higher than 1.18, because then all the incident photons are absorbed.

In the U.V., however, the experimental data exceed this limit (see Fig. 4 and Kirschfeld et al., 1983). A possible explanation is that the fraction of photons entering the rhabdomere (i.e. the excitation efficiency) in the U.V. is slightly higher than that in the blue–green. Because the excitation efficiency of the first order mode is virtually independent of wavelength (Smakman et al., 1984), the conclusion must be that additional light is coupled into the rhabdomere via a higher order mode. With on-axis illumination the only possible candidate is the mode 02 (Marcuse, 1974), which is excited at $V \geqslant 3.8$. A number of our investigated cells had V-numbers that exceeded this value (see Smakman et al., 1984), so some of these cells can have achieved a higher relative U.V. sensitivity. Consequently, the estimated value of $\alpha_x + \alpha_s$ at 349 nm then becomes somewhat lower than 1.75.

Absolute sensitivity

The variation in absolute sensitivity can be well understood from the variation in visual pigment content. This validates the common assumption that in R1–6 photoreceptors, irrespective of the visual pigment content, the electrical response amplitude is equal when equal numbers of light quanta are absorbed. Evidence for this assumption was also provided by Razmjoo and Hamdorf (1976), who correlated relative sensitivity measurements with difference spectrophotometry on isolated retinas of the white-eyed mutant chalky. In our experiments the visual pigment content in wild type flies could be calculated from selfscreening. From these results we also conclude that the gain of the electrical response does not vary substantially among fly photoreceptor cells.

CONCLUSION

The spectral sensitivity of R1–6 photoreceptors of the blowfly can be well understood from the spectral absorption properties of the visual pigment xanthopsin and the ultraviolet absorbing sensitizing pigment. The spectral absorption is modified by the waveguide properties of the rhabdomere and by selfscreening.

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