PHOTORECONVERSION OF BLOWFLY VISUAL PIGMENT PROCEEDS THROUGH A SLOWLY (13 MS) DECAYING INTERMEDIATE

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Photoreconversion of blowfly visual pigment proceeds through a slowly (13 ms) decaying intermediate

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Summary. The photochemical cycle of the visual pigment molecules in the blowfly *Calliphora erythrocephala* was investigated by transmission measurements, making use of the fact that intermediate states of the visual pigment molecules each have a characteristic absorption spectrum.

It is shown that the conversion of metaxanthopsin (M580) to the native xanthopsin state (P490) induced by an orange-red light pulse proceeds through a newly discovered intermediate (N), which thermally decays with a time constant of about 13 ms at room temperature.

The absorption spectrum of N peaks in the blue-green at about 490 nm. In the green and orange N absorbs more strongly than the native xanthopsin, but in the blue N and xanthopsin absorb almost equally. The latter finding explains why N has remained undetected in earlier studies.

Introduction

Vision starts with the absorption of light by the visual pigment molecules in the photoreceptor cells. The visual pigment of the fly photoreceptor cells R1–6 is a xanthopsin (Vogt 1983; Vogt and Kirschfeld 1984) which absorbs maximally at 490 nm. Upon light absorption xanthopsin converts via a number of thermolabile intermediate states into a thermostable metaxanthopsin absorbing maximally at 580 nm (for reviews see Hamdorf 1979; Stavenga and Schwemer 1984). This photochemical process has been analyzed by Kruizinga et al. (1983), who found that metaxanthopsin is formed via so-called bathoxanthopsin and lumixanthopsin states, decaying with time constants of 700 ns and 80 μs, respectively (room temperature; see also Kirschfeld et al. 1978; Stark et al. 1979).

On the reverse photoconversion, i.e., of metaxanthopsin into the xanthopsin state, Kirschfeld et al. (1978) reported that at 0 °C this process is completed within 300 μs. Kruizinga et al. (1983) have characterized an intermediate K, decaying with a time constant of 4 μs.

The results of our recent electrophysiological experiments on the early receptor potential (ERP; Gagné et al., in press) forced us to reconsider the process of photoregeneration, i.e., the conversion of metaxanthopsin into xanthopsin. Minke and Kirschfeld (1980) and Stephenson and Pak (1980) measured a positive monophasic ERP in the blowfly and the fruitfly upon photoconversion of metaxanthopsin to xanthopsin. However, we have found that this ERP actually has a biphasic time course, i.e., an initial positive phase followed by a second negative phase lasting 20–30 ms (Gagné et al., in press). This second phase indicated the existence of an intermediate, converting thermally in the order of 10 ms, i.e., much slower than the conversions found hitherto. Here we present optical experiments which demonstrate and characterize this hypothetical intermediate in the photochemical cycle of the main visual pigment of the blowfly.

Material and methods

Experiments were performed on females of the blowfly *Calliphora erythrocephala* (wild type, 7–14 days after emergence) at room temperature. The animals were fixed with wax and mounted on a goniometer in a microspectrophotometer. A hole was made at the back side of the head by removing a small piece of chitin, and a small plastic light guide was inserted through this hole for antidromic illumination.

Abbreviations: ERP early receptor potential; *M* metaxanthopsin; *P* xanthopsin

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The microspectrophotometer was constructed from an Ortholux 2 microscope (Leitz). Antidromically transmitted light was measured by imaging the deep pseudopupil with a NPL10 objective (0.20, Leitz) in the plane of a diaphragm in front of a photomultiplier (EMI9862).

Orthodromic adaptation light and antidromic test light were supplied by a 150 W Xe lamp controlled by shutters. In the adaptation beam a blue filter (BG12, Schott), creating about 30% xanthopsin and 70% metaxanthopsin in the photosteady state (Hamdorf 1979), or a 610-nm cut-on filter (OG610, Schott), creating nearly 100% xanthopsin, was used. In the test beam interference filters, bandwith 10–15 nm, were used. Orthodromic visual pigment-converting high-intensity flashes were delivered by a Xe flash lamp ($\tau = 0.7$ ms) mounted with a blue (BG12, Schott) or an orange-red filter (OG570, Schott). The light path of the flash lamp was closed 1 ms after the flash was triggered, in order to measure the transmission without interference from the tail of the high intensity flash.

The stimulation sequence consisted of 1 s adaptation light, 90 s darkness, 0.1 s test light, a flash and 0.4 s test light. The blue (BG12) or red (OG610) adaptation light was sufficiently bright to bring the visual pigment into the photosteady state within the 1-s illumination time. However, the adaptation light activated the pupil mechanism (Franceschini and Kirschfeld 1971; Stavenga 1975a) and therefore the 90-s dark period was given to allow reopening of the pupil. To protect the photomultiplier, the shutter in front of the photomultiplier was closed during the flash (see Figs. 1, 2). After another period of 5 s darkness, the sequence was repeated. Stimulus control and sampling of the photomultiplier signal (2 kHz) were performed by an intelligent laboratory interface (1401, Cambridge Electronic Design). Data, after transfer to a computer, were stored on hard disk for further analysis. Least-squares exponential fits of the data (see Theory) were performed with the Asyst software package (Macmillan Software Company).

Theory

Conversion of the fly visual pigment state metaxanthopsin (M) to the native state xanthopsin (P) is characterized by $M \rightsquigarrow K \rightarrow N \rightarrow P$ (Kruizinga et al. 1983; see Fig. 6). The formation and the thermal decay of intermediate K are very fast: the time constants are <40 ns and 4 µs, respectively (Kruizinga et al. 1983). These time constants are negligibly short with respect to that of the thermal decay of N, τ_N (Figs. 2B, 3). The change in the fractions of metaxanthopsin (f_M), intermediate N (f_N) and xanthopsin (f_P) of the visual pigment molecules after a pigment-converting flash ($M \rightsquigarrow P$) in the dark is then given by the following set of differential equations:

$$\frac{d}{dt} f_M(t) = 0 \tag{1}$$

$$\frac{d}{dt} f_N(t) = -\tau_N^{-1} f_N(t) \tag{2}$$

$$\frac{d}{dt} f_P(t) = \tau_N^{-1} f_N(t). \tag{3}$$

Suppose the fraction of molecules existing in the M state initially equals q and a fraction r is converted by a brief flash; or, $f_M(0^-) = q$, $f_M(0^+) = q - r$, $f_N(0^-) = 0$, $f_N(0^+) = r$, and $f_P(0^-) = f_P(0^+) = 1 - q$. Then Eqs. (1)–(3) lead to the solution:

$$f_M(t) = q - r \tag{4}$$

$$f_N(t) = r \exp[-t/\tau_N] \tag{5}$$

$$f_P(t) = (1-q) + r(1 - \exp[-t/\tau_N]). \tag{6}$$

Transmission of test light through a rhabdomere of a fly photoreceptor cell can be described by Lambert-Beer's law (see Stavenga 1975b; Kruizinga et al. 1983):

$$I_l(\lambda, t) = I_0 \exp[-C l \sum \alpha_i(\lambda) f_i(t)] \tag{7}$$

with I_0, intensity of light entering the rhabdomere; C, concentration of the visual pigments in the rhabdomere; i, state of visual pigment molecule (P, xanthopsin; M, metaxanthopsin; N, intermediate N); l, rhabdomere length; $\alpha_i(\lambda)$, molecular absorption coefficient of state i at wavelength λ; $f_i(t)$, fraction of visual pigment molecules in state i at time t.

Substituting Eqs. (4)–(6) in (7) yields:

$$\begin{aligned} I_l(\lambda, t) = I_0 \exp[-C l \{ & \alpha_M(\lambda)(q-r) \\ & + \alpha_P(\lambda)(1+r-q) \\ & + (\alpha_N(\lambda) - \alpha_P(\lambda))\, r \exp(-t/\tau_N)\}]. \end{aligned} \tag{8}$$

When all the visual pigment molecules are in the xanthopsin (P) state, or $f_P = 1$, $f_M = 0$, then ($q = r = 0$):

$$I_l = I_0 \exp[-C l \alpha_P(\lambda)]. \tag{9}$$

The difference in absorbance with respect to this case is

$$\begin{aligned} \Delta E(\lambda, t) &= -\log_{10}[I_l(\lambda, t)/I_l(q = r = 0)] \\ &= A(\lambda) + B(\lambda) \exp[-t/\tau_N], \end{aligned} \tag{10}$$

where

$$A(\lambda) = 0.43\, C l (q-r)[\alpha_M(\lambda) - \alpha_P(\lambda)] \tag{11}$$

represents the absorbance difference after the thermal decay of N has been completed and

$$B(\lambda) = 0.43\, C l r [\alpha_N(\lambda) - \alpha_P(\lambda)] \tag{12}$$

represents the change in absorbance due to the thermal decay of N.

The absorbance difference of the blue-adapted case ($q = 0.7$, $r = 0$) with respect to the red-adapted case ($q = r = 0$) is

$$\Delta E_b(\lambda) = 0.43\, C l q [\alpha_M(\lambda) - \alpha_P(\lambda)]. \tag{13}$$

The fraction r which is converted by an orange-red flash can thus be calculated from the above formulae. From Eqs. (11) and (13)

$$A(\lambda)/\Delta E_b(\lambda) = 1 - (r/q), \tag{14}$$

and from Eqs. (12) and (13)

$$B(\lambda)/\Delta E_b(\lambda) = (r/q)[\alpha_N(\lambda) - \alpha_P(\lambda)]/[\alpha_M(\lambda) - \alpha_P(\lambda)]. \tag{15}$$

Finally, Eqs. (14) and (15) yield

$$\alpha_N(\lambda) = \alpha_P(\lambda) + [\alpha_M(\lambda) - \alpha_P(\lambda)]\, B(\lambda)/[\Delta E_b(\lambda) - A(\lambda)]. \tag{16}$$

According to Eq. (16), the absorption spectrum of N can be calculated from the absorbance differences $A(\lambda)$, $B(\lambda)$ and $\Delta E_b(\lambda)$ without prior knowledge of r and q. However, because a background contributes to the transmission signal, this background has to be subtracted before the absorbance difference can be calculated, and a least squares exponential fit (Eq. 10, see Fig. 3) can be performed, yielding values for $A(\lambda)$ and $B(\lambda)$ (Eqs. 11, 12). Therefore, the procedure was to first estimate the background at the various test wavelengths under the condition that r is constant (Eq. 14).

In the derivation given above the waveguide properties of the rhabdomeres have been neglected. Furthermore, it has been implicitly assumed that the distribution of the visual pigment molecules over the various states is the same throughout the rhabdomere. This condition is not entirely fulfilled because the orange-red flash is not sufficiently intense to bring the visual pigment into photoequilibrium. It can be easily shown that the derivation taking both aspects into account leads to expressions (14) and (15) where r is replaced by an average r given by:

$$\bar{r} = \int_0^l \eta(x)\, r(x)\, dx \Big/ \int_0^l \eta(x)\, dx \tag{17}$$

where $\eta(x)$ is the fraction of light propagated within the rhabdomere boundary (see, e.g., Stavenga 1975b). η is not a constant (fly rhabdomeres taper) and because η is a function of wavelength, $\bar{r}$ will also be wavelength dependent. We estimate, however, that the effect of this wavelength dependence on the resulting absorption of N will be minor.

Results

Each state in the photochemical cycle of visual pigments has a characteristic absorption spectrum and therefore the time course of the photochemical process can be studied by transmission measurements (e.g., Hamdorf 1979). In Fig. 1 the transmission of fly photoreceptors is measured at wavelength $\lambda_t = 570$ nm. Preceding the measurements of Fig. 1 the red (>610 nm) adapting illumination was given, which established a photochemical steady state with virtually pure xanthopsin (P490), i.e. $f_M = 0$. A blue flash (BG12) at $t = 0$ then converts a substantial fraction into the metaxanthopsin (M580) state; we calculated $f_M = 0.3$ (Fig. 1A). An orange-

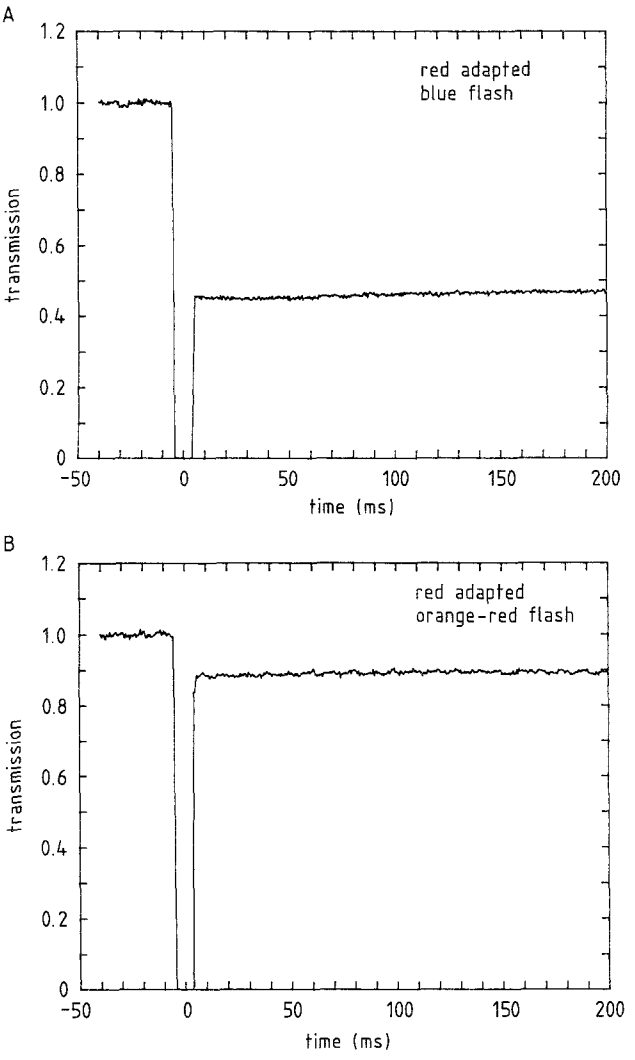

Fig. 1A, B. Transmission measurements of fly photoreceptor cells at $\lambda_t = 570$ nm after red adaptation (OG610), which created approximately 100% P490. At $t = 0$ an intense flash of light is given. **A** Blue flash (BG12) converting net 30% xanthopsin (P490) into metaxanthopsin (M580). **B** Orange-red flash (OG570) converting net 3% P490 into M580. During the flash the photomultiplier is protected by closing a shutter in front of it. The changes in transmission are due to the considerable absorption of M580 at the test wavelength. The transmission has reached a stable level before the restart of the measurement after the flash

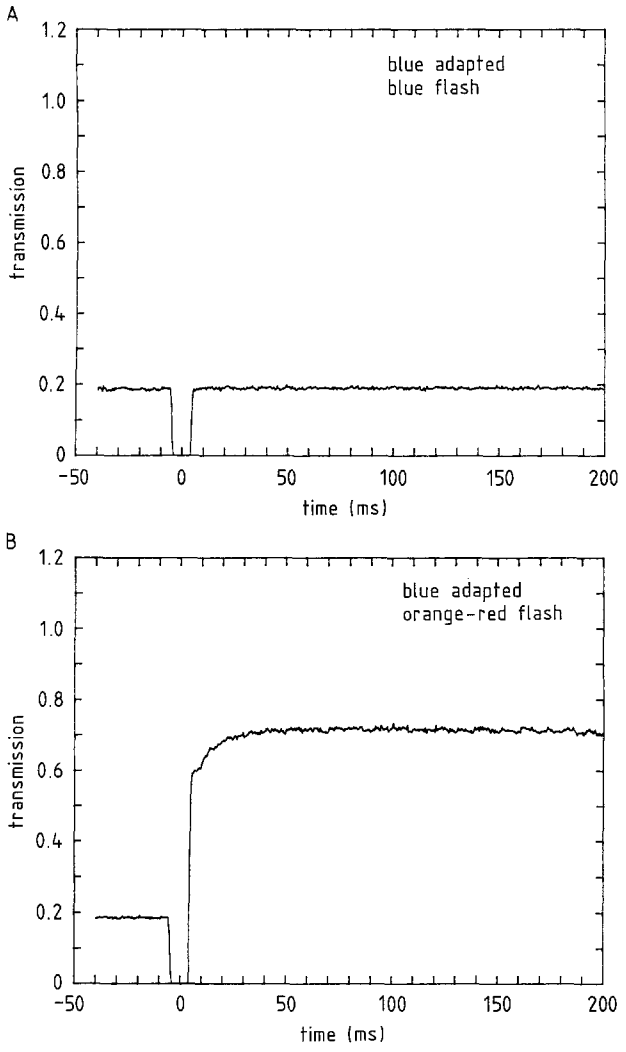

Fig. 2A, B. Transmission measurements of fly photoreceptor cells at $\lambda_t = 570$ nm after blue adaptation (BG 12), which created a photosteady state with 30% P490 and 70% M580. At $t=0$ an intense flash of light is given. **A** Blue flash (BG 12) converting net 0% M580 into P490, so no change in transmission occurs. **B** Orange-red flash (OG 570) converting net 57% of the visual pigment from M580 into P490. The relatively slow change in transmission after the flash reflects the thermal decay of an intermediate N, which absorbs less than M580 and more than P490 at the test wavelength

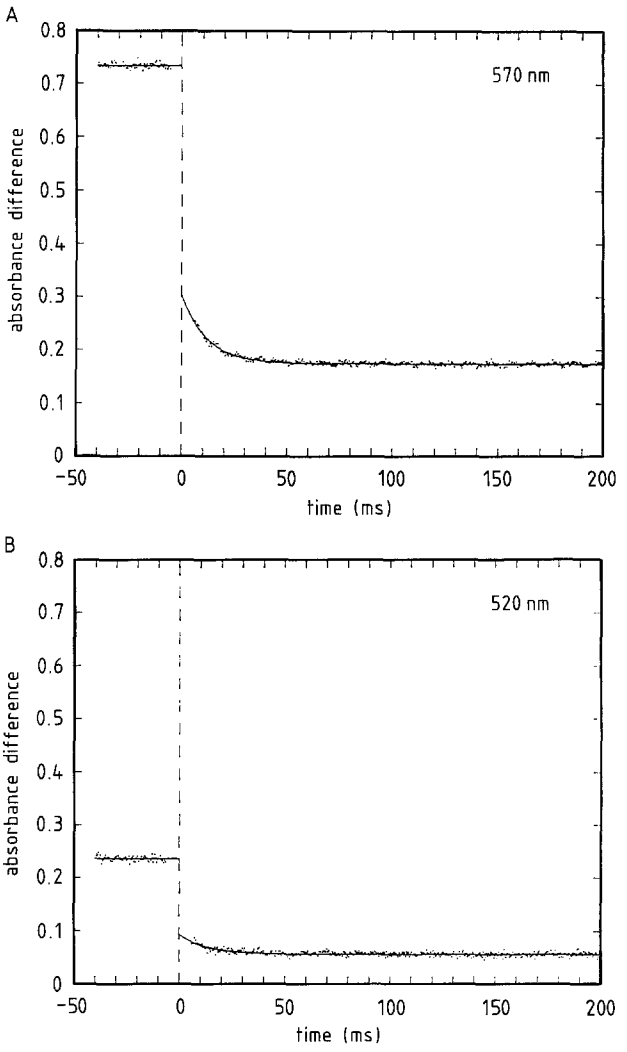

Fig. 3A, B. Absorbance difference after blue adaptation with respect to a red adapted eye (i.e., $q=0$, $r=0$) before and after an orange-red flash at $t=0$, calculated from transmission measurements as in Fig. 2B. A least squares exponential fit [$\Delta E = A + B \exp[-t/\tau_N]$; Eq. (9), Theory] was performed on the data (*solid line*). **A** Absorbance difference at $\lambda_t = 570$ nm, yielding $A=0.17$, $B=0.13$ and $\tau_N = 11.7$ ms. **B** Absorbance difference at $\lambda_t = 520$ nm, yielding $A=0.06$, $B=0.04$ and $\tau_N = 13.1$ ms. The data are corrected for background stray light (see text) and the calculated fraction of M580 converted by the flash (r) is 0.53

red flash (OG 570) shifts the visual pigment population only very slightly; we calculated $f_M = 0.03$ (Fig. 1B). Even with this small conversion, the drop in transmission is considerable, due to the high absorption of metaxanthopsin at the test wavelength (570 nm).

The opposite situation is considered in Fig. 2. Here, preceding to the measurement a blue (BG 12) adapting light was given, which created a photosteady state with about 70% of the visual pigment molecules in the metaxanthopsin state, i.e., $f_M = 0.7$. Of course, an additional blue flash (BG 12) at $t=0$ does not cause a change in transmission because the visual pigment population is already at the blue-adapted photosteady state (Fig. 2A). However, an orange-red flash (OG 570) yields a large transmission change, and this change appears to proceed during several milliseconds after the flash (Fig. 2B).

A comparison of the transmission value in Fig. 2A with that resulting after the flash in Fig. 1A shows that one blue flash is not sufficiently

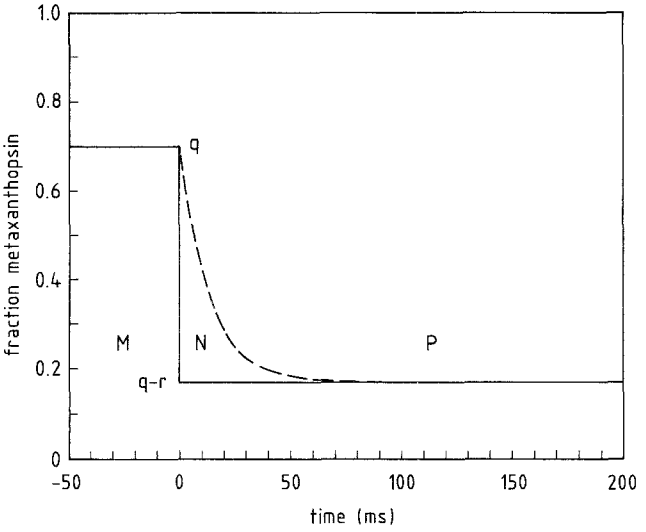

Fig. 4. Schematic representation of the change in distribution of the visual pigment in fly photoreceptor cells. The solid line represents the fraction of M580. Blue adaptation creates a high initial fraction of M580, $f_M = q = 0.7$. At $t = 0$ an orange-red flash converts a fraction r of the visual pigment into the intermediate N ($r = 0.53$; see Fig. 3B). This conversion can be considered to occur instantaneously with respect to the thermal decay of N (see text, Fig. 6). After the flash $f_M = q - r = 0.17$ stays constant. Intermediate N decays with time constant $\tau_N = 13.1$ ms (dashed line, $f_N = r \exp[-t/\tau_N]$; see Fig. 3B) into xanthopsin (P490; $f_P = 1 - q + r\{1 - \exp[-t/\tau_N]\}$)

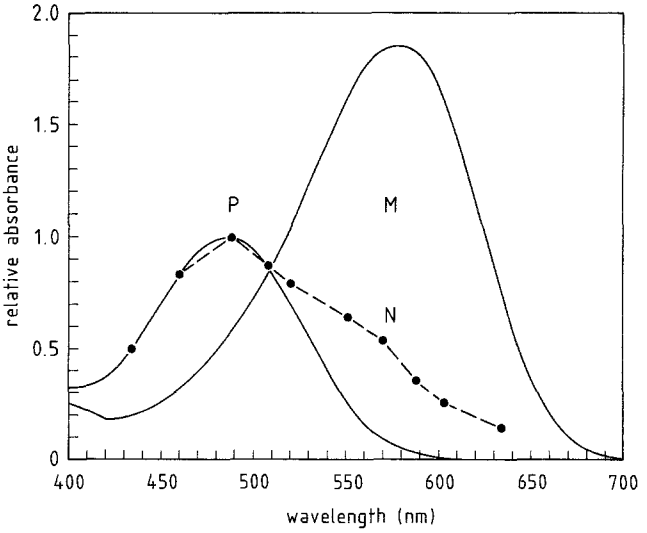

Fig. 5. Relative absorption spectra of xanthopsin (P490), metaxanthopsin (M580) (Schwemer 1979; Minke and Kirschfeld 1979), and intermediate N (N490)

intense to establish a photosteady state. The same conclusion follows for the orange-red flash when comparing the final transmission value in Figs. 1B and 2B.

The only obvious interpretation of the unexpected, slow transmission change in Fig. 2B is the existence of a hitherto undetected spectral intermediate, which thermally decays to the native xanthopsin state of the visual pigment molecules. In order to study the spectral properties of this intermediate, we have measured the orange-red flash-induced transmission change at various wavelengths. We found that the time course of the absorbance change after the orange-red flash, of which examples at two different wavelengths are given in Fig. 3, can always be well fitted with an exponential (see Theory). The calculated time constant was 13.1 ± 1.2 ms ($n = 5$). Kruizinga et al. (1983) found that metaxanthopsin converts into xanthopsin via an intermediate K, which is formed within 40 ns after the flash and decays with a time constant of 4 μs. Clearly, intermediate K converts into a second intermediate, N, which subsequently decays into xanthopsin. This thermal conversion has not been described before.

Figure 4 schematically shows the time course of the fractions of xanthopsin (f_P), metaxanthopsin (f_M) and intermediate N (f_N). After blue adaptation, which produced a high f_M content (q), an orange-red flash at $t = 0$ converts a fraction (r) of metaxanthopsin into intermediate N. The formation of N occurs with an overall time constant of 4 μs (see above) and thus can be considered to be instantaneous with respect to the time course of its decay. This conversion leads to a drop in absorbance when intermediate N has a lower absorption coefficient than metaxanthopsin at the test wavelength (Fig. 3). Intermediate N decays with a time constant of about 13 ms to the native xanthopsin (room temperature, Figs. 3, 4). The thermal decay of N leads to a further drop in the absorbance when native xanthopsin has a lower absorption coefficient than intermediate N at the test wavelength (Fig. 3).

Because measurements are performed from the deep pseudopupil, part of the photomultiplier signal is due to stray light. The main screening pigment is red, and therefore the stray light component in the transmission increases progressively with longer test wavelengths. An estimate of the stray light component as a function of wavelength was made by assuming that the fraction of metaxanthopsin converted by the flash was constant and independent of the test wavelength. This fraction (r) was calculated according to the method described in the Theory section after subtracting a certain background level, i.e., the stray light component. Values for the stray light component at the different test wavelengths where chosen in such a way that the fraction r was a constant during each experiment.

With values of the relative absorption of xanthopsin and metaxanthopsin from the literature (Schwemer 1979; Minke and Kirschfeld 1979) and the derived value for r, the relative absorption of the intermediate N can be estimated (see Theory). Figure 5 shows the absorption spectra of xanthopsin and metaxanthopsin and that derived for intermediate N. The spectra of native xanthopsin and N coincide in the short-wavelength range because after the orange-red flash the transmission changed, but no measurable further decay occurred.

Discussion

Conversion of xanthopsin into metaxanthopsin takes place with a time constant of 0.1 ms at room temperature in the fruitfly (Kirschfeld et al. 1978; Stark et al. 1979). Studies with laser methods revealed that the formation of metaxanthopsin occurs via two thermolabile intermediates, batho- and lumixanthopsin, decaying with time constants of 700 ns and 80 µs, respectively, at room temperature (Kruizinga et al. 1983). The experimental method used in this study does not allow measurement of transmission changes within 4 ms after the flash. Within this time the formation of metaxanthopsin is completed, and indeed no change in transmission occurs after 4 ms (Fig. 1).

Kirschfeld et al. (1978) found that at 0 °C xanthopsin is photoregenerated from metaxanthopsin within 300 µs. This conclusion, in principle in agreement with the finding by Kruizinga et al. (1983) of an intermediate K decaying with a time constant of 4 µs, is in conflict with the results of the present study, however. We have shown that metaxanthopsin converts into xanthopsin via an intermediate N, subsequent to K, decaying with a time constant of 12–14 ms (room temperature; Figs. 2B, 3). The apparent discrepancy can be explained by the choice of test wavelength of the transmission measurement of Kirschfeld et al. (1978), this being 480 nm. In our experiments with blue test lights, we have been unable to discriminate intermediate N from its xanthopsin, and thus we are forced to conclude that both visual pigment states absorb approximately equally well in the blue. For the same reason, Kruizinga et al. (1983), who investigated the conversion of metaxanthopsin into xanthopsin at 456 nm, also failed to detect the transition of K to xanthopsin through the N state.

After blue adaptation an additional blue flash does not give rise to a change in transmission (Fig. 2A), although this flash converts a small fraction (<0.09) of the visual pigment molecules from xanthopsin into metaxanthopsin and a similar amount from metaxanthopsin into intermediate N. We calculated that the thermal decay of intermediate N into xanthopsin after the flash in Fig. 2A causes a change in transmission of less than 1%. This change in transmission falls within the accuracy of the measurement and cannot be seen in Fig. 2A.

The shape of the absorption spectrum deduced for N (Fig. 5) deviates from the usual shape for visual pigments. We do not have a clear interpretation for this aberrant finding. One cause may be the assumption, implicit in our analysis, that the waveguide properties of the rhabdomeres do not substantially affect the spectra. Fly rhabdomeres, however, can carry one or two waveguide modes (in the green-orange and in the blue, respectively; van Hateren 1984), which do influence the absorption properties of the rhabdomeres. We estimate, nevertheless, that the effects on the absorption spectrum of N are minor. Measurements in an optical system less complex than the living eye are needed to clarify this point.

Spectra with long wavelength tails have been presented for photoproducts of octopus rhodopsin by Tsuda et al. (1980). However, it cannot be ruled out that these spectra represent a mixture of photopigment states. Because the time course of the transmission change at various wavelengths was virtually identical (12–14 ms) it seems unlikely that in the present case of the blowfly more than one photoproduct is involved.

In Fig. 6 a schematic representation of the photochemical cycle of the blowfly visual pigment is given, together with the time constants of the conversion steps.

The conversion of xanthopsin into metaxanthopsin occurs with an overall time constant of around 80 µs while the reconversion takes place with an overall time constant of about 13 ms (Fig. 6). The forward conversion of P⇝M thus proceeds more than 2 orders of magnitude faster than the backward conversion M⇝P. However, the relatively slow reconversion of xanthopsin is not in any way restrictive for the functioning of the visual system. It is the conversion of xanthopsin into metaxanthopsin which triggers the phototransduction process, eventually leading to the late receptor potential (LRP). The time constant of the forward conversion (80 µs) easily accommodates for the delay of the LRP. In order to prevent a continuous triggering of the phototransduction process, metaxanthopsin must be inactivated, which is believed to be achieved by phosphoryla-

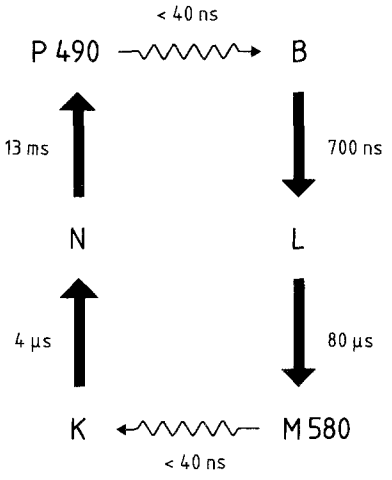

Fig. 6. Photochemical cycle of the blowfly visual pigment with thermal decay time constants. Upon photon absorption, xanthopsin (P490) converts via two thermolabile intermediates, bathoxanthopsin (*B*) and lumixanthopsin (*L*) into the thermostable metaxanthopsin (M 580) state (Kruizinga et al. 1983). Reconversion of xanthopsin out of metaxanthopsin takes place via intermediate K (Kruizinga et al. 1983) and the subsequent intermediate N characterized here

tion (Paulsen and Bentrop 1984; Bentrop and Paulsen 1986). After photoregeneration of a molecule into the xanthopsin state it needs first to be dephosphorylated before it can be converted again into the active form of metaxanthopsin. This dephosphorylation is 3 orders of magnitude slower than the regeneration of xanthopsin (Paulsen and Bentrop 1984), and hence the latter process is not a limiting factor in the performance of the visual system of the fly.

The existence of intermediate N, decaying with a time constant of 12–14 ms in the photoreconversion pathway of xanthopsin appears to be in agreement with our recent electrophysiological experiments on the early receptor potential (Gagné et al., in press).

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