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ENIGMA OF EARLY RECEPTOR POTENTIAL IN FLY EYES

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Abstract—The early receptor potential (ERP) of fly photoreceptors R1–6 has been recorded in the blowfly *Calliphora erythrocephala*, and quantitatively analyzed. Photoconversion of the native visual pigment (P) into the meta-state (M) does not induce a measurable ERP. Photoconversion of M into P induces a biphasic ERP, presumably due to the slow thermal decay of intermediate N, recently discovered by Roebroek, Gagné and Stavenga (1989). The experimentally measured ERP's are interpreted with an *RC*-model which incorporates the time constant of the flash, the time constant of the thermal decay of intermediate N, the electrical properties of the photoreceptor cell and the charge displacements within the visual pigment molecules occurring upon photoconversion. The model satisfactorily describes the ERP for the M to P conversion by assuming that effectively 0.03 electron charges are moved across the cell membrane during conversion of the M to the N state and that 0.04 electron charges are moved in the opposite direction during conversion of N to P. The net 0.01 electron charge movement during conversion of P to M would, according to the simple *RC*-model, induce a measurable ERP, in conflict with the experimental results. The longstanding enigma of the ERP of fly photoreceptors appears largely but not completely resolved.

Early receptor potential   Fly photoreceptor   Visual pigment   Anoxia   Charge displacements

INTRODUCTION

The early receptor potential (ERP) is a fast photovoltage that is recorded across the eye or the retina in response to an intense flash of light. It arises from charge displacements within the visual pigment molecules occurring upon photoconversion of the visual pigment (for reviews see: Cone & Pak, 1971; Rodieck, 1973; Fein & Szuts, 1982). Both the light-induced conversions and the thermal transitions of the intermediates in the photochemical cycle of the visual pigment cause a charge displacement in the molecules, and thus each transition is in principle capable of generating a distinct phase in the accordingly complex waveform of the ERP (e.g. Cone & Cobb, 1969). The charge displacements result in a change in transmembrane potential which spreads throughout the electrical circuit of photoreceptor cell and surrounding medium. This view was firmly established by the initial extracellular measurements of the ERP in both vertebrates and invertebrates (see Rodieck, 1973) and has been confirmed more recently by intracellular recordings of the ERP (Hodgkin & O'Bryan, 1977).

The specific advantage of invertebrates in studying the ERP is that their visual pigments do not bleach. Photoconversion of the native visual pigment P yields a thermostable meta-state M, which can readily be photoconverted back into the native state. Intracellular recordings from photoreceptors in the squid, the barnacle, the scallop as well as in the horseshoe crab *Limulus*, show that conversion of P to M results in a monophasic hyperpolarization, whereas the M to P transition causes a monophasic depolarization (Hagins & McGaughy, 1967; Hillman, Hochstein & Minke, 1972; Cornwall & Gorman, 1983; Lisman, 1985).

Flies are the only insect order where an ERP has been reported so far. It is of historical interest to note that the fly ERP was discovered as a component of the electroretinogram in *Drosophila* (Pak & Lidington, 1974). It should be known that the visual pigment (P) of fly photoreceptor cells R1–6, xanthopsin (Vogt, 1983), after light absorption reaches a state B within 40 nsec. B thermally decays with a time constant of 700 nsec to L, which finally converts

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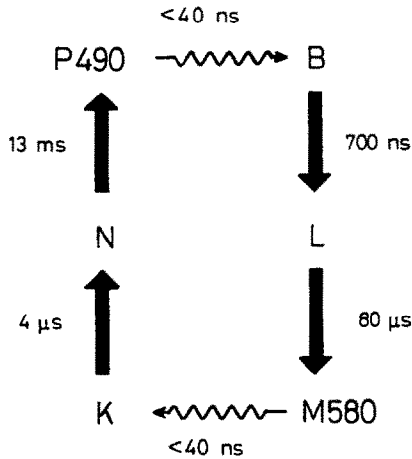
Fig. 1. Photochemical cycle of the blowfly visual pigment with thermal decay time constants. Upon photon absorption xanthopsin (P490) converts via two thermolabile intermediates, bathoxanthopsin (B) and lumixanthopsin (L), into the thermostable metaxanthopsin (M580) state (Kruizinga et al., 1983). Reconversion of xanthopsin out of metaxanthopsin takes place via intermediate K (Kruizinga et al., 1983) and intermediate N (Roebroek et al., 1989).

to the thermostable state M with a time constant of 80 μsec (Kruizinga, Kamman & Stavenga, 1983). The reverse pathway, M to P, is: photoconversion of M to K within 40 nsec, thermal decay of K to N with a time constant of 4 μsec (Kruizinga et al., 1983), and finally conversion of N to P with a time constant of 13 msec (Roebroek et al., 1989); all at room temperature (Fig. 1). Xanthopsin P absorbs predominantly in the blue-green, and metaxanthopsin M absorbs maximally in the orange. Prolonged blue light thus establishes a photosteady state with a large part of the visual pigment population in the M-state ($\approx 70\%$), whilst orange-red light results in a photosteady state with virtually all molecules in the P-state (see e.g. Hamdorf, 1979; Stavenga & Schwemer, 1984).

Pak and Lidington (1974) found in the Drosophila norp A (no receptor potential) mutant that a bright orange flash, after blue pre-illumination, induces a positive waveform in the electroretinogram. This potential was coined the M-potential, because it was evidently coupled to M-conversion. Subsequent investigations (Minke & Kirschfeld, 1980; Stephenson & Pak, 1980) have shown that the M-potential is a complex summation of retina and lamina components, related to the ERP of the photoreceptor cells. When measured intracellularly in the photoreceptor cells of Drosophila (fruitfly), Musca (housefly) and Calliphora (blowfly), the ERP appeared to be enigmatic. Whereas the M

to P conversion was positive, as in other invertebrates, the P to M conversion was silent (for discussion, see Minke & Kirschfeld, 1980). We have reinvestigated this enigma and observed that the M to P conversion induces, when recorded under appropriate conditions, a biphasic ERP (first wave positive, second wave negative). The time course of this second wave indicated the existence of a hitherto undetected intermediate in the photoconversion of M to P. We therefore performed optical measurements to check this conjecture and, indeed, this revealed an intermediate state, called N (Roebroek et al., 1989). Because the photochemical cycle of the fly visual pigment now is known in exhaustive detail we have been able to model the ERP measurements, using electrical data for the photoreceptor cells from the literature. The ERP results, presented in the present paper, are interpreted with a model incorporating the time constant of the flash used to generate the ERP, the time constant of the photoreceptor cell and the time constants of the intermediate states.

MATERIALS AND METHODS

Experiments were performed on females of the blowfly, Calliphora erythrocephala (mutant chalky, 7–14 days after emergence). The animals were immobilized with wax and mounted on a goniometer. For intracellular recordings, a small hole was made in the dorsal part of the cornea through which a microelectrode was inserted. Conventional glass microelectrodes filled with a 3 M KAc, 0.05 M KCl solution, were used, the resistance was 120–200 MΩ. The indifferent electrode (chlorided silver wire) was placed in the ventral part of the retina, through a second small hole.

Adaptation light was supplied by a 150 W Xe lamp controlled by an electronic shutter. The adaptation beam contained either a broadband blue filter (BG12, Schott), creating in the photosteady state about 30% xanthopsin and 70% metaxanthopsin, or a 610 nm cut-on filter (RG610, Schott) creating in the photosteady state almost 100% xanthopsin (Hamdorf, 1979). The pigment converting flash was delivered by a Xe-flash lamp (time constant $\tau_f = 0.8$ msec) mounted with a blue (BG12, Schott) or an orange-red filter (OG570, Schott). The adaptation light and the pigment converting flash were delivered to the eye via an NPL10 objective (0.20, Leitz).

The stimulation sequence consisted of a 1 sec blue (BG12) or red (RG610) adaptation light, which was sufficiently bright to bring the visual pigment into the photosteady state. A 90 sec dark period was given in order to allow the cell to recover from a prolonged depolarizing or hyperpolarizing afterpotential (see e.g. Tsukahara, Horridge & Stavenga, 1977); when the fly was anaesthetized with nitrogen, which abolished the late receptor potential, the dark period lasted 15 sec. Following the dark period a blue (BG12) or orange-red (OG570) flash was given. After another period of 5 sec darkness the sequence was repeated.

Stimulus control and sampling of the receptor potential (10 kHz) were performed by a laboratory interface (1401, Cambridge Electronic Design, U.K.). Sampled data were transferred to a computer and stored on harddisk for further analysis. A Gauss–Newton least square curve fitting algorithm, as implemented in the high level language Asyst (Macmillan Software Company), was used to fit the recorded ERPs with equation (2).

ERP MODEL

The ERP model used here is identical to the one developed by Hodgkin and O'Bryan (1977) for the ERP in turtle cones. Briefly, the electrical model is a simple RC-circuit (see inset of Fig. 3), which is fed by a current source created by the light-induced pigment isomerization and the thermal transitions of the intermediates. We note here that the electrical characteristics of fly photoreceptors are determined in part by electrical coupling to other cells (Van Hateren, 1986). The electrical properties of the cell are still quite well described by an RC-circuit, however, where the effective resistance, R, and capacitance, C, are only indirectly related to the membrane resistance and capacitance (Van Hateren, 1986). The cumulative effect of the pigment isomerization and the transitions of all intermediates living much shorter than the time constant of the cell (5–8 msec; Van Hateren, 1986) is equivalent to that of a charge movement occurring instantaneously (i.e. as a δ function). This is the case for the P to M conversion, since the overall time constant of this pathway is 0.08 msec (Kruizinga et al., 1983). In the M to P pathway only the decay of N to P has a time constant (13 msec; Roebroek et al., 1989) exceeding the cell time constant. The ERP model for the M to P transition is then reduced

to the RC-circuit of the receptor cell fed with a current source made of two parts: a delta function component and an exponential component. However, the duration of the flash eliciting the ERP is not negligible with respect to the cell time constant. Following Hodgkin and O'Bryan (1977), the effect of the finite flash time is that of a single exponential function. The membrane voltage then is, in Laplace transform (see Hodgkin & O'Bryan, 1977):

$$V(s) = (a_4)(a_1)[s + a_3(1 - B)]/[(s + a_1)$$
$$\times (s + a_2)(s + a_3)]; \quad (1)$$

with:

s = complex frequency;

a_1 = inverse of the flash time constant τ_f;

a_2 = inverse of the cell time constant $\tau_c = RC$ (R = cell resistance), (C = cell capacitance);

a_3 = inverse of the time constant τ_N of the thermal decay of intermediate N to P;

$a_4 = N_0 K/C$ = a scaling factor proportional to the quantity of charge transferred by a single isomerization (N_0 = number of molecules isomerized by the light flash), (K = proportionality constant which depends on the difference in the effective dipole movement in the conversion of M to N);

B = the charge transfer ratio during the transition of N to P and of M to N.

Fitting was performed with equation (1) converted to the time domain (see Hodgkin & O'Bryan, 1977):

$$V(t) = a_4 a_1 [\{[a_3(1 - B) - a_1]/[(a_2 - a_1)$$
$$\times (a_3 - a_1)]\} \exp(-a_1 t)$$
$$+ \{[a_3(1 - B) - a_2]/[(a_1 - a_2)$$
$$\times (a_3 - a_2)]\} \exp(-a_2 t)$$
$$+ \{[a_3(1 - B) - a_3]/[(a_1 - a_3)$$
$$\times (a_2 - a_3)]\} \exp(-a_3 t)]. \quad (2)$$

RESULTS

Early and late receptor potential

Illumination of fly photoreceptor cells induces a change in the membrane potential, the receptor potential. As illustrated in Fig. 2 two types of receptor potential can be distinguished (Minke, Hochstein & Hillman, 1973; Järvilehto, 1979); i.e. the early receptor potential (ERP),
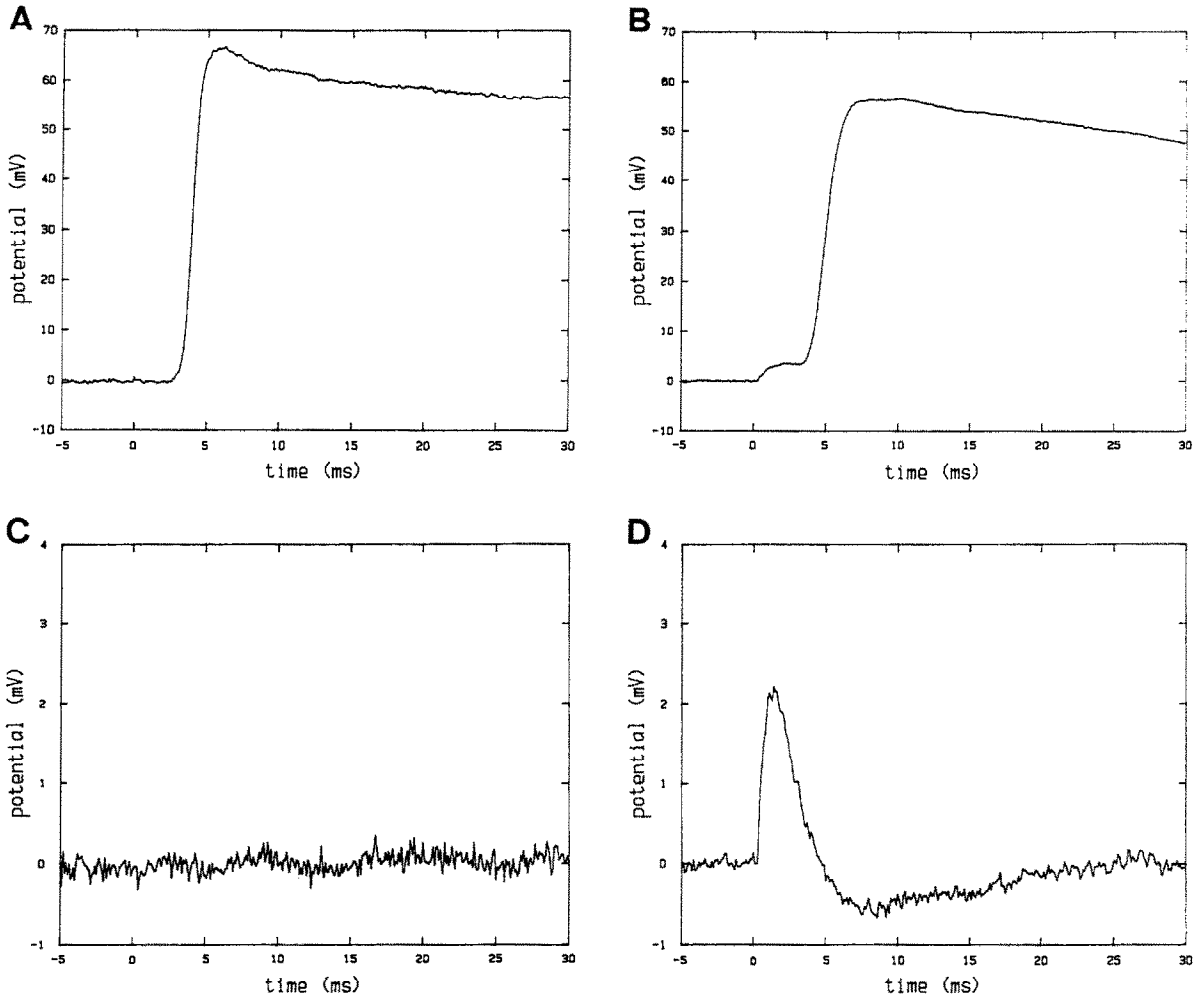
Fig. 2. Membrane potential of a photoreceptor cell after an intense flash of light is given at $t = 0$. (A) Cell red adapted, blue flash. An LRP is recorded and no ERP component is seen when converting P to M. (B) Cell blue adapted, orange red flash. Prior to the LRP a small depolarizing potential, an ERP component, is recorded without a detectable delay, when converting M to P. In (C) and (D) the fly has been anaesthetized with nitrogen to abolish the LRP, while the other conditions where similar as in (A) and (B). (C) No ERP is detected when converting P to M. (D) In addition to the positive ERP phase, a second negative phase is recorded when converting M to P. This second negative phase is under normal conditions masked by the LRP (see B).

resulting from charge movements accompanying visual pigment transformations, and the late receptor potential (LRP), being the product of the phototransduction process, which is triggered by conversion of the native visual pigment only.

Figure 2A shows the receptor potential in a red-adapted cell (i.e. having $\approx 100\%$ P), induced by an intense blue flash. The flash intensity was sufficiently high to convert a large proportion of the visual pigment molecules, thus causing a saturating LRP. In Fig. 2B the cell was blue adapted (i.e. having $\approx 70\%$ M) and illuminated with an orange-red flash. The flash intensity was high, and therefore of the present P molecules

($\approx 30\%$) a sufficient number was converted to create also a fully saturating LRP. However, a distinct foot, the ERP, due to the conversion of a large number of M molecules, precedes the LRP in this case. A subsequent orange-red flash induced a similar, saturating LRP but the initial foot was lacking, proving the successful conversion of the large majority of M into P by the first flash (not shown).

Isolation of the ERP by anoxia

The LRP can be abolished reversibly by anoxia, e.g. by nitrogen (Payne, 1981), whereas the ERP is preserved (Rodieck, 1973). Figure 2C shows that under anoxia the signal,

Table 1. ERP simulation values for the 5 and 3 parameter fit, together with mean and standard deviations for 13 recorded cells. $\tau_f = 1/a_1$: the flash time constant (msec). $\tau_c = 1/a_2$: the cell time constant (msec). $\tau_N = 1/a_3$: the time constant (msec) of the transition of N to P (see Fig. 1). a_4: a scaling factor. B: the charge transfer ratio during the transition of N to P and of M to N

Cells	5 Parameter fit					3 Parameter fit		
	τ_f (msec)	τ_c (msec)	τ_N (msec)	a_4	B	τ_c (msec)	a_4	B
ERP 0803	0.74	2.66	8.13	4.27	1.51	2.00	4.71	1.78
ERP 0806	0.74	1.73	6.98	5.24	1.36	1.25	5.97	1.68
ERP 1102	1.11	2.05	10.77	4.05	1.22	2.48	3.37	1.28
ERP 1202	0.90	4.49	3.76	4.27	1.05	2.19	4.36	1.37
ERP 1205	0.68	2.93	5.11	3.91	1.07	1.63	4.71	1.33
ERP 1209	1.00	1.40	3.89	4.57	1.08	0.98	4.43	1.45
ERP 1212	0.97	3.10	3.15	3.18	0.93	1.65	3.14	1.09
ERP 1215	0.81	2.49	7.34	5.00	1.28	2.00	5.50	1.10
ERP 2004	0.56	3.30	5.81	3.15	1.19	1.75	4.02	1.49
ERP 2009	0.54	3.73	4.10	2.28	1.16	1.47	3.06	1.58
ERP 2011	0.87	1.88	4.71	2.31	1.18	1.24	2.46	1.59
ERP 2015	1.17	1.20	6.09	2.67	1.30	1.26	2.16	1.66
ERP 2701	1.10	2.50	5.32	2.68	0.99	2.09	2.38	1.19
Mean	0.86	2.57	5.78	3.66	1.18	1.69	3.87	1.43
Standard deviation	0.20	0.91	2.03	0.97	0.15	0.42	1.16	0.22

elicited in a red-adapted cell by a bright blue flash, is negligible with respect to the noise, confirming the conclusion of e.g. Minke and Kirschfeld (1980), that in the fly the ERP of the P to M conversion is silent. The ERP of the reverse conversion, also under anoxia, is presented in Fig. 2D. It now appears that the initial depolarization, already noticeable in Fig. 2B, is followed by a hyperpolarization. The first phase lasts about 5 msec and the second one about 25 msec. Clearly, under normal conditions the second phase will be swamped by the LRP.

Modeling the ERP

We have quantitatively modeled the ERP measurements, like that of Fig. 2D, with equation (2) of the ERP model. Of the five parameters in equation (2) two are known rather accurately: the time constant of the flash ($\tau_f = 1/a_1 = 0.8$ msec) and that of the last intermediate ($\tau_N = 1/a_3 = 13$ msec; Roebroek et al., 1989). Accordingly, we have conducted two series of fit procedures on 13 ERP recordings. In the first series, all five parameters were fitted: a_1, a_2, a_3, a_4 and B. In the second series, parameters a_1 and a_3 were fixed to their known values, and fitting proceeded on three parameters: a_2, a_4 and B. Note that parameter a_4 is just a scaling factor in both fit procedures. The reason for conducting also the first series of fits, even if a_1 and a_3 were known, was to appraise the predicting power of the model on known parameters and to compare both series of fit parameters.

The fit parameters for the two series are given in Table 1 together with the mean values and

standard deviations. The fits with 5 parameters were excellent in all 13 cells (exemplified by the continuous curve in Fig. 3), while the fits with three parameters, also perfect for all cells in the positive phase, show a small, systematic deviation in the negative phase (Fig. 3, dashed curve). The fits are still quite acceptable, however. The value for the flash time constant following from the 5 parameter fits, 0.86 msec, corresponds well with the value determined photometrically: 0.8 msec.

The ERP in the presence of the LRP

The first, positive phase of the ERP measured in the unanaesthetized fly is larger than the corresponding wave of the ERP recorded under anoxia. Figure 4 shows the three parameter fits (with $\tau_f = 1/a_1 = 0.8$ msec and $\tau_N = 1/a_3 = 13$ msec) at the experimental curves of Fig. 1B and 1D. In the case of the receptor potential of Fig. 2B only the first phase can be fitted, of course, since the LRP is taking over after about 2 msec. The resulting value for the cell time constant is $\tau_c = 1/a_2 = 7.0$ msec, distinctly larger than the 1.7 msec calculated for the ERP under anoxia.

DISCUSSION

A biphasic ERP is measured in blowfly photoreceptor cells under anoxia when visual pigment molecules are massively converted from the metaxanthopsin (M) to the xanthopsin (P) state. Previous studies (Minke & Kirschfeld, 1980; Stephenson & Pak, 1980) concluded to a
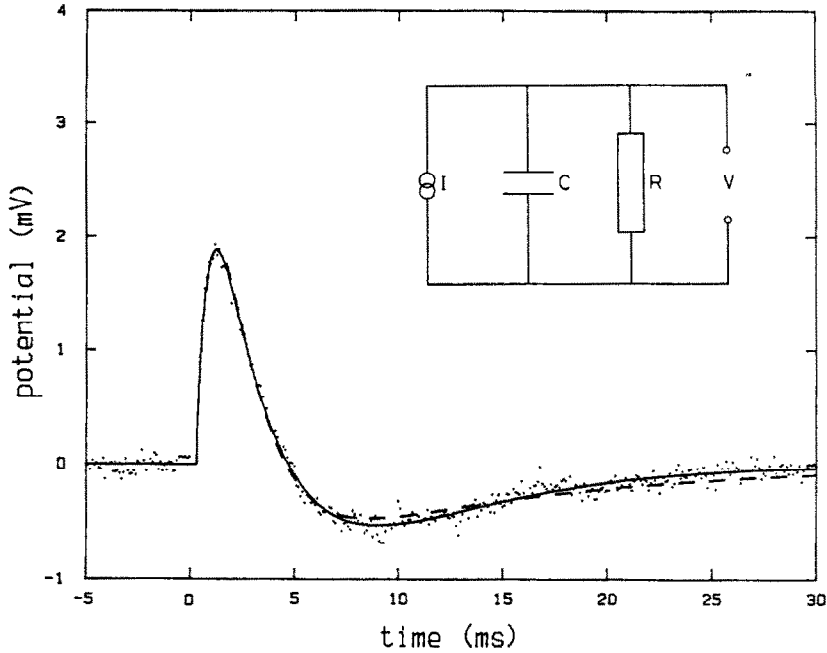
Fig. 3. Modeling of the recorded ERP (dots) with a simple RC-circuit as shown in the inset. For an explanation of the model, see text. The continuous curve, which fits the data almost perfectly, is a fit of equation (2) with five parameters (see Table 1, cell ERP 2004). The dashed curve is a fit of equation (2) with three parameters (see Table 1, cell ERP 2004); two parameters were fixed to their known value ($\tau_f = 0.8$ msec and $\tau_N = 13$ msec). It can be seen that the positive phase is also very well fitted, but that the negative phase slightly lags behind the recorded potential.
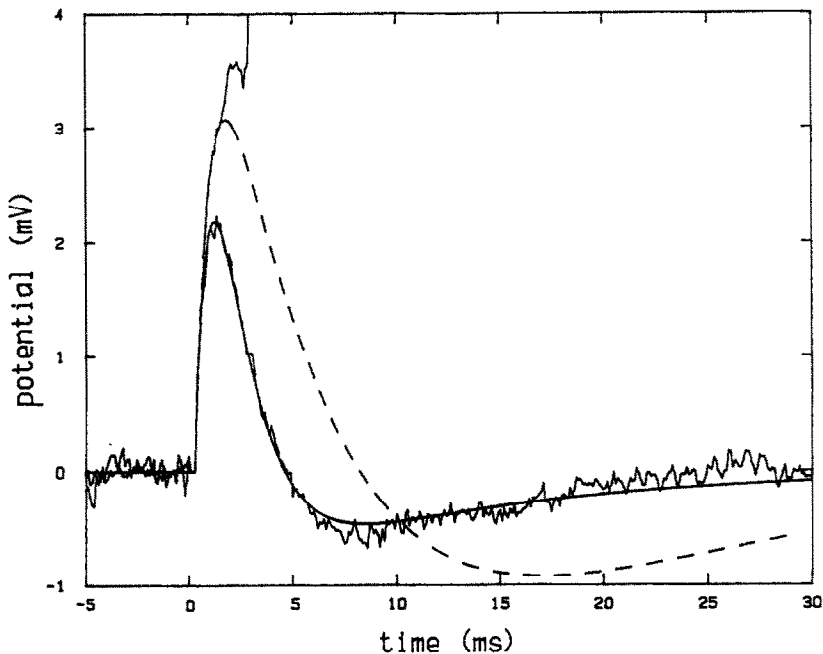

Fig. 4. Reconstruction of an ERP in the presence of an LRP. The noisy curve is the ERP, recorded when the LRP is abolished with nitrogen, and the continuous curve is a best fit with three parameters (see Table 1, cell ERP 1205). The ERP of the unanaesthetized fly has been superposed on the ERP measured under anaesthesia. In this case, only the beginning of the signal is seen because the large LRP response, superposed on the ERP, is out of range of the scaled Y-axis. A fit of this ERP (first 2 msec) was performed with all previous parameters, except the cell time constant, fixed. The best fit predicts a cell time constant of 7 msec: the normal value for a dark adapted, unanaesthetized photoreceptor. The dashed line is the predicted normal ERP, which would be seen provided the cell time constant remains unchanged and the ERP were not masked by the LRP.

monophasic ERP for this transition. However, close inspection of the published records (e.g. Fig. 8a in Stephenson & Pak, 1980) shows that they contain clear signs of a biphasic shape, as in Fig. 2D.

The measurements can be well modeled with the simple model of Hodgkin and O'Bryan (1977) for the ERP of turtle cones. This strengthens the view that the ERPs of vertebrate and invertebrate photoreceptors have an identical origin, namely that they are the result of charge movements across the photoreceptor membrane, which acts as a parallel RC-circuit. The amount of charge transferred by a single photoisomerization can be calculated from the obtained values of a_4 and B (Table 1). Taking $C = 230\,\text{pF}$ ($\tau_c = 7\,\text{msec}$ and $R = 30\,\text{M}\Omega$; Van Hateren, 1986), and from Hamdorf (1979) that a photoreceptor contains 2.5×10^8 visual pigment molecules, or $N_0 = 0.7 \times 2.5 \times 10^8$, we obtain, with $a_4 = 3.77\,\text{mV}$ (Table 1, average of 3 and 5 parameter fit) that $K = a_4 C/N_0 = 5.0 \times 10^{-21}\text{C}$. In other words, the "instantaneous" conversion of a visual pigment molecule from the M- to the N-state moves effectively 0.03 electron charges across the membrane. The value for the charge transfer ratio $B = 1.3$ (Table 1, average of 3 and 5 parameter fit) yields that N to P conversion induces an opposite movement of 0.04 electron charges. Comparable values were found for the visual pigment systems in other photoreceptor membranes (Rüppel & Hagins, 1973; Hodgkin & O'Bryan, 1977; Lisman & Bering, 1977).

The time constant ($\tau_c = 1/a_2$), of a dark adapted photoreceptor is 5–8 msec (Van Hateren, 1986). The three parameter fit to the initial phase of the early receptor potential measured in the unanaesthetized fly (Figs 2B and 4) yielded a comparable value of 7 msec. Anoxia, however, causes a substantial drop in membrane resistance and a large shift in resting potential of about 30 mV (Payne, 1981). Hence the decrease of the cell time constant by more than a factor of 2 in cells under anoxia, resulting in a similar and more rapid first phase of the ERP.

Roebroek et al. (1989) determined in wild type *Calliphora* that the time constant of the last intermediate τ_N is 13 msec, whereas a value of 5.8 msec was obtained in the model calculations with a five parameter fit to the ERP data measured in the white eyed mutant chalky. It seems unlikely that such a difference would exist in the reaction time of the last intermediate

between wild type and chalky *Calliphora*. Possibly, the thermal decay of intermediate N to P depends on the strength of the electric field across the membrane, which changes when the fly is anaesthetized with nitrogen.

In the P to M pathway all intermediates decay with a time constant much shorter than that of the cell (see Fig. 1). The generated ERP then can be regarded to be the effect of an instantaneous charge movement (a δ-function current source), proportional to $(1 - B)$. All our experimental recordings of the ERP for the conversion P to M were silent, in agreement with Pak and Lidington (1974), Stephenson and Pak (1980) and Minke and Kirschfeld (1980). This indicates that the net charge movement is negligible, i.e. the charge transfer ratio $B \approx 1$. The 5 parameter fit for the cells of Table 1 shows indeed that in a few cases B is approximately equal to 1. However, calculating the ERP with the average value for B, i.e. $B = 1.18$, yields a monophasic positive signal with amplitude 0.3 mV, which is well distinguishable from the noise as measured in Fig. 2C. The same calculation with the data from the 3 parameter fit yield an average ERP amplitude of 0.6 mV.

We conclude that by applying the simple RC-model of Hodgkin and O'Bryan (1977) we have largely, but not completely, resolved the longstanding enigma of the ERP in fly photoreceptor cells. Presumably a full quantitative description of the fly ERP requires a more detailed electrical model of the photoreceptor. The monophasic positive ERP when M is converted to P actually appeared to be a biphasic ERP, and this notion triggered the discovery of a slowly decaying intermediate N (Roebroek et al., 1989). The study of the ERP thus is helpful in revealing steps in the visual pigment cycle and, because it can serve to determine membrane parameters (Rüppel & Hagins, 1973; Hardie, 1985), the ERP can be a valuable tool in the study of photoreceptor properties and function.

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