Biophys Struct Mech (1983) 10: 129–142

Biophysics of Structure and Mechanism

Voltage Noise in Honeybee Drone Photoreceptors

M. Ferraro[1], R. Levi[2], D. Lovisolo[2], and M. Vadacchino[3]

[1] Istituto di Fisiologia Veterinaria, Università di Torino, V. le Mattioli, 25, Torino, Italia
[2] Istituto di Fisiologia Generale, Università di Torino, C. so Raffaello, 30, Torino, Italia
[3] Dipartimento di Fisica, Politecnico di Torino, C. Duca degli Abruzzi, 24, Torino, Italia

Abstract. Voltage noise analysis was performed on membrane potentials recorded from the photoreceptor cells of the honeybee drone. Voltage power spectra showed an increase in noise amplitude on passing from the dark to moderate light; with strong light noise fell to near the dark level.

At intermediate light intensities the noise was reduced by application of tetrodotoxin.

The probable effects on the power spectra of electrical coupling between cells are discussed. It is tentatively estimated that the unitary event in weak light is a conductance increase of 20 pS. The results are compared with previous results from photoreceptors of other species that appear to be specially adapted to weaker illuminations.

Key words: Photoreceptor noise – Phototransduction – Tetrodotoxin

Introduction

It is known that, at low light intensities, the photoreceptors of several invertebrates show discrete responses to single photons (quantum bumps; see e.g., Laughlin 1981). At higher intensities the bumps summate to produce a sustained, more or less noisy response.

The photoreceptors of the honeybee drone are less sensitive to weak light than most invertebrate photoreceptors in which noise has been examined. This might be expected on evolutionary grounds, since the main activity of the drone that is subject to evolutionary pressure is the pursuit of the queen during the nuptial flight, which takes place in bright sunlight. In the drone, the quantum bumps are too small to be examined individually. Consequently, we analysed the voltage noise at different light intensities in an attempt to deduce properties of the unitary event.

The six large photoreceptors of the drone ommatidium are electrically coupled (Shaw 1969), and the complications that this introduces are discussed.

Methods

Heads of honeybee drones (*Apis mellifera*) were cut and dissected by a section perpendicular to the cornea, according to the technique described by Baumann (1968), in order to expose the retinula cells along their longitudinal axis. The two halves of each head were fixed in a small Perspex chamber and perfused with an oxygenated physiological solution of the following composition: (mM/l) Na^+, 280; K^+, 3.2; Ca^{2+}, 1.8; Cl^-, 287; *Tris* HCl, 9; Glucose, 10 (Bader et al. 1976); pH was 7.3 ± 0.1; all experiments were performed at temperatures between 21° and 23° C.

Receptor potentials were recorded intracellularly by means of glass microelectrodes, filled with 2.5 M KCl, that had resistances between 20 and 40 M Ω. In most of the experiments, electrodes were then beveled according to a simplified version of the procedure developed by, among others, Brown and Flaming (1974). The electrode was brought into contact with a wet surface of abrasive alumina powder (Ialta, Torino, Italy) until the resistance dropped to 7–15 M Ω. Voltage signals were picked up by an M707 Electrometer Amplifier (WPI Instr. Inc., New Haven, CT, USA), then amplified and stored on magnetic tape on a Hewlett Packard 3964A recorder. In order to perform noise analysis, signals were sent to an AC-coupled amplifier. Attenuation caused by this amplifier was about 5% at 5 Hz and less than 2% at 10 Hz; for this reason, spectra were plotted between 5 and 500 Hz. Noise analysis was performed using a Nicolet Sc. Instr. Ubiquitous FFT Analyzer, which, among other functions, gave the power spectrum and the autocovariance function of the signal. Analysis was performed up to 500 Hz, because tests with spectra extending up to 1,000 Hz gave no significant differences.

Light stimulation was obtained by focusing a 100-W halogen lamp on a 2-mm-diameter spot of the dissected eye. Unattenuated irradiance of the white light source at the eye surface was 22.6 mW. At the sensitivity peak for the drone photoreceptor, 450 nm (obtained inserting an interference filter of half-peak bandwith 15 nm), this corresponded to 2.2×10^{15} photons/cm^2/s. A Uniblitz shutter (Vincent Assoc., USA) driven by a Digit 3T Signal generator (Romagnoli, Livorno, Italy) modulated the light beam. Stimuli were usually of 90-s duration, in order to obtain responses long enough for the Nicolet analyzer to perform a high number of averages (70-s stretches were enough for obtaining spectra based on 150 averages). Unattenuated light stimuli elicited responses near the saturation level; neutral density filters (Kodak Wratten) were used to attenuate the stimulus.

Analysis was started after the first 10–20 s of response, discarding the fast transient and the subsequent, slower drifts.

Results

Intracellular recordings obtained in darkness and with stimulation of the eye, bathed in normal physiological solution, with 90-s lights of different intensities are shown in Fig. 1A, while Fig. 1B shows stretches from the same recordings at a higher amplification. In Fig. 2 the power spectra obtained from the same experiment as in Fig. 1 are shown. (The bottom trace in Fig. 2D is instrument noise.)

Even from a qualitative observation, some distinctive features can be noted:

1. Since the area under each spectrum gives the noise amplitude, it can be seen that the noise amplitude reaches a maximum at intermediate light intensities (Log $I = -1.8$), while at the strongest light intensity the noise level is reduced.

2. While in most biological membranes resting noise has a $1/f$ slope (Neher and Stevens 1977), in all the cells investigated in this study the slope of the high-frequency side was somewhat steeper, about $1/f^2$ (see Fig. 2).

3. At intermediate light intensities (and sometimes also at high ones) a pronounced peak appears in the spectra; it shows a close similarity to those seen in the voltage spectra of the squid axon by Wanke et al. (1974).

We changed the bath by adding 10^{-5} g/l tetrodotoxin (TTX), a drug that abolishes the initial spike, but affects neither the amplitude nor the shape of the receptor potential itself (Baumann 1968). As can be observed in Fig. 3, in solutions containing TTX the peak at intermediate intensities was abolished. In the dark and with full light, no major differences could be observed between cells bathed in normal solution and in a solution containing TTX; only an

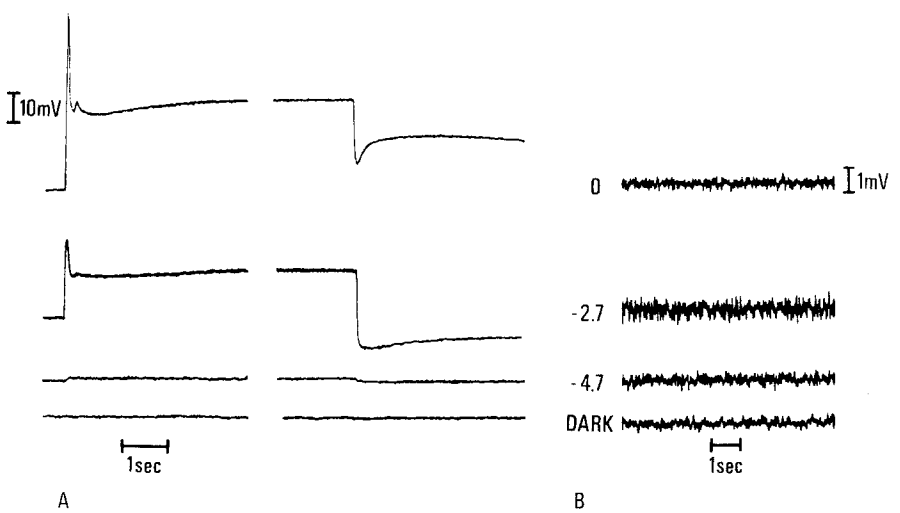

Fig. 1. A Intracellular recordings of receptor potentials obtained with light of different intensities. Bottom trace is membrane resting potential. **B** The same recordings as in **A** shown at higher amplification. Numbers indicate log of relative light intensity

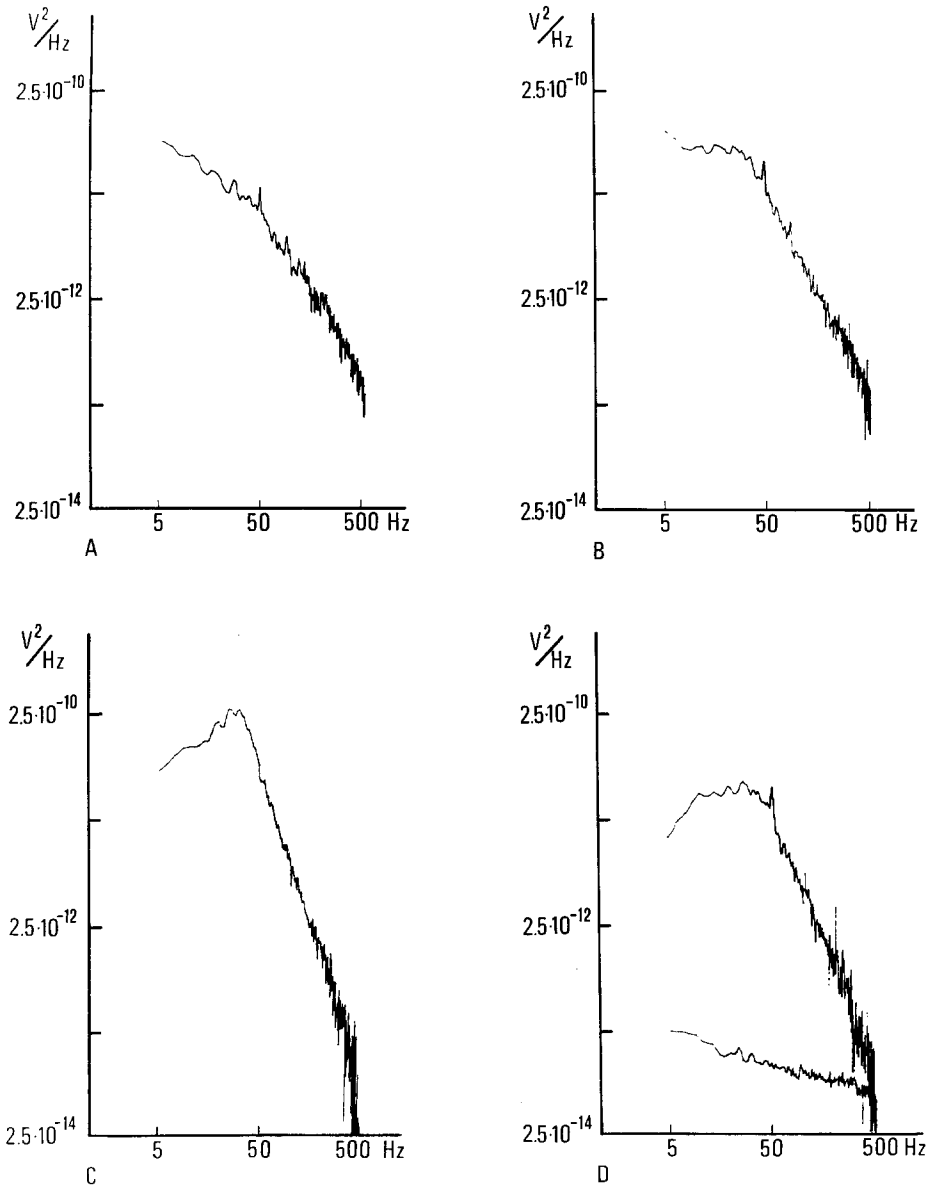

Fig. 2A–D. Noise power spectra from the same cell as in Fig. 1. **A:** dark. **B:** Log $I = -4.7$. **C:** Log $I = -1.8$. **D:** Log $I = 0$. Bottom trace in **D** is instrument noise recorded with the electrode in the bath

increase in the high-frequency slope was observed, particularly in dark-adapted conditions (see below).

The presence of a noise component abolished by TTX (TTX-dependent noise) and the change in the shape of the spectra are in agreement with data in the literature (Baumann 1968, 1975), which indicate that the mechanism of

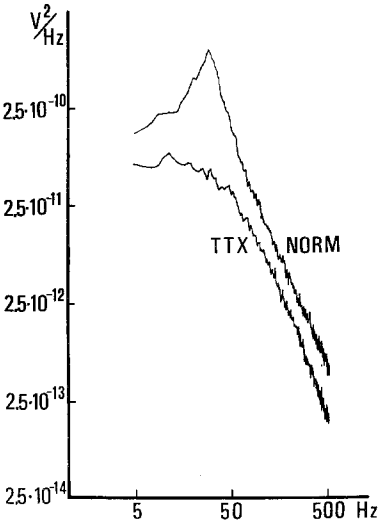

Fig. 3. Power spectra from the same cell bathed in normal solution and in a solution containing TTX. Log $I = -2.7$

generation of the single spike in the drone photoreceptor is of the same kind as that of the nerve action potential. The noise that remains in TTX-containing solutions (TTX-independent noise) can be ascribed to the fluctuations of the light modulated channels and of any other channels not blocked by TTX, that may be present in the photoreceptor membrane. The subsequent analyses of the changes in noise with light have been performed on this component, which was obtained from cells bathed in solutions containing TTX.

Quantitative Analysis of Light-Induced Noise

Of the approximately 20 cells that gave stable and successful recordings in solutions containing TTX, seven were selected for which noise was recorded at several different light intensities. Table 1 shows the values of the steady-state depolarization, V, and of the variance at different light intensities, σ^2, and in the dark, σ_D^2. The bottom row of Table 1B shows instrument noise variance, σ_I^2. Variance was calculated taking the value of the autocovariance function at $t = 0$.

Unlike the observations that have been made in other invertebrate photoreceptors (Smola 1976; Wu and Pak 1978; Payne 1980, 1981), it can be seen that the difference between noise recorded in the dark and that recorded in the presence of light is not large enough to allow us to consider the dark noise as negligible. It is not that dark noise levels in the drone photoreceptor are higher than those reported for other preparations, but noise recorded in the presence of light is generally lower, as can be seen comparing Table 1 with data from the authors cited above. This could be expected on the grounds of the functional properties of this photoreceptor, which is adapted to work in bright light (see Introduction).

Table 1. *A. Steady-state depolarization, V* [mV]

Cell	Log *I*					
	− 4.7	− 3.7	− 2.7	− 1.8	− 0.8	0
1	2	8.5	21	24	29	29.5
2	2	10	20	30	39	40
3	2	11	20	32	36	36
4	1	5.5	11.5	26	31	33
5	2.5		10	14		21
6	0.5		9	15	20	23
7		4	11	20	23	28
Mean (± SE)	1.6	7.8	14.6	23.0	29.7	30.1
	± 0.3	± 1.3	± 2.0	± 2.6	± 3.0	± 2.6

B. Variance, σ^2 [10^{-8} V^2]

Cell	Log *I*							
	− 4.7	− 3.7	− 2.7	− 1.8	− 0.8	0	σ^2_{dark}	σ_i^2
1	0.98	2.50	1.98	1.35	0.73	1.18	0.73	0.27
2	1.60	3.84	2.48	1.90	1.52	1.53	0.86	0.27
3	2.44	4.15	2.54	1.81	1.48	1.28	1.41	0.61
4	1.25	2.02	2.16	1.98	1.48	1.38	0.82	0.61
5	1.90		3.50	3.27		1.61	0.90	0.26
6	0.27	0.84	1.24	0.95	0.62	0.39	0.27	0.06
7	0.75	1.11	1.70	1.18	1.23	0.42	0.26	0.05
Mean of $(\sigma^2-\sigma_i^2)$	1.00	2.10	1.92	1.47	0.86	0.79	0.43	
(± SE)	± 0.22	± 0.50	± 0.25	± 0.27	± 0.13	± 0.14	± 0.09	

The low level of noise in these cells, however, has some drawbacks. It is not possible to neglect dark noise as one of the components of the recorded noise, nor is it generally possible to subtract it from the noise observed at different light intensities, as some authors have done (e.g., Wu and Pak 1978).

In the drone, the six large photoreceptor cells in each ommatidium are electrically coupled, and the effect of the coupling, which is strong in the dark, is considerably reduced by strong light (Shaw 1969). The contribution of the noise component observed in the dark must change with light intensity, because of the change in the input resistance of the membrane, and cannot be regarded as a constant. Hence, it is not possible to separate noise induced by light from the spontaneous component, particularly at high light intensities. For this reason, our analysis could only be applied, for the complete range of light intensities used, to TTX-insensitive noise as a whole (but the case for low light intensities will be treated in more detail below).

Only instrument noise has been subtracted from the recorded noise. In Fig. 4, the mean values (± SE) of $\sigma^2-\sigma_i^2$ from the cells of Table 1 are plotted as a

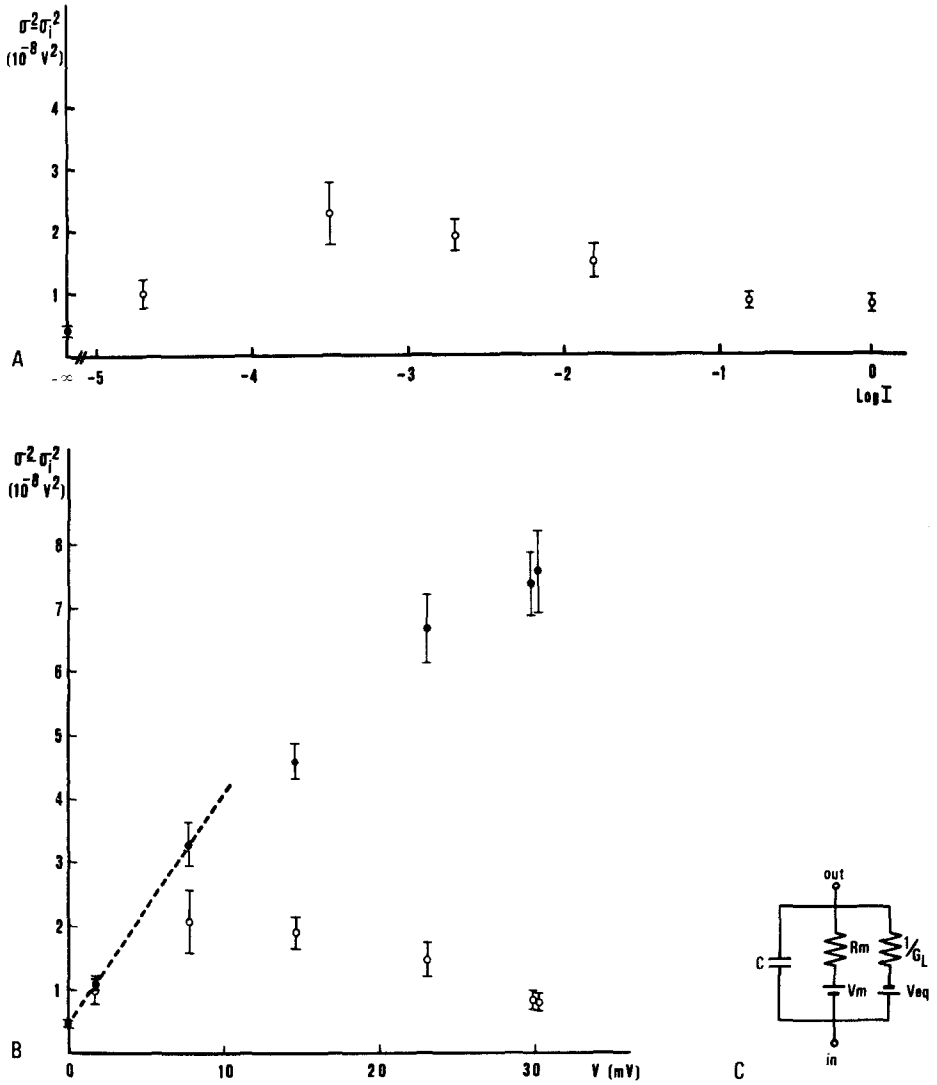

Fig. 4. A Difference between recorded noise and instrument noise variances as a function of log of relative light intensity. Mean and SE of seven cells. **B** The same data as in **A** plotted as a function of steady-state depolarization, V. *Filled circles* (± SE) are the result of Martin's correction (Eq. 1). *Dotted line* through the first three points is a regression line $y = a + bx$ with $a = 0.435 \cdot 10^{-8}\ V^2$, $b = 3.7 \cdot 10^{-6}$ V ($r^2 = 1$). **C** Equivalent circuit of the photoreceptor membrane adopted for Martin's correction. V_m = membrane resting potential; V_{eq} = equilibrium potential for light-induced current; R_m = membrane passive resistance; G_L = light activated conductance

function of the log of relative light intensity (Fig. 4A) and of the mean steady-state depolarization, V (Fig. 4B).

It can be seen that the noise reaches a maximum around Log $I = -3.7$, and that at the highest light intensity it is only slightly above the level of spontaneous noise. This finding is consistent with a self-shunting model for the receptor

membrane (Martin 1955; Katz and Miledi 1972). Due to the increase in membrane conductance, induced in our case by light through an increase in G_L, variations in voltage do not bear a constant relation to the variations in conductance. According to Fig. 4C variance will be related to depolarization, V, by the following equation (Katz and Miledi 1972):

$$\sigma^2 = \left[\frac{V_D - V}{V_D}\right]^3 \cdot V \cdot h\,, \tag{1}$$

where $V_D = V_{eq} - V_m$ has been taken as +58 mV, the average of the resting potential of the cells of Table 1 with changed sign, because the peak of the transient depolarization is close to the zero potential value, and h is the mean amplitude of the unitary event. If the measured noise variance is multiplied by the correction factor $[V_D/(V_D - V)]^3$, then noise should increase linearly with voltage. The filled circles in Fig. 4B are the results of this correction for our data; bars are errors calculated taking into account also the error implied in the correction. All the points could not be reasonably fitted by a single straight line, as some saturation in the noise appears for higher depolarizations. However, a straight line can be drawn through the first three points, corresponding to the resting potential and to the depolarization induced by the two lowest light intensities (see Fig. 4B). The slope of the regression line gives an evaluation of the magnitude of h, the amplitude of the elementary event; from Fig. 4B one obtains $h = 3.7 \times 10^{-6}$ V. From this value, an estimate of elementary event conductance change, δg, can be derived from the relationship: $\delta g \cdot R_m = h/V_D$ (Martin 1955), with $R_m = 3.10^6\ \Omega$ (Shaw 1969; Baumann and Hadjilazaro 1971). The resulting value for δg is 20 pS.

It must be remembered, however, that Martin's correction and the underlying model of Fig. 4C are oversimplifications, for they take into account neither the cable properties of the cell nor possible membrane electrical nonlinearities. Moreover, for events as short as the membrane time constant (as will be shown to be the case for the drone, at least partially), Stevens (1976) has pointed out that Martin's correction leads to an overcorrection. The correct relationship between noise and steady-state depolarization would then lie between the two curves, the experimental and the corrected one.

Spectral Analysis: Spontaneous Noise

For the seven cells examined above, difference power spectra were obtained by subtracting the spectrum of the noise of the electrode in the bath from the spectra recorded from the cell bathed in a TTX-containing solution. Figure 5 shows a spectrum recorded in a dark-adapted cell. The slope of these spectra was about $1/f^3$, whereas in dark-adapted cells bathed in normal solution the slope was usually $1/f^2$ (see above, Fig. 2A). We could not decide whether this was actually due to an effect of TTX on the slope of the spectra recorded from dark-adapted cells, or if it was an artifact due to different degrees of dark adaptation. In any

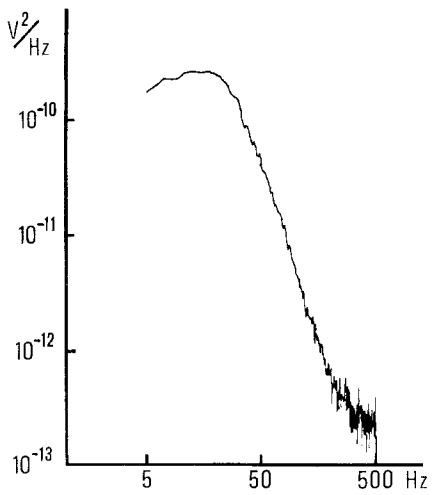

Fig. 5. Power spectrum of TTX-insensitive noise in a dark-adapted cell

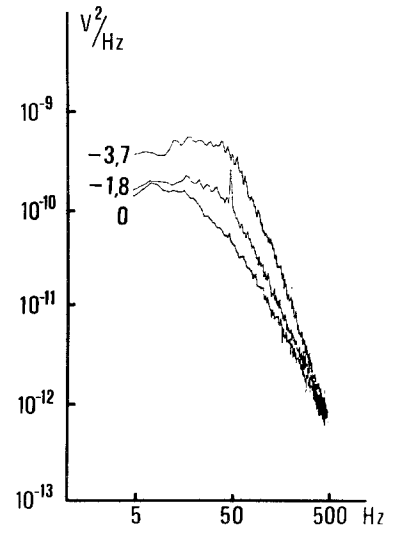

Fig. 6. Power spectra of TTX-insensitive noise from the same cell at different light intensities. Numbers on the left are log of relative light intensity

case, this rather high slope for a resting noise could not lead to quantitative interpretations, again because of the electrical coupling between the photoreceptor cells, which, acting as a low-pass filter, might change the shape and amplitude of the spectra.

Change of Noise with Light

For the reasons outlined above, only a qualitative analysis of the spectra and the way they change throughout the whole range of light intensities used can be performed. From Fig. 6 it can be observed that the slope of the high frequency

side falls from about $1/f^3-1/f^4$ at low light intensities to about $1/f^2$ with strong lights, in agreement with the findings of Payne (1980, 1981) on locust photoreceptors. He ascribed this effect either to the shunting of the cell's input resistance by the light-induced conductance increase [as the membrane impedance falls below 1 M Ω for strong light intensities (Shaw 1969) its filtering characteristics no longer influence the voltage spectra, which become simple Lorentzians] or to the adaptation of the underlying current events (see also Wong and Knight 1980).

Neither of these suggestions could be tested in our case, but some more detailed observations can be made on spectra obtained at the lower light intensities (Log $I = -3.7$, Log $I = -4.7$). With these lights, giving responses within or near the linear range, the electrical coupling between the photoreceptor cells in an ommatidium can be assumed to be constant, and the spectrum in the dark can be subtracted from the spectra recorded at these intensities. The result can be regarded as representing the contribution of light-induced noise (either directly, through the fluctuations of light-modulated channels, or indirectly, through possible voltage-dependent channels activated by the depolarization induced by light).

Figure 7 shows two spectra obtained from the same cell by subtracting the noise recorded in the dark from that recorded at Log $I = -4.7$ (Fig. 7A) and at Log $I = -3.7$ (Fig. 7B). The slope is again between $1/f^3$ and $1/f^4$. Spectra with a slope like that shown in Fig. 7 could be fitted by a product of two Lorentzian

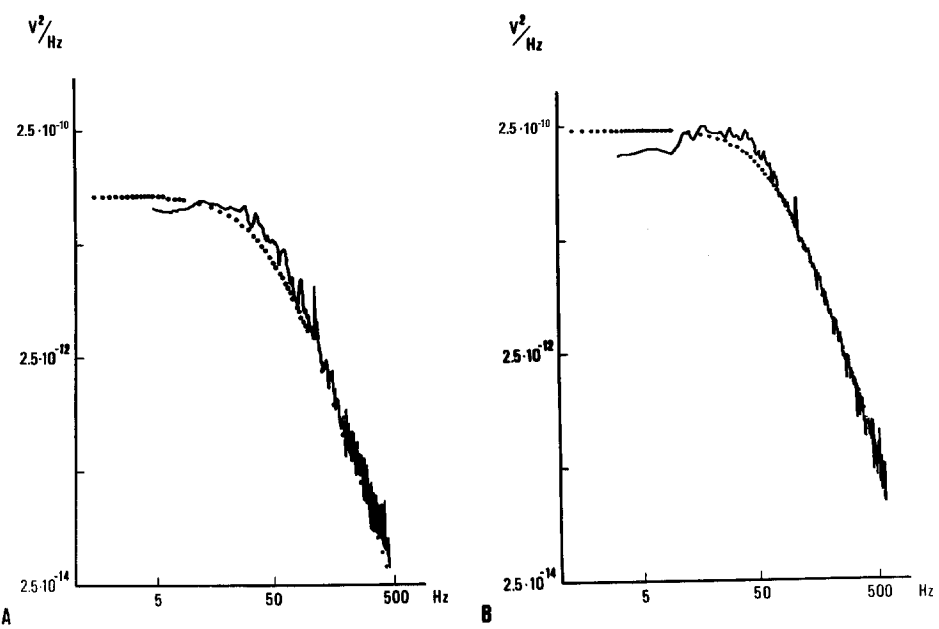

Fig. 7A and B. Power spectra obtained by subtracting the spectrum recorded in the dark from those recorded at two low light intensities in the same cell. *Dotted lines* are drawn in accordance with Eq. (7). **A.** Log $I = -4.7$; $R_mC = 2.2$ ms; $\tau = 4.5$ ms. **B.** Log $I = -3.7$; $R_mC = 2.2$ ms; $\tau = 2.7$ ms

functions, and this can lead to a phenomenological approach to the explanation of their features, under some simplifying assumptions:
1. Voltage noise spectra are related to current noise spectra by the following equation (Bendat and Piersol 1971; Stevens 1972):

$$S_V(f) = S_I(f) \cdot |Z(f)|^2, \tag{2}$$

where $Z(f)$ is the membrane complex impedance.
2. Using the model of Fig. 4C:

$$|Z(f)|^2 = \frac{R_m^2}{1 + (2\pi R_m C f)^2}. \tag{3}$$

Instead of using R_m as the membrane resistance in Eq. (3), one should also take into account the contribution of the light-induced conductance, G_L; but for low light intensities, like those used to obtain these spectra, G_L is still very small, so the difference is not significant.
3. The current noise spectrum has a Lorentzian shape with a time constant, τ, of the same order of magnitude as the membrane time constant, R_mC. A simple physical model that produces a Lorentzian spectrum is a source of identical, random and uncorrelated events, each of them defined as a conductance change of exponential shape:

$$g(t) = \delta g \cdot e^{-t/\tau}. \tag{4}$$

This in turn gives rise to a current event:

$$i(t) = V_D \cdot g(t) = \delta i \cdot e^{-t/\tau}, \tag{5}$$

where $\delta i = V_D \cdot \delta g$.
The current spectrum will then be given by (De Felice 1981):

$$S_I(f) = \frac{n\delta i^2 \tau^2}{1 + (2\pi f\tau)^2}, \tag{6}$$

where n is the frequency of events; from Eqs. (2, 3, and 6) the voltage spectrum will be:

$$S_V(f) = \frac{S_V(0)}{[1 + (2\pi f\tau)^2] \cdot [1 + (2\pi R_m C f)^2]}, \tag{7}$$

with $S_V(0) = n \cdot \delta i^2 \tau^2 R_m^2$.

We fitted our experimental spectra with curves obtained from Eq. (7) (see dotted lines in Fig. 7); $S_V(0)$ has been taken considering the zero frequency limit of the experimental spectra; R_mC and τ were fitted by trial and error, starting from values of R_mC around 2.2 ms. Taking $R_m = 3.10^6\ \Omega$ (see above), this would

mean a capacitance of about 0.7 nF. Assuming a specific membrane capacitance of 1 $\mu F/cm^2$, the total surface of the cell would be around 7.10^4 μm^2, a value of the same order of magnitude as that given by Coles and Tsacopoulos (1979) of 4.10^4 μm^2.

Fitting on four cells gave a mean value for τ of 6.6 ± 1 ms at Log $I = -4.7$ and of 3.87 ± 0.77 ms at Log $I = -3.7$, showing a decrease in single event duration even with slight increases in light intensity. Considering that the average depolarization is given by $V = I \cdot R_m$, where I, the average inward current is related to δi by $I = n \cdot \int_0^\infty \delta i \cdot e^{-t/\tau} = n \cdot \delta i \cdot \tau$, one obtains $V = n \cdot \delta i \cdot \tau \cdot R_m$; from this and the definition of $S_V(0)$, n can be derived:

$$n = \frac{V^2}{S_V(0)}. \tag{8}$$

For the four cells fitted, one obtains $n = 5.8 \pm 1.8 \cdot 10^4\ s^{-1}$ at Log $I = -4.7$ and $n = 5.4 \pm 0.78 \cdot 10^5\ s^{-1}$ at Log $I = -3.7$. In this range, therefore, the rate of events increases linearly with light intensity.

An exponential shape for the unitary event is, however, "arbitrary and indeed, unlikely" as pointed out by Katz and Miledi (1972) and, more recently, by De Felice (1981). An alternative and more plausible model is the "random switch" model, representing a population of channels flipping between an open and a closed state (Neher and Stevens 1977; De Felice 1981). This one also gives a current power spectrum of Lorentzian shape, provided the opening and the closing are independent and Poisson distributed. However, as pointed out by Katz and Miledi (1972), changing the shape of the unitary event would not greatly alter the values obtained for event parameters. If an exponential event is described in terms of amplitude, h', and time constant, τ, the equivalent square event should have an amplitude $h = h'/2$ and a duration $T = 2\tau$.

Discussion

Notwithstanding the limitations of voltage noise analysis and the presence of electrical coupling between the cells, which prevent a fully detailed analysis of our data over the whole range of intensities used, some interesting features of the mechanism that is responsible for the generation of the receptor potential in the photoreceptors of the honeybee drone can be discussed. Voltage noise amplitude (and, consequently, single event voltage amplitude) is considerably lower than those found in most other photoreceptors: one order of magnitude lower than noise in locust photoreceptors (Payne 1980, 1981), two orders lower than in *Limulus* (Wong and Knight 1980). However, the value we obtained for single event conductance change is only slightly below the value given by Payne (1980, 1981), 40 pS for a double exponential shape. This could be due to the fact that the input resistance is lower than in other photoreceptors, particularly because of the electrical coupling between cells in the same ommatidium. Locust photoreceptors are electrically coupled, too, but the coupling is less strong (Shaw 1969).

In general, electrical coupling between photoreceptors tends to increase the signal to noise ratio (e.g., Smola 1976).

At the higher light intensities, noise increases less than proportionally to voltage, even after applying Martin's correction, as some saturation appears for voltage above 10 mV. A similar effect was observed by Payne (1980) on *Locust* photoreceptors treated with anaesthetics for depolarizations above 15 mV. This could mean that single event amplitude decreases at high light intensities, as also found on other invertebrate photoreceptors (Wu and Pak 1978; Dodge et al. 1968; Wong and Knight 1980; Wong et al. 1982).

At low light intensities, at which the contribution of light-induced noise can be isolated, from the fit of the experimental spectra we have shown that the duration of the elementary event decreases with increasing light intensities. This does not confirm the findings of Wu and Pak (1978) for *Drosophila* photoreceptors, but is in agreement with the data on *Limulus* (Dodge et al. 1968; Wong and Knight 1980; Wong et al. 1982). The unitary events in the drone photoreceptors thus appear to adapt, both amplitude and duration being reduced. The linearity of increase of n at low light intensities is a finding common to other invertebrate photoreceptors. It must be noted that the values found in the drone are about two orders of magnitude greater than those reported for *Drosophila* photoreceptors (Wu and Pak 1978) and about three orders greater than those reported for *Limulus* (Wong and Knight 1980; Wong et al. 1982) at comparable depolarizations. From these observations it can be concluded that due to the electrical coupling between cells in the same ommatidium and the smallness of the elementary event, the drone photoreceptor has a better signal to noise ratio than most invertebrate photoreceptors.

Acknowledgements. We wish to thank the research staff of the Materials Department of the National Electrotecnic Institute "G. Ferraris" for their kind permission to use the Nicolet FFT Analyzer and particularly Prof. Piero Mazzetti for his helpful advice and discussion of the results.

References

1. Bader C, Baumann F, Bertrand D (1976) Role of intracellular Ca^{2+} and Na^{2+} in light adaptation in the retina of the honeybee drone. J Gen Physiol 67: 475–491
2. Baumann F (1968) Slow and spike potentials recorded from retinula cells of the honeybee drone in response to light. J Gen Physiol 52: 855–875
3. Baumann F (1975) Electrophysiological properties of the honeybee retina. In: Horridge GA (ed) The compound eye and vision of insects. Clarendon Press, Oxford
4. Baumann F, Hadjilazaro B (1971) A depolarizing aftereffect of intense light in the drone visual receptor. Vision Res 12: 17–31
5. Bendat JS, Piersol AG (1971) Random data: Analysis and measurement procedures. Wiley, New York
6. Brown KT, Flaming DG (1974) Bevelling of fine micropipette electrodes by a rapid precision method. Science 185: 693–695
7. Coles JA, Tsacopoulos M (1979) Potassium activity in photoreceptors, glial cells and extracellular space in the drone retina: changes during photostimulation. J Physiol (Lond) 290: 525–549
8. De Felice LJ (1981) Introduction to membrane noise. Plenum Press, New York London
9. Dodge F, Knight BW, Toyoda J (1968) Voltage noise in *Limulus* visual cells. Science 160: 88–90

10. Katz B, Miledi R (1972) The statistical nature of the acetylcholine potential and its molecular components. J Physiol (Lond) 224: 665–699
11. Laughlin SB (1981) Neural principles in the visual system. In: Autrum H (ed) Handbook of sensory physiology, vol VII/B. Springer, Berlin Heidelberg New York
12. Martin AR (1955) A further study of the statistical composition of the end-plate potential. J Physiol (Lond) 130: 114–122
13. Neher E, Stevens CF (1977) Conductance fluctuations and ionic pores in membranes. Annu Rev Biophys Bioeng 6: 345–381
14. Payne R (1980) Voltage noise accompanying chemically induced depolarization of insect photoreceptors. Biophys Struct Mech 6: 235–251
15. Payne R (1981) Suppression of noise in a photoreceptor by oxydative metabolism. J Comp Physiol 142: 181–188
16. Shaw SR (1969) Interreceptor coupling in ommatidia of drone honeybee and locust compound eyes. Vision Res 9: 999–1029
17. Smola U (1976) Voltage noise in insect visual cells. In: Zettler F, Weiler R (eds) Neural principles in vision. Springer, Berlin Heidelberg New York
18. Stevens CF (1972) Inferences about membrane properties from electrical noise measurements. Biophys J 12: 1028–1047
19. Stevens CF (1976) A comment on Martin's relation. Biophys J 16: 891–895
20. Wanke E, De Felice LJ, Conti F (1974) Voltage noise, current noise and impedance in space clamped squid giant axon. Pfluegers Arch 347: 63–74
21. Wong F, Knight BW (1980) Adapting-bump model for eccentric cells of *Limulus*. J Gen Physiol 76: 539–557
22. Wong F, Knight BW, Dodge FA (1982) Adapting-bump model for ventral photoreceptors of *Limulus*. J Gen Physiol 79: 1089–1113
23. Wu CF, Pak WL (1978) Light induced voltage noise in the photoreceptor of *Drosophila melanogaster*. J Gen Physiol 71: 249–268