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THE DYNAMIC BEHAVIOUR OF PHOTORECEPTOR CELLS IN THE FLY IN RESPONSE TO RANDOM (WHITE NOISE) STIMULATION AT A RANGE OF TEMPERATURES

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SUMMARY

1. Photoreceptor cells in *Calliphora stygia* were stimulated with randomly fluctuating green light while the resulting fluctuations in membrane potential were recorded with intracellular micro-electrodes.

2. Fourier analysis was used to obtain the frequency response functions between the light intensity fluctuations and the membrane potential fluctuations at a range of different temperatures.

3. The results show that for small light fluctuations the transducer function can be modelled by a cascade of five identical linear exponential filters whose time constants decrease as the temperature of the cell is increased.

4. The time constants of the linear filters and their rate of change with temperature are similar to the electrical behaviour of cell membranes. However, a series of chemical reactions with similar activation energies could also explain the observed behaviour.

5. Evidence is presented that the total light response is a linear summation of discrete waves of depolarization (bumps), which become longer in duration but of constant area as the temperature is reduced.

INTRODUCTION

Photon capture in arthropod photoreceptors causes a graded depolarization of the cellular membrane potential. The dynamic, or time varying, behaviour of this response to light has proved difficult to characterize accurately and particularly difficult to interpret in terms of a physical transduction process. The response to a short flash of light is usually a slower wave of depolarization with a peak amplitude significantly delayed from the initial flash. Fuortes & Hodgkin (1964) proposed a model to explain this behaviour in the eye of *Limulus*, having about ten identical resistor-capacitor low pass filters cascaded together with high impedance buffer amplifiers between each stage. This model gives a good approximation to the observed behaviour for small intensity flashes. The model was further examined by Borsellino,

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Fuortes & Smith (1965), who suggested that the effects of temperature upon light transduction could be accounted for if the time constants of the filter elements were functions of temperature. They also suggested that a physical transduction process underlying the model might consist of a series of chemical reactions which were coupled together via products and reactants. A similar model has also been proposed to describe the electrical responses of turtle cones to flashes and steps of light (Baylor, Hodgkin & Lamb, 1974) but in this case only six or seven filter stages were required to explain the experimental observations.

Although most photoreceptors give non-linear responses to large changes in light intensity, their behaviour for small changes in light intensity is very well approximated by linear time-invariant models. Direct evidence for this conclusion has been provided by McCann (1974) and by Eckert & Bishop (1975), who have shown that second order contributions to the response are very small. For a linear system the response to a short flash of light (impulse response function) and the response to a series of sine wave light intensity fluctuations (frequency response function) theoretically contain identical information and are related to each other by the Fourier transform. A number of authors have used the sine wave method to examine the linear behaviour of photoreceptors (DeVoe, 1966; Pinter, 1966, 1972; Zettler, 1969; Knight, Toyoda & Dodge, 1970; Dodge, Shapley & Knight, 1970; Gemperlein & McCann, 1975; Leutscher-Hazelhoff, 1975). However, the results obtained from these experiments have not been used to test the validity of the Fuortes & Hodgkin model.

The Fuortes & Hodgkin model accounts for the long delay between a flash and the peak response, which in the frequency response function becomes a phase lag between stimulus and response which increases with frequency. Another possible model to explain this behaviour would be one in which a pure delay element replaced some of the filter stages (DeVoe, 1966; Zettler, 1969). However, although a pure delay element might approximate the measured phase lags quite well, it could not explain the reduction in amplitude of the response with increasing frequency, and so some filter elements are essential to any model. The frequency response function might be expected to discriminate quite clearly between a pure delay and a cascaded filter, since the former should have a phase lag which increases without bound as frequency increases, while the latter should have a maximum phase lag asymptote. Unfortunately, the decreasing amplitude of the response at higher frequencies makes the accurate measurement of phase shifts most difficult in the frequency range where it could differentiate between the two mechanisms.

In the present work we have used random (white noise) light fluctuations to determine the frequency response of light transduction in *Calliphora*. This method has the advantage of yielding more accurate estimates of the amplitude and phase characteristics in a noisy environment than is possible by the sine wave method, and also provides a measure of the contribution of a linear noise-free model to the total response. Since the phase lag between stimulus and response increases with decreasing temperature, we have measured the frequency response function at a range of temperatures below and including room temperature. The results show that the transduction mechanisms may be modelled as a fifth order linear system under our experimental conditions. Therefore a model of the type proposed by Fuortes &

Hodgkin, but having five stages, can be used. The experimental results are also discussed with respect to the effects of temperature upon the time constants of the system, and to the relationship between discrete waves of depolarization (bumps) in the receptor and the total light response.

METHODS

Wild *Calliphora stygia* were caught locally and maintained in the laboratory for a maximum of 5 days before use. The animals were immobilized in wax and mounted on a fixed platform. Glass micro-electrodes filled with 3 M-KCl and having resistances of approximately 100 MΩ were used to penetrate the retina from the back of the head. This preparation has been described in detail before (Zettler & Järvilehto, 1971). A pseudo-random binary signal was generated by a shift register generator (Beastall, 1972) and was filtered by a six pole active filter to produce random noise having a flat power band width over the range 0–200 Hz. The noise signal was amplified and then fed to a green light emitting diode (Hewlett-Packard 5082-4984) via a 500 Ω resistor. This light emitting diode has a peak light output at 565 nm and a spectral distribution which is approximately gaussian with half intensity points at 550 nm and 575 nm. The spectral characteristics do not change appreciably with current over the usable range of forward currents. The mean light output used in all experiments was 3·5 $\mu W/cm^2$ and the randomly fluctuating current caused a total AC modulation of approximately 0·75 $\mu W/cm^2$ r.m.s. The light emitting diode was mounted on a Carden arm system which allowed it to be moved in two polar dimensions to any desired position in front of the eye at a fixed distance of 3 cm from the eye. The luminous area of the light emitting diode was measured to be 0.25 mm^2 and it subtended an angle of less than 1° at the surface of the eye. The stimulus may therefore be regarded as punctiform.

The light fluctuations were monitored by the current flowing through the light emitting diode, and the receptor potential was measured and amplified by the micro-electrode and an electrometer amplifier. Both signals were fed to an analogue to digital convertor connected to a PDP-8/E computer. A crystal clock was used to sample both input and output signals at 2 msec intervals and the digital values were stored immediately on a magnetic disk. The data was stored in segments containing 256 sample values from each of the two signals. Each segment was then transformed to yield 128 pairs of complex Fourier coefficients, which were in turn used to compute 128 values each of the input power spectrum, the output power spectrum, and the cross spectrum. This process was repeated 20 times for each experiment and the average spectra for the twenty segments were used to compute twenty-four amplitude and phase measurements at exponentially increasing frequency values. A more detailed description of the analysis and the software needed to conduct the analysis have been described before (French, 1973).

The six pole active filter used on the input signal caused the input power spectrum to fall to a very low level above a frequency of 200 Hz, and the output power spectrum of the micro-electrode signal similarly fell to a very low level above 200 Hz. The folding frequency of 250 Hz resulting from the 2 msec sampling rate was therefore sufficiently high to prevent any aliasing of the input or output signals.

The temperature of the preparation was controlled by passing cooled air continually over the head of the fly. The temperature of the head was monitored by a thermocouple embedded in the head and connected to a sensitive temperature gauge, and could be maintained within ± 0·5 °C during an entire experiment.

THEORY

Linear systems analysis

A time invariant linear system with single input and single output may be completely characterized by its impulse response, $g(t)$, which relates the output, $y(t)$, to the input, $x(t)$, by the convolution integral

$$y(t) = \int_{-\infty}^{+\infty} g(u)\, x(t-u)\, du, \tag{1}$$

where t and u are independent time variables. An alternative representation of the system may be obtained from the frequency response function, $G(f)$, which is the Fourier transform of the impulse response:

$$G(f) = \int_{-\infty}^{+\infty} g(t)\, e^{-2\pi jft}\, dt, \tag{2}$$

where $j = \sqrt{-1}$, and f is the frequency in Hz.

The frequency–response function is complex but may be separated into two real functions of frequency. The first is the ratio of the output signal amplitude to the input signal amplitude. The second is the phase shift between the input and output signals. The frequency–response function is usually displayed as a Bode plot, in which the phase shift and the logarithm of the amplitude ratio are plotted versus the logarithm of the frequency.

The frequency–response of an unknown system may be obtained by using a set of sinusoids with different frequencies as input signals. The response to each of the separate sinusoids will be another sinusoid of the same frequency but differing in phase and amplitude from the input. The differences between the input and output are used to produce the Bode plot.

An alternative means of measuring the frequency–response function of an unknown system, which we have used here, is to provide an input signal consisting of random white noise. The output is then also a random process. The input white noise may be considered to be made up from sinusoids at all frequencies and with random amplitudes and phases. The information required to construct the Bode plot may therefore be obtained by comparing the amplitudes and phases of all the sinusoidal components in the input and output signals. This can be achieved by transforming the input and output random signals directly into the frequency domain by use of the fast Fourier transform (Cooley & Tukey, 1965).

There are two major advantages to the use of random white noise for obtaining the frequency response function. First, only one experiment of relatively short duration is required and so the method is very efficient. Secondly, a side product of the measurement scheme is the coherence function (Bendat & Piersol, 1966) which is a normalized measure of the linear correlation between the input and output signals as a function of frequency. A coherence function of unity indicates a linear noise-free system, while a coherence function of zero indicates that there is no linear correlation between the input and output signals. The coherence function is therefore very useful in determining whether a linear model can account for the behaviour of a system and whether there is a suitable signal to noise ratio to allow a valid determination of the frequency response function.

Analysis of systems containing cascaded filters

Complex linear systems are often analysed or synthesized in terms of simple elements such as attenuators, delays, integrators and differentiators. Amongst the most important elements are the single time constant, or first order, filters. Any set of electrical, mechanical, hydraulic, or other components may be used to construct such a filter provided that they obey a standard set of differential equations (D'Azzo & Houpis, 1966). A common example of a first order filter is the combination of a resistor and a capacitor to produce a low pass electrical filter, as in the Fuortes &

Hodgkin model. The Bode plot of such a filter has an amplitude characteristic with low and high frequency asymptotes of zero and -6 dB/octave respectively, and the low and high frequency asymptotes of the phase plot are zero and $-90°$ respectively. Other types of first order filters may have the low and high frequency asymptotes reversed or may have amplitude slopes of $+6$ dB/octave or phase asymptotes of $+90°$. This time constant of the filter is determined from the corner frequency of the Bode plot, which is that frequency at which the phase curve passes through $-45°$, and is also the frequency at which the amplitude asymptotes intersect when extrapolated towards each other.

Two or more simple first order filters may be cascaded together in series to make a more complex linear system. If this is done and an isolating element (usually consisting of a unity gain amplifier) is connected between each pair of filters, then the Bode plot of the resultant system may be derived immediately by summing together the Bode plots of the individual elements. If the elements are joined together without isolating amplifiers, then it is still possible to determine the over-all order of the system by the use of asymptotes, but the intermediate behaviour of the Bode plots may be more complex.

In the case of the Fuortes & Hodgkin model there are isolating elements between each pair of filters, so that simple summation of the Bode plots of the individual filters should occur. If the number of filter stages is n, then the high frequency asymptotes should be given by $-6\,n$ dB/octave and $-90\,n°$. Determination of n is therefore possible if the high frequency asymptotes of the Bode plot can be determined. This approach has been used in the present work.

RESULTS

Fig. 1 illustrates typical membrane fluctuations observed in a receptor cell as the result of random light stimulation at four different temperatures. At room temperature these fluctuations had the form of a continuous random signal. As the temperature was reduced the amplitude of the membrane potential fluctuations decreased significantly and it was possible to discern stereotyped waves of deploarization, or bumps, having a similar shape to one another. However, the bumps were not all of the same amplitude and often appeared to be superimposed upon each other. These bumps could also be seen with constant light stimulation at lower temperatures.

The experiments were conducted in a dark room under a dim red light, to which the eye is very insensitive (Burkhardt, 1962). However, the continuous green light of the stimulus must have caused partial light adaptation, at least to the cell being stimulated. The mean light response during the fluctuations shown in Fig. 1 was about 5 mV, which is near the bottom of the $V/\log$ I curve (Järvilehto & Zettler, 1971).

The response of the receptors was increasingly attenuated as the frequency of the light fluctuation increased. The result of this attenuation was that the response above 150 Hz was too weak to allow any meaningful measure of the frequency response function. For all of the experiments described here the coherence function was between 0·8 and 0·9 over the frequency range 0–50 Hz. Above 50 Hz the coherence dropped progressively and was generally below 0·5 by 150 Hz. The system is well described by linear models (McCann, 1974; Eckert & Bishop, 1975) and so the

relatively low values of coherence above 50 Hz must be due to a falling signal to noise ratio as the amplitude of the response decreases.

Fig. 2 shows the phase difference between the input and output signals of a single receptor cell, as a function of frequency, at four different temperatures. In this

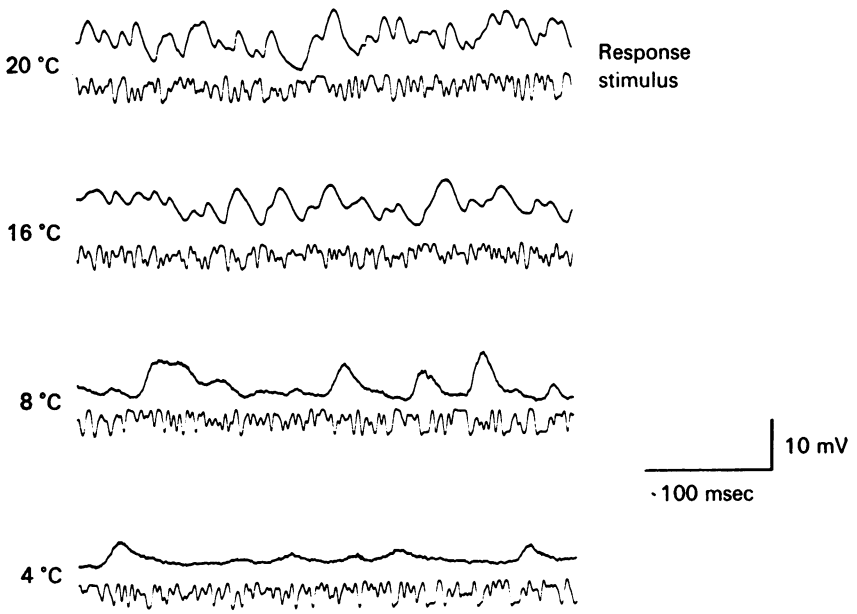

Fig. 1. Oscilloscope traces of the random current applied to the light emitting diode (stimulus) and the resultant membrane potential fluctuations (response) at four temperatures. The four traces shown are short but typical sections of the total data obtained in each case. The 10 mV ordinate scale refers to the membrane potential traces. Note the reduction in total response amplitude and its separation into discrete 'bumps' as the temperature is lowered.

diagram a negative phase shift represents the photoreceptor response lagging behind the light stimulus. In each case the phase shift is about zero at low frequencies and reaches a lag of about $-450°$ at high frequencies. The major difference between the results at different temperatures is not in the low and high frequency asymptotes but in the corner frequencies of the curves. The lower the temperature the lower the frequency at which the phase lag begins. It is important to note that all of the curves reach a similar high frequency asymptote. Even the lowest temperature curve, which lags most strongly at low frequencies, reaches an asymptotic phase lag. This is quite contrary to what would be expected of a system containing a pure delay, where the phase lag would be expected to continue decreasing steadily with frequency, without reaching any asymptote.

The expected asymptotic phase lag from a cascade of n filters would be $-90\,n°$. In all of the curves of Fig. 2 the high frequency asymptote is very close to $-450°$, corresponding to $n = 5$. This result seems quite clear when compared with the expected values for $n = 4$ ($-360°$) and $n = 6$ ($-540°$). The smoothness and lack of any detectable double inflexions in the phase curve suggests a system of five cascaded

filters, each having a similar time constant. The change in the shape of the curve with temperature indicates that the time constants of the filters all decrease with temperature, again with very similar or identical behaviour to each other.

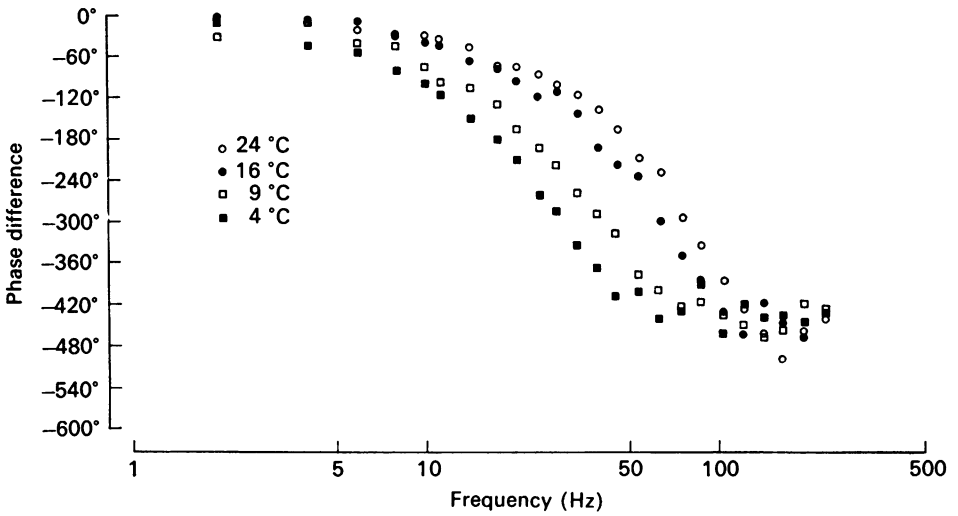

Fig. 2. The phase difference between stimulus and response signals as a function of frequency for four different temperatures. The low frequency asymptote is 0° and the high frequency asymptote is about −450° for all four curves. However, the inflexion of the curves occurs at increasing frequency as the temperature is raised.

A fifth order low pass linear system would be expected to have a frequency response function whose amplitude characteristic has zero slope at low frequency and a slope of −30 dB/octave at the high frequency asymptote (−6 n dB/octave, $n = 5$). Fig. 3 shows the amplitude curves of the frequency–response function between the input and output of the same receptor cell as for Fig. 2. The zero slope at low frequency is quite clear, and the high frequency slopes are quite compatible with the predicted slope at all temperatures. Again, the lower temperature results give the most satisfactory fit because they start to drop at lower frequencies. The amplitude characteristic therefore confirms the finding of the phase characteristic, that the light transduction process may be modelled by a cascade of five identical first order filters.

The time constant of a first order filter may be determined from the corner frequency of the Bode plot. This can be measured from the frequency at which the phase curve passes through −45° or by extrapolating the amplitude asymptotes towards each other and observing the frequency at which they intersect. We therefore measured the frequencies at which the phase curves passed through −225° (−45 n°, $n = 5$). The measured corner frequencies were then checked against the amplitude curves and found to be in good agreement with the intersections of the asymptotes.

A total of twenty-three experiments was carried out on four different receptor cells over a range of different temperatures, and for each the Bode plots were drawn and the corner frequencies measured. In each case the results were similar to those of Figs. 2 and 3, with the system always displaying a clear fifth order characteristic. All of

the time constants derived from the corner frequencies are shown in Fig. 4 as functions of temperature. It can be seen that the same trend of decreasing time constant with increasing temperature was always found, although there is a significant spread in the actual time constants measured.

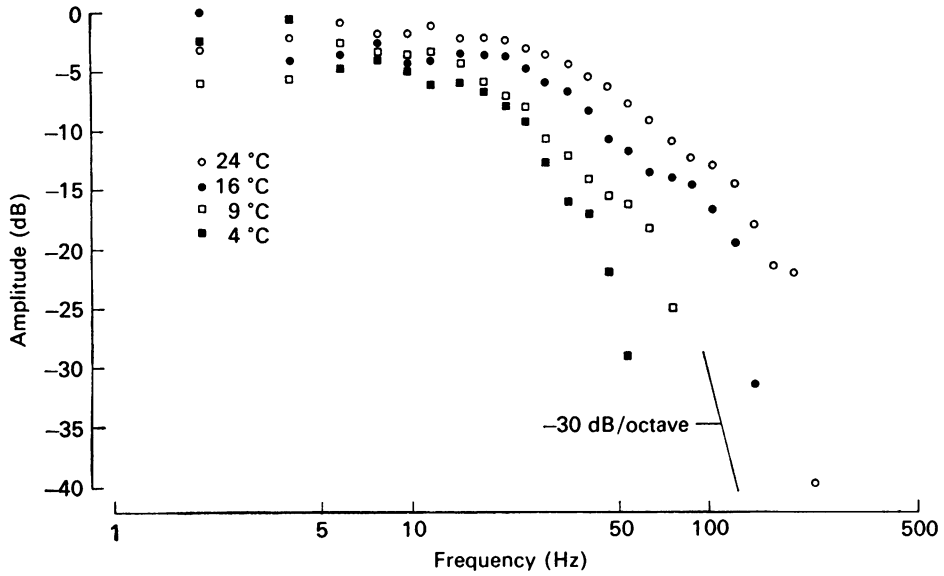

Fig. 3. The amplitude of the gain between stimulus and response as a function of frequency for four different temperatures. The slope of −30 dB/octave is the expected high frequency asymptote for a fifth order linear system as predicted by the phase curves of Fig. 2.

The photoreceptor response at lower temperatures contained quite distinct individual wave forms or bumps, but also contained more complex depolarizations which could be due to two or more bumps being superimposed upon each other with different time shifts. We chose ten of the largest, clearest and apparently single bumps from an experiment at 8 °C and measured their profiles accurately using magnified oscilloscope photographs. The profiles were then normalized to the same peak amplitude and the average profile for the ten bumps was computed. The power spectrum of this profile was computed using the fast Fourier transform, and compared with the power spectrum for the entire record of this experiment at 8 °C. The two spectra are almost identical, indicating that the power spectrum of the entire sensory signal, under the conditions of our experiments, may be obtained by summation of the power spectra of the individual bumps. Any non-linear interaction between the bumps, or the presence of any signal independent of the bumps, would have been expected to cause a significant difference between the two power spectra.

The relationship between bump size or shape and photon capture is not well established in *Calliphora* and so we cannot be sure that the bumps which we used were the results of single photons, particularly as we chose bumps which were large and therefore easy to measure accurately. However, in the locust, where it is possible to relate bump production to photon capture, there is a wide variability in bump amplitude (P. G. Lillywhite, submitted for publication). We have also compared the

power spectra of individual bumps to the overall output power spectrum in locusts (S. Laughlin, P. G. Lillywhite & A. S. French, in preparation) and have found a similar agreement to that shown in Fig.5.

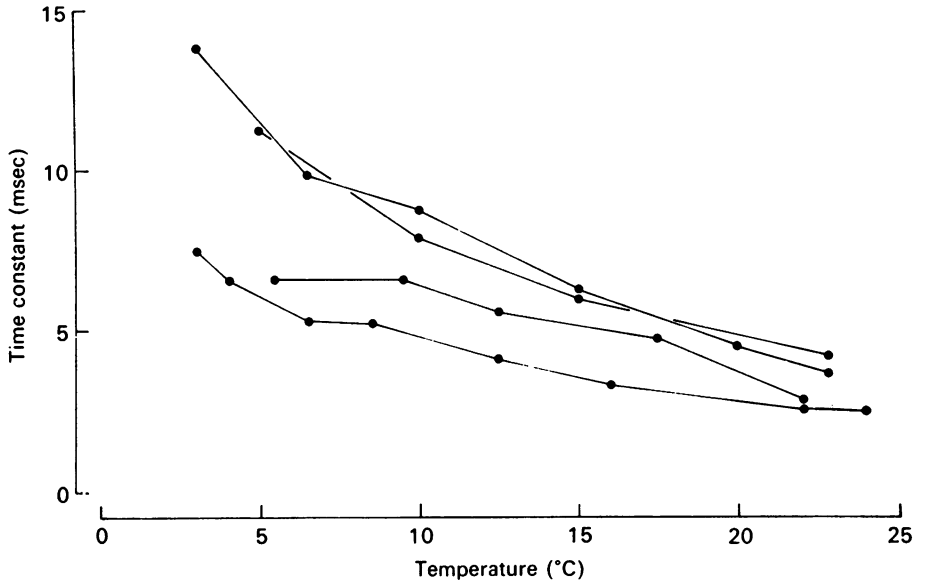

Fig. 4. The time constant of the linear elements as functions of temperature. Each line represents a set of experiments similar to those described by Fig. 2 and 3.

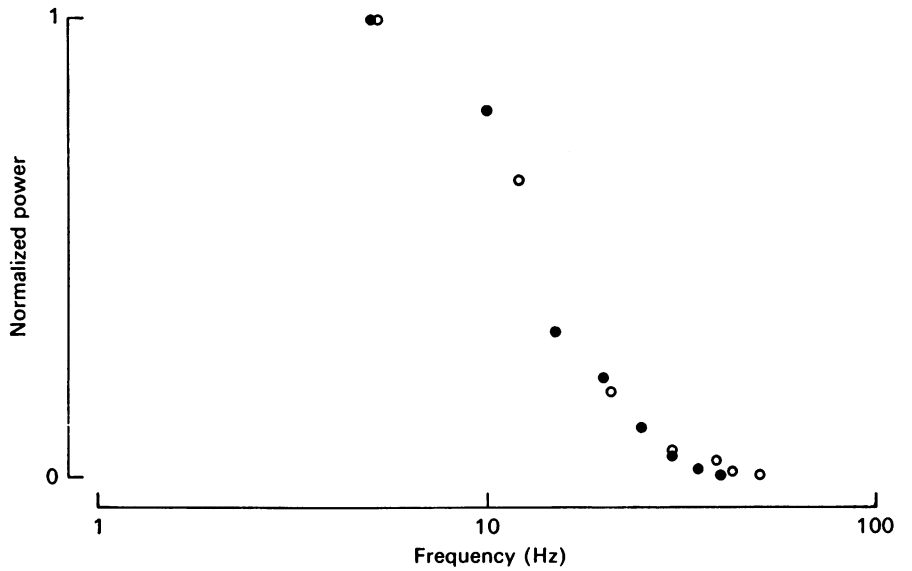

Fig. 5. A comparison of the power spectra of individual bumps in membrane potential for a randomly stimulated cell at 8 °C (filled circles), with the measured power spectrum of the entire response for the experiment (open circles).

DISCUSSION

The frequency–response functions which we have measured can all be completely accounted for by a model of the type proposed by Fuortes & Hodgkin for light transduction in *Limulus* (1964). For *Limulus* the number of filter stages required in the model was about ten or eleven. DeVoe (1966) has used a similar model to describe light transduction in the eye of the wolf spider, *Lycosa*, using seven filter stages. Baylor *et al.* (1974) have also used a similar model to describe light transduction in turtle cones, using six or seven stages. Our results can only be explained by a system of five cascaded filters. The significance of the range in the number of filters which have been found in different preparations will not become apparent until the physical nature of the filter elements is understood.

Both Zettler (1969) and Leutscher-Hazelhoff (1975) have measured the frequency–response function of light transduction in *Calliphora* at similar frequencies to those which we have reported, using sine wave stimuli. However, Zettler found much lower phase lags at 100 Hz (about $-300°$) while Leutscher-Hazelhoff found much higher phase lags at 100 Hz (about $-600°$). This wide divergence emphasizes the great difficulty of measuring such a large phase shift by comparing the peaks of small sine waves in a noisy environment. The clear asymptotic behaviour of our phase curves over a wide range of temperatures, the good agreement with the amplitude slope, and the high value of the coherence function, convinces us that our values are more reliable. The low temperature results were particularly valuable in revealing the asymptotic behaviour because of their earlier phase lag with frequency.

The Fuortes & Hodgkin model includes an isolating element between each pair of filters to prevent interaction between components in adjacent filters. The frequency response functions which we have measured are of the form which would be expected from such a system. However, they could also result from a more complex fifth order system which was critically damped to produce the flat amplitude characteristic and smooth phase characteristic. Most authors who have measured frequency–response functions for light transduction have found that although the amplitude characteristics are often flat, as we have found, they can also display peaks of response in the mid-frequency range before falling off at high frequency. This peaking seems to become more pronounced with higher light intensities, and is echoed in the responses to light flashes, which become more oscillatory with higher light intensity. Such behaviour is typical of a second or higher order system in which interaction between adjacent filter elements occurs. A possible hypothesis to explain this change is that at low light intensities there is a cascade of elements which are well isolated from each other, but at higher light intensities more interaction between the components of the filters takes place. Alternatively, the system could be more complex but critically damped at low intensities, becoming slightly underdamped at higher light intensities.

Baylor *et al.* (1974), in modelling light transduction in turtle cones, have suggested that one of the filter stages in the cascade must have a significantly longer time constant than the others. In our case, such a situation is clearly not possible, since it would cause a separate inflexion in the phase and amplitude curves at a lower frequency than the main corner frequency. However, our results do not rule out the possibility of additional filters in the cascade having much shorter time constants,

since they would not cause inflexions until higher frequencies were reached than we have observed.

The time constants of the five filters suggested by Fig. 4 are quite typical of cell membrane time constants, so a model containing five membranous elements could account for the results. Passive membrane conductance increases by about 2·7 % per degree Celsius, or by a factor of about 1·3 for a 10 °C rise in temperature (Cole, 1968). Inspection of Fig. 4 shows that the time constants of the transduction process decrease by an average factor of about 1·7 between 10 and 20 °C. The time constants are therefore increasing faster than might be expected for a membrane, although probably not so much as to rule out the possible involvement of membranous structures.

Any number of other physical and chemical processes could also be postulated to fit the data. A number of authors have suggested that a series of chemical reactions could explain the cascade of filters. Baylor *et al.* (1974) have determined that the time constants of their filters change by a factor of 1·8 over the range 15–25 °C, which they suggest may be due to a chemical reaction having an activation energy of 10 kcal/mole. In our case the change of 1·7 between 10 and 20 °C could be explained by a reaction with an activation energy of 3 kcal/mole.

The data presented in Fig. 5 suggests that the total light response may be a summation of the discrete waves of depolarization, or bumps. This is not a novel conjecture but has been proposed before by several authors (Dodge, Knight & Toyoda, 1968; Dodge *et al.* 1970; Srebro & Behbehani, 1972; Martinez & Srebro, 1976). If this hypothesis is correct, then the amplitude results of Fig. 3 are of interest since they all have approximately the same low frequency asymptote. The extreme low frequency portion of a signal is merely its mean value, and if the total signal is made up from a linear summation of many bumps, then the total area of the bumps in each signal must be the same at all of the temperatures which we used. However, a reduced temperature causes a reduction in the high frequency amplitude and so the shape of the bumps must change, becoming slower. Lillywhite (1977) has produced statistical evidence that each bump is caused by the transduction of one photon, in the locust eye, and that the photon to bump efficiency is greater than 60 % at room temperature. If we can therefore regard each bump as the impulse response of the cascaded filters, then the total area under each bump should not change as the time constant changes. This is true because integrating the impulse response of a low pass filter gives a function which is independent of the time constant of the filter. The amplitude results of Fig. 3 are therefore consistent with a bump being the impulse response of the cascaded filter to a single photon.

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