

LINEAR AND NON-LINEAR PERFORMANCE OF TRANSDUCER AND PUPIL IN *CALLIPHORA* RETINULA CELLS

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SUMMARY

1. Intracellular recordings have been made from the blowfly (*Calliphora erythrocephala*) retinula cell; apart from the transducer mechanism, these cells also feature a pupil mechanism.

2. At several mean intensity levels, within the apparently linear range of response, frequency characteristics of amplitude and phase and responses to 'delta'-flashes and 'delta'-flash pairs have been obtained.

3. Fourier methods have shown these responses to be mutually compatible, confirming linearity in these circumstances.

4. Non-linear behaviour can be made to appear at the lower frequencies when the modulation depth is increased.

5. Non-linearities can also appear through application of the superposition test: a low frequency sine wave, modulated so as to elicit an apparently linear response, and a high frequency sine wave which does not give rise to non-linearity even at the highest modulation depths can, when superimposed, yield a greater response to the latter when situated at the minima of the former than at its maxima.

6. At frequencies above approximately 1 Hz these superposition non-linearities are attributed to the transducer mechanism gain control. Below this frequency the pupil mechanism takes part considerably in the retinula cell's total observed gain control: its characteristics remain yet to be cleared up.

7. The transducer's linear and non-linear properties fit in closely with those of the Fuortes-Hodgkin model which couples increases in gain and time constants.

8. The Fuortes-Hodgkin model will probably require some quantitative modifications in the originally treated case of *Limulus*, on account of its pupil.

9. Finally, the merits of Veringa's diffusion model, and the possibility of eventually joining this model with the Fuortes-Hodgkin one are pointed out briefly.

INTRODUCTION

When one wishes to gain knowledge about the processes of light absorption and the ensuing photochemical and membrane processes, visual receptor cells are the most sensible choice for electrophysiological observations.

In this study, also published more extensively in the form of a thesis (Leutscher-Hazelhoff, 1973), these primary processes have been lumped together and called by the name of transducer process. Information will be provided regarding the input-output performance of blowfly receptor cells, more specifically, their frequency characteristics of amplitude and phase and their dependence on mean intensity.

Such characteristics have previously been measured in *Calliphora* (= blowfly) retinula cells by Zettler (1969), Gemperlein & Smola (1972*a,b*) and Smola & Gemperlein (1972). Furthermore, similar work has been presented for both reticular and eccentric cells in *Limulus* (Knight, Dodge & Toyoda, 1970; Dodge, Knight & Toyoda, 1968; Pinter, 1966) and locust and cricket (Pinter, 1972).

Pinter provides evidence that, though non-linear as a whole, the transducer system in the latter three species behaves in a linear way for small signals on a steady level of intensity, whether these small signals are sinusoidal or approximate delta functions. And that, as a consequence of this linearity, Fourier methods can reliably predict responses to delta flashes from frequency response characteristics and *vice versa*. He notes, moreover, that in many cases linearity exists to very high modulation depths.

However, he has judged it superfluous to apply the superposition test, which is the most stringent test for linearity and which requires that superposition of two wave forms on one another yields a response by simple linear addition of the responses to each of the two stimulus wave forms separately. In this study evidence will be presented that in the *Calliphora* retinula cell this test does yield non-linearities, although the present measurements confirm those reported by Pinter in all respects named.

It will be argued that the non-linearities revealed by the superposition test form the link between the linear behaviour at each adaptation level and the 'logarithmic' behaviour between adaptation levels, or rather, the dependence of gain on mean intensity.

Furthermore, the applicability of the Fuortes-Hodgkin (1964) model will be discussed.

Meanwhile, in *Calliphora*, gain control is performed partly by its pupil mechanism, which is located in the retinula cell. The consequences of its contribution to the gain control of the retinula cell as a whole will be discussed.

Anatomy

Apart from the usual cellular components the retinula cells, like all visual sense cells, possess a specialized membrane region which harbours the photopigments. This rod-like structure, the rhabdomere, is $200\ \mu\text{m}$ long and $1\text{--}2\ \mu\text{m}$ in diameter and functions as an optical wave guide, its refractive index being higher than that of its surroundings. Furthermore, the fly retinula cells contain as a special feature a large number of mobile pigment granules (not to be confused with the photopigments) which migrate under the influence of changes in light intensity. In the dark-adapted state they are located diffusely throughout the cytoplasm but light adaptation induces them to move close to the rhabdomere and to absorb and scatter a substantial fraction of the light conducted by it.

This so-called pupil mechanism (Kirschfeld & Franceschini, 1969; Stavenga, Zantema & Kuiper 1973) causes a drastic reduction of maximally 1.3 log units (Stavenga, 1974) in the effectiveness of the incident light.

METHODS

Preferably, flies caught outdoors were used. They were kept intact except for a sliver of chitin taken away from the back of the head exposing the visual layers.

Equipment

The highest mean intensity in our experimental set-up is in the following indicated as $I = 1$. This corresponds to $20\ \text{W}/\text{m}^2$ at the spot where the fly's eye was placed and it was achieved by a Sylvania glowtube nr 1113 C at a current of 15 mA. Its output was controlled in two different ways: one way was to simply drive it with current fluctuations of the chosen wave form, the resulting wave-length fluctuations being judged negligible to the insect eye owing to its spectral sensitivity, and the other method consisted of pulse-width modulation, using square-wave pulses of 11.4 kHz. In this way the spectral composition of the light emitted by the glow-modulator remained the same throughout.

A wave guide placed in the beam near the fly's eye conducted part of the glow-modulator output to a photomultiplier, revealing the difference between the two driving methods while these differences were not detected in the retinula cell recordings.

The recording equipment consisted of a picometric amplifier, input impedance $10^{13}\ \Omega$, grid current $2 \times 10^{-13}\ \text{A}$, an Ampex CP 100 instrumental tape recorder, band width 0–2.5 kHz, tape speed 7.5 in./sec, and an average response computer, CAT 1000.

Procedures

The pick-up electrode (3 M-KCl filled micropipette, resistance approximately $20\ \text{M}\Omega$) penetrated the visual tissues from a point proximal to the lamina layer under an angle judged to coincide approximately with the long axis of the retinula cell aimed at. During penetration the light source was continually delivering light flashes, as the potentials elicited by them are a valuable indication of the whereabouts

of the electrode tip. In order to elicit maximum response amplitude the light source position was meanwhile repeatedly adjusted. When the sequence of potential jumps encountered resembles that shown in Fig. 1 this suggests successful impaling of a retinula cell body. Other criteria for retinula cell recordings are:

- (a) bumps at low light intensities;
- (b) at high light intensities a wave shape in response to a step of light which corresponds to that identified as a typical retinula cell response in marking experiments by Zettler & Jährvilehto (1970); and,
- (c) a fluctuating response amplitude in reaction to rotation of a polaroid filter in front of the light source.

Before starting a stimulus program retinula cells were allowed to adapt to a chosen mean intensity for two minutes. Stimulus programs did not exceed 20 min, as almost all cells when light-adapted do not maintain a stable output for a longer period of time.

The stimuli chosen consisted of brief increments and decrements of light (0.5 msec, which to all intents and purposes approximate delta flashes for the blowfly eye), flash pairs, sine waves and single sinusoids, superimposed on several mean intensities. The modulation depth (in all cases meaning the amplitude of the deviation from the mean intensity divided by that mean intensity) and frequency and/or repetition rate were varied.

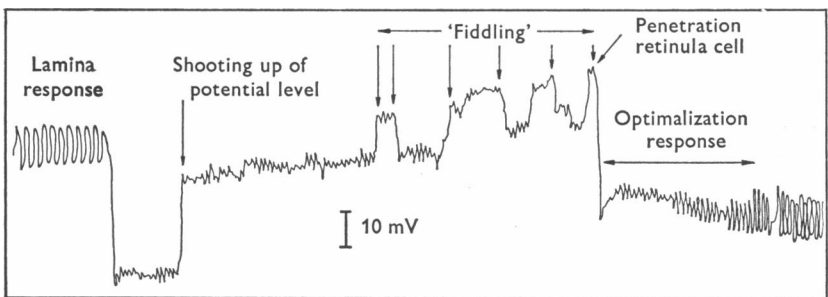


Fig. 1. Sequence of potential jumps during penetration of the visual tissues ending in the successful impaling of a retinula cell, followed by the optimization of its response to a continually present 3 Hz on-off light stimulus. Downward deflexions correspond to negative-going potentials.

RESULTS

'Delta'-flashes

At mean intensity = 1 Bloch's law holds for light flashes up to at least 1 msec; i.e. stimulus height and stimulus duration up to 1 msec are interchangeable in giving rise to a certain response, which has equal shape and size but opposite sign for equal sized brief increments and decrements of light. On the strength of this result increments and decrements of 0.5 msec duration are in this study henceforth called positive and negative 'delta'-flashes.

The responses are small (a few hundred μV) and have to be averaged in order to be distinguishable from the noise. An example is shown in

Fig. 2. The response amplitude is proportional to the stimulus amplitude which in Fig. 3 is presented in terms of modulation depth.

A further indication of linearity is given by the fact that the shape of the response is independent of stimulus amplitude, as is shown in Fig. 4, where the magnitude of the response at different modulation depths has been normalized. It is seen that the maximum response height occurs here at 11 msec after the beginning of the stimulus and that the rising slope is only slightly steeper than the descending one. There is a small under-shooting (for negative 'delta'-flashes overshooting) 'tail' which returns to pre-flash level after about 50 msec. This tail is best seen in Fig. 2.

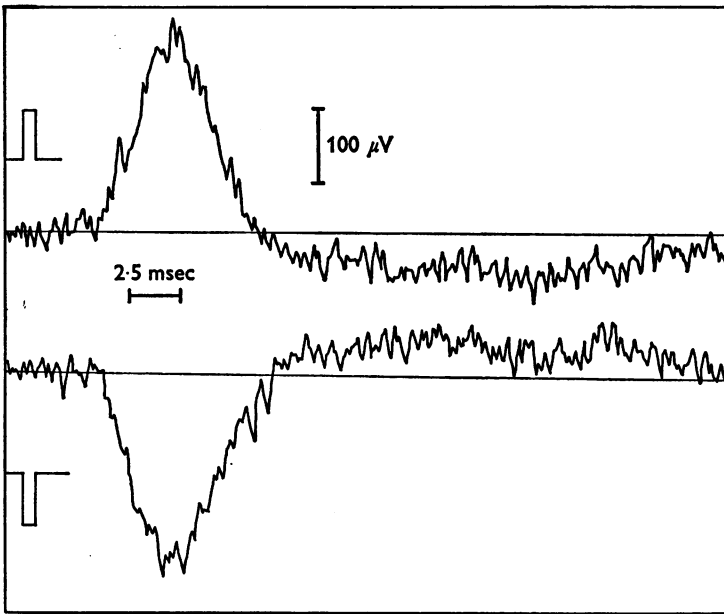


Fig. 2. Response to positive-going and negative-going 'delta'-flash (0.5 msec duration), superimposed on the same mean intensity. Modulation depth of the flashes is 80%. Averaged 85 times.

When the repetition rate of the stimulus is increased to more than once in 50 msec, the successive responses interact, so that when 'delta'-flash pairs are offered of, for instance, 12.5 msec between flashes, the response to the second flash peaks to a lesser height than the response to the first one. Positive-positive and negative-negative 'delta'-flash pairs again yield responses which are equal in amplitude and shape. An interval of 1 msec between flashes leads to a response equal in time course but double the amplitude of the response to a single flash, whereas increasing interval

first broadens and flattens the response and leads to a double-peaked one starting at 4.5 msec interval between 'delta'-flashes.

The responses to positive-negative and negative-positive 'delta'-flash pairs on the other hand, are hardly discernible at 1 msec intervals, whereas larger interflash distances result in ever larger responses. Again it follows that Bloch's law applies to just about 1 msec. Some examples are shown in Fig. 5. These responses can be reliably predicted by, respectively, summation and subtraction of responses to single 'delta'-flashes, confirming the linear nature of these responses.

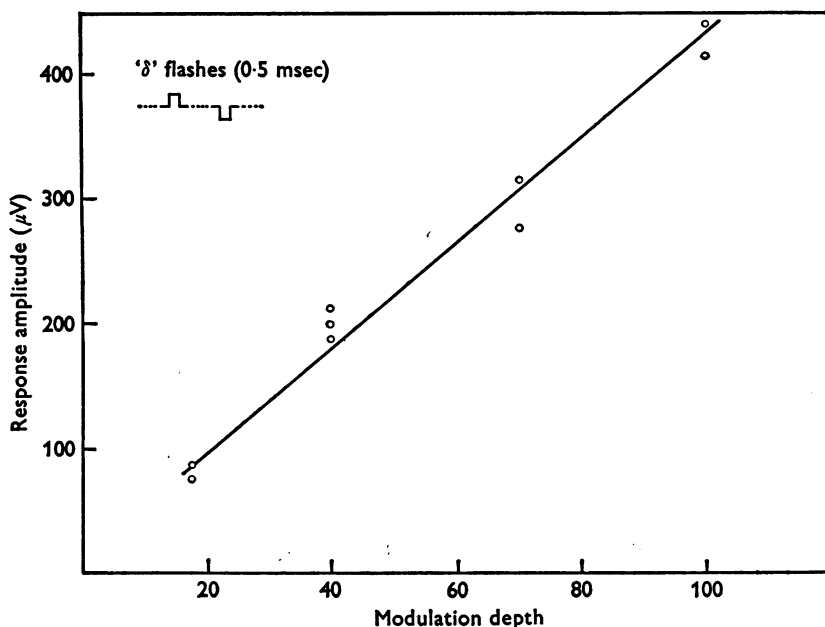


Fig. 3. Amplitude of the response to positive and negative 'delta'-flashes versus their modulation depth.

Sine waves

Sine-wave stimuli produce sine-wave responses, lagging more or less behind and the peak-to-peak response amplitude is again proportional to modulation depth. However, this is true only with some restrictions: wave form distortions become apparent at lower frequencies and higher modulation depths. These deviations consist of the ascending slope being steeper than the descending one and the positive half of the response being more rounded, and the negative half sharper than a sine wave. Also, when the modulation of the input is temporarily replaced by steady light of the same mean intensity, it becomes evident that the amplitude of the

negative half of the response is markedly greater than that of the positive half. An example is shown in Fig. 6.

When for different modulation depths the positive and negative excursions of both input and output are plotted on either side of the mean intensity and its response value, then it is revealed that the output amplitude is not proportional to the input, which fact remains obscured when the peak-to-peak response amplitude is plotted versus modulation depth. Both ways of plotting are shown alongside in Fig. 7.

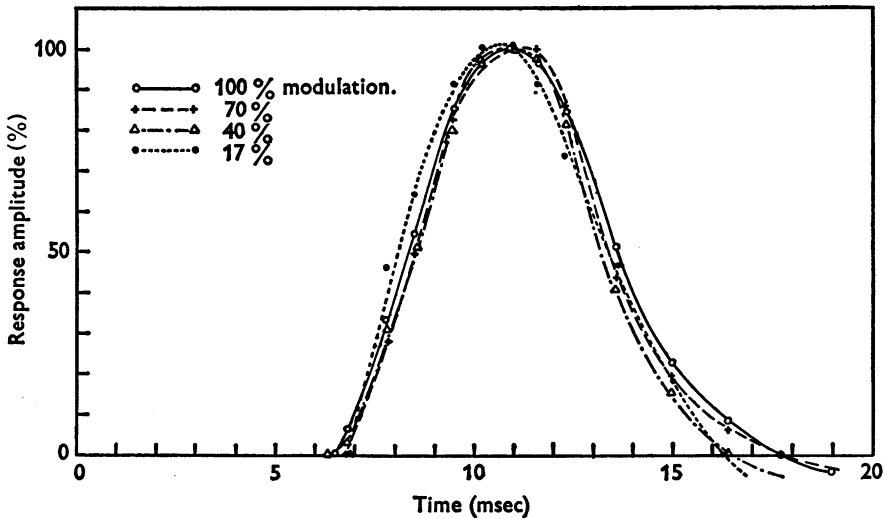


Fig. 4. Shape of the response to 'delta'-flashes at four different modulation depths (maximum response amplitude normalized to 100%). (The earlier peaking of the response at the lowest modulation depth is not significant.)

The shape of the input-output relationship plotted on either side of the mean value suggests a logarithmic element in the distortion.

Furthermore, it is related to the result obtained when a distorted sine-wave response is analysed by plotting the deviations from the mean of the output versus those of the input while disregarding the phase difference. Fig. 8 shows the resulting Lissajous figure, illustrating the greater steepness of the ascending than the descending slope.

This method reveals that at intensity level = 1 distortions do not appear below 30% modulation at any one of the applied frequencies or at any modulation depth above 60 Hz, but that below 60 Hz modulation depth and frequency must decrease together in order to maintain an undistorted sine-wave response.

Keeping within bounds of truly linear and undistorted performance of

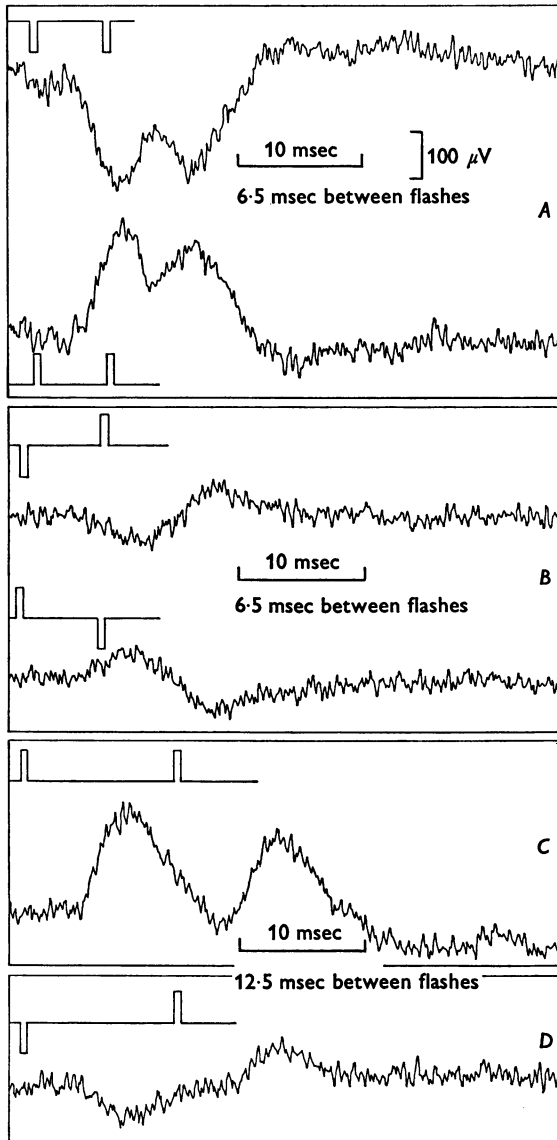


Fig. 5. *A*: responses to double-positive and double-negative 'delta'-flash pairs, 6.5 msec between flashes. *B*: responses to negative-positive and positive-negative 'delta'-flash pairs, 6.5 msec between flashes. *C* and *D*: responses to double-positive and negative-positive 'delta'-flash pairs, 12.5 msec between flashes. Averaged 85 times.

the retinula cell, the responses obtained at different frequencies can now be gathered in a frequency or attenuation characteristic: the response amplitude is plotted against frequency (both on log scale), keeping the modulation depth constant. In actual fact, the responses were either

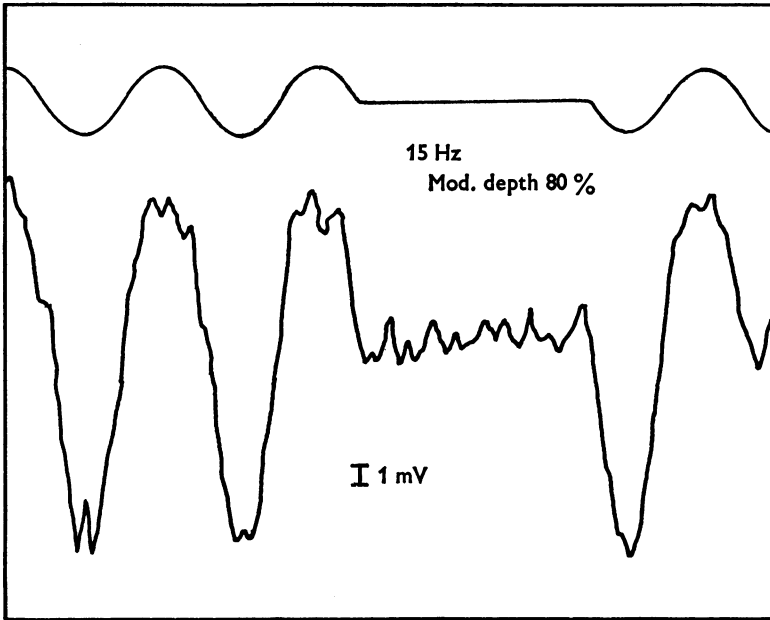


Fig. 6. Wave form of the response to a 80% modulated 15 Hz sine wave which is temporarily replaced by steady light of the same mean intensity.

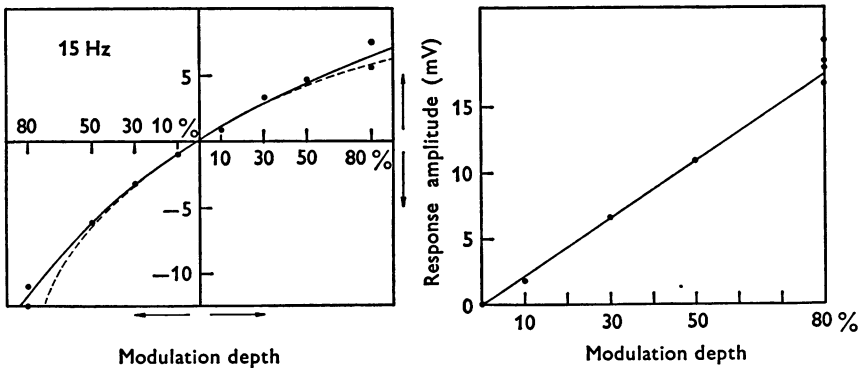


Fig. 7. Response amplitude versus modulation depth of 15 Hz sine waves; on the left plotted as positive and negative excursions on either side of the mean intensity and its response value, and on the right, as peak-to-peak amplitude values. The dashed line in the left half of the picture represents a purely logarithmic distortion.

obtained with 30% modulation depth at frequencies below 60 Hz and 80% modulation depth at the higher frequencies, or with several modulation depths at every frequency. Response amplitudes obtained at modulation depths other than 80% were all linearly converted to values corresponding to 80% modulation depth.

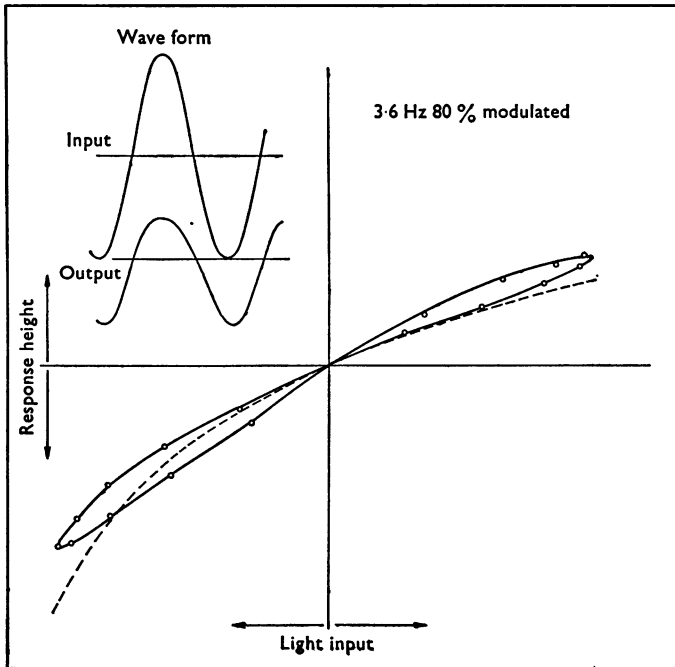


Fig. 8. Wave form of the response to a sine wave of 3.6 Hz and 80% modulation depth plotted as a function of the input wave form when the phase difference (8.5°) is compensated for. The dashed line again represents a purely logarithmic distortion.

Fig. 9 shows four such attenuation characteristics, indicating that individual cells are not completely alike. It is seen that flickering light yields a response up to 180–200 Hz (up to 240 Hz in one of the cases shown in Fig. 10), while peaking occurs at 15–20 Hz.

The high frequency end, on the other hand, there is below 15 Hz down to 1 Hz a decline of a factor 2–3, the response amplitude remaining constant below 1 Hz down to the lowest measured frequency of 0.1 Hz. In Fig. 9 the phase relationship between stimulus and response is given as well in two cases: it is seen that the response may lag behind more than 500° at high frequency. This is more than the minimum phase: at an amplitude cut-off of 24–30 dB the phase lag amounts to 360–450 degrees at the high

frequency limit, so either the system is not a minimum phase system or the asymptote is not yet reached in the measured frequency range. The phase relationship is independent of modulation depth as long as linear behaviour persists.

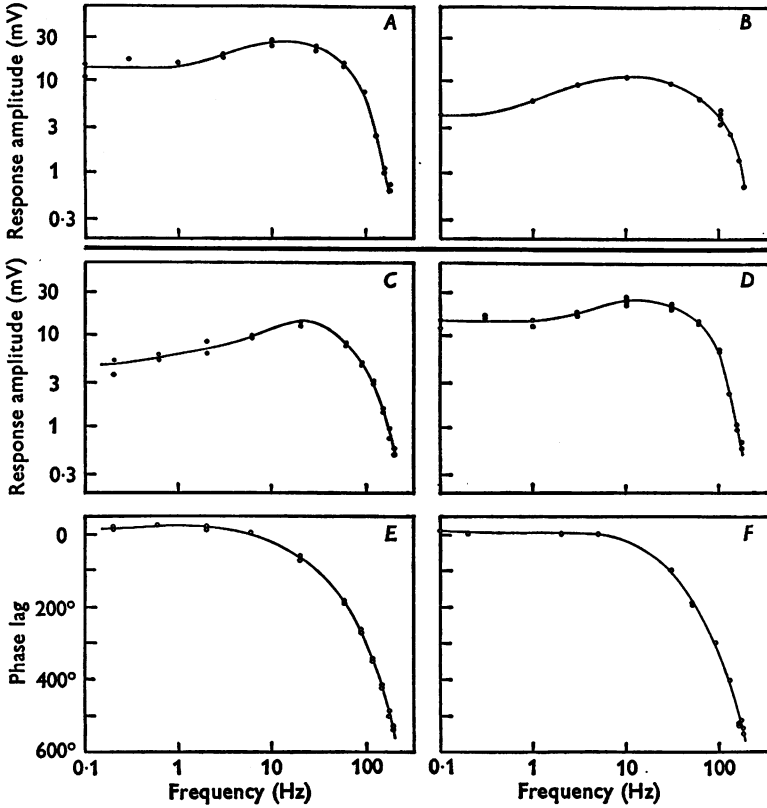


Fig. 9. *A-D*: attenuation characteristics (response amplitude vs. frequency) for four different retinula cells, all obtained at mean intensity 1. *E* and *F*: phase characteristics accompanying the attenuation characteristics in *C* and *D*.

Gain

The reported linear relationship between response amplitude and stimulus intensity is observed only at fixed intensity levels. Between levels this relationship is lost owing to the adaptive processes involving changes in gain and time constants.

Gain is defined as the ratio of the amplitudes of response and stimulus and is a measure of sensitivity. A change in adaptation level sets the gain or sensitivity of the system to another value: this is indicated by the term

gain-control or gain-setting. Its magnitude is illustrated by the different heights of the attenuation characteristics obtained at different mean intensities at the low frequency limit.

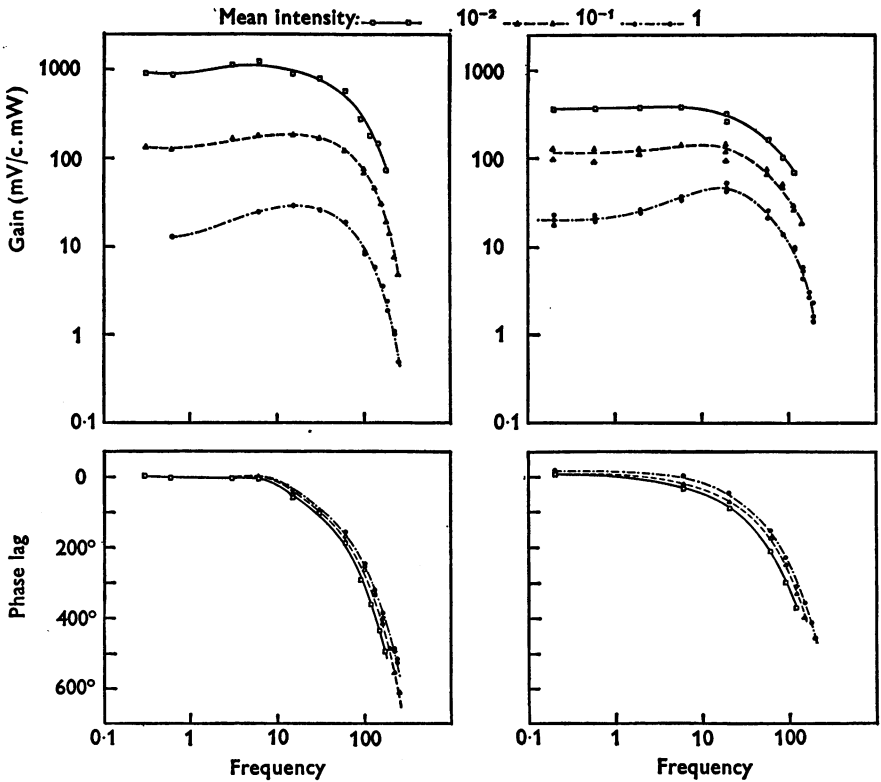


Fig. 10. Attenuation and phase characteristics as obtained from two different cells. In the two upper plots the attenuation is represented in terms of gain at three different mean intensities a factor 10 apart. In the lower plots the accompanying phase behaviour is shown.

Attenuation and phase characteristics obtained at different adaptation levels are not identical in shape. In Fig. 10 it is seen that lowering of the mean intensity involves an increase in gain; with rising frequency, however, the phase characteristics keep diverging, whilst the attenuation characteristics first converge, and from 60 Hz onwards maintain a constant mutual distance.

In summary, the retinula-cell response mechanism may be described as a mechanism in which gain-control is employed to realize useful response amplitudes over a large range of intensity levels while a predominantly linear performance is maintained at every adaptation level examined.

This gain control is performed partly by the pupil mechanism. The pigment granules remain effectively immobile above approximately 1 Hz (D. G. Stavenga, personal communication) and hence they make no contribution to the shape of the frequency characteristics above this value, but they do take up different positions at each mean intensity level. Therefore, the mutual distance of the attenuation characteristics in Fig. 10 is achieved by pupil mechanism and transducer mechanism jointly.

Superposition of two sine waves

Superposition stimuli in this study serve a double purpose. They form a means of getting rid of the pupil mechanism and they are the most stringent test for linearity of the transducer mechanism. A linear system should respond to two superimposed sine waves with a simple addition of the responses to either sine wave alone. And if this stimulus may be regarded as occurring at a steady state of adaptation, this is what might have been expected. On the other hand, if the lower frequency sine wave does induce changes in adaptive state, the higher frequency sine wave should be subject to gain-control, and yield a smaller response at the lower frequency sine-wave maxima than at the minima. When the low frequency sine wave is chosen above 1 Hz, any such observed non-linearity can be attributed to gain-control which is entirely due to the transducer mechanism alone.

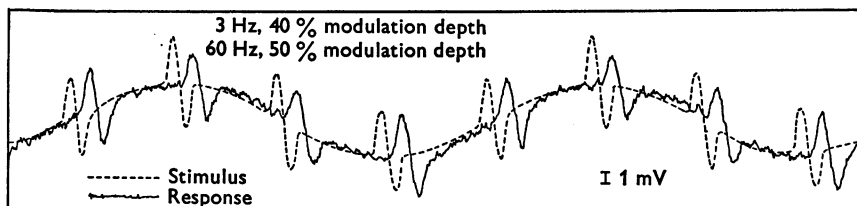


Fig. 11. Shape of the response to a stimulus consisting of 40 % modulated free-running 3 Hz sine waves on which are superimposed 50 % modulated 60 Hz single sinusoids.

As the superimposed stimulus single sinusoids have been chosen instead of free-running sine waves. This has the advantage of allowing the response to the lower frequency sine wave to be seen and judged as to linearity, simultaneously with the response to the high frequency sinusoids.

Fig. 11 shows a stimulus consisting of a 3 Hz 40 % modulated sine wave with superimposed on it 50 % modulated 60 Hz single sinusoids, together with the response to it. This response as a whole is obviously non-linear, though the 3 Hz part of it is not and the 60 Hz single sinusoids when presented alone yield a linear response too, even when 90 % modulated

At low modulation depths of both superimposed sine waves the response is linear; it is by increasing the modulation depth of the low frequency sine wave rather than that of the high frequency one that non-linearity can be made to appear in the response.

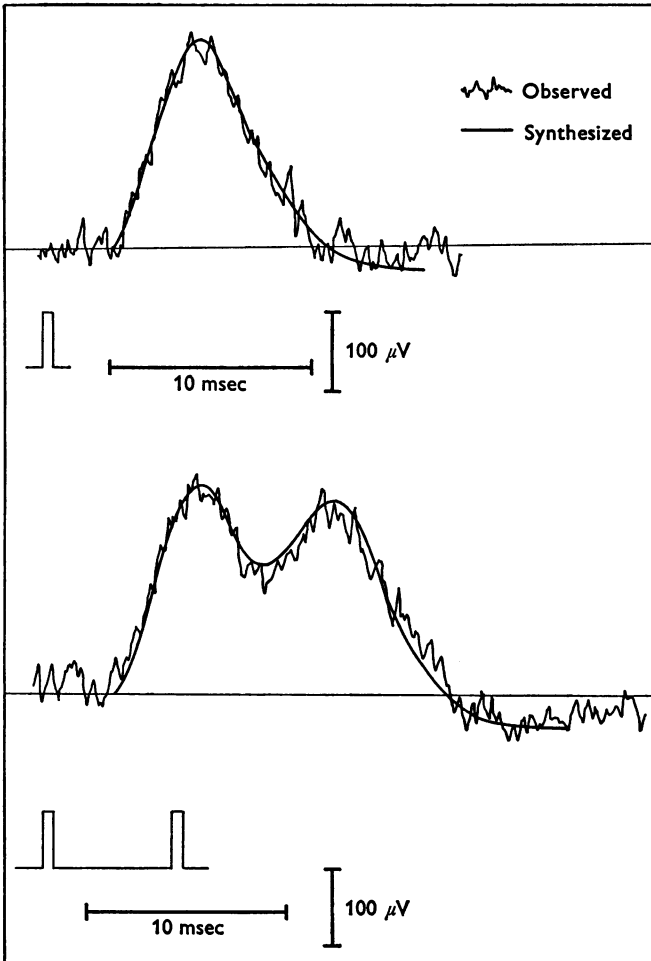


Fig. 12. Observed and synthesized wave forms in response to a 'delta'-flash and a 'delta'-flash pair, 6.5 msec between flashes.

This latter fact may be viewed in relation to the earlier appearance of non-linearities (i.e. at lower modulation depths) in case of low frequencies than in case of high frequencies; this leads to speculation regarding the nature of the non-linearity, which will be reserved for the Discussion.

DISCUSSION

Linear behaviour

The frequency characteristics obtained from blowfly retinula cells at fixed adaptation levels are very similar to the formerly reported ones that were obtained extracellularly (Leutscher-Hazelhoff & Kuiper, 1964; Kuiper & Leutscher-Hazelhoff, 1965). Above 1 Hz they are expressive of the linear behaviour of the transducer mechanism, while below approximately 1 Hz the pupil mechanism contributes to the frequency characteristics, presumably through being linked to the transducer mechanism in a feed-back loop.

That the cell responses are indeed linear is shown by the fact that not only does a sine wave input produce a sine wave output, but that (as in Pinter's (1972) work on locust and cricket, mentioned in the Introduction) responses to a number of different stimulus wave forms can be reliably predicted by means of Fourier methods from the frequency characteristics. Some examples of predicted and observed wave forms are shown in Fig. 12. A more detailed discussion will be given in a following paper (Van Barneveld & J. T. Leutscher-Hazelhoff, in preparation).

Non-linear behaviour

The non-linear behaviour of the retinula cell cannot be analysed as straightforwardly. Apart from the usual greater difficulties encountered with non-linear than with linear systems, this is due to the different static position taken up above approximately 1 Hz by the pupil's pigment granules at different adaptation levels, which must lead to marked differences in gain (but not in time constants) of the retinula cell output. Besides this, below 1 Hz there must be a contamination of the transducer mechanism dynamics (amplitude and phase) by those of the pupil.

Summing up the observed retinula cell behaviour and relating it to what is known from the literature, it may be said that between adaptation levels there are marked differences in gain and in phase behaviour. Zettler's (1969) observation to the contrary, e.g. that the mean intensity influences the gain but not the phase behaviour (which observation considerably puzzled Pinter, 1972) is not confirmed, neither by Smola & Gemperlein (1972) nor in the present study (Fig. 10).

In accordance with this is the fact that responses to 'delta'-flashes show distinct changes in gain and time constants with changing mean intensity. This has also been observed in studies on a pupil-less mutant form of *Calliphora*, the variety 'Chalky' (Dörrscheidt-Käfer, 1972). This latter fact points to the probability that it is, also in the *Calliphora* wild form, not the pupil only which is responsible for the gain-control displayed by

the retinula cell (as might be deduced from the parallel course of the attenuation curves in the high frequency region, Fig. 10), but that the transducer mechanism exhibits gain-control as well.

The non-linearities in wave form observed above 1 Hz, which must be attributed to the transducer mechanism alone, are quite consistent with the idea of transducer gain control: the greater response amplitude for negative than for positive signals, the appearance of distorted sine-wave responses at lower modulation depths the lower the frequency, and, most of all, the form of the response to a stimulus consisting of single sinusoids superimposed on a low frequency sine wave are all suggestive of some kind of low frequency adaptive parameter setting in the transducer mechanism.

This description fits in closely with the properties of the well known Fuortes-Hodgkin (1964) model, which links the increase in gain with the increase in time constants associated with dark adaptation as observed in the *Limulus* photoreceptor and which consists of a number of n cascaded integrators whose leakage conductance is changed on illumination by feed-back from the output.

It must be noted, however, that a pupil mechanism is present not only in *Diptera*, but also in *Limulus* (Miller, 1958; Behrens, 1974; Miller & Cawthon, 1974) and many other arthropods, for example in locust (Horridge & Barnard, 1965; Horridge, 1966), cockroach (Butler, 1971), ant (Menzel, 1972; Brunnert & Wehner, 1973), bee (Kolb & Autrum, 1972), bumble bee, wasp, locust, cricket, butterfly and dragonfly (Stavenga, 1975).

Unlike Hamdorf and co-workers (1969) who have chosen to experiment on retinula cells not containing a pupil, Fuortes & Hodgkin have probably not been aware of the existence of a pupil in *Limulus* and of the necessity of taking into account its contribution to the gain-control displayed by the retinula cell.

All the same, though the impact of the existence of a pupil mechanism on this model will have to be evaluated, the attraction of the idea on which it is based remains.

The link between adaptive changes in gain and time constants, and even these adaptive changes themselves, are missing from another attractive and rather simpler approach, viz. Veringa's diffusion model (1961*a,b*, 1970), which is supported by Kelly (1969). This latter model is a linear one which, while adequately describing human high frequency behaviour, requires extension by diverse and possibly non-linear operations when applied to flies.

The possibility of joining the two models should not be disregarded.

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