

Comparative Physiology and Evolution of Vision in Invertebrates

C: Invertebrate Visual Centers and Behavior II

By

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With 216 Figures



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Preface

Volume VII, Part 6 brings to a conclusion the Handbook of Sensory Physiology, the publication of which has spanned 9 years. In the General Preface of Volume I it was stated that: "The purpose of this handbook is not encyclopedic completeness, nor the sort of brief summaries provided by periodic annual reviews." The Editorial Board and the editors hope that this golden mean has been achieved: An absorbing, thorough, but nevertheless exemplary presentation should, with the aid of relevant examples, enable the reader to become accustomed with the numerous facets of the sensory system without sacrificing an overview of the subject.

The main issues of sensory physiology were formulated in the nineteenth and early twentieth centuries by JOHANNES MÜLLER, H. VON HELMHOLTZ, E. HERING, S. EXNER, J. VON KRIES, W. TRENDELENBURG, and E. D. ADRIAN, to name but a few. Modern development in the field has been characterized by interdisciplinary cooperation, the foundation for which was laid in the second half of the nineteenth century by VON HELMHOLTZ, EXNER, MAXWELL, and others. Progress made in biochemistry, physics, mathematics, and information theory has not only made possible unanticipated refinement of methods of measurement; it has above all permitted the transformation of mere hypotheses into established, accepted theories as well as revealing new problems. However, at the same time such development has, in recent decades, resulted in the literature becoming dispersed in specialist journals; consequently, it has grown increasingly difficult to survey. The editors have considered it an essential task to bring together the often very divergent areas of study in this handbook. Thus, sensory physiology is treated at all levels, from molecular processes to the phenomena of perception.

It has proved possible to implement the plan for the handbook as set out in 1970: "The series begins with a volume on general features of receptor processes in all modalities. It then progresses, in specialized volumes, to treatments of somesthesia, electroreception, chemical senses, audition and vestibular sensitivity and vision in all of its aspects. A concluding volume is planned to deal with problems of perception in so far as they transcend the individual sensory modalities" (Vol. I, p. VI). The original plan was extended in two directions: in Volume IX the development of sensory systems is treated and, finally, the physiology of vision in vertebrate and invertebrate animals has been handled in separate volumes. Both are topical areas, and their progress has nowhere been compiled in the form of a handbook.

The editors hope that the reader will try to uncover deficiencies in the handbook; deficiencies for which one cannot blame the editors but rather which show lacunae in our knowledge and will stimulate excursion into unresearched areas. It is precisely in this respect that this handbook is of value, since it provides a survey of the present state of research.

The editors are profoundly grateful to the nearly 400 authors who have made contributions to this handbook. "The writing of the chapter should be enjoyable rather than a chore" wrote the deceased member of the Editorial Board, Professor HANS-LUKAS TEUBER. Professor TEUBER himself admitted, however, that it can constitute one further obligation. The Editorial Board, editors, and readers owe special thanks to Springer-Verlag: Dr. Götze inspired the work; he dared to accept the undertaking and, together with his colleagues, did everything possible to give the work its present scope.

Munich

H. AUTRUM

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Chapter 1

Light and Dark Adaptation in Invertebrates

H. AUTRUM, München, Germany

With 47 Figures

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A. Introduction

The term "adaptation," in the broadest sense, denotes all those events that change the structure, form, function, or behavior of organisms in such a way that they are better adjusted to their surroundings. Such adjustment can span more than three billion years; this is adaptation in the evolutionary sense, a process that extends over many generations. An individual organism can also adapt to its changing environment, by maintaining homeostasis under altered conditions – adjusting to the winter cold, for example, and to the heat of summer. Annual rhythms (such as bird migration, diapause, or dormancy during drought) are adaptations to variation in climatic conditions. The diurnal rhythm of nearly all organisms, and nearly all physiologic processes down to the molecular level, is an example of an adaptive phenomenon that takes only a few hours. Environmental conditions can change in even shorter periods, within minutes or fractions of a second: a cloud passes across the sun, a butterfly flits between light and shade at the edge of a forest, and in both cases the eyes adapt to the changes in light intensity.

The time courses of adaptation, then, range from more than 10^9 years to 10^{-3} s; they vary by a factor of nearly 10^{20} . It comes as no surprise that the phenomena the word "adaptation" describes, and the mechanisms these involve, are enormously diverse.

Sense organs inform the organism about the current states of the internal and external milieu. Because the two have become quite different as animals evolved, the sense organs have adapted to quite different conditions – adapted in the evolutionary sense. Many sense organs are capable of adjusting rapidly, within hours, minutes, or seconds, to changing environmental conditions. This property is called sensory adaptation. A number of environmental factors change only slightly (examples include the content of ions in the blood, blood pressure, and the acceleration due to gravity). The associated sensors adapt over only a small range, and the sensory systems have a more or less linear characteristic (for example, baroreceptors in the carotid sinus and stretch receptors). Light intensity, by contrast, can vary by a factor of 10^{10} . In many cases visual adaptation is "adapted" (to combine the phylogenetic and physiologic senses) to this range of variation. In functional terms, visual adaptation shifts the working range of the visual system, and the characteristic curves are exponential (see Sect. C.III).

In the discussion that follows, visual adaptation is presented from two points of view: (1) Because the ability to respond to light developed very early in phy-

logeny, the mechanisms of visual processes as well as those of adaptation are rather similar in the various phyla. These few mechanisms form the basis on which this chapter is organized. (2) During evolution the different groups of animals, and often even different related species, developed a great number of variations and special adaptations (in the evolutionary sense). Within the animal kingdom, photoreceptors and eyes arose from unmodified cells with not-yet-determined special structures, along at least 40 different lines of phylogenetic development (SALVINI-PLAWEN and MAYR, 1977). Because the causes of this heterogeneity are not well known, and relatively few species have been studied, it is often difficult to fit the particular aspects of visual physiology that have been discovered into an orderly scheme, and premature schematization is very likely to obscure unsolved problems. Thus, the reader may feel that the assortment of detailed findings presented in the following sections is confusingly diverse; each such observation, however, deserves mention in a handbook. And after all, continual variations upon a few central themes are characteristic of biology and among its chief attractions.

Two basic mechanisms of visual adaptation are identifiable. First, in many eyes the photic environment of the primary receptor cells, which transform light into excitation, can be changed. This function is accomplished by regulation of the light flux from the outside world to the receptor cells by means of pupils of many different kinds (dynamic stimulus control; see Sect. E.I). Second, the sensitivity of the receptor cells themselves can change (dynamic sensitivity control; Sect. E.II). Several mechanisms are involved in sensitivity control. The initial event in the receptor cells is the absorption of light in photopigments (Sect. E.II.2). After certain intermediate steps, these photochemical processes are followed by electric phenomena (Sect. E.II.3). Because the response to light stimuli – in association with the wide range of possible light intensities – is nonlinear (Sect. C.III), special care must be taken in discussing such concepts as effectiveness (Sect. C.III) and sensitivity (Sect. C.IV).

The events involved in visual adaptation are far from being fully understood. They occur at many levels between stimulus and behavior and have been studied at many sites within the organism, and they are not always reflected in behavior. Some of the observations mentioned in the following discussion, though at first thought to reflect processes of adaptation, may have little to do with visual adaptation, e.g., the membrane shedding and renewal known to occur in the eyes of spiders (see Sect. E.I.6).

The most useful definition we can provide at present is: Visual adaptation as detected in physiologic and psychophysical experiments is a change in sensitivity of the visual system and its neuronal components. The crucial aspect of this definition is variability in time, depending on the light intensities. If a prolonged constant stimulus elicits a constant response, or if the responses to repeated identical stimuli are identical over a long period, the system is nonadapting. Visual adaptation is indicated whenever the response to a constant stimulus changes in time, or when the response can be kept constant over time only by varying the stimulus. In psychophysical experiments, for example, the time course of dark adaptation is determined by following the change in the intensity of a test stimulus just sufficient to elicit a visual sensation; this sensation represents a constant response, the threshold. In all threshold measurements, whether on humans or animals, the method

used should, of course, take into account the quantal nature of the light stimuli. For details of human measurements see the reviews by BARLOW (1972), BAUMGARDT (1972), NACHMIAS (1972), and BLACKWELL (1972); for insects see the review by SNYDER (1979). A different way to determine sensitivity is the measurement of behavioral or electrophysiologic response to a constant stimulus. Note that the test stimulus by which the time course of adaptation is measured (even with threshold measurements) must not itself bring about a change in the sensitivity of the system.

Whenever an entire organism is under study, whether human or animal, the site at which the adaptation occurs is problematic. To specify it, one would have to know either:

- 1) that the representation of the time course of the stimulus is isomorphic in all parts of the system – that is, uniformity must be demonstrable in the particular case concerned; or

- 2) what the laws are that govern the transformations that occur between the different parts of the system – that is, the transfer functions operating at each level must be available.

In no case so far studied has either of these conditions been met, although a partial analysis has been done in some instances (e.g., the action of the pupil in control of the light input; see below).

There is a possibility of semantic confusion in that “adaptation” has been applied both to the process of change and to the state eventually achieved. BARLOW (1972) has suggested that the term “temporal adaptation” be used with reference to a system that is not yet in equilibrium – one that is still changing in time. Under constant conditions, the system approaches equilibrium; because the approach is asymptotic, the decision as to when equilibrium has been achieved is somewhat arbitrary, and different time constants are sometimes given for a particular system by different authors. The state of equilibrium, in which (under constant conditions) the response remains essentially the same indefinitely, is called “steady-state adaptation” (the term “completed adaptation” is also occasionally used).

B. The Function of Adaptive Processes

Many organisms live in environments where the mean light intensity can vary considerably. Their visual systems master this situation, having the capacity to alter their range of sensitivity (see Sect. C.IV.4). It is important to the organism that not only should its visual system shift its range of light sensitivity as the brightness of the surroundings changes, but that as far as possible, the contrasts in the environment should be maintained (contrast constancy) – both the brightness contrasts and the contrasting colors of objects. Only at the limits of the system’s capacity – when the mean brightness of the surroundings is very low or high – do both contrast sensitivity and certain color parameters change. An example of extreme dependence of color perception on brightness in vertebrates is given by the Purkinje effect. This effect depends on the presence of two anatomically and functionally

different receptor systems, the rods and cones. Among the invertebrates – perhaps with the exception of *Limax* (SUZUKI et al., 1979) – there is no phenomenon comparable to the vertebrate Purkinje effect (THOMAS and AUTRUM, 1965; bee). The differences between the peripheral visual cells R 1–6 and the central R 7/8 of dipterans cannot be discussed in this regard, in particular as their functions have not yet been clarified unequivocally (see HARDIE, 1979; SMOLA and MEFFERT, 1979).

Two types of units exist in the eyes of the scallop, *Pecten*. The depolarizing receptor cells in the proximal layer are inactivated by higher light intensities (2 log units) which were adequate stimuli for the distal photoreceptors. The threshold of the proximal layer cells is 2 log units lower than the threshold of the distal hyperpolarizing photoreceptors (MCREYNOLDS and GORMAN, 1970b). There is, however, no indication either of color vision or of any sort of Purkinje shift (see also MESSENGER, Chap. 2, this volume).

C. Electrophysiology and Adaptation

Adaptation processes in receptor cells and neurons are mostly measured by electrophysiologic techniques. This method raises the questions: Of what kind are the relationships between electric responses, either receptor potentials or axonal spikes, and adaptation, i.e., sensitivity changes? Is the electric response an adequate measure of adaptation? And: As the word “sensitivity” is given different meanings, the concept of sensitivity needs precise definition(s).

Electrophysiologic recordings from photoreceptors show that the receptor potential in response to a square-wave stimulus initially rises rapidly to a maximum and then declines, first sharply and then more slowly (transient phase). This phase is followed by a plateau during which the potential falls off much more slowly (BERNHARD, 1942; HARTLINE et al., 1952; BURKHARDT and AUTRUM, 1960; DeVoe, 1962; STIEVE, 1965; PINTER, 1966; and others; for a review see, e.g., GOLDSMITH and BERNARD, 1974; for the forms of different receptor potentials see FUORTES and O'BRYAN, 1972, this handbook, Vol. VII/2, Fig. 22, p. 308). In arthropods and many other invertebrates these potentials are depolarizing; hyperpolarizing receptor potentials occur, for example, in the photoreceptors of the distal layer of the eyes of the scallop *Pecten* (TOYODA and SHAPLEY, 1967; MCREYNOLDS and GORMAN, 1970a, b; for a review see FUORTES and O'BRYAN, 1972) and have shapes which are mirror images of those of the depolarizing receptor potentials.

All-or-none impulses are rare in invertebrate photoreceptor cells (a few scorpions: BELMONTE and STENSAAS, 1975; cephalopods: MACNICHOL and LOVE, 1961; *Pecten*: HARTLINE, 1938). The eccentric cells in the ommatidia of *Limulus* are second-order neurons (see Sect. E.I.3.a).

I. The Plateau of the Receptor Potential is Not the Steady State

The use of brief stimuli can mislead one into regarding the plateau as a constant level; the time constant of potential decay can be so large that over short times (a few seconds) no change is recorded (cf. STIEVE et al., 1976). Steady state (final equilibrium) and plateau are thus different things, and the two should not be used as synonyms.

Frequently the transient phase of the receptor potential is used to measure the time course of adaptation (for example, during adaptation to different intensities or different durations). The changes in the transient potential (latency, slope, amplitude) are then said to reflect short-term adaptation, whereas changes associated with the plateau indicate long-term adaptation. To the extent that simultaneous measurements of sensitivity are made, there is no objection to these terms.

II. Electrophysiologic Responses as a Measure of Adaptation

In electrophysiologic experiments, as a rule (with invertebrates) the electric response observed is that of a single photoreceptor or interneuron when intracellular recording is used, and the summed potentials of several receptors (electroretinogram, ERG) when the electrode is extracellular. A light stimulus elicits responses which are measured – depending on the conditions of the experiment – as a current, voltage, or impulse frequency. But changes in magnitude and time course of response need not be associated with adaptation. The level of response (current, voltage, or impulse frequency) can be quite different in a given state of adaptation and vice versa (see below, Sects. E.II.1. and E.II.3.).

III. Efficiency

The relationship between a stimulus and the electric response is called the efficiency of the stimulus. If the response is plotted as a function of the log of the intensity of the stimulus, an efficiency curve is obtained (Fig. 1). Its shape, to a first approximation, is that of a hyperbolic function of the form

$$V = \mu \cdot V_{\max} \cdot \frac{I}{\mu I + 1}$$

where V_{\max} is the magnitude of the maximal response at saturation, I is the stimulus intensity, V is the magnitude of the response, and μ is the sensitivity parameter (LAUGHLIN, 1975 a). μ is the reciprocal $1/I$ of a stimulus of intensity I that elicits a response of amplitude $V_{\max}/2$. μ is thus a measure of sensitivity (see Sect. C.IV).

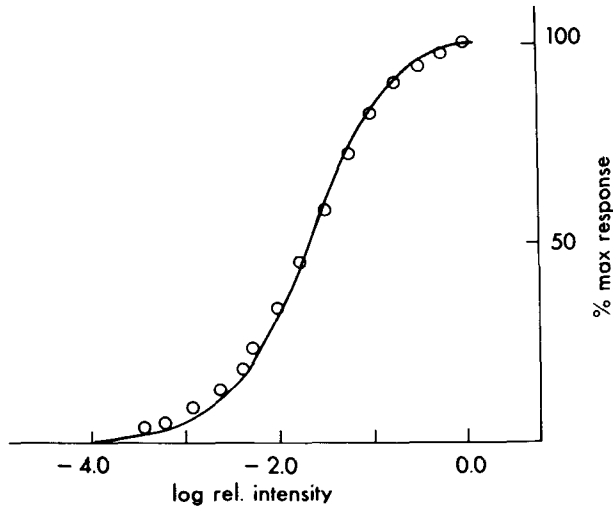


Fig. 1. A typical dragonfly (*Hemicordulia*) retinula cell intensity/response function plotted as a $V/\log I$ curve. Each point shows the peak response (normalized to percent maximum response at 56 mV) at the corresponding stimulus intensity. The points have been fitted by eye with a hyperbolic tangent function (LAUGHLIN, 1975a)

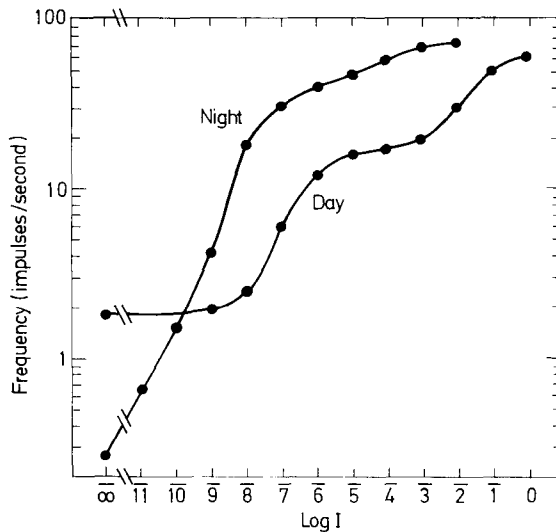


Fig. 2. Intensity (I) characteristics for daytime and nighttime responses from an ommatidium of *Limulus* lateral eye in situ with the optic nerve trunk uncut. The mean firing rate of the single optic nerve fiber during the last 3 s of a 6-s flash is plotted on the ordinate as a function of the logarithm of the relative light intensity plotted on the abscissa. "Day" responses were responses from 9 to 10 p.m. The animal remained in the dark between the test flashes and between the daytime and nighttime recording periods. In darkness ($\log I = -\infty$) the spontaneous activity of the optic nerve fiber was about 2 impulses per s during the day and 0.2 impulse per s at night. At $\log I = 0$, approximately 10^{12} quanta per second are incident on the ommatidium at the cornea from 400 to 650 nm (BARLOW et al., 1977)

As a rule, the efficiency curve is called the $V/\log I$ function. It agrees with the theoretical curve obtained under the assumption that each absorbed photon opens the same number of conductance channels in the membrane (SHAW, 1968), independent of the number of conductance channels already open. (It should be mentioned that the experimental $V/\log I$ curves agree, in general, only to a good approximation with the theoretical form. Often the function is modified with I^n and n varies between 0.5 and 1. For details see LAUGHLIN, Vol. VII/6B of this handbook, Chap. 2., Sect. E.II.3.c)

This is not always the case. When the voltage gain – the number of conductance channels opened per absorbed quantum – changes with adaptation, the $V/\log I$ function is shifted vertically, parallel to the V axis (Fig. 2). Such a shift occurs during efferent control of sensitivity in the lateral eye of *Limulus* (BARLOW et al., 1977; see Sect. E.I.2.a.γ) and in higher-order neurons of insects (see LAUGHLIN and HARDIE, 1978; and Vol. VII/6 B of this handbook, Chap. 2).

IV. Sensitivity

During temporal adaptation (see Sect. A), there is a change in the sensitivity of the system (or of one or all of its elements). The word “sensitivity” is also given different meanings, so that in each case it should be specified which connotation of the general term is intended. Traditional sensory physiology regarded the receptors as energy transformers (VON FREY, 1896). Even disregarding the sense organs that fire (spontaneous) impulses in the stationary state, there are two arguments against this view:

(1) In photoreceptors the effective quantity is not the energy but the number of quanta absorbed, and (2) sense organs often consist not only of the receptor cells but of associated accessory devices that transform the stimulus. For the organism and its behavior, the content of the signal (the “information”) is of concern, not the measurement of energies and quantum numbers. Thus, in many sense organs the properties of the accessory apparatus are more important to behavior than the process of transformation in the receptor cells (e.g., the stretch receptors of crustaceans, proprioceptors of the sinus caroticus, Pacinian corpuscles (see review by LOEWENSTEIN, 1972), muscle spindles (review by OTTOSON and SHEPHERD, 1972), viscoelastic deformation in the stimulus-conducting apparatus of campaniform sensilla in the cockroach *Blaberus* (CHAPMAN et al., 1979); for mechanoreceptors see reviews in SCHWARTZKOPFF, 1974).

Spectral efficiency curves (Sect. C.III) are obtained by stimulation with monochromatic lights having equal numbers of quanta; the amplitude of the receptor potential characterizes the relative effectiveness of lights of different wavelengths or intensities ($V/\log I$ function). A more physiologically relevant description, however, is given by sensitivity curves. In order to determine the sensitivity of a receptor under different conditions of adaptation, the efficiency ($V/\log I$) curve must be measured over the entire voltage range of the receptor or neuron. From this curve one can then find, for each potential amplitude V , the corresponding (relative) illuminance (of the eye or an ommatidium or a rhabdom or rhabdomere) of the

stimulus light in numbers of quanta. The sensitivity is the reciprocal of the stimulus levels eliciting responses of equal magnitude (AUTRUM and VON ZWEHL, 1964, p. 361). The relative spectral sensitivity is given by $I(\lambda)/I_{\max}$ for a specified response magnitude (e.g., $V_{50} = 50\%$ of the maximal response; see equation in Sect. C.III), whereas $V(\lambda)V_{\max}$ is the relative spectral efficiency.

Because sensitivity can be related to entirely different aspects of the response of a cell, a visual interneuron or a neuronal system (re behavior see below, Sect. C.I), it must be defined in each individual case by the nature of the response observed (e.g., transient phase, plateau) and the methods used. The forms of sensitivity commonly considered are as follows.

1. Absolute Sensitivity

The *absolute sensitivity* of a receptor is measured for any desired state of adaptation, for a constant response, and as a rule for a response amplitude 50% of the maximum response (V_{\max} according to LAUGHLIN, 1976a; other terms include, for example, the h_{\max} of STIEVE, 1973, and his group).

A V_{\max} of 50% is not entirely an arbitrary choice, for it is at this level that the slope of the $V/\log I$ function is maximal. The reciprocal of the corneal irradiance in quanta $\cdot \text{cm}^{-2} \cdot \text{s}^{-1}$ gives the absolute sensitivity. Prerequisites for comparison of the absolute sensitivities of different photoreceptors are (1) the use of parallel [from a point light source at a sufficient distance (cf. also SNYDER, 1979, this handbook, Vol. VII/6A, Chap. 5, Sect. C, pp. 268–279; for comparison of the absolute sensitivities of the eyes of insects and vertebrates see KIRSCHFELD, 1974; see also the review by SNYDER, 1979, this handbook, Vol. VII/6A, Chap. 5, Sect. C.I, p. 269 ff. and 290)] monochromatic light with maximal spectral efficiency; (2) that the light be directed exactly along the optical axis of the dioptric apparatus; and (3) that the $V/\log I$ functions of the cells can be superimposed by shifting along the $\log I$ axis – that is, that they have the same shape. The quantal corneal irradiance under these precisely defined conditions has been called PAQ_{50} (peak axial quantal irradiance to produce a response of 50% of maximal) by LAUGHLIN (1976a). The sensitivity for these conditions is the reciprocal of PAQ_{50} , and is called APS_{50} (axial peak sensitivity at 50% V_{\max}).

Note that this definition of absolute sensitivity does not involve measurement of the absolute threshold, i.e., the minimal number of quanta that produce a response just barely distinguishable from the noise. But given constant conditions it does enable comparison between different receptors (see, e.g., KIRSCHFELD, 1974; LAUGHLIN, 1976; SNYDER, 1979).

For the study of photoreceptor sensitivity, LAUGHLIN and HARDIE (1978) and HARDIE (1979) have given three further operational definitions:

2. Increment Sensitivity

This is the instantaneous gain, defined as $d(\text{output})/d(\text{input})$; for measurement of the receptor potential in volts (V) the units of increment sensitivity are dV/dI (WERBLIN, 1974).

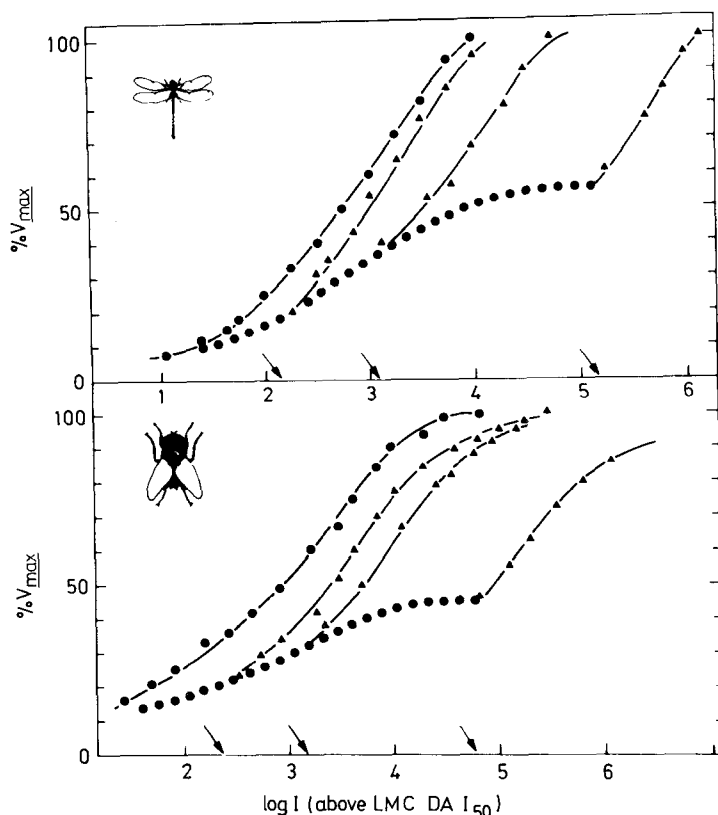


Fig. 3. Dark- and light-adapted intensity/response functions of fly (*Calliphora*) and dragonfly (*Hemicordulia*) photoreceptor cells presented as $V/\log I$ curves. Total amplitudes of the peak voltage responses, measured as total deflection from dark-adapted rest potential, are plotted against log of total intensity during the test flash, $\log(I_o + I_t)$. —●—●— = responses from dark-adapted cell; -▲-▲- = responses from cells light-adapted at intensities indicated by arrows; ●●●●● = amplitudes of steady-state responses to continuous background illumination (LAUGHLIN and HARDIE, 1978)

3. Detection Sensitivity

Also called quantum sensitivity, this is the reciprocal of the stimulus intensity required to produce a criterion signal-to-noise ratio. All else being equal (e.g., voltage gain per quantum and membrane noise), it is proportional to quantum capture efficiency — i.e., the fraction of quanta in the stimulus that is effectively absorbed by the photopigment.

4. Range Sensitivity

This is the reciprocal of the intensity required to produce a criterion absolute voltage response (e.g., 50% V_{\max}). Range sensitivity defines the intensity region within which the dynamic range lies (in a galvanometer, for example, the reciprocal

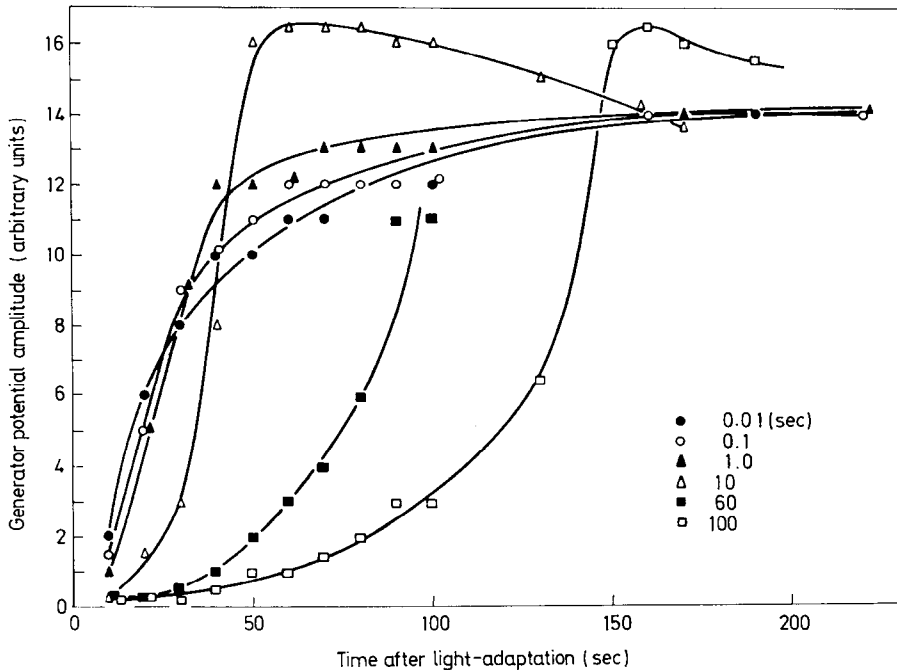


Fig. 4. *Limulus* lateral eye. Dark adaptation curves plotted for constant-stimulus runs which were preceded by light adaptation periods of various durations. The intensity of the adapting light was 0.00 log units for all runs. The durations of the light adaptation periods are tabulated on the figure. The run numbered 60 s was a short control run (BENOLKEN, 1962)

of the input signal producing maximal deflection). For curves with comparable $V/\log I$ slope, range sensitivity defines the position of the response-intensity function on the log-intensity axis. For different levels of steady-state adaptation, the $V/\log I$ curves can be superimposed by shifting parallel to the abscissa (NAKA and KISHIDA, 1966; GLANTZ, 1968; DÖRRSCHEIDT-KÄFER, 1972; BADER et al., 1976; LAUGHLIN and HARDIE, 1978) (Fig. 3).

All these terms are used in the context of optimal conditions, specified above. If the incident light is not exactly axial, the amplitude of the response decreases. This *angular sensitivity* can change with state of adaptation – e.g., in arthropods with effective pupil size (see SNYDER, 1979, this handbook, Vol. VII/6A, Chap. 5, Sect. D.II).

5. Polarization Sensitivity

The sensitivity to polarized light demands special definitions. The following terms are applied (WEHNER et al., 1975; WEHNER and BERNHARD, 1976; BERNHARD and WEHNER, 1977; personal communication by R. WEHNER); different definitions are cited by WATERMAN (Vol. VII/6B of this handbook, Chap. 3):

(1) Polarization *sensitivity* refers to the capacity of a photoreceptor, a visual interneuron, or the whole animal to change its response with changing *e*-vector di-

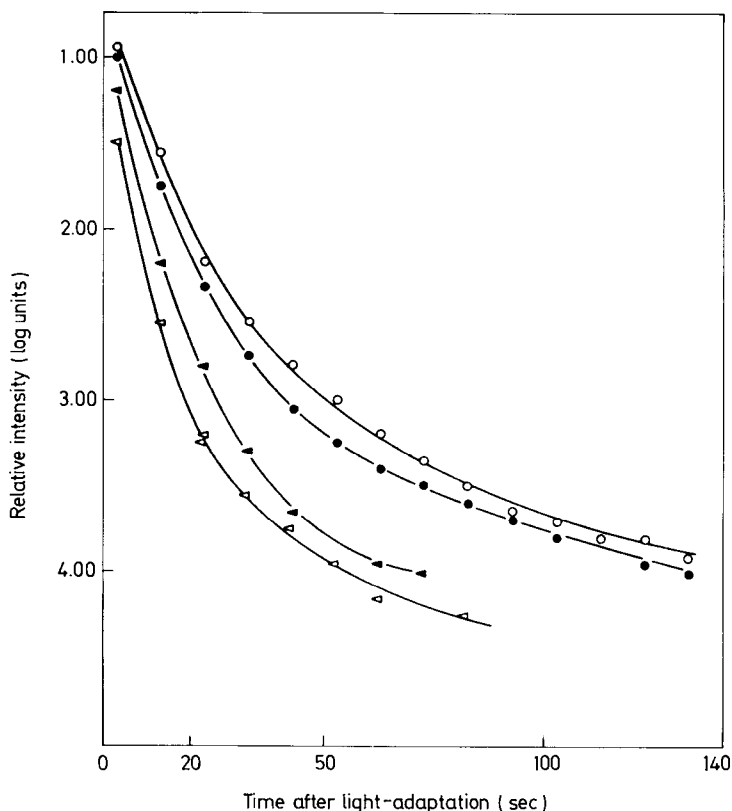


Fig. 5. *Limulus* lateral eye. Dark adaptation curves plotted for constant-response runs which were preceded by light-adaptation periods of various durations. The intensity of the adapting light was 0.00 log units for all runs. The durations of the light adaptation periods were 120 s, 70 s, 30 s, and 10 s, respectively, for the upper through the lower curves. The same constant-response criterion was used to plot all curves. The sensitivity of the eye increases in a downward direction on the curves (BENOLKEN, 1962)

rection Φ . Physiologic responses depend on Φ . (2) Polarization *detection* refers to the way *e*-vector directions are determined within the visual system. For polarization detection to occur, *e*-vector directions must be determined independent of the intensity and degree of polarization; Φ is determined irrespective of *I* and *d*. (3) *Orientation* by polarized light in addition requires some knowledge of the pattern of polarized light in the sky (*e*-vector pattern).

6. Efficiency and Sensitivity

Measurements of the constant-stimulus/response function or of the constant-response/stimulus function of a given preparation do not always give the same curves for the time course of adaptation, as one might expect. As a rule, the response measured (in invertebrates) is the amplitude of an electric potential. Even