of the beam. However, one can assume homogeneous spatial distributions to obtain estimates of the average cross sections of large numbers of observed insects. Estimates of the number of insects as a function of height can also be made. Figure 3 is an example of such an estimate for an 18-hour observation period at the Salton Sea under clear sky conditions. Because of the inherent minimum range of the radar, no insect could be detected below 50 m. Furthermore, no correction has been made for either the increase of the sampling volume with height (inherent with a conical beam) or the decrease of signal intensity with height. Two pronounced features are evident in Fig. 3: (i) the large increase in the insect density after sunset and after sunrise, indicating nocturnal and daytime insects, respectively; and (ii) the two-layer structure for the nocturnal insects. One layer of insects is centered around 150 m, the other at 400 m. This nocturnal layering appeared to be associated with atmospheric structure. A meteorological sounding balloon released at 1943 P.S.T. revealed a small temperature inversion and humidity decrease at 350 m which is located between the two layers of maximum insect density. The apparent localization of insect flight elevations above and below the region of changing atmospheric structure may result from the influence of certain atmospheric conditions or winds (wind information was not available during this test period), or, more likely, may represent different species of insects.

These results suggest that the FM-CW radar is capable of simultaneously sensing insects and atmospheric structure and that insect flight is influenced by atmospheric structure. Correlations between atmospheric structure and insect activity were detected in both arid and humid locations.

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26 February 1973; revised 2 April 1973

Intracellular Recordings from Single Rods and Cones in the Mudpuppy Retina

Abstract. *Mudpuppy rod and cone responses differ both in time course of recovery and in absolute sensitivity. Rods are about 25 times more sensitive than cones and appear to generate a larger voltage per quantum absorbed. Comparison of mudpuppy receptor sensitivities to those of other vertebrates suggests that the difference in sensitivity between rods and cones may be a general phenomenon.*

Most vertebrate retinas contain two kinds of photoreceptors—rods and cones. These photoreceptors, together with the interneurons that process receptor signals, form two relatively independent visual systems. Much has been learned about the different properties of these two (often called the scotopic and photopic) systems (*1*), but little is known about the differences between the two kinds of photoreceptors themselves. For example, it is well known that rod vision is more sensitive than cone vision, but much of this difference may be due to differences in the connections of interneurons that process the two kinds of receptor signals. It is not yet known whether the photoreceptors themselves differ in sensitivity. Previous investigations have suggested that rod and cone responses may have different time courses of recovery (*2*), but this difference has not yet been demonstrated directly.

In order to compare the responses and sensitivities of rods and cones, the signals of the rods must be isolated from those of the cones, and the signals of the receptors must be isolated from those of other visual neurons. One way to do this is to record intracellularly from single photoreceptors. Intracellular recordings have been made from single rods and cones (*3*), but the responses of both kinds of photoreceptors have not yet been recorded from the same retina. This report will describe recordings from both the rods and cones, made from the retina of the mudpuppy, *Necturus maculosus*. This animal was chosen for these experiments because it has large retinal cells and because it appears to have only one rod pigment (λ_{max} about 525 nm) and only one cone pigment (λ_{max} about 575 nm) (*4*). Our recordings confirm that rod and cone responses differ greatly in their time course of recovery after brief flashes of light; they also show that single rods are more sensitive than single cones.

Eyes from dark-adapted mudpuppies were enucleated in dim red light. The cornea and lens were dissected away, and the eyecup was placed on moist cotton. Before the insertion of each micropipette, the retina was allowed to dark-adapt further until the threshold for the b-wave of the electroretinogram stabilized (approximately 10 minutes) (*5*). Fine micropipettes, 200 to 800 megohms in resistance as measured in the vitreous, and filled either with 1*M* potassium acetate or 2*M* potassium chloride, were used to penetrate photoreceptors. The retina was illuminated from above with one of two dual-beam photostimulators (*6*). The last lens in the light beam of both stimulators had a small diameter and long focal length, so that the light illuminating the retina was nearly collimated (*7*). Since penetrations were always made into the central region of the eyecup, the light from the photostimulators was approximately parallel to the long axis of the receptors whose responses were measured.

The penetration of a photoreceptor was signaled by a sudden negative shift in potential (~30 mv). Receptor responses could be distinguished from those of other cells in the retina by their small receptive fields, short absolute latencies, fast rise times, and characteristic waveforms to brief flashes of light (*8*). Spectral sensitivity curves, constructed by measuring intensity-response curves at a number of different wavelengths, were used to separate

receptor responses into two groups: one maximally sensitive at 525 nm and the other maximally sensitive at 572 nm. Two spectral sensitivities chosen from each group are plotted in Fig. 1A. The solid curves are the log relative absorbances of mudpuppy rod and cone photopigments obtained from macrospectrophotometry on whole mudpuppy retinas by Brown (*9*). The spectral sensitivities of the receptors are in excellent agreement with the curves for photopigment absorbance. Since mudpuppy rods appear to have a photopigment which absorbs maximally at about 525 nm (*4*), receptors with peak sensitivity at 525 nm were identified as rods; similarly, those with peak sensitivity at 572 nm were identified as cones.

Figure 1B compares the dark-adapted responses of a rod and a cone to short (0.2-sec) flashes of diffuse, monochromatic light. The number to the left of each response gives the equivalent intensity at the λ_{max} of the photoreceptor in log quanta/cm^2-flash. Both receptor types respond with graded hyperpolarizations. The cone response consists of an initial transient peak, followed by a brief plateau and then by a rapid return of the response to the baseline. Flashes of longer duration increase the duration of the plateau but leave other features of the response unchanged. The waveform of the rod response is similar to that of the cone. Both response types have comparable latencies and rise times at any intensity

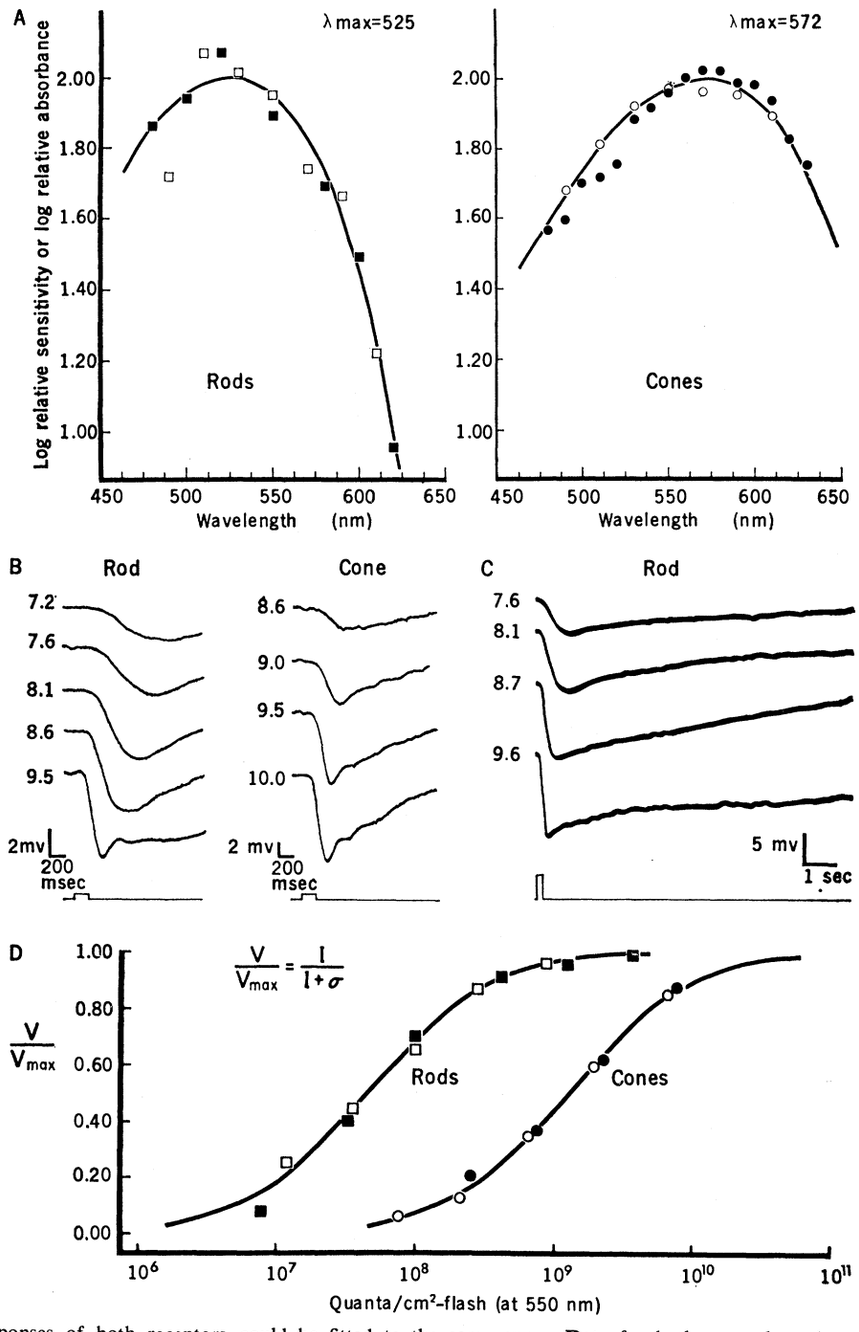

Fig. 1. Responses and sensitivities of single rods and cones. (A) Spectral sensitivities of mudpuppy photoreceptors, plotted against absorbance curves for rod and cone photopigments (*9*). The spectral sensitivity at each wavelength is the inverse of the intensity of light necessary to evoke a criterion response. The criterion responses were chosen to be one-half of the maximum light-evoked response (½ V_{max}). Since intensity response curves for different wavelengths were all parallel to one another along the intensity axis for both groups of receptors, the selection of a criterion response did not affect the shape of the spectral sensitivity curves. (Left) The log relative spectral sensitivities from two cells classified as rods (open and filled squares) and the rod pigment log relative absorbance from macrospectrophotometry on whole mudpuppy retinas (curve). (Right) The log relative spectral sensitivities from two cells classified as cones (open and filled circles) and the cone pigment log relative absorbance from macrospectrophotometry on whole mudpuppy retinas (curve). (B) Comparison of rod and cone responses. Amplitude calibration for rod is twice that for cone. Flashes were 180 msec long and at 510 nm for the rod and 600 nm for the cone. Relative absorbance curves of Fig. 1A were used to convert the quantum intensities of the flashes into equivalent intensities at the λ_{max} of the rod or cone visual pigment. The number to the left of each response gives the equivalent intensity in log quanta/cm^2-flash. Rod and cone responses have comparable absolute latencies and rise times when measured at the same intensity, but they have different time courses of recovery. (C) Responses of a second rod on a much longer time scale, showing the slow recovery of the rod response. Even at the dimmest intensity, the rod response does not completely recover 10 seconds after stimulation. Flashes were 190 msec long at 550 nm and were given at 25-second intervals. The quantum intensities of the flashes were converted into equivalent intensities as in Fig. 1B, and the equivalent intensities in log quanta/cm^2-flash are given to the left of each response. (D) Intensity-response curves of mudpuppy photoreceptors. Peak amplitude of response measured as a fraction of the amplitude at saturation for the two most sensitive rods and cones, plotted against the log of the incident quantum intensity at 550 nm. At this wavelength, the relative percent absorptions of rod and cone photopigments are almost identical. Open and filled symbols are used to refer to the same cells as in Fig. 1A. Data for both rods have been shifted 0.1 log unit along the intensity axis (filled squares to left and open squares to right) so that the responses of both receptors could be fitted to the same curve. Data for both cones have been shifted 0.04 log unit (filled circles to right and open circles to left). The equation given in the figure has been fitted to both sets of data by choosing appropriate values for σ. The average value of σ for the two rods is 7.66 and for the two cones 9.10 log quanta/cm^2-flash. The rods are over 1.4 log units more sensitive than the cones.

at which they both could be measured. However, the initial transient of the rod response is more variable in size from cell to cell than that of the cone and is present only at saturating light intensities. In other species, receptors show an initial transient which appears to be formed by horizontal cell inhibition feeding back onto receptors (*10*). It is possible that the initial transients of mudpuppy rods and cones also reflect receptor-horizontal cell interaction. Since horizontal cells in the mudpuppy receive much of their synaptic input from cones (*11*), it is likely that they would inhibit receptors only at light intensities bright enough to produce large amplitude responses in the cones. This may explain why rod responses show initial transients only at bright light intensities.

Although rod and cone responses resemble one another in many respects, they do differ strikingly in their time course of recovery. Rod responses return to the baseline much more slowly than cone responses, whether the two are compared at the same amplitude of response or at the same intensity. Figure 1C illustrates the slow recovery of the rod response. In addition, rods consistently appear to be more sensitive than cones. For example, a light of 8.6 log quanta/cm^2-flash gives a nearly saturating response in a rod (Fig. 1, B and C) but barely stimulates a cone.

Figure 1D gives the normalized intensity-response curves of the two most sensitive dark-adapted rods and the two most sensitive dark-adapted cones for short flashes (*12*) of full-field illumination at 550 nm (*13*). At this wavelength, the relative percent absorptions of rod and cone photopigments ($A_{550}/A_{\lambda max}$) are almost identical. The data points for both kinds of photoreceptors have been fitted with the equation

$$\frac{V}{V_{max}} = \frac{I}{I+\sigma} \qquad (1)$$

where V is the peak amplitude of the light-evoked response at intensity I, V_{max} is the peak amplitude at the saturation of the response, and σ is the intensity necessary to give a response of ½ V_{max}. This equation has been shown to describe the intensity-response curves for full-field illumination of the rods of the rat (*14*), skate (*15*), and nocturnal gecko (*16*), and of the cones of the turtle (*17*) and pigeon (*18*). The intensity-response curves of mudpuppy rods and cones also closely fit this equation, but the rods are over 1.4 log units more sensitive than the cones.

Table 1. σ (quanta absorbed per receptor-flash at the half-maximal response) for receptors of mudpuppy and several other vertebrates.

Animals	σ	
	Rods	Cones
Mudpuppy	31	275
Rat (*14*)	30 to 50	
Skate (*15*)	30	
Turtle (*17*)		1150 to 2300
Primate (*22*)		3500

There are several possible explanations for this difference in sensitivity. Rods could have a greater density of pigment than cones and so could absorb a greater percentage of the quanta passing through their outer segments. However, measurements of mudpuppy rod and cone pigment densities suggest that the two kinds of photoreceptors absorb nearly the same percentage of quanta (*4*). A second possible explanation is that rod outer segments could have a larger cross-sectional area and so intercept larger numbers of quanta. However, the ratio of rod to cone cross-sectional areas in mudpuppy can account for less than 0.5 log unit of the difference in sensitivity (*19*). Thus even when rod and cone sensitivities are corrected for differences in pigment absorption and in diameter, they still differ by about 1 log unit.

This remaining log unit appears to be the result of an intrinsic difference in *gain* between the two kinds of photoreceptors. We define gain as the magnitude of the response per quantum absorbed, or V/I. Equation 1 predicts that, at dim light intensities ($I \ll \sigma$), photoreceptor responses will be linearly proportional to light intensity [see, for example, (*15*)] and will follow the equation

$$V = \frac{V_{max}}{\sigma} I \qquad (2)$$

Hence, near threshold, the gain of a photoreceptor will be equal to the ratio V_{max}/σ. The gains of mudpuppy rods and cones in the linear regions of their responses can be compared by comparing the ratios V_{max}/σ; but since the values of V_{max} were similar for the most sensitive rods and cones (*20*), the gains can be compared simply by comparing σ's. Table 1 lists σ for mudpuppy rods and cones in quanta absorbed per receptor-flash calculated from the intensity-response curves of Fig. 1D, the pigment concentrations given by Liebman (*4*), the receptor dimensions of Brown *et al.* (*19*), and the pigment absorbance curves of Fig. 1A. Since σ is smaller for the rods than for the cones, the gain (V_{max}/σ) is larger; the average gain for the two rods is about 280 μv per quantum absorbed and for the two cones about 45 μv per quantum absorbed. The rods generate a large voltage change per quantum absorbed than do the cones.

Table 1 also lists σ for the rods and cones of several other species. Since σ is the number of quanta absorbed per receptor-flash at the half-maximal response, it is a measure of the sensitivity of the various rods and cones (*21*). The sensitivity of mudpuppy rods is in good agreement with the sensitivity of rat and skate rods. The rods from these animals are much more sensitive than the cones from the mudpuppy, turtle, and primate. This suggests that rods, wherever they occur among vertebrates, may all have about the same sensitivity and that rods may be universally more sensitive than cones.

Note added in proof: D. A. Baylor and A. L. Hodgkin (*24*) have recently made extensive measurements of the absolute sensitivities of turtle cones. They calculated that the two most sensitive cones had gains of about 25 μv per quantum absorbed. Since V_{max} for these two cones was about 15 mv, we estimate σ to be about 600 quanta absorbed per receptor per flash. This estimate of σ is close to the value reported here for mudpuppy cones and indicates that cones may be more uniform in their sensitivity from species to species than is suggested by the measurements of Table 1.

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(giving 67 percent absorption at λ_{max}) and for the cones 0.384 (giving 59 percent absorption at λ_{max}). These densities are probably too high, since the spectral sensitivities of the photoreceptors are narrower than pigment absorption curves based upon these peak densities.

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12. Experiments on mudpuppy horizontal cells (*11*) have demonstrated that dark-adapted cone receptors show complete temporal summation of absorbed photons for flash durations up to 500 msec (that is, the product of the duration of stimulation and the intensity of light necessary to produce a criterion response is a constant for durations as long as 500 msec). Rod responses decay more slowly than cone responses, and so rods probably sum photons for durations at least as long as cones. The flashes of light used to measure rod and cone absolute sensitivity (as in Fig. 1D) were less than 200 msec in duration and so were almost certainly within the summation times of both receptors.
13. Both stimulators were calibrated for absolute light intensity by placing a United Detector Technology PIN-5 diode in the position normally occupied by the eyecup. The output of the diode in the unbiased mode measured against a calibrated Kipp and Zonen compensated thermopile was 2.80 ± 0.47 watts/amp at 550 nm (13 measurements). A calibrated Eppley thermopile gave a second value within the standard deviation of the first. Lamps in both stimulators were driven by regulated power supplies, and lamp outputs did not vary from day to day by more than ± 10 percent. Variations of intensity across the field of stimulation were no greater than ± 5 percent.
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20. V_{max} ranged from 3.5 to 21 mv for rods and 5 to 14.5 mv for cones. For the photoreceptors shown in Fig. 1, A and D, V_{max} was 5.6 mv (open squares) and 13 mv (filled squares) for the two rods and 12.5 mv (open and filled circles) for the two cones. V_{max} for the cones was not actually measured but was estimated from the shapes of the intensity-response curves for all of the wavelengths where the sensitivity was determined. The largest responses actually measured for the two cones were 11.1 mv (open circles) and 11.8 mv (filled circles). Hence it is unlikely that V_{max} was overestimated. It is possible that V_{max} was underestimated; but if V_{max} was underestimated, σ would also have been underestimated, and the difference between the sensitivities of rods and cones would be even greater than that given in Table 1.
21. Table 1 includes only determinations of σ made from recordings of receptor potentials. The determinations of σ for skate and rat rods and for primate cones were made by extracellular recording; those for mudpuppy rods and mudpuppy and turtle cones were made by intracellular recording. Since the isolated extracellular receptor response has been shown to be proportional to the intracellular receptor potential (*16*), the values of σ determined extracellularly can be compared to those determined intracellularly. However, the values of V_{max} measured extracellularly cannot be compared to those measured intracellularly. Hence Table 1 can be used to compare only the sensitivities of these various rods and cones and not their gains.
22. R. M. Boynton and D. N. Whitten, *Science* **170**, 1423 (1970). We have calculated σ from their data assuming equal numbers of two kinds of cones in the primate fovea (λ_{max}'s of 535 and 570 nm) each 1 μm in diameter and with peak absorption of 50 percent. It should be noted that these authors reported that primate cones have a broader intensity-response curve than any vertebrate photoreceptor so far recorded. Their data fit the equation, $V/V_{max} = (I^n)/(I^n + \sigma^n)$, with n equal to 0.7. If primate cones have an intensity-response function similar to that of other vertebrate receptors (that is, $n = 1.0$, σ would be smaller than the value given in Table 1. In that case, we estimate that σ could be as small as 350 quanta absorbed per receptor-flash, which is close to the value we report for mudpuppy cones.
23. Preliminary results of these experiments were reported at the meeting of the Association for Research in Vision and Ophthalmology, Sarasota, Florida, 24–28 April 1972. Supported in part by an NIH traineeship to G.L.F. (P10-6606) and an NIH research grant to J.E.D. (EY-00824). This research was begun at the Wilmer Institute, Johns Hopkins University School of Medicine, Baltimore. We thank Paul K. Brown, Daniel G. Green, John E. Lisman, and William R. Wooten for helpful advice and for critical readings of the manuscript, Ralph Nelson and Jung Ming Wu for assistance in designing and building electronic equipment, and P. S. Sheppard for preparing the illustrations. This report is part of a dissertation submitted by G.L.F. in partial fulfillment of the requirements for a Ph.D. degree from the Biophysics Department, Johns Hopkins University.
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23 March 1973

Enzyme Release from Polymorphonuclear Leukocyte Lysosomes: Regulation by Autonomic Drugs and Cyclic Nucleotides

Abstract. *Osmotic release of β-glucuronidase from polymorphonuclear leukocyte lysosomes is inhibited by catecholamines and adenosine 3′,5′-monophosphate, and accelerated by cholinergic agents and guanosine 3′,5′-monophosphate. These actions are specific for the sympathetic and parasympathetic neurotransmitters and for the two cyclic nucleotides, as phenylephrine, tyramine, choline, adenosine 5′-monophosphate and guanosine 5′-monophosphate do not modify lysosomal enzyme release.*

That norepinephrine and epinephrine inhibit the release of enzymes from liver lysosomes in vitro (*1*) may be an indication that the sympathetic nervous system participates in modulating lysosome membrane integrity and that the action of the catecholamines is mediated by adenosine 3′,5′-monophosphate (cyclic AMP), since phosphodiesterase inhibitors enhance and β-adrenergic receptor antagonists block the action on lysosomes. The significance of these re-

Table 1. Inhibition by sympathomimetic and acceleration by parasympathomimetic amines of release of β-glucuronidase from polymorphonuclear leukocyte lysosomes. Data represent the mean ± S.E.M. from three separate experiments. Release of enzyme from a granule suspension incubated without compound for 0 and 60 minutes, respectively, yielded extinction values (540 nm) of 0.170 to 0.215 and 0.470 to 0.540.

Agent*	Release of β-glucuronidase (percent of control) at concentrations of the agent:			
	$10^{-4}M$	$10^{-5}M$	$10^{-6}M$	$10^{-7}M$
Norepinephrine	27 ± 2.4	42 ± 5.2	53 ± 5.5	64 ± 5.1
Epinephrine	14 ± 1.2	25 ± 2.7	42 ± 5.0	58 ± 4.1
Phenylephrine	99 ± 7.3	102 ± 6.6	98 ± 5.7	100 ± 4.8
Tyramine	100 ± 3.9	98 ± 6.1	99 ± 5.3	101 ± 4.5
Acetylcholine	191 ± 14	157 ± 9.2	124 ± 7.2	110 ± 4.7
Acetyl-β-methylcholine	172 ± 12	144 ± 6.8	121 ± 6.0	104 ± 5.5
Choline	99 ± 3.9	102 ± 5.1	98 ± 5.0	99 ± 4.3

* The forms of the agents tested: *l*-norepinephrine bitartrate, *l*-epinephrine bitartrate, *l*-phenylephrine hydrochloride, tyramine hydrochloride, acetylcholine chloride, and acetyl-β-methylcholine chloride.