The Spectral Sensitivity of
Single Units in the Nucleus
Rotundus of Pigeon, *Columba livia*

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**ABSTRACT** Responses to diffuse monochromatic light were recorded from single units in the diencephalon of pigeon. Units were both excited and inhibited by light stimulation. Intensity-response functions based on latency measures to the first spike after stimulation were used to generate action spectra. One class of spectral sensitivity functions presumably from rods, showed peak sensitivities near 500 nm: these functions were unaffected by changing criterion values used to generate the functions. A second class of cone functions showed multiple peak sensitivities at 540 nm and 600-620 nm. These units shifted their peak sensitivities with a change in criterion values. Unit response types tended to be localized differentially in the nucleus rotundus. Excitatory units were located in the dorsal half of the nucleus, while inhibitory units were located in the ventral half, with a few exceptions. An attempt was made to integrate the present findings with previous behavioral, electrophysiological, photochemical, and anatomical data in the pigeon.

**INTRODUCTION**

The activities of pigeons are dominated by vision, a fact supported by the elaboration of visual structure in these animals. The eyes and the tectal lobes are large and well-developed, and easily dominate the brain morphology. But the remainder of the afferent pathway is more difficult to determine. Older work traced the anatomical connections of the optic tectum more rostrally to the diencephalon, in particular, to the nucleus rotundus of the thalamus (Cajal, 1952; Papez, 1929; Huber and Crosby, 1929). The connections described, however, were unclear, and the conclusion of an homology between the nucleus rotundus and the ventral nucleus of the mammalian thalamus was somewhat questionable. More recently, the relation between the optic tectum and the nucleus rotundus has been investigated further in a set of studies using the Nauta-Gygax technique of staining, as well as electrical methods of stimulation and recording (Karten and Revzin, 1966; Revzin and Karten, 1966–1967). These studies have described a large pro-
jection from the optic tectum to the nucleus rotundus, a projection more massive than previously thought. Using electrical stimulation to the deeper layers of the optic tectum, particularly the stratum griseum centrale, Revzin and Karten found evoked potentials largely limited to the nucleus rotundus. The authors concluded that the nucleus rotundus which receives its major input from the optic tectum probably serves to convey visual information, although no direct projection from the retina to the nucleus rotundus was found to exist as it does to the tectal lobe (Cowan, Adamson, and Powell, 1961; Karten and Revzin, 1966). More evidence implicating the nucleus rotundus was reported in a later behavioral study by Hodos and Karten (1966). They showed that selective bilateral lesions in the nucleus rotundus produced fairly severe impairment of visual discrimination for both pattern vision and brightness.

If the nucleus rotundus is involved with vision, then there is very good reason to believe that it may be concerned with color, for since the classic study of Hamilton and Coleman (1933), it has been accepted that pigeons can discriminate different wavelengths. Efforts to uncover the physiological mechanisms of color vision have been confined largely to the eye (Graham, Kemp, and Riggs, 1935; Granit, 1942; Ikeda, 1965), or the optic nerve (Donner, 1953). These studies have established a scotopic spectral sensitivity curve with a λmax near 500 nm together with photopic curves in the longer wavelengths. There are, in addition, two bodies of electrical work concerned with wavelength-sensitive processes in later portions of the afferent pathway which are, alas, unpublished. Wylie (1962) made a preliminary analysis of a single unit in the optic tectum and derived both scotopic and photopic sensitivity functions with a Purkinje shift to relate them under appropriate conditions. His results are in agreement with previous work. The only electrophysiological work of any kind having to do with color in the nucleus rotundus was reported by Galifret (1966). He recorded responses from two inhibitory units to an equal quantal light input. The spectral curves unfortunately are not presented, but are described as having peak responsivities of 500 and 540 nm, respectively.

The study reported here is one in which we have recorded in considerable detail the responses of single units in the nuclear mass of rotundus to colored light. A few units in closely allied structures also have been included.

**METHODS**

**Stimulus System**

Light was provided by a 150 w xenon arc lamp in conjunction with a 0.25 m Ebert monochromator (Jarrell-Ash Co., Waltham, Mass.). Entrance and exit slits were adjusted to provide a bandwidth down 3 db, 4 nm either side of the nominal wavelength. Light from the monochromator was collected into a
meter length of a Crofon light guide (Du Pont & Co., Inc., Wilmington, Del.) and presented to the eye in Maxwellian view with a subtended visual field of 60°. Light intensity was varied over a six log unit range by neutral density filters interposed in the stimulus pathway. The duration of the stimulus was controlled by a programmed electromagnetic shutter. Calibration of the entire stimulus system was accomplished with an Eppley thermopile (The Eppley Laboratory, Inc., Newport, R. I.) in conjunction with a Keithley Model 150B microvoltmeter (Keithley Instruments, Cleveland, Ohio). The intensity of unfiltered light at 500 nm measured $2.93 \times 10^{13}$ quanta/sec-cm$^2$.

**Recording System**

Extracellular action potentials were recorded in the diencephalon by tungsten (Hubel, 1957) or stainless steel (Green, 1958) microelectrodes. Tip diameters ranged from 1 to 4 μ with a passive resistance of 5–25 MΩ. The potentials were referred to a chlorided silver wire inserted into the muscle tissue of the neck. Responses were led into a Bak negative capacitance electrometer (Electronics for the Life Sciences, Rockville, Md.), amplified a thousandfold via a Tektronix 122 preamplifier (Tektronix, Inc., Beaverton, Oreg.), and displayed on one beam of a dual-beam cathode-ray oscilloscope. A parallel circuit permitted monitoring of action potentials by sound. A marker signaling light onset and offset was displayed on the second beam. Permanent records were obtained by photographing the oscilloscope trace on moving film (Grass Kymograph Camera, Grass Instruments, Quincy, Mass.). The initial deflection of the response is positive, shown upward in all text-figures.

**Subjects**

The subjects were 20 adult White Carneaux pigeons (*Columba livia*) of indeterminate age obtained from a commercial source (Palmetto Pigeon Plant, Sumter, S. C.). They ranged in weight from 350 to 500 g.

**Preparation**

Each pigeon was anesthetized with Penthrane (methoxyflurane, Abbott Laboratories, Chicago, Ill.). A tracheal cannula was inserted with local application of xylocaine to reduce irritation. The animals were then secured in a stereotaxic instrument (Kopf Instruments, Tujunga, Calif.). Approximately 40 mm$^2$ of bone covering the left postero medial portion of the cerebrum was removed and the exposed dura was punctured and retracted. Warm mineral oil was applied to the pial surface for heat insulation and conservation of moisture. The lower lid of the contralateral eye was sutured in an open position and Neo-synephrine (10% viscous ophthalmic solution) or atropine sulfate (1% aqueous solution) was applied to the eye for mydriasis. Tubocurarine (0.3 cc, 3 mg/cc solution) or gallamine triethiodide (Flaxedil, 0.2 cc, 20 mg/cc solution) was injected into the right pectoralis muscle. These dosages administered at 2 hr intervals throughout the recording session were sufficient to prevent body movements. The animal was then artificially ventilated in an open system.
at 12 strokes/min. All surgical cuts were periodically bathed in tetracaine hydrochloride (Pontocaine, 0.5% solution) to insure maximal comfort.

Procedure

Each animal was dark-adapted for at least 40 min prior to active recording. A microelectrode was then lowered into the brain at a predetermined stereotaxic location, anterior plane (A 6.0–6.5) according to the coordinates of Karten and Hodos (1967). All units were tested for their ability to be driven by diffuse light. Units were held for 2–3 hr, sufficient to complete a spectral run. Stimuli of 0.5 or 1 sec duration were presented to the animal every 50 sec. The cycle permitted sufficient time for recovery as witnessed by the level of spontaneous activity and reliability of recording. A balanced design of stimulus intensity presentation, as well as standard flashes of light distributed throughout the experimental run, was used as control procedures for the stability of the preparation. A series of monochromatic stimuli of nominal wavelengths 420, 440, 460, 480, 500, 520, 540, 560, 580, 600, 620, 640, and 660 nm were presented over a six log unit intensity range.

The locations of all driven units were later confirmed by histological procedures. With tungsten, the electrode was left in situ. The brain was first fixed in 10% formalin for 7–14 days and then frozen according to the method of Siegel (1968). The electrode was removed and identification of the tract easily made in cross-section. Although anterior and lateral placements were confirmed, the depth of the electrode tip could only be estimated. With stainless steel electrodes, the method of Green (1958) was used with good success. Upon passage of 100 µamp for 20 sec, spots as small as 100 Å could be clearly identified in histological sections cut at 100 Å thickness.

Results

Extracellular action potentials were isolated from 65 units, of which 69% were broadly classified as excitatory and the remainder inhibitory. The units were further classified into several subtypes listed below. The classification is descriptive and not intended to be exhaustive.

General Properties

Excitatory Units

Phasic Units  This type of excitatory unit responded to light onset with a very fast, short burst of 3–10 spikes lasting about 20–30 msec. The rest of the stimulus period was marked by an absence of firing, or at most one or two spikes. These units normally exhibited little spontaneous activity either before or after stimulation. 18 units were of this type (cf. Fig. 1 A).

Tonic Units 18 units responded with increased firing to stimulus onset and lasted for the duration of the stimulus. The units slowed rather abruptly at stimulus offset. An example of this type of unit is shown in Fig. 1 B.
Sustained Units Six units began firing with the onset of light and continued their responses into the dark period (cf. Fig. 1 C). At high intensities of light, the responses often continued for as long as 9 sec, far beyond the duration of the stimulus.

On-Off Units Three units were isolated that responded in typical on-off fashion; i.e., with an increased burst of activity to both stimulus onset and offset. An example is shown in Fig. 1 G.

Inhibitory Units

Phasic Units Analogous to the excitatory phasic units, eight units responded with a transient interruption of short duration following stimulation by light. Typically, the inhibitory phase lasted about 100 msec before resumption of firing. Units of this type were characterized by moderately high levels
of spontaneous activity, about 50 spikes per sec. An example is shown in Fig. I D.

**Tonic Units.** Five inhibitory units were isolated that stopped or markedly reduced their firing for the duration of the stimulus (cf. Fig. 1 E). Spontaneous firing, fairly slow in these units, resumed promptly at stimulus offset.

**Sustained Units** A third type of inhibitory unit responded with a burst of activity 1–2 sec after stimulus offset (cf. Fig. 1 F). There was little spontaneous activity. While the latency of the response was remarkably long, it is not unusual. Pickering (1968) and Pickering and Varju (1967, 1969) have reported delays of more than 20 sec for responses to occur after stimulation while recording from frog retinal ganglion cells. This type of unit is different from the typical off-unit in that the latency of discharge is longer to the more intense light; i.e., the effect of inhibition is stronger. This relationship with intensity can be seen in Fig. 5. Seven units of this type were isolated.

**Intensity-Response Functions**

Of the units isolated, 21 were held long enough to afford complete analyses. Intensity-response functions were generated for 15 excitatory units, one on-off unit, and one inhibitory unit. We found the excitatory responses more directly related to variations with light intensity. On the other hand, only one of the five inhibitory units for which sufficient data were collected showed a systematic variation of response with stimulus intensity.

Latency to the first spike after stimulus onset or offset afforded the most satisfying relationship with changes in stimulus energy in agreement with Galifret (1962). The problem of conveying information to the central nervous system on the basis of latency has been raised often, for there is no separate information source available to the organism as to when the stimulus actually occurred. There is the rationale offered by Galifret (1962), who justifies the use of latency measures based on the avoidance of complex lateral interactions that could affect a frequency code. There is also the position advanced by Uttal and Krissoff (1968, p. 272), who argue that temporal coding is shared among several channels and comparisons between them constitute the neural information code to be analyzed in some more central neural structure.

An increase in latency with a decrease in stimulus intensity is shown in Fig. 2 for the excitatory sustained unit 34. The increase is orderly and progressive over a six log unit range. The relationship of reciprocal latency to the appropriate first spike plotted against the logarithm of light intensity was derived for each of the units for which completed runs were obtained. A typical plot is shown in Fig. 3 for unit 34, the same unit displayed in Fig. 2. Functions were fit by the method of least squares. The linearity of the plot is quite striking extending over five to six logarithmic units, a span covering
Figure 2. An intensity series at 500 nm for unit 34 showing increasing latency with decreasing intensity. Numbers at left are in density units.

Figure 3. Intensity functions for same unit shown in Fig. 2, plotted as reciprocal latency to the first spike against relative intensity. Plotted values are for single responses. Points were fitted by the method of least squares. Wavelength is indicated at the top of each function. The abscissa is marked on a log unit scale.
Figure 4. An intensity series at 420 nm for unit 36 showing decreasing latency with decreasing intensity suggesting an inhibitory mechanism. Numbers at left are in density units.
response latencies of about 55–500 msec. All the excitatory units showed plots similar to this one.

The discharge of the inhibitory sustained unit 36 is shown in Fig. 4, in relation to stimulus intensity. In Fig. 5, plots of reciprocal latency now show a negative slope, for the strength of the inhibition lies in its ability to prolong the latency of discharge: more stimulus energy results in longer delays to the first spike. Latencies here are quite long, from better than 1 sec to as long as 5 sec. The points do not fit the linear regression lines as well as the data displayed in Fig. 3. At the extreme wavelengths of 420 nm and 620 nm, particularly, the departures are quite noticeable. In the middle wavelengths, however, the linear fit is good.

![Intensity functions for the same unit shown in Fig. 4 plotted as reciprocal latency to onset of unit activity against relative intensity. Plotted values are for single responses. Points were fitted by the method of least squares. Wavelength is indicated at the top of each function. The abscissa is marked on a log unit scale. Note the negative slope which is typical of latency of offset of inhibition; with more light, the longer the inhibition.](image)

**Figure 5.** Intensity functions for the same unit shown in Fig. 4 plotted as reciprocal latency to onset of unit activity against relative intensity. Plotted values are for single responses. Points were fitted by the method of least squares. Wavelength is indicated at the top of each function. The abscissa is marked on a log unit scale. Note the negative slope which is typical of latency of offset of inhibition; with more light, the longer the inhibition.

*Spectral Functions*

**Curves related to $\lambda_{max}$ of 500 nm**

Based on the intensity-response functions, action spectra were derived by determination of the numbers of quanta at the several wavelengths needed to produce a constant response. Action spectra for 10 excitatory units are shown in Fig. 6. Five of these units show a $\lambda_{max}$ near 500 nm and have been plotted as a range of points clustered around the absorption spectrum of Bridges's 502 pigment for the pigeon, shown in solid black (Bridges, 1962). The mean value for the units at 500 nm has been matched to Bridges's curve. The other response values have been displaced accordingly at the several wavelengths with the extreme ranges at different wavelengths shown in solid black brackets. The ranges agree fairly well at the shorter wavelengths with the absorption curve, but there are systematic increases in sensitivity at longer wavelengths. The ranges do not overlap the curve at all after 560 nm. Five additional excitatory units, with a $\lambda_{max}$ of 520 nm, are
also indicated in Fig. 6. A dashed line connects the mean values of these units, with dashed brackets showing extreme ranges. The curve for these units appears to be different from Bridges's curve in the shorter wavelengths. Above 520 nm, however, the two ranges cluster fairly closely and all the units from both distributions tend to coincide.

While all excitatory, the units analyzed in Fig. 6 were of different subtypes: six units were excitatory tonic, three units were excitatory sustained, and one was an excitatory phasic unit. No relationship was found with regard to

![Figure 6. Spectral sensitivity curves for 10 units. The heavy black line is the absorption spectrum of pigment 502 nm (Bridges, 1962). The dark solid vertical lines are the ranges of five units which had their max at 500 nm. The dashed line is the average curve of five units with a \( \lambda_{\text{max}} \) at 520 nm. Their range is indicated by vertical dashed lines.](image)

the determined \( \lambda_{\text{max}} \). This is not surprising since the latency measures used here ignore the unit discharge after the first spike; the remainder of the discharge does not enter into the determinations.

In none of these units did changes in criterion values used to derive action spectra produce differences in the \( \lambda_{\text{max}} \) of the derived spectral sensitivity functions.

All the units whose action spectra are shown in Fig. 6 are located in the nucleus rotundus save three: two units are from the nucleus superficialis parvocellularis (dorsal to the nucleus rotundus) and display a \( \lambda_{\text{max}} \) of 520 nm; one unit is from the nucleus geniculatus lateralis pars ventralis, \( \lambda_{\text{max}} \) of 500 nm.

The action spectrum for an inhibitory sustained unit is shown in Fig. 7. This type of unit (see above) is inhibited by light. The latency of discharge is
longer to the more intense light. The figure plots single points derived from the intensity plots of Fig. 5 at a reciprocal criterion latency of \((1/L) 0.00022\) (4500 msec). The absorption spectrum of Bridges's 502 pigment is drawn for comparison. This fit is exceptionally good, with close alignment at both short and long wavelengths. This unit was located just ventral to the nucleus rotundus in the tractus tectothalamicus.

**Distribution of \(\lambda_{\text{max}}\) Other Than 500 nm**

Spectral sensitivity curves plotted for two excitatory phasic units in the nucleus rotundus together with one in the dorsolateral thalamus showed an additional prominent peak. A family of curves for several criterion values is shown in Fig. 8 for unit 61. The curves show two peaks which change their relative sensitivities as a function of light intensities. At a criterion value of reciprocal latency \(0.008\) (125 msec), to a fairly dim light, two peaks are seen: one near 500 nm and an additional one at longer wavelengths near 580-600 nm. A portion of the topmost curve in Fig. 8, plotted at criterion \(1/L = 0.008\) (125 msec), has been fitted to Bridges's 502 pigment (dotted line). Up to 560 nm the two curves are virtually superimposable. But the longer wavelengths clearly do not belong to a unimodal curve. The additional peak at 600 nm is a separate function and represents an additional long wave sensitivity. With increases in light intensity, criterion values of reciprocal latency...
0.010 (100 msec) to 0.012 (83.3 msec), the sensitivity of the unit shifts from 500 nm to 540 nm. The smaller, longer wavelength peak also moves further into the red, but the shift is not as great nor so clearly defined. The results presented here for unit 61 were similar to those for units 8 and 63. These latter units showed essentially the same peaks and shifts as a function of light intensity.

The spectral curves for the one on-off unit 29 are plotted in Fig. 9. Families of curves that demonstrate spectral sensitivities as a function of different criterion values are shown. The on family of curves shows a peak at 540 nm which is fairly prominent and is seen at all criteria. However, with more intense light stimulation, a well-defined 600 nm peak develops. This red peak is not readily apparent at the dimmest light level plotted, a criterion value of $1/L = 0.005$ (200 msec), but systematically increases with shorter criterion latencies until at $1/L = 0.01$ (100 msec) it is the most prominent peak seen.

The off family of curves shows peaks that are displaced toward longer wavelengths when compared to the on portion. There is a prominent 560 nm peak at the dimmest light required to elicit a response at $1/L = 0.0078$ (128 msec). The peak is not evident at the more intense levels. There is here, too,
FIGURE 9. Family of action spectra as a function of changing criteria for an on-off unit. For the on portion, the criteria from top to bottom are 0.0050 (200 msec), 0.0060 (167 msec), 0.0075 (133 msec), 0.0090 (111 msec), and 0.010 (100 msec). For the off portion the criterion values from top to bottom are 0.0075 (133 msec), 0.010 (100 msec), 0.0125 (80 msec), 0.015 (66.7 msec), and 0.0175 (57 msec).

A red process at 620 nm which becomes the dominant peak at the higher intensities. Similar to the on portion, there is evidence of a blue-green sensitivity near 520–540 nm.

Because the off discharge responds with shorter latencies on the whole, the criterion values used to define the two sets of curves do not completely overlap. The lower criterion values of reciprocal latency 0.0075 through 0.010 for the off portion do, however, overlap with the higher criterion values of the on portion. The off portion curves are displaced 20 nm to the red region relative to the on portion (cf. criterion values of 0.010 and 0.0075 for both on and off curves).

Two units, one, an excitatory phasic unit, the other an excitatory sustained unit, were found to lie within the optic tract below the nucleus rotundus. Mean action spectra for the two units are shown in Fig. 10 for two selected criterion levels. The upper curve for dimmer light is plotted at a reciprocal latency of 0.0083 (120 msec) with the single unit values indicated at each nominal wavelength. The curve is wide and while it has a $\lambda_{\text{max}}$ near 500 nm it is far too broad to match a 502 $\lambda_{\text{max}}$ pigment absorption curve. The lower curve for more intense light is plotted at a criterion reciprocal latency of 0.0167 (60 msec). It shows a curiously shaped curve peaking near 540 nm.
Figure 10. Action spectra for two units of the optic tract. The vertical lines indicate the range of values about the average curve. The lower curve is for a reciprocal latency criterion value of 0.0165 (60.5 msec), the upper curve for 0.0085 (118 msec). Note the shift to the shorter wavelengths with dimmer light (upper curve).

with slight indications of a red and blue process near 620 and 450 nm, respectively.

Histology

Small lesions in the tissue were easily located in sections cut at 100 μ. A photomicrograph of a section at A 6.50 in Fig. 11 shows the lesion made by passing 100 μamp for 20 sec. The lesion is clearly defined in the dorsomedial rotundus.

Of the 65 units isolated, 45 units were located in the nucleus rotundus proper, 11 units were located just dorsal to the nucleus, 4 in the tractus tectothalamicus, 2 in the tractus opticus just ventral to the nucleus rotundus, 2 in the nucleus superficialis parvocellularis (dorsal to the rotundus), and one in the nucleus geniculatus lateralis pars ventralis. A summary of these placements is shown in Fig. 12 where line drawings are taken from frontal plates A 6.00, 6.25, and 6.50 in the Karten and Hodos atlas. Small arrows are placed next to the units for which complete spectra were determined. Those units which were excitatory are displayed as open squares, solid circles indicate inhibitory units. The one unit from the nucleus geniculatus lateralis pars ventralis is not indicated in the figure. It lies at A 7.25 and could not be accommodated.

Within the nucleus rotundus itself, the units tend toward a dichotomy of function. Most excitatory units appear to be located in the dorsal half of the nucleus. The ventral half of the nucleus is almost completely inhibitory.
DISCUSSION

There are single units located in the thalamus of the pigeon that respond differentially to lights of various wavelengths. The majority of units described in this paper were located in the nucleus rotundus of the thalamus with several more lying within the diencephalon in closely adjacent structures.
Both Huber and Crosby (1929) and Papez (1929) have described a pathway from the tectum to the thalamus which could mediate visual information, and Karten and Revzin (1966) and Revzin and Karten (1966–67) have shown that the nucleus rotundus of the thalamus receives most, if not all, of its input from the optic tectum. None of its input comes directly from the retina. The nucleus rotundus therefore represents at least 4th order, probably 5th order neurons in the processing of visual information.

The extracellular responses recorded in the nucleus rotundus can be classified broadly as excitatory or inhibitory within the classical definition of responses to light. We have described several response types within this broad
dichotomy but have found no close correlation between these types and derived spectral functions.

We should note that our response types bear a superficial resemblance to the classes of ganglion cells described in the frog by Maturana, Lettvin, McCulloch, and Pitts (1960). We are reluctant to make a closer comparison for we used neither the stimulus objects of various shapes that they did nor did we confine our stimuli to the receptive fields of the units concerned. The kinds of units isolated and the shapes of the spectral sensitivity functions derived from them may very well be influenced by the use of diffuse light as opposed to light restricted to portions of the receptor field, but the $\lambda_{\text{max}}$'s do not appear to be affected. Michael (1968), in his study of color processes of optic nerve fibers in the ground squirrel, compared spectral sensitivities under conditions of diffuse light and light restricted to the receptive field. While the shapes of the curves were narrower and steeper for diffuse light, the $\lambda_{\text{max}}$'s were virtually unchanged under the two sets of conditions.

**Action Spectra of the Rods**

Several units in the nucleus rotundus show a $\lambda_{\text{max}}$ that is close to 500 nm. There is sufficient evidence from photochemistry (Wald, 1958; Bridges, 1962; Sillman, 1969), electrophysiology (Graham et al., 1935; Granit, 1942; Donner, 1953; Ikeda, 1965), and behavior (Hamilton and Coleman, 1933; Blough, 1957) to support the validity of a spectral process with a $\lambda_{\text{max}}$ localized in this region of the spectrum. The match to Bridges’s 502 pigment displayed in Fig. 6 is fairly easy to make because of the few corrections involved. Our resolution does not permit discrimination of an interval of only 2 nm and we have taken the two $\lambda_{\text{max}}$'s of 500 and 502 nm to be the same. The transmissions of the preretinal media, lens, and cornea have been measured by Blough (1957) and found by him to be clear within the range of 400 to 700 nm. In front of the rods, presumed carriers of the 502 pigments, there are none of the oil globules otherwise prevalent in this eye (Walls, 1942). The match to the absorption curve is good until about 560 nm. Thereafter there is a systematic increase in sensitivity that overlaps the long wavelength leg of a second “process” although we are loath to call it so. This second process has a $\lambda_{\text{max}}$ near 520 nm and is distinct from the process at 500 nm in the shorter wavelengths. But in the longer wavelengths the two curves virtually coincide and this is what makes us hesitant to propose a second process at 520 nm. There is some support for a process here, however, from Laurens’ work (1923) in which he used a pupil response to spectral lights of equal energy content and found a maximum sensitivity at 524 nm. But his measurements of human pupillary responses in the dark-adapted eye with dim light in the same apparatus show a $\lambda_{\text{max}}$ of 514 nm, a sizable discrepancy from the accepted $\lambda_{\text{max}}$ for the human C.I.E. scotopic luminosity function.
(505 nm). We are uneasy, therefore, with the 524 nm value for the pigeon. Added to this is the fact that no photopigment with a maximum absorption at 520 nm has been found in the eye of the pigeon (Wald, 1958; Bridges, 1962; Sillman, 1969), and it is unlikely that pigments at both 500 and 520 nm, presumably rod pigments, exist in this eye concurrently. Ikeda (1965) has suggested that a similar increased red sensitivity obtained in his electroretinographic study of the pigeon may be due to a contribution from cone mechanisms. He found, when he directed his stimulus light to the periphery, a much better fit to the rhodopsin absorption curve. The periphery has a greater proportion of rods than the central area and would therefore imply less of a cone contribution (Waelchli, 1883; Walls, 1942).

What mitigates against a cone contribution in the data presented here, is the constancy of the spectral sensitivity curves regardless of the criterion values used to define the function. Whether values denoting intense or dim stimulus lights were used, the $\lambda_{\text{max}}$'s of the curves were unchanged. If the cones were a contributing factor, one could expect their relative contribution to a mixed rod-cone system to vary as a function of intensity, the so-called Purkinje shift. The effect, if present, can easily be seen in spectral sensitivity curves derived from electrical data (Granda and Biersdorf, 1963; Granda and Stirling, 1966). Too, in the one inhibitory unit we succeeded in analyzing completely, the fit of the derived action spectrum is very close to Bridges's 502 pigment and shows none of the red sensitivity although the stimulus location was unchanged. Whatever the explanation of the increased red sensitivity, it is clearly a complicated matter and demands further study.

**Action Spectra of the Cones**

Several units showed a $\lambda_{\text{max}}$ together with inflections in the action spectrum different from a $\lambda_{\text{max}}$ of 500 nm. Inflections have traditionally inferred additional processes that are combined in the over-all sensitivity curve (Granit, 1947). The main peaks isolated in this study are centered at 540 and 600 nm. In several units there was, in addition, a pronounced Purkinje shift from a $\lambda_{\text{max}}$ of 500 nm at dim lights to one at 540 nm for lights a thousand times more intense (cf. Fig. 10). There is also a smaller shift for the $\lambda_{\text{max}}$ of 600 nm, but it is not so clearly defined nor does it always occur. Both Granit (1947) and DeValois (1965) have shown Purkinje shifts in single cells similar to what we have indicated here.

The two additional peaks associated with more intense lights accord very well with Ikeda's (1965) results for the electroretinogram in this same animal. Ikeda isolated two photopic processes: one at 547 nm to coincide with the cone pigment of Bridges (1962), the other process was found to lie at a $\lambda_{\text{max}}$ of 605 nm. Donner (1953), too, has shown peak sensitivities in his work on the massed discharge of pigeon retinal ganglion cells that lie at 543 nm.
and somewhere between 596 and 613 nm. But the remainder of the work done on the pigeon, from whatever source, supports processes at other regions of the spectrum. Granit (1942) and Donner (1953) both show in their electrical work curves that peak near 580 nm. They claim that the curves represent a photopic process that operates for daylight vision in the pigeon. The curve has been carefully reproduced recently in a behavioral study by Graf (1969) that utilized flicker photometry. His curves show a peak at 580 nm and display very little variance with repeated measures. Blough (1957) in his behavioral study on dark adaptation in the pigeon was able to show a photopic curve in the early stages of dark adaptation that peaked at 565 nm. However, the $\lambda_{\text{max}}$ is scarcely different from that at 580 nm (about 0.02 log unit), and is really very similar to the sensitivity curves presented by Graf.

Now, the earliest known cone pigment in the pigeon eye was reported by Wald (1958) in the Teddington Symposium honoring Selic Hecht, where he claimed that iodopsin ($\lambda_{\text{max}} = 562$ nm) was successfully extracted from the pigeon’s eye in his laboratory. Bridges (1962) who found a new 544 pigment but not iodopsin, and Sillman (1969) who looked for both and found neither, failed to corroborate Wald’s claim. It is unfortunate that the cone pigments remain undetermined, for any photopic sensitivity that is operative presumably depends on their presence. The process is even more complicated, for in this eye, indeed in the eyes of most sauropsida, there are oil globules of various colors and high optical density. Described first by Hannover (1840), and more recently by King-Smith (1969) in the pigeon, these structures are judiciously placed in front of the outer segments so that the light to be absorbed by the pigments must first pass through the globules. Since the globules absorb in the longer wavelengths they act to limit the transmission of light to that region of the spectrum. The resultant sensitivity of the receptor is therefore a function of both pigment and globule. In the pigeon eye, the globules are colored yellow, orange, and red (King-Smith, 1969) and in conjunction with either a 544 pigment or a 562 pigment (iodopsin) can only displace the peak sensitivity to longer wavelengths. For this reason there is some evidence against Wald’s 562 pigment in that there is no way to shift the $\lambda_{\text{max}}$ of the pigment to shorter wavelengths say, at 540 nm (cf. Figs. 8-10), by combination with the long wavelength oil globules. One is either left with a pigment of $\lambda_{\text{max}}$ sufficiently displaced to shorter wavelengths to account for the electrical peak sensitivity (e.g., Bridges's 544 pigment) or an appeal to “... nervous interaction in the retina...” as Donner (1960) has done in a similar attempt to explain his work on the pigeon. In our work, both 500 and 562 pigment-generated signals could combine to yield a 540 electrical peak sensitivity. There is some indirect support for this combination in terms of a Purkinje shift demonstrated in some of the cells.

The photopic sensitivity of $\lambda_{\text{max}}$ 580 nm described by Granit (1942),
Donner (1953), Blough (1957), and Graf (1969) can be derived by a combination of the 540 and 620 nm spectral sensitivities as suggested by Ikeda (1965). In our data a simple additive combination suffices crudely but we should be in a better position to assess this combination if we had some idea of the numbers of each pigment-oil globule pairing for proper weighting. These data are not yet available.

Histology

Within the nucleus rotundus there is a functional differentiation of responses such that excitatory units are localized in the dorsal half and inhibitory units localized in the ventral half of the nucleus. This finding is reminiscent of the early results of DeValois, Smith, Karoly, and Kitai (1958) who found excitatory on-responses in the dorsal layers of the macaque lateral geniculate body and inhibition in the ventral layers, a finding later disputed in part by Wiesel and Hubel (1966). It is not our intent to propose the nucleus rotundus as a homologue to the lateral geniculate body of mammals, for the comparison is specious at best. True, the nucleus rotundus projects rostrally to higher centers as does the lateral geniculate body; it also appears to have the functional dichotomy found by DeValois et al. (1958). Unlike the lateral geniculate body, however, the nucleus rotundus receives no direct input from the retina (Cowan et al., 1961; Karten and Revzin, 1966). Karten (1969), moreover, has claimed recently that the tectorotundal pathway forms part of a general tectofugal system leading from the retina by way of the contralateral tectum to the nucleus rotundus and then to the ectostriatum. He compares this pathway directly with the tectal projection to the nucleus lateralis posterior thalami in mammals. This tectofugal system is distinct from a thalamofugal system which embodies a direct retinal projection to the contralateral dorsal thalamus and then to the telencephalon. The avian thalamofugal system, then, which does not include the nucleus rotundus, is compared directly to the geniculocortical projection in mammals.

What this description implies for the physiological functioning of the nucleus rotundus is difficult to say. There are few physiological data bearing on the point. We know that units in the nucleus rotundus have differential sensitivity to wavelength. They also exhibit a localization of excitation and inhibition. From Revzin (1967) we learn that the units possess extremely large receptive fields, greater than 42°, with sensitivity to movement, a fact recently confirmed in our own work. But beyond these data we know very little. To fit them into a homologic description at this time is hardly possible.

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