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Critical Flicker Frequency in a Harp Seal, *Pagophilus groenlandicus* (Erxleben, 1777)

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CRITICAL FLICKER FREQUENCY IN A HARP SEAL, PAGOPHILUS GROENLANDICUS (ERXLEBEN, 1777)

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ABSTRACT

CRITICAL FLICKER FREQUENCY IN A HARP SEAL, PAGOPHILUS GROENLANDICUS (ERXLEBEN, 1777)

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University of Guelph, 1973

Supervisor:
Professor M. L. Matthews

Critical flicker frequency (CFF) in a free-swimming harp seal (Pagophilus groenlandicus) was investigated using behavioral techniques. The resulting CFF versus intensity contour indicates a definite rod-cone break, confirming a duplex photoreceptor population whose presence had not been observed in previous morphological reports.

This thesis is dedicated to

ERNST WOLF, Ph.D.

for introducing me to the

study of vision

ACKNOWLEDGEMENTS

I wish to thank Prof. M. L. Matthews for serving as my Supervisor and for his support and encouragement throughout this exercise. Thanks are due also to Prof. D. J. Piggins and Prof. E. D. Bailey for serving on my Committee and for their many helpful comments.

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Everything in the vertebrate eye means something.

Walls (1942)

INTRODUCTION

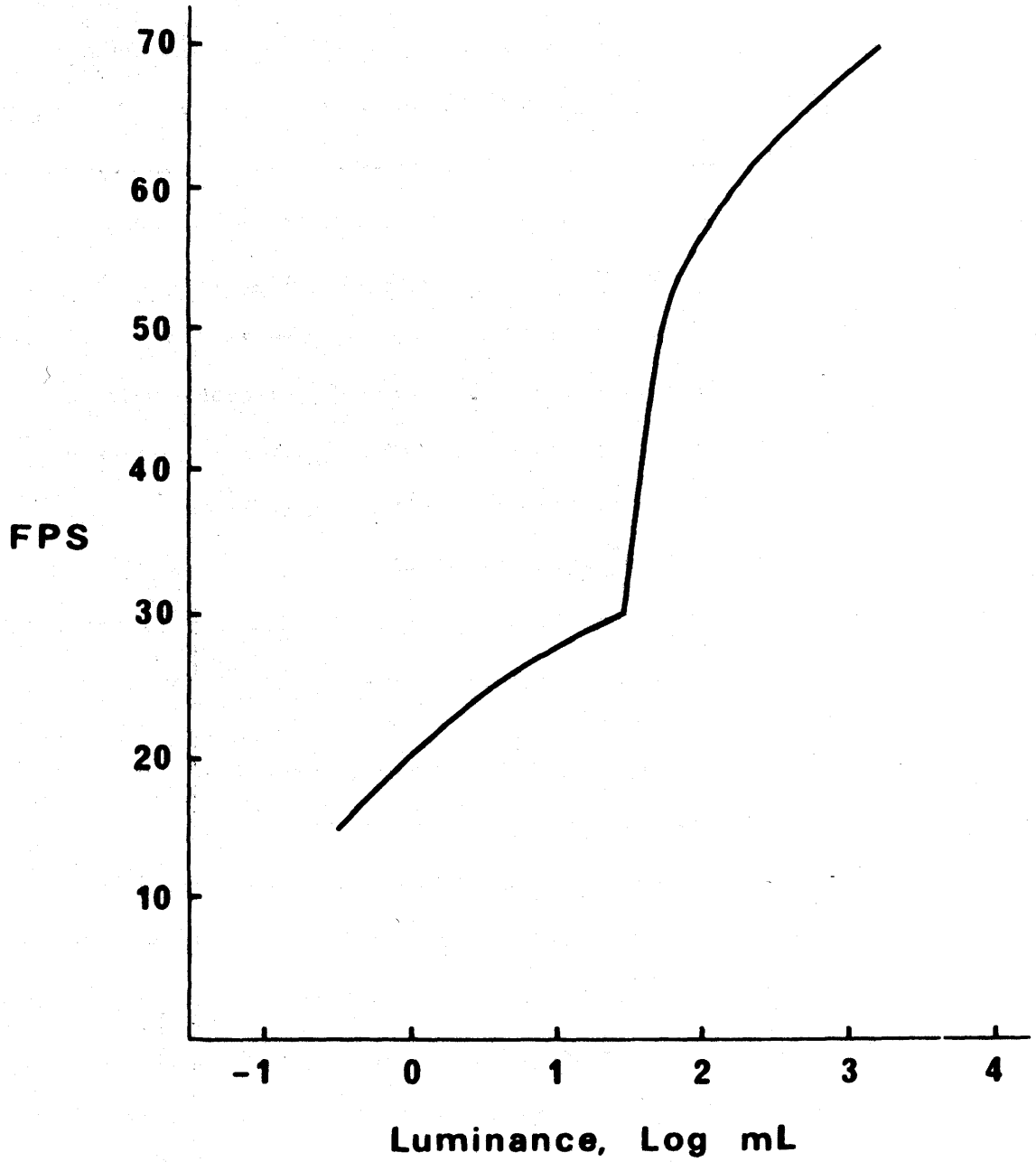
Critical flicker frequency (CFF) may be thought of as an index of the temporal resolution power of the visual system. It may be defined as the lowest flash rate at which an observer sees a train of intermittent light pulses as continuous, or fused. The measurement of CFF is also, according to Walls (1942), "one of the best criteria of the comparative objective capacities of vertebrates for movement perception," a capacity, as with visual acuity, strongly tied to photoreceptor type and population.

Initial work by Porter (1902) specified two branches of the human CFF-intensity function. Schaternikoff (1902) and Von Kries (1903) further showed that CFF-rates decreased with dark adaptation, and that color-blind observers had CFF values 20% lower than normals. Based on this evidence, Von Kries attributed the two-part curve to different sensitivities of rod and cone vision. Early electroretinographic work by Piper (1911) showed response differences in the electrophysiological performance of rod retinae and duplex retinae. Later experiments in electroretinography performed by Granit and Riddell (1934) and by Granit (1935) provided evidence that, in animals with mixed retinae, photopic CFF-rates were higher than scotopic rates. Also, by comparing the different wave components of the electroretinogram (ERG), it was possible to identify the separate contributions of rods and cones. The

response latency for cones was found to be shorter than that for rods. These important characteristics have been confirmed and further specified in other experiments: Shipley and Fry (1966) used flicker perimetry during dark adaptation to isolate and identify photoreceptor contributions; analysis of early and late receptor potentials suggests that cones resolve higher flicker rates than rods (Brown and Watanabe 1962 a, b; Brown, Watanabe, and Murakami 1965; Whitten and Brown 1973 a).

The ERG-waveform has been found to reliably follow the flicker stimulus with a response for each individual flash of light until, at CFF, the waveform becomes smooth. In animals with pure rod retinae, the ERG-CFF response rate is low, usually below 30 flashes per sec. (fps), such as the hedgehog, Erinaceus europaeus (Horsten and Winkleman 1962), or the bushbaby, Galago crassicaudatus (Dodt 1967; Ordy and Samorajski 1968). Pure cone retinae animals exhibit higher response rates, for instance the tree shrew, Tupaia glis (90 fps; Tigges, Brooks, and Klee 1967), or squirrel, Sciurus vulgaris (103 fps; Horsten and Winkleman 1962). In mixed retinae, Dodt (1952) demonstrated light adaptation yields higher CCF-rates than dark adapted conditions. The cat (Fig. 1), possessing a poor but nonetheless valid mixed retina, produces a duplex contour, defining rod and cone responses. Dodt and Enroth (1954) showed that the cone contributions to this contour can be elicited by using high flash intensities. Gouras and Link (1966) and Gouras (1967), in their study with the rhesus monkey (Macaca mulatta), have presented evidence to show that while the thresholds and response speed of the receptive field of a ganglion cell of converging rod and cone photoreceptors increase with illumination, the much shorter response latency of the cones (50 versus 150 msec) is sufficient to control the ganglion cell output

Fig. 1 Critical flicker frequency in the cat. The ordinate represents the frequency in flashes per second (fps) at which the electroretinogram failed to respond to each stimulus. The abscissa represents the stimulus intensity in log milliLamberts. (Redrawn from Dodt and Enroth 1954)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Luminance, Log mL

whenever adequately stimulated. This situation is further enhanced by the higher response speed of the ganglion cell itself, produced by the increasing illumination.

When plotting CFF against a wide range of stimulus intensities, a response contour may be produced showing a shift in function from one type of photoreceptor to another, as in the cat (Fig. 1), or the lack of such a transition as in the pure rod Tokay gecko, Gekko gekko, and the pure cone iguana, Iguana iguana (Fig. 2) (Meneghini and Hamasaki 1967). These latter curves are excellent examples of three fundamental points:

1) cone photoreceptors follow higher rates of flicker than rods;

2) the slopes of rod and cone curves are different; and

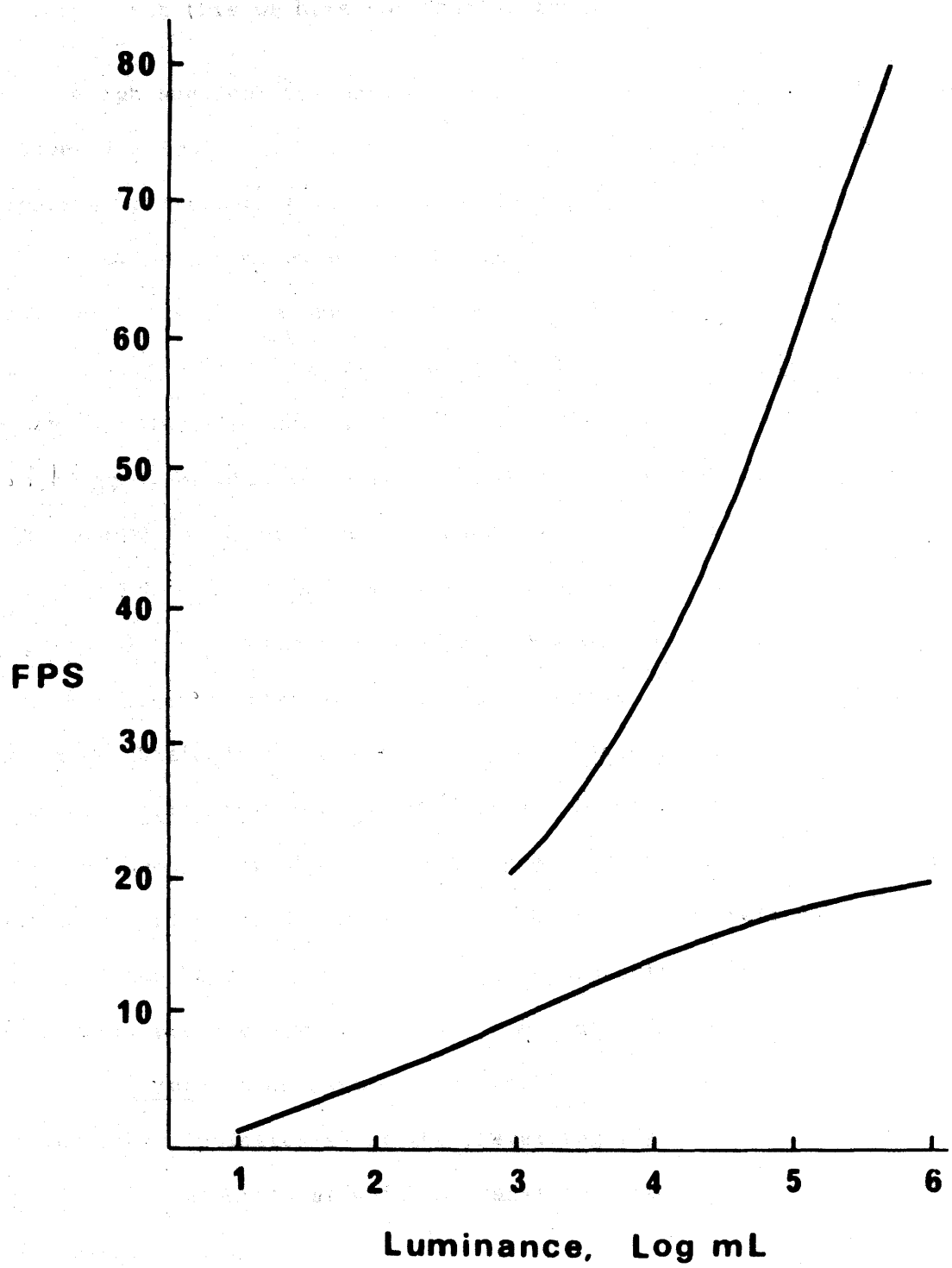
3) simplex retinae show no discontinuity in such functions. The cat's response contour (Fig. 1) obtained by Dodt and Enroth (1954) combines the properties of rod and cone performance. The discontinuity in the curve indicates a mediational transfer from rods to cones.

Behavioral work by Crozier and co-workers yielded analogous results (Fig. 3). In morphologically distinct duplex retinae, duplex flicker contours were found (Wolf and Zerrahn-Wolf 1936; Crozier, Wolf, and Zerrahn-Wolf 1936, 1937 a, b, c, 1938; Crozier and Wolf 1939 a, c, 1940 b, 1944 b); whereas with simplex retinae (and also in the foveal region of man), simplex contours were observed (Crozier, Wolf, Zerrahn-Wolf 1939; Crozier and Wolf 1940 a, 1941 a, b, 1942, a, b, 1943, 1944 a). As stated by Crozier and Wolf (1944 c):

> What one is required to say is that, in duplex performance curves we have to do with the occurrance of two populations of neural effects in the constitution of the response contours. This might well be found to occur in cases where only "cones" or only "rods" are revealed by ordinary histological inspection, but where either might really

Fig. 2 Critical flicker frequency in the iguana, Iguana iguana (upper) and the gecko, Gekko gekko (lower). The ordinate represents the frequency in flashes per second (fps) at which the electroretinogram failed to respond to each stimulus. The abscissa represents the stimulus intensity in log milliLamberts.

The iguana is thought to have a pure cone retina, whereas the gecko possesses a pure rod retina. (Redrawn from Meneghini and Hamasaki 1967)


80
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FPS
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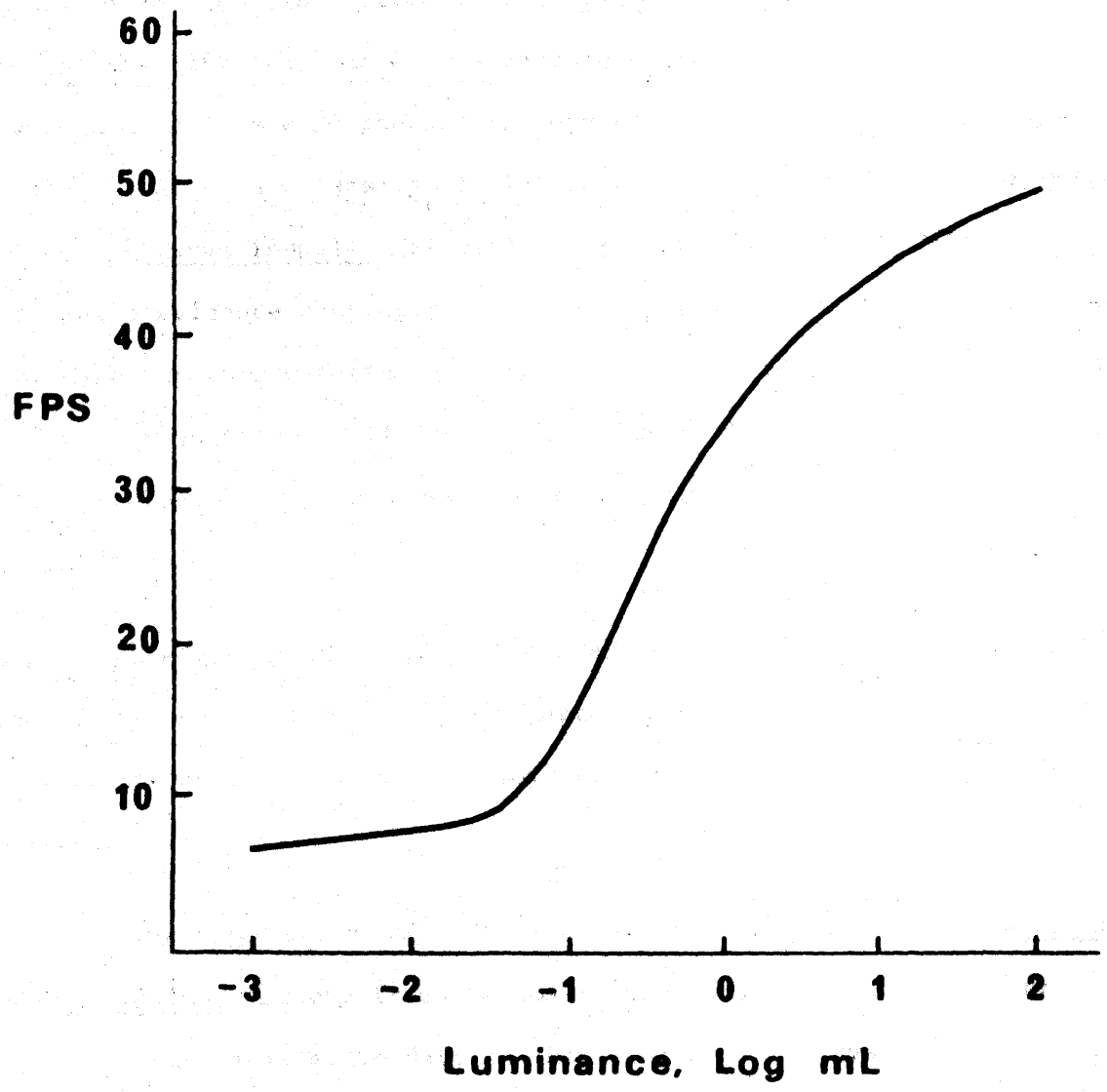
6
Luminance, Log mL

include more than one functional type. Reciprocally, it might easily happen that a structurally duplex retina should be associated with a simplex performance curve, but this we have not thusfar found.

High and low ERG- and behavioral CFF values have been recorded in several animal species, but under different conditions of flash intensity, pulse duration, and, especially, adaptation (see Landis 1954), much confusion has developed in attempts to specify the true retinal characteristics of the organism examined. Animals with pure cone retinae, such as the American red squirrel, Tamiosciurus hudsonicus loquax (Tansley, Copenhauer, and Gunkel 1961), or the tree shrew, Tupaia glis (Tigges, Brooks, and Klee 1967; Ordy and Samorajski 1968) show high ERG-CFF of 65 and 90 fps, respectively, and pure rod animals, such as the gecko, Gekko gekko (Meneghini and Hamasaki 1967), show low values of 20 to 25 fps. While a single peak CFF value may suggest a rod or a cone photoreceptor population, it says nothing about a mixed retina. The rates obtained in the squirrel monkey, Saimiri sciureus, 60 fps; marmoset, Callithrix jacchus, 60 fps; and lemur, Lemur catta, 50 fps (Ordy and Samorajski 1968) are all suggestive of cone performance, but fail to describe the duplex nature of these animals' retinae. A continuous investigation covering both photopic and scotopic stimulus intensities is the only procedure which can yield a) contours indicating the presence of a rod and/or a cone segment, b) specify the peak CFFs of the contributing receptor population(s) at the prevailing light intensity, and c) indicate the intensity at which a transition from higher to lower CFFs (if present) occurs.

With the development of additional morphological criteria (Walls 1942; Pedler 1965; Cohen 1969) to supplement Schultze's (1866) original

Fig. 3 Critical flicker frequency in the sunfish, Lepomis. The ordinate represents the number of flashes per second (fps) passing a given point on the circumference of a rotating cylinder within which the animal is placed. The critical response is a change in orientation to the alternate transparent and opaque stripes on the cylinder wall which cause the flashing. The abscissa represents the stimulus intensity in log milliLamberts. (Redrawn from Crozier, Wolf and Zerrahn-Wolf 1936)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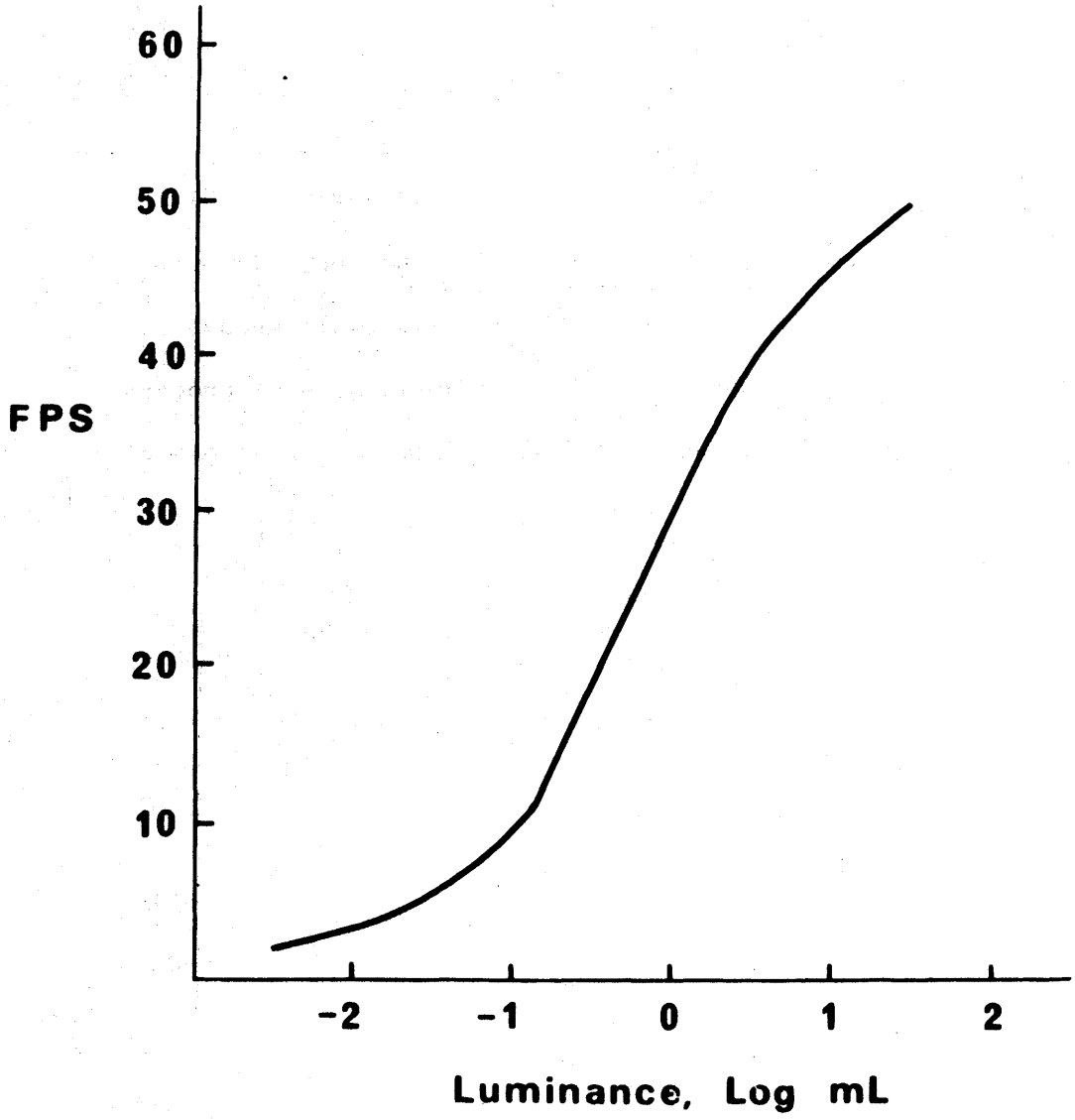
Luminance, Log mL

notion of two types of receptors, further confusion has developed. While flicker contours and histological data for individual species are usually in accord, occasional contradictions between anatomical and functional distinctions have been observed. As early as 1944, Crozier and Wolf (1944 c), in a behavioral experiment, observed a duplex contour (Fig. 4) in the soft-shelled turtle, Trionyx (Amyda) emori, which according to Gillett (1923) has an exclusive cone retina. Also the Phelsuma species of geckos were thought to possess pure cone retinae (Tansley 1961) but Arden and Tansley (1962) reported breaks in the ERG-CFF curves of the Phelsuma inunglis (Fig. 5). Furthermore, Hamasaki (1967) presented evidence showing that the owl monkey, Aotes trivirgatus, does not have a pure rod retina as defined by Jones (1965), but generates a flicker curve with a definite rod-cone break (Fig. 6). In such cases, the histological criteria were inadequate to define the true retinal compositions.

The technique of CFF has therefore shown itself to be a valid and indispensable tool in photoreceptor detection and analysis. Dodt (1967) has defined CFF as the "most reliable" indicator of a rod or cone mammalian eye.

The application of a CFF analysis to the harp seal, Pagophilus groenlandicus, follows from the small, and sometimes contradictory evidence, accumulated to date on this seal's visual system. Nagy and Ronald (1970) analyzed the harp seal's retina histologically. While their study did not reveal the presence of cone outer segments, cone-type pedicles were observed. This combination of characteristics is suggestive of Pedler's (1965) type B cell, a relatively sensitive poly-synaptic receptor, found in the fovea of rhesus monkeys. A high

Fig. 4 Critical flicker frequency in the soft-shelled turtle, Trionyx emoryi. The ordinate represents the number of flashes per second (fps) passing a given point on the circumference of a rotating cylinder within which the animal is placed. The critical response is head nystagmus to the alternate transparent and opaque stripes on the cylinder wall which cause the flashing. The abscissa represents the stimulus intensity in log milliLamberts. (Redrawn from Crozier and Wolf 1944c)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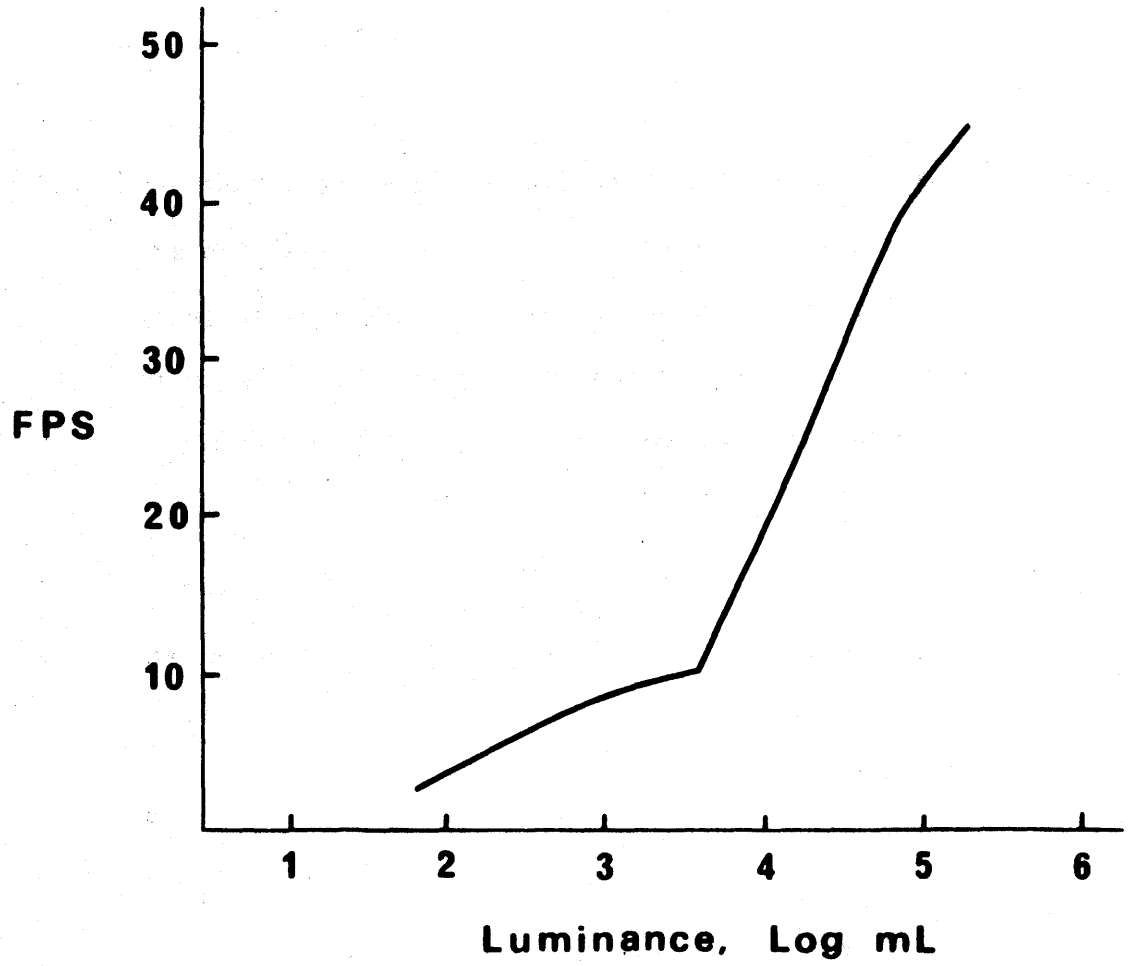
Luminance, Log mL

Fig. 5 Critical flicker frequency in the diurnal gecko, Phelsuma inunguis. The ordinate represents the frequency in flashes per second (fps) at which the electroretinogram failed to respond to each stimulus. The abscissa represents the stimulus intensity in log milliLamberts. (Redrawn from Arden and Tansley 1962)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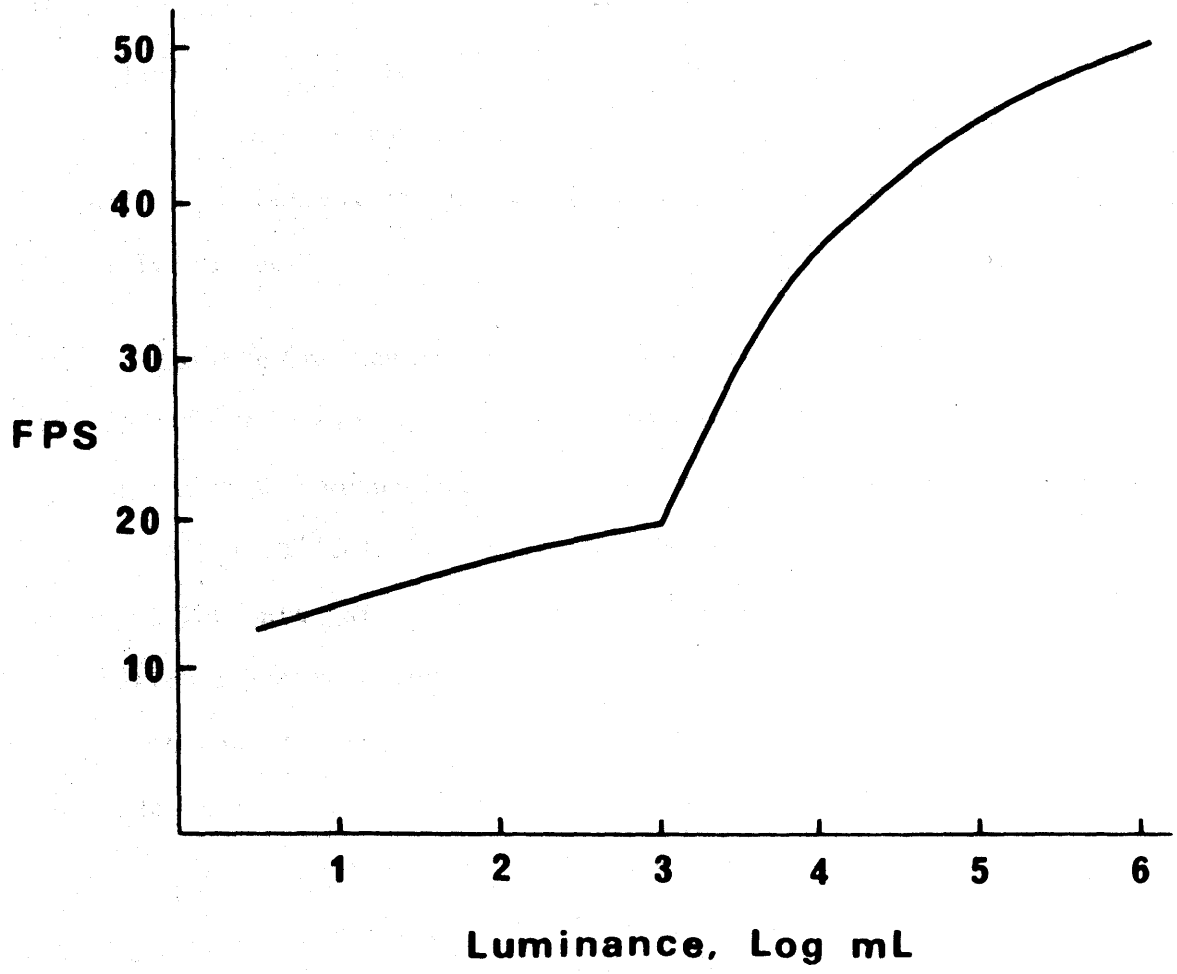
Luminance, Log mL

Fig. 6 Critical flicker frequency in the owl monkey, Aotes trivirgatus. The ordinate represents the frequency in flashes per second (fps) at which the electroretinogram failed to respond to each stimulus. The abscissa represents the stimulus intensity in log milliLamberts. (Redrawn from Hamasaki 1967)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Luminance, Log mL

convergence ratio of receptor to bipolar to ganglion cells (100:10:1) nonetheless suggests a rod-populated retina.

The harbor seal, Phoca vitulina, has been examined using Pedler's definitions (Jamieson and Fisher 1971). It was found that "cone-type receptors are present, although not perhaps in the classical context ...." While the ratio of rod- and cone-like pedicles was estimated to be 23:1, Jamieson and Fisher felt that the poly-synaptic nature of these pseudo-cones made up for their low density. In contrast, Landau and Dawson's histological report (1970) stated that no cones could be found in the harbor seal.

Lavigne and Ronald (1972) demonstrated through operant techniques that the harp seal's eye is adapted to dim light sensitivity, supporting Nagy and Ronald's morphological evaluation. Extremely low threshold values ($6.7 \times 10^{-5} \mu W/m^2$) at peak scotopic sensitivity (about 525 nm) and an eight log unit gain in relative sensitivity during the course of dark adaptation point to a very sensitive retinal organization. This agrees well with the high convergence ratio mentioned earlier. However, a Purkinje shift of approximately 25 nm was observed, suggesting the presence of two photopigments, if not of two photoreceptor systems. Nagy (1971) concludes the harp seal's retina is populated by a single class of photoreceptor outer segments, containing at least two types of photopigments. The two photopigments are assumed to be sufficient for mediating Lavigne and Ronald's photopic and scotopic conditions. Nagy further states that Lavigne and Ronald's photopic spectral sensitivity curve is mediated by the outer segments with pedicle terminals.

A critical flicker frequency analysis was therefore undertaken

in order to facilitate making a more definitive statement about the functional composition and organization of the harp seal's retina.

METHOD

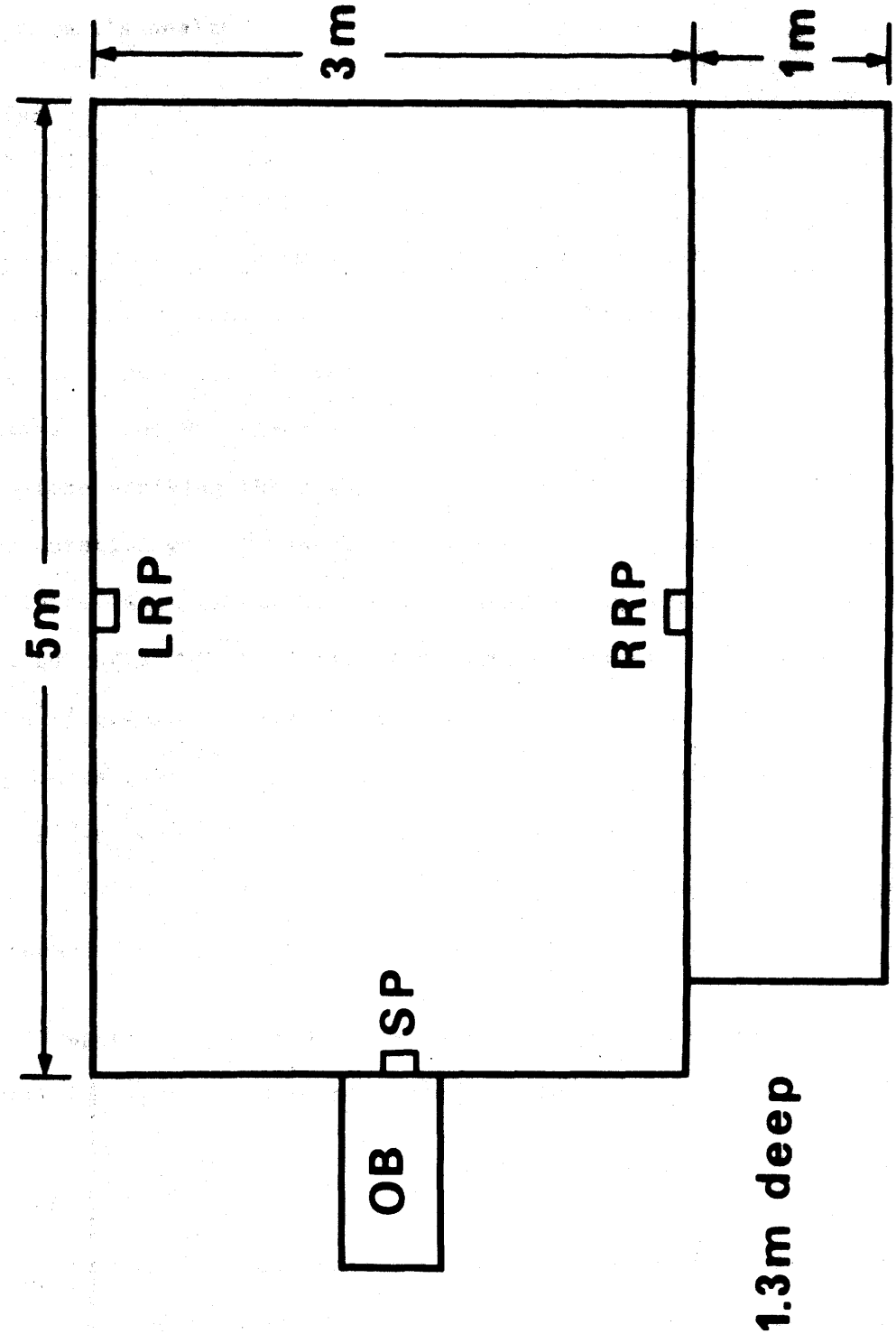
SUBJECT

The subject was a four year old immature female harp seal, Pagophilus groenlandicus (Erxleben 1777). She had served in a previous visual experiment (Lavigne and Ronald 1972) using the same operant techniques.

The seal was visually isolated from other seals belonging to the Department of Zoology, University of Guelph, in an indoor fiberglass tank (Fig. 7) containing a total volume of approximately 6,000 gallons. Continuously flowing well-water of approximately 10°C provided a water change once every four hours. Tank cleaning was carried out periodically. A ledge, 1m wide, ran along one side of the tank, providing an area for the animal to rest out of water. The area around the tank was sectioned off from the rest of the facility by an opaque black plastic wall. An overhead lighting array, controlled through an automatic timer giving a light-dark photoperiod of about 12:12 hr, was positioned 2m above the water, and consisted of eight, 100 W 125 V light bulbs.

Atlantic herring, Clupea harengus, served as food. Daily consumption was approximately 4,000g, divided over two meals. This was further supplemented by a daily vitamin dose (Appendix 1). Weighing

Fig. 7 An overhead schematic representation of the indoor fiberglass tank used to house the experimental animal. The 1m-wide segment was a deck above the waterline providing an area for the animal to rest out of water. Walls approximately 1m high extended above the waterline and deck surface. The optical bench (OB) was aligned behind an underwater window, providing a stimulus next to the stimulus paddle (SP). Responses were made to the left response (LRP) and right response (RRP) paddles.


3m
1m
5m
LRP
RRP
SP
OB
1.3m deep

and bleeding (Ronald, Foster, and Johnson 1969) were carried out monthly as part of a standard maintenance program, giving a general indication of the animal's health.

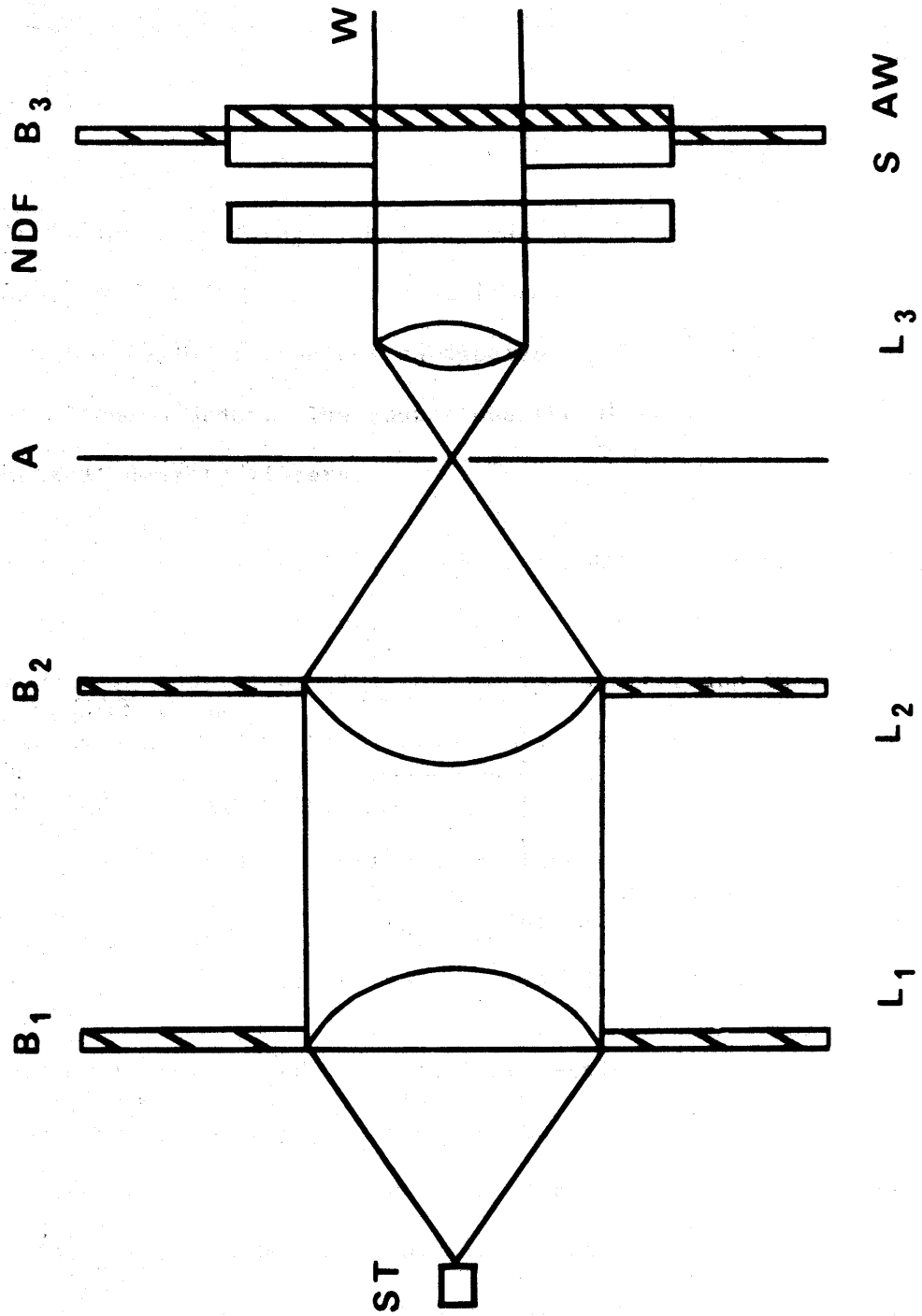
APPARATUS

The optical apparatus (Fig. 8) consisted of a General Radio strobe whose condensed beam was focused on an aperature. A third lens collimated the beam which then passed through Kodak neutral density filters and a Uniblitz electronic shutter of 2.5 cm diameter. This beam then passed through a clear acrylic window and approximately 15 cm of water before striking the right eye of the self-positioned seal. The shutter duration was 500 msec. Appropriate baffles were used to cut down stray light. Neutral density filters used during the testing sessions attenuated the strobe's initial intensity of 170 lux, measured at the position of the seal's eye, by 1.0, 2.0, 3.0, 4.0, 4.5, 5.0, 5.5, 6.0, and 7.0 log units. The entire optical apparatus was placed in a lightproof house. Flash rate was indicated by a Dawe Instruments frequency counter coupled to an International Rectifier photovoltaic cell whose surface was attached to baffle #2.

Response logic, under the control of the experimenter, defined the correct response and reinforcement pattern.

Calibration: Calibration of the source was carried out using a Gamma 700 photometer coupled to a fiber optics probe in a waterproof housing. A R.C.A. 931A photomultiplier tube served as the sensing element. Its housing included a photopic correction filter facilitating

Fig. 8 A schematic representation of the optical bench. General Radio strobe (ST); condensing lenses (L_1 and L_2); aperature (A); collimating lens (L_3); Kodak neutral density filters (NDF); Uniblitz electronic shutter (S); acrylic window in side of tank (AW); water (W); baffles (B_1, B_2 and B_3).


W
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L1
ST

direct illuminance measurements. Calibration of the photometer itself was against a N.R.C. standard lamp. To determine the incident lux at the animal, the fiber optics probe was lowered into the water to a position equal to that of the seal's right eye.

PROCEDURE

Preliminary Training: The seal was shaped using operant techniques (Blough 1958). It was conditioned to discriminate between a flickering stimulus of 15 fps and an apparently fused stimulus of 40 fps, presented in random order. The source was the above optical apparatus without neutral density filters.

The seal began a trial by pressing a submerged stimulus paddle with her nose, simultaneously positioning her head in a relatively consistent viewing position. This opened the shutter and initiated the response logic system. The seal responded to the presence of a flickering stimulus by pressing a response paddle on the left side of the tank, or to the presence of a fused stimulus by responding to the right side of the tank. Only one view of the stimulus was allowed per trial; the animal was forced to respond in order to view the next stimulus.

During training, and later testing sessions, the order of stimulus presentations was formulated using Gellerman's (1932) schedule, yielding an equal number of catch (fused stimulus) and test (flickering stimulus) trials. Experimenter biasing and paddle preference by the seal were thus minimized. The order was read from a prepared listing, and was used by the experimenter to simultaneously match the stimulus conditions and the response logic system.

Detection of a test stimulus caused the seal to press the left response paddle, receiving a piece of herring as reinforcement. Responding to the right response paddle for a test stimulus caused a solenoid to close loudly, indicating to the animal that an incorrect response had been made and that no food reinforcement would be presented. Catch trials required the seal to respond in the opposite sequence; right side responses were reinforced, left side paddle responses were not. The experimenter reset the response logic after each incorrect response to prepare for the next trial.

Two sessions of about 30 min. each were run daily, during both training and testing time periods. The animal worked at her own speed. Failure to work caused the paddles to be withdrawn and the session terminated. During training and testing days, the daily food allocation was given only if both sessions were completed. On 'days off,' the two meals were given by hand.

Testing: Testing sessions were preceded by dark adaptation periods of at least one hour. Overnight dark adaptation of approximately ten hours was also used but did not cause any significant difference in performance when compared to one hour dark adaptation times. All testing was carried out in the dark.

Data collection was through the Up-Down Transformed Response (UDTR) rule of Wetherill and Levitt (1965). This simple technique facilitates quick but accurate threshold estimations, and may be used to determine threshold values ranging from 50% to 89% correct performance (Wetherill and Levitt 1965). The function selected for this procedure

produced a threshold level (L) of 70.7%. The test stimulus value is varied above and below this threshold by the animal's responses. The threshold percentage is determined in the following manner: two correct responses at a single stimulus value, in this case a single flickering rate, causes the stimulus to be increased by a step value of 2 fps. An incorrect response causes the stimulus to be decreased by the same step size. If the correct response probability at any level x is F(x), this procedure will yield a threshold where $F^2(x) = 0.50$ or a level of $L_{0.707}$ (Wetherill and Levitt 1965).

Test conditions consisted of making the best estimate of $L_{0.707}$ from past observations. This flash rate was set on the strobe through adjustment relative to the readout of the photocell-frequency counter arrangement. Gellerman's (1932) schedule was then followed to furnish a sequence of test (flickering) and catch (fused) trials. If the first response to a test trial was correct, the flash rate was increased by the step value of 2 fps. Such appropriate increases were continued until the animal made an error on a test trial. The following test trial after this error was set at 2 fps lower. This first incorrect test trial response signalled the beginning of run #1 (Wetherill and Levitt 1965). The UDTR rules for the $L_{0.707}$ paradigm were then used on following trials. Two correct responses increased the flash rate by the step size; one incorrect response decreased the flash rate by the same amount. Each unidirectional series of moves up or down the frequency scale defined a run. Ten runs were collected in each testing session. The peak and valley scores, with the exception of the first incorrect test trial response, were averaged to obtain the $L_{0.707}$ estimate. Standard deviations were also computed (Wetherill and Levitt 1965).

Catch trial performance was computed using the number of correct catch trial responses divided by the total number of catch trials presented. This value served two purposes: it indicated the overall reliability of the animal's responses during the session, and served later on as a criterion for data analysis.

RESULTS

A total of 139 testing sessions was performed during the months of April, May, and June, 1973. These sessions were distributed over an intensity range of 170.0 to 0.000017 lux, producing six to twelve complete and useable sessions at each of the ten intensities.

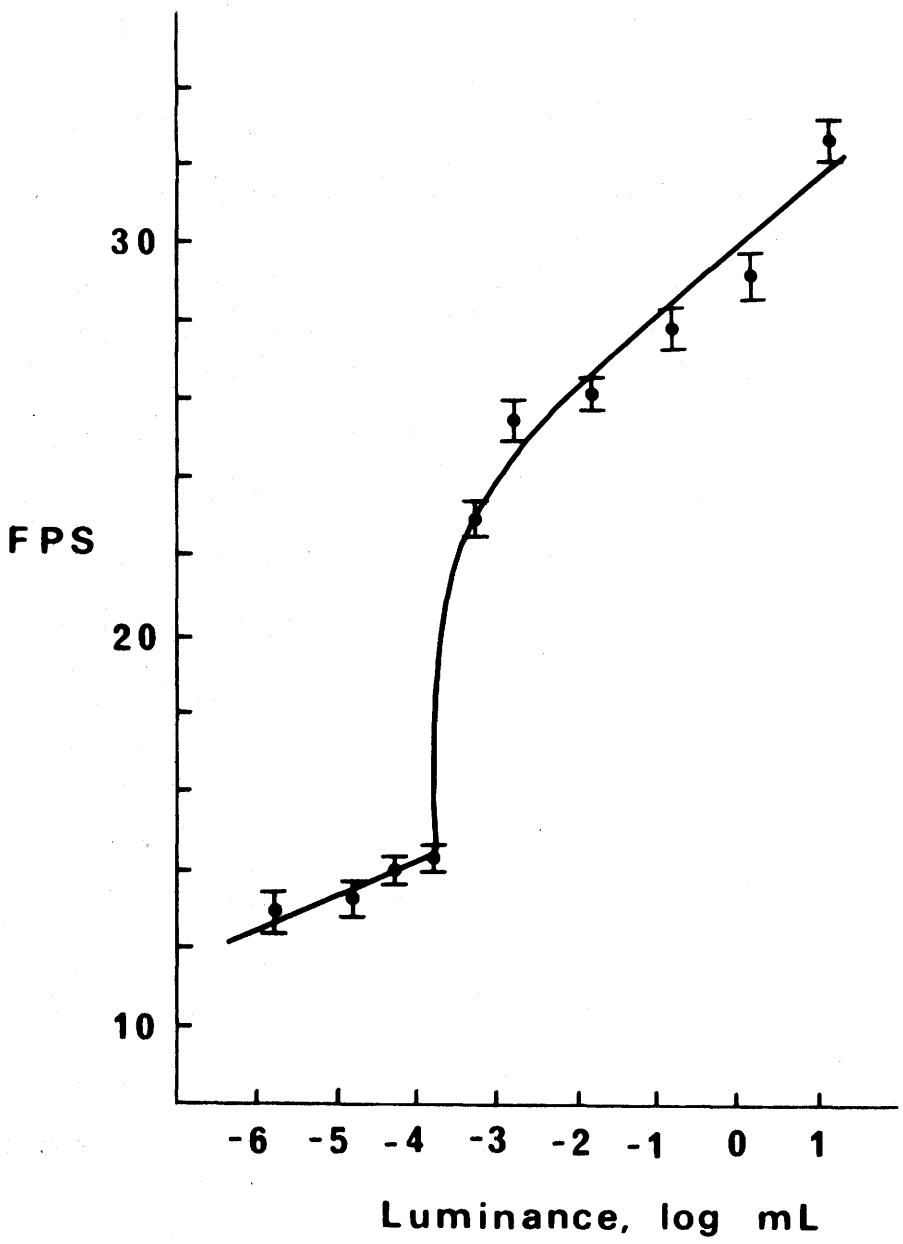
The mean values of four sessions at each intensity, selected on best catch trial performance, were used to compile a $L_{0.707}$ mean for that specific illuminance. Standard deviations from the compiled means and average catch trial performance were computed (Table 1). The probable error (PE) for each intensity's mean was calculated using the value 0.6745 standard error (Table 1) (Peatman 1947; Sokal and Rohlf 1969). The computed means, plus and minus their respective PE to denote the 50% confidence response band about these means (Crozier, Wolf and Zerrahn-Wolf 1937 c), have been plotted as a function of luminance (Fig. 9)

A probit function, based on a maximum response value of 32.70 fps at 170.0 lux was calculated (Table 1) and plotted (Fig. 10). The light intensity was converted from incident lux to milliLamberts (Hurvich and Jameson 1966) to facilitate comparison with other seal psychophysical data. This plot described a two-branched function with unequal slopes.

Table 1 Critical flicker frequency (CFF) determinations for a harp seal, Pagophilus groenlandicus (Erxleben, 1777).

Luminance (log mL)	Mean (fps)	Std. Dev. of mean	Probable error of mean	Mean catch trial	Probit score
1.23	32.70	1.37	0.46	76.50%	----
0.23	29.20	1.77	0.60	77.75%	6.24
$\bar{1}$.23	27.80	1.59	0.54	82.00%	6.03
$\bar{2}$.23	26.15	1.07	0.36	84.25%	5.84
$\bar{3}$.23	25.55	1.37	0.46	78.00%	5.77
$\bar{4}$.77	22.95	1.19	0.40	73.50%	5.53
$\bar{4}$.23	14.35	0.83	0.28	78.00%	4.85
$\bar{5}$.77	14.00	0.89	0.30	74.75%	4.82
$\bar{5}$.23	13.35	1.46	0.49	83.00%	4.77
$\bar{6}$.23	13.00	1.59	0.54	86.25%	4.74

Fig. 9 Critical flicker frequency in a harp seal, Pagophilus groenlandicus. The line has been fitted by eye. The ordinate represents the frequency in flashes per second (fps) of the $L_{0.707}$ thresholds, plotted as a function of luminance. The abscissa represents the stimulus intensity in log milliLamberts. Vertical deviations denote the probable error of each $L_{0.707}$ threshold.


30
FPS
20
10
-6
-5
-4
-3
-2
-1
0
1
Luminance, log mL

Since this function is suggestive of two contributing photoreceptor populations (Crozier, Wolf and Zerrahn-Wolf 1937 c), regression lines and a t-test between the slopes of these two lines were calculated (Sokal and Rohlf 1969). Computed regression line equations for the two lines of the probit plot were: $\hat{y} = 5.06 + 0.06x$ for the lower branch, and $\hat{y} = 6.19 + 0.18x$ for the upper segment (Fig. 10). The r^2s or coefficients of determination were 0.9452 and 0.9570, respectively.

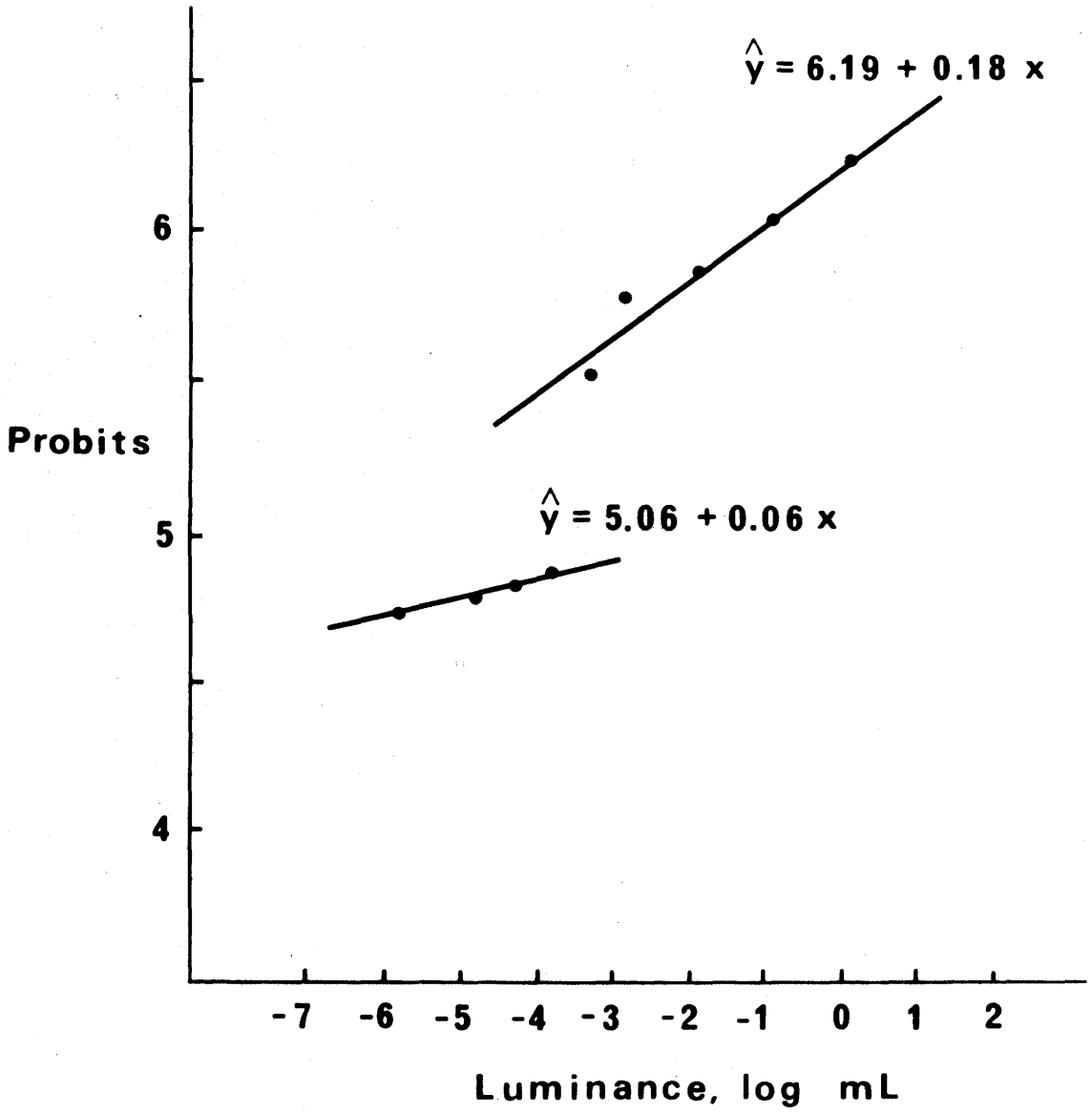
The resulting t-score of 5.68 (3df) suggests the slopes of the two probit line segments are significantly different ($p < 0.05$).

DISCUSSION

Examination of the plotted CFF contour (Fig. 9) and comparison with CFF curves of animals with known photoreceptor compositions, the cat (Fig. 1); the Tokay gecko and the iguana (Fig. 2); and the sunfish (Fig. 3), strongly indicate the harp seal has a duplex retinal composition. Of special interest is a comparison with the flicker contour of the diurnal gecko, Phelsuma (Fig. 4), whose eye was originally thought to be exclusively cone populated until Arden and Tansley's (1962) electro-retinographic study. A duplex break is evident in both the harp seal (Fig. 9) and this gecko's flicker curve.

The probit plot (Fig. 10) reinforces the view of a duplex receptor system in this seal's retina. The computed regression lines fit the data in two segments very closely. The presence of two line segments instead of only one strongly suggests two different receptor populations (Crozier, Wolf, and Zerrahn-Wolf 1937 c). The r^2 values and the significant

Fig. 10 Critical flicker frequency in a harp seal, Pagophilus groenlandicus, expressed in probits, plotted as a function of luminance. The ordinate represents the probit values, derived from the observed CFF thresholds. The abscissa represents the stimulus intensity in log milliLamberts. The slopes of the two line segments are significantly different ($p < 0.05$).


ŷ = 6.19 + 0.18 x
ŷ = 5.06 + 0.06 x
Probits
6
5
4
-7
-6
-5
-4
-3
-2
-1
0
1
2
Luminance, log mL

result derived from the t-test between the slopes of these two line segments verify the existence of two photoreceptor populations contributing to the overall flicker contour.

The compiled means and standard deviations for the $L_{0.707}$ thresholds (Table 1) indicate that the operant procedure used in this experiment is a viable technique of data collection in a free-swimming harp seal. The small standard deviations, ranging from 0.83 to 1.77 fps, suggest the animal had learned well the necessary paradigm for this experimental procedure. Each mean was derived from forty threshold observations; each of the four test sessions used in compiling these means was made up of ten runs, each run itself estimating the threshold value. The entire CFF curve (Fig. 9) is therefore generated from 400 threshold observations. The catch trial performance for the forty test sessions ranged from 70% to 97% correct.

The presence of two photoreceptor types in the harp seal retina has also been suggested by other recent psychophysical data. A spectral sensitivity analysis of the harp seal (Lavigne and Ronald 1972) indicated a Purkinje shift in sensitivity. While Purkinje shifts have been observed in animals with only one morphologically distinct type of photoreceptor, as well as those with two types (Dodt 1967; Granit 1943; LaMotte and Brown 1970), the flicker contour obtained in this experiment strongly suggests the existence of two photoreceptors. Thus, the Purkinje shift observed by Lavigne and Ronald can be thought to reliably reflect the duplex nature of this animal's retina. In addition, monochromatic dark adaptation curves have been obtained for this seal (Lavigne, in preparation). These curves likewise suggest a duplex retina (Lavigne, personal communication), supporting the CFF results.

Further evidence for duplex retinal function is revealed by a pupillary response experiment using the harp seal (Lavigne and Bernholz, in preparation). This procedure generated a sigmoid function describing the interaction between luminance and pupil area. A probit plot of this function suggests the pupillary response is also tied to a rod-cone break in adaptation. Differences in the break point of the pupillary response and the CFF plots may be due to the procedure used.

Functional aspects of this seal's physiology are evident from its interaction with the environment. The harp seal has been shown to dive as deeply as 275 m (Nansen 1925), as well as remain on ice floes for three to four weeks at a time (Mansfield 1967). Ice illumination of approximately 35,000 lux is not uncommon (Lavigne, personal communication), while diving to depths of this magnitude subjects the animal to almost total darkness. Duntley (1963) has shown that at 520 nm, close to the peak scotopic sensitivity of the harp seal (Lavigne and Ronald 1972), only about 0.005% of the light incident at the water's surface penetrates to 250 m, even assuming zero scattering. Such extremes in illumination raise the question of whether one photoreceptor type, with or without a highly mobile pupil, can adequately handle such a range.

Environmental influences can force an animal to adapt in order to maximize its efficiency. One adaptation to this seal's visual system has already been shown; the harp seal's peak scotopic sensitivity of about 525 nm, (Lavigne and Ronald 1972) is very close to the wavelength with the second lowest attenuation coefficient of those tested by Duntley (1963). It would be illogical to think that an animal who has evolved such an excellent deep diving aid as this would not retain cones for activities on ice floes. Nonetheless, through a light microscopy study

and on morphological criteria, Nagy and Ronald (1970) have defined the harp seal retina as pure rod. However, a further study, using electron microscopy, has resulted in Nagy stating that the harp seal has a single class of photoreceptor outer segments, rod-like in appearance, housing at least two types of photopigments. Those outer segments with pedicle-like terminals are thought to mediate Lavigne and Ronald's (1972) photopic spectral sensitivity responses (Nagy 1971).

The important comparison however is between the harp seal contour and that of the owl monkey, Aotes trivirgatus, (Fig. 6). Jones' (1965) light microscopic examination of this monkey's retina suggested a pure rod photoreceptor population. Subsequently, Hamasaki's (1967) electroretinographic study revealed a duplex flicker contour (Fig. 6), thereby suggesting that Jones' histological conclusions were erroneous.

Nagy and Ronald (1970), also using light microscopy, stated that only rod photoreceptors could be found in the harp seal's retina, adding:

> The absence of cone-type photoreceptors in the seal should be stressed. Although pedicle-like receptor terminals, characteristic to that of cones, have been observed, no cone outer segments have been seen using morphologically accepted criteria.

Conclusions of this sort, based on accepted morphological criteria and not on the animal and its environment, may lead to descriptive errors. If they had followed the morphological suggestions of Pedler (1965), their "pedicle-like receptor terminals" coupled to rod outer segments would have suggested receptors similar to those found in the fovea of the rhesus monkey (Pedler 1965). Jamieson and Fisher (1971) used Pedler's criteria and performed a histological examination of the harbour seal,

Phoca vitulina, retina. Their results showed that the harbour seal's retina is histologically similar to that of the harp seal reported by Nagy and Ronald (1970) but that the receptor terminals in the harp seal retina report, when analyzed using Pedler's suggestions, indicate a duplex retina. Pedler's criteria and therefore Jamieson and Fisher's results deviate from "the classicial context as described by Polyak (1941)" (Jamieson and Fisher 1971), a context strongly relied upon by Nagy and Ronald to describe the results of their light microscopy.

As the present experiment has shown, a duplex retina is strongly indicated by the observed CFF contour, a functional index. Other supporting psychophysical data have been cited above. One therefore must make a decision, at least in this animal's case, whether to describe the type(s) of photoreceptor(s) present on grounds of classicial appearance, or function.

Reliance upon morphological criteria has occasionally been shown to be highly restrictive. Crozier and Wolf (1944 c) showed the soft-shelled turtle, Trionyx empori, has a duplex flicker contour, conflicting with Gillett's (1923) histological report of an exclusive cone retina in this animal. They were very careful nevertheless in stating that the retina was duplex, basing their final decision on "subsequent histological examination," rather than on their observed CFF contour. Comparison to some of their other CFF results was given lower preference. Their caution though was well founded. They had previously (Crozier and Wolf 1939 b) examined the gecko Sphaerodactylus inague, whose retina "by cytological criteria ... is devoid of cones." When compared to the CFF contour obtained in the turtle Pseudemys (Crozier, Wolf, and Zerrahn-Wolf 1939), an almost pure cone animal with a negligible

amount of rods, Crozier and Wolf found the gecko's CFF curve to be almost identical. From this evidence they made three statements:

1) ... these observations do not support the idea that a rod retina necessarily functions best at low illuminations, even in a nocturnal animal.

2) Nor is it indicated that a rod retina performs less ably than a cone retina at high illuminations.

3) The danger of associating histological appearance and functional capacity in matters of visual performance is sharply emphasized. (Crozier and Wolf 1939 b).

Crozier and Wolf, with apparent confidence in the reported retinal composition, thereby rejected basic functional characteristics of rods and of cones and argued that the problem could not be solved by thinking the gecko possessed a "peculiar kind of retinal rod; this merely destroys the complex accepted conception of rod with which we started" (Crozier and Wolf 1939 b). Inspection of the CFF contours for these two animals (Crozier and Wolf 1939 b, pp. 560 and 565) and the probability plot (p. 563) shows reasons to question the validity of this gecko's histologically appointed photoreceptor composition, and to firmly accept their third statement, cited above, though now on functional rather than morphological grounds.

One consideration missing from this gecko examination was the transmutation theory of Walls (1942). This theory suggests that, structurally, 'cones' of some geckos have evolved into 'rods,' without changing their cone operational characteristics. Pedler (1965) also points out the possibility of one class of outer segments retaining the terminal indicative of the complementary photoreceptor. Pedler and Tilly (1964) have shown that in some geckos "changes in intracellular components have evolved, to meet the demands of sensitivity and acuity by using the facilities of one basic cell variety." Dodt and Jessen's

(1961) electroretinographic study of a "nocturnal gecko," Tarentola mauritanica, in which no Purkinje shift was recorded, resulted in a duplex flicker contour. Brown and Watanabe (1962 b) in their examination of the owl monkey, Aotes trivirgatus, concluded that Dodt and Jessen's duplex results were feasible, and that observed rod and cone potentials from the owl monkey suggested "that functional differences may occur among receptors which show no differences in structure or contained photopigments." Such changes in structural versus functional characteristics can and do occur, and make photoreceptor classification, on the basis of morphological criteria, at times a very tenuous situation. Some geckos have been forced to adapt from a diurnal to a nocturnal environment, only later to be forced back into a dirunal setting (Walls 1942; Underwood 1951; Tansley 1965). Such environmental changes can result in transmutation of retinal cells, as indicated above. The seal has had to move from the water, onto land, and subsequently back to the water during its evolution (Harrison and King 1965; Peterson 1968). These changes might cause anatomical changes, mandatory to survival, to occur. A resulting photoreceptor structure however, may no longer be easily identifiable, in the sense of old (Schultze 1866), intermediate (Polyak 1941), or new (Pedler 1965) morphological criteria.

Kelly (1972), in discussing human spatio-temporal resolution, suggests that in evolutionary terms the most efficient place to make bandwidth limitations is at or near the input level. He mentions that a species would be unlikely to develop an elaborate high frequency collecting receptor system if, at some later stage in the visual process, this specific information is always discarded. The actual limitation is most likely "governed by the response of individual receptors or receptive

fields" (Kelly 1972). By suggesting that receptor cells, bipolar cells, and horizontal-bipolar cell combinations each have specific adaptation exponents, Kelly theorizes that photopic CFF mediation is accomplished at the retina (Kelly 1971, 1972) and not at some higher site as put forward by Sperling and Sondhi (1968).

If the photopic temporal resolution limit is set by cones as indicated by Kelly, the frequencies above -2 log mL in the harp seal CFF contour (Fig. 9) may also be mediated and limited by cones. The high luminance level precludes the possibility of rod interference. Evidence from the rhesus monkey, Macaca mulatta (Gouras and Link 1966; Gouras 1967) points out that the shorter response time by the cones (50 versus 150 msec for the rods) controls ganglion cell output when stimulated at suprathreshold intensities. Still shorter latency is derived from the faster response speed of the ganglion cell itself under increasing illumination. As a further complement to this system, it was shown that the earliest signal to the ganglion cell leaves a transitory refractory period; stimulation of both rods and cones simultaneously results in a higher probability of a cone controlled response (Gouras and Link 1966; Gouras 1967). Whitten and Brown (1973 b) have suggested that at stimulus intensities generating cone late receptor potentials with larger than threshold amplitudes, the rod late receptor potentials are so strongly suppressed by this cone stimulation that they disappear. A cone-rod lateral inhibitory arrangement is hypothesized by these authors to free the cones from the degrading effect of very slowly decaying rod potentials at photopic intensities. Once freed, the cones can then perform at peak temporal resolution rates. At threshold levels, the same reaction time superiority is displayed by the cones (Gouras 1967).

Progressive light adaptation was shown to reduce the effective size of receptive field centers, agreeing with Hubel and Wiesel's (1960) findings in the spider monkey (Ateles) fovea that some ganglion cell receptive field centers may in fact be only the size of single cone photoreceptors. This shift during light adaptation to smaller receptive field centers, most likely controlled by cones, plus the faster reaction time of the ganglion cell itself leads to the increase in temporal resolution at higher luminances.

Nagy and Ronald (1970) and Nagy (1971) found no area centralis in the harp seal retina. No midget bipolar or midget ganglion cells, associated with single cone-controlled receptive field centers should therefore be evident (Hubel and Wiesel 1960). Also, the ganglion cell population, relative to the photoreceptor count, was found to be very low. The two types of ganglion cells observed, however, had larger dendritic fields in the periphery and far periphery than in the center (Nagy 1971), suggesting larger receptive fields in these areas. These ganglion cells were influenced by bipolar to amacrine to ganglion cell connections, suggesting that a great deal of visual processing is done at the retina. Large numbers of interneurons from horizontal cells in the outer plexiform layer of the harp seal retina may act as the mediators of a lateral inhibitory arrangement (Brown and Murakami 1968; Whitten and Brown 1973 b). Care however must be taken in this interpretation; Steinberg (1969 a, b) has shown that the cone-rod suppression is not as complete in the cat as it appears in the Macaca investigation of Whitten and Brown. Caution with relating this suppression to the harp seal retina is taken from Balliet and Schusterman's (1971) suggestion that visual acuity in some pinnipeds resemble more closely the visual acuity of the cat than that of the otter, an evolutionary marine relative of

the seal. The disparity between the seal's superior and the otter's inferior visual acuity is thought to stem basically from the poorer resolving power of the otter's retina (Balliet and Schusterman 1971). Complete cone-rod suppression, missing in the cat (Steinberg 1969 a, b), and possibly in the seal retina, may not be required if sufficient high resolving retinal elements are present to meet the minimum acuity requirements of the animal.

While Nagy states that the bipolar cells of the harp seal retina look like those associated with rod photoreceptors, the amacrine and the ganglion cells present may not show such affiliation. Work with the rhesus monkey, Macaca mulatta, indicates that different amacrine cell types are not exclusively associated with rod or with cone photoreceptor populations, and that there is no difference in amacrine cell types between the fovea and parts of the retina where rod bipolar terminals are found (Boycott and Dowling 1969). Further work on these animals has suggested that there are no exclusive rod-responding ganglion cells (Gouras and Link 1966). If the observations from the rhesus monkey retina may be applied to the harp seal retina, photoreceptor control of the ganglion cell may be the important key to the high amount of visual information processing at the retina thought to be exhibited by this seal. With the presence of high CFF rates at photopic stimulus levels, the existence of cone photoreceptors is strongly indicated.

The observed CFF contour (Fig. 9) can therefore be in agreement with the observed second and especially the third order neurons of the harp seal retina (Nagy and Ronald 1970; Nagy 1971) but would suggest that the conclusion that only rod photoreceptors are present (Nagy and Ronald 1970) is incorrect. A duplex photoreceptor population in the harp

seal retina, suggested by Lavigne and Ronald's (1972) spectral sensitivity results, and by Nagy's (1971) electron microscopy proposals, is supported by these results.

BIBLIOGRAPHY

Arden, G. B. and Tansley, K. 1962. The electroretinogram of a diurnal gecko. J. Gen. Physiol., 45, 1145-61.

Balliet, R. F. and Schusterman, R. J. 1971. Underwater and aerial visual acuity in the Asian "Clawless" otter (Amblonyx cineria cineria). Nature, 234, 305-6.

Blough, D. 1958. A method for obtaining psychophysical thresholds from the pigeon. J. Exp. Anal. Behav., 1, 31-43.

Boycott, B. B. and Dowling, J. E. 1969. Organization of the primate retina: light microscopy. Phil. Trans. R. Soc. B., 225, 109-84.

Brown, K. T. and Murakami, M. 1968. Rapid effects of light and dark adaptation upon the receptive field organization of S-potentials and late receptor potentials. Vision Res., 8, 1145-71.

____ and Watanabe, K. 1962 a. Isolation and identification of a receptor potential from the pure cone fovea of the monkey retina. Nature, 193, 958-60.

____ ____. 1962 b. Rod receptor potential from the retina of the night monkey. Nature, 196, 547-50.

____ ____ and Murakami, M. 1965. The early and late receptor potentials of monkey rods and cones. Cold Spring Harb. Symp. Quant. Biol., 30, 457-82.

Cohen, A. I. 1969. Rods and cones and the problem of visual excitation. In: The Retina, B. R. Straatsma, M. O. Hall, R. A. Allen, and F. Crescitelli, Editors. Univ. of California Press. Berkeley.

Crozier, W. J. and Wolf, E. 1939 a. The flicker contours of genetically related fishes. II. J. Gen. Physiol., 22, 463-86.

____ ____. 1939 b. The flicker response contour for the gecko (rod retina). J. Gen. Physiol., 22, 555-66.

____ ____. 1939 c. The flicker response contour for the frog. J. Gen. Physiol., 23, 229-38.

____ ____. 1940 a. Temperature and critical illumination for reaction to flickering light. VI. Flash duration varied. J. Gen. Physiol., 23, 531-51.

____ ____. 1940 b. Reaction to visual flicker in the newt Triturus. J. Gen. Physiol., 23, 667-76.

____ ____. 1941 a. The flicker response contour for Phrynosoma (horned lizard; cone retina). J. Gen. Physiol., 24, 317-24.

____ ____. 1941 b. The simplex flicker threshold contour for the zebra finch. J. Gen. Physiol., 24, 625-33.

____ ____. 1942 a. Theory and measurement of visual mechanisms. VIII. The form of the flicker contour. J. Gen. Physiol., 25, 369-79.

____ ____. 1942 b. The wavelength sensitivity for the zebra finch. J. Gen. Physiol., 25, 381-90.

____ ____. 1943. Theory and measurement of visual mechanisms. IX. Flicker relations within the fovea. J. Gen. Physiol., 27, 119-38.

____ ____. 1944 a. Theory and measurement of visual mechanisms. X. Modifications of the flicker response contour, and the significance of the avian pecten. J. Gen. Physiol., 27, 287-313.

____ ____. 1944 b. Flicker response contours for the sparrow, and the theory of the avian pecten. J. Gen. Physiol., 27, 315-24.

____ ____. 1944 c. Theory and measurement of visual mechanisms. XII. On visual duplexity. J. Gen. Physiol., 27, 513-28.

____ ____ and Zerrahn-Wolf, G. 1936. On critical frequency and critical illumination for response to flickered light. J. Gen. Physiol., 20, 211-28.

____ ____ ____. 1937 a. Temperature and critical illumination for reaction to flickering light. II. Sunfish. J. Gen. Physiol., 20, 411-31.

____ ____ ____. 1937 b. Critical illumination and flicker frequency in related fishes. J. Gen. Physiol., 21, 17-56.

____ ____ ____. 1937 c. Intensity and critical frequency for visual flicker. J. Gen. Physiol., 21, 203-21.

____ ____ ____. 1938. Critical illumination and flicker frequency, as a function of flash duration for the sunfish. J. Gen. Physiol., 21, 313-34.

____ ____ ____. 1939. The flicker response function for the turtle, Pseudemys. J. Gen. Physiol., 22, 311-40.

Dodt, E. 1952. Beitrage zur electrophysiologie des auges. II. Mitteilung. Ueber hemmungsvorgange in der menschlichen retina. Von Graefes Arch. Ophthal., 153, 152-62.

____. 1967. Purkinje-shift in the rod eye of the bush baby, Galago crassicaudatus. Vision Res., 7, 509-17.

____ and Enroth, C. 1954. Retinal flicker response in cat. Acta Physiol. Scand., 30, 375-90.

____ and Jessen, K. H. 1961. The duplex nature of the retina of the nocturnal gecko as reflected in the electroretintogram. J. Gen. Physiol., 44, 1143-58.

Duntley, S. Q. 1963. Light in the sea. J. Opt. Soc. Amer., 53, 214-33.

Gellerman, L. W. 1932. Chance orders of alternating stimuli in visual discrimination experiments. J. Genet. Psychol., 42, 206-08.

Gillett, W. G. 1923. The histological structure of the eye of the soft-shelled turtle. Amer. Jour. Ophthal., 6, 955-73.

Gouras, P. 1967. The effects of light-adaptation on rod and cone receptive field organization of monkey ganglion cells. J. Physiol., 192, 747-60.

____ and Link, K. 1966. Rod and cone interaction in dark adapted monkey ganglion cells. J. Physiol., 184, 499-510.

Granit, R. 1935. Two types of retinae and their electrical responses to intermittent stimuli in light and dark adaptation. J. Physiol., 85, 421-38.

____. 1943. The spectral properties of the visual receptors of the cat. Acta Physiol. Scand., 5, 219-29.

____ and Riddell, H. A. 1934. The electrical responses of light- and dark-adapted frogs' eyes to rhythmic and continuous stimuli. J. Physiol., 81, 1-28.

Hamasaki, D. I. 1967. An anatomical and electrophysiological study of the retina of the owl monkey, Aotes trivirgatus. J. Comp. Neurol., 130, 163-74.

Harrison, R. J. and King, J. E. 1965. Marine Mammals. Hutchinson. London.

Horsten, G. P. M. and Winkleman, J. E. 1962. Comparison of critical fusion frequency in diurnal and nocturnal retina of vertebrates. Arch. Intern. Physiol. Biochem., 70, 660-70.

Hubel, D. H. and Wiesel, T. N. 1960. Receptive fields of optic nerve fibers in the spider monkey. J. Physiol., 154, 572-80.

Hurvich, L. M. and Jameson, D. 1966. Contemporary Topics in Experimental Psychology. Allyn and Bacon, Inc. Boston.

Jamieson, G. S. and Fisher, H. D. 1971. The retina of the harbor seal, Phoca vitulina. Can. J. Zool., 49, 19-23.

Jones, A. E. 1965. The retinal structure of (Aotes trivirgatus) the owl monkey. J. Comp. Neurol., 125, 19-28.

Kelly, D. H. 1971. Theory of flicker and transient responses. I. Uniform fields. J. Opt. Soc. Amer. 61, 537-46.

____. 1972. Adaptation effects on spatio-temporal sine-wave thresholds. Vision Res., 12, 89-101.

LaMotte, R. H. and Brown, J. L. 1970. Dark adaptation and spectral sensitivity in the cat. Vision Res., 10, 703-16.

Landau, D. and Dawson, W. W. 1970. The histology of retinas from the pinnipedia. Vision Res., 10, 691-702.

Landis, C. 1954. Crozier and Wolf on flicker-fusion, 1933-44. J. Psychol., 37, 3-17.

Lavigne, D. M. and Ronald, K. 1972. The harp seal, Pagophilus groenlandicus (Erxleben, 1777). XXIII. Spectral sensitivity. Can. J. Zool., 50, 1197-1206.

Mansfield, A. W. 1967. Seals of Arctic and Eastern Canada. Fisheries Research Board of Canada. Ottawa.

Meneghini, K. A. and Hamasaki, D. I. 1967. The electroretinogram of the iguana and Tokay gecko. Vision Res., 7, 243-5.

Nagy, A. R. 1971. A light and electronmicroscopic study of the structure of the retina of the harp seal, Pagophilus groenlandicus (Erxleben, 1777). Ph.D. thesis, Univ. of Guelph.

____ and Ronald, K. 1970. The harp seal, Pagophilus groenlandicus (Erxleben, 1777). VI. Structure of retina. Can. J. Zool., 48, 367-70.

Nansen, F. 1925. Hunting and Adventure in the Arctic. Duffield. New York.

Ordy, J. M. and Samorajski, T. 1968. Visual acuity and ERG-CFF in relation to the morphological organization of the retina among diurnal and nocturnal primates. Vision Res., 8, 1205-25.

Peatman, J. G. 1947. Descriptive and Sampling Statistics. Harper. New York.

Pedler, C. 1965. Rods and cones - a fresh approach. In: Color Vision. Ciba Foundation Symposium. A. V. S. De Reuck and J. Knight, Editors. Churchill. London.

____ and Tilly, R. 1962. The nature of the gecko visual cell. Vision Res., 4, 499-510.

Peterson, R. S. 1968. Social behavior in pinnipeds with particular reference to the northern fur seal. In: The Behavior and Physiology of Pinnipeds. R. J. Harrison, R. C. Hubbard, R. S. Peterson, C. E. Rice, and R. J. Schusterman, Editors. Appleton-Century-Crofts. New York.

Piper, H. 1911. Uber die netzhautstrome. Arch. Anat. Physiol., Lpz. 85-132.

Polyak, S. 1941. The Retina. Univ. of Chicago Press. Chicago.

Porter, T. C. 1902. Contributions to the study of flicker. II. Proc. Roy. Soc., 70A, 313-29.

Ronald, K., Foster, M. E., and Johnson, E. 1969. The harp seal, Pagophilus groenlandicus (Erxleben, 1777). II. Physical blood properties. Can. J. Zool., 47, 461-68.

Schaternikoff, M. 1902. Ueber den einfluss der adaptation auf die erscheinung des flimmerns. Z. Psychol., 29, 241-54.

Schultze, M. 1866. Zur anatomie und physiologie der retina. Arch. Mikrosk. Anat. Entw. Mech., 2, 175-286.

Shipley, T. and Fry, A. 1966. Critical flicker fusion perimetry and the adaptation level of the eye. Nature, 211, 1315-17.

Sokal, R. R. and Rohlf, F. J. 1969. Biometry: The Principles and Practice of Statistics in Biological Research. W. H. Freeman. San Francisco.

Sperling, G. and Sondhi, M. M. 1968. Model for visual luminance discrimination and flicker detection. J. Opt. Soc. Amer., 58, 1133-45.

Steinberg, R. H. 1969 a. Rod-cone interaction in S-potentials from the cat retina. Vision Res., 9, 1331-44.

____. 1969 b. The rod after-effect in S-potentials from the cat retina. Vision Res., 9, 1345-55.

Tansley, K. 1961. The retina of a diurnal gecko, Phelsuma madagascariensis longinsulae. Pflugers Arch. ges. Physiol., 272, 262-69.

____. 1965. Vision in Vertebrates. Chapman and Hall, Ltd. London.

____, Copenhauer, R. M. and Gunkel, R. D. 1961. Some aspects of the electroretinographic response of the American red squirrel, Tamiosciurus hudsonicus loquax. J. Cell. Comp. Physiol., 57, 11-19.

Tigges, J., Brooks, B. A., and Klee, M. R. 1967. ERG recording of a primate pure cone retina (Tupaia glis). Vision Res., 7, 553-63.

Underwood, G. L. 1951. Reptillian retinas. Nature, 167, 183-85.

Von Kries, J. 1903. Uber die wahrnehmung des flimmerns durch normale und durch total farbenblinde personen. Z. Psychol., 32, 113-17.

Walls, G. L. 1942. The Vertebrate Eye and its Adaptive Radiation. Cranbrook Institute of Science. Bloomfield, Michigan. Reprinted 1963 Hafner Publishing Co. New York.

Wetherill, G. B. and Levitt, H. 1965. Sequential estimation of points on a psychometric function. Brit. J. Math. and Stat. Psychol., 18, 1-10.

Whitten, D. N. and Brown, K. T. 1973 a. The time courses of late receptor potentials from monkey cones and rods. Vision Res., 13, 107-35.

____ ____. 1973 b. Photopic suppression of monkey's rod receptor potential, apparently by a cone-initiated lateral inhibition. Vision Res., 13, 1629-58.

Wolf, E. and Zerrahn-Wolf, G. 1936. Threshold intensity of illumination and flicker frequency for the eye of the sunfish. J. Gen. Physiol., 19, 495-503.

APPENDIX 1

Daily Vitamin Supplement

30 500 mg Sodium chloride tablets.
Drug Trading Co., Toronto.

2 10 mcgm Novo-B vitamin B compound with vitamin C capsules.
Novopharm Ltd., Toronto.

2 100 mg Thiamine hydrochloride tablets.
Empire Laboratories, Toronto.

1 5000 International unit A, 400 International unit D halibut liver oil capsule.
Novopharm Ltd., Toronto.

3 400 International unit vitamin E capsules.
Empire Laboratores, Toronto.

* * * * *

1 Neo-Maturex Hematopoietic capsule each Wednesday.
Ayerst Laboratories, Montreal.