NAVAL RESEARCH

REVIEWS

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PROFILES IN SCIENCE

Dr. Weyl

Dr. Weyl came to the Office of Naval Research in 1947 from the Bureau of Ordnance; where he successfully used new mathematical techniques in the design of high explosive weapon systems. At ONR Dr. Weyl helped organize the Mathematics Program, which under his direction was an important instrument for encouraging American Scientists to do research in applied mathematics. During his twenty years at ONR Dr. Weyl is best known for his ability to anticipate the needs of the Navy and then direct the scientific research to satisfy these needs. While at ONR Dr. Weyl was Head of the Mathematics Division, Director of Research, and for six years the Chief Scientist and Deputy of Naval Research.

After leaving ONR he served as Special Assistant of the President of the National Academy of Sciences and in 1968 became Dean of the newly established Division of Sciences and Mathematics at Hunter College of the City University of New York where he is today.

The Vision of Sharks: A Perspective

Samuel H. Gruber
University of Miami

Introduction

The Navy's interest in sharks is axiomatic; because of their distribution, size, and potential danger,, they can interfere with certain Naval missions. Besides the real physical hazard, however, the shark problem also involves considerations of a psychological nature. The old adage that ignorance breeds fear provides one basis for Navy-supported studies which yield a greater understanding of sharks. Ideally, the end result of these investigations should allow Naval personnel to predict and eventually control the activities of sharks within areas of military operations. Prediction of animal behavior, however, falls within the sphere of a relatively new branch of biology known as Ethology. One of the pioneers and foremost authorities in this field, N. Tinbergen (1), has clearly explained the relation between sensory physiology and ethology. He correctly pointed out that the first task in investigating the behavior of an animal is a careful study of its sensory capacities. These studies involve both psychophysics and neurophysiology. Their objective is to provide data on physiological mechanisms subserving a particular sensory modality as well as to give some insight into the subjective world of the animal. It should be understood that each animal has its own "Merkwelt" or perceptual world which is frequently different from our own. For example, we are barely aware of the rich olfactory world open to dogs. Any such differences must be known to the ethologist if a meaningful understanding of an animal's behavior is to be gained. Thus, ONR's Oceanic Biology branch has vigorously supported research on the sensory biology of sharks.

My studies on vision at the University of Miami's Rosenstiel School of Marine and Atmospheric Science have been included within this program and the stated objective is to characterize the visual system of sharks in terms of structure, physiological mechanisms and visual capability. In other words, we have taken a broadly based and interdisciplinary approach to the question of eyesight in sharks.

Systematic investigation of vision in sharks dates from the middle of the 19th century. These early studies attempted to describe the

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anatomy and fine structure of the eye, retina, and visual pathway and to predict visual capability from these anatomical features. By the 1940's, enough information had been amassed to include data on shark vision in two of the great works on the vertebrate eye, by Walls (2) and Rochon-Duvigneaud (3). Later reviews (4,5) summarized knowledge of the shark's visual system to the 1940's and I am presently working on a 12-year update of this information. Throughout these reviews, the ideas of two early workers – Victor Franz and Marie-Louise Verrier – prevailed and sharks came to be thought of as having extremely poor eyesight. According to Verrier (6), the retina was crudely organized with a relatively coarse grain of receptor cells and, most damaging for visual capability, completely lacking in cone receptor cells. Cone cells are the light receptors which are associated with acute color vision and rapid temporal resolution. While Walls (2) agreed with Verrier's views, certain paradoxes about the shark's visual system were noted. He wrote that "the whole philosophy of the basis of contrast between the fish eye ... and the typical "air" eye ... is rather rudely disturbed by the elasmobranchs." What "disturbed" Walls was the number of important optical specializations independently evolved by sharks and their allies. Why would an animal with rudimentary vision have evolved a complex and unique set of optical structures?

This was the state of information when we began to look into the question of vision – especially color vision – in sharks. The older literature, as indicated above, seemed to rule out the possibility of color vision and "clearly demonstrated" that sharks have notoriously poor eyesight. However, at the urging of my colleagues from the Bascom-Palmer Eye Institute, University of Miami, we collected eyes from several local species and were surprised to find both rods and cones in all retinas (Figure 1). Of course, scientific literature yields only very slowly and the question now became: are these cone cells truly cones or merely artifacts? Thus, our first job was to determine whether the few species with cones were special cases or whether the so-called duplex retina (i.e. containing both rods and cones) was a general feature of elasmobranchs. In seven species, the lowest cone: rod ratio we found was 1:13 and we concluded that the typical elasmobranch does, in fact, possess both rods and cones in its retina. In retrospect, it seems that the early workers had problems on two accounts: first, their conclusions were too broadly applied; and second, working in Europe, they did not have access to the larger and perhaps more typical sharks.

Duplexity Theory of Vision

Clearly, then, sharks have cones; but do these cones function? Again the early investigators concluded that if an animal possessed a

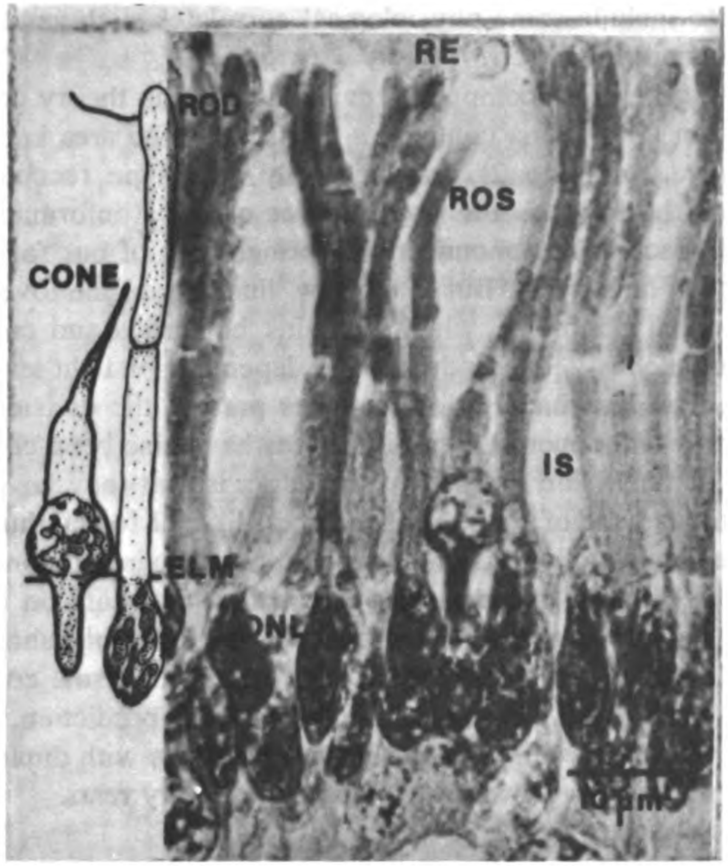


Figure 1 — Photoreceptors of the white shark, Carcharodon carcharias *(Linnaeus): Lamnidae. Abbreviations used in Figs.: ELM = external limiting membrane; HC = horizontal cell; IS = inner segment of photoreceptor; MF = Muller fibre; ONL = outer nuclear layer; RE = retinal epithelium; ROS = rod outer segment. (From Gruber* et al.*, 1975, with kind permission of the editor of the Bulletin of Marine Science.)*

certain type of cell, it must be functional. We made no such claim. Instead, the shark was subjected to a variety of experimental procedures designed to separate out the relative activities of rods from cones. The experiments were based on a theoretical framework known as the Duplexity Theory of Vision (7). For more than a century, visual scientists have explored the bases of this theory and, in general, it has stood the test of time (8). Thus, there is a wealth of comparative animal and human data with which to compare my results on sharks. While development of the duplexity theory is rather complex, the theory itself is simple. Its author, Schultze, a classical histologist, discovered a relationship between behavior and type of photoreceptor. Animals with pure-rod retinas (such as the gecko lizard) were found to be nocturnal; those with pure-cone retinas (such as the ground squirrel) were diurnal. This was later expanded to include some physiological correlates such as color vision and visual acuity.

Perhaps the most compelling evidence for this theory comes from human vision. Our retina contains a tiny specialized area known as the *fovea centralis* (Figure 2) in which only cone-type receptors occur. In addition, the fovea is the major source of visual information during daylight. In fact, an autonomic reflex brings both of our fovea to bear on any object of interest. But under low illumination the fovea is blind, and our retinal periphery, which contains both rods and cones, takes over. Simultaneously, acuity drops; and depending on light levels, colors disappear. This graphically demonstrates part of the division of labor between rods and cones. These differences have also been confirmed in lower vertebrates. The problem with sharks is that they have a homogenous retina devoid of any specialized areas like the fovea; thus studying both rod and cone activity is more difficult. Since rods and cones operate optimally at different intensities, we reasoned that data on any visual parameter sampled at different brightness levels would show a characteristic "kink" at the point where rods took over visual control from the cones. Such a curve is shown in Figure 3. This prediction, confirmed in many experiments on humans and other animals with duplex retinas, is another foundation on which the duplexity theory rests.

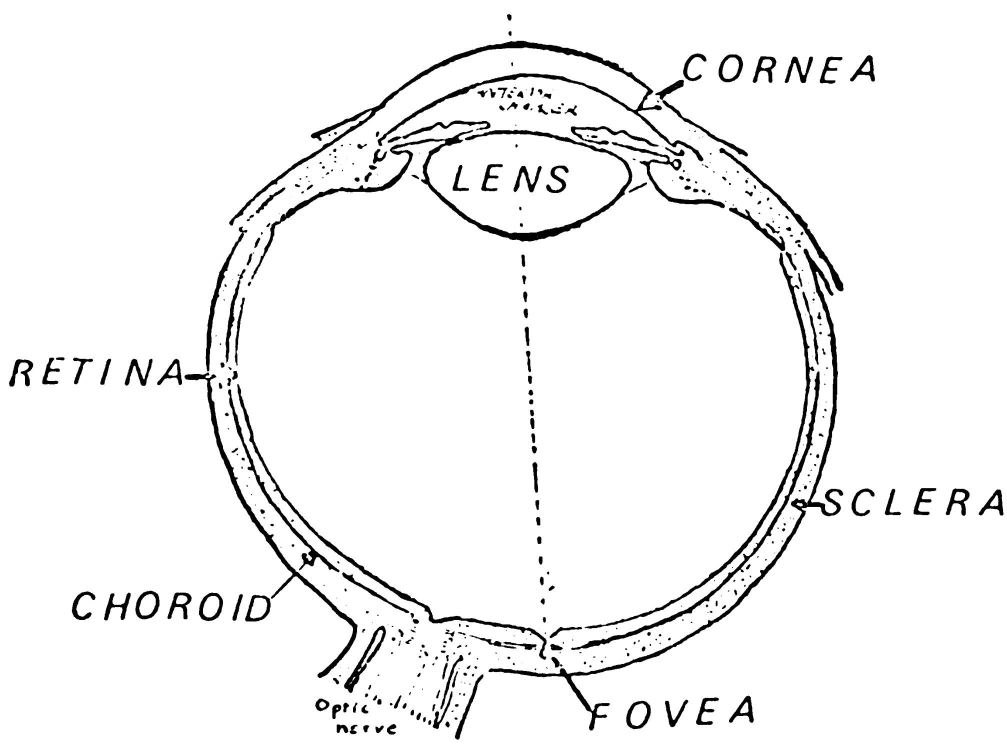


Figure 2 – Horizontal section through the human eye (diagramatic). Fovea is the shallow pit to the right of the optic nerve. Dotted line shows the optical axis of the eye. (Modified from Wolff, The Anatomy of the Eye and Orbit, *H. K. Lewis and Co.)*

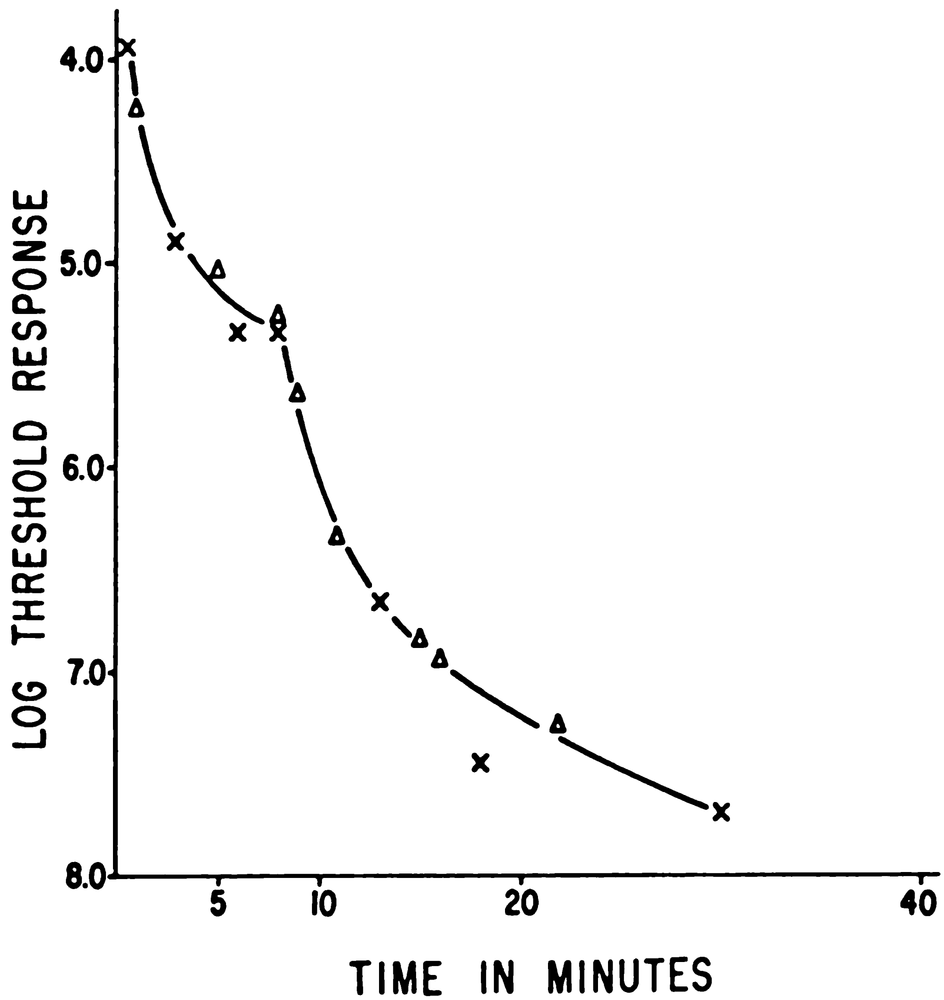


Figure 3 — Course of dark adaptation in two human subjects. Abscissa is time in darkness after 5 minutes of intense light adaptation. Ordinate is the light intensity just noticable to the subjects. At 8-10 minutes a "kink" can be seen which signals the switch over from cone- to rod-control of dark adaptation.

How to Investigate Visual Systems

Some years ago, Hess (9) identified four basic methods for obtaining experimental data on sensory systems. These included: (A) extirpation and ablation; (B) electrophysiological recording from sensory tissue; (C) natural orientations to sensory stimuli, and (D) learned responses to conditioned stimuli. Because of the restricted information obtainable by the method of extirpation (A), and the capriciousness of natural orientation (C), we have concentrated on (B) and (D) to collect reliable data on visual capability of sharks.

Electrical recording from the fish retina was attempted in the 19th century (10). Nearly 100 years later, Kobayashi (11) was the first to attempt this method on sharks. By stimulating the retina with brief flashes of light it is possible to measure a potential or voltage difference between an indifferent electrode placed on the head of an anesthetized shark and a recording electrode placed on the cornea or in the vitreous body of the eye. With suitable amplification and display, this response, known as the electroretinogram (ERG), can be easily visualized (Figure 4).

My primary interest, however, has been in a behavioral technique known as classical conditioning (12). In 1928, Pavlov had already established that a so-called conditioned reflex could be formed between a neutral stimulus such as the ringing of a bell and the presentation of food. Pavlov found that repeated pairings of bell and food would modify a dog's behavior through the formation of a conditioned reflex, so that it salivated when it heard the bell. The dog, in effect, expected to receive food when it heard the bell and anticipated the food by salivating "prematurely." In Pavlov's pioneer experiments, the bell was called the conditioned stimulus while the food was the unconditioned stimulus, which, in hungry dogs, always elicited the unconditioned salivation

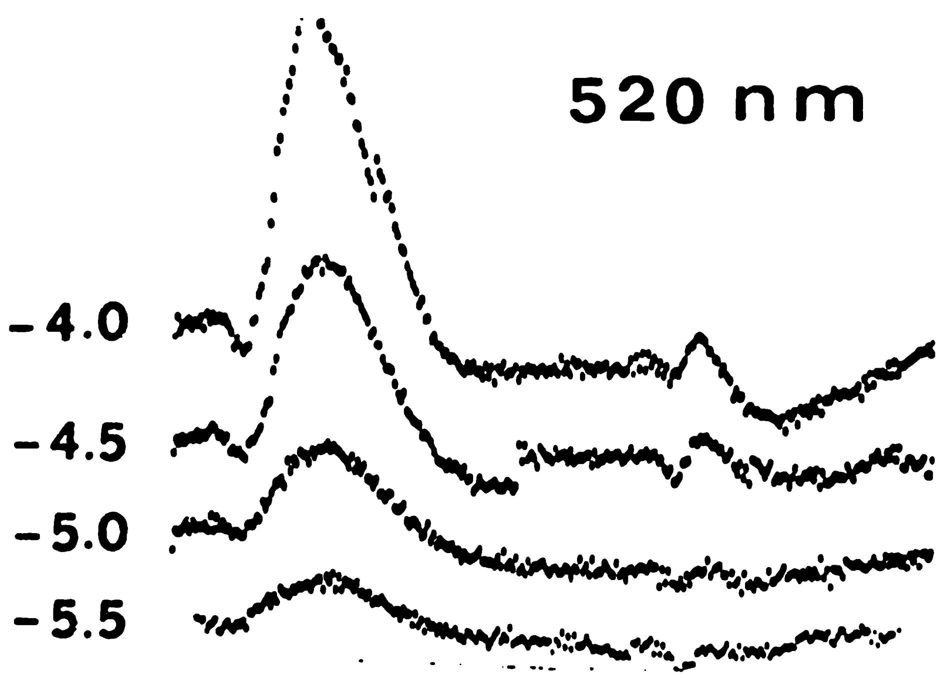


Figure 4 — Electro retinograms (ERG) of the lemon shark. ERGs are generated by the retina each time it is stimulated by a flash of light. ERGs above demonstrate that response amplitude increases as light increases (4.0 is brightest). Computer has summated responses from 16 flashes of light for each ERG shown. The stimulus wavelength is 520nm.

response. The novel conditioned salivation, an analogy of the unconditioned response, always preceded the presentation of food. At first only glandular responses and smooth muscle contractions were considered classically conditioned responses because they are presumably autonomic, that is, not under conscious control. But this was later expanded to include movements of striated muscle (13).

Our first attempt to train lemon sharks (Figure 5) was by the method of classically conditioned, heart-rate deceleration. This technique, profitably used in bony fishes (14), depends upon an electric shock which causes the animal's heart to "miss a beat" and decelerate. In our early studies, we harnessed lemon sharks and connected them to an electrocardiograph machine. A small electric shock was paired with a brief flash of light to form a conditioned reflex between light and shock. While this method worked well with goldfish, we were completely unsuccessful in getting consistent conditioned responses in the shark. The major problem was that the shark's EKG had to be monitored through a chronically implanted cardiac electrode. In every case, the electrode sutures caused internal infections and the animal died shortly

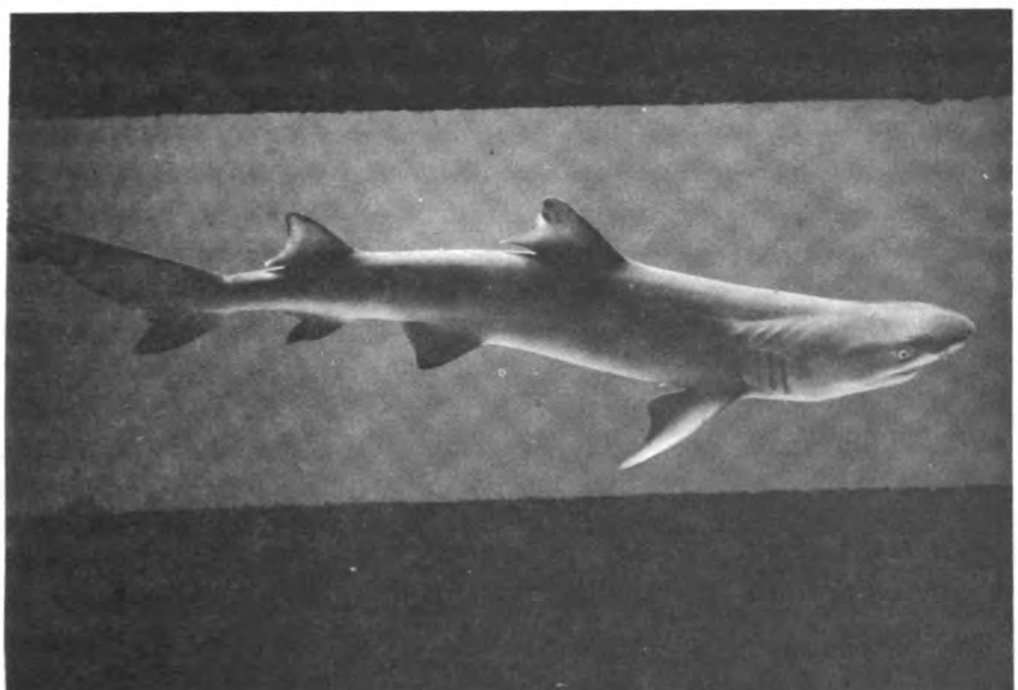


Figure 5 — Lemon shark, **Negaprion brevirostris** *(Poey), family Carcharhinidae, was chosen because it lives in captivity and is available year round. Most importantly, it need not swim to respire and can thus be harnessed and restrained. This is impossible for most other sharks since they cannot actively pump water over their gills and must swim to respire.*

thereafter. Our real break came when we noticed one animal responding to the light by moving its third eyelid, the so-called nictitating membrane (Figure 6). By luck, the shocking electrodes had been so positioned as to stimulate receptors which activate the blinking response. By pairing for heart rate, we coincidentally conditioned the third eyelid. After systematic experimentation with electrode position, intertrial interval and other conditioning factors, an optimal procedure was evolved which rapidly and reliably produced what appeared to be conditioned blinking responses. The latest apparatus for conditioning lemon sharks is shown in Figure 7.

The reason for training in the first place was to be able to unambiguously ask the shark questions about its visual world without the aid of language instruction. Naturally, we had to correctly interpret the shark's answer. We also had to demonstrate that the behavioral answer was valid and under strict control of the visual stimulus. Therefore, a series of control studies was absolutely necessary if the final sensory data were to have a high degree of reliability. For example, what if sharks blink frequently as does man? This would mean that the animal

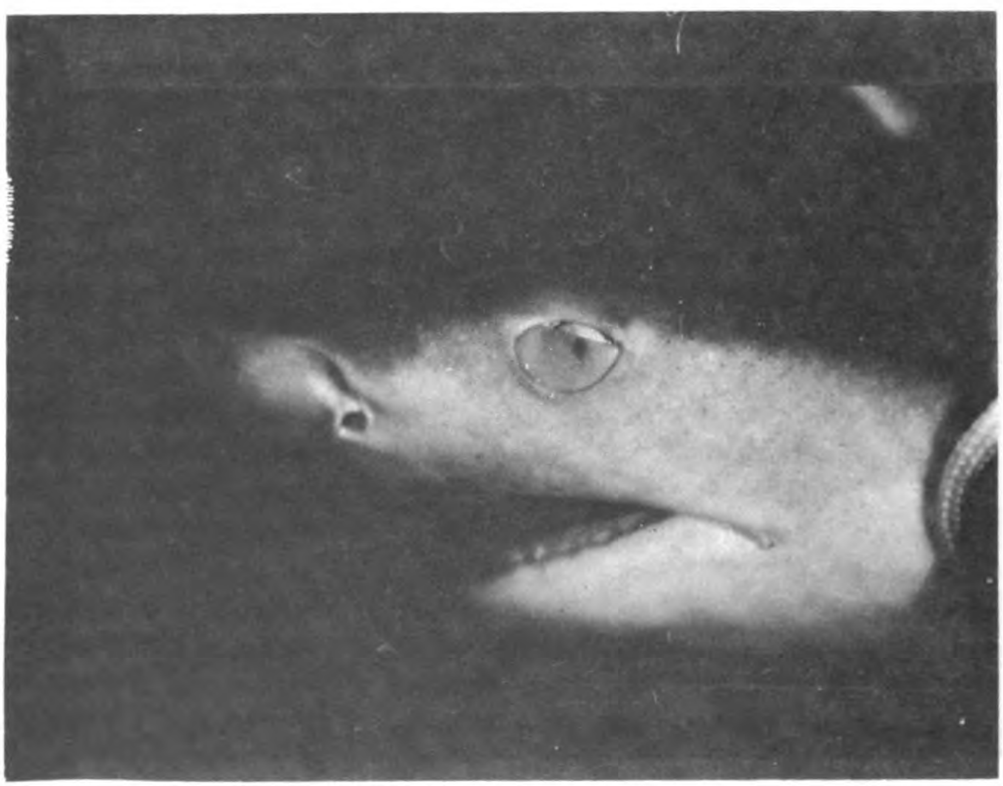
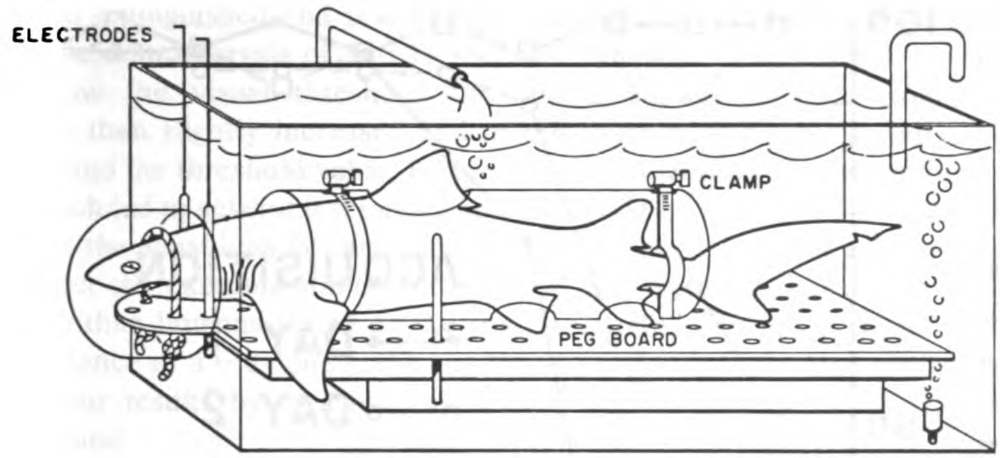


Figure 6 – The lemon shark's nictitating membrane or third eyelid (covering all but the top of the eye). Such lids are only found in a few shark species; not in any other fish. The basis of classical conditioning described in the text is the reflex movement of the lid when a brief, small electric field is set up around the shark.



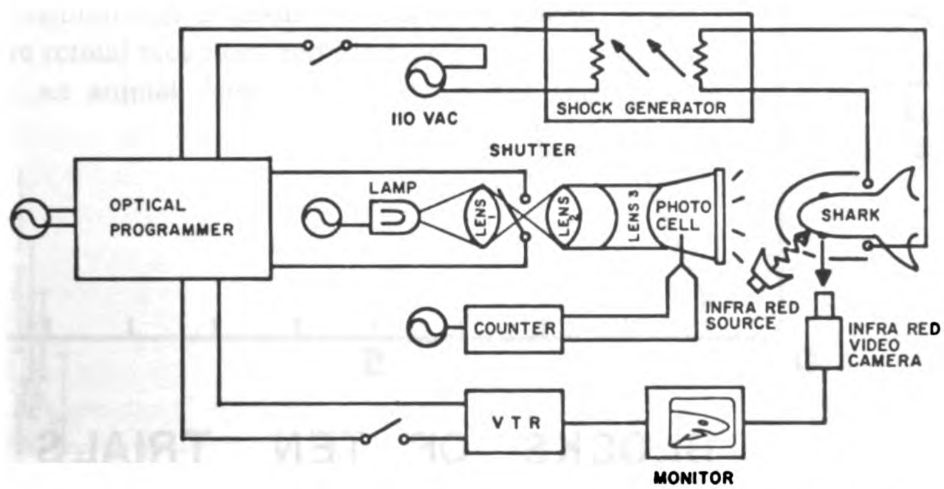


Figure 7 – Restraining apparatus (upper) and electro-optical stimulator used in the experiments. Optical programmer automated training and testing procedures and CRs were recorded on video tape for later analyses. (From Gruber, 1975b by kind permission of the editor of Vision in Fishes, *Plenum Press.)*

sometimes blinked as a conditioned response to light and at other times because "it felt like blinking." As it turned out, this particular factor was not a serious problem.

The strategy of our experiment involved the sensory threshold. Animals were individually conditioned by pairing light and shock 100 times a day for 8 days. Figure 8 shows the course of acquisition of the conditioned response. The sharks gave very reliable responses by the second day! Later, the bright conditioning flash was lowered over several more sessions until a point was reached where the stimulus brightness fell below the shark's threshold of vision. The animal was further trained near this threshold level. At this point we were ready to ask the shark experimental questions.

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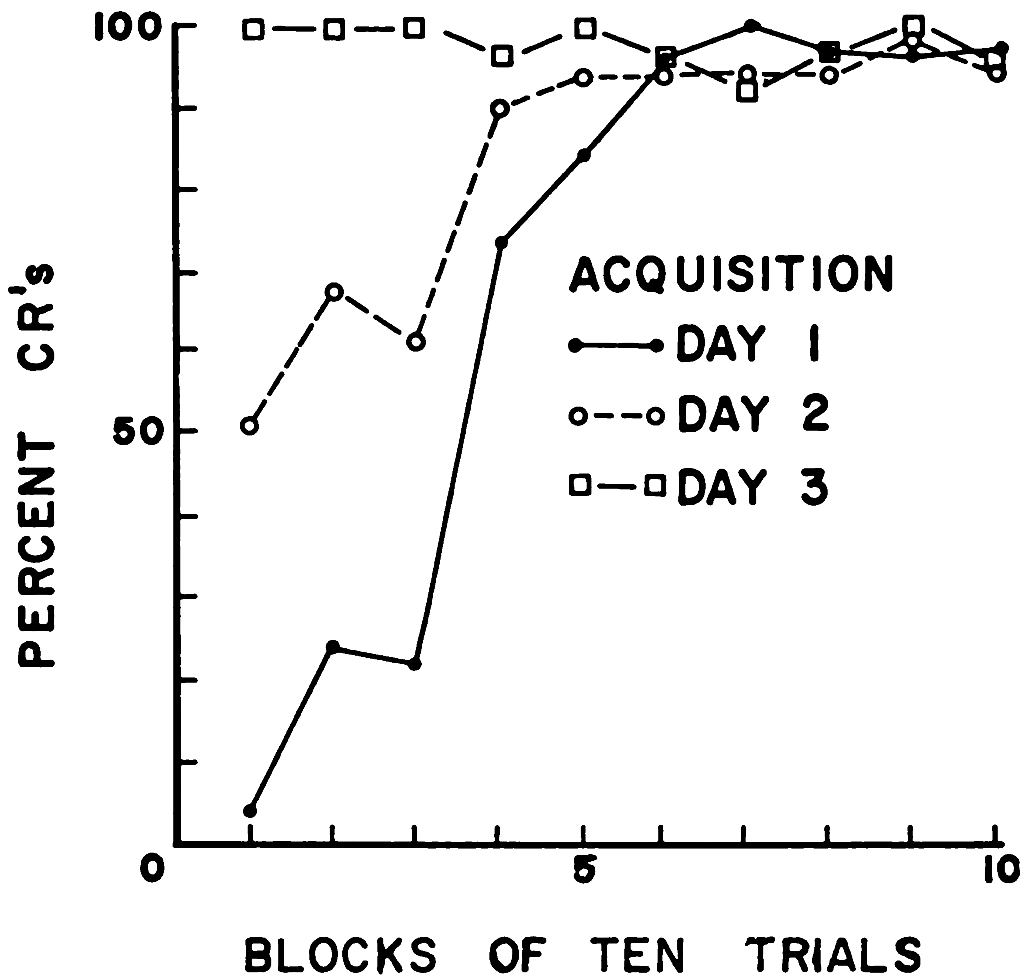

Figure 8 – Acquisition of the conditioned nictitating membrane response in the lemon shark during 3 days of training at 100 trials/day. Trials consisted of a 500 ms pulse of light accompanied by a 100 ms low voltage electric shock. Responses were very reliable by the end of 200 trials. (From Gruber and Schneiderman, 1975, with kind permission of the editor of Behavioral Research Methods Instrumentation.)

Visual Experiments

We had rather specific questions to ask. These did not originate with us but had previously been asked in visual investigations on animals ranging from the dragonfly to man. The experimental questions were framed in the duplexity theory as described above.

The most useful first experiment seemed to be a determination of the rate and range of dark adaptation. Thus, we directly measured the changes in sensitivity as the shark's eye adjusted to darkness. What we actually asked the shark was: "Do you see this flash of light?", and the shark replied "yes" if it blinked and "no" if the nictitating membrane did not move. In practice, we light-adapted the shark overnight and then intensely adapted it to 1550 ft-candles for 45 minutes. Room lights were then extinguished and test flashes decreasing in brightness were given at random intervals of 3 to 15 seconds. When the stimulus was lowered below the visual threshold, the animal answered "no." Brightness was then slightly increased and in this way tracked rapidly four times around the threshold value. Figure 9 shows the results of this experiment, which led to several fascinating conclusions. For example, the data show that the sensitivity of our sharks increased more than one million times under the experimental conditions, and they were ten times more sensitive than humans tested on the same apparatus. However, we found no evidence of a rod-cone break and thus turned to independent verification of our results by measuring dark adaptation with an entirely separate method.

As stated, the ERG is a well-known method for the study of vision. This method tells us about the relation between the absorption of photons by the retinal receptors and the bioelectric activity created by that action. What an animal "sees," however, is the sensation or the impression

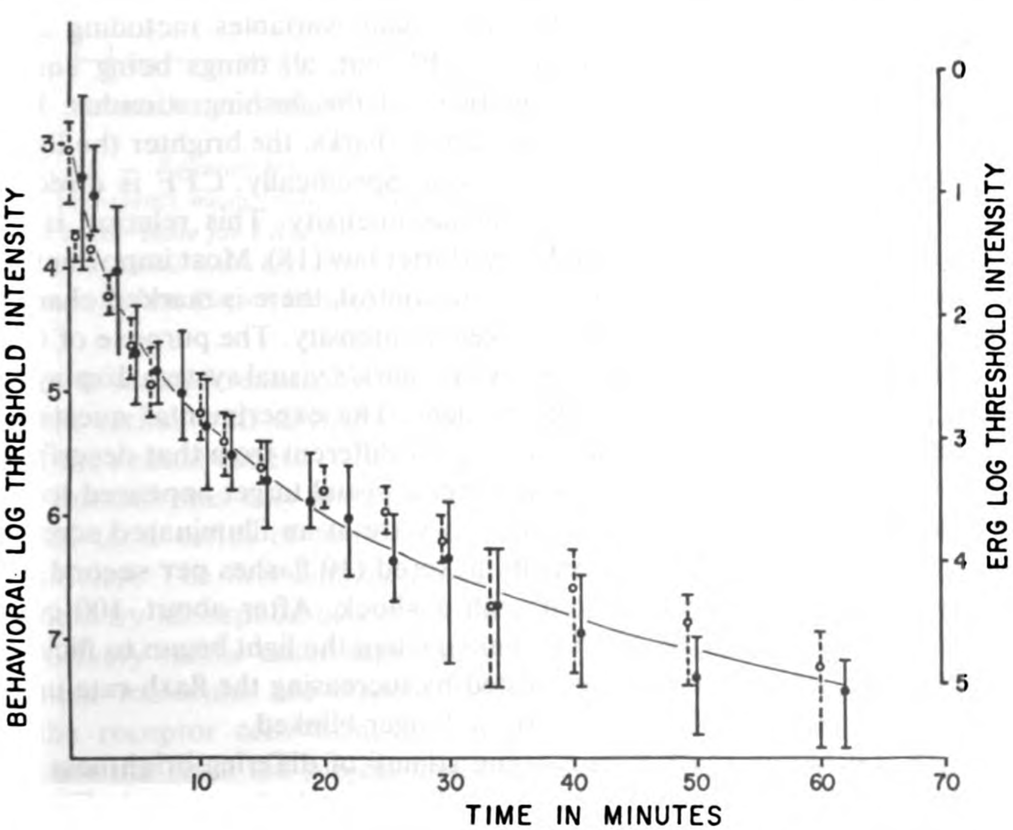

Figure 9 – Course of dark-adaptation in the lemon shark. Left ordinate represents the psychophysical measures. Solid conventions are mean psychophysical thresholds and bars represent the range of variation in 5 animals. Right ordinate represents ERG data from Hamasaki and Bridges (1965). The curves were aligned at 60 min. Open conventions are mean ERG thresholds with range of variation in 8 experiments. (From Gruber, 1975, with kind permission of the editor of Vision in Fishes, *Plenum Press.)*

created by signal processing at the retina and brain. Thus, correlations between ERG and seeing must be demonstrated. Such correlations have, in fact, been found for human data (15). Hamasaki and Bridges (16), in an independent study, determined the rate of dark-adaptation in the lemon shark by use of the electroretinogram. Their data are plotted with my behavioral data on Figure 9. While the agreement was almost perfect, no sign of a rod-cone break was noted and so we turned to a second parameter—flicker-fusion frequency—to determine whether the cone photoreceptors were actually functional.

If the rate of flashing of light is slowly increased, a critical point is reached when the light no longer appears to flicker. This point is known as the critical frequency of flicker-fusion, or CFF. This phenomenon has been systematically investigated since 1742 and is even used in clinical tests to signal certain eye diseases (17). The test actually measures temporal resolution of the visual system. The important point is that vertebrate rods are notoriously poor at temporal resolution. The highest flash-rate that the vertebrate rod system can follow is ordinarily 18 to 20 flashes per second. Actually, many variables including age, temperature and even altitude affect CFF but, all things being equal, the most important variable is brightness of the flashing stimulus. For man, and, as we later found out, for lemon sharks, the brighter the light, the better it can be temporarily resolved. Specifically, CFF is directly proportional to the logarithm of stimulus intensity. This relation is so universal that it is known as the Ferry-Porter law (18). Most importantly, when the visual system switches to cone control, there is marked change in the slope of the curve relating flicker to intensity. The purpose of this experiment was to determine whether the shark's visual system displayed such a rod-cone break for flickering light. The experimental question, and thus training methodology, was slightly different from that described above. Now we asked the shark whether a visual target appeared to be flashing or not. The shark was made to stare at an illuminated screen. The steady visual target was briefly flickered (10 flashes per second for 1/2 second) and this was paired with a shock. After about 100 conditioning trials, the shark reliably blinked when the light began to flicker. After final training, sharks were tested by increasing the flash-rate until a point was reached when the shark no longer blinked.

By testing the shark with flashing stimuli of differing brightness on different days, we eventually collected the data which appear in Figure 10. Also shown are results of a complementary ERG study completed with the help of D. I. Hamasaki. These curves can be resolved by simple statistical methods into two intensity-dependent branches. The data in Figure 11 graphically demonstrate the significance of this study. Animals with duplex retinas show double branched CFF curves. Additionally, rods are "slow" (20 fps) while cones are "fast" (40-90 fps).

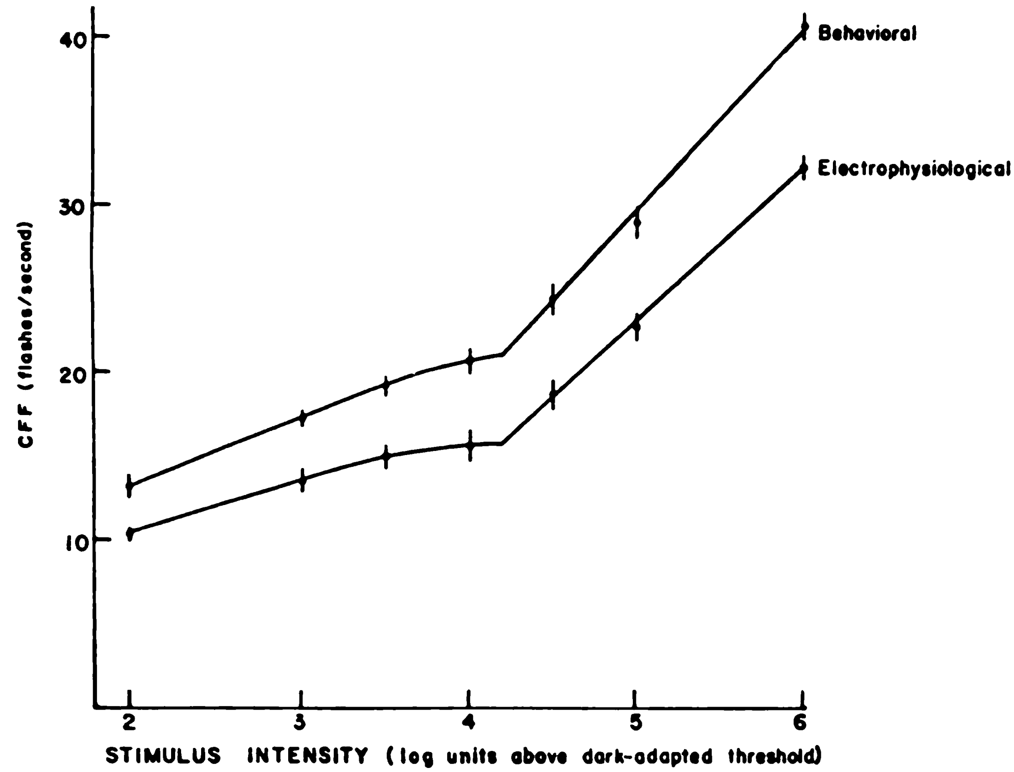

Figure 10 — Relation between CFF and stimulus intensity in the lemon shark. Upper curve represents mean (± one std. error) of the behavioral CFF values from 5 animals. Lower is the same for ERG data from 8 eyes. Curves were fitted by eye after statistical resolution into 2 branches. (From Gruber, 1975, with kind permission of the editor of Vision in Fishes, *Plenum Press.)*

Thus, it seemed reasonable to conclude that the shark has a functionally duplex retina with daylight visual mechanisms presumably associated with the retinal cones.

But this was only one piece of evidence. To strengthen our case, we turned to a series of tests known as photopic and scotopic spectral-sensitivity. The first biological event in vision is bleaching of a visual pigment by absorption of a quantum of light. These pigments are located exclusively in the outer segments of the rods and cones. When a few pigment molecules are bleached, events are set in motion which lead to the receptor cell "firing" an electrochemical signal. If this signal reaches the brain the subject might report that a flash of light was seen. Pigment molecules which absorb the photon energy prefer certain frequencies (colors) of light. For example, rhodopsin, found in man's retinal rods, absorbs best in the green and reflects red and blue. The admixture of this reflected light naturally gives rhodopsin its characteristic purple color. But, more importantly, selective absorption sets physical limits on the band width of visually detectable light frequencies. In fact, one of the clearest, most fully supported relationships in visual

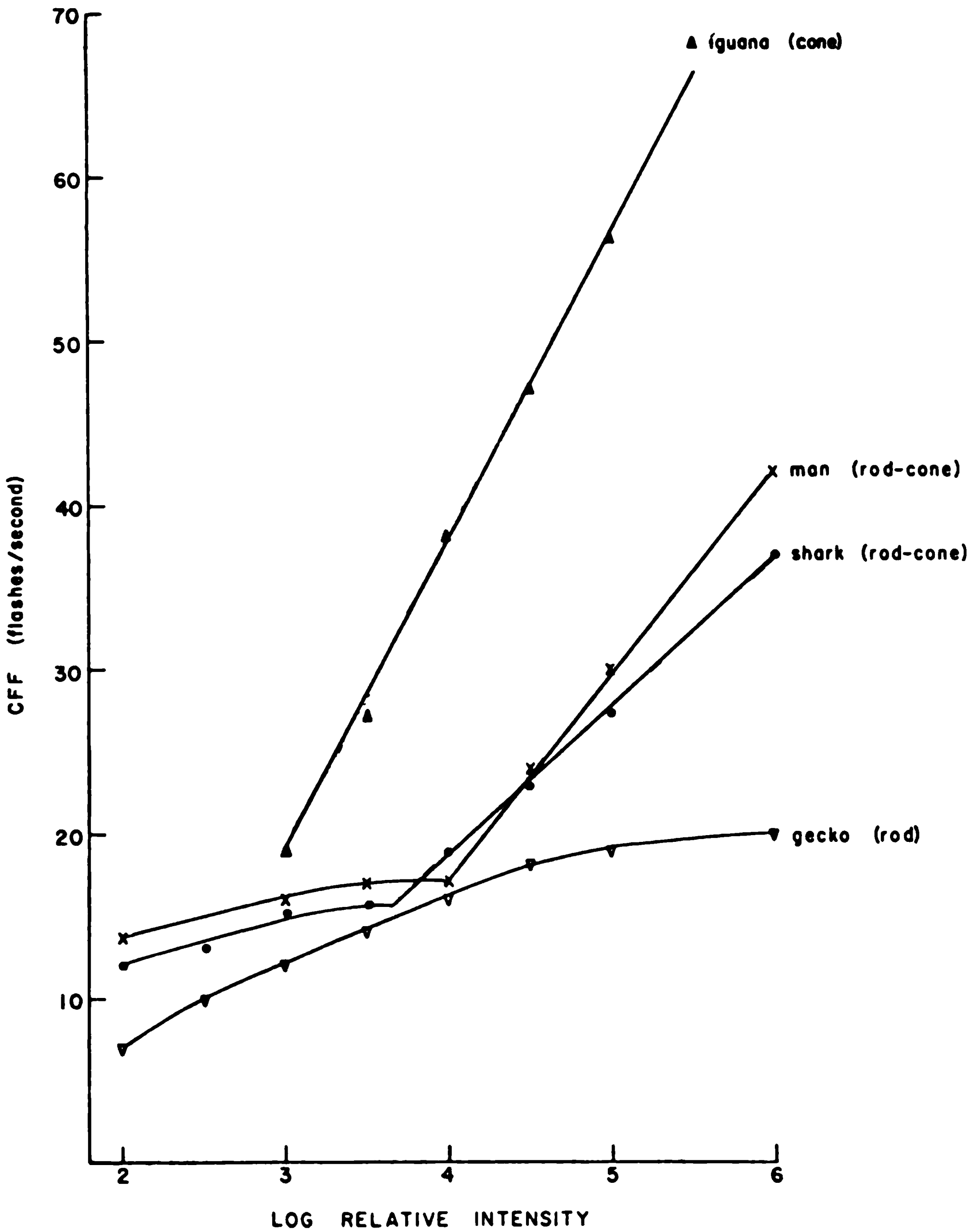

Figure 11 — CFF vs Stimulus intensity for man, iguana, gecko, and shark. The non-human data were obtained from the same apparatus under identical stimulus conditions and therefore are directly comparable. The human curve is shown for reference only. These curves demonstrate differences between pure and mixed retinas with respect to flicker-fusion. (From Gruber, 1969.)

science is the relation between the sensitivity of the eye to spectral lights (spectral sensitivity) and the absorption spectra of the visual pigments.

The next point is that rods and cones have different pigments and therefore different spectral responses. This means (for man) that yellow green is most readily seen in daylight, while at night, when the rods alone function, the eye is most sensitive to the blue green region of the spectrum. This change from yellow green to blue green is known as the purkinje shift and is characteristic of animals with duplex visual systems. Animals with either pure rod or pure cone systems do not shift sensitivity upon light adaptation.

Thus, our next step was to determine whether the purkinje shift is a feature of the shark's visual mechanisms. The experimental question put to the shark again became "do you see this flash of light?" This time, however, the flashes were spectrally pure colors. By counting the relative number of photons at threshold for each color, we were able to determine the (rod-dominated) spectral sensitivity in the dark-adapted shark. Unfortunately, the light-adapted (cone-dominated) spectral sensitivity proved more difficult to measure reliably and we eventually settled on a method which was less than ideal. The shark was light-adapted and then tested by extinguishing the adapting lights and quickly obtaining a threshold. The adapting lights were again turned on and this procedure repeated until a stable, repeatable threshold value was obtained. Comparison of the experimental results showed a small purkinje shift, but the best evidence came from our ERG study. In our earlier ERG studies described on page 12, *each* ERG was laboriously handmeasured. When the signal to noise ratio was high it was difficult indeed to get a reliable value for response amplitude. In the spectral-sensitivity study, however, computer averaging was employed, increasing the number of data points collected by more than two orders of magnitude. Figure 4 shows such a computer-averaged ERG representing 160 summated individual retinal responses.

The results of this study (Figure 12) were quite clear. The lemon shark's visual system shifts some 20 nm toward the yellow after moderate light-adaptation. This purkinje shift was further evidence of duplex function. It also indicated the range of photon frequencies which the shark detects. However, it does not necessarily indicate that sharks perceived these stimuli as colored. For this, an entirely separate experiment is being undertaken.

So, we can say quite a bit now about the shark's visual system. First, sharks definitely have an anatomically duplex retina. This finding differs dramatically from the classical literature, which indicates that sharks have a poorly organized, rod-pure retina, and are thus visually deprived. These first results on actual visual capability of sharks have provided some insight into their sensory world. We have known that the

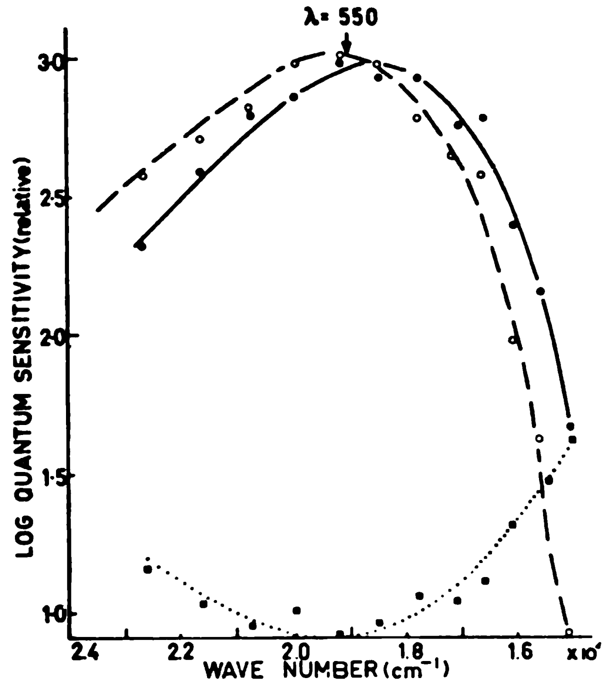

Figure 12 — Spectral-sensitivity of the light- and dark-adapted lemon shark retina. Open circles are scotopic measures; closed circles photopic measures of sensitivity. The two curves were aligned at their maximum sensitivity points. Closed squares show the difference between photopic an scotopic data. Results are ERG recordings from 12 eyes. Abscissa is given in wave numbers to facilitate comparison with visual pigment curves. (From Gruber, 1975, with kind permission of the editor of Vision in Fishes, *Plenum Press.)*

shark's eye can adjust to darkness, i.e., the pupil dilates (19) (Figure 13), and the reflecting tapetum uncovers (20). What we now know is the extent of that adaptation in quantitative terms. We have obtained data on both kinetics of adaptation and sensitivity levels. Most importantly, we have shown that the absolute sensitivity of the shark exceeded that of man by an order of magnitude. This means that, in favorable hydrographic conditions, sharks probably can hunt visually by moonlight, and possibly by starlight.

Many sharks are known to actively pursue and capture healthy prey. Thus, a high degree of temporal resolution is necessary to keep the rapidly moving visual world from degenerating into an optical smear. The rod-pure retina could not sustain such rapidly changing retinal images. Fortunately for the sharks, they are provided with cones in sufficient numbers to yield a flicker rate, at moderate intensities, of about 40-45 flashes/sec. Assuming that CFF is the most important factor,

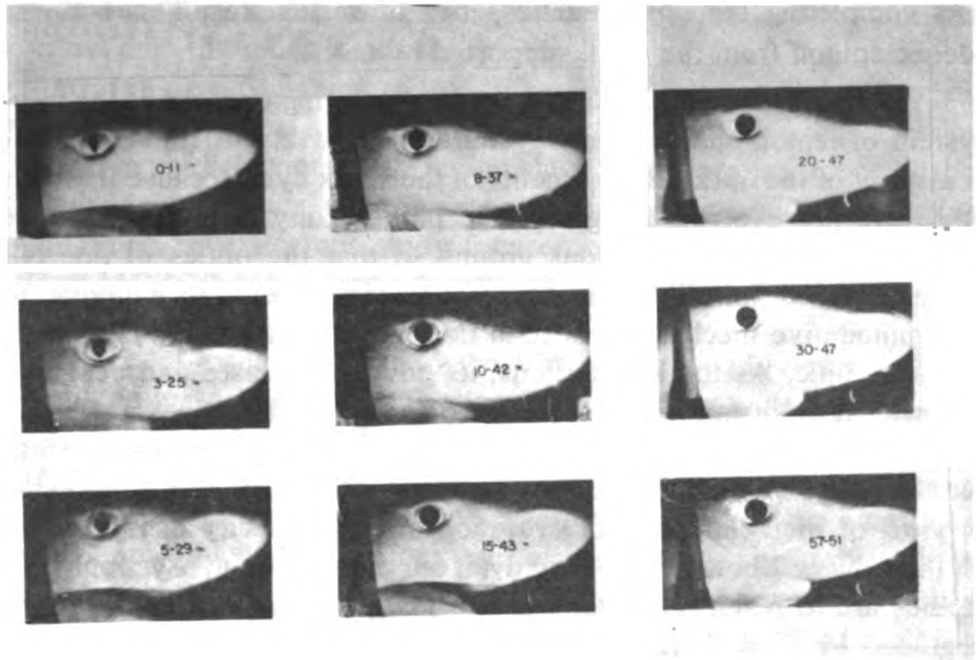

Figure 13 – Infrared photographs of dark adaptation of the pupil (pupillary dilation) in the lemon shark. Numbers in each photograph represent the time in darkness and area of the pupil. The average increase in area upon dark adaptation was 10-fold.

sharks can probably resolve temporally intermittent information about as well as man's *peripheral* retina. Movement detection is quite good in our periphery.

The shark's vision appears to be fairly well adapted to the range of photon frequencies transmitted by the aquatic medium. The red sensitivity of the shark is low, as is the red transmission of seawater, and the peak sensitivity is near to peak transmission in shallow water.

Future Work

For various reasons, convenience not being the least, visual scientists have settled on a limited number of animal "models" as subjects in comparative vision research. Presumably these form a natural phylogenetic series, including such animals as goldfish, frog, boxturtle, pigeon, cat, and several primates. The elasmobranchs – a distinct vertebrate class – have been omitted from this list and until now only the most rudimentary information on their vision was available. However, with completion of the work described below, we will be in a good position to compare the vision of sharks with that of the other "model" systems, thus completing the phylogenetic series of vertebrates. This is an academic spinoff from the work supported by ONR.

Work underway in my laboratory is attempting to describe the visual system of lemon sharks from several distinct levels. At the basic level is a study of the optical components of the shark eye. Because the vertebrate eye has evolved along separate paths, many distinct adaptations have been retained by various groups so that the optics of one type of eye may be quite different from those of another. For example, the accommodative mechanism of man involves the stretching elastic lens within a tunic. As the lens flattens, its power decreases and best focus shifts to more distant objects. In contrast, the fish lens does not change shape, but rather swings in a pendulum fashion toward or away from the retina. Thus, investigation of the optics of the shark eye is necessary in view of their independent evolution and the paucity of information on the subject. But more importantly, if our physiological, psychophysical studies are to reach full potential, we must know how aerial images are degraded by passage through the optical media comprising the shark's eye. In other words, we must be able to refer to illumination at the retinal level. This is the standard in most human studies: the unit of retinal illumination is the Troland. Consequently we are measuring optical parameters such as refractive indices of humors, lens and cornea, spherical and chromatic aberration, precise distances from one optical element to the next, nodal points, etc. The outcome will be a mathematical model of the eye which should allow us to predict values of a retinal image from any environmental image. Once the image falls on the retina, light is absorbed in the outer segments of the photoreceptors, which eventually produces an electrochemical signal that makes its way through the retina to the brain via the optic nerve. This is the "raw material" of vision.

Neural information processing takes place at many levels in the visual system. The greatest retinal processing occurs in the lower vertebrates, while mammals process more complex information in the brain. To understand the amount and type of visual processing in the shark's retina, we will be sampling the activity of two types of retinal neurons: horizontal and ganglion cells. This research involves the technically difficult process of penetrating and holding individual retinal neurons with microelectrodes and recording the electrical activity of these cells under various stimuli and conditions. We are extremely interested in whether the shark retina encodes information present in wavelength variations of light. Such color-coded responses, known as chromatic S-potentials (horizontal cells) and opponent responses (ganglion cells) have been found in fish retinas but not, for example, in the cat, an animal with notoriously poor color vision. We will also be looking for interaction between rod and cone photoreceptors under low illumination. Thus, our basic goal will be to understand the kind of visual data the retina sends the brain.

We are also beginning to investigate processing at higher levels in the CNS, but are most intensively studying the output of such processing, namely, visual behavior in the lemon shark. This is being accomplished through psychophysical experiments involving both classical and operant conditioning. The operant study focuses on whether sharks can truly discriminate between colors, while the classical conditioning study looks into mechanisms of color capability in these animals. The classical studies are an extension of the behavioral work already described. The operant study, well underway, utilizes a 12,000-liter, underwater, single-choice maze (Figure 14). By use of food reward, young lemon sharks have been trained to choose one of two doors, each of which has a fiber-optic array connected to optical projectors. Presently, the sharks are making intensity discriminations by correctly choosing the brighter of the two doors irrespective of position (Figure 15). After completion of the brightness discrimination study the sharks will be switched to a color discrimination task. It should be noted that color vision can be demonstrated only by behavioral testing. With brightness eliminated as a possible cue, an attempt will be made to train the sharks to choose a particular color (again irrespective of position) and thereby demonstrate that sharks possess color vision.

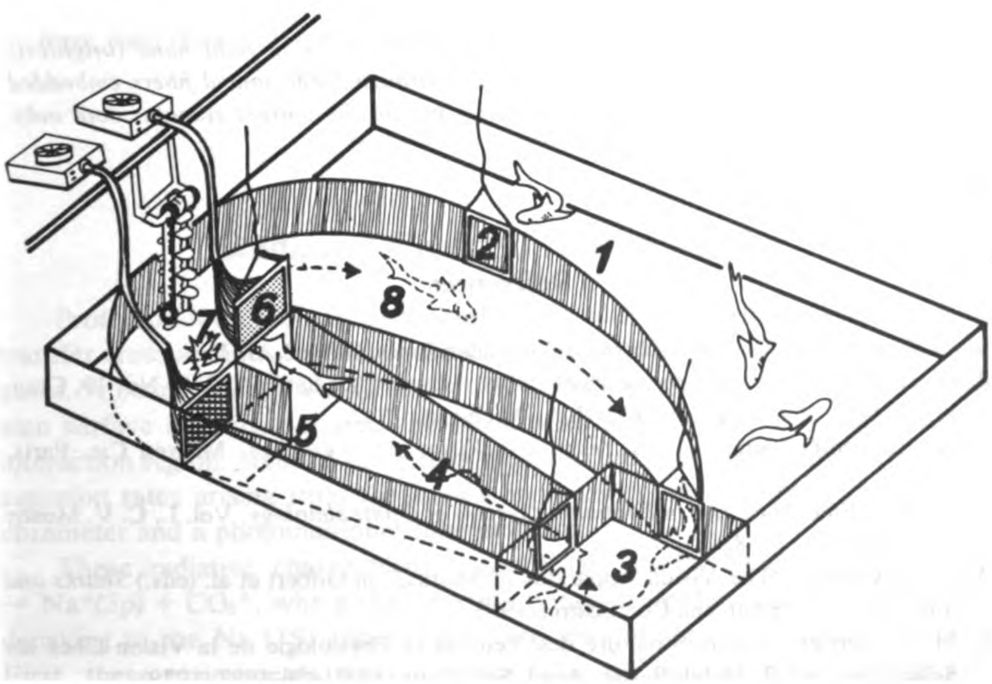

Figure 14 — Simplified sketch of the single choice maze. Sharks live in (1), enter maze through door (2) an swim to start box (3). When door is lifted sharks enter central alley (4) swim to choice point (5) and choose a stimulus door (6). A feeder automatically drops a 5 g fish reward for correct behavior. Shark cycles back to 3 for futher trials.

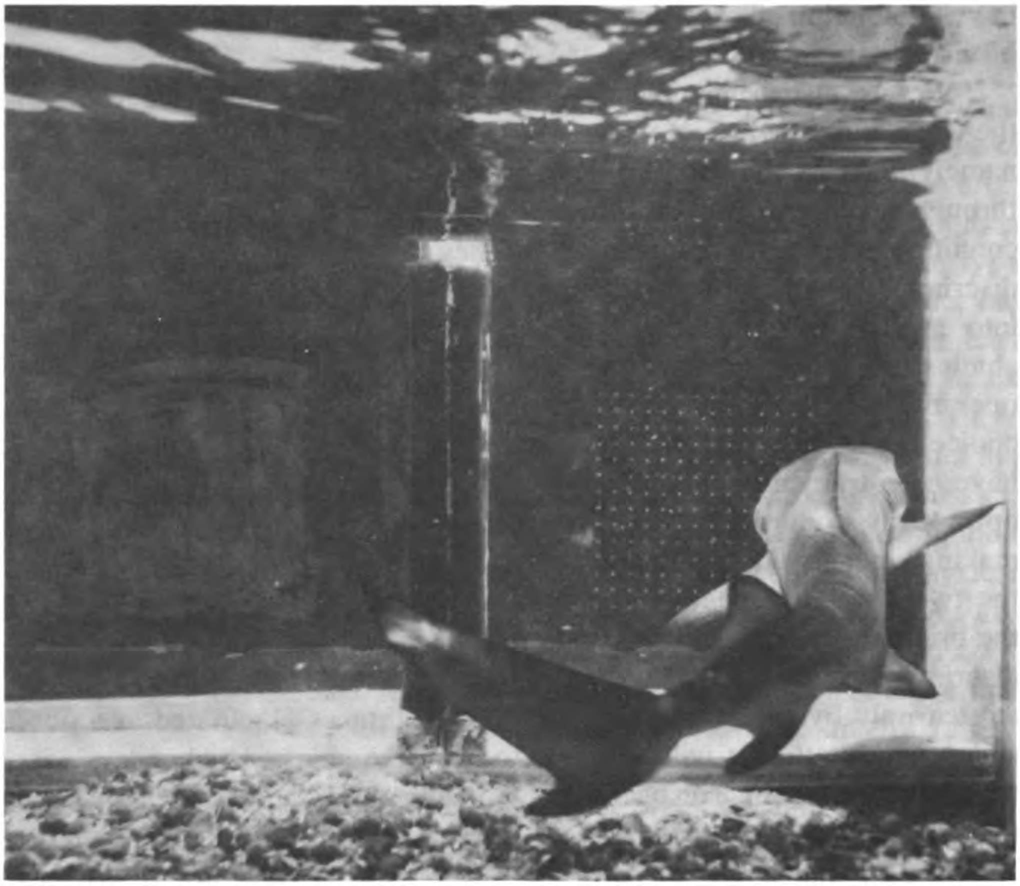

Figure 15 — Underwater photograph of lemon shark choosing right hand (brightest) stimulus door. Stimulus consists of light passing through 3000 optical fibers embedded in each door. Shark receives food reinforcement behind the correct stimulus door only. (Photo credit, C. Bray.)

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Radiative Charge Transfer Studies

Professor John Weiner Dartmouth College, has measured radiative charge transfer cross sections for the reactions between alkali ions and various molecular gases. A beam of alkali ions (Li^+, Na^+, K^+, Rb^+ and Cs^+) is produced by a tungsten surface ionization source and electrostatically focused into a well defined interaction region. Neutral gas is then bled into the vacuum chamber and photon emission rates arising from the ion-gas-interaction are measured with a monochrometer and a photomultiplier tube detector.

These radiative charge transfer processes, as, for example, $Na^+ + CO_2 \rightarrow Na^*(3p) + CO_2^+$, where the emission comes from the excited $Na^*(3p)$ state decaying to the Na (3S) ground state, are very important for several reasons. First, these experiments measure absolute cross sections for charge transfer into specific excited states of the neutralized specie. These absolute cross sections are necessary for calculations of the rate constants for modeling of

(Continued on Inside Back Cover)

30th Anniversary Article

Early Years of the Mathematics Program at ONR

Mina Rees
City University of New York

At the end of World War II, thirty years ago, the birth of the Office of Naval Research signalled the beginning of a series of federal programs that provided significant investments in scientific research and stimulated an expansion of scientific activity that placed the United States in the forefront of scientific achievement. In particular, substantial support of the research of university mathematicians introduced a new dimension into the relationship between the government and mathematicians. It changed the life style of many university people, encouraging young people to seek careers in mathematics and stimulating work in new or previously neglected sub-fields of mathematics. Many of these fields have since blossomed and become familiar aspects of college and university programs. This article will recount some aspects of the genesis of the military support of mathematics, beginning in 1946, and comment on some of the early achievements of the program.

In 1945, even before the end of World War II, many scientists who had been involved in wartime research were asked for opinions on the creation of an office within the Navy that would give money to universities for basic research in mathematics. My response was one of grave doubts because I thought that mathematicians probably would not be enthusiastic about receiving financial support for their peacetime research from the government, and especially from the military. But the plans went forward and the Office of Naval Research (ONR) was created by an act of Congress in 1946. Later, counterpart offices were created by the other military services, and the three offices together

Dr. Rees is well known for her service on many scientific and educational committees. She was director of the Mathematical Sciences Division at ONR, President of the American Association for the Advancement of Science, and until recently Dean of the Graduate Division of the City University of New York.

provided wide support for scientific research in American universities within their broad mandate to support research of interest to the Defense Department.

In spite of my doubts I was invited to Washington in 1946 to help set up the mathematics program of the new Office of Naval Research. After consulting with some of my wisest friends, I decided to participate in what still seemed to me a somewhat uncertain venture. When I arrived in Washington in August of 1946, it was impossible to find a place to live. No apartments were available and most hotels permitted a guest to stay only five days. When I found one that extended its hospitality for two weeks at a time, I was enchanted. I made a virtue of necessity, and every two weeks vacated my room and went on a trip to a leading mathematics department. On my return I registered for another two weeks.

These were the conditions under which I consulted many of the senior mathematicians of the United States. Together we evolved the first outline of the ONR mathematics program. While it evolved through criticism and change by my Washington colleagues, of course, our basic decision was to support pure and applied mathematics, statistics, and computer development with its related numerical analysis to insure the sophisticated use of electronic digital computers when they became available. Also, we had to establish the philosophy to guide the Navy in providing funds to buy time for able mathematicians to carry on their research and to establish research assistantships for young mathematicians whose support seemed to us the key to the flowering of mathematical research in the country. Because ONR was not authorized to carry on an educational program, the teaching aspects of setting up these new mathematics studies would have to be handled by the universities.

Before World War II, there had been relatively little emphasis in American universites on "applied mathematics" which was strongly represented at a number of German centers, particularly Goettingen, and at other continental universities as well as on British campuses. After the war, with some of the world's most distinguished emigre mathematicians on our campuses, it was possible to contemplate a strong development in these fields in the U.S. ONR seized the opportunity to support emerging groups like that at New York University under Richard Courant whose work at Goettingen had made his name magic throughout the world. There were also individuals, such as Szego and Polya at Stanford, about whom strong groups could be expected to grow. There was a small number of very able probabilists and statisticians; these included some emigres who were already eminent, such as Feller and Kac at Cornell and Neyman at Berkeley, as well as some native mathematicians who were well established and whose work was just beginning to be acclaimed. All these received encouragement and support from ONR as part of a plan to expand the U.S. activity in applied mathematical research and to increase the numbers of able young people being educated to carry on research in these fields. Only by working toward these goals could ONR be counted on to produce results not only significant for mathematics but useful to the Navy.

Although ONR support of research in the more abstract fields of mathematics was in our original planning, it had not been explicitly authorized without regard to relevance to the Navy's mission when the ONR Mathematics Branch was established. Nevertheless, it seemed clear to us in the Mathematics Branch that the argument for increasing the number of well educated and experienced research mathematicians was a strong one. During the war, the effectiveness of mathematicians in handling troublesome and pressing problems had often depended not so much on their specific fields as on their quality as research investigators. Of course there were some problems, such as the malfunctioning of a rocket, which required specific work in a relevant field but, in general, the pure mathematicians were among the most admired and sought after in seeking answers to many urgent problems. Moreover, there was considerable feeling among us that our program must strive to strengthen mathematical research in the United States, not fragment it, and we did not want to exclude any first class research.

One night early in my tenure, I was working late at my desk when Captain Robert Conrad came in. Captain Conrad was the spiritual father of the Office of Naval Research, a great man and a great leader, whose energy and enthusiasm set the tone of ONR. He sat down and said to me, after a little chit-chat: "Mina, if you want to include pure mathematics in your program, I'll support you in your decision." This was a great day for all of us, for it meant an end to the constant worry as to whether the Navy would see the needs of mathematics as we saw them.

Within this framework, many mathematicians supported by the Navy continued to work in the abstract parts of mathematics that were of greatest interest to them. But there were others who, to quote A. W. Tucker of Princeton, "felt an obligation to reach out beyond customary courses, seminars, and research, to make two-way contact with industrial labs and government undertakings." My own evaluation is that those who were lured into new fields by the Navy's interest were mathematicians who welcomed a reason for exploring new aspects of work in which they had been interested for a long time. When this kind of new research commitment was accompanied by the offering of related courses and seminars at their universities, a lively campus activity was apt to come into being. Thus, Solomon Lefschetz set up at Princeton a broadly based program in differential analysis that provided a home for the work of a number of vigorous young mathematicians. These men became leaders in creating new developments in such areas as stability theory of differential equations, mathematical theory of control processes, and dynamic programming. And the project in the logistics program under Professor Tucker, also at Princeton, produced many of the leading figures now pursuing research in universities or working in business or industry in fields related to the project. Tucker and his former students, particularly David Gale and Harold W. Kuhn made important contributions to the development and systematization of the underlying mathematical theory of linear inequalities. Their work led to significant advances in the related field of game theory and in linear programming.

The Navy's program had a broad effect not only on individual mathematicians across the nation, but also on some departments and institutions as well, who changed their character under the stimulus of federal dollars. The ONR emphasis on analysis, with considerable interest in questions related to continuum mechanics, stimulated increased activity in several university departments. The New York University Graduate Mathematics Department is one of the most striking in its use of the new resources, originally in support of analysis. With the new funding, that Department expanded its activities, assumed a new role in its university, and became one of the most distinguished departments in the country. Some very substantial engineering-oriented mathematical research was supported by ONR's Mechanics Branch. When that Branch joined the Mathematics Division after a few years, the Division's influence was extended into the engineering schools of many universities. Stanford was one of those where the new resources were applied across the span of science and engineering as well as mathematics, including applied mathematics and mathematical statistics.

In the early days, we recognized that ONR had a special obligation to provide for the balanced support and growth of mathematical research in the United States within the framework of the Navy's established policy. In time, it became clear that dedication to these purposes would also provide the Navy with access to first class mathematical talent to aid in the attack on major problems. Thus, when the Defense Department needed help in considering the DEW Line defense of the continent against air attack, a number of our computer mathematicians were asked for advice. When the fleet needed a coordinated system of defense, similar invitations were extended to appropriate mathematicians. And when, in the late 1940's, the staff of our office became aware that some mathematical results obtained by George Dantzig, who was then working for the Air Force, could be used to reduce the burdensome costs of the Navy's logistics operations, the possibilities were pointed out to the Deputy Chief of Naval Operations for Logistics. His enthusiastic reaction led in a short time to the establishment of a Logistics Branch in ONR with a separate research program. This has been a most successful activity of the Mathematics Division, both in its usefulness to the Navy and in its impact on industry and the universities. Our support for the quantitative side of economics, to which two recent Nobel Laureates contributed, was motivated by our concern with decision making processes. The "decision mathematics" fostered by our program strongly affected developments in agricultural economics as well as military command decision systems. Along with the Rand Corporation, we had a major influence on the introduction of operations research and its subdiscipline, management science, into business schools. Operations research also found roots in many universities in new departments and in existing departments of computer science and industrial engineering. The content of operations research as it is taught in these disciplines reflects research areas supported by ONR. ONR's journal, the Naval Research Logistics Quarterly, is highly respected and is extensively used as a reference for source materials in these fields. Game Theory and Gaming as an instructional technique, as well as the mathematical theory of optimization and other aspects of mathematics for social scientists, have also provided teaching content and research interests for members of various university departments.

Another important aspect of the early Mathematics Branch program was the work in computers. It not only made the Logistics program possible but broadly touched the whole span of Naval operations and our society. When I first went to Washington in 1946, ONR was supporting some projects dealing with analog computers. However, little attention was being given to automatic digital computers, although other parts of the Navy had supported significant work in this field. ONR's entry into the field was extensive, much of it in collaboration with the National Bureau of Standards. Initially, we emphasized the development of mathematical results that would be needed if the machines, when they became operative, were to be used properly. With the passage of time, however, a substantial program for component and computer development did emerge. The two computers we supported that had the greatest influence on subsequent developments in the field were the computer at the Institute for Advanced Study, known particularly because of John von Neumann's critical role in its design, and the Whirlwind computer at MIT, which provided Jay Forrester with his first claim to fame. As F. J. Weyl summarized it: "The decisive aspects of stored program computer logic, high speed parallel electrostatic and magnetic core memories, the interaction of high speed small memories with slower, much more capacious ones in the same computer, and many important simplifications in programming and coding were first realized on one or the other of these machines."

The Whirlwind was originally conceived as an element in an advanced flight trainer. After many changes and adaptations to the state of the art, it evolved as a general purpose computer of unusual design.

Within months after its completion, it became clear that this computer was particularly well suited to serve as a data processing component in a prototype integrated defense system, then under development at MIT. The experience gained on Whirlwind during the second half of the fifties laid the groundwork for the development of the computerized air traffic control systems, the automated reservations facilities, and the computer-managed learning systems of our day. Components of Whirlwind have recently been installed as a permanent display in the Smithsonian Institution.

ONR supported many projects concerned with numerical analysis, which often were led by investigators widely known and respected for their work in pure mathematics. In 1947, the Institute for Numerical Analysis was established at UCLA under the auspices of the Bureau of Standards and with ONR support. It's staff of distinguished mathematicians and mathematical physicists came from the United States and Europe. D. H. Lehmer, a leading U.S. number theorist and a Director of the Institute commented on the nature and quality of the Institute's research in an October, 1969 interview at the Smithsonian Institution. He observed that the Institutes program had naturally focussed on the research interests of its staff. There was work on partial differential equations and systems of linear equations that produced a great variety of significant results. Much of the mathematics was concerned with experiments in methods for the new kinds of numerical analysis problems that would arise with the use of the new, very fast, very sophisticated electronic digital computers. A number of very able young people were trained at the Institute, and large numbers of older mathematicians learned the new approaches that computers required. When the Institute was terminated as a government agency, many of these people went to new positions across the country and spread the word about the computer revolution to many universities that had not yet been involved. Professor Lehmer comments: "It was a little rough on the lot of us, because the laboratories we went to or the campuses we returned to were not supplied with the hardware we needed ... and it took another ten years for [these] to show up at every university."

Another major application field that owes much to the pioneering support of ONR is mathematical statistics. At first, the principal feature of the ONR work was a basic research program in statistics and probability at those universities which, in the late 1940's, either had such programs or were developing them. The people who headed these university programs were acknowledged leaders in the field or some times junior people who have since assumed positions of leadership. With support from ONR, departments of mathematical statistics flourished on university campuses, and research activity in the field prospered in the United States.

Looking back, we can see that many of the research results produced in the ONR programs have been important both to science and to applications for the Department of Defense, other federal agencies, and industry. Abraham Wald's work in sequential analysis and decision theory, launched during World War II, was carried forward under ONR sponsorship; William Feller produced a notable exposition of probabilistic methods in his two-volume treatise; and a number of theoretical investigations into applied problems such as weather modification, models in medicine, design of experiments and data analysis, were carried on separately by Jerzy Neyman and S. S. Wilks. Junior colleagues and students of these early ONR investigators are now prominent statisticians; and their students, in turn, made possible the staffing of the fifty or more statistics departments that were begun after 1950.

An important part of the statistics program, which continues to this day, evolved from steps taken just prior to and at the beginning of the Korean war. About 1949, the Joint Services Program in Quality Control (now Quality Control and Reliability) was established. Its purpose was to continue World War II work on quality control and acceptance sampling and to address new reliability problems arising in inspection and quality measurement. A number of Department of Defense Inspection Manuals developed from this research are still in use.

I have not tried to describe the extent of the ONR program in pure mathematics since the Navys' influence was felt primarily in the availability of increased research support rather than in the fields chosen for research. However, a number of very able mathematicians did participate during the fifties in summer studies on a highly classified project and generated new research interests which grow into major mathematical efforts. But on the whole, research in pure mathematics moved forward propelled by its own inner forces; and it was natural that the National Science Foundation should gradually assume the major responsibility for its support.

As I reflect on ONR's thirty years of existence, and particularly the early years when I was part of the organization, I believe there may be some lessons of value to those who are considering the future course of ONR's mathematics program. The most basic of these is the realization that the old perception of what constitutes "applied mathematics" is too limited, and that virtually all mathematics is applicable. In ONR, this was perhaps most striking in some of the work done in the early years for the National Security Agency. This basic precept justifies a policy of constant watchfulness for new developments in mathematics and access to the most productive mathematicians. Such a policy, vigorously encouraged and practiced, can do much to enhance the contributions of mathematics to national needs.

A further implication derives from the recognition that many new applications lie in fields other than the classical fields of physics and engineering. Such applications require collaboration between mathematicians and practitioners who may be less sophisticated mathematically than physicists and engineers. Environmental protection, biomedical research, and medical and public health economics abound with problems in which known methods of data treatment are inadequate. Many of these problems can benefit from skillful model building and research to obtain new mathematical results. But experience has indicated that the best hope of success in such applications lies in immersing an interested and suitably trained mathematician in the field and encouraging close collaborative work toward solutions. Results are seldom obtained quickly, and support for two or three years away from usual academic commitments is needed generally.

Such a program would give able young mathematicians an opportunity to broaden their mathematical perspectives in applications important to the national welfare and could thereby greatly enrich the country's mathematical resources. Concurrently, it could bring new program vitality to many of the nation's mathematics departments and provide ONR with a cadre of able and enthusiastic young mathematicians capable of addressing urgent Navy problems.

The management of a program of this type, involving applications of mathematics in new and unfamiliar fields, is a major challenge to the federal scientific officers who must monitor it. The intrinsic difficulty of collaboration across disciplinary boundaries is compounded by the problems of fitting such a program into the appropriate budget categories and pigeonholes, obtaining support money from various sources, and being responsive to the divergent interests of more than one sponsor. We know from experience that such programs sometimes do succeed, and with proper care and courage the results can be extremely worthwhile for the sponsors and the scientists alike.

Research Notes

Hibernation Studies

Groundhogs don't seem to be very exciting creatures. They burrow under the earth and hibernate a lot, and some people even believe that they are harbingers of spring. But when it comes to hibernation, they're champions at it, says Dr. Tom Albert, a veterinarian from the University of Maryland. Dr. Albert is at the Naval Arctic Research Laboratory to capture marmots, the arctic relative of the lower-48 groundhog, and start a marmot colony at NARL's Animal Research Facility.

For six years Dr. Albert has been studying the hibernation physiology of groundhogs. These animals hibernate about three-quarters of the year, spending all that time without eating or drinking. During hibernation, they actually lower their body temperature from its normal 98-99° F to about 40° F, and in this way spend very little energy in heating their bodies throughout the winter. Every seven to ten days of hibernation, groundhogs wake up and spontaneously begin to rewarm to their normal body temperature. The rewarming process is essentially completed within four hours, and the next eight to twenty hours are spent awake. The groundhog then goes back into hibernation, and the cycle continues throughout the winter. Its body does not rewarm uniformly, though, for different parts warm up faster than other parts. In fact, the front half of the body is able to reach normal temperature within three hours, while the rear half takes up to four. This process of maintaining different regions of the body at different temperatures is called regional heterothermy, the subject Dr. Albert will be investigating.

The Office of Naval Research has funded Dr. Albert to study the marmot for a year at NARL starting this July. He is presently here to do preliminary research for the project. Dr. Albert chose the marmot because it is essentially a groundhog, except half as big. Also, the marmot has adapted to a colder climate than its relative. Groundhog den temperatures seldom go below freezing, and when they do the groundhogs begin to rewarm. Marmots, on the other hand, hibernate in similar temperatures. Dr. Albert hopes to get twelve marmots to conduct experiments on. He will build two artificial marmot dens above ground consisting of a wooden tube, or runway, connected to a wooden den enclosure. Hopefully, a couple of marmots will accept the dens as their new homes and will hibernate there in the winter. Thermocouples (temperature-sensitive wires) connected to a multi-channel temperature recorder will be placed at strategic points in the dens to measure air, soil, and nesting material temperatures. One of the questions Dr. Albert is trying to answer is whether marmots can hibernate at ambient temperatures well below freezing.

Another series of experiments involves surgical implantation of thermocouples to monitor regional heterothermy over different parts of the marmot's body. Three sets of animals will be used, two of which will be kept at room temperature, and the third consisting of hibernating animals. With each set, thermocouples will be implanted in the bodies, after which the animals will be placed in the Animal Research Facility's metabolic chamber at various cold temperatures, and their temperatures and oxygen consumption rates measured. The second set of marmots kept at room temperature will be injected with a serum that induces hibernation, after which they will be placed in the metabolic chamber. This serum has been obtained from the blood of hibernating groundhogs, and has been found to induce hibernation in nonhibernating groundhogs. In each experiment, Dr. Albert will be looking at the effects of regional heterothermy in response to cold exposure.

Dr. Albert hopes that knowldge gained from hibernation and regional heterothermy research can be applied to human beings. He foresees future uses of such knowledge in organ preservation and long-term space travel. In the latter case, many problems of space travel that involves months or even years can be obviated if hibernation at regular intervals is induced in the astronauts.

Research on Automating the Process of Programming

Though present day computers are often called Automatic Machines, they are, in fact, far from being totally automatic. While it is true that computers provide a mechanical means for quickly processing large amounts of data, we have not yet automated the pre-data processing functions of problem analysis and design, and program coding, testing, and debugging.

Unfortunately, these still largely people-intensive activities account for an increasingly high share of the costs of computer systems.

ONR, concerned both with cost and quality issues in the creation of computer software, is funding research on automating the function of computer program writing. As attractive as the objective of reducing software development costs is the fascinating possibility that computer programs could be produced for wide classes of professionals without the prerequisites of extensive computer training and laborious efforts, or alternately recourse to middleman computer application programmers.

There exist two fundamental approaches to the goal of automatic programming. The most ambitious one, under development at MIT, envisions the computer as processing not only programming knowledge, but also ability to acquire expertise in a specific application area which is equal or superior to the proficiency of the user. The user would then be required to supply description of his circumstances, environment, and objectives, whereupon the computer would generate programs that would serve the user in a near optimal manner. The viewpoint and progress at the University of Pennsylvania, reported upon below, represents a more modest attack on the problem. In this case, while the system is designed to ensure that the user benefits from the experience of others, he is considered to have superior proficiency in the area of his application and to be the ultimate decision maker of the best services for his purposes. Basically, the computer possesses only a programming knowledge base, and the information on specific requirements must come from the user.

More particularly, the Penn approach views the user as an expert in the application field in which the computer program is to be applied, e.g., accounting, production control, engineering, etc. The applications area professional regards the computer as a black box and his description of requirements is entirely n terms of data or documents used as input or output, as well as formulae employed in the computation. He understands that when a function is properly specified, it can be executed by a computer.

The stating of requirements has been made as simple as possible. The user communicates with the machine in short declarative sentences; each sentence containing a "chunk" of information such as the name of an item of data or an expression of an algebraic or logical relationship among items of data. The aggregation or synthesis of a number of statements is left to a Machine Processor.

The Processor is tolerant of the user's ambiguities and omissions. To fully specify a requirement would necessitate composing many statements which may appear to a user to be self evident and superfluous. The Processor, in synthesizing the statements into a program, recognizes such ambiguities or omissions and guesses the required statements, relieving the user of much tiresome detail. The guessed statements are reported to the user for verification.

If the specification of a requirement is still incomplete, the missing statements are solicited by the Processor from the user, incrementally, one statement at a time. Inconsistencies among statements that cannot be resolved by the Processor are also reported to the user. This dialogue continues until the specification is found by the Processor to be complete.

Self (automatic) program documentation is attained during the expert/machine dialogue. The Processor produces a variety of reports including a listing of statements, a cross referencing output, a decision table derived from the logic of the statements, and flow charts.

The Processor is application independent and embodies only computer related methods. Therefore, its potential use includes such broad areas as logistics, manpower, and command and control decision making. The ultimate output of the Processor is a completed application computer program ready for machine processing. Current research is being applied to make COBOL the final output language of the described automatic programming system.

Re-emphasizing the objective of this project, it is to make computer programming so easy that large classes of professionals who have had no exposure to computer training will be able to satisfy their computational needs via a direct, simple dialogue with the machine. The Penn methodology employed to ultimately satisfy this goal has involved: (1) the design of a user oriented language to enable direct user – machine interaction, and (2) the development of a Processor which, in addition to synthesizing and organizing all user application statements, automatically produces machine code (computer programs).

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radiative energy loss in electron beam heated plasma phenomena. They are also relevant to the understanding of alkali resonance line emissions originating in the ionospheric night glow. Second, in the course of determining the absolute cross sections, the polarization ratios of the atomic emissions are also measured. It is thought that these polarization measurements will provide a sensitive probe of the relative spatial orientation of the collision partners in the quasi-molecule-ion intermediate complex. In addition, polarized emission arising from a non-random population of degenerate atomic orbitals can be used to construct bond overlap models of the quasi-molecular intermediate, and thus some insight can be obtained into the preferred collision geometries. Third, the appearance of structure in the emission cross sections can be used to study the possible occurrence of quantum interferences between charge transfer and other energy processes.

The essential thing is that these studies can yield detailed information on the molecular nature of the collision complex, in spite of the relatively high ion beam energy used in these experiments. Finally, the functional dependence of the ratiative charge transfer process is analyzed in terms of the collision energy, the principal quantum numbers of the active electron, and the endoergicity or energy defect of the overall process.

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