# VISUAL CONTRAST THRESHOLDS OF THE GOLDFISH (*CARASSIUS AURATUS*)

FRANK J. HESTER

Bureau of Commercial Fisheries, Fishery-Oceanography Center, La Jolla, California

## INTRODUCTION

THE VISUAL sense in fishes has been the subject of numerous investigations. These have included studies of size, shape, form, and color discrimination; examination of fish-eye dioptrics; and electrophysiological, histological, and behavioral investigations of light and motion perception and of visual acuity. Visual acuity may be considered a special case of contrast discrimination—the ability to distinguish a target from its background because the target is lighter or darker than the background.

The ability of a fish to detect an object by contrast discrimination has not been quantitatively measured, but it may be the most important factor in any visual system. Furthermore, contrast transmittance is much poorer in water than in air. Even in the clearest water most targets are visible for only a few tens of meters. Underwater sighting ranges can be calculated readily if certain characteristics of the water mass are known (DUNTLEY, 1963), and if the contrast sensitivity of the observer is known. Once the contrast sensitivity of fishes is determined, many problems are open to solution, among which are spacing of the individuals in a school, object avoidance, predator avoidance, and food detection.

DENTON and NICOL (1965) suggested that silver-sided fishes may be difficult for predators to detect because they so nearly match the brightness of their water background. The effectiveness of this camouflage can be determined only when the contrast sensitivity of the predator is known. BAYLOR and SHAW (1962) suggested that the double-cone mosaics in the teleost retina increase contrast sensitivity. BRIGGS and HATCHETT (1965) pointed out that, because contrast transmission in water is so poor, it would not be surprising to find better contrast discrimination in fishes than in terrestrial vertebrates, but did not suggest a mechanism whereby the sharper discrimination could be brought about.

In the light-adapted human eye, contrast thresholds are lowest at the fovea and increase toward the periphery of the retina in rather good agreement with the number of cones in the corresponding retinal regions (e.g. BLACKWELL and MOLDAUER, 1958; TAYLOR, 1961). Since the cone density in the teleost retina, even in pseudo-foveate species, is at most about 10 per cent of the human fovea (TAMURA, 1957; O'CONNELL, 1963), it seems unlikely that fish eyes have lower contrast thresholds than the light-adapted human fovea.

Contrast, as used above, can be defined as the ratio of the difference between the radiance of an object and its background to the radiance of the background. The more usual way of defining contrast is to use brightness or luminance instead of radiance. These terms, however, are based on the sensitivity of the human eye and are difficult to interpret when the detector, the fish retina, may have a different spectral sensitivity. The use of

radiance surmounts this difficulty, since the units are in actual units of energy for a specified band of wave lengths within the visible spectrum for the organism.

Contrast can assume any value from $-1$ (when the target radiates no flux and the background does) through zero (when the target and background have equal radiance) to some large positive number (when the radiance of the target is large with respect to the background). Threshold values of the light-adapted human eye for stimuli of moderate area typically are fractional and are distributed symmetrically on either side of zero. Under usual conditions, the threshold is independent of whether the target is lighter or darker than its background; only the absolute value of contrast is important (BLACKWELL, 1946). This generalization greatly simplifies the problem of target generation and measurement. That is, the test object may be a spot projected on a background of some uniform radiance. In the procedure outlined below all the contrast values are positive. This arrangement has the additional advantage of permitting the use of contrast values greater than unity. Such values do occur in nature and are especially important at low adaptation levels, and for objects that subtend small angles in the visual field.

Contrast threshold values for the human eye vary with target size, position of the target image on the retina, and the radiance level to which the eye is adapted, as well as with duration and color of the stimulus. (The latter two are not considered in the present study.) It is highly probable that similar relations will be found to hold for fishes. For this reason a contrast discrimination experiment on a fish, to yield useful data, should involve targets of several different areas, should cover a wide range of adaptive states from full-dark to full-light, and should examine several regions of the retina. This last point is especially important for experiments with most fishes, since their visual field is extremely large and nearly spherical, and since visual stimuli can operate anywhere in this field.

Two other considerations, stimulus duration and the subject's spectral sensitivity, arise when experimental techniques used on humans are transferred to fishes. The human eye covers a search field in a series of steps, each of which ends in a brief pause before the point of fixation is again shifted in space. For a stimulus to be "realistic" its duration should be the same as the dwell time of the eye. Since reportedly the typical fish eye remains fixed in space, and ocular movement compensates only for body-swimming movement (WALLS, 1942), a suitable stimulus duration for the fish must be chosen arbitrarily. It should not be so short as to be unrealistic and yet should not be so long that natural moving targets, such as other fish, will appreciably change position, or that prey will have time to sight the fish and escape. An arbitrary duration of 0·5 sec seems to fulfill the above condition as a first approximation.

The spectral sensitivity of the human eye, for both light- and dark-adapted (photopic and scotopic) vision, has been standardized and a science of measurement based on this sensitivity—namely photometry—has been developed to a high degree. Fish photometry is, at best, poorly defined. Spectral-sensitivity curves for fishes are based chiefly on pigment-absorption spectra, such as those reported by BAYLISS, LYTHGOE and TANSLEY (1936), MUNZ (1958), and WALD (1941), and apply primarily at low-adapted (scotopic) levels. The behavioral studies (for example, by GRUNDFEST, 1932) and electrophysiological studies (GRANIT, 1941) demonstrate a shift in the peak spectral sensitivity between light- and dark-adapted eyes in several species of fish (a frequent response in a duplex retina). These sensitivity curves show marked interspecific differences. The only warranted generalization is that the curves for fresh-water and inshore fishes generally are more red-sensitive than those for pelagic and deep-sea fishes. Since the curves for all fishes examined differ from

those for the human eye, photometric expressions of stimulus and background levels appear to be of doubtful meaning. Water is an excellent monochromator, however, so that underwater light in most natural waters below a few meters of depth is confined to the blue-green portions of the spectrum. These wave lengths can be approximated in the laboratory by the use of proper narrow-pass filters such as a Wratten 611, with peak at 534 m$\mu$, to simulate underwater light in fresh-water and near-shore water, and a Wratten 45, with peak at 480 m$\mu$, to simulate oceanic water. By use of such filters, radiance measurements can be made with reasonable accuracy and the interspecific differences and the differences due to the duplex nature of the retina are reduced to some common physical measure.

Under certain circumstances, color discrimination may affect contrast discrimination (McCLEARY and BERNSTEIN, 1959, and others have demonstrated color vision in fishes). For the human eye, however, and probably for that of fishes, the visibility of objects depends primarily on luminance contrast at all levels of illumination, and entirely on luminance contrast at low levels of illumination, at which color vision is inoperative (MacADAM, 1946). Chromatic contrast is undoubtedly of even less importance in the aquatic environment, due to the rapid loss of all but a narrow band of wave lengths below a certain depth; it can be eliminated completely by the use of narrow-pass filters.

At least one visual function in fishes, namely critical flicker fusion, is known to be temperature dependent (CROZIER, WOLF and ZERRAHN-WOLF, 1938; TAMURA and HANYU, 1959; HANYU and ALI, 1963). Similar temperature effects should be considered in contrast threshold experiments and should be controlled carefully (a need that does not arise in experiments on human vision).

As the eye of the fish grows, the density of cones declines more slowly than is required to compensate for the calculated expansion of the image area in the larger eye (TAMURA, 1957; LYALL, 1957; O'CONNELL, 1963) leading to increased acuity or sensitivity, or both, in larger fish of any species. Such an increase in acuity with growth has been reported in the cichlid *Aequidens portalegrensis* (BAERENDS, BENNEMA and VOGELZANG, 1960). The size of the fish, then, should be considered when any visual data are collected.

Some of the most interesting problems open to analysis when contrast threshold data are available pertain to the open ocean, where sighting ranges are relatively great and vision probably plays an important role. It is therefore desirable that experiments on contrast thresholds be run on open-water fishes. This initial study, however, has been so complex that additional complications caused by choosing a subject that is difficult to obtain and maintain have been avoided. Pelagic fishes in general are not easy to work with; some of the more interesting ones require special life-support systems, and even then they show a disturbing inclination to die at the most inopportune time. Near-shore species are easier to collect and keep but also require salt water, which is highly corrosive to electronic equipment. These difficulties have been avoided by choosing the goldfish, *Carassius auratus*, one of the many hardy and readily available fresh-water fishes that have been widely used in previous behavioral and physiological investigations, and a species that has been the subject of several studies pertinent to the present investigation.

## METHODS

*Apparatus*

In the apparatus (Fig. 1) used throughout the studies the fish is held in a vacuum-formed plastic holder

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in a plastic tank. The holder was so designed that the anterior part of the fish, including the eyes, is free, but the fish is immobilized. The holder and fish can be rotated, raised and lowered, so that nearly every part of the visual field can be directed toward one end of the tank.
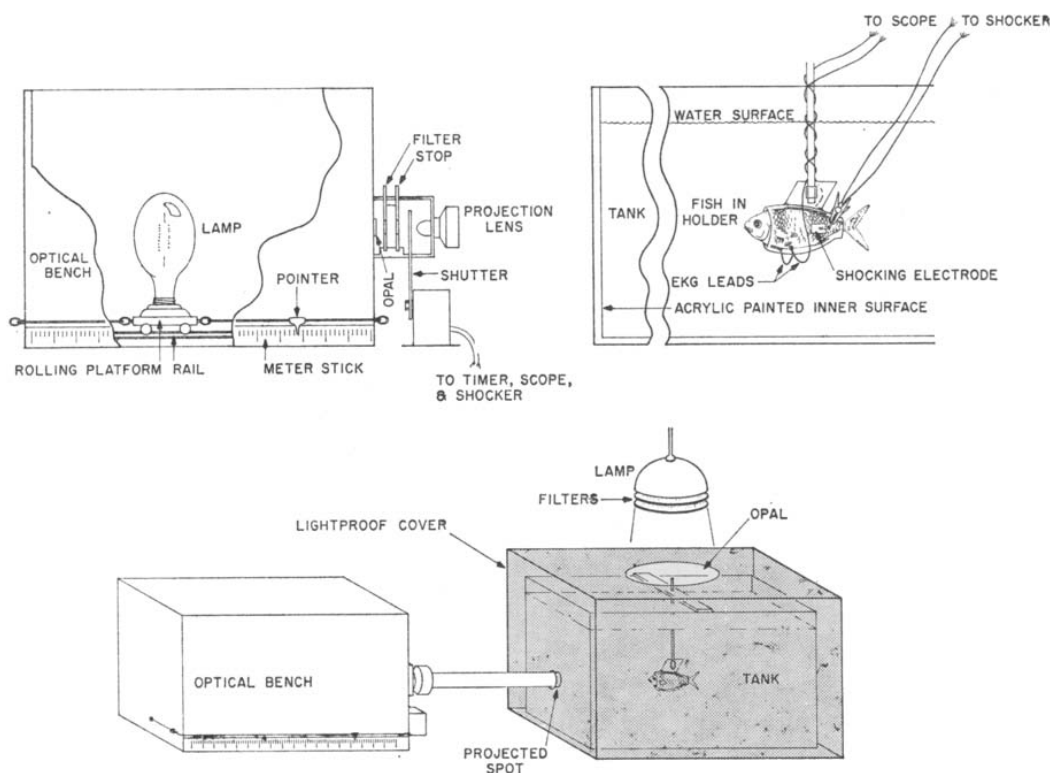


FIG. 1. Apparatus used in the determination of contrast thresholds of the goldfish.

The inner surface of the tank in which the fish is held is coated with a white acrylic paint. A thin layer of this paint acts as an effective diffuser, yet allows the conditioned stimulus, a spot of light, to be projected upon it from outside the tank, with little edge degradation.

The tank is covered by a sheet of opal plastic and is lighted from above by a single tungsten-filament lamp. This lamp is equipped with a water-bath filter; a narrow-pass filter, Wratten 61 (peak $\lambda$ 533·8 m$\mu$); and neutral density filters as required. This combination of tank, diffusers, light, and filters provides rather uniform radiance distribution, varying less than 20 per cent on the walls and bottom of the tank. The measured radiance of the end of the tank on which the target is projected (see below) is the background radiance used for calculating target contrast and also the adapting radiance for the subject.

A circular target can be projected on one end of the tank by opening the electronically controlled shutter on the optical bench. The spectral content of this stimulus is set by a Wratten 61 filter. The diameter of the target is varied by a series of optical stops. Stepwise adjustment of the target radiance is regulated by neutral-density filters. The optical bench provides fine adjustment of the target radiance over a 1·4-log range.

An electronic timing device was constructed to control both the shutter and an electric shocker, the unconditioned stimulus. The time sequence used was 0·5 sec open for the shutter and 0·2 sec on for the shock. The shock was timed to occur 0·4 sec after the shutter opened. During training, the time between stimulus presentations was controlled by a motor-driven potentiometer and varied from 40 to 60 sec, with a mean of 50 sec. During data runs the inter-trial interval was fixed at 45 sec.

*Radiometry*

The radiance of the tank interior and the projected spot were measured with a Gamma Scientific Model 200 M log-linear photometer equipped with a fiber-optic probe which allows measurements to be made underwater. The photometer was calibrated with a Gamma Scientific Model 200 luminance standard and Wratten 61 filter. The standard was calibrated with an Eppley thermopile. The cumulative calibration error for absolute measurements was estimated to be ±20 per cent.

Contrast as previously defined is $C_0 = \dfrac{N_t - N_o}{N_o}$, where $N_t$ is the radiance of the target and $N_o$ is the radiance of the background. Target radiance was measured independently of background radiance ($N_o = O$).

Computed values for $C_0$ were reproducible to within $\pm 5$ per cent.

The fish holder was positioned 40 cm from the target-end of the tank. The water in the tank had a spectral volume attenuation coefficient $\alpha_{533} \sim 0.40$, measured with a Marine Advisers alphameter having a 1-m path length. Contrast transmittance in a scattering and absorbing medium is given by $\dfrac{C_r}{C_0} = e^{-\alpha r}$

(DUNTLEY, 1963) where $C_0$ is inherent contrast measured at the target, $C_r$ is apparent contrast measured at distance $r$ (the distance from the observer to the target), $e$ is the base for natural logarithms, and $\alpha$ is the spectral volume attenuation coefficient. Computed $C_0$ was corrected for the 40-cm path by the factor 0·85 to obtain $C_r$.

*Psychophysical methods*

There are three classical methods of determining psychophysical thresholds: the direct method or method of adjustment, the method of limits, and the method of constant stimuli or indirect method. There is no reason to expect the threshold obtained by these three different methods to be the same. The direct method is usually based on the dispersion of the observed values as measured by the standard deviation. The method of limits takes the arithmetic or the geometric mean between the upper and lower stimulus intensity. The indirect method is based on the medium of an ogive calculated from the experimental data. HOLWAY (1937), however, related the direct method and the indirect method through Crozier's Law

$\dfrac{\sigma}{T_{0.50}} =$ a constant. The method of limits is more subject to the observer's criteria of "just perceptible" and "just imperceptible" and usually results in a higher threshold than is obtained with the other two methods.

These then were the three choices for determining contrast thresholds of the goldfish. The method used was determined from the requirements of the experiments and the physical ability of the subject. The method of limits was not considered since thresholds obtained in this manner are difficult to relate to the thresholds obtained with the other two methods. Of the remaining two, the method of constant stimuli was selected for the present study because it is generally considered to be the most desirable (BLACKWELL, 1952), since the threshold is computed rather than specified by the subject.

Because careful control of target diameter, location, and contrast were required, the movements of the goldfish necessarily had to be restricted. Immobilization precluded use of the usual motor responses ordinarily preferred by animal psychologists; instead, the cardiac response suggested by OTIS, CERF and THOMAS (1957) was chosen. A second reason for choosing the cardiac response was that the method of constant stimuli requires many observations for each set of data points. An additional advantage of cardiac response over motor response is that conditioning is more rapid; consequently many trials can be made in a short time.

There are two ways to conduct an experiment in which the method of constant stimuli is used. One is to require the subject to make a phenomenal report of the stimulus: respond "yes" if the stimulus is perceived and "no" if it is not. The second is to require a forced-choice: the subject giving some verifiable attribute of the stimulus other than whether or not it is perceived. BLACKWELL (1952), in his discussion of psychophysical methods, concluded that data obtained by forced-choice are generally superior to data obtained with the yes–no response. The difficulties in devising a forced-choice experiment for goldfish in which the cardiac response is used seemed to outweigh the benefits expected from the increase in the precision of the data. Instead the stimuli were presented at unexpected intervals and a yes–no cardiac response was recorded.

*Conditioning and response*

The method used to determine stimulus perception was an adaptation of the classical conditioning described by OTIS, *et al.* (1957). The goldfish was placed in the holder, wired, and positioned in the tank so that the desired part of the visual field was directed toward the end of the tank where the target would appear, a distance of 40 cm. The electrocardiogram electrodes were two insulated #22 copper wires with bare tips, one of which was placed on each side of the body beneath the pectoral fins. To avoid damage to the subject, the electrodes were in contact with the sides of the fish, rather than implanted.

Heartbeat was monitored on one channel of a Tektronix 564 storage oscilloscope with a type 3A3 dualtrace differential amplifier and a type 2B67 time base. The other channel was used for the conditioned stimulus marker. The EKG so obtained could be stored and photographed. The output of the oscilloscope preamplifier was also fed to a Sanborn 299 d.c. amplifier-recorder.

After the fish was properly positioned it was allowed to acclimate for a short period until the heartbeat was normal. Conditioning was effected by using the target with an angular subtense of 194' of arc at a contrast level sufficiently high to produce an orientation response. The target was presented for 0·5 sec. After 0·4 sec a mild shock, 0·2 sec in duration, was given the fish. The shocking voltage, typically 3·0 V d.c., was adjusted to produce a strong cardiac inhibition. The interpresentation interval was

randomized $\pm 10$ sec about a mean value of 50 sec. Conditioning usually required 15–20 training presentations.

After the fish was conditioned, the target contrast was decreased to a low level and raised in 0·3-log increments until a response was noted. The fish was then tested at a contrast level 0·1 log lower for 5 trials and the number of responses noted. If the number of responses was 2 or 3, making this contrast near the 50-per cent response level, a higher and a lower 0·1-log increment of contrast were taken to give three contrasts, 0·1 log apart, that included the level of approximately 50-per cent response.

The fish was then reinforced 3 times and tested with 5 trials at each of the 3 levels of contrast, reinforced 3 times, and retested until 25 trials were run at each of the 3 levels.

During testing, due to the nature of the recording apparatus, it was desirable to change the inter-trial interval to a fixed period of 45 sec. Since the responses were always below the 90-per cent level it can be argued that this procedure did not result in the subject's anticipating the time of stimulus onset.

The conditioning described above resulted in a generalization of the stimulus by the subject. Fish conditioned to the 194′ target responded to targets of smaller dia. and targets located elsewhere in the visual field. In addition, fish conditioned binocularly responded to targets in the monocular field; however, in the experiments involving the monocular field the fish was conditioned with one eye covered.

The 3 contrasts in an experiment were presented in a random order, and 5 trials were run at each contrast. After 2 sets of 5 trials, each fish was reinforced 3 times at a higher contrast. The last 3 sets of 5 trials each were run consecutively without reinforcement. The 3 contrasts were presented in a fixed order, low to high. When this schedule of trials and reinforcements was used, extinction never was apparent.

McCLEARY and BERNSTEIN (1959) used the cardiac response to demonstrate color vision in the goldfish. In their experiments the stimulus duration was 10 sec. Response was measured by comparing statistically the number of heartbeats counted during this 10-sec period with the number counted during a 10-sec period throughout which a neutral stimulus was presented. For the stimuli of short duration used in the present study, the cardiac response was markedly different. The heart rate was constant except immediately after stimulus presentation, when only one or occasionally a few beats were skipped or were of decreased amplitude. Statistical comparison of the number of beats following stimulus presentation and the number of beats during some other period were not significant; however, the single-beat inhibition was so pronounced (Fig. 2) that it alone was a reliable indication of response.
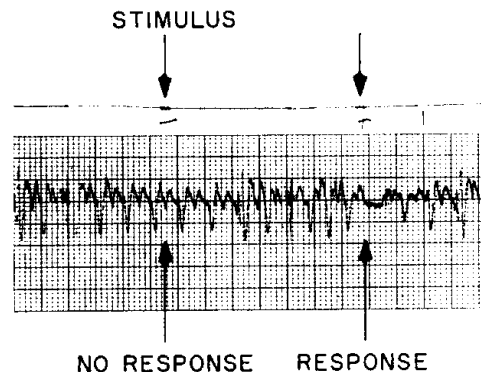


FIG. 2. EKG recording from a goldfish showing the cardiac response to a circular spot of light having a duration of 0·5 sec, a contrast of 0·26, and an angular subtense of 194′ of arc. Background radiance was 0·07 $\mu$Wcm/2/$\omega$.

Regardless of the contrast level used, there was no tendency for an increased latency or a decreased amplitude. Similarly, latency and amplitude changes were not noted during the experiments in which temperature and consequently heart rate were higher or lower. The cardiac response reflected the all-or-none character of the visual phenomenon over the entire range of contrasts. The response seemed to be an excellent and easily observed indicator for yes–no phenomenal reporting.

Unfortunately, the initial success of the technique did not continue throughout the course of the experiments. The number of conditioning failures was near a constant 20 per cent for all the experiments at the 3 highest adaptive levels. Some of the subjects (and the experimenter) had bad days but the same subject often performed well at a later date. When the adaptive level was lowered to 0·07 $\mu$W/cm²/$\omega$, the rate of failure increased slightly: several reliable subjects no longer performed well; the heartbeat of one fish, a veteran of some 20 sessions, became erratic; and other fish would not condition at all. Despite these difficulties it was possible, by using new subjects, to complete this series of experiments. At the next lower level, 0·007 $\mu$W/²cm/$\omega$, the rate of failure was 100-per cent. The experiments were terminated at this point.

*Processing of psychophysical data*

Biological assay is a term meaning the measurement of the potency of any stimulus by means of the reactions which it produces in living material. Often the response is quantal; that is, an all-or-nothing response—as in the goldfish experiments, in which a cardiac response is or is not elicited by a given stimulus. Probit analysis provides a method of statistically treating quantal biological assay data.

The history of the probit method was thoroughly discussed by FINNEY (1952). Although probit analysis has been widely used, the calculations are tedious and many workers have resorted to a graphical method. Recently RICHARDSON (1967) and others have developed computer programs for probit analysis that greatly speed the calculations.

BLACKWELL (1953), in a study of the form of visual threshold data, showed that in a series of experiments all the data for four subjects could be fitted by one or another Poisson sum. In the same series he found that the data for three of the subjects were fitted by normal ogives and the data for the fourth were fitted by log-normal ogives. The circumstance that predictions concerning the magnitude of the threshold were not verified by using Poisson sums, however, led Blackwell to conclude that threshold data could probably be analyzed adequately by either normal or log-normal ogives.

BLACKWELL (1953) used a special version of the $\chi^2$ test to determine the number of observations required to separate statistically data log-normal in form from data normal in form. This is the number of observations that must be made to obtain an unacceptable fit to a normal ogive by data actually log-normal in form (or the reverse). If 10 stimulus levels were used in an experiment, 209 presentations at each level, or 2090 observations, would be required.

For goldfish, the contrast threshold was taken to be the contrast at which positive responses were elicited 50 per cent of the time. Typically, each experiment provided data from 25 trials at 3 contrasts. Both a normal and a log-normal probability integral were fitted to these data by the probit analysis computer program of RICHARDSON (1967). The fit was slightly better if the log-normal transformation was used; however, the 25 observations at each of 3 levels used in the goldfish experiments fall far short of the required number (see above). Therefore the lower $\chi^2$ values for the log transformation found in most of the experiments cannot be considered of statistical significance. Either curve will give a good estimate of the threshold (less than 2 per cent difference in most of the goldfish data).

*Biological material*

The fish used throughout were "wild-type" goldfish, *Carassius auratus*, obtained from a local dealer. They were fed a commercial dry fishfood which they supplemented with the vegetation in their tanks. Day length was artificially controlled, 12 hr light, 12 hr dark. During the experiments at low radiance levels the light-dark in the holding tanks was reversed. Water temperature was held at 20° C (except during one experiment on temperature effects).

All measurements of fish were standard length (tip of snout to base of tail, measured to the nearest mm). The fish were 49–110 mm long. Lens dia. was measured on material preserved in 70 per cent alcohol.

During the study it was customary to use the same group of fish (usually 5) for each particular experiment. When other fish had to be substituted they were selected to approximate the performance of the original subjects as nearly as possible.

*Histology*

For histological preparations of the retinae, specimens were decapitated, the corneas pierced, and the whole heads fixed in Bouin for 24 hr. The left eye was then removed and enucleated, a snip of the ora was removed for orientation, and the eye was returned to Bouin. After the eye remained in fixative for at least an additional 24 hr, it was cleaned in 70 per cent ethyl alcohol for several days, dehydrated, and cleared in cedarwood oil. The eye was then embedded in paraffin and divided into sections—usually 12, although some additional sections near the ora were taken on one fish. These sections were reembedded and sectioned as near to the center of the convex surface as possible. Tangential serial sections 6–8 $\mu$ thick were made and stained with Mallory triple stain. Photo micrographs of the sections were made and the number of single and double cones counted on the photographs. The numbers of cones per 0·00125 mm² were counted from 4 locations on each photograph and the total of the 4 counts doubled to get the number of cones per 0·01 mm². Whenever possible the average of two or more sections from the serial were used to estimate these numbers.

# THE GOLDFISH EYE

*Anatomy*

The eye-cups of goldfish appear hemispherical, with equal horizontal and vertical axes. The 6 oculomotor muscles are developed, the *inferior rectus* weakly. Both obliques tend steeply inward in the socket, suggesting limited movement of the eye in the equatorial plane. The lens rests against the

immovable iris and is suspended dorsally and slightly temporally by the well-developed ligament. The weakly developed *retractor lentis* is attached to the lens ventrally and slightly nasally and runs radially to the retina at the ora. The *retractor lentis* lacks the lateral component necessary to move the lens along the temporal-nasal line. This attachment, however, seemingly could roll the lens inward toward the fundus, but such movement is doubtful, since the muscle is developed so poorly. Furthermore, KIMURA and TAMURA (1966) found that the muscle failed to contract when stimulated electrically. Their results indicate that the goldfish apparently lacks a functional accommodative apparatus; and, indeed, it is difficult to see why one is necessary in a hemispherical eye. According to PUMPHREY (1961), the usual shape of the fish eye-cup is semi-ellipsoidal with the long axis running temporal-nasal. Accommodation of such an eye is effected by a movement of the lens along this axis. The center of the lens of a hemispherical eye-cup is everywhere equidistant from the retina and the image is in equal focus regardless of its angular position in the visual field. This would hold true for objects farther than about 2 m from the fish if the distance from the lens to the retina and the focal length obey Matthiessen's ratio (focal length = 2·55 lens radius·. Objects closer than 2 m would be slightly out of focus.

Presumably the 40-cm target-to-subject distance used throughout the experiments was viewed by the goldfish with the refractive state of the eye constant regardless of the position of the target in the visual field. For a lens having a focal length of 3·3 mm (2·55 × 1·3 mm lens radius) an image on the retina at the *limitans*, of an object at infinity, will be shifted 62 $\mu$ toward the sclera when the object is moved to a distance of 40 cm. Since the receptive layer in the goldfish retina is about 40 $\mu$ thick, the image of an object at 40 cm will fall outside the layer of visual cells. For large targets this refractive error should have a negligible effect on contrast perception.

The goldfish eye lacks a choroid gland and a falciform process. Instead, hyaloid vessels radiate over the retina from the optic papilla. In the sectioned eye of a 72-mm goldfish having a 7-mm dia. optic cup, the dia. of the papilla was about 0·024 mm. The visual cell layers that surrounded it were compressed over an area about 0·083 mm in dia. In an ophthalmoscopic examination of enucleated, preserved eyes the papilla appears surrounded by radiating lines of nerve fibers overlying the retina. The hyaloid vessels are few but prominent. No tapetum is observable.

The binocular field was measured on two goldfish immobilized in plastic holders. With the eye free to move, the field of overlap was about 45° in the horizontal plane and about 54° for a path of sight directed 15° upward or downward. If the fish were anesthetized with MS 222, so that the eyes were immobile, the binocular field was about 10° narrower.

In anesthetized fish the eyes could be moved in the socket some 60° forward and 20° to the rear and +10° to −50° vertically. Eye movements of this magnitude were not observed in free-swimming fish. These fish moved their eyes somewhat when swimming or when prodded with a pencil. The eye of a fish contained in a holder could be made to follow the spot from an ophthalmoscope. Movements of about 20° forward were observed. Rearward movement was very slight—less than 5°. The eye was not observed to move above the horizontal but did follow the beam downward about 20°. A downward jerk of at least 40° was observed occasionally, apparently associated with a respiratory cleaning movement.

## Histology

ENGSTROM (1960) found two types of single cones and unequal double cones in the goldfish retina. In one of his two goldfish he described a distinct pattern similar to the square pattern reported for trout (LYALL, 1957). The pattern in the goldfish is most readily distinguished in the equator of the eye. In my material a pattern is not discernible; the lack of it made cone counts difficult.

In the three whole eyes examined for the present study, double cones are more numerous than both types of single cones combined. Double and single cones are both more numerous in the dorsal and temporal regions than in the nasal and ventral regions (Fig. 3). Rods are presumed to be present, since the absorption spectrum for the dark-adapted goldfish eye has been shown to differ from the photopic spectrum (BURKHARDT, 1966). The photopic curve has a maximum at 560 m$\mu$, whereas the scotopic curve has two maxima, one at 560 m$\mu$ and a slightly higher one at 500 m$\mu$. Rods are not discernible in any of my material and must be small. Numerous rod nuclei can be seen in cross-sections of dark-adapted eyes, but counts have not been attempted.

LYALL (1957), MÜLLER (1952), and O'CONNELL (1963) all reported that cone density for several species decreased with retinal growth but at a lesser rate than would be expected if the total number of elements remains constant. Lyall and Müller found new elements being added by mitosis at the retinal margins. If the number of cones in the retina remains constant during the growth of the eye, the number of cones per unit area should decrease proportionally to the increase in area of the retina. The number of cones per unit area then should be proportional to the square of the lens diameter (assuming that Matthiessen's ratio holds) and the regression of log number of cones per unit area on log lens diameter should have a negative slope of −2. If new cones are added in the retina during the growth of the eye, the number of cones per unit area should decrease at a lesser rate, and the slope of the regression log number of cones per unit area on log lens diameter should be between 0 and −2.
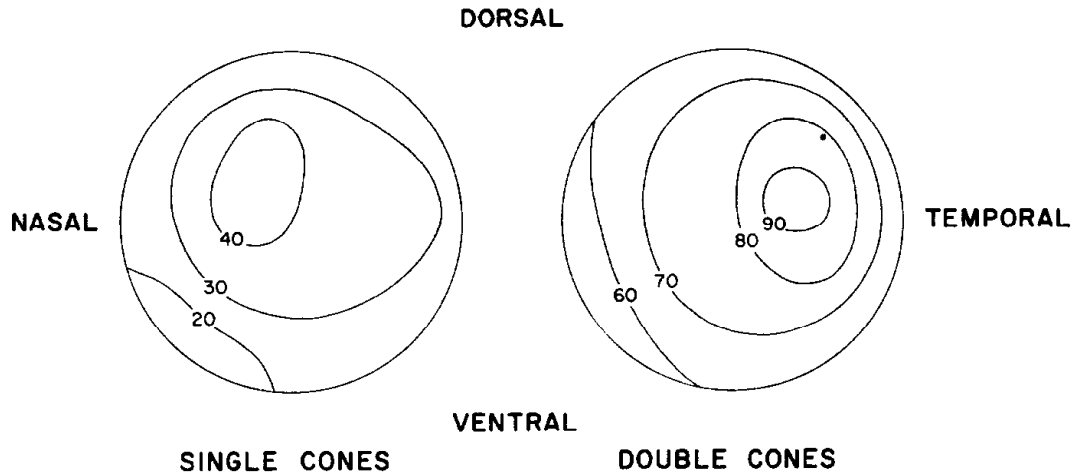
DORSAL



NASAL

40

30

20

TEMPORAL

90

80

60　70

VENTRAL

SINGLE CONES　　　　DOUBLE CONES

Fig. 3. The probable cone topography of the goldfish retina in number of cones per 0·01 mm²
of retina. No correction was made for shrinkage.

Single and double cones per 0·01 mm² in sections from the ventral-temporal region of the retina were counted for 8 goldfish with lens dia. of 2·40–3·00 mm. The slopes of the two regression lines are $-1·53$ for single cones and $-1·36$ for double cones. The variability is so great, however, that neither line differed significantly from either 0 or $-2$.

## RESULTS

### Relation of contrast threshold to fish size

The histological examination of the goldfish retina indicates that as the eye increases in size, cone density decreases at a lesser rate than that predicted on the basis of area alone. Similar observations on other species led O'CONNELL (1963) to suggest that some aspects of the visual performance in a fish may vary in relation to the size of the eye. To study the relation of contrast threshold and fish size, binocular contrast thresholds $^{(P=0.50)}$ were determined for 14 fish (49–92 mm standard length), at 20° C. The target subtended 194' of arc, and was positioned in the binocular field directly in front of the fish at 0° elevation and 0° bearing. Adaptive radiance was $10^2$ $\mu W/\overline{cm}^2/\omega$.

Fish length and contrast threshold were negatively correlated at a significant level $(r=-0·709^{**})$.[2] The comparison of lens dia. with length shows sufficient variation to suggest that lens dia. is a better index of visual performance; the correlation is improved considerably $(r=-0·819^{**})$[2] for the new regression (Fig. 4):
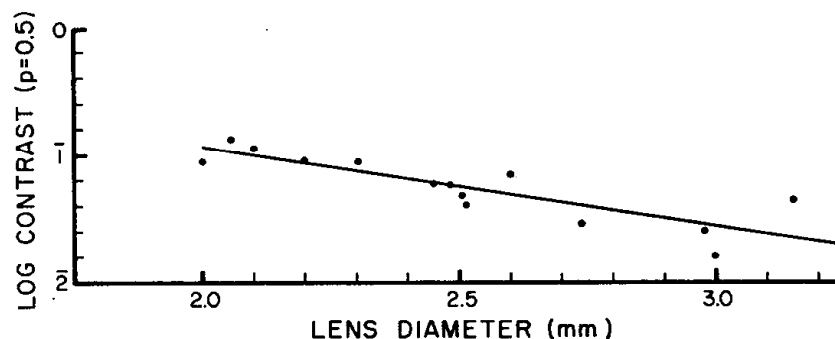


Fig. 4. The relation of contrast threshold to lens diameter for 14 goldfish. The line is the regression equation $y = -0·60x + (0·230)$.

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[2] Significant at the 0·01 level.

$$y = -0.60x + (0.230)$$
where            $y = \log \text{threshold}^{(P=0.50)}$
and              $x = \text{lens dia. mm.}$

These data suggest that the performance of at least one visual task, namely contrast perception, improves with growth, confirming the observations of BAERENDS, et al. (1960) who reported an increase in acuity with growth in the cichlid *Aequidens portalegrensis*.

## Relation of contrast threshold to temperature

Because the relation between threshold and eye size was significant, goldfish of approximately the same standard length (70–90 mm) were used in this and the following experiments.

Binocular contrast thresholds $^{(P=0.50)}$, were obtained for 5 fish at 15, 20, 25, 30, 35° C. Target dia. was 194' of arc. Adaptive radiance was $10^2 \mu W/\overline{cm^2}/\omega$. The fish were allowed to acclimate for at least 48 hr at each temperature except 35° C. Thresholds at 35° were taken by using fish acclimated 48 hr at 30° C, raised to 35° C during 1 hr, and acclimated at 35° C for 1 hr. Threshold was lowest at 20° C and increased at higher and lower temperatures (Fig. 5).
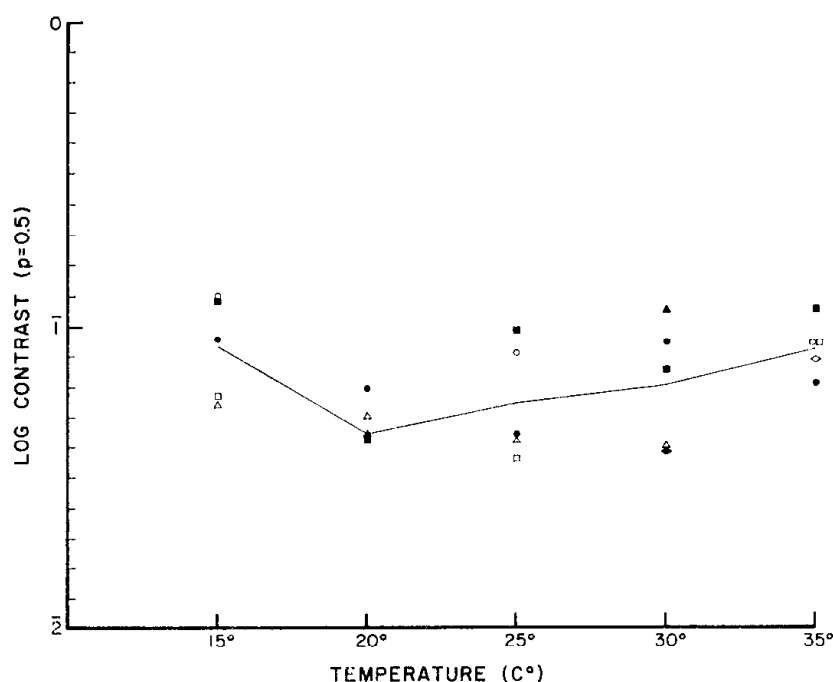


FIG. 5. The relation of contrast threshold to temperature. Each symbol performance for an individual fish.

Two aspects of vision have been shown to be temperature-dependent in poikilotherms. CROZIER, et al. (1938) found that critical intensity for the turtle *Pseudemys* was decreased if temperature was increased from 21.5° C to 29.5° C and flash frequency was held constant. HANYU and ALI (1963) described a linear increase in the maximum flicker fusion frequency of the goldfish over a temperature range of 5–25° C.

AREY (1916) found more uniform pigment distribution in the light-adapted goldfish retina at 25 than at 5° C. In the retina of dark-adapted goldfish, pigment contraction was less at the lower temperature. Arey also found an increase in the elongation of the

chief cone myoid of the double cones at the higher temperature. The accessory cone myoid did not change with temperature.

The threshold temperature data for the goldfish suggest that the mechanisms linking the two operate more efficiently at 20° C than at the higher or lower temperature. The relation between flicker frequency and temperature reported by HANYU and ALI (1963), however, showed no inclination to change in slope even at 25° C. Although no clear relation exists between flicker-frequency and contrast perception, their observations suggested that the mechanism responsible for the threshold minimum at 20° C might be at least a step removed from processes in the retina.

At least two temperature related phenomena in the goldfish have been shown to be maximal near 20° C. FRY (1957) found that the scope for activity, the difference between the active and standard metabolism of the goldfish, was maximal at about 27° C. In a later study BEAMISH and MOOKHERJII (1964) reported a maximum at 20° C in the average routine oxygen consumption of the goldfish; they attributed this maximum to an increase in spontaneous activity at 20° C.

*Relation of contrast threshold to retinal position*

The nonuniform cone density of the goldfish eye suggested that differences in contrast threshold depend on the position of the image on the retina. Threshold differences (Fig. 6) appear to be related to cone density. The fish were immobilized in the usual manner and the contrast thresholds were obtained for the binocular field, with target at 0° elevation and bearing. Monocular contrast thresholds were also taken with the target at 12 different positions in the visual field: 4 in the horizontal plane, 4 with the fish in the plane 15° below the target and 4 with the fish in the plane 15° above the target. Bearings of 45° increments measured from the nose also were used. Target dia. was 194', temperature was 20° C, $N_0$ was $10^2$ $\mu$W/$\overline{mc}^2$/$\omega$. Monocular thresholds were taken with a blinder over the right eye of the fish; the left eye was uncovered and both eyes were free to move in their sockets.

The goldfish data show that the difference between the binocular and monocular threshold is about 0·17 log units (binocular threshold = 0·67 monocular threshold). LE GRAND (1957) discussed the difference between monocular and binocular threshold in terms of a simple summation of probabilities. If the assumption is made that at any instant there is no correlation between the sensitivities of the two eyes, the calculated ratio of binocular to monocular thresholds for the goldfish is 0·68 monocular threshold, a difference of 0·17 log units—in good agreement with the data.

Monocular threshold in the horizontal plane increased at the center of the eye. Since the area of the retina covered by the target image included the optic papilla, an increase in threshold (decrease in sensitivity) might be expected. A target with a dia. of 194' of arc would project as a spot approximately 0·15 mm in dia., on the retina of an eye 7 mm in dia. The diameter of the papilla in an eye this size was 0·024 mm (0·083 mm across the region of retinal deformation). Thus, the target covers an area of the retina considerably greater than that of the papilla.

The average monocular threshold for an upward or downward path of sight decreased slightly toward the center of the retina. This decrease might be related to the increase in cone density toward the center of the eye (Fig. 3); however, additional complications were found to be involved which makes these two data sets suspect.

A similar relation—a lower threshold in regions of high cone density—has been described for the human eye (TAYLOR, 1961). JACOBSON and GAZE (1964) and SCHWASSMANN and
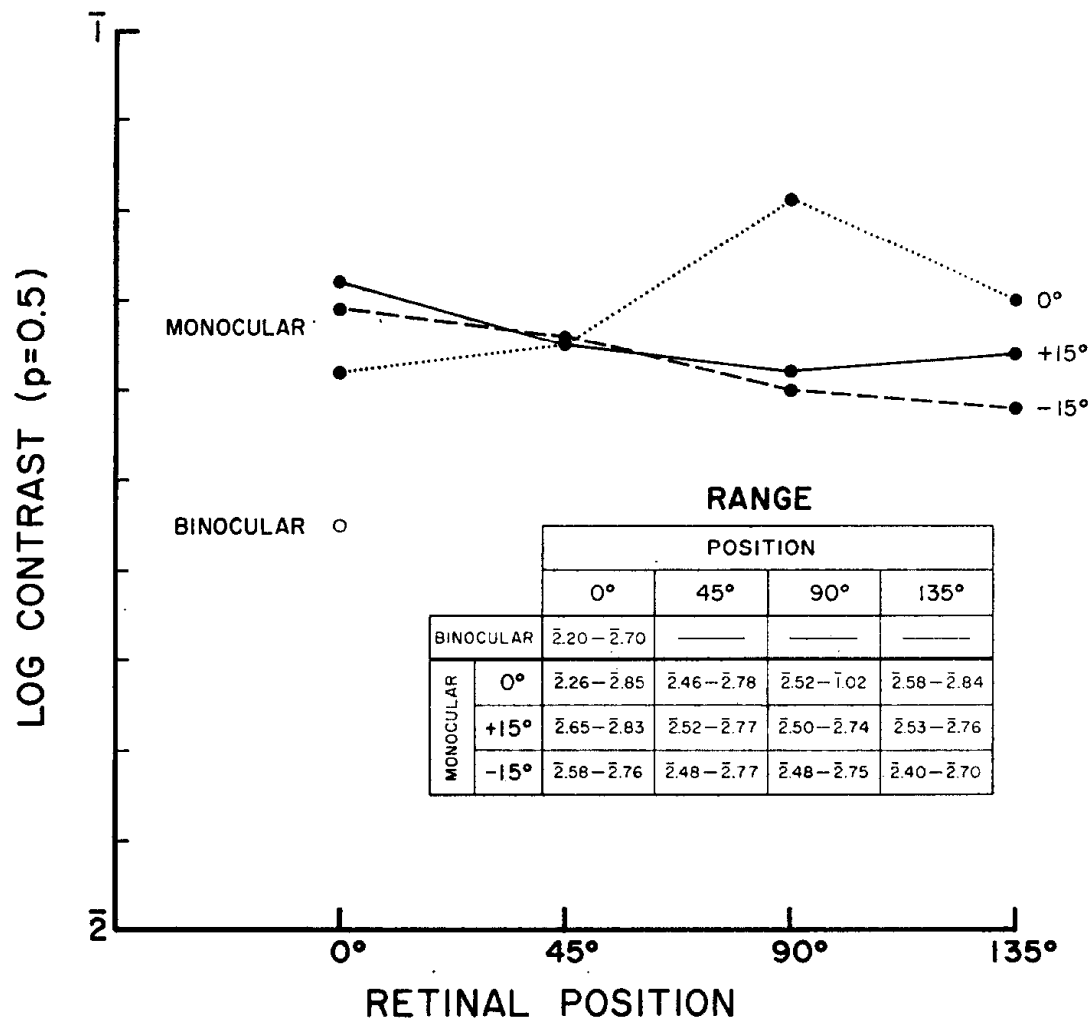
FIG. 6. Variation of contrast threshold for different positions of the target in the visual field. Each point is the mean for five fish. Target position in degrees is measured in the horizontal plane from directly in front of the fish (0°) rearward in the visual field to 135°. The points are for monocular thresholds—the dotted line for paths of sight in the horizontal plane, the solid line for paths of sight directed upward 15°, and the dashed line for paths of sight directed downward 15°. The open circle is the mean binocular threshold, target in the horizontal plane at 0° bearing. The log of the ranges for each point is given in the table.

KRUGER (1965), however, did not find areal differences in flash perception on the goldfish retina in the optic tectum, and concluded that there was no indication of a specialized area in the visual field in this species.

*Relation of contrast threshold to target size and adaptive radiance*

Binocular contrast thresholds were obtained for groups of fish at 4 adaptive radiance levels for targets of 5 dia. (Fig. 7). Difficulty with conditioning at low-adaptive levels caused the experiments to be terminated at $7 \times 10^{-2}$ $\mu$W/$\overline{cm^2}$/$\omega$.

The curves for goldfish show similarities to the curves for the human eye (BLACKWELL, 1946). The curves for both sets of data (Fig. 8) have negative slopes. The slope of the curve for the human eye tends to approach zero at the higher adaptive levels. A similar trend might be expected for goldfish if the experiments had been extended to higher levels of adaptation.

At lower adaptive levels the slopes are steeper except for a break at the change from photopic to scotopic vision in the human data. A similar break appears to occur between
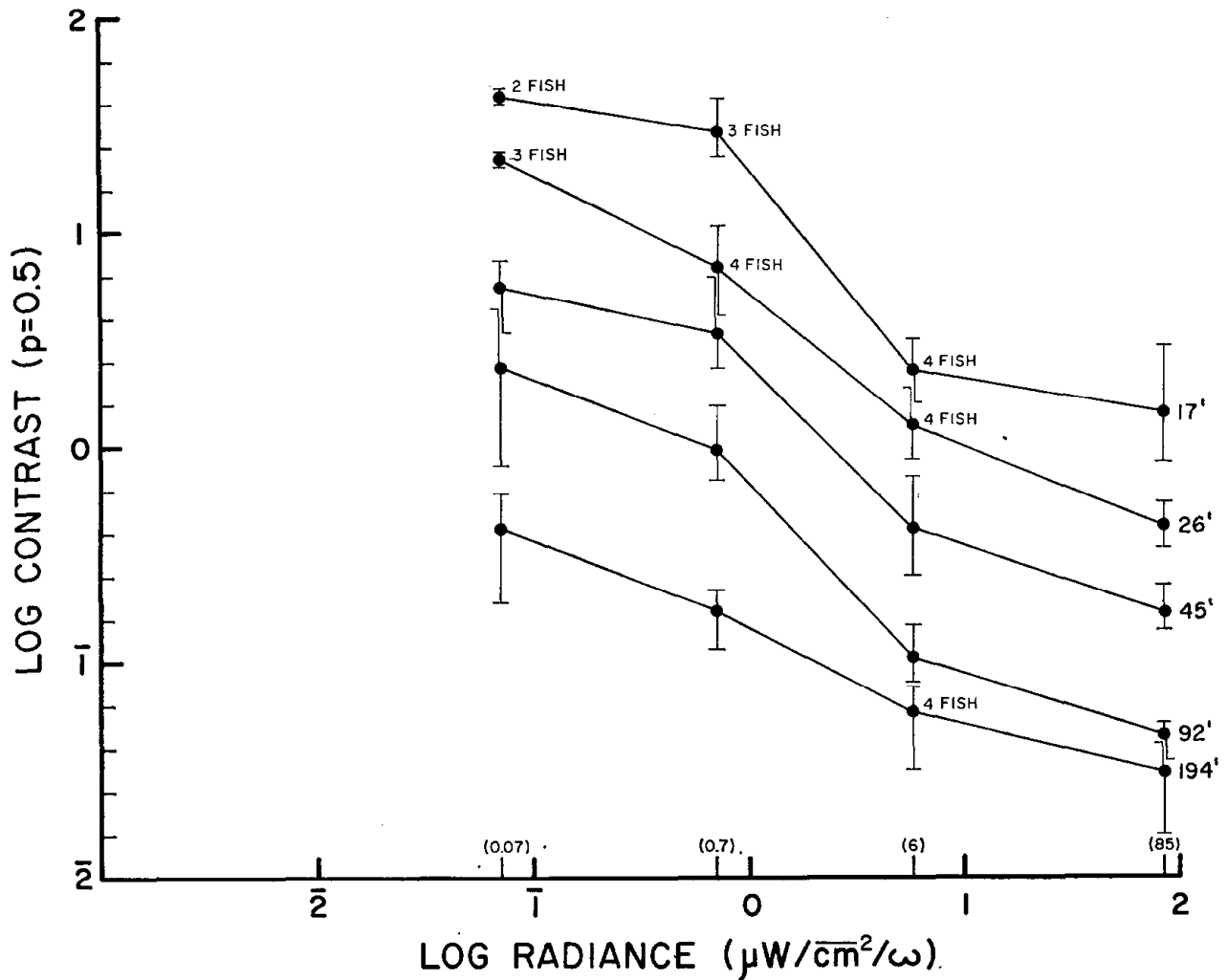
FIG. 7. Relation of contrast threshold to adaptive-radiance for targets of different diameters (17 to 194 min of arc). Points are means for five fish except where specified.
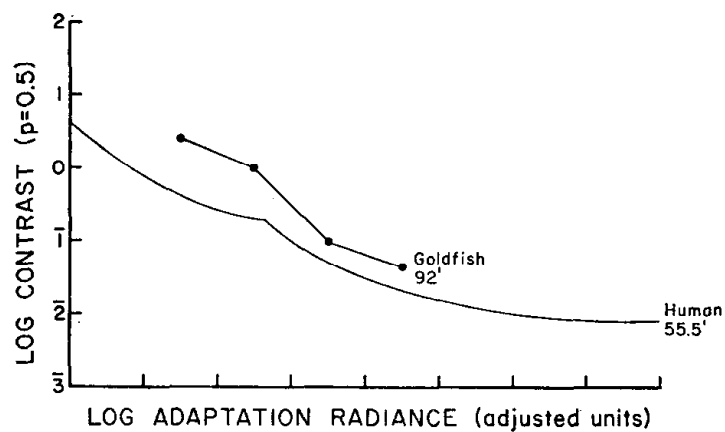
FIG. 8. The relation of contrast threshold to adaptive radiance for the goldfish and for the human eye (after BLACKWELL, 1946). The radiance units have been adjusted to cause the mesopic regions of the two curves to coincide.

1 and $10^{-1}$ $\mu W/\overline{cm}^2/\omega$ in the goldfish data. Unfortunately, data are lacking for the scotopic portion of the goldfish curves.

Histological examination of eyes from goldfish adapted at $7 \times 10^{-2}$ $\mu W/\overline{cm}^2/\omega$ shows that some pigment migration had occurred and indicates partial dark adaptation. This level appears to be close to those reported by ALI (1959) for the young of two species of salmon ($10^{-1}$, $10^{-2}$ ft-c, about the same as $7 \times 10^{-2}$ $\mu W/\overline{cm}^2$), although differences in the two experiments render the comparison speculative. Other reports of the mesopic region in fishes (WOODHEAD, 1966) are generally several orders of magnitude lower, but again direct comparisons are impossible.
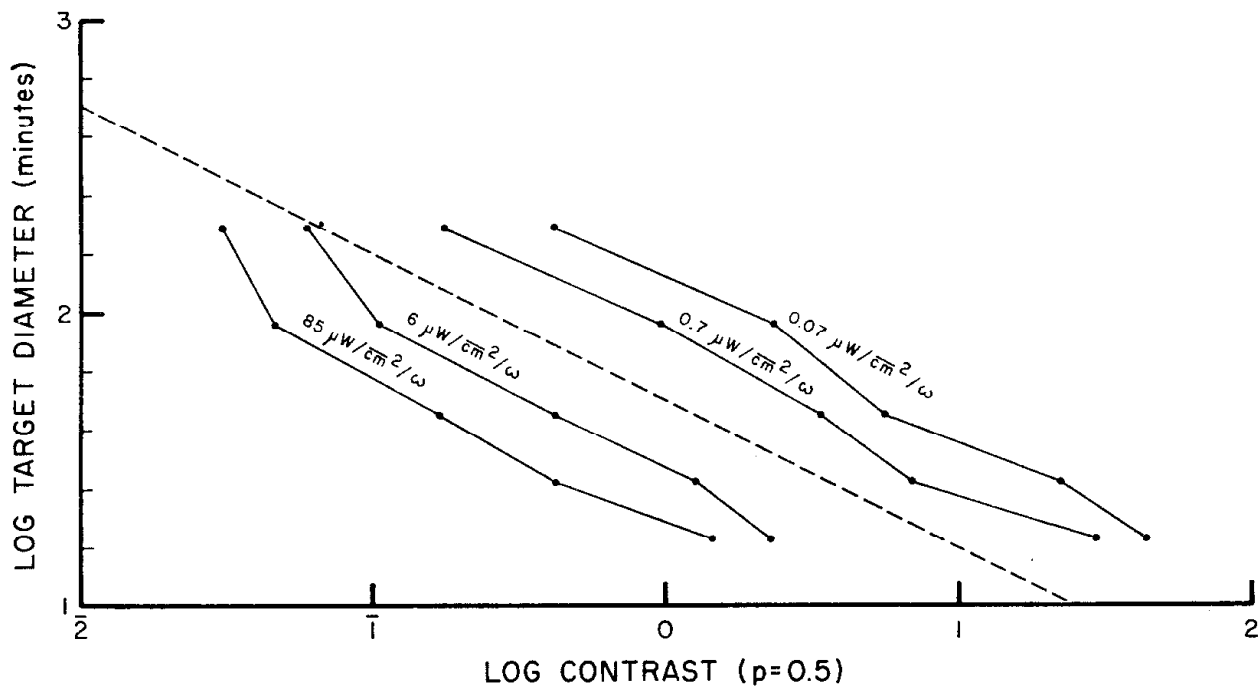


FIG. 9. The relation of target diameter to contrast threshold at each of four levels of adaptive radiance. The dashed line has a slope of $-0\cdot5$.

The curves obtained when log target diameter is plotted against log contrast threshold (Fig. 9) show several features that are remarkably similar to those in the human data. At high contrasts both sets of data yield curves with slopes very close to $-0\cdot5$. A slope of $-0\cdot5$ would be expected if complete summation of the radiant flux occurs regardless of the size of the retinal area covered. Of interest are first that the goldfish data have slopes so near to the $-0\cdot5$ expected with complete summation; and second that the data do not depart from this slope even for target diameters greater than 100' of arc (low adaptive levels).

The general interpretation of spatial summation is that a number of receptor elements, rods or cones, are connected into a functional unit, probably in the inner nuclear layer of the retina. The size of these functional units has been postulated to decrease as the retina adapts to higher radiance levels (HECHT, 1928; HECHT and WALD, 1934). Although the mechanisms involved are likely to be more complex than Hecht suggested (PIRENNE, 1962), the general concept has been accepted. Interpreting the goldfish data in terms of Hecht's theory indicates that the size of a functional unit in the goldfish retina must, at any adaptive level, be much greater than that in the human retina.

Hecht originally proposed his theory to explain the relation between acuity and intensity. He later extended the theory to include intensity discrimination. Both acuity and intensity discrimination are special cases of contrast discrimination. One definition

of visual acuity is the reciprocal of the minimum separable angle in minutes of arc, when the adaptive state of the eye and the target contrast are specified. The targets usually used are Snellen letters, Landolt's C's, and bar gratings. The target contrast is typically 1·0 and the eye light-adapted. Human visual acuity based on these tests varies from 1·0 to 2·0, corresponding to minimum separable angles of 1·0′ to 0·5′ of arc (WESTHEIMER, 1965). Minimum separable angle has been calculated for a number of species of fish (TAMURA, 1957), on the basis of the separation distance between alternate cones in the retina. In the 27 species examined the smallest calculated minimum separable angle was 4·2′ of arc (0·24 acuity) for *Epinephelus septemfasciatus*. The other 26 species had calculated minimum separable angles which ranged up to 15·4′ of arc (0·065 acuity) for *Chlorophthalmus albatrossis*. Unfortunately, the goldfish was not included in Tamura's study; however, it is possible to calculate minimum separable angle for goldfish by using Tamura's formula and the density of cones for the goldfish eye (Fig. 3). Tamura's formula, based on Matthiessen's ratio, is:

$$a = \frac{1}{F}\left[\frac{0·1\,(1+0·25)}{\sqrt{n}} \times 2\right]$$

where
    $a$ = minimum separable angle (radians)
    $F$ = focal length of the lens (2·55 × lens radius)
    $n$ = maximum number of cones (both single and double) per
      0·01 mm² of retina (0·1 mm on a side).

The 0·25 is a correction factor for shrinkage and the factor two is to select alternate cones. For a goldfish having a 2·6 mm dia. lens:

$$F = 3·3$$

$n$ (dorsal/temporal) = 90 double and 30 single = 120

$$a = \frac{1}{3·3}\left(\frac{0·25}{11}\right) = 0·0138 \text{ radians or } 24′ \text{ of arc.}$$

A vertical line at contrast 1·0 (Fig. 9) would be the locus for single-point acuity of the goldfish. Single-point acuity for the highest adaptive radiance is about 0·05 (minimum separable angle, 20′ of arc). This value is amazingly close to the calculated minimum separable angle. The problem of detecting a single point is usually considered as a visual acuity task, but one that is difficult to relate to the tests described previously, namely Snellen letters, Landolt's C's, bar gratings, and retinal measurements. With this difficulty in mind the acuity curve for the goldfish over the range of four adaptive radiances is given in Fig. 10.

For targets which exceed a certain size the relation, threshold × target area = a constant, no longer holds. The slope of the curve changes sharply and becomes asymptotic to the ordinate. This concept of the critical visual angle (BLACKWELL, 1946)—the point at which each curve departs from linearity—is a fundamental property of the eye. One interpretation of this phenomenon that results in a useful generalization is that the threshold is constant for targets subtending angles greater than a certain critical angle. For approximations of sighting ranges this generalization has proven very useful (DUNTLEY, 1963). The critical angle for the goldfish in well-lighted waters is (from Fig. 9) about 100′ of arc and corresponds to a contrast threshold of 0·05.

*Relation of contrast threshold to probit slope*

The standard deviation ($\sigma$) of per cent positive responses about the mean is represented
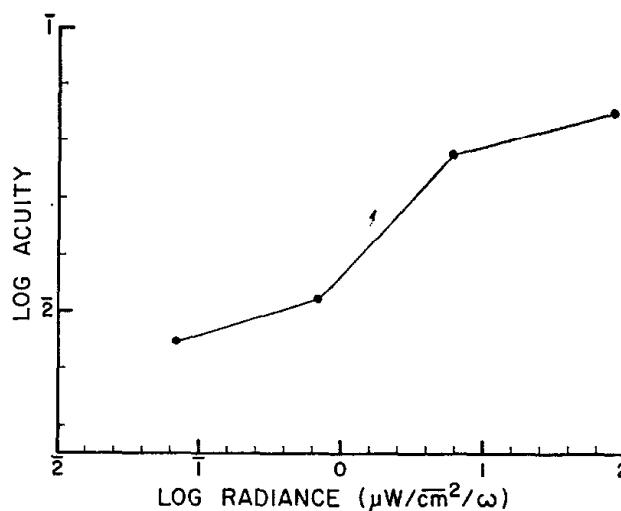
FIG. 10. The relation of single-point acuity to adaptive radiance for the goldfish.

by the reciprocal of the slope of the probit line in probit analysis. In agreement with Crozier's Law, the ratio of $\sigma$ to the mean $T_{0.50}$ is constant. This relation was found to hold for the human eye by BLACKWELL and MCCREADY (1958), where $\sigma/T_{0.50} = 0.390$ over a range of threshold values of a million to one. The ratio, arithmetic mean $\sigma/T_{0.50}$, for goldfish binocular thresholds was 0.585 (S.E. $\pm$ 0.0647). Departures from this ratio were not significant in any of the experiments in which binocular vision was tested. The monocular threshold experiments had a mean $\sigma/T_{0.50} = 0.403$ for targets in the horizontal plane.

Since the binocular threshold data do not show significant departures from a mean $\sigma/T_{0.50} = 0.585$ regardless of the experimental variable (target size, adaptive radiance, temperature, or fish size), the probit for the normal distribution of per cent positive response and contrast can be used to adjust these data to any other desired detection probability. Values of $t$ corresponding to the desired probability level (Table 1) are to be found in a table of areas of the normal curve of error.

TABLE 1. CORRECTION FACTORS FOR DETECTION LEVELS OTHER THAN 0·50 (NORMAL DISTRIBUTION)

| Detection probability | $t$ | $\dfrac{\sigma \cdot t}{T_{0.50}}$ | $\dfrac{T_p}{T_{0.50}}$ |
|---|---|---|---|
| 0·90 | 1·29 | 0·75 | 1·75 |
| 0·95 | 1·65 | 0·96 | 1·96 |
| 0·99 | 2·33 | 1·36 | 2·36 |

If the log-normal distribution of the threshold is used instead of the normal, the standard deviation (0·612 for the binocular data) can be considered to be constant regardless of the magnitude of the threshold. For the goldfish data the log-normal distribution gave a smaller $\chi^2$ nearly two-thirds of the time; however, there is little justification for preferring the use of this transformation (BLACKWELL, 1953), and the differences in the thresholds obtained by the two methods were never greater than a few per cent. The values for converting thresholds from log-normal data to some other probability are given in Table 2.

## DISCUSSION: THE UNDERWATER VISUAL PROBLEM

DUNTLEY (1963) has shown that for horizontal paths of sight the underwater sighting

TABLE 2. CORRECTION FACTOR FOR DETECTION LEVELS OTHER THAN
0·50 (LOG-NORMAL DISTRIBUTION)

| Detection probability | $e^{-t_p\sigma}$ |
|---|---|
| 0·90 | 2·08 |
| 0·95 | 2·74 |
| 0·99 | 4·18 |

range of a target is determined by the exponential degradation of the inherent target contrast along the path of sight:

$$\frac{C_r}{C_o} = e^{-ar}$$

where
$C_o$ = inherent target contrast (measured at the target),
$C_r$ = apparent target contrast (measured at distance $r$),
$e$ = base for natural logarithms,
$a$ = the spectral volume attenuation coefficient for the water mass,

and
$r$ = range to target.

For the light-adapted human eye the contrast threshold $_{(P=0·50)}$ was found to be approximately 0·01 for targets exceeding 15′ of arc in a series of forced-choice temporal method experiments in which binocular viewing, foveal fixation, and a 0·33-sec target duration were used (TAYLOR, 1964). This threshold can be corrected by a series of "field factors" (TAYLOR, 1964) to compensate for unexpected appearance (1·40) and an uncertainty in location of ±4° or more (1·31), and by a confidence-level factor to raise the threshold to the 95 per cent level (1·64). The corrected threshold will be 0·01 × (1·40)(1·31)(1·64), or about 0·032. If this corrected threshold is used in the contrast-reduction formula the underwater sighting range by a swimmer for targets having an inherent contrast of 1·00 would be $\frac{3·5}{a}$ meters when $r$ is measured in meters and $a$ in $\frac{\ln}{m}$. (The inherent contrast of 1·00 is an absolute value. Dark objects viewed against a light background have inherent contrasts close to −1·00. Such targets are common in the underwater environment.)

The contrast threshold $_{(P=0·50)}$ for a goldfish in well-lighted waters for targets greater than 100′ of arc is about 0·05 (Fig. 9). This threshold was determined by the yes–no rather than the forced-choice method. Thresholds determined by the yes–no method are expected to be slightly greater than thresholds determined by the forced-choice procedure (BLACKWELL, 1953); however, this discrepancy is ignored.

Since the goldfish experiments contained both a temporal and spatial uncertainty factor, corrective field factors have already been applied. To raise the threshold to the 0·95 probability level it must be multiplied by 1·96 (Table 1) to get a corrected threshold $_{P=0·95)}$ of 0·098 and an underwater sighting range $\frac{2·32}{a}$ m.

The fresh water used in the experiments had a spectral volume transmission of 67 per cent/m at 534 mμ; the spectral volume attenuation coefficient is $a_{534}$=0·40. For the goldfish, horizontal sighting ranges of some 6 m would be expected for targets in the binocular field having a contrast 1·0 and an angular subtense greater than 100′ arc. Such a target might be a fat 17 cm black goldfish. Such sighting ranges may seem small when compared with the performance of a human swimmer (8·8 m for a 15′ target), but they are not. The exponential attenuation of contrast tends to minimize any range advantage

that might be gained by decreasing the target contrast threshold. The circumstance that threshold becomes asymptotic for targets above a certain size and that this threshold value for goldfish is very close to that for human means that only the smaller critical target-size gains an advantage for the human.

The critical angles of some other fishes are smaller than that of goldfish (TAMURA, 1957; and TAMURA and WISBY, 1963). All of those calculated are smaller than that of the goldfish. This difference would indicate that the critical angles for these fishes are also smaller than the critical angle of the goldfish. On the other hand, the goldfish data show that there is yet little reason to suppose that the contrast-enhancement mechanism postulated by BAYLOR and SHAW (1962) does exist in fishes. Therefore, even though the critical angle is smaller, the contrast threshold of the critical angle may well be the same for all fishes. As an example, the skipjack tuna, Katsuwonus pelamis, has a bar grating acuity of about 0·18 (NAKAMURA, 1968)—nearly four times better than the 0·05 single-point acuity of goldfish. Despite the higher resolution of this tuna's optical system, the contrast sensitivity at the critical angle most probably is close to that of the goldfish.

Underwater sighting ranges are much shorter than are the sighting ranges in air. For this reason most targets of interest—predators or navigational aids—will subtend large angles even at the limits of visibility. Smaller objects and food particles are of interest at closer ranges where again the angular subtense will be large. Although the resolution of the fish eye may show manifold differences among species, underwater sighting ranges for large objects (detection) probably are remarkably uniform.

## CONCLUSIONS

The goldfish data presented in this paper have implications that probably may be generalized to apply to visual performance in other fishes.

1. Contrast thresholds vary with fish size (lens dia.). The decrease in threshold with increase in size probably may be attributed to the density of the visual elements per unit area of retina, which decreases at a lesser rate than that predicted from the increase in area alone.

2. Contrast threshold is temperature dependent. Visual performance is best at some temperature intermediate between the lower and upper lethal temperatures. For the goldfish this temperature coincides with the temperature of maximum spontaneous activity.

3. Contrast threshold varies with the position of the target in the visual field (retinal position of the image). Threshold is lowest in the binocular field, which is attributed to the increase in probability of detection for binocular vision (binocular threshold is 67 per cent of monocular threshold). For targets in the monocular field thresholds are lower for areas of higher retinal cone density.

4. Contrast threshold varies with target size and the adaptive state of the eye. Targets smaller than a certain critical size are related to contrast in a manner indicative of complete retinal summation. For the dark-adapted eye complete summation is indicated even for targets larger than 200' of arc. No evidence was found to indicate a special contrast-enhancement mechanism in fishes.

5. The light-adapted goldfish eye has a critical angle (the angular target diameter greater than which contrast threshold does not decrease) of 100'. The critical angle contrast threshold is 0·05, a useful value for calculating underwater sighting ranges. The precision of the experimental determinations of critical angle threshold and binocular contrast thresholds for other target diameters and other adaptive levels are sufficient to permit

the calculation of correction factors for detection levels other than the 0·50 probability level.

6. Acuity is a special case of contrast perception. Single-point acuity for the goldfish interpolated from the experimental data is 0·05 (corresponding to a minimum separable angle of 20′ of arc) for the light-adapted eye. Both acuity and contrast perception show the changes of decreasing adaptive levels characteristic of a duplex retina.

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**Abstract**—Contrast thresholds of the goldfish eye were determined by the method of constant stimuli using a yes-no conditioned cardiac-response. Computerized probit analysis was used to treat the data. Thresholds were determined for varying temperatures, target sizes, fish sizes, target positions and adaptive radiance levels. Positive contrast, circular targets were used throughout. Both target and adaptive radiance were monochromatic light. Threshold was found to decrease as fish size increased. This change was attributed to the density of cones which decline more slowly as the eye grows than is required to compensate for the calculated expansion of image area in the larger eye. Threshold was found to be temperature dependent, being lowest at 20°C. Threshold was found to vary with the position of the target image on the retina in general agreement with cone topography. Binocular thresholds were lower than monocular thresholds. The relation between target size and contrast threshold was studied at four adaptive levels from a photopic level of 85 $\mu$W/cm$^2$/$\omega$ to a near scotopic level of 0·07 $\mu$W/cm$^2$/$\omega$. The data were examined to determine critical visual angle and the region of complete summation. Single-point visual acuity for the goldfish was interpolated from the data. The use of contrast threshold data in underwater visibility

problems is discussed. No evidence was found to indicate a special contrast-enhancement mechanism in fishes.

**Résumé**—On détermine les seuils de contraste du poisson rouge par une méthode de stimuli constants utilisant une réponse cardiaque conditionnée oui-non. On traitait les données par une analyse électronique. On mesurait les seuils pour diverses températures, dimensions de tests, dimensions de poissons, positions des cibles et niveaux d'adaptation. On utilisait constamment un contraste positif et des tests circulaires. Des lumières monochromatiques étaient employées à la fois pour le test et pour l'adaptation. On trouve que le seuil baisse quand la taille du poisson augmente. On attribue ce changement à la densité des cônes qui, lorsque l'oeil grandit, diminue moins qu'il ne faut pour compenser l'agrandissement calculé de l'image dans l'oeil plus grand. Le seuil dépend de la température, avec un minimum à 20°C. Le seuil varie avec la position de l'image de la cible sur la rétine en accord avec la topographie des cônes. Les seuils binoculaires sont inférieurs aux monoculaires. On étudie la relation entre taille de la cible et seuil de contraste à quatre niveaux d'adaptation, depuis le niveau photopique de 85 $\mu$W/cm$^2$/$\omega$ jusqu'à un niveau presque scotopique de 0,07 $\mu$W/cm$^2$/$\omega$. On détermine avec ces résultats l'angle visuel critique et la région de sommation complète. On interpole à partir de ces données l'acuité visuelle du poisson rouge pour un seul point. On discute l'emploi des seuils de contraste dans les problèmes de visibilité dans l'eau. Aucune évidence n'indique de mécanisme spécial pour augmenter le contraste chez les poissons.

**Zusammenfassung**—Die Kontrastschwellen beim Goldfischauge wurden mittels der Methode des konstanten Reizes bestimmt, wobei eine konditionierte ja-nein-Antwort der Herztätigkeit verwendet wurde. Die Meßwerte wurden durch Probitanalyse mit einem Computer ausgewertet. Die Schwellen wurden für verschiedene Temperaturen, Testgrößen, Testlagen und Adaptationsniveaus bestimmt. Es wurden immer positiver Kontrast und ringförmige Testobjekte verwendet. Adaptations-und Testbeleuchtung waren monochromatisch. Die Schwellen nahmen ab, wenn die Fischgröße zunahm. Die Änderung wurde der Zapfendichte zugeschrieben, die bei wachsender Größe des Auges langsamer abnimmt als notwendig ist, um die berechnete Bildvergrößerung im vergrößerten Auge zu kompensieren. Die Schwelle erwies sich als temperaturabhängig; sie war am niedrigsten bei 20°C. Sie änderte sich auch in Übereinstimmung mit der Netzhauttopographie entsprechend der Lage des Bildes auf der Netzhaut. Die binokularen Schwellen waren niedriger als die monokularen. Der Zusammenhang zwischen Testgröße und Kontrastschwellen wurde für vier verschiedene Adaptationsniveaus, ausgehend von einem photopischen Niveau von 85 $\mu$W/cm$^2$/$\omega$ biz zu einem nahen skotopischen Niveau von 0,07 $\mu$W/cm$^2$/$\omega$, untersucht. Die Meßwerte wurden untersucht, um den kritischen Sehwinkel und den Bereich vollständiger Summation zu ermitteln. Aus den Meßwerten wurde die Punktsehschärfe des Goldfischs interpoliert. Die Verwendung von Kontrastschwellen bei Problemen über das Sehen unter Wasser wird diskutiert. Es konnte keine Hinweis auf einen speziellen Kontrast-Verstärkermechanismus bei Fischen gefunden werden.

**Резюме** — Были определены пороги различения контраста для глаза золотой рыбки методом постоянных раздражителей, с использованием условно-рефлекторной «да-нет» сердечной реакции. При оценке результатов был применен «пробит»-анализ с помощью счетно-решающего устройства. Пороги были определены: при разной температуре, разных величинах тестовых объектов, величинах рыб, положениях объектов и уровнях адаптивного облучения. Определялся всегда положительный контраст и объекты были круглыми. Как тестовые объекты, так и адаптивное облучение создавалось монохроматическим светом. Пороги уменьшались пропорционально увеличению размеров рыб. Эти изменения были связаны с плотностью колбочек, которая уменьшается медленнее, когда глаз растет, чем это нужно для компенсации высчитанного расширения области изображения в большем по размерам глазе. Было найдено, что пороги зависят от температуры, они минимальны при 20$^0$С. Найдено, что пороги изменяются с изменением положения изображения объекта на сетчатке, в общем в согласии с топографией колбочек. Бинокулярные пороги были меньше, чем монокулярные. Соотношение между величиной объекта и пороговым контрастом было изучено на четырех адаптивных уровнях, начиная от фотопического уровня (85 μW/cm$^2$/ω) и до уровня близкого к скотопическому

(0,07 $\mu$W/cm$^2$/$\omega$). Данные были просмотрены с целью определения ·критического угла зрения и области полной суммации. Отдельные показатели остроты зрения золотой рыбки были интерполированы на основании полученных фактических данных. Обсуждается вопрос об использовании данных о контрастных порогах в проблеме видности под водой. Не было найдено доказательств того, что у рыб имеется специальный механизм усиливающий контраст.