THRESHOLD INTENSITY OF ILLUMINATION AND FLICKER FREQUENCY FOR THE EYE OF THE SUN-FISH

By ERNST WOLF and GERTRUD ZERRAHN-WOLF

(*From the Biological Laboratories, Harvard University, Cambridge*)

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I

Light which is interrupted with sufficiently high frequency appears continuous to the human eye. If at a given illumination the frequency of flashes is gradually decreased, the light impressions begin to be perceived separately at a certain flicker frequency. We therefore have the possibility of examining the relation between critical flicker frequency and illumination.

A large body of work has been done to determine critical flicker frequencies in relation to illumination for the human eye. In a recent series of papers (Hecht, Shlaer, and Verrijp, 1933–34) a complete account of the facts has been given. With organisms other than man, critical flicker frequencies have been determined for the eye of the dragon fly larvae (Sälzle, 1932) and of the bee (Wolf, 1933–34). In both cases a reflex motion was used for the determination of threshold reaction at critical illumination. Since the method applied to the study of these two organisms is intrinsically different from the one used for the study of the human eye, an effort was made to use a similar reflex method for the study of an eye which is anatomically more similar to the human eye than that of the arthropods mentioned. For test object the sun-fish *Lepomis* was chosen.

II

If a *Lepomis* is placed in a glass tank surrounded by a system of alternating opaque and translucent stripes it will react with a movement of its body to a displacement of the stripe system. The fish's reaction consists in a motion in the direction of the stripe movement.

Lyon (1904) proved that the response of the fish is a reaction to seen movement. Grundfest (1931–32*a*, *b*) made use of this reaction in fishes for the study of sensitivity to spectral lights. He found that *Lepomis* was particularly definite in its response. Since a good deal of information was secured by Grundfest's experiments, *Lepomis* was used for the study of critical flicker frequencies.

For observation a fish is placed in a cylindrical glass jar which stands on a glass-topped table (Fig. 1). The jar containing the fish is surrounded by a glass cylinder on which black opaque paper stripes are pasted, leaving translucent spaces of equal width between them. The striped screen is mounted on an axle which runs in brass bearings and can be driven by a motor at various speeds. To make a

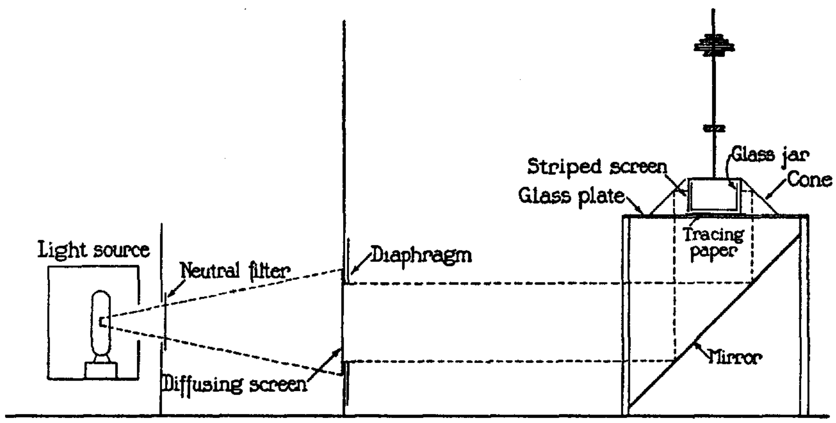

FIG. 1. Diagram of apparatus for measuring threshold intensity of illumination at different flicker frequencies for the eye of the sun-fish.

certain number of stripes pass in front of the fish's eye to produce a constant flicker frequency, two methods are employed. First, the velocity of rotation of the screen can be varied by adjusting a rheostat controlling the voltage of the motor and by changing pulleys in the transmission system. The second way of changing flicker frequencies consists in the use of different striped screens. There are three screens available with 10, 20, and 40 stripes each. The cylinders with a greater number of narrower stripes will give a higher flicker frequency with a slow speed of rotation. Since the quietness of motion is essential for the precise judgment of threshold reaction, efforts were made to keep the number of revolutions of the screen always as low as possible.

The striped screen is viewed by the fish against a white reflecting surface. This is a hollow 45° cone made of sheet metal and painted with zinc oxide. The cone is illuminated from underneath. The light comes from a source (500 watt concentrated filament lamp) which can be placed at different distances on an optical bench. For experimentation three fixed positions of the source were chosen from the diffusing screen (*D*) at the end of the optical bench. Behind this screen there is placed a diaphragm which controls the area of the radiating surface of the diffusing screen. The light then falls on a mirror which is inclined at an angle of 45° and reflects through the glass top of the table on to the reflecting cone. The light intensities falling on the eye of the fish are measured by means of a Macbeth illuminometer. By means of the diaphragm and the different distances of the source from the diffusing screen the brightness can be varied over 4 logarithmic units. For each position of the light source, and for the different diaphragm openings, calibration curves are plotted from which during experimentation the intensity values for a given diaphragm opening can be read with sufficient accuracy. The intensity range thus secured is not large enough to determine a complete flicker curve for the eye of *Lepomis*. For higher intensities which were desirable we had to use a 1000 watt lamp instead of the 500, and in some cases we had to use an additional source consisting of another 1000 watt lamp which was placed at a slight angle to the optical axis. This source then was kept constant and the one on the optical rail varied. By these means we were able to secure brightnesses sufficiently high to cause the fish to react at flicker frequencies as high as 50 per second. For intensities lower than the ones which could be obtained with the 500 watt lamp at the far end of the optical bench and by the diaphragm, we used another source consisting of a 100 watt bulb at a fixed position and placed in front of it Eastman Kodak "neutral" filters of different transmissions. The neutral filters were calibrated with a Martens polarization photometer. First a 1/10 filter was calibrated, then, keeping the 1/10 filter in place, a 1/100 filter is put into the path of the other beam of the photometer. The difference between the two is then about 1/10, which can be read with the necessary accuracy on the scale of the photometer head. In the same way a 1/1000 filter is calibrated against the 1/100 and finally a 1/10,000 filter against the 1/1000. For each filter in the light path a calibration curve for the diaphragm is plotted. The intensity range is thus extended over another 4 logarithmic units so that a total range of 9 logarithmic units can be covered.

For experimentation we selected 12 animals which gave rather precise reactions to moving stripes. These were among a great number of individuals which we obtained from the Boston city aquarium. The 12 selected animals were kept in separate glass jars. For tests they were transferred into culture dishes 10 cm. in diameter and 5 cm. in height. Each dish was filled with 250 cc. of clean tap water which was at room temperature before the fish were put into it.

Before experimentation the fish were kept in darkness for at least 2 hours, to secure a sufficient degree of dark adaptation. The first animal then is placed on the glass top of the table and left in the dark for a short time so as to avoid any interference with our first reading by the shock produced by the transportation. Then the stripe system is set into motion at a certain flicker speed, which was previously fixed. The light is turned on while the diaphragm is completely closed. By means of a gear transmission the observer is able to open the diaphragm slowly while watching the animal. As soon as a small amount of light strikes the fish it shows a slight "shock reaction" by moving backward; it then stays quiet. This "shock response" is certainly not due to the flicker, since it can also be obtained with the stripes quiet. The fish's reaction to the moving stripes at threshold intensity consists in a sudden motion of the body in the direction in which the stripes are moving. For this threshold reaction the reading of the scale of the diaphragm is noted down which later on can be translated into the corresponding light intensity. At low flicker frequencies, *i.e.* 3 to 10 stripes per second passing in front of the fish's eye, the animal usually follows the stripes. It often stays right in the middle of the tank and turns around like a galvanometer needle keeping the same stripes in its field of vision. At speeds up to 15 or 20 flickers per second the fish stays to the wall of the glass jar and moves in circles. If the flicker frequency is above 20 per second the reaction mostly consists after a short forward motion, in swimming backward. This backward motion becomes faster with increasing flicker frequency. It therefore seems as if the fish moves in such a way as to make the flicker disappear by moving just fast enough against the motion of the stripes so that the visual field looks as if it was evenly illuminated.

Even while the kind of reaction can be quite different in nature the threshold illumination for initiation of response can be determined with accuracy. We usually took three successive readings with each fish at a given flicker frequency. Such a set of successive measurements gives approximately the same reading in each case. For each flicker frequency our 12 animals were tested and the threshold intensities for response recorded. The intensity values obtained for the whole group agree among each other fairly well. The animals are of the same species and of one strain. It therefore seemed justifiable to treat the data *en masse* for plotting a flicker curve for the eye of *Lepomis*.

III

The data for critical flicker frequency for the eye of the sun-fish are presented in Fig. 2, where we plot critical flicker frequencies against the logarithms of threshold intensities. The points of the curve are mean values of the observations taken on our 12 animals. It is at once apparent that the curve is made up of two distinct parts. For flicker frequencies between 3 and 10 flickers per second the slope of the central part of the curve is 1.3. Above flickers of 10 per second the curve takes a different slope up to about 43 flickers per second. The slope of this part is 16.8. Above 45 flickers the curve shows a bend to the right and comes to a maximum level a little above 50 flickers per second.

The two distinct parts of the curve indicate that we meet in the eye of the fish a dual visual system. The lower portion of the curve represents the function of the rods up to intensities a little above 1/100 millilambert. At higher intensities the cones come into play.

If we attempt to compare the flicker data for the fish's eye with those obtained for the human eye (Hecht, Shlaer, and Verrijp, 1933–34) we have to take three points into consideration.

1. The intensity range covered by the fish is considerably greater for the rod section of the curve than for man. The fish will react to the

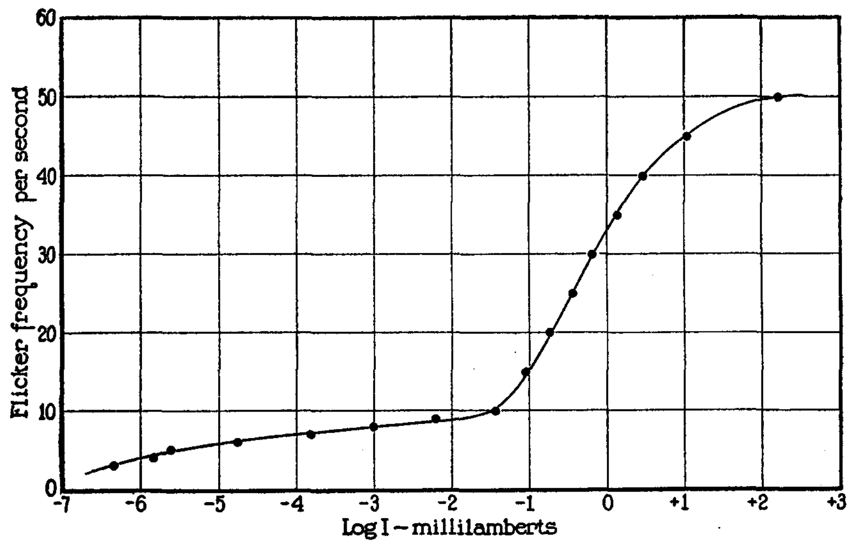

FIG. 2. Relation between critical flicker frequency and illumination for the eye of the sun-fish. The points represent mean values of threshold intensities for 12 fish tested at different flicker frequency.

moving stripes at intensities which are lower than necessary for the human eye to recognize flicker at all. The curve for the fish extends so far that at the very lowest intensities it is hardly possible to see the fish or to decide whether the fish was reacting to the flicker even before the light intensity was sufficient for the observer to see the fish. The fish is certainly capable of recognizing flicker at intensities 2 logarithmic units below that required for man.

The slopes of the rod sections of the curve for the human eye and for the fish are quite different and are hard to compare. The human curve shows a plateau in that section which covers about 3.25 logarithmic units, whereas the curve for *Lepomis* shows a steady rise. Hecht, Shlaer, and Verrijp (1933–34) have given a slope value between 4.5 and 5 for the rod part of the human eye; for the fish it is 1.3.

2. The transition from rod to cone vision occurs for the human eye at about -2.5 of the log I scale[1] and at a flicker frequency between 9 and 10. For *Lepomis* the transition occurs at the same intensity and at the same flicker frequency.

3. For white light the cone sections of the human and the fish curves are quite different in slope. For the human eye the values average around 11, whereas for the fish we find a slope of 16.8. The maximum flicker frequency which can be perceived by the human eye varies between 45 and 53 per second. The maximum for *Lepomis* is very similar. Some of the animals will not give a clear response at 50 flickers per second, some will still react at frequencies slightly over 50. It has to be stated, however, that the response at illuminations higher than 100 millilamberts is not as clear as at lower intensities. It seems therefore probable that very bright illuminations might have some injurious effect which prevents proper reaction. For the human eye there is found a drop in flicker frequencies at intensities close to 1000 and over 1000 photons. With our present experimental arrangement we are not able to obtain light intensities as high as those used for investigations on the human eye. We therefore are not able to state at present whether the same drop in critical flicker frequencies could be found at very high intensities for *Lepomis*.

It remains to compare the flicker curve for *Lepomis* with that for the bee (Wolf, 1933–34), since for both organisms the same kind of reaction to moving stripes was taken for the determination of threshold reaction. The flicker curve for the bee is quite different, in two respects. First, the slope of the curve is very steep over the middle range; second, there is no evidence for the presence of a dual visual system. We might deduce from these facts that the ommatidial mosaic of the bee's eye is not divided into two distinct groups of

[1] Hecht's measurements are given in photons. On converting his intensity values into millilamberts the change is found to be insignificant for the purposes of this comparison.

receptors of which one is acting in dim light, like the rods, and the other in bright light, like the cones. We probably meet only one system of receptor elements which covers the whole visual range.

The relationship between threshold light intensities and flicker frequencies suggests that there exists a connection between the effect produced during each period of excitation by light and the duration of the dark period within each complete flicker cycle. Reaction to flicker ceases at the moment when, at a given intensity of illumination, the duration of the light and the dark periods becomes shorter than necessary to unbalance the photochemical receptor system, which would cause a response. At this instant we encounter a steady state condition in which during exposure to light the amount of photolytic products required to initiate an impulse, is below threshold concentration, and where during the dark period the time is shorter than necessary to rebuild a sufficient amount of photosensitive material which could be acted upon by the next flash of light. For the stationary state condition a photochemical equation has been derived. If we attempt to fit the flicker data for *Lepomis* to the stationary state equation we obtain a very good fit for the rod part of the curve, and also for the cone part. Since the general theory of stimulation by intermittent light has been discussed recently in a number of papers (Hecht and Wolf, 1931–32; Hecht, Shlaer, and Verrijp, 1933–34) it is not necessary to give a theoretical interpretation of the flicker data secured with *Lepomis*.

SUMMARY

The sun-fish *Lepomis* responds to a moving system of stripes by a motion of its body. By changing the velocity of motion of the stripe system different flicker frequencies can be produced and thus the relation of flicker frequency to critical intensity of illumination can be studied. Threshold illumination varies with flicker frequency in such a way that with increasing flicker frequency the intensity of illumination must be increased to produce a threshold response in the fish.

The curve of critical illumination as a function of frequency is made up of two distinct parts. For an intensity range below 0.04 millilambert and flicker frequencies below 10 per second, the rods are in function. For higher intensities and flicker frequencies above 10,

the cones come into play. The maximum frequency of flicker which can be perceived by the fish's eye is slightly above 50 per second.

The flicker curve for the eye of *Lepomis* can easily be compared with that for the human eye. The extent of the curve for the fish is greater at low illuminations, the fish being capable of distinguishing flicker at illuminations lower than can the human eye. The transition of rod vision to cone vision occurs for the fish and for the human eye at the same intensity and flicker frequency. The maximum frequency of flicker which can be perceived is for both about the same.

CITATIONS

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