haves similarly (R. B. Huey and T. P. Webster, in preparation). B. Lister (in preparation) has found comparable situations in *A. sagrei* on Great Abaco Island, Bahamas, and *A. monensis* on Mona Island, Puerto Rico.
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17 September 1973; revised 17 December 1973 ■

Temporal Summation of Light by a Vertebrate Visual Receptor

Abstract. *Using aspartate to isolate mass receptor activity, we have investigated the reciprocity of flash intensity and flash duration in determining the response of the frog's cone receptor. The durations over which reciprocity holds decrease with increases in either flash energy or ambient light intensity. These findings parallel those of human psychophysical experiments.*

In 1885 Bloch suggested that the visual effect of brief flashes of light is determined by the total quantity (flash intensity × flash duration) of light (*1*). There followed an unusually large number of psychophysical studies confirming what became known as Bloch's law (*2*). It states that for flash durations up to some critical duration, the visual system responds equally to flashes of equal energy. As flash duration is further increased this reciprocity of intensity and duration decreases until the visual response is determined solely by flash intensity. It has also been shown that critical duration is dependent upon a number of factors including ambient light intensity and response measure (*3, 4*). Data from electrophysiological studies (*5*) with a variety of different animals and response measures also exhibit these relations.

While the extent of the reciprocity of intensity and duration, sometimes called temporal summation, has been measured at various levels in the visual system, a direct measure of temporal summation has not been made for any vertebrate photoreceptor. Using aspartate to isolate mass receptor activity, we have measured the extent of this reciprocity for the frog's 580-nm cones. The magnitude of the critical duration and how it is affected by light adaptation and response measure are comparable to the results from human psychophysics and animal electrophysiological recordings. This suggests that perhaps some of the temporal phenomena observed in human psychophysical studies are determined by receptor characteristics.

Gross extracellular receptor potentials, isolated with aspartate, were recorded from isolated frog (*Rana pipiens*) retinas. The details of the preparation, the optical system, and the recording apparatus have been presented previously (*6*). Aspartate isolates the receptor response of the electroretinogram (ERG) by blocking postsynaptic activity and thus eliminating the other components of the ERG (*7*). This allows the recording of receptor potentials with conventional gross electrodes.

To record cone responses, a 5-minute adapting light was used to bleach about 90 percent of the rod pigment, rhodopsin (*8*). The retina was then dark-adapted for 50 minutes. The rod pigment does not regenerate in the isolated retina (*9*), but 90 percent of the cone pigment does (*10*), and the cone receptor threshold returns to within 0.16 log unit of its prebleach sensitivity (*6*). In this state, the cones containing a visual pigment absorbing maximally at 580 nm (580 cones) have been shown to control the response to 630-nm light. In fact, they are over 1.5 log units more sensitive to a 50-msec, 630-nm flash than any of the other frog receptors, including the rhodopsin-containing rods (*8*). All the responses recorded in this study were from the 580 cones.

Figure 1 shows polygraph records of cone responses. All stimulus presentations for each column were of equal energy (that is, as duration was increased the intensity was decreased such that energy was held constant). The stimulus energy for columns 2 and 3 was 0.6 log unit higher than for column 1. For column 3, a background was added which decreased the peak amplitude to the 20-msec stimulus of column 2 to the amplitude of column 1. The X's under the responses give the peak amplitude and latency for the response to the 20-msec flash for that column. In all three columns, the peak response amplitude is approximately the same for equal-energy 20- and 40-msec flashes. However, for successive stimulus durations within each column, the peak response amplitude decreases while the latency increases. This implies that as the duration is increased, the light energy is not as effective, as measured by the peak amplitude. Compare the responses to the 20- and 80-msec flashes across columns. In column 1, the peak for the 80-msec flash is the same as that for the 20-msec flash. In column 2, it is 90 percent, and in column 3 it is 76 percent. Thus,

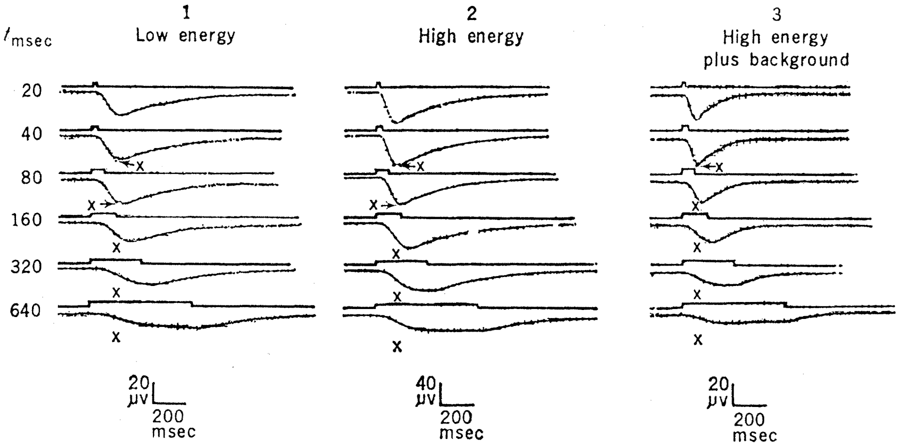

Fig. 1. Polygraph records of cone responses to equal-energy, 630-nm flashes. The stimulus energy for columns 2 and 3 was 0.6 log unit higher than for column 1 (*19*). The flashes of column 3 were presented as increments upon a steady, 501-nm background. The bandpass was d-c to 100 hertz.

raising the flash energy (between columns 1 and 2) or adding a background (as in column 3) decreases the amount of summation during the 80-msec flash.

To get a more detailed and a quantitative description of temporal summation for the cones, we determined the intensity necessary to evoke a response of a constant peak amplitude (10 or 60 μv) for the durations used in Fig. 1. This procedure was repeated for both dark-adapted and light-adapted (501-nm background) conditions. Figure 2 gives the results on a log intensity (I) versus log time (t) plot. Consider the data for the dark-adapted 10-μv condition (bottom curve). The points for 20, 40, and 80 msec are well fitted by a line with a slope of -1. Thus at these durations, a constant amount of light energy evokes the same peak amplitude. At 320 msec, the data point clearly falls above the diagonal line. Since an increased amount of total energy ($I \times t$) is needed to evoke the 10-μv response at this duration, the critical duration has occurred by 320 msec. However, the threshold at this duration is lower than for the 160-msec flash. This indicates that while the energy in the last 160 msec of the 320-msec flash is not as effective as the energy in the first 160 msec, some of the energy in the last 160 msec does have an effect in determining the peak amplitude. This is known as partial summation. For the 640-msec flash the intensity necessary for the 10-μv response is essentially the same as that for the 320-msec flash. Therefore, the light during the additional 320 msec does not affect the peak amplitude. That is, no further summation is taking place and the data points fall along a horizontal line. Compare this curve with the filled triangles, representing the 60-μv dark-adapted condition. The two curves have the same general shape, but the 60-μv curve shows less summation. One way of making a quantitative comparison between such curves is to find the intersection of the diagonal and the horizontal lines. Besides being easy to compute, the intersection method gives a combined measure of both partial and complete summation. The intersections are 186 and 108 msec for the 10- and 60-μv dark-adapted conditions. The curves for the 10- and 60-μv light-adapted conditions again show the same general shape, but the intersection values are 137 and 73 msec. Thus, increasing either criterion amplitude or background intensity decreases temporal summation.

When a constant peak amplitude is used as the criterion response, the frog's 580 cones show substantial temporal summation. This summation decreases with increased background intensity and criterion amplitude. These findings are quite similar to those of human psychophysical experiments in which constant detectability or brightness is used as the criterion response. For example, the critical duration for detection by the dark-adapted human cone system is between 100 and 200 msec (*11*), and this decreases to below 10 msec as the background intensity is increased (*3*). Also, for flashes which are suprathreshold, as the criterion brightness is increased the critical duration decreases (*4, 12*).

It is important to note that although the cones' peak amplitude may be constant for short flashes of equal energy, the response waveforms are not identical. For example, the responses to 20 and 40 msec in Fig. 1 (column 1) have the same peak amplitude but different response shapes. Interestingly, Zacks (*13*) has shown that humans can discriminate between two equal energy flashes that are equally detectable, even when each is shorter than critical duration. One difference between the cone receptor response to 20- and 40-msec flashes of equal energy is the longer latency to peak of the response to a 40-msec flash (a difference of 12 msec in column 1). If the intensity is increased, as it was for the 40-msec flash in column 2 of Fig. 1, then the slope of the leading edge of the response becomes steeper. Thus to obtain a constant latency (for example, time to peak or a given criterion amplitude) to the 20- and 40-msec flashes in any column, the intensity of the 40-msec flash would need to be increased. Therefore, had we used a constant latency as the criterion response, then the critical duration, if it could be measured, would have been much shorter than that found in Fig. 2. This offers a possible explanation for the psychophysical observation that the critical duration for a constant human reaction time is considerably shorter than for a constant detectability (*14*).

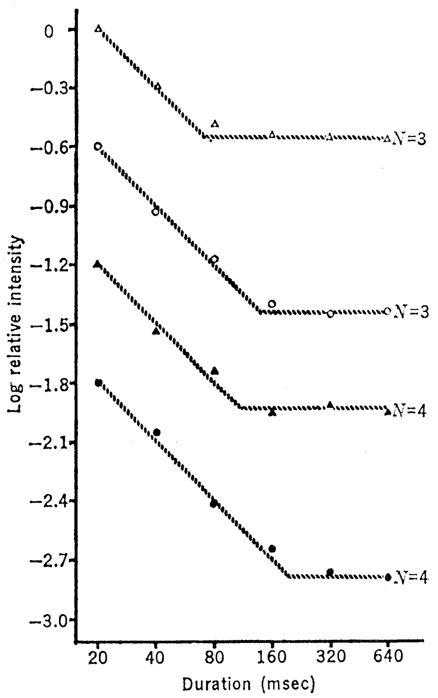

Fig. 2. Log relative intensity necessary for a constant peak response amplitude as a function of stimulus duration (axis logged). The diagonal lines have a slope of −1.0 and are loci of equal-energy flashes. The horizontal lines are loci of equal-intensity flashes. Two criteria of peak amplitude were used: 60 μv (△, ▲) and 10 μv (○, ●). The difference in intensities necessary to evoke these criterion reponses was approximately 1 log unit (at 20 msec). Closed symbols represent data from dark-adapted preparations, and open symbols, data from light-adapted (steady, 501-nm background) preparations. The background light raised the intensity necessary to evoke the criterion responses an additional log unit (at 20 msec). Curves have been shifted vertically for clarity. N on the figure refers to the number of preparations averaged in each curve.

At least three psychophysical findings have no counterpart in our recordings: (i) (brightness enhancement), long-duration flashes of suprathreshold intensity are sometimes reported as appearing dimmer than shorter-duration flashes of equal intensity (*4, 12, 15*); (ii) critical duration has been shown to decrease as the area of stimulation is increased (*16*); and (iii) temporal summation can be demonstrated for two successive flashes presented to different parts of the retina (*17*). If present in the frog's cones the equivalent of brightness enhancement should have shown up in our recordings. However, we have no possible counterpart for the last two findings (*18*). On the other hand, the similarities between our data and those of human psychophysical experiments suggest that the temporal characteristics of the receptor response may well be a main determinant of the temporal summation of the visual system.

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20. Supported in part by NIH grant MM-19322 and a grant from the Institutional Scientific Research Pool of Columbia University. We thank Drs. N. Graham and B. Schneider for their helpful comments and Dr. E. Galanter for making available the facilities of his laboratory, which are supported in part by a contract with the Office of Naval Research.

12 November 1973

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Learning by Following a Food Source

Abstract. *Hungry pigeons first learned to eat grain from the experimenter's hand. When the hand approached and "pecked" a small disk to produce grain in a food hopper, the pigeons followed the hand and rapidly learned to peck the disk. Birds given operant conditioning training took significantly longer to learn the same response. Under natural conditions, young animals may learn to behave like their parents simply by following parental sources of food.*

Although some behaviors are transmitted from one generation to the next by genetic mechanisms, others, acquired during the lifetime of the parents, must be transmitted differently. In the research described here, we examined a simple, but possibly important, means by which learned behaviors are transmitted. Young animals follow their parents—notably during weaning, after imprinting, or when part of a social group (*1*). However, there have been few experimental studies of what and how the young learn by following. Church (*2*) showed that rats learned to approach food in the lighted arm of a maze by following previously taught leader rats. Galef and Clark (*3*) showed that a learned preference for one of two food sources was transmitted from adult rats to pups; the pups learned by following their parents to the preferred source. Galef and others suggest that rats may be subject to peculiar selective pressures because of human attempts to eradicate colonies of wild rats through poisoning. Rats may have evolved the learning-through-following mechanism, thereby avoiding poisoned foods. In this present research, we extend the Church and Galef demonstrations by showing that members of a different species, pigeons, rapidly learned an operant response, pecking a disk, by following an arbitrary source of food, grain held in a human hand. Learning through following is not specific to rats in the presence of conspecifics, nor specific to a given type of response or mode of feeding. "Following" may be a general means by which some behaviors are socially transmitted from one organism to another.

Twenty experimentally naive White Carneaux pigeons, 2 months old at the start, were maintained at approximately 85 percent of their normal body weights The experimental chamber, a box 76 by 51 by 36 cm, had an opening of 31 by 11 cm to permit the experimenter's hand to move freely within it. The front wall contained a Gerbrands response disk and a hopper in which mixed grain could be presented. The response disk was similar in color to the surrounding metal panel and was never transilluminated. Two overhead white 7-watt bulbs provided continuous illumination of the chamber, and four overhead red 7-watt bulbs served as a stimulus signal.

In the first of four experimental conditions, five pigeons were taught to eat grain from the experimenter's hand and to follow the hand about the chamber. When red stimulus lights then flashed, the hand slowly moved to the disk and "pecked" it, thereby causing grain to appear in the hopper. The main question was whether the pigeons would learn to peck the disk. This method of training was then compared with three control conditions.

For the first 7 days in condition 1, each pigeon was fed mixed grain in its living cubicle from a small cup, about 3.8 cm in diameter and 3.8 cm high, held in the experimenter's hand. Then, during nine sessions in the experimental chamber, each bird learned to follow and eat grain from the handheld cup. Sessions averaged 18 minutes, during which the birds each ate about 12 g of grain. The experimenter intermittently covered the cup with her palm so that during the last few sessions grain was accessible for only a few seconds; nevertheless, all pigeons followed the hand through most of each session.

After these preliminary sessions of following a food source, training to peck the disk was begun. At the start of the first session, the hopper was operated until the bird ate for 10 seconds; at the beginning of all subsequent sessions the bird was permitted to eat grain in the handheld cup for 10 seconds. During the remainder of each session, the cup was covered by the experimenter's palm so that the grain could not be seen. The experimenter occasionally "pecked" at grain in the cup with her index finger to maintain the bird's attention but covered the cup before the bird could eat. The procedure consisted of S+ trials with red lights flashing (1.5 flashes per