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EARLY LIGHT AND DARK ADAPTATION IN FROG ON-OFF RETINAL GANGLION CELLS[1]

JAMES GORDON[2] and NORMA GRAHAM[3]

Rockefeller University, Hunter College, and Columbia University, New York, N.Y., U.S.A.

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INTRODUCTION

LIGHT and dark adaptation—the effect of the previous history of light stimulation on present responses—is being extensively studied in the vertebrate visual system (EASTER, 1968; CLELAND and ENROTH-CUGELL, 1968, 1970; DOWLING and RIPPS, 1970, 1971; BURKHARDT and BERNSTON, 1972, for example). Psychophysical results suggested that, in the human visual system at least, light and dark adaptation effects are not strictly monotonic with time when short time periods are involved. Psychophysical thresholds do not continuously increase as time in the light is increased nor continuously decrease as time in the dark is increased. Rather, at times near the onset or offset of an adapting light (early light or early dark adaptation) the threshold for a test stimulus is elevated even further than it is during a very long exposure to a steady-state adapting light (CRAWFORD, 1947; BAKER, 1963). To find out whether such early light and dark adaptation effects exist in a vertebrate retina, "transient *on–off*" cells in the frog retina were studied using brief test flashes presented at various times with respect to longer adapting flashes. It seemed likely that the study of early light and dark adaptation would also be useful in understanding the mechanisms that produce transient *on* and *off* responses.

METHODS

The frog (*Rana pipiens*) eye cup preparation was used in these experiments. A light adapted frog was decapitated, the jaw removed, and the head bisected down the mid-line. The nictatating membrane and the skin around the eye were removed. The eye was hemisected in front of the ora serrata and the front half of the eye (cornea and lens) removed. The eye, still in its socket, was placed facing downwards on a paper towel for about five minutes to drain off most of the vitreous. The eye was then placed facing upwards in the apparatus on a bed of sea sand moistened with frog Ringer's. Pure O_2 which had been moistened by bubbling through distilled water was continuously circulated through the chamber containing the eye cup. Experiments were carried out at room temperature (about 20°C).

Electrical potentials from single retinal cells were isolated using 2 M NaCl filled micropipettes with a tip diameter of about 1 μ. It was possible to get excellent signal to noise ratios with these electrodes (at least 6:1 and often 20:1) although they presented difficulty in maintaining long-term recording from a single cell. The indifferent electrode was a chlorided silver wire inserted in the Ringer-moistened sea sand. The signals were amplified with a high impedance, low noise a.c. preamplifier; the high and low frequency cut-offs were set at 1000 Hz and 100 Hz, respectively. The amplified signals were displayed on a Tektronix 502A oscilloscope; the vertical output of the oscilloscope was recorded with a Sanborn F.M. tape-recorder. Electrical signals were also recorded, on other tape channels, which indicated the onset and offset of the stimuli. The tapes were played back through impulse height discriminators and analysed with a CDC 160A computer.

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[2] Department of Psychology, Hunter College, CUNY. Please send reprint requests to Dr. JAMES GORDON, Rockefeller University, New York, N.Y. 10021, U.S.A.

[3] Department of Psychology, Columbia University.

The optical system was a three channel projection system (HARTLINE and MCDONALD, 1947) in which an 18 A 6 V tungsten filament bulb was used as the source. The maximum field size in the system was 100 mm in dia. and this was optically reduced by 20:1 to form a maximum circular image in the retinal plane of 5 mm. There was little scattered light within the optical system; diffuse illumination across the retina due to stray light was over 3 log units dimmer than the stimulus image itself. Images from the channels were also formed on a screen so that the positions of the stimuli in each channel could be monitored. The intensity of each channel was controlled with a circular neutral density wedge and the duration of the stimuli was controlled with electromagnetic shutters which provided rise and fall times of less than 1 msec. A programmed timer was used to control the onset and offset times of the stimuli.

Single cells were isolated by slowly driving an electrode into the retina while a uniform full field stimulus (5 mm dia. on the retina) flashed on and off once per second. The criteria for specifying single-cell isolation were uniform impulse waveform, no overlapping of two impulses and uniform impulse height for impulses which were reasonably far apart in time. (When there was a burst of impulses it was common to observe a decrease in impulse height in succeeding impulses.)

In the frog retina impulse-producing cells show many response patterns (HARTLINE, 1938; MATURANA, LETTVIN, MCCULLOCH and PITTS, 1960; REUTER, 1969). The cells used in this study were those that showed transient responses containing approximately equal numbers of impulses at the onset and offset of the light; in general, the response at onset or offset contained fewer than 20 spikes and lasted less than 0·5 sec. These impulse-producing cells are probably retinal ganglion cells although there is some evidence that other cells in the frog retina produce impulses (KANEKO and HASHIMOTO, 1968).

Procedure. All experiments involved the presentation of two stimuli to the frog's eye: (1) an "adapting" stimulus which was illuminated for 10 sec out of every 20; and (2) a "test" stimulus which was illuminated for 0·1 sec once (or not at all) during each 20 sec on–off cycle of the adapting stimulus. In early light (dark) adaptation experiments, the onset of the test stimulus occurred 4 sec before the onset (offset) of the adapting stimulus, 4 sec after the onset (offset) of the adapting stimulus, or at various times within 0·4 sec of the onset (offset) of the adapting stimulus. The 10-sec on/10-sec off adapting cycle was chosen because 20 sec is usually long enough for the test stimulus on one cycle not to affect the responses during the next cycle. However, this occasionally was not the case, and cells showing longer-lasting effects were discarded from the present sample.

The two stimuli were always circular, although various sizes, locations, and relative illuminances of the two stimuli were used in order to explore the effect of these variables. See figures for exact values used. For a given cell, the sizes, location, and illuminances were always chosen so that a response to the test flash was elicited whenever its onset was at least 4·0 sec before or after the onset or offset of the adapting light.

RESULTS

Total responses

For the early light adaptation experiments, the total number of impulses occurring from six seconds before the onset of the adapting stimulus to seven seconds after the onset of the adapting stimulus were counted. This interval included the responses to both the test stimulus and the onset of the adapting stimulus. Similarly for the early dark adaptation experiments, the total number of impulses occurring from 6 sec before the offset of the adapting stimulus to 7 sec after the offset of the adapting stimulus was counted, thus including the responses to the test stimulus and to the offset of the adapting stimulus.

For most transient *on–off* cells, this "total response" depended on the time of the test stimulus onset. Examples of the total responses from four cells are plotted in Fig. 1 as a function of the time of onset of the test stimulus relative to the adapting stimulus onset (for

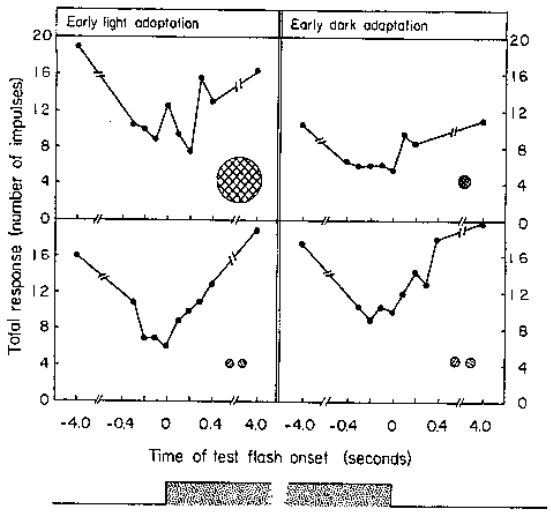

FIG. 1. Total responses as a function of time of test-stimulus onset. See text for complete definition of total response. The test stimulus was 100 msec long and the adapting stimulus was 10 sec long. For the early light adaptation results (left graphs), time zero is the time of the adapting flash onset; for the early dark adaptation results (right graphs), time zero is the time of the adapting flash offset. The time-course of the adapting flash is also indicated in the drawing at the bottom of the figure.

The spatial configuration of the stimuli is diagrammed in the lower right of each graph: A circle filled with diagonal lines from bottom left to top right designates an adapting stimulus; diagonal lines from top left to bottom right designate a test stimulus. Upper left: A (adapting stimulus) was 5 mm (in diameter on the retina) at 1·5 ft-c and T (test stimulus) was 5 mm at 18 ft-c, and there was no background illumination. Each point is the average of two presentations of the stimuli. Lower left: A was 0·1 mm at 5 ft-c, T was 0·1 mm at 18 ft-c, separated from A by 0·07 mm; A and T were superimposed on a background (5 mm in dia., illuminated constantly) of 0·2 ft-c. One stimulus presentation determined each point. Upper right: A was 0·25 mm at 13 ft-c, and T was 0·25 mm at 15 ft-c, and there was a background of 0·3 ft-c. Average of two stimulus presentations. Lower right: like lower left but average of two stimulus presentations.

early light adaptation experiments—left column) or to adapting stimulus offset (for early dark adaptation experiments—right column). The top row are results when the test stimulus was superimposed on the adapting stimulus, and the bottom row when the test stimulus was spatially separate from the adapting stimulus. (Sketches in the bottom right of each graph show the stimulus spatial configuration. Exact sizes and illuminances are given in the figure legends.) It is clear that the total response was greatest when the test stimulus occurred in the middle of the 10-sec adapting stimulus or in the middle of the 10-sec dark period. The total response was always smallest when the test stimulus occurred near the onset or offset of the adapting stimulus. Occasional transient *on–off* cells did not show this pattern. On inspection of these cells' records, one of two things always appeared: (1) there was no response to the adapting stimulus alone; or (2) there were late *off*-discharges or other "stray" impulses (impulses occurring more than a second after the test or adapting stimulus onset or offset) that were contributing a great deal of variability. If these stray impulses were avoided by counting only impulses within some small period of time after the test and adapting stimuli

onset and offset, these cells also displayed the decrease in response magnitude for test stimulus times near the adapting stimulus onset and offset.[4]

Response components

Impulse histograms for one series of records in an early light adaptation experiment are shown in Fig. 2. The time of the adapting stimulus is indicated by an arrow underneath each record and is also diagrammed at the bottom of the figure. The time of the test stimulus onset is indicated by a small square underneath each record and is also written to the left of each record. The total number of impulses in each of the records shown in this figure has already been plotted in Fig. 1, lower left.

When the test stimulus occurred well before (top record) or well after (bottom record) the onset of the adapting stimulus, there were two distinct bursts in the response to the test

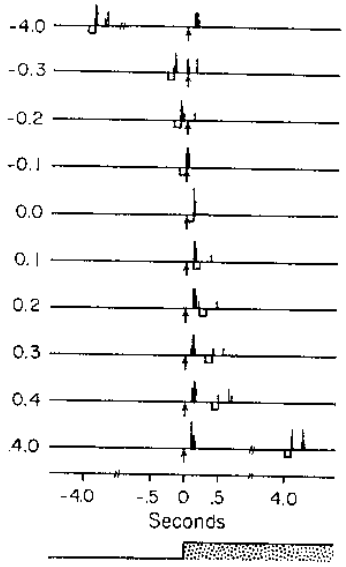

FIG. 2. Histograms for early light adaptation, showing responses to test stimuli (indicated by small squares underneath each histogram) occurring at various times with respect to the onset of the adapting stimulus (arrows underneath each histogram and drawing at bottom of figure). Each histogram is the response to one presentation of the stimuli and shows the number of impulses occurring within 20-msec time periods plotted against time. The shortest bar in the histogram represents one impulse occurring in a 20-msec period. Like Fig. 1 lower left for stimulus parameters.

stimulus (the first occurring between 0·08 and 0·15 sec after test stimulus onset and the second occurring between 0·24 and 0·31 sec after test stimulus onset), and there was one burst in the response to the adapting stimulus (occurring between 0·08 and 0·20 sec after

[4] Occasionally, cells other than these transient *on–off* cells were studied, in particular cells that responded with a longer and larger response (30 or more spikes lasting about 1 sec) at either onset or offset (but never at both). For these cells, the plots of total response against test stimulus onset time did not show any regularity such as that described here.

adapting stimulus onset). Notice what happens, however, when the test stimulus is presented 0·3 sec before the adapting stimulus onset (second record). Two bursts still occur after the onset of the test stimulus; these bursts have the same latencies after test stimulus onset and approximately the same number of impulses as did the bursts in the top and bottom records. However, the time period between 0·08 and 0·20 sec after the adapting stimulus onset contains only two impulses, instead of the seven or nine in the top and bottom records. Thus, what will be called the "adapting stimulus response component" appears to have been decreased or "inhibited" in the second record as compared to the top and bottom records, but the "test stimulus response component" appears full strength. Notice also what happens when the test stimulus is presented shortly after the adapting stimulus (the 0·4 record for example). Here the test stimulus response component contains only a few impulses rather than the nine or ten it contains in the bottom and top records. In short, it appears that whenever the stimuli are close together in time, the response component that is due to come second is decreased by the presence of the first response component. A similar series of impulse histograms from an early dark adaptation experiment is shown in Fig. 3. Again, a response component is decreased in magnitude whenever it occurs shortly after another response component.

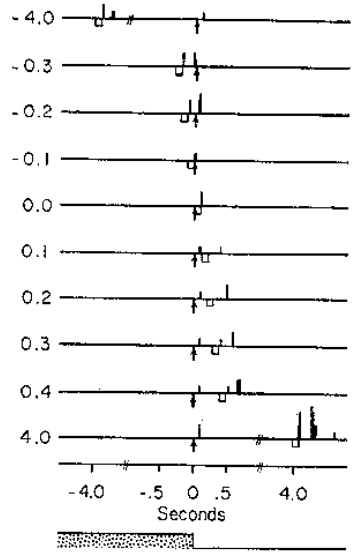

FIG. 3. Histograms for early dark adaptation. Conventions as in Fig. 2. The adapting stimulus was 5 mm in dia. at 0·15 ft-c, the test stimulus was 0·5 mm in dia. centered on the test stimulus and illuminated at 18 ft-c, and there was no background illumination.

To confirm this observation, plots of the number of impulses in each response component as a function of test-stimulus-onset-time are shown in Figs. 4 and 5. (The results from the histograms of Fig. 2 are plotted in the upper left of Fig. 5 and those from Fig. 3 enter into the averages shown in the lower right of Fig. 4.) As indicated in the above description, a response component is identified as those impulses occurring within certain intervals

of time after the test stimulus onset or after the adapting stimulus onset or offset. These time intervals are determined by the responses when the test and adapting stimulus onsets and offsets are well separated in time. Depending on the particular time intervals involved, there will be ambiguous impulses—impulses that might be said to belong to either the test or adapting response components, as, for example, the impulses in the 0·0 records of Figs. 2 and 3. These ambiguous impulses are shown in Figs. 4 and 5 as ×'s for completely ambiguous records. In cases where most of the impulses could be unambiguously assigned but some

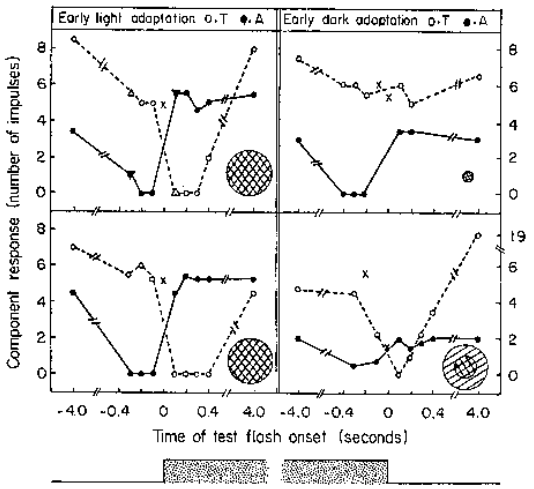

FIG. 4. Response components as a function of time of test stimulus onset when the test stimulus is superimposed on the adapting stimulus. See text for complete definitions of adapting response component (closed symbols) and test response component (open symbols). ×'s are plotted in cases where none of the impulses could be unambiguously assigned to either the test or adapt response components. Triangles are plotted in other ambiguous cases and point toward the "true values". That is, a triangle points up if the response component it represents could be said to contain either the number of impulses plotted or more and a triangle points down if the response component it represents could contain the number plotted or fewer. In such cases the sum of the number represented by the two triangles (one pointing up and one pointing down) is the total number of impulses. Thus the response component which comes earlier is always represented by a triangle pointing up and the response component which comes later by a triangle pointing down. This use of the triangles is tantamount to assigning all the ambiguous impulses to the later response component which tends to hide any decrease in the magnitude of the later response component. Other conventions as in Fig. 1.

Upper left: Like Fig. 1 upper left. Lower left: A was 5 mm at 0·5 ft-c, T was 5 mm at 1·8 ft-c, and there was no background illumination. Average of two stimulus presentations. Upper right: Like Fig. 1 upper right. Lower right: Like Fig. 3 but average of four stimulus presentations.

could not (as in the −0·2 record of Fig. 2 where the last impulse is ambiguous) triangles were used which point toward the "true" numbers; that is, a triangle points up if it represents the minimum number assignable to a component and points down if it represents the maximum number assignable. See Fig. 4 legend for other details.

In all the cells shown, and indeed in almost all the cells analyzed, there is clear evidence that the magnitude of whichever response component is due to come later is decreased when it closely follows the other response component This decrease or inhibition can be seen in

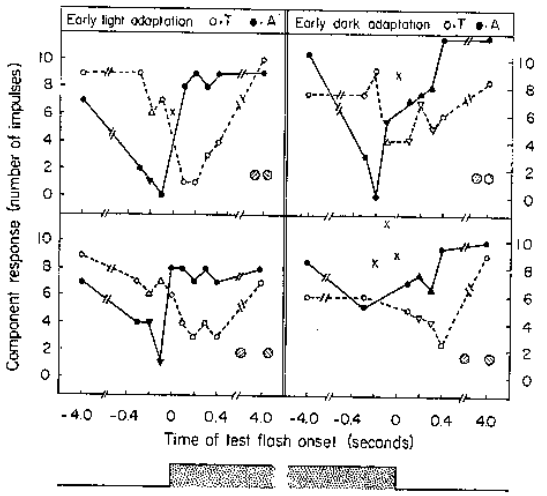

FIG. 5. Response components as a function of time of test stimulus onset when the test stimulus is not superimposed on the adapting stimulus. Conventions as in Fig. 4. Upper left: like Fig. 1 lower left. Lower left: A was 0·1 mm at 5 ft-c, T was 0·1 mm at 6 ft-c separated from A by 0·2 mm, and there was a background of 0·2 ft-c. One stimulus presentation determined each point. Upper right: like Fig. 1 lower right. Lower right: like lower left in this figure.

Figs. 4 and 5 as dips in the adapting stimulus curves (solid symbols) for some negative times (test stimulus onset before adapting stimulus event) and as dips in the test stimulus curves (open symbols) for some positive times (test stimulus onset after adapting stimulus event). These dips are seen to occur in the plots for both early light and dark adaptation although

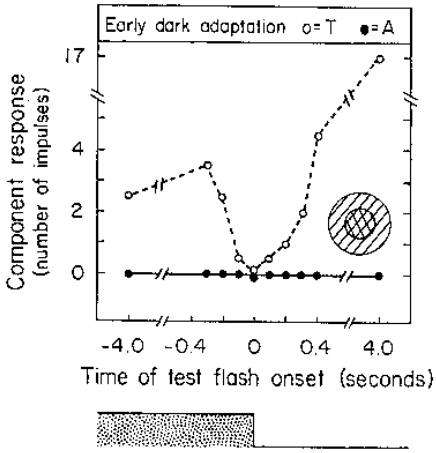

FIG. 6. Response components as a function of time of test stimulus onset in a case where there was no response to the adapting stimulus offset. Conventions as in Fig. 4. A was 5 mm at 0·05 ft-c, T was 0·5 mm at 1·8 ft-c centered on A, and there was no background illumination. Average of two stimulus presentations.

they are more clearcut and more likely to occur for both response components in the case of early light adaption. They also occur both for spatially superimposed stimuli (Fig. 4) and for spatially separate stimuli (Fig. 5). As can be seen in these figures, the duration of the dip varies. For some cells, the second response component is back up to almost full strength when it comes a few hundred msec after the first component; in other cells, the response component is completely inhibited for the entire 0·4-sec period studied here. Very occasionally summation of the test and adapting response components was seen when both components occurred at exactly the same time instead of one occurring slightly before the other. The results shown in Figs. 4 and 5 are representative of the cells studied except that the results for occasional cells (less than 10 per cent of sample) did not show any such dips.

The decrease or inhibition of the second response component when it follows shortly upon the first is not necessarily dependent on the existence of impulses in the first response component, at least not for early dark adaptation. In the experiment shown in Fig. 6 the adapting stimulus offset produced no impulses at all. Even so, the test stimulus elicited fewer impulses when the response to it occurred shortly after the adapting stimulus offset (test stimuli onsets from −0·1 to 0·2) than when its response occurred either before or long after the adapting stimulus offset. Although inhibition in the absence of impulses was never encountered during early light adaptation experiments, such an effect may only occur for a narrow range of stimulus intensities (high enough to produce inhibition but too low to elicit impulses) and thus may have been missed.

Thresholds

The question can be asked—how intense must the test flash be so that the total response to the combination of test and adapting stimuli contains just one impulse (or some other arbitrary number) more than the response to the adapting stimulus alone? This kind of

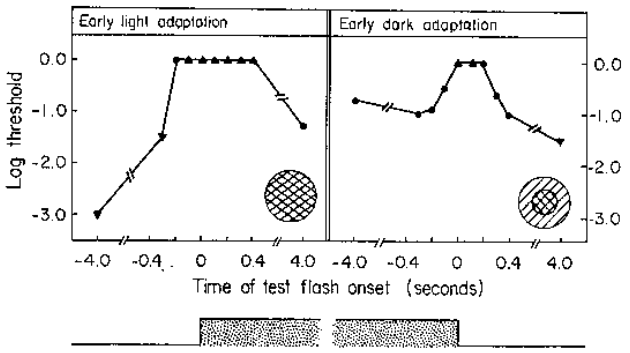

FIG. 7. Threshold as a function of time of test stimulus onset. Threshold is the test stimulus intensity such that the total response to both adapting and test stimuli was one impulse bigger than the response to the adapting stimulus alone. 0·0 on the log threshold scale represents 18 ft-c. A triangle pointing up indicates that the intensity it represents was the highest intensity used and the response was smaller than the criterion. A triangle pointing down indicates that the intensity it represents was the lowest used and the response was larger than the criterion. Other conventions as in Fig. 1.

Left: A was 5 mm at 1·5 ft-c, T was 5 mm, and there was no background illumination. There were two presentations of each intensity of test stimulus. Right: A was 5 mm at 0·15 ft-c, T was 0·5 mm centered on A, and there was no background illumination. There were four presentations of each intensity of test stimulus.

question is often asked, for example, in order to compare physiological results to certain psychophysical results. Unfortunately it is not always possible to answer that question unambiguously for this experiment. As the illuminance of a test flash is increased, the total number of impulses in the response might first increase and then decrease. There would then be two values of test stimulus intensity producing a given criterion response. For two cells in this study, however, experiments like those in Figs. 1–6 were run at a large number of test stimulus illuminances, and ambiguities caused by non-monotonic stimulus–response functions did not arise. For these two cells, "thresholds"—test stimulus illuminances such that the total response to both adapting and test stimuli was one impulse bigger than the response to the adapting stimulus alone—are plotted in Fig. 7. If there was no stimulus eliciting a response of exactly criterion magnitude but there were stimuli eliciting greater and smaller responses, the threshold was found by interpolation between the two stimuli that produced responses bracketing the criterion. In a number of cases, the test stimuli used were either too intense or not intense enough to produce a response of criterion magnitude. In these cases, triangles are plotted pointing toward the presumed thresholds. As is expected from Fig. 1, the threshold was elevated near the onset and offset of the adapting stimulus.

DISCUSSION

Responses of some cells in the frog retina (probably retinal ganglion cells) that discharge impulses at the onset and offset of long-duration illumination were studied using early light and dark adaptation paradigms. The total number of impulses in the response to the test and adapting stimuli was less when a 100-msec test stimulus was presented near the onset or offset of a 10-sec adapting stimulus than when the test stimulus was presented either in the middle of a 10-sec adapting stimulus or in the middle of a 10-sec dark period. This decrease in total response magnitude when the test stimulus was near the onset or offset of the adapting stimulus was the result of what will be called "post-excitation inhibition". Immediately following the response of a cell to one stimulus, there is a period of time during which the response to a second stimulus is decreased or completely inhibited. This is true for both transient *on* and transient *off* responses and is true whether the adapting and test stimuli illuminate the same retinal areas or illuminate close but separate areas.

Thus, the response of a frog transient *on–off* cell to test flashes near the onset or offset of an adapting light is quite different from the response to test flashes occurring several seconds or more away from any onset or offset. This time-dependency suggests that results from experiments on the goldfish and frog in which the adapting stimulus onset preceded the test stimulus onset by 0·5 sec or less (EASTER, 1968; BURKHARDT and BERNSTON, 1972) might well not be directly comparable to the results from experiments on the cat in which the adapting stimulus onset preceded the test stimulus onset by several seconds or more (CLELAND and ENROTH-CUGELL, 1968), even if the experiments had all been done on the same species.

Mechanisms for on–off cells

It is tempting to suggest that post-excitation inhibition represents the overshoot of a mechanism which cuts off long-lasting responses thereby producing transient *on* and *off* responses. It is not obvious, however, how to formulate this suggestion rigorously; in fact, one model which might be said to embody such an overshooting mechanism can be rejected.

NYE and NAKA (1971) suggested that a receptive field model like that of Rodieck and Stone (RODIECK and STONE, 1965a, 1965b; RODIECK, 1965) for the cat retinal ganglion cell would explain their results for frog retinal ganglion cells. In this model, the cell's response

is the sum of the responses from two separate mechanisms. The center mechanism is most sensitive to stimuli in the receptive field center, and the surround mechanism is sensitive not only to stimuli in the center of the receptive field but also to stimuli in the periphery of the field. Further, to account for the time course of the responses to stimuli in the center or periphery of the receptive field, it is assumed that the response of each mechanism is itself the sum of the responses from two sub-mechanisms—an excitatory mechanism (E) and an inhibitory mechanism (I). The time-courses of the responses of each mechanism to the onset and offset of a light are diagrammed in Fig. 8. The firing frequency of the ganglion cell is assumed proportional to the height above the zero line of the slow-potential responses shown in Fig. 8. (Thus, net inhibition which is shown as dips below the horizontal line will not be represented in the train of impulses discharged by the ganglion cell.)

As NYE and NAKA (1971) showed, this model will predict their results, which were somewhat similar to the early light adaptation results reported here. Further, in two studies of masking (where the test and adapting stimuli were both brief) in single neurons of the cat optic nerve and lateral geniculate nucleus, the time-courses of the responses were explained on the basis of antagonism between a center mechanism and a surround mechanism (SCHILLER, 1968; NAKAYAMA, 1968). Application of the model of Fig. 8 would probably predict the time-courses of those masking results well.

The "post-excitation inhibition" seen after *on* responses in the present experiments can also be predicted by the model of Fig. 8, as long as the stimulus producing the *on* response is assumed to be affecting both the center and surround mechanisms. This prediction can be seen in the bottom line of Fig. 8: Immediately after the *on* response there is a period of inhibition. However, this model cannot predict the inhibition that occurred after the *off* response in the early dark adaptation experiments. It predicts instead a period of inhibition before the *off* response, which was never seen in these experiments.

In a rather different model for *on–off* responses, the underlying slow potentials do not have transients at *on* and *off* but the mechanism for generating impulses from the slow potentials produces transients (proposed for goldfish retinal ganglion cells; BICKING, 1965). The adaptation or "depressive process" that is part of the postulated impulse-generating mechanism might well predict post-excitation inhibition after both *on* and *off* responses. However, in the model as it is now stated, such inhibition would depend on the occurrence of impulses and the observed inhibition does not (Fig. 6).

As the above discussion shows, although these experimental results showing post-excitation inhibition cannot uniquely specify a model for frog transient *on–off* cells, they do impose constraints on such a model.

Psychophysical analogy

If the threshold test stimulus intensity (the test intensity such that the total response to the test stimulus and adapting stimulus together contains just one more impulse than the response to the adapting stimulus alone) is plotted as a function of the relative time of the test stimulus onset (Fig. 7), the threshold is elevated near the times of the onset and offset of the adapting stimulus. A similar elevation is seen in plots of the psychophysical threshold for human observers (CRAWFORD, 1947; BAKER, 1963). Further, both for the physiological experiment described here and for the psychophysical experiments, the effect at adapting stimulus onset is more dramatic and more reliable than that at adapting stimulus offset (TELLER, 1971; TELLER, MATTER, PHILLIPS and ALEXANDER, 1971).

For a number of reasons, however, it is premature to identify the frog *on–off* retinal

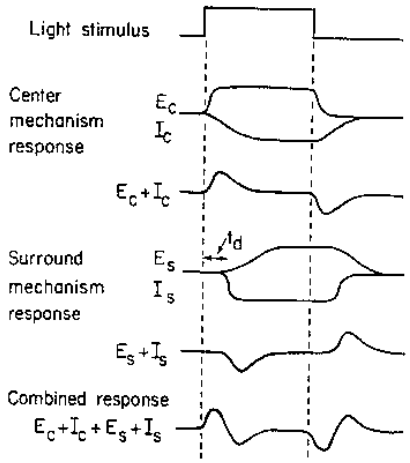

FIG. 8. Diagram of time-courses for the sub-mechanisms of a receptive field in a model of the type suggested by RODIECK and STONE (1965) for the cat retinal ganglion cell and by NYE and NAKA (1971) for the frog retinal ganglion cell. Because the excitatory sub-mechanism in the center (E_c) has a faster time-course than the inhibitory sub mechanism in the center (I_c), excitation dominates the center response producing an increase of firing rate at the onset of light and a depression of firing rate at the offset ($E_c + I_c$). Similarly, inhibition dominates the surround mechanism producing a depression in firing rate at the onset of light and an increase of firing rate at the offset ($E_s + I_s$). There is also a time delay (t_d) between the center mechanism and the surround mechanism. Thus a response to equal stimulation of both mechanisms ($E_c + I_c + E_s + I_s$) shows net excitation followed by inhibition at the onset of light and inhibition followed by excitation at the offset of light.

ganglion cell as a neural model of human psychophysical early light and dark adaptation. For example, the dependence of the psychophysical early light and dark adaptation effect on the spatial configuration of the stimuli (TELLER, 1971; TELLER *et al.*, 1971) may not be duplicated in the frog *on–off* cell responses. Further, the obvious species difference, strengthened by the well-known results showing that cells in the frog retina are substantially different from those in the primate retina (MATURANA *et al.*, 1960; HUBEL and WIESEL, 1969; DOWLING, 1968) argues against such an identification. This argument can be partially countered by noting that frog retinal ganglion cells are more like primate cells higher in the visual system and that those higher primate cells may actually be the neural substrate for early light and dark adaptation.

Another problem that arises in using the frog *on–off* cell or any other visual cell as a neural model of psychophysical thresholds is the difficulty of satisfactorily defining a physiological "threshold" equivalent to the psychophysical threshold. The results shown in Fig. 7 define the threshold as that test intensity that produces one additional impulse. However, the response to the test stimulus-adapting stimulus combination is not always the same as the response to the adapting stimulus plus some extra impulses due to the test stimulus (Figs. 2 and 3). Therefore, even if the frog possessed only a single visual neuron, the one studied in the experiment, the frog's ability to tell whether or not a test flash was present might very well depend on something other than the total number of impulses.

Although it may be premature to identify the frog *on–off* cell as a neural model of psychophysical early light and dark adaptation, such an identification is interesting to consider for the model it suggests of the psychophysical results. The psychophysical elevation of threshold is often thought of as resulting from an increase in the cell's activity during the onset and offset of the adapting stimulus. This increase in activity is thought to "mask" the smaller constant response of the cell to the test stimulus. The elevation in threshold shown in Fig. 7, however, indicates that a very different model of the psychophysical results is possible—a model in which the threshold increase is due to post-excitation inhibition.

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Abstract—Transient *on–off* cells in the frog eyecup preparation were studied. Short test flashes were presented at various times with respect to a ten second adapting flash. The total number of impulses in the response was least when the test flash was near the onset or offset of the adapting flash as a result of "post-excitation inhibition"—the decrease or inhibition of a response whenever it closely follows another response. Some modification of existing models for *on–off* cells is required to explain this inhibition. Post-excitation inhibition also provides a possible model for psychophysical effects.

Résumé—On étudie les cellules transitoires *on–off* dans une prépration en coupelle d'oeil de grenouille. On présente de brefs éclairs tests à divers instants après un éclairement d'adaptation de dix secondes. Le nombre total d'impulsions dans la réponse est minimal quand l'éclair test est voisin du début ou de la fin de la période d'adaptation, ce qui est un effet d'inhibition "post-excitatoire", à savoir la baisse ou l'inhibition d'une réponse qui suit de près une autre réponse. Il faut modifier les modèles existants de cellules *on–off* pour expliquer cette inhibition. L'inhibition post-excitatoire fournit aussi un modèle possible pour les effets psychophysiques.

Zusammenfassung—Transiente On–Off-Zellen wurden am präparierten Froschauge untersucht. In verschiedenem zeitlichen Abstand zu einem Adaptationsblitz von 10 Sekunden Dauer wurden kurze Testblitze dargeboten. Die Gesamtzahl der Impulse in der Reizantwort war am geringsten, wenn der Testblitz in kurzem Abstand zum Ein- oder Ausschalten des Adaptationsblitzes erfolgte, als Wirkung der "post-exzitatorischen Inhibition" d.h. der Abschwächung oder Inhibition einer Reizantwort in unmittelbarer Folge auf einen anderen Reiz. Um diese Inhibition zu deuten, sind die bestehenden Modelle der On–Off-Zellen etwas abzuändern. Die post-exzitatorische Inhibition kann als mögliches Modell für psychophysische Effekte dienen.

Резюме—Были исследованы транзиторные on–off клетки препарата глазного бокала лягушки. Краткие тестовые вспышки света подавались в разное время на фоне десятисекундной адаптирующей вспышки. Общее число импульсов в реакции было наименьшим, если тестовая вспышка была близка к началу или концу адаптирующей вспышки, что являлось следствием "поствозбудительного торможения" и выражалось в уменьшении или торможении реакции, если она близко следовала за другой реакцией. Для того, чтобы объяснить это торможение, необходима некоторая модификация существующей модели для on–off клетки. Поствозбудительное торможение также представляет возможную модель для психофизических эффектов.