Electrophysiology of the Insect Dorsal Ocellus

III. *Responses to flickering light of the dragonfly ocellus*

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ABSTRACT The ERG of the dragonfly ocellus has been analyzed into four components, two of which originate in the photoreceptor cells, two in the ocellar nerve fibers (Ruck, 1961 *a*). Component 1 is a sensory generator potential, component 2 a response of the receptor axons. Component 3 is an inhibitory postsynaptic potential, component 4, a discharge of afferent nerve impulses in ocellar nerve fibers. Responses to flickering light are examined in terms of this analytic scheme. It has been found that the generator potential can respond to higher rates of flicker—up to 220/sec.—than can the receptor axon responses, the postsynaptic potential, or the ocellar nerve impulses. The maximum flicker fusion frequency as measured by fusion of the ERG is that of the sensory generator potential itself.

INTRODUCTION

Two previous papers (Ruck, 1961 *a*, *b*) were concerned with analysis of the ocellar ERG and the mechanisms controlling the discharge of ocellar nerve impulses. This paper is concerned with responses to flickering light. The dragonfly ocellus contains two kinds of neural elements, photoreceptor cells and ocellar nerve fibers. Synapses between the two occur in the distal end of the ocellar nerve in the region where it joins the ocellar cup. The ERG is complex. It can be resolved into a generator potential (component 1), a receptor axon response (component 2), an inhibitory postsynaptic potential (component 3), and ocellar nerve impulses (component 4). Responses of each component to flickering light have been studied. The generator potential can follow higher rates of flicker than any of the other components. The maximum flicker fusion frequency of the ERG, therefore, is that of the generator potential itself.

Autrum and Gallwitz (1951) presented evidence which indicated that ability of the compound eye of the dragonfly (*Aeschna*) to follow high rates of flicker depended upon electrical interaction between photoreceptor cells and neurons of the optic ganglion. They found that surgical removal of the first layer of synapses of the optic ganglion, the *lamina ganglionaris*, resulted in reduction of the maximum flicker fusion frequency. Ruck (1958) suggested that the hypothesis of electrical interaction was inadequate, and that injury incurred during surgery probably accounted for the lowering of the f.f.f. This suggestion was based largely upon comparative studies of the f.f.f. of dorsal ocelli and compound eyes. In dragonflies, dorsal ocelli and compound eyes have approximately the same maximum f.f.f., but the ocelli lack the *lamina ganglionaris*. Ruck concluded tentatively that ability to resolve high rates of flicker was determined by properties of the receptor cells themselves. This conclusion is borne out in the present study.

MATERIALS AND METHODS

Methods of recording ocellar responses have been described (Ruck, 1961 *a*). Two optical stimulators were used in the present studies. In one a tungsten lamp served as the source. Light passed through a heat filter, a series of lenses, and was eventually brought to a focus on the cornea of an experimental ocellus. Stimulus intensities were controlled by Wratten neutral density filters, stimulus duration and frequency by a combination of a rotary sector disc and a manual shutter (Ruck, 1957, 1958 *a*, *b*). The other stimulator had a Sylvania glow modulator tube as a light source. Stimulus intensity, duration, and frequency were controlled by the output of an electronic stimulator (Ruck, 1961 *a*). Stimulus intensity is expressed as the logarithm of the illumination produced at the experimental cornea. Log $I = 0$ is equivalent to a corneal illumination of 12,000 foot-candles. Illumination produced by the tungsten lamp was measured directly. That produced by the glow modulator was obtained by "bioassay." Responses elicited by stimuli of known intensity delivered by the tungsten lamp system were matched in wave form and amplitude by the glow modulator. Glow modulator stimulus intensities were given the values in log I of the stimuli from the tungsten lamp system which produced the same responses (Ruck, 1961 *a*).

RESULTS

1. Responses of the Photoreceptor Cells to Flickering Light

The responses of the photoreceptor cells were described in the first paper of this series (Ruck, 1961 *a*). A convenient way to record them is to place one active electrode just beneath the cornea and an indifferent electrode in contact with hemolymph just under the exoskeleton in the midline of the frons. This lead was used in obtaining the data of this section. The receptor cell responses include a sensory generator potential (component 1) which appears as a cornea-negative potential change. It evokes component 2, a cornea-positive

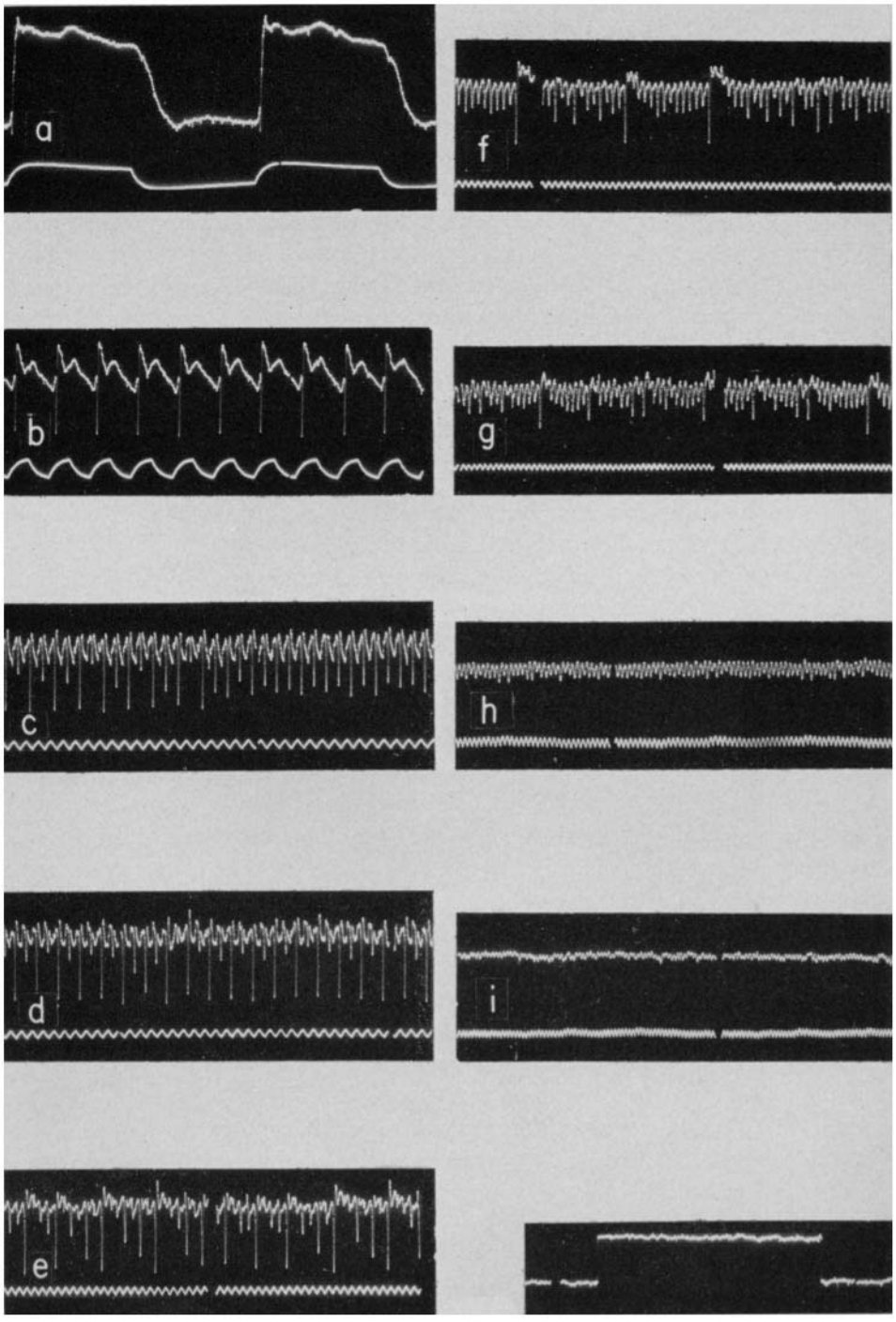

FIGURE. 1. Flicker responses of the lateral ocellus of *Tetragoneuria sp.* Corneal lead. D.C. amplification. Log $I = 0$. Light:dark ratio = 1. Flicker frequencies, *a*, 2.5/sec.; *b*, 16.2/sec.; *c*, 53/sec.; *d*, 60/sec.; *e*, 84/sec.; *f*, 98/sec.; *g*, 113/sec.; *h*, 138/sec.; *i*, 183/sec. Calibration, 1 mv. Negativity of corneal electrode gives upward deflection.

potential, believed to be a depolarizing response of the receptor cell axons. The corneal lead also records responses of the ocellar nerve fibers (components 3 and 4). These events may be quite prominent at low stimulus intensities. At high intensities, however, the photoreceptor cell responses so dominate the total ERG that they can be studied in virtual isolation (Ruck, 1961 *a*).

The responses of Fig. 1 were obtained from the lateral ocellus of *Tetragoneuria* sp. at high stimulus intensity. Components 1 and 2 dominate the records. Component 1 is the sustained upward (cornea-negative) deflection, component 2 the phasic downward deflection at 'on.' Stimulus intensity was maintained constant at $\log I = 0$. Flicker frequency was varied while maintaining the light:dark ratio constant at 1.0. Components 1 and 2 behave quite differently in flickering light. Component 1 follows every cycle of the stimulus in approximately sinusoidal manner up to the fusion frequency. Component 2, on the other hand, can follow each cycle of the stimulus only in the lower range of stimulus frequencies.

Before proceeding with an analysis of Fig. 1 it is worth while to examine the records of Fig. 2. These were obtained from a lateral ocellus of *Anax junis*. Some minutes before making the recordings this ocellus responded to flickering light in much the same manner as the ocellus of Fig. 1. Then rather abruptly component 2 disappeared, leaving component 1 in isolation. Records *a*, *b*, and *c* illustrate component 1 in response to single flashes of increasing intensity. Component 1 is a monophasic, cornea-negative potential. It responds to flicker, records *d* to *h*, in an approximately sinusoidal manner. As flicker frequency increases the amplitude of component 1 diminishes in a regular, graded manner to the fusion point. The flicker fusion frequencies for component 1 in isolation at stimulus intensities of $\log I = -1.0$ and $\log I = 0$ were, respectively, 150/sec. and 175/sec.

Returning to Fig. 1 it can be seen that component 2 arises low on the ascending limb of component 1. This is consistent with the view (Ruck, 1961 *a*) that component 1, the generator potential, evokes component 2. Component 2 is unable to follow each cycle of the flicker stimulus to frequencies as high as those which component 1 can follow. At 2.5/sec. (*a*), and 16.2/sec. (*b*), component 2 has the same amplitude in each cycle. In the first half of the record at 53/sec. (*c*), however, it shows a tendency to follow alternate cycles of the stimulus; *i.e.*, it is large in one cycle, small in the next. In the latter half of the record it has an approximately equal "compromise" amplitude in all cycles. At 60/sec. (*d*), 84/sec. (*e*), 98/sec. (*f*), and 113/sec. (*g*) the amplitude of component 2 varies conspicuously from cycle to cycle. The records suggest that component 2 is the algebraic sum of numerous "unit events" which are activated synchronously at 'on' below a certain flicker frequency (about 50/sec. in Fig. 1). Above this frequency they segregate into groups, each following a frequency component lower than the

flicker frequency. Tentatively, this behavior may be explained on the assumption that the unit event has an absolute refractory period.

Another property of component 2 may be recognized in Fig. 1. The amplitude of component 2 increases from 2.5/sec. (*a*) to 16.2/sec. (*b*). Since the stimulus intensity remained constant this increase may be ascribed to a kind of temporal facilitation. Component 1 does not display this property.

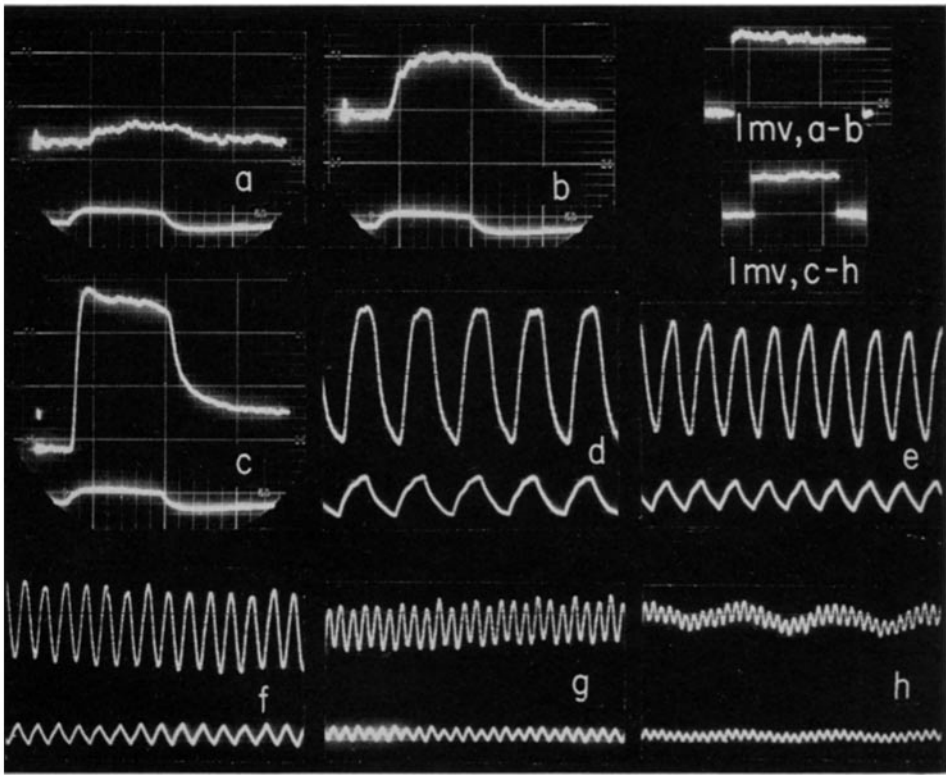

FIGURE 2. ERG's of lateral ocellus of *Anax junius*. Corneal lead. Preparation has deteriorated to the extent that component 1, the generator potential, remains in isolation. D.C. amplification. Records *a*, *b*, and *c*, responses to single flashes of 0.125 sec. duration; log $I = -4.0, -3.0, -1.5$. Records *d* to *h*, responses to flickering light; log $I = -1.0$; *d*, 19.6/sec.; *e*, 32.5/sec.; *f*, 54/sec.; *g*, 91/sec.; *h*, 135/sec. Negativity of corneal electrode gives upward deflection.

At flicker frequencies from 138/sec. (*h*) to 183/sec. (*i*) individual component 2 deflections cannot be discriminated. The fusion frequency of the ERG at log $I = -1.0$ was about 195/sec., at log $I = 0$ about 220/sec. (not illustrated). From a study of deteriorating preparations, *e.g.* that of Fig. 2, in which component 1 is the only remaining component of the ERG, it is concluded that the maximum f.f.f. of the normal preparation is that of component

1. Ability to resolve highest rates of flicker is therefore a property of the generator potential mechanism which resides in the rhabdomere-bearing ends of the receptor cells (Ruck, 1961 *a*). There is no need to invoke electrical interaction between generator potential and other excitatory events in the ocellar pathway, either pre- or postsynaptic, to account for the high flicker fusion frequencies.

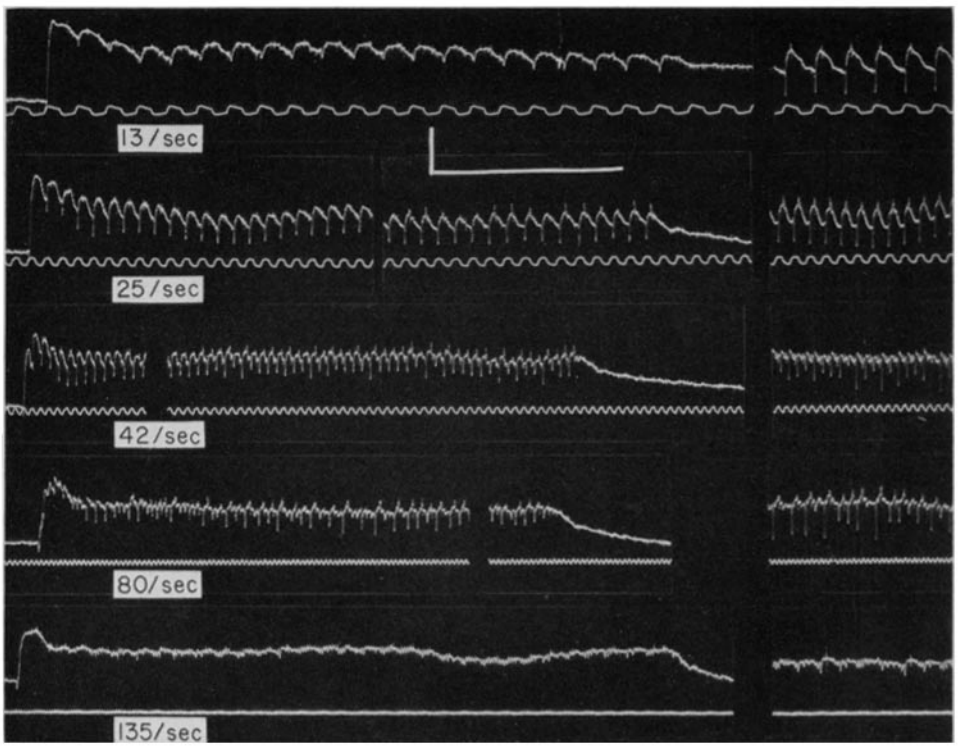

FIGURE 3. Flicker responses of the median ocellus of *Aeschna* sp. Corneal electrode. Log I = 0. D.C. amplification. Records at left, responses of dark-adapted ocellus; at right, after 30 sec. continuous exposure to flicker. Calibrations, 1 mv. and 0.5 sec.

Fig. 3 illustrates other properties of the flicker response of the receptor cells. The preparation was a normal median ocellus of *Aeschna* sp. Stimulus intensity was constant at log I = 0. Flicker frequency was varied. At each frequency two series of responses were recorded, the first of the dark-adapted ocellus (left), the second of the light-adapted ocellus (*i.e.*, after a 30 sec. exposure to the stimulus). At each of the five flicker frequencies the first response of the dark-adapted ocellus brings the generator potential to a high level from which recovery is incomplete when the second cycle of the stimulus arrives. The result is that the second component 1 response is superimposed

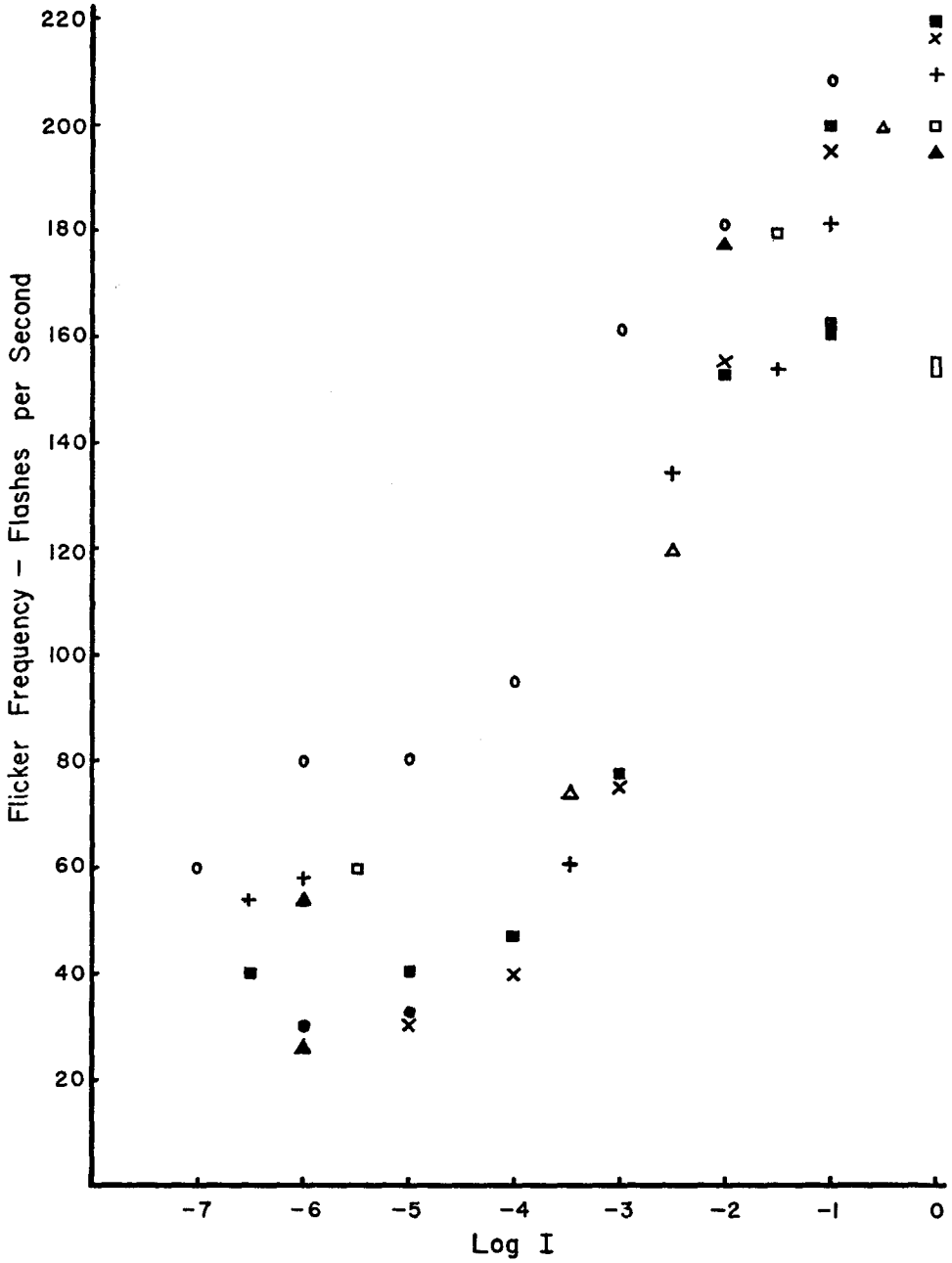

FIGURE 4. Flicker fusion frequencies of the ERG's of eight dragonflies (six species). Corneal lead was used in obtaining all data. All preparations were in normal condition; *i.e.*, all ERG components were present. Fusion frequencies are those of component 1, the generator potential.

upon a residue of the generator potential left by the first. With increase of flicker frequency the flicker response becomes smaller and smaller until eventually discrete responses to each cycle no longer appear. The phenom-

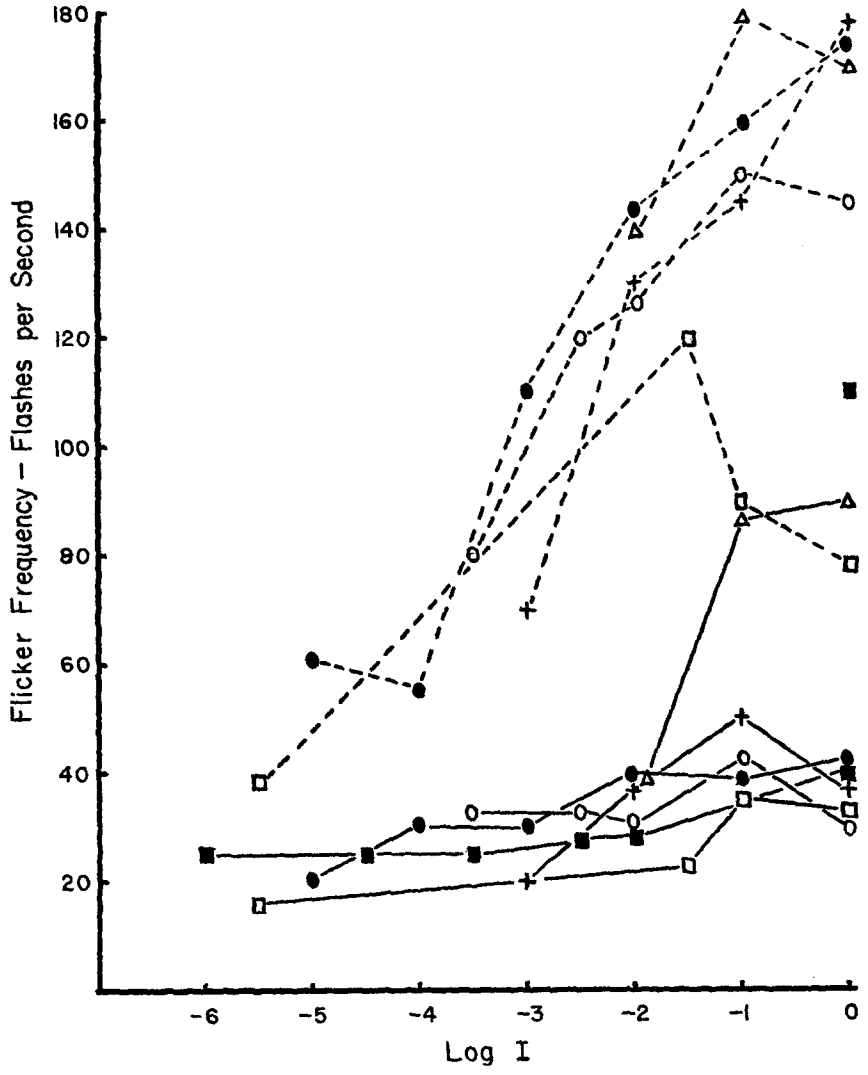

FIGURE 5. Flicker response data for component 2 only from lateral ocelli of six dragonflies (five species). Lower (solid) curves, highest frequencies at which component 2 can follow each cycle with on-deflections of equal amplitude. Upper (dashed) curves, flicker fusion frequencies of component 2.

enon is roughly analogous to the transition from single twitches to tetanus in skeletal muscle. Flicker frequency for this preparation was about 160/sec. A response at the fusion frequency was indistinguishable from a response to a sustained stimulus of appropriate intensity (not illustrated).

Fig. 3 illustrates temporal facilitation of component 2 very well. Component 2, small in early responses of the dark-adapted ocellus, increases in amplitude up to a steady state level after continuous exposure to flicker for about 30 sec. (records at right). The flicker frequency at which component 2 failed to follow all cycles of the stimulus with deflections of equal amplitude was about 38/sec., lower therefore than in the preparation of Fig. 1. This frequency varies somewhat from preparation to preparation.

The graphs of Figs. 4 and 5 summarize certain properties of the receptor cell responses to flickering light. Flicker fusion frequency of the normal ERG of several lateral ocelli is plotted as a function of log I in Fig. 4. Over a range of 7 logarithmic units of intensity change the f.f.f. increases from about 40/sec. to over 200/sec. Since the f.f.f. of preparations in which component 1 is the only surviving response increases in the same way, it is concluded that Fig. 4 describes the behavior of the sensory generator potential.

Fig. 5 summarizes the frequency response of component 2 only. Two points are plotted at each stimulus intensity for each preparation. The lower set, connected by solid lines, gives the frequencies at which the amplitude of component 2 in alternate cycles begins to fluctuate. These frequencies vary relatively little over a range of 6 logarithmic units. With a light:dark ratio held constant at 1.0, the duration of the dark phase of the flicker cycle provides a measure of the "refractory period." This has values between 25 and 12 msec., corresponding to frequencies between 20 and 40/sec. (Several points lie outside this range.) The upper set of points (dashed lines) gives the frequencies at which component 2 deflections can no longer be discriminated in the ERG. These frequencies show marked increase with increase in log I. The highest frequencies attained by component 2, using this criterion, are somewhat lower at the highest stimulus intensities than those attained by component 1.

Thus far the following conception of the flicker response of the receptor cells has emerged: Component 1, a graded event which shows no sign of having an absolute refractory period, determines the flicker fusion frequency of the ERG. Component 1 "drives" component 2. Component 1 appears to be the algebraic sum of a large number of unit events, each of which has an absolute refractory period. The unit events can respond synchronously in each cycle of the stimulus only up to frequencies of about 40/sec. At higher frequencies the unit events break up into separate populations, each following a frequency component lower than the stimulus frequency.

2. *Responses of Ocellar Nerve Fibers to Flickering Light*

A convenient way to record the responses of ocellar nerve fibers is to place an active electrode on the end of the ocellar nerve at the point where it enters the brain. The nerve is then sectioned free of the brain and the proximal

end is lifted just above the level of the hemolymph. An indifferent electrode is placed in contact with hemolymph just under the exoskeleton of the frons. This lead is illustrated in a previous paper (Ruck, 1961 *a*). Responses of the ocellar nerve fibers include a hyperpolarizing postsynaptic potential (component 3) and nerve impulses. The latter occur as a spontaneous discharge in the dark-adapted state. The postsynaptic potential inhibits the dark discharge. Postsynaptic potential and nerve impulses are recorded at a distance from their sites of origin in a volume conductor (the hemolymph); both have electrical signs opposite to those obtaining at sites of origin. The postsynaptic potential appears as a negative wave, the nerve impulses as positive spikes (Ruck, 1961 *a*). The lateral ocellar nerve contains three or four nerve fibers, one of which is much larger than the others. Most often spikes in only the largest fiber are recorded.

The ocellar nerve is only a millimeter or so long. The active electrode therefore lies close to the receptor cells. It is not surprising therefore that receptor potentials (components 1 and 2) are also recorded superimposed upon the responses of the ocellar nerve fibers. Component 2, presumably the response of the receptor cell axons, may be quite conspicuous in the nerve lead. When it can be discriminated it appears as a negative wave preceding the postsynaptic potential. This is illustrated in Fig. 6. The records were obtained from the lateral ocellar nerve of *Sympetrum rubicundulum*. Those at the left were elicited by a stimulus intensity of $\log I = -5.5$. Components 2 and 3 are designated by arrows in the upper two records. At higher flicker frequencies and at higher stimulus intensities it is frequently difficult to resolve components 2 and 3. For example, in the records at the right in Fig. 6, obtained at $\log I = -2.0$, components 2 and 3 have summed in such a way that neither component can be discriminated independently of the other. Because of this it is not possible to determine accurately the f.f.f. of component 3 in the nerve lead.

Ocellar nerve impulses, however, are easily discriminated as Fig. 6 shows. They are inhibited during the light phase of each flicker cycle at lower flicker frequencies and appear as an off-discharge during the dark phase. There is always a limiting frequency above which the nerve impulses fail to follow the flash frequency. There are two ways in which "failure to follow" manifests itself. (*a*) The impulse discharge persists in the presence of flicker but shows no relation to the cycles of the stimulus. In this case the responses resemble those elicited by a sustained light flash of low to intermediate intensity to which the nerve impulse discharge has adapted. The record at $\log I = -5.5$, 62/sec., illustrates this. The record immediately below shows the non-adapted discharge characteristic of the dark-adapted state in this preparation. (A 1 mv. calibration signal is superimposed.) (*b*) The impulse discharge remains

totally inhibited in the presence of the flicker stimulus. The record at log $I = -2.0$, 90/sec., illustrates this. Similar total inhibition is characteristic of the response to a sustained stimulus of high intensity.

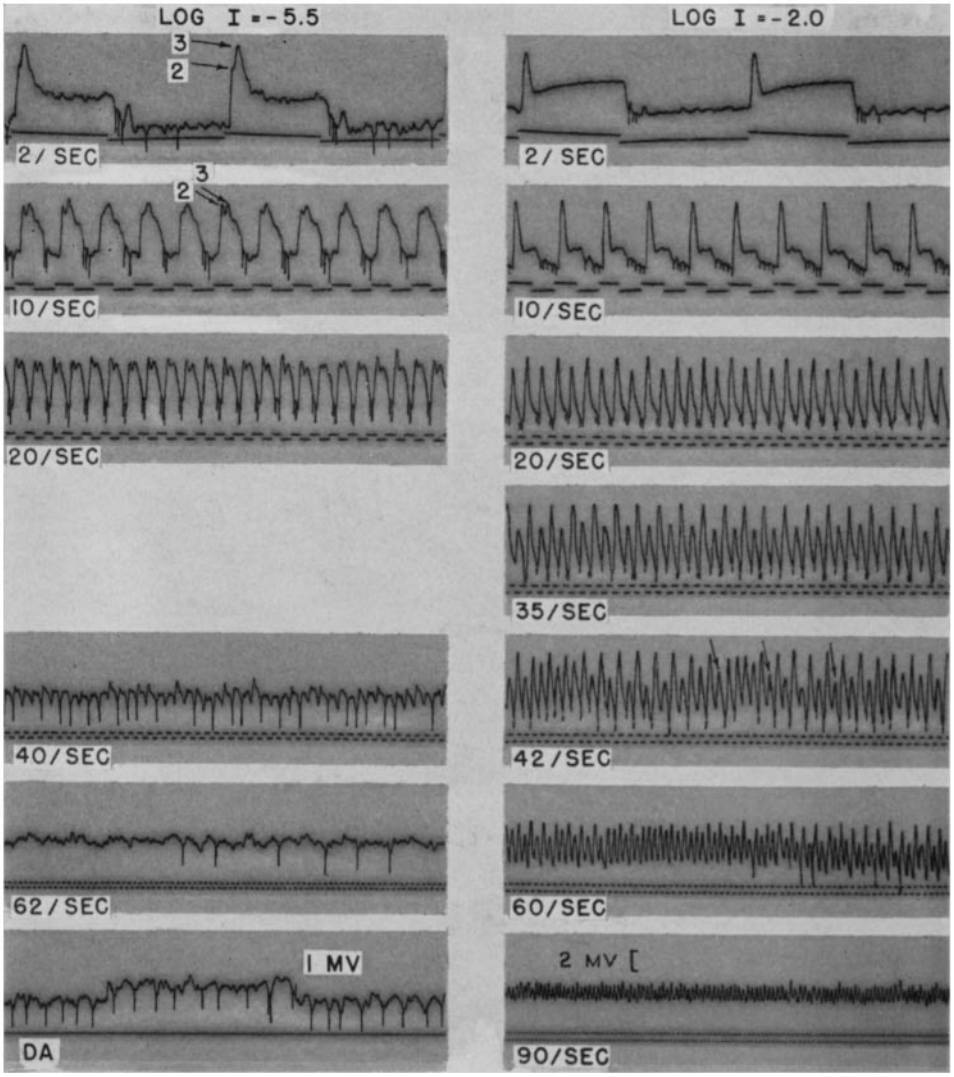

FIGURE 6. Flicker responses of the lateral ocellus of *Sympetrum rubicundulum*. Nerve lead. D.C. amplification. Negativity of nerve lead gives upward deflection. Components 2 and 3 indicated by arrows in upper two responses of left column.

At higher stimulus intensities, before total inhibition sets in, there is a range of frequencies within which the nerve impulses are "driven" by the flicker stimulus, but do not appear in every cycle. In Fig. 6, log $I = -2.0$,

impulses appear in every cycle from 2/sec. to 35/sec., but at 42/sec. appear in some cycles but not in others. The same is true for the response at 60/sec. where impulses are very infrequent but are nevertheless driven by the stimulus.

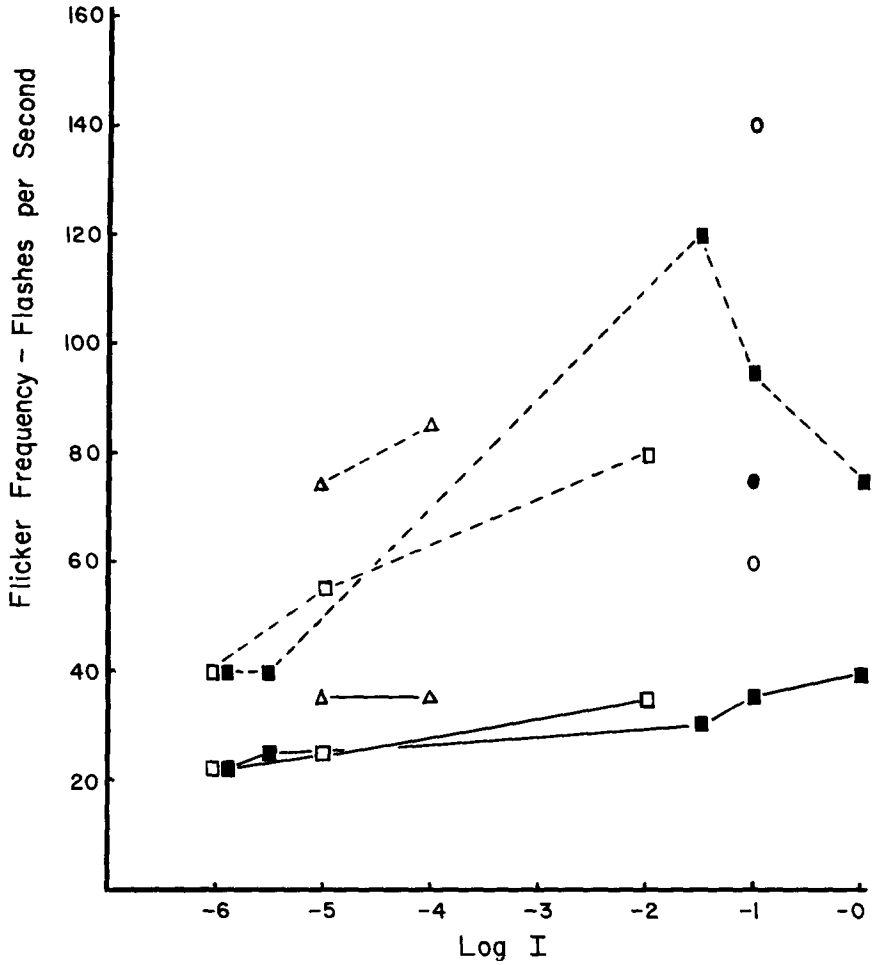

FIGURE 7. Flicker response data for nerve impulses in the largest fiber of lateral ocellar nerves of several dragonflies. Lower (solid) curves and lower empty circle at log $I = -1.0$: highest frequencies at which off-impulses occur in each flicker cycle. Upper (dashed) curves, upper empty circle and solid circle: "flicker fusion frequencies" of off-impulses (see text).

The flicker response of the ocellar nerve impulses may be explained on the basis of simple assumptions concerning the functional relationships of components 2 and 3: Impulses appear during the dark phase of a flicker cycle when component 3 has sufficient time to decay to a level permitting the

release from inhibition of the nerve impulses. Whether off-impulses appear or do not appear in a given cycle depends on the duration of the dark period and on the magnitude of component 3. The larger component 3 is, the longer is the requisite decay time. Large component 3 deflections are evoked by large component 2 deflections.

In the lower frequency range, from about 20/sec. to about 40/sec., there is sufficient time during the dark period of each cycle for components 2 and 3 to decay, even though both may be large. Off-impulses appear in each cycle. At higher flicker frequencies, with shorter dark periods, there may or may not be sufficient decay time depending on the magnitudes of components 2 and 3. The unit events underlying component 2 segregate at higher frequencies into populations following different submultiples of the flicker frequency. In one cycle (Fig. 1) component 2 may be large, in the next small. When component 2 is large, so is component 3. *E.g.*, in Fig. 6, log $I = -2.0$, 42/sec., nerve impulses tend to occur in alternate cycles, and to follow the smaller of the upward deflections (arrows). These deflections represent the algebraic sums of components 2 and 3. Presumably there is insufficient time following the larger upward deflections (large sums of components 2 and 3) for the postsynaptic potential to decay and release the off-impulses.

Fig. 7 summarizes certain features of the flicker responses of ocellar nerve impulses in several preparations. A lower set of points gives the highest frequencies at which impulses occur in each cycle of the stimulus. Over a range of 6 logarithmic units these frequencies lie between about 20/sec. and 40/sec., the same range in which the component 2 "units" (Fig. 5) occur synchronously with each cycle. An upper set of points gives the frequencies at which the impulses, if present, bear no relation to the cycles of the stimulus; *i.e.*, resemble the record at log $I = -5.5$, 62/sec., in Fig. 6; or gives the frequencies at which total inhibition sets in, as in the record at log $I = -2.0$, 62/sec., in Fig. 6.

DISCUSSION

There are at least four links in the chain of events leading to inhibition of ocellar nerve impulses. The sensory generator potential (component 1) evokes component 2, believed to represent receptor axon responses. These probably lead to the release of inhibitory transmitter substance which evokes a hyperpolarizing postsynaptic potential (component 3). The latter directly inhibits the ocellar nerve impulses (Ruck, 1961 *a*, *b*). Component 2 is the "link" most difficult to interpret. The unit event has not yet become accessible to direct analysis. Presumably this will require penetration of individual receptor cells with ultramicroelectrodes. The flicker experiments and others reported in previous papers provide considerable indirect information con-

cerning the properties of the unit event. The following is a summary of these properties.

(*a*) Component 2 originates in the receptor cells. (*b*) It is evoked by component 1. (*c*) Polarity of component 2 in the extracellular medium, negative deep in the ocellus, and positive near the cornea, are what would be expected for depolarizing responses of the receptor axons. (*d*) Component 2 can be removed reversibly by high concentrations of K ion. (*e*) Synaptic transmission fails if component 2 drops out of the ERG (Ruck, 1961 *a*, *b*). (*f*) In the honeybee ocellus, component 1 may appear in isolation at threshold and increase in amplitude with increase in stimulus intensity in graded fashion. Above a certain stimulus intensity a slight increase may bring in component 2 abruptly as a well developed on-deflection. Component 2, therefore, may be nongraded with increase in stimulus intensity near threshold (Goldsmith and Ruck, 1957–58). (*g*) The fractionation of component 2 at intermediate flicker frequencies indicates that many units contribute to it. Apparently the on-deflection of component 2 in response to a single flash is simply the envelope of many unit events active simultaneously (Figs. 1 and 3).

Now if component 2 is an essential link in the chain of events leading to synaptic inhibition, one would expect it to persist as long as synaptic inhibition persists. In response to a single sustained light flash, however, component 2 usually appears to be a single sharply phasic on-deflection of several milliseconds' duration; synaptic inhibition may persist as long as the light is on (many seconds or minutes). In response to flickering light the phasic on-deflections of component 2 may disappear at frequencies below that at which the generator potential fuses, though synaptic inhibition may persist at the fusion frequency and above. The following two hypotheses attempt to reconcile the *apparently* non-sustained nature of component 2 with the sustained nature of synaptic inhibition:

(1) The generator potential arising in each receptor cell excites the axon of that cell, producing one or more unit component 2 events which are like nerve impulses in some of their properties (above). A sustained generator potential evokes a repetitive discharge of these "impulses." Individual impulses are too small to be detected with large external electrodes such as those used in this study. Synchronous firing of many impulses, however, can be detected. The onset of a single light flash evokes a synchronous discharge in many or all receptor axons. This manifests itself as the large on-deflection of component 2. Later during the flash the impulses fall out of synchrony; then, throughout the receptor population, impulses occur at random intervals. A smooth envelope of component 2 activity is the result. Component 2 may then *appear* to have dropped out of the ERG. Evidence suggesting that component 2 can be repetitive in response to single flashes has been obtained from the lateral ocellus of the honeybee. The records of Fig. 8, particularly those of the lower row, illustrate the repetitive nature of component 2.

(2) The unit component 2 event has an initial spike-like phase at on, followed by a sustained potential change during the remainder of the stimulus. Either hypothesis would explain the persistence of synaptic inhibition. Available data do not permit a clear choice between the two, nor do they suggest alternative hypotheses.

Temporal facilitation of component 2, shown in Figs. 1 and 3, and described for the honeybee ocellus (Goldsmith and Ruck, 1957–58), is not clearly understood. It may be that a conditioning flash delivered to the dark-adapted ocellus triggers component 2 in some but not all receptor axons, while it brings other receptor axons nearer to the "firing" point. In this case a subse-

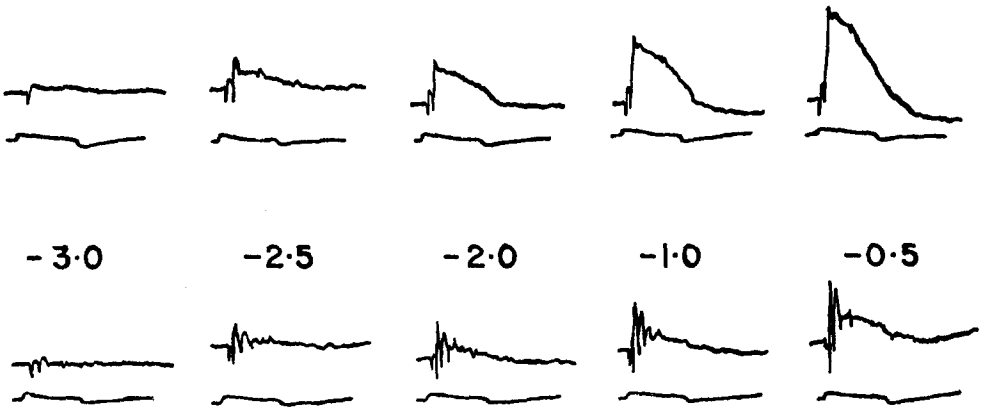

FIGURE 8. ERG's of lateral ocellus of honeybee. Active electrode subcorneal; indifferent electrode in dark compound eye. A.C. amplification; frequency band pass of 0.5 cycle/sec. to 2 kilocycles/sec. Stimulus duration 0.125 sec. Log *I* given between records. Upper records, ERG's of the dark-adapted ocellus. Lower records, ERG's of the light-adapted ocellus; *i.e.*, steady state responses to stimuli presented at 1/sec. Records show that component 2 may be repetitive in response to single stimuli.

quent test flash might excite all the receptor axons to "fire" simultaneously with increase in amplitude of component 2. Temporal facilitation, if this were true, would amount to recruitment by the test flash of a subliminal fringe. The fact that temporal facilitation occurs with flashes of high intensity, which might be expected to excite all the receptor axons, suggests that this explanation is inadequate. An alternative explanation might be that the size of the unit component 2 event can be increased by repetitive stimulation.

The flicker responses of the dragonfly ocellus may be summarized as follows: (*a*) The sensory generator potential has a f.f.f. which increases from about 30/sec. to over 200/sec. as the stimulus intensity increases over a range of 7 logarithmic units. (*b*) The unit events of component 2 are excited synchronously with each cycle of the stimulus within the frequency range, 20/sec. to 40/sec. Above this range refractoriness of the unit events prevents syn-

chronous responses of component 2 in each cycle. Asynchronous responses of the unit events, still driven by the flicker stimulus, may occur up to 150/sec. or slightly higher, depending on stimulus intensity. (*c*) Off-discharges of ocellar nerve impulses in the largest fiber of the lateral ocellar nerve may occur in each cycle of a flicker stimulus within the range, 20/sec. to about 40/sec. At higher flicker frequencies, just as in the case of component 2, off-impulses may occur in some cycles but not in others. The f.f.f. of these impulses corresponds to total inhibition or to a state of partial adaptation as if in response to a sustained flash. This f.f.f. depends on stimulus intensity and ranges from about 40/sec. to about 140/sec. Flicker data for the smaller fibers of the ocellar nerve are difficult to obtain. In one or two preparations in which small fiber impulses were visible along with the large the f.f.f. of the small ones appeared to be about the same as or lower than that of the large.

The part played by the ocellar response in insect behavior remains mysterious. The output of the ocellus is capable of measuring differences between lower levels of illumination by degree of inhibition of ocellar nerve impulses. At high levels of sustained illumination, inhibition of the largest ocellar nerve fibers and those smaller ones whose activity has sometimes been observed is complete. Within the range of intensities of sustained stimuli in which inhibition is complete, increases of intensity may still produce off-impulses (Ruck, 1961 *b*). Output of the ocellar nerve may be related to cycles of flicker stimuli of high intensity up to frequencies as high as 140/sec., but the ocellar nerve fails to exploit the much higher fusion frequencies characteristic of the sensory generator potential. It is rather unlikely in any event that the ocellus is specifically adapted to resolving high rates of flicker generated in flight by movement relative to objects in the visual field. When an image is formed by the ocellar cornea it lies well behind the retina (Homann, 1924; Wolsky, 1931; Parry, 1947; Cornwell, 1955). Also visual angles of ocelli are quite large (Cornwell, 1955), while the number of ocellar nerve fibers is quite small. It is more likely that the ability to resolve high rates of flicker in the experimental situation reflects simply the rapidity of the processes of dark adaptation, a property shared with the compound eye (Ruck, 1958 *b*). The optics of the compound eye seem much better adapted to utilizing rapid dark adaptation in the naturally occurring flicker situation.

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