THE ELECTRORETINOGRAM OF CYNOMYA

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The electroretinogram (ERG) of vertebrates obtained in response to a flash of light (one-half second or longer) consists of a complex wave in which there are usually four distinct peaks known as the a-, b-, c-, and d-waves (Fig. 1). This complex change of electrical potential is commonly regarded as the algebraic sum of the EMF from three sources, all of which are located in the retina. The EMF from each source is considered to be a component produced by a particular process. The a-wave is the result of the timing of components II and III (referred to as P II and P III) P III rising faster than P II. The b-wave is the peak of P II, and the c-wave is the sum of P I, P II and P III, but its magnitude is determined largely by P I. The d-wave (or "off effect") occurs after the flash is terminated and results from the fact that P III declines more rapidly than P I and P II (Granit, 1933, 1935, 1938; Therman, 1938; Bernhard, 1940, 1942).

It has been pointed out previously (Jahn and Crescitelli, 1938, 1939, 1940; Jahn and Wulff, 1942) that the ERG of insects may consist of four major waves which in general form are quite similar to the a-, b-, c-, and d-waves of vertebrates. It is also known that in *Trimerotropis* the wave form is the result of summation of at least two components, one of which arises in the eye and one in the optic ganglion (Jahn and Wulff, 1942). The nomenclature of the vertebrate ERG has been adopted for insects as a matter of convenience and without assuming that the two wave forms arise in the same way or are strictly comparable to each other.

It is the purpose of the present paper to present strictly comparable records of the ERG of *Cynomya cadaverina* taken at two temperatures, at various intensities and durations of flash, and at slightly different stages of adaptation, and to examine these records in view of the possibility that the wave form might be interpreted in the same manner as those taken from vertebrate eyes.

The effect of temperature, of intensity, of duration of flash and of adaptation have been studied separately on other insects, but there is no published set of records in which these four factors
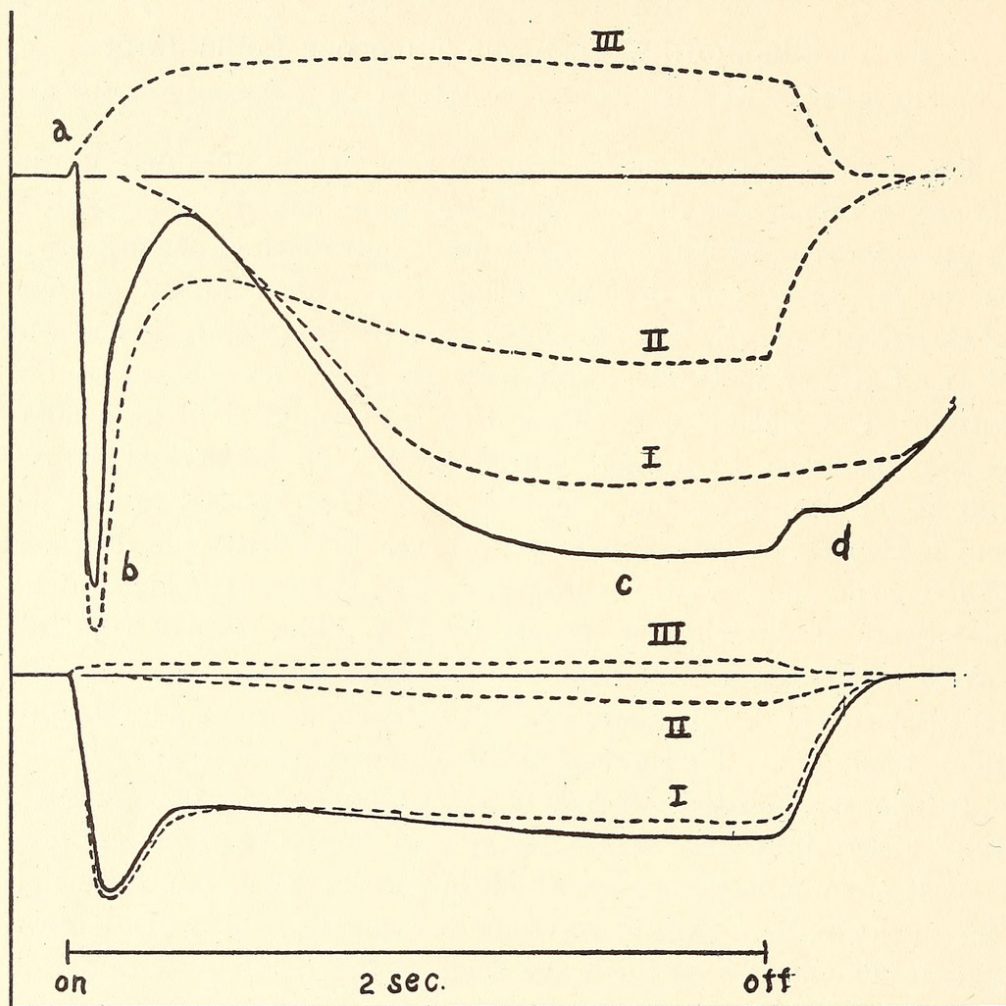
FIG. 1. A diagram showing the analysis of a composite retinal electric response of a dark adapted cat's eye at two intensities of illumination, 14 ml. (upper) and 0.14 ml. (lower), of an area of 1661 sq. mm. viewed at a distance of 70 mm. The continuous line is the composite or recorded response; the broken lines represent the various components. The duration of the light stimulus is 2 seconds. (From Granit, 1933)

have been varied in an otherwise strictly comparable series of experiments.

MATERIAL AND METHODS

The flies were collected locally and used immediately. After temporary inactivation by low temperature the fly was mounted

in the electrode chamber, and electrical contact was made with the cornea of the eyes by means of chambers containing salt solution. One eye only was exposed to the stimulating light of 10,000 foot-candles (unit intensity), and the responses were recorded with a condenser-coupled high-gain amplifier, cathode ray oscillograph and camera.

A double wall around the electrode chamber permitted changing the chamber temperature by passing hot or cold air between the walls. The temperature was frequently recorded by means of a resistance thermometer placed in the chamber near the animal.

Numerous records were made from twelve animals. All the records shown in Figure 2 were made from the same animal on the same day and at the same amplification. Therefore they are strictly comparable. Records from other animals were similar, and those presented comprise the most typical of the complete series obtained. In order to facilitate the dicussion certain records have been copied and are shown enlarged with the waves labelled in Figure 3. In Figure 2, responses to the first four exposures at the rate of one per second are shown in each column. Records from further stimulation showed few differences from those of the fourth stimulus, and no differences which would affect the following discussion.

In referring to the records the following system is used. The row, column, and number of exposures are given successively, e.g., 4C3 refers to row 4, column c, exposure 3. The same system is used for the enlargements shown in Figure 3. Three seconds elapsed between records 7D1 and 7D2, and 7D2 is in response to a 350 msec. stimulus; in several other series one or two flashes were omitted.

RESULTS

I. The Electroretinogram of *Cynomya* at Room Temperature (26–28° C.)

A. Changes produced by intensity at short exposure.

With a light stimulus of unit intensity (10,000 foot-candles) and 17 msec. exposure, the response of the eye is a negative wave which consists of a sharp downward deflection, the b-wave, followed by a slow c-wave on which there is a negative peak, the
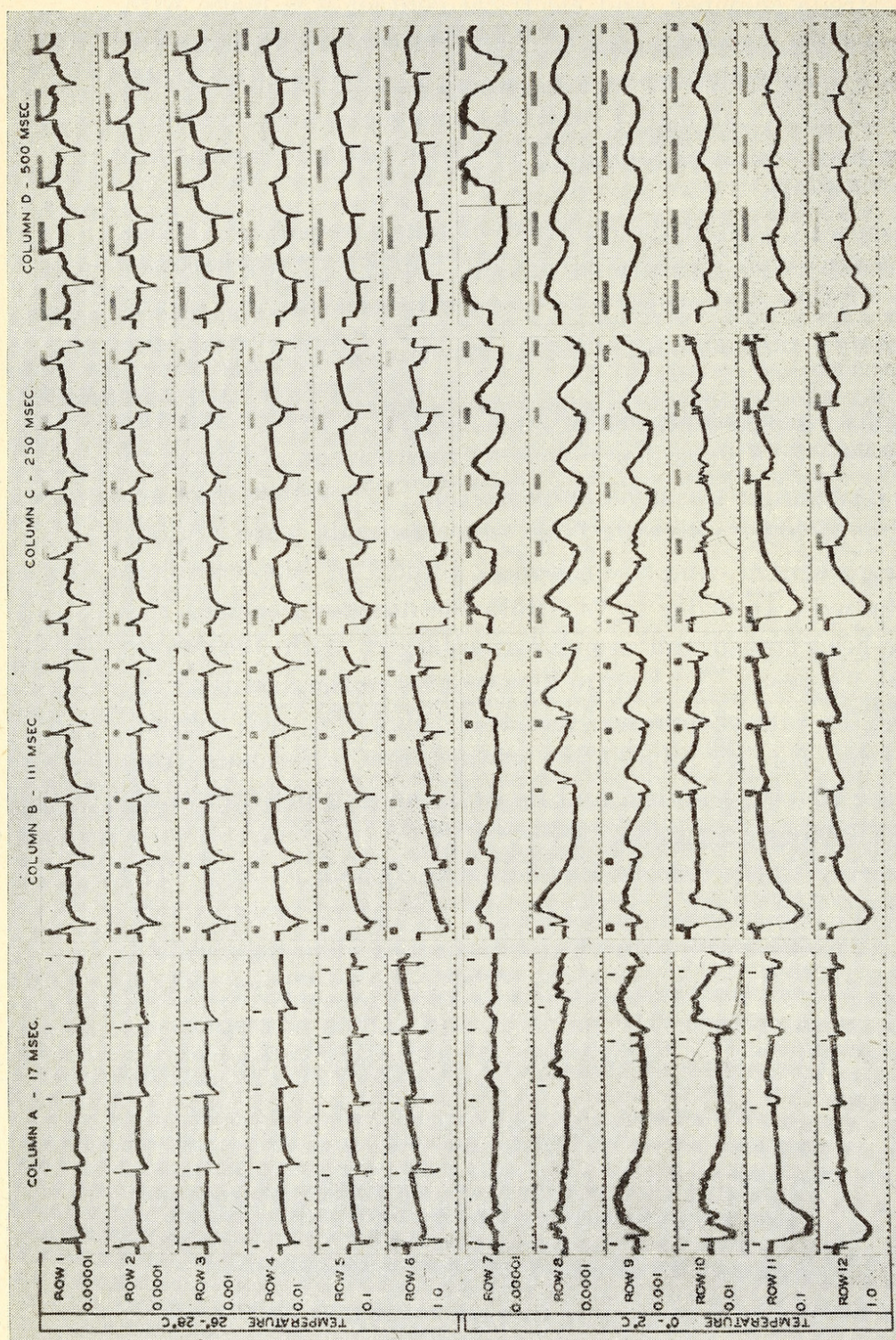
FIG. 2. Photographs of electric responses obtained from the photoreceptor of Cynomya. The responses have been arranged in columns (A through D) according to the duration of the light stimulus, in rows (1 through 12) according to the intensity of the light stimulus and in two blocks according to the temperature of the eye. Records in rows 1 through 6 were obtained with the eye at 26–28° C.; records in rows 7 through 12 were obtained with the eye at 0–2° C. The intensity is given as fractions of unit intensity, which is approximately 10,000 foot candles. Time lapse is indicated by the dots at the bottom of each record; the distance between consecutive dots represents 0.1 second.

d-wave. Following the d-wave there is a slow return to the base line. The b-wave is sometimes preceded by an a-wave, but the a-wave is usually seen as a notch on the b-wave. (record 6A, Figure 2). Upon light adaptation the magnitude of this response decreases slightly, the a-wave notch becomes more prominent, and the return to the base line is more rapid.

When the stimulus is similar to the above but of a low intensity (0.00001 unity) the electrical response consists of an a-wave, followed by a small negative deflection which is probably a d-wave (record 1A, Figure 2). This response changes a little upon light adaptation.

As the intensity of the stimulating light is increased, the exposure and temperature remaining constant, the positive a-wave spike gradually diminishes, eventually becoming a notch on the b-wave which increases in magnitude as the intensity approaches unity and becomes distinct from the d-wave at 0.1 unit intensity (records 2A, 3A, 4A, and 5A).

B. Changes produced by intensity at long exposures.

The response of the eye to a half-second light stimulus of unit intensity is a rather complex negative wave (record 6D, Figure 2). The wave starts with a downward deflection, the b-wave, on which there is an a-wave notch. There is a c-wave which is followed by a spike-like d-wave, and the response is terminated by a slow return to the base line. Upon light adaptation the magnitude of the b-wave decreases, and the response begins with a small positive deflection or a-wave. The d-wave also increases in size as light adaptation proceeds.

When the stimulus is similar to the above but of a low intensity (0.00001 unity) the response consists of two spikes, an initial positive a-wave spike and the terminal negative d-wave spike. The intermediate b- and c-waves are entirely absent (record 1D, Figure 2).

As the intensity of the stimulus is increased the c-wave makes its appearance (record 3D, Figure 2) and the a-wave becomes smaller and disappears (records 3D and 4D, Figure 2). The b-wave is seen as a slight hump on the c-wave (3D1) and later as a distinct peak (4D1 and 6D1). The d-wave is persistent through-

out the intensity changes and becomes more spike-like at the higher intensities (compare records of column D, 1 through 6).

RESPONSES TO 17 MSEC. STIMULI

6A1

6A4

12A1

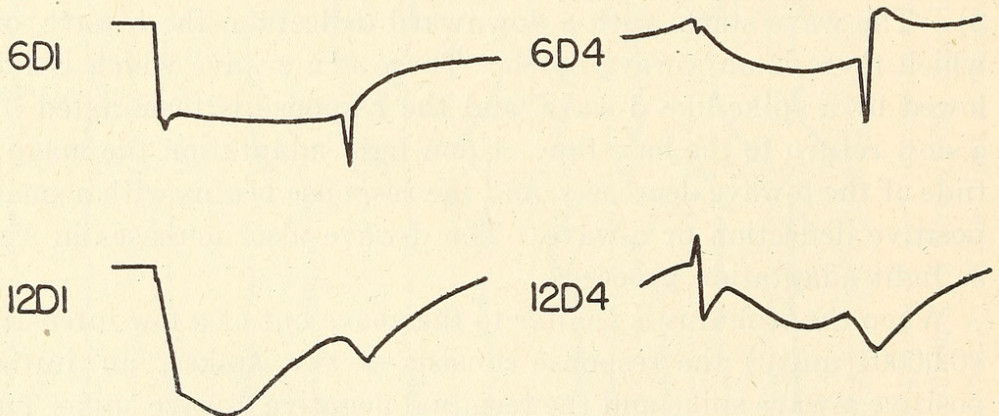12A4
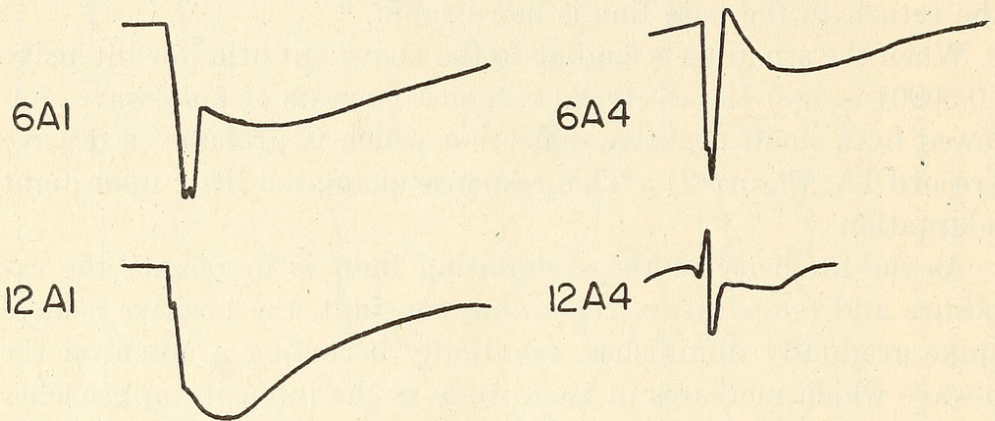
RESPONSES TO 500 MSEC. STIMULI

6D1

6D4

12D1

12D4

FIG. 3. Enlarged drawings of records selected from Figure 2. The numbers refer to the original records in Figure 2.

C. Changes produced by intensity at intermediate exposures.

The wave form of the electroretinogram elicited by stimuli of exposure of 111 and 250 msec. is similar to those already discussed and hence needs little further elaboration. The d-wave which is very small at 17 msec. is as large as the a-wave at 111 msec. (1A

and 1B, Figures 2) and changes little as the duration of flash is increased.   The b-wave gradually replaces the a-wave with increasing intensity as in 17 or 500 msec. exposures.

II. THE ELECTRORETINOGRAM OF *Cynomya* AT LOW TEMPERATURE (0–2° C.)

A. *Changes produced by intensity at short exposures.*

With a short (17 msec.) exposure of unit intensity the initial response of the dark-adapted eye near zero ° C. is a negative wave consisting of a sharp b-wave, bearing a notch, which is presumably the a-wave, and a rather slow c-wave.   The response is terminated by a slow return to the base line (record 12A, Figure 2). This response is strikingly modified by light adaptation, as can be seen from the succeeding responses on the same record. These are characterized as consisting of an a-wave spike, a small b-wave and a small c-wave.   This type of response is perhaps better illustrated in the responses of record 12B, Figure 2, in which the c-wave is better developed.

With a short exposure of low intensity (0.00001 unity) the response consists of a slow and relatively long positive wave (record 7A, Figure 2) which undergoes little modification upon repetitive stimulation.   As the intensity increases this slow positive wave is differentiated into an a-wave spike and a slow positive component whose classification is uncertain.   Further increases in intensity result in a reduction of the a-wave, the appearance of a b-wave and an increase in the magnitude of the slow positive component (record 9A, Figure 2).   As the intensity approaches unity the a-wave completely disappears and the slow positive component is replaced by a slow negative component as seen in the first response of record 12A, Figure 2.

B. *Changes with intensity at long exposures.*

When the light stimulus is of unit intensity and 0.5 seconds long, the initial response is a negative wave similar to that initiated by the short stimulus.   The response consists of a b-wave which bears the a-wave as a notch near the top, an atypical c-wave and a much reduced d-wave or off effect.   The succeeding responses are very much modified and exhibit an initial a-wave

spike (probably arising from the notch on the b-wave), a small b-wave and a c-wave.   The d-wave is present but is not spike like (record 12D, Figure 2).

At low intensity (0.00001 unity) the half-second exposure elicits a large slow positive wave which bears a number of irregularities difficult to identify (record 7D, Figure 2).   In record 8D, Figure 2, it can be seen that the first of these irregularities has been slightly isolated from the rest of the response and is probably the a-wave.   In record 9D, Figure 2, the a-wave is still more prominent, and the slow wave has decreased in magnitude. These tendencies are accentuated as the intensity is further increased (record 10D, 11D, and 12D, Figure 2), and the slow positive wave is gradually replaced by the slow negative wave.   The d-wave does not become typical until the intensity is 0.1 unity (record 11D, Figure 2).

C.   Responses at intermediate exposures.

The changes resulting from intensity differences at exposures of 111 and 250 msec. are essentially similar to those already discussed.   It is perhaps necessary only to point out the responses of records 10B and 10C, Figure 2, which attain a considerable complexity which is quite constant for this intensity, exposure and temperature.   It is not proposed at present to identify the numerous spikes which are present in this response.

III.   THE EFFECT OF TEMPERATURE ON LATENT PERIOD

In general, the latent period of the electrical response of the eye is greater the lower the temperature.   It is, however, also quite apparent that the latency varies with the intensity of the stimulating light.   Latencies measured on records 7A, 12A, 1A and 6A are given in Table I.

TABLE I

LATENCY OF ERG

	Low intensity (0.0001)	High intensity (1.0)
0– 2° C.	0.18 sec.	0.045 sec.
26–28° C.	0.03 sec.	0.015 sec.

DISCUSSION

In previous publications from this laboratory the variation in wave form and magnitude of the ERG has been described for several insects under a variety of conditions, and it has been stated that most of these variations could be explained as the resultant of three components. However, no overt attempt was made to do so except in *Trimerotropis* where the ganglion potential is measured as part of the ERG (Jahn and Wulff, 1942), but even in that publication no effort was made to carry the three component theory to its logical conclusion for the various peaks of the ERG. *Cynomya* seems to be very favorable material for the study of the component hypothesis because of the presence of all four of the peaks (a-, b-, c-, and d-waves) recorded from other eyes and an additional prolonged positive wave which might be homologized with P III.

Therefore, in the present discussion it is proposed to assume that the insect ERG is the sum of three components similar to those assumed for the vertebrate eye (Granit, 1933) and to make an unbiased examination of the difficulties to which this assumption leads us. The variations and possible origins of each wave will be considered individually.

The a-wave

In the response of *Melanoplus* to very low intensities, the a-wave appears as a typical positive spike. As the intensity is increased the combined b- and c-waves become prominent and the a-wave becomes a notch on the front of the b-wave. When the intensity is greater than fifty foot-candles the a-wave notch is usually imperceptible (Jahn and Crescitelli, 1938; Crescitelli and Jahn, 1939). In *Trimerotropis* there is a notch on the b-wave, but the possible presence of a typical a-wave has not been investigated. This b-wave notch increases with slight light adaptation but disappears if light adaptation is prolonged (Jahn and Wulff, 1942).

In cecropia and polyphemus moths the a-wave is present in the response of the dark-adapted but not of the light-adapted eye. During dark adaptation the a-wave appears first as a notch on the descending phase of the b-wave and migrates forward over

the b-wave until it becomes the initial wave. In Hydrous a-waves have not been detected. In *Chlænius* the a-wave is absent in the day phase, and is present in the night phase only when the eye is dark adapted. In *Dytiscus* the a-wave is quite prominent at both low and high intensity during both the day and night phases, and during light adaptation it first decreases and then increases in prominence (Wulff and Jahn, 1943).

In the present data on *Cynomya* at 26–28° C., the a-wave is typically present at low intensities and becomes a notch on the b-wave at high intensities (as in *Melanoplus*), and it also becomes more prominent with light adaptation (3D, 4D, 5D, 5C, Figure 2). At 0–2° C. the a-wave is prominent, especially at low intensities. At high intensities in the dark-adapted eye it is a notch on the b-wave, but it becomes a prominent and typical a-wave as a result of light adaptation (rows 11 and 12, Figure 2).

In vertebrates the a-wave is supposed to result from the sharp rise of P III. In *Trimerotropis* the notch on the b-wave arises from the ganglion potential. If, for purpose of discussion, we consider this notch the equivalent of an a-wave, we may then consider the a-wave to result from the ganglion potential. The ganglion potential, then, must rise more sharply than the eye potential when the eye is stimulated with low intensities and also when partially light adapted. If one assumes that the magnitude of the recorded ganglion potential varies much less with intensity and slight adaptation than the EMF in the eye, then this explanation becomes plausible. If the EMF of the sense cells is a measure of the amount of photochemical product present (Peskin, 1942; Wulff, 1943; Jahn and Wulff, 1943, Jahn, 1944) then it should be greater in response to high intensity in the dark-adapted eye than in response to low intensity under any condition of adaptation or to high intensity in the light-adapted eye. Under either of these latter conditions, the relative magnitude of the ganglion potential would be greater. This explanation would fit the present data, and that for *Melanoplus,* but not that for *Samia cecropia* and *Polyphemus* where the a-wave increases with dark adaptation. The explanation of the behavior of the a-wave of *Dytiscus* and *Chlænius* is also apparently complex.

The b- and c-waves

The b- and c-waves are consistently present in the ERG of all insects so far studied. In *Melanoplus* the major wave in response to a short flash on the dark-adapted eye is the combined b- and c-waves, and these may be separated by light adaptation (Jahn and Crescitelli, 1938), especially if the exposure is prolonged and made repetitive (*e.g.,* half-second flashes, one per second). These waves are greatly prolonged and decreased in voltage by low temperatures (especially below 10° C.), and the c-wave is also decreased by temperatures above 25° C. so that at 40° C. the response to a brief flash consists only of a b-spike. In *Trimerotropis* and in *Basilarchia* the b- and c-waves are quite prominent (Jahn and Wulff, 1942; Crescitelli and Jahn, 1942) and distinct from each other. In *Cecropia* and *Polyphemus* and in *Chlænius* and other beetles, the b-wave may consist of two peaks (Jahn and Crescitelli, 1939).

In all species studied the b- and c-waves are decreased in voltage by light adaptation. In *Melanoplus* the wave form is not appreciably changed by removal of the optic ganglion (Jahn and Wulff, 1942), and it has been assumed that at least in *Melanoplus* the b- and c-waves are closely linked with the photochemical reaction (Wulff and Jahn, 1943; Wulff, 1943). The effect of temperature (*i.e.,* the variation of temperature coefficients with adaptation and temperature range) can be explained by assuming the photochemical product is the catalyst for the potential producing reaction. In species where the wave form is more complex, and especially when the ganglion potential may be recorded from the front of the eye (*e.g., Trimerotropis,* Jahn and Wulff, 1942) the measured voltage may not be directly related to the photochemical reaction.

In the present data the b- and c-waves are typical of those for the diurnal insects studied in that the magnitude increases with intensity and decreases with light adaptation. This decrease with light adaptation is especially prominent at low temperature where the recovery process should be greatly retarded. At low temperature the c-wave is greatly prolonged as in *Melanoplus.* One outstanding feature of the present records is the apparent reversal in polarity of the c-wave at low temperature and low

intensity (rows 7, 8, and 9, Figure 2). This prolonged positive wave which is not considered to be the c-wave, will be discussed below.

On the theory of three components the b-wave is caused by the spike of P II and the c-wave by P I. These components, then, especially P I, may be considered to decrease with light adaptation and to increase with intensity.

The d-wave

The d-wave occurs after the cessation of illumination and is usually detectable as a distinct wave only if the flash is one-half second or more in duration. The d-wave is absent from the dark-adapted eye of *Melanoplus* but is present in the light-adapted eye (Jahn and Crescitelli, 1938; Crescitelli and Jahn, 1939). It is quite prominent in the dark-adapted eyes of *Trimerotropis* (Jahn and Wulff, 1942) and *Basilarchia* (Crescitelli and Jahn, 1942) but seems to be completely absent in *Samia cecropia* and *Dytiscus* (Jahn and Crescitelli, 1939; Jahn and Wulff, 1943a) and in all other moths and beetles studied. In *Trimerotropis* the d-wave disappears with removal of the optic ganglion as does the notch on the b-wave.

In the vertebrate eye the occurrence of a d-wave is closely associated with the occurrence of an a-wave, and both are supposed to be the result of rapid changes in the voltage of P III. The factors which control the occurrence of the d-wave are more complex than those which control the a-wave in that the former is the result of summation of three components rather than of only two as is the a-wave. In *Trimerotropis* the d-wave and the notch on the b-wave are also associated in that they result from the summation of the voltage from the ganglion and that from the eye.

In *Cynomya* at 26–28° C. the d-wave is more prominent than in any of the other insects studied, even *Trimerotropis*. Its voltage is only slightly affected by intensity, becoming somewhat smaller and more spike-like at high intensities (colums C and D, Figure 2), and slightly larger with adaptation (6C, 6D). At low intensities the a- and d-waves (rows 1 and 2, columns B, C, and D) are of approximately equal voltage and of very similar waveform. At 0–2° C. the d-wave is present but of decreased voltage and increased duration (5D and 6D).

The prolonged positive wave

The most unusual characteristic of the present records of *Cynomya* is the prolonged positive (*i.e.*, front of the eye becomes positive) wave found at low temperature and low intensity (rows 7 and 8, Figure 2). The only other prolonged positive wave we have ever recorded from insects was from injured eyes of *Trimerotropis* (Jahn and Wulff, 1942) and because of the conditions of the experiment these have so far been disregarded. The prolonged positive wave of *Cynomya* is quite constant in its occurrence and was found in every animal examined at low temperature and low intensity. The effect of low temperature is reversible; if the animals are again placed at 26–28° C. records similar to rows 1–6 are obtained. In vertebrate eyes P III, whenever it occurs alone, is supposed to constitute a "negative" wave. Since in the vertebrate literature the voltage change is considered in relation to the back of the eye (*i.e.*, back of the eye becomes negative) the negative wave of vertebrates has the same polarity as the positive wave of *Cynomya*. Therefore, we may tentatively consider the prolonged positive wave to represent P III.

Since the normal ERG is assumed to be composed of three components we must consider that components I and II are affected more by temperature than component III. The difference, for instance, between record 7D1 and record 1D1 would be explained by a decrease in record 7D1 of components I and II, especially of P I. Since the prolonged part of P II is of low voltage, the level of the measured voltage a quarter of a second after beginning of illumination is mostly a balance between I and III. At 26–28° C. this balance occurs at intensities of 0.00001 and 0.0001 units; at 0–2° C. the balance is about 0.001 for the first flash and between 0.001 and 0.01 for later flashes. If P III is only slightly affected by intensity and partial light adaptation, then P I must increase with intensity and decrease with light adaptation, as has been assumed above (section on the b- and c-waves). It also seems necessary to assume that P III is affected only slightly by temperature. Components I and II are apparently decreased in voltage by low temperature but are also somewhat prolonged (*e.g.*, 9D, where the increase of negativity continues after cessation of stimulation). This is in accordance with the

behavior of the c-wave of *Melanoplus* (Crescitelli and Jahn, 1939).

A prolonged "negative" wave (P III) has been recorded numerous times from vertebrate eyes (literature cited by Kohlrausch, 1931; Granit, 1933, 1938; Therman, 1938). It occurs under conditions of etherization, asphyxiation, high concentration of potassium ions, low temperature, and in isolated retinas during degeneration. The effect of low temperature is strictly reversible in the frog eye (Nikiforowsky, 1912), and for many years this was one of the major items of evidence that P III is a normal component. Crescitelli and Jahn (1939a) made an unsuccessful attempt to produce a pure "negative" wave with the eye of *Melanoplus*. At zero ° C. the ERG became reduced in voltage and prolonged, but the polarity was never reversed. In contrast to these results on *Melanoplus*, the polarity of the ERG of *Cynomya* has been reversed in every animal examined. However, in *Cynomya* the reversal occurred only at intensities considerably below the range used by Crescitelli and Jahn on *Melanoplus*.

Applicability of the three-component theory

It seems apparent that if one assumes three components similar in wave-form to those assumed for the vertebrate eye, the present records on *Cynomya* and also other published records from *Melanoplus*, *Trimerotropis*, and *Basilarchia* can be explained on a logical basis. The next consideration is whether or not these components have a real existence in the insect eye, and if so, whether or not they are homologous to the components of the vertebrate eye. This leads us directly to the question of where the components originate in the insect eye.

In *Trimerotropis* there are at least two components: one positive and one negative. In *Melanoplus* the positive component is greatly reduced. In *Cynomya* the reversal of polarity at low temperatures is best explained by assuming two opposed components, and the changes in the b- and c-waves make the assumption of three components seem plausible.

The alternative explanation to the three-component theory would be that one process may produce a potential of different wave form as the intensity, temperature, and state of adaptation

are varied. For purposes of experimental treatment it is easier to consider only changes in magnitude or duration for each of several processes.

If P III is considered to be the ganglion potential, then it undoubtedly makes a considerable contribution to the ERG of *Trimerotropis* and presumably at low intensities (especially when the temperature is low) to the ERG of *Cynomya*. In *Melanoplus* the ganglion potential apparently contributes little to the ERG at high intensity but might be the cause of the a-wave at low intensity.

In the vertebrate eye P III is the least affected by most chemical agents and low temperature. However, it is the most susceptible of the components to ethyl alcohol (Bernhard and Skoglund, 1941). The action of these agents on the ganglion potential is unknown. Furthermore, the experiments of Granit and Eccles (1932, unpublished) and of Granit and Helme (1939) that antidromic impulses in the nerve do not affect the ERG indicate that no component originates in the ganglionic layer of the retina. Therefore it seems best to reserve judgment on the possible homology of the positive wave of *Cynomya*, the ganglion potential, and P III.

Another disturbing thing about the possible homology of P III and the ganglion potential is that the ganglion potential would be less sensitive to low temperatures than the components which we have assumed above to be catalyzed by the photochemical product (*i.e.*, P I and P II). If a ganglion potential can exist when the b- and c-waves are undetectable, then the theory that the electrical change in the eye initiates the nerve impulse should be re-examined. One possibility which has not been investigated is that low temperature may produce a positive wave in the deganglionated eye and that the positive wave of *Cynomya* does not arise in the ganglion.

Another group of data which at present can not be explained on the tricomponent theory are those in which the c-wave is greatly prolonged (moths, and beetles during the night phase of a diurnal rhythm). The origin of this large and greatly prolonged c-wave has not been determined, but its presence clearly separates the electroretinograms into two groups—those with and

those without the prolonged c-wave, the former being nocturnal and the latter diurnal. The animals with a long c-wave may also have a double spiked b-wave of unknown origin.

From the foregoing analysis it is clear that apparently insurmountable problems present themselves in any attempt to homologize the components of vertebrate and insect electroretinograms. We may consider, then, that the components of the insect eye may have quite different origins from components of similar sign and wave form in the vertebrate eye.

The next question is, "Where do the components originate?" For the insect eye the only evidence is that obtained by Jahn and Wulff (1942) who found that both the eye and the ganglion contributed to the ERG. Although this same question cannot be answered yet with any certainty for vertebrates, there are several lines of research which seem promising.

The complexity of the retinal action potential increases with increasing complexity of the retina and with increasing complexity of the receptor-conductor relationships. For example, the electrical response obtained from the eye of *Limulus* (Hartline, 1927–28), which has a single layered receptor and a simple ganglion free retina-nerve relation, is a simple monophasic negative potential. Other arthropods, such as the grashopper *Trimerotropis* (Jahn and Wulff, 1942) perhaps possessing a dual retina (Hanstrom, 1928) exhibit more complex responses. However, upon removal of the optic ganglion *Trimerotropis* exhibits a response similar in simplicity to that obtained from *Limulus*. Most vertebrates, possessing dual retinas of variable rod-cone composition, exhibit a characteristic complex retinal action potential. However, in the tortoise, *Testudo græca*, which has almost no rods, Bernhard (1941) has shown that P III dominates the ERG and that P III is correlated with cone vision. In complex retinas P III is correlated with pre-excitatory inhibition which is supposed to be a feature of the synaptic organization of the cones (Granit, 1944). Furthermore, Adrian (1944) has demonstrated that the wave form of the ERG of man varies with wave-length of the stimulating light, depending upon whether rods, cones, or both are stimulated.

It seems likely that some of the complexity of the vertebrate

and some invertebrate electroretinograms may be attributed to
the involved structural (Walls, 1942) and functional (Adrian
and Matthews, 1927, 1927a, 1928) receptor-conductor relation-
ships. The researches of Adrian (1931, 1937) and Eccles (1943)
and others adequately describe the occurrence of slow negative
potentials in all ganglia and synapses which are excited by nerve
impulses. In fact, to quote Eccles (1943), ''It has been shown
that synaptic transmission may be mediated by the local negative
potential (the synaptic potential) which is set up by a nerve
impulse incident upon a nerve cell.'' In view of the intricate
receptor, nerve, ganglia and synaptic relationships of the ver-
tebrate photoreceptor, it is probable that slow negative potentials
of retinal neurones and synapses play a part in the slow action
potential obtained from the eye. This view has also been ex-
pressed by Adrian and Matthews (1928) in a discussion of their
work on the eel, *Conger vulgaris*.

The latent period

In *Cynomya* the latent period of the ERG increases with low-
ering of the temperature; a similar effect is found for *Melanoplus*
(Crescitelli and Jahn, 1939). The present data also show that
the latent period of *Cynomya* decreases with increasing intensity;
this is also true for *Melanoplus* (Crescitelli and Jahn, 1939, and
unpublished data; this effect is not shown in the published rec-
ords of Jahn and Crescitelli, 1938, because of errors introduced
in the process of engraving). However, no careful study of the
variation in latent period under various conditions has been
made for any of the insects studied.

SUMMARY

The electroretinogram of *Cynomya* was studied at two temper-
atures over a wide range of intensity and flash duration of the
stimulating light. At 26–28° C. and low intensity the response
to a 17 msec. flash is a sharp a-wave (positive). As the intensity
is increased the response becomes diphasic and then becomes a
typical complex b-c-wave (negative). As the flash duration is
increased these same changes occur and in addition a spike-like
d-wave appears, even at the lowest intensity used. At 0–2° C.
the low intensity brief flash resulted in a prolonged positive

wave. As the intensity is increased the response becomes diphasic and then complex and negative. As the duration is increased the positive wave at low intensities is prolonged and the complex negative wave at high intensities becomes somewhat similar to that at 26–28° C. except that the d-wave is less pronounced and the a-wave much more pronounced.

The existence of these complex wave-forms is discussed from the viewpoint of the tricomponent theory. It is concluded that although a three component theory might explain the results it is not possible that the components could have the same significance as those of the vertebrate eye.

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