RETINAL ACTION POTENTIAL — EFFECT OF TEMPERATURE ON MAGNITUDE AND LATENCY IN THE GRASSHOPPER [1]

W. J. FRY,[2] V. J. WULFF[3] AND MANFRED BRUST[3]
[2] *Bioacoustics Laboratory, University of Illinois*
[3] *Department of Zoology, Syracuse University*

TWO FIGURES

INTRODUCTION

The investigation of the effect of temperature on the magnitude and latent period of the retinal action potential elicited by illuminating the compound eye of grasshoppers was undertaken for three reasons: (1) to provide additional evidence in support of the contention that the potential magnitude and latent period are controlled by different processes; (2) to evaluate the effect of temperature on some of the constants in the kinetic model; and (3) to determine the validity of certain predictions suggested by the kinetic model developed in the preceding paper (Wulff, Fry, Linde, '55).

The model for the potential generating mechanism postulates that the action of light on a photosensitive material produces a material designated by C which manifests itself, after the lapse of the latent period, as an e.m.f., the response magnitude of the retinal action potential. The material C accumulates at a rate proportional to the intensity of illumination and it is depleted, during illumination, at a rate proportional to the difference in its concentration at any time and the concentration in the dark adapted eye. This idea is formally represented by equation 2, page 253. If the depletion reaction is thermolabile and the accumulation reaction is thermostable

[1] These studies were aided by a contract between the Office of Naval Research, Department of the Navy, and Syracuse University, NR 119-266.

then a reduction in temperature should increase the plateau magnitude of the potential versus log t_f (t_f — flash duration) curve but should have negligible effect on the rising phase of the same curve if the assumption is made that the equilibrium concentration of C does not vary much over the temperature range 10°–30°C. The experimental results summarized herein show that the response magnitude versus log t_f relation has this characteristic for all but the highest intensities.

The kinetic model controlling the latent period postulates that light acting on a photosensitive substance produces a state or factor P. The rate at which P accumulates is the sum of two rates, one autocatalytic and one proportional to the light intensity. It is assumed that the latent period terminates when the magnitude of P reaches some critical value. These ideas are formally presented in equations 5, 6 and 7, page 256. The model indicates that increasing temperature should produce shorter latent periods and, in particular, that the slope (absolute value) of the linear portion of the curves of latent period versus logarithm of intensity should be greater the lower the temperature. In addition the theory also indicates that the extended linear portions of these curves should intercept the log I (I — intensity) axis at values such that the critical value of P is lower at higher temperatures. The results of temperature studies on grasshopper eyes (Jahn and Crescitelli, '39, Jahn and Wulff, '42) and those on other photoreceptors (Hecht, '19, Nikiforowsky, '11) show that the duration of the latent period is inversely related to the temperature. The experimental data presented herein verify the two specific predictions indicated by the theory of the latent period regarding the changes with temperature.

MATERIALS

Grasshoppers *(Melanoplus differentialis)* used in these experiments were prepared in a manner described previously (Wulff, et al., '55). In these experiments the temperature of the experimental chamber was held at 10°, 20° and 30°

for periods of days to permit the collection of adequate data. The experimental animals seemed not to be adversely affected by the experimental procedure. In all other respects the methods employed were identical to those already described (loc. cit.). Temperature experiments were performed on 15 animals.

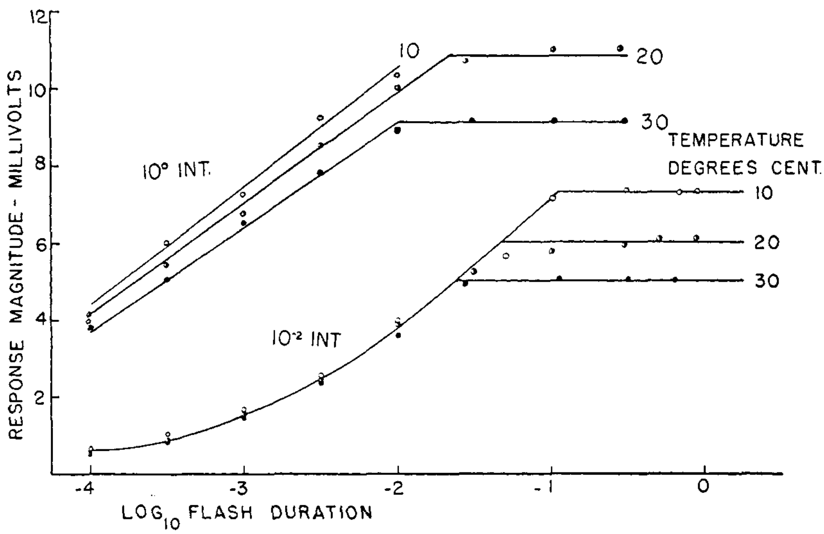

Fig. 1 Magnitude of the grasshopper retinal action potential plotted as a function of the logarithm of the flash duration, for two intensities of illumination and three temperatures. Unit intensity represents 11,800 foot candles at the cornea.

RESULTS

A. The effect of temperature on the potential magnitude. The relation between temperature, duration, and intensity of illumination is presented in figure 1. The data in the lower set of curves were obtained with an illuminating intensity of 118 fc. at the cornea and at three different temperatures. The data in the upper set of curves were obtained with an illuminating intensity of 11,800 fc. on the cornea. Similar results were found in 14 other temperature experiments on grasshoppers.

B. The effect of temperature on the latent period. The relation between temperature, intensity of illumination and latent period is given in figure 2. An intensity value of unity on the scale of figure 2 corresponds to 11,800 fc. The lowest set of points was obtained upon illumination at given intensities for 0.05 secs. duration at 30°C. The upper set of points was obtained under the same conditions of illumination but at 10°C. The middle set of data was obtained upon

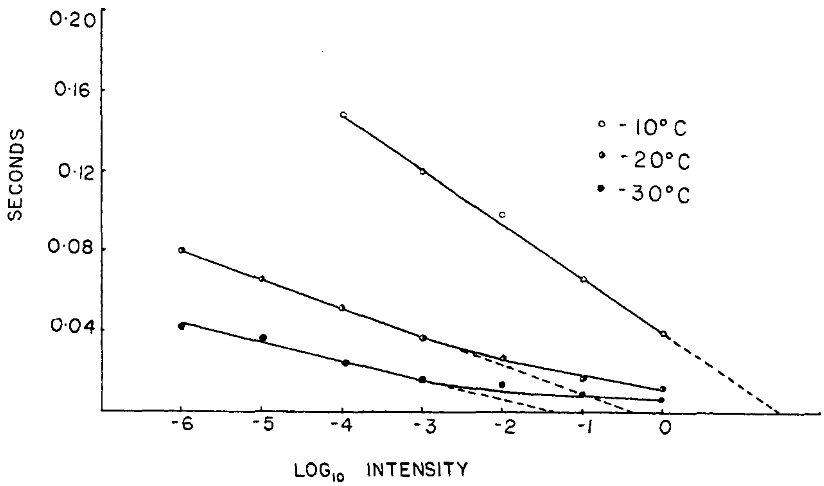

Fig. 2 The latent period of the grasshopper retinal action potential plotted as a function of the logarithm of the intensity for three temperatures. The 10°C. and 30°C. data were obtained from one animal using exposures of 0.05 secs. The 20°C. data were obtained from a different animal using exposures of 0.01 secs. Unit intensity represents 11,800 foot candles at the cornea.

illumination at given intensities for 0.01 sec. duration at 20°C. Similar results were found in 4 experiments of this type on grasshoppers.

C. The ratio of constants at different temperatures. For intermediate intensities (the lower curves of fig. 1) the constant, k, of the depletion reaction in the kinetic model (loc. cit.) is simply related to the reciprocal of the flash duration at the inflection point of the magnitude vs. log t_f curve; i.e. $k = \frac{1}{t_f}$. The temperature coefficient of k expressed as a ratio of its values at two temperatures 10°C apart varies between 1.9 and 2.4 with an average of 2.2.

The rate constant, h, of the autocatalytic reaction in the latent period process (loc. cit.) can be evaluated from the slope, m, of the experimental curves in figure 2, as follows:

$$m = \frac{-\ln(10)}{h}.$$

The temperature coefficient of h expressed as a ratio of its values at two temperatures 10°C apart, and determined from the data of figure 2 is 1.7. This value is obtained using only the 10°C and 30°C curves of figure 2. The average temperature coefficient of h from 3 experiments is *1.50* with a range of *1.25* to *1.70*.

The constant p_c/n, which appears in the model for the latency process (loc. cit.), is evaluated from the intercepts of the linear portions of the curves in figure 2 on the log I axis by using the relation

$$I_i = \frac{hp_c}{n}.$$

Numerically p_c/n is 3.84 $(10)^{-1}$ at 10°C, 2.46 $(10)^{-3}$ at 20°C and 1.64 $(10)^{-4}$ at 30°C.

DISCUSSION

The summary of experimental results, presented herein, concerning the changes in the magnitude and the latency of the retinal action potential of the grasshopper as a function of temperature constitute further support for the kinetic model (Wulff, Fry and Linde, '55) dealing with these characteristics at a single temperature.

The predictions of this model concerning the changes in latency with temperature are verified. The rate constant, h, of the autocatalytic process in the latent period mechanism should increase as the temperature rises. It follows from the theory that h is inversely proportional to the absolute value of the slope of the linear portion of the curves of latent period versus logarithm of intensity. The experimental data (fig. 2) show that the slope increases as the temperature decreases. Thus, the prediction concerning the variation of the rate constant, h, as a function of temperature is verified. It is of interest to note that the value of the temperature coefficient of h (average *1.5*) is low for a chemical reaction. It is, of course, possible that the model for the latent period does not imply a chemical process.

The model also indicates that the intercepts of the linear portions of the curves of latent period versus logarithm of intensity on the log I axis should satisfy a specific inequality relation. That is, the intercepts should have values such that the magnitude of the factor P, derived from the experimental data, which determines the time of initiation of an electrical response, decreases as the temperatures increases. Since the parameter n is the rate constant for a light initiated process it would not be expected to vary much over the temperature range used in these experiments. The variation in the quantity p_c/n with temperature is then essentially a measure of the variation of p_c with the temperature. The numerical values for p_c/n given above, which are derived from the intercept values of the experimental curves, then verify the prediction of the model. The quantity p_c decreases rapidly as the temperature increases, between 10°C and 20°C it decreases by a factor of 156 and between 20°C and 30°C it decreases by a factor of 15.

The variation in the response magnitude at all but the highest intensities exhibits a striking behavior, which is consistent with the model. At a constant intensity, response magnitude as a function of the flash duration is expressed as a rising curve independent of the temperature until it increases to a value which, for further increases in flash duration, becomes constant. This constant value is temperature dependent.

It was predicted on the basis of the model that the plateau value should certainly vary with the temperature since the rate constant, k, of the chemical reaction determining the rate of depletion of C determines the value of the flash duration at which the plateau starts. The temperature coefficient of k (average $Q_{10} = 2.2$) calculated from the experimental data is within the usual range of values characteristic of many chemical reactions.

It is not possible to conclude theoretically that the rising phase of the relation between response magnitude and flash duration should be independent of the temperature; actually a variation with temperature is not opposed by the model. However, the nonvariation of this rising phase with temperature constitutes strong support for the model since this particular characteristic is realized by assuming that the equilibrium concentration of C in the dark adapted eye is practically constant over the temperature range of interest in this paper.[4]

Such an assumption is not unreasonable but it is not implied that because this situation obtains in grasshopper eyes that this would be characteristic of eyes in general.[5]

The deviation from the model which occurs at the highest intensities is exhibited as a compression of the plateau values and change in slope of the linear rising phase of the relation between response magnitude and logarithm of flash duration. This sort of deviation at the highest intensities and constant temperature appears to be at least partially associated with the appreciable depletion of the light sensitive substance during the time of the flash (Wulff, Fry and Linde, '55).

[4]The constants b and a are also involved in determining the form of this relation. However, b is the rate constant of the light initiated process and consequently should not vary much over the temperature range of the data presented here. The constant a which is the proportionality parameter relating emf to logarithm of concentration would not be expected to vary much over this same temperature range if it is assumed that this parameter has a temperature coefficient similar to that characterizing many voltaic processes.

[5] The effect of temperature on the characteristics of the retinal action potential of the lateral eye of Limulus is being investigated. The results indicate that the effect of temperature on response magnitude of the Limulus retinal action potential is different from that of the grasshopper but the effect on latency is similar.

LITERATURE CITED

CRESCITELLI, F., AND T. L. JAHN 1939 The effect of temperature on the electrical response of the grasshopper eye. J. Cell. and Comp. Physiol., *14:* 13–27.

HECHT, S. 1919 The effect of temperature on the latent period in the photic response of Mya arenaria. J. Gen. Physiol., *1:* 667–685.

JAHN, T. L., AND V. J. WULFF 1943 Effect of temperature upon the retinal action potential. J. Cell. and Comp. Physiol., *21:* 41–51.

NIKIFOROWSKY, P. M. 1912 Über den Verlauf der photoelektrischen Reaktion des Froschauges bei abkühlung. Zeitschr. f. Biol., *57:* 397–412.

WULFF, V. J., W. J. FRY AND F. A. LINDE 1955 Retinal action potential — Theory and experimental results for grasshopper eyes. J. Cell. and Comp. Physiol., *45:* 247.