THE EFFECT OF SEX AND AGE ON THE TEMPERATURE AT WHICH REVERSAL IN REACTION TO LIGHT IN ERISTALIS TENAX OCCURS

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Introduction

One of the most tantalizing phenomena facing the physiologist is the change of sign of reaction to light that occurs in many organisms. In this reversal an organism which is normally photopositive, moving toward the light, becomes negative and avoids the light, or a normally photonegative organism, moving away from the light, becomes positive. Some even consider this phenomenon "unapproachable," according to Maier and Schnierla (1935). Although this has claimed the attention of extremely able investigators for over 75 years, Holmes' statement (1916) holds good today. "The mechanisms involved are still unknown." The need for information concerning this problem is shown by the brevity of the paragraphs devoted to it by Wigglesworth (1939) and Heilbrunn (1943).

Reversal in reaction to light occurs "spontaneously" with no change in external conditions in Daphnia (Ewald, 1914; Clarke, 1932) and in Spondylomorum (Mast, 1918). It occurs rhythmically in some animals, according to Bohn (1905, 1907, 1909), Ewald (1914), and Warden, Jenkins, and Warner (1940), and in the course of normal development in others (Fraenkel and Gunn, 1940). For example, lobster larvae (Hadley, 1908) are positive for two days after hatching when they become negative and remain so until shortly before molting when they again become positive. They are negative in the early second stage and third stage but become positive before molting. In the fourth and later stages they are negative.

Various investigators maintain that a reversal of sign of the reaction to light can be produced in many organisms by the following changes: I. In the organism itself: metabolic rate, muscle tonus, water content, concentration of certain hormones, adaptation in sense organs, orientation to gravity, mode of locomotion (e.g., from swimming to crawling), mechanical stimulation, operations (such as removal of all or part of the wings or brain), training, and genetic constitution. II. In the immediate environment: temperature, food supply, background, light intensity (both gradual and rapid), wave length of light, osmotic pressure, oxygen pressure, hydrogen ion concentration, viscosity, and other changes produced by the addition of various inorganic and organic compounds.

Of all these methods none is more important than the use of alterations in temperature to produce changes in the sign of the reaction. An increase in temperature makes some photopositive organisms negative and some, that are negative, positive, while a decrease in temperature makes some positive organisms negative and some, that are negative, positive.

The animals and plants used in previous studies on the effect of temperature on reversal in reaction to light are as follows; swarm spores of *Haematococcus, Uloth-*

rix, and other algae (Strasburger, 1878); *Euglena, Volvox, Spondylomorum,* and other algae (Mast, 1911, 1918, 1927, 1932, 1936); the flagellate, *Chromulina* (Massart, 1891); *Rana clamata* (Torelle, 1903); *Arenicola* larvae (Kanda, 1919); *Polygordius* larvae (Loeb, 1893, 1905, 1906, 1918); *Lumbricus* and *Eisenia* (Prosser, 1934; Mast, 1936); *Cyclops, Cypris,* and a water spider (Mast, 1911); certain marine copepods (Loeb, 1893, 1905; Parker, 1901; Rose, 1929); *Daphnia* (Groom and Loeb, 1890; Loeb, 1906; Mast, 1911; Dice, 1914; Rose, 1929; Clarke, 1932); the copepod, *Leptodora* (Siedentop, 1930); *Artemia salina* (Bujor, 1911); *Balanus* nauplii (Groom and Loeb, 1890; Ewald, 1912; Rose, 1929); nauplii of the barnacle, *Chtamalus* (Rose, 1929); various amphipods (Phipps, 1915; Holmes, 1916); *Ranatra* (Holmes, 1905, 1916); *Notonecta* (Essenberg, 1915); the Mayfly nymphs, *Epeorus* and *Leptophlebia* (Allee and Stein, 1918); the beetle, *Anthrenus muscorum* (Janda, 1931); *Drosophila* (Carpenter, 1908); mosquito larvae, *Culex pipiens* (Miller, 1940); the tsetse fly, *Glossina morsitans,* and the stable fly, *Stomoxys calcitrans* (Jack and Williams, 1937).

The small number of species of insects tested furnishes no basis for Holmes' statement (1916), "In the insects reversal of the positive reaction is rather uncommon."

Because nothing is known about the effect of age and sex on the temperature at which reversal occurs in any organism, and because nothing whatever is known about reversal in *Eristalis tenax,* a study of reversal in reaction to light in this insect was made. For this work the drone fly proved as excellently adapted as it has for many other phases of physiological research.

In this paper are presented the results of a study of the effect of sex and age on the temperature at which reversal of reaction to light occurs. *Eristalis* at ordinary temperatures is highly photopositive. Preliminary experiments showed that between approximately 10°C. and 30°C. the flies crawl or fly directly toward a source of light. Outside these limits they are highly negative, moving directly away from a source of light. Since it was found impractical to study in detail the behavior of these flies at low temperatures but comparatively easy at high temperatures, this paper deals almost entirely with the latter.

Materials and Methods

The apparatus used (Fig. 1) consists of a box made of 6.3 mm. plywood (50 × 35 × 34 cm.). There are two main compartments, a light one, *A,* and a dark one, *B.* The light compartment is lined with white cardboard on the bottom, two sides and one end. The two compartments, 6.25 cm. deep, are separated by a wooden slide, *a,* painted white on the side toward the light compartment, which can be raised. Above the light compartment are two sliding glass panels, *b, c,* 6.3 cm. apart. A thermometer, *r* is inserted through a hole, *d* at the level of the white floor, *e.*

The dark compartment, *B,* has the same dimensions as the light compartment, but is lined with dull black cardboard and has a removable wooden cover, *f,* through the center of which a thermometer, *g,* is inserted. A glass window, *h* (3.8 × 12.5 cm.), covered by a removable shade on the outside, is at one end of this compartment.

Below the detachable floors, *i, j,* of each compartment the construction is identical. Five centimeters below these floors is a sheet of galvanized steel on which rests a cardboard, *k*. Below the metal bottoms are two heat chambers, 12.5 cm. deep, *C, D,* lined with corrugated cardboard, *l,* and asbestos sheeting, *m*. The heat is supplied by two 100-watt Mazda lamps, *n,* with constant voltage, each lamp being wired separately.

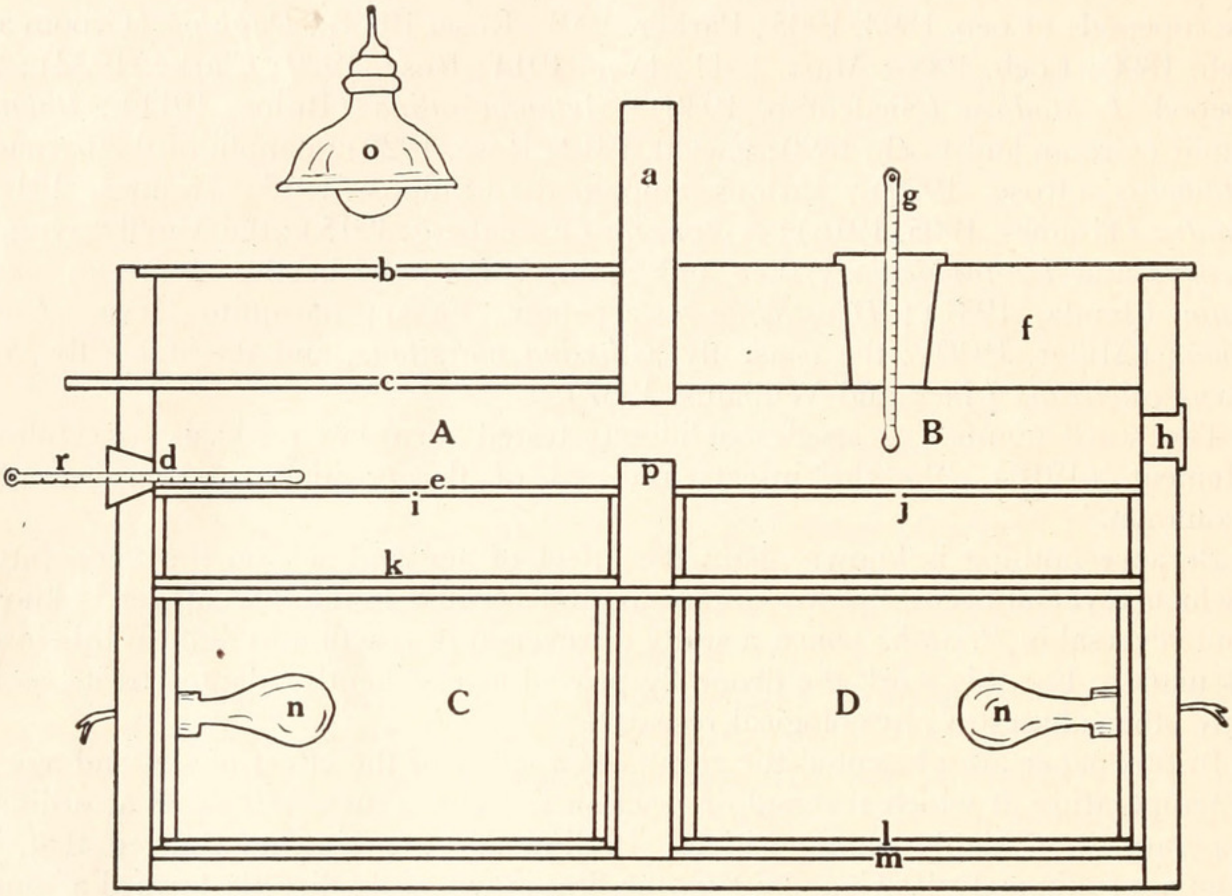

FIGURE. 1. Sectional view of the apparatus used. See text.

A 100-watt Mazda lamp, *o,* was suspended 81.25 cm. over the center of the white floor of the light compartment. The luminous intensity on this floor was 700 f.c., as recorded by a Weston exposure meter.

In these experiments only flies of known age and sex were used. They were raised in the laboratory according to the methods previously described (Dolley et al., 1937, p. 410). The exact temperature at which the flies became negative to light and went into the dark chamber was ascertained for six groups of flies whose sex and age are as follows:

1. Young males, 5–16 days.
2. Young females, 5–16 days.
3. Middle-aged males, 28–36 days.
4. Middle-aged females, 28–36 days.
5. Old males, 48–77 days.
6. Old females, 48–77 days.

Two hundred and seventy observations were made on members of each of these groups. No more than three were made on an individual insect and at least twenty-four hours elapsed between successive observations on the same fly.

All experiments were performed in a dark room. A typical experiment was made as follows: The temperature in the dark compartment was raised to between 35° C. and 37° C., that in the light compartment was raised to 28° C. Throughout the experiment the temperature in the dark compartment was seven to nine degrees higher than that in the light compartment. Ten to fifteen flies of the same age and sex, and with unclipped wings, were placed in the light compartment by sliding back the glass plates, *b, c*. These plates were replaced; the heating unit under the light chamber was turned on; and the center slide, *a*, was raised, making an opening (18 × 4 cm.) connecting the two chambers, *A, B*.

As the temperature in the light chamber rose the flies became restless, crawling and flying about. Soon individuals moved out of the light into the darkness of the dark chamber. A fly was considered to have reversed when it had passed completely beyond the center ridge, *p*. When this occurred the investigator recorded the temperature in the light compartment. The flies followed one another, and one by one entered the dark compartment. Frequently a fly returned to the light compartment after a few minutes in the dark, and then after a few seconds returned again to the dark compartment. Sometimes a given fly made three or four such successive reversals. The temperature at which the final reversal of a given fly took place was recorded and considered one observation. After approximately twenty-five minutes all the flies had reversed and entered the dark compartment. The organisms were then removed and those that had survived were placed in a cage with food and water. They were used for a maximum of two other experiments similar to that described above. An interval of at least twenty-four hours elapsed between successive tests on the same flies. About twenty-five per cent of the insects used in a given experiment did not survive their exposure to the high temperature of the dark compartment.

Results

The results obtained are given in Figure 2 and Table I. As is shown in this table, the mean temperatures in degrees centigrade at which the flies reversed are as follows: old males, 33.18 ± 0.09; old females, 33.822 ± 0.091; middle-aged males, 34.450 ± 0.088; middle-aged females, 35.06 ± 0.11; young males, 35.500 ± 0.099; young females, 36.106 ± 0.082. The standard deviations (Table I) are as follows: old males, 1.485 ± 0.064; old females, 1.489 ± 0.064; middle-aged males, 1.440 ± 0.062; middle-aged females, 1.742 ± 0.075; young males, 1.623 ± 0.070; young females, 1.318 ± 0.057.

Are the differences between the mean temperatures just given at which the two sexes reversed significant? According to Pearl (1940, p. 287), "the odds are 369.4 to 1 against the occurrence of a deviation in either the plus or minus direction as great or greater than 3 × S.E. These are long odds, and are conventionally regarded as amounting to practical certainty."

The differences between the means of the two sexes of the old, middle-aged and young flies are, respectively, 5 +, 4 +, and 4 + times the standard errors of the differences. This means that the odds against the occurrence from chance of these differences are, respectively, over 1,744,000; 15,770; and 15,770 to 1. It is evident that the differences between the means of the sexes in the above three age groups are clearly significant. Consequently, it is obvious that in each group the female flies reversed at a higher temperature than the male flies.

Age also has a definite effect on the temperature of reversal. This is shown when the observations on the individuals, both males and females, of the same age, are put together, as is done in Figure 2 and the lower portion of Table I. It is clear from this figure and table that the mean temperatures at which the old, middle-aged and young flies reversed are: 33.50 ± 0.07, 34.781 ± 0.071, and 35.786 ± 0.064, respectively. The differences between the means of the old and middle-aged, the old and young, and the middle-aged and young flies are, respectively, 12 +, 22 +, and 10 + times the standard errors of the differences. Consequently, age is an important factor in determining the temperature at which *Eristalis* changes its reaction to light. The younger the fly, the higher the temperature at which reversal occurs.

TABLE I

The effect of sex and age on the temperature at which reversal in reaction to light in Eristalis occurs. See text

Age	Sex	Mean temperature in degrees centigrade ± standard error	Standard deviation ± standard error
Old	male	33.18 ± 0.09	1.485 ± 0.064
	female	33.822 ± 0.091	1.489 ± 0.064
Middle-aged	male	34.450 ± 0.088	1.440 ± 0.062
	female	35.06 ± 0.11	1.742 ± 0.075
Young	male	35.500 ± 0.099	1.623 ± 0.070
	female	36.106 ± 0.082	1.318 ± 0.057
Old		33.50 ± 0.07	1.522 ± 0.046
Middle-aged		34.781 ± 0.071	1.652 ± 0.050
Young		35.786 ± 0.064	1.477 ± 0.045

It is patent that in the young flies the females with a standard deviation of 1.318 ± 0.057 showed less variation than did the males with a standard deviation of 1.623 ± 0.070; that in the middle-aged series the females showed greater variation than the males; that in the old flies the variation in the two sexes was about the same; and that between the three groups of different ages, each being composed of flies of both sexes, the young flies showed the least variation. The significance of the differences given above is not at present known, but it is true that the young flies were a more homogeneous group so far as age is concerned than were the old flies. The maximum difference in age between the members of the young series was eleven days, while the maximum difference in age between the members of the old series was twenty-eight days, a long period of time in comparison with the duration of life of *Eristalis*.

The reversals described above are unquestionably reversals to light and not to heat energy. The flies in going from the light compartment into the dark compartment were not going from a region of high temperature to one of lower heat energy. The reading on the thermometer (Fig. 1, *r*) in the light compartment was compared with that of a black bulb thermometer made by coating a thermometer with lamp black. During the experiments the temperature as recorded by the latter was only 1.5 degrees higher than that recorded by the one used. Consequently, even if the flies had absorbed as much heat energy as did the black bulb thermometer, still the effective temperature in the dark compartment would have been from 5.5 to 7.5 degrees higher than that in the light compartment.

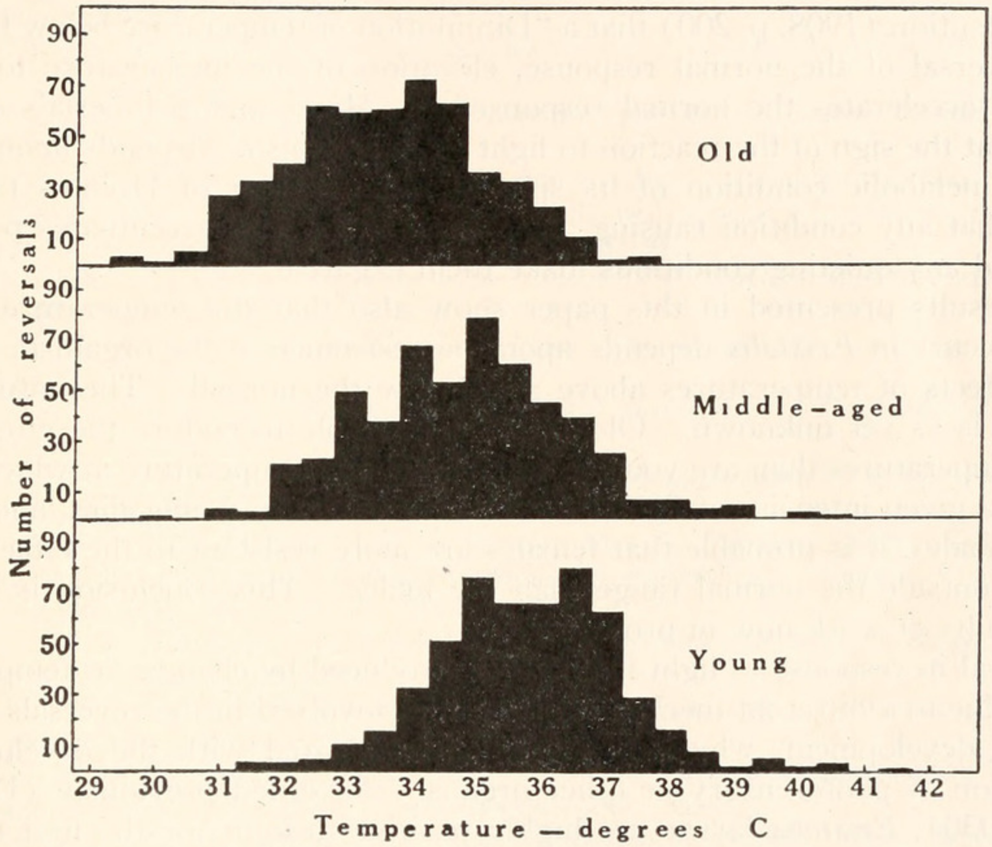

FIGURE. 2. Histogram showing the effect of age upon the temperature at which reversal in reaction to light in *Eristalis* occurs. Note that the means of the reversals for the older flies are at lower temperatures than are the means for the younger ones. See Table I.

DISCUSSION

The results presented in this paper show that the temperature at which *Eristalis* reverses in its reaction to light is not correlated specifically with either a decrease or an increase in heat energy for it can be caused by both. Reversal in sign of reaction occurs both when the temperature is raised above a certain point and when it is lowered below approximately 10°C., as stated previously.

This conclusion is in harmony with the following: 1. Mast's contentions (1918) that a decrease in heat energy and an increase in light energy produce similar effects in photopositive euglenae and other algae, and (1936) that reversal in *Volvox* and *Euglena* is due to "internal changes" and "is not specifically correlated with the immediate environment"; 2. the conclusion of Phipps (1915) that reversal in certain amphipods is associated with changes in their "physiological states"; 3. that of Welsh (1930) that reversal in the water mite, *Unionicola*, "is probably a central nervous phenomenon"; 4. that of Washburn (1936, p. 208) that the "complex influence of external and internal conditions on phototropism" . . . "is based on innate factors"; 5. that of Allee and Stein (1918) that reversal in reaction to light in certain Mayfly nymphs is associated with either increase or decrease in metabolic rate; and 6. those of Jack and Williams (1937) that if the temperature is raised sufficiently high the normally photopositive reactions of the tsetse fly, *Glossina morsitans*, and the stable fly, *Stomoxys calcitrans*, become reversed, and that "the temperature at which the negative reaction develops appears to depend somewhat upon the flies' physiological conditions."

The conclusion stated above is not in harmony with the following: 1. Davenport's contention (1908, p. 200) that a "Diminution of temperature below the normal causes reversal of the normal response, elevation of the temperature to near the maximum accelerates the normal response"; 2. Maier and Schnierla's conclusion (1935) that the sign of the reaction to light in an organism "depends upon the characteristic metabolic condition of its species"; and 3. that of Holmes (1905) for *Ranatra* that any condition causing an increase in activity accentuates positive reactions and any quieting conditions make them negative.

The results presented in this paper show also that the temperature at which reversal occurs in *Eristalis* depends upon the resistance of the organism to the injurious effects of temperatures above and below the normal. The nature of this resistance is as yet unknown. Old flies are less able to endure the effects of abnormal temperatures than are young ones. Since the temperature at which reversal occurs in a given intensity of light is lower in old than in young flies, and in males than in females, it is probable that females are more resistant to the effects of temperatures outside the normal range than are males. This conclusion is confirmed by the results of work now in progress.

Reversal in response to light in *Eristalis* produced by changes in temperature is probably due to a different mechanism from that involved in the reversals occurring in normal development, which are doubtless associated with the development or degeneration of photosensory or other organs. As stated previously (Dolley and Haines, 1930), *Eristalis* larvae are highly positive to light for the first few hours after hatching. They then become negative to light and remain so until they pupate. The imagos are at first negative but soon become positive at ordinary temperatures, and remain so throughout their lives. Similar phenomena have been described for blowflies (Herms, 1911; Gross, 1913; Patten, 1916), *Amaroucium* larvae (Grave, 1920; Mast, 1921), and for other organisms. According to Pause (1918) Chironomus larvae are positive until they have formed haemoglobin when they become negative.

SUMMARY

1. Over 1,620 observations were made on over 1,000 flies in ascertaining the temperature at which *Eristalis tenax* becomes negative to light.

2. In a luminous intensity of 700-foot candles *Eristalis* is highly photopositive within a temperature range between approximately 10° and 30°C. Outside these limits it is highly negative. Reversal of the photopositive reaction can be produced either by increase or decrease of the temperature.

3. In high temperatures the temperature at which *Eristalis* changes in its reaction to light depends on the sex of the flies. Females cease their positive reaction to light and become negative at a higher temperature than do males.

4. In high temperatures the temperature at which *Eristalis* changes in its reaction to light depends also on the age of the flies. The younger the fly, the higher the temperature at which it ceases its positive reaction to light and becomes negative.

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