THE SPECTRAL SENSITIVITY OF CALLIPHORA MAGGOTS

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If fly larvae are put on a table by a window they immediately begin to travel away from the light. Turn the table round, and the maggots change direction so as to move directly away from the light again. They travel by a ‘tacking’ process—the head end is extended to right and left alternately, and each time the rear end is drawn after it. The animal moves on a straight course if this process is symmetrical; should a movement of the head bring it into a region of higher illumination or other undesirable condition the head is withdrawn, and a second step made to the opposite side, turning the animal round.

Placed between two opposing lights, the maggots will travel towards the weaker, and the direction of travel may be reversed by increasing the intensity of the weaker light until it, in turn, is the brighter. In the present work this reaction is used to equate the luminosity of lights of different wavelengths to a standard, and hence to draw a spectral sensitivity curve.

Bolwig (1946) performed a series of detailed experiments, behavioural and micro-anatomical, on the larva of the related Musca domestica, and says: ‘The search for the light-sensitive cells has resulted in finding some cells at the bottom of a pair of pockets (directed forward) in the anterior end of the pharyngeal skeleton; these cells must undoubtedly be regarded as the light-sensitive cells.’

The gulf which separates the maggot from the adult fly, with its compound eyes and array of ocelli, is crossed in the 10 days or so of pupation. Ellsworth (1933) had thought that the tips of the maxillary lobes of the fleshfly larva were its light receptors, and that they must degenerate at metamorphosis without taking part in the formation of the compound eyes; this is not the case in larvae with lateral ocelli. Bolwig’s finding, that these maxillary papillae are chemoreceptors in the housefly larva, means that the compound eye may evolve from the rudimentary lateral larval structure. It would be interesting to know if any light-sensitive pigment used by the maggot is retained through metamorphosis, or whether the emancipated fly has replaced the whole chemical basis of its larval light sense.

Much attention has been paid to the spectral sensitivity of adult blowflies, using behavioural methods (Schneider, 1956) and electrophysiological means (e.g. Wålther & Dodt, 1959; Autrum, 1955). Apart from the work of Mast (1917) on unidentified blowfly maggots, and Bolwig (1946) on housefly larvae, however, there appears to be no information about spectral sensitivity of larval Diptera.

The wealth of information about adult flies appears rather inconsistent at first sight. Comparison of the various spectral sensitivity curves, which are illustrated in
Figs. 6 and 7, is reserved for the discussion; it will then be possible to include the present results, and to try to show an emerging pattern of dependence on intensity and other experimental conditions.

**APPARATUS**

A metal bridge was made, covered with black adhesive plastic film. The platform of the bridge was 12 in. long by 4 in. wide, and the sides were turned up to form 1 1/2 in. high walls to prevent the maggots from straying. The ends of the platform were turned down to form sloping ramps 4 in. high, each leading down into a steep-walled dish to collect the maggots. Fig. 1 illustrates the experimental arrangement.

The bridge and the two dishes were placed symmetrically in a black box 17 in. long. In the end-walls of the box, on a level with the platform, were 2 cm. square holes filled with flashed-opal glass, illuminated respectively by the two light sources. Behind one opal square was a calibrated monochromatic light source. This consisted of a 32 V., 100 W. Philips projector lamp, $S$, fan-cooled. Two pieces of Chance glass absorbed heat from the lamp, an achromatic lens combination of focal length 1/4 in. collimated the beam, which passed through a 2 cm. square Balzer interference filter, $\lambda$ (type B, 40% transmission, the width of the band of wavelengths being about 10 m$\mu$ at the 20% transmission level), and through neutral density filters to the opal square. The wavelengths used in all the experiments were 402, 417, 442, 462, 489, 499, 513, 531, 554, 579, and 602 m$\mu$. At the lower intensity level (level $B$) filters at 362, 392, 621 and 640 m$\mu$ were included. A filter at 470 m$\mu$ was added to the later series, at the higher intensity level (level $A$).

Suitable screening masks were provided, and the opal square was inspected from inside the black box before each run to confirm that stray light was excluded.

Behind the second opal square, at the other end of the bridge, was the standard light source, which consisted of a 12 V., 6 W. car headlamp bulb, $S'$, another piece of opal glass to diffuse the light, and a neutral density filter. (Both incandescent lamps were supplied by 50 cyc./sec. a.c., using suitable transformers.)

The standard light, without its neutral filter, gave a reading of 0.3 f.c. at the middle of the bridge, measured with a Holophane photometer. Two values of neutral filters were used, one (level $A$) giving approximately 0.001 f.c. at the middle of the bridge, and the other (level $B$) 0.001 f.c. (1 f.c. = 1.076 lumens per square metre).
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The relative energy of the monochromatic source was found at each wavelength by a null method: the photo-current of a Mazda type 27 M 1 photomultiplier, of known relative spectral sensitivity, was kept constant by the addition of neutral density filters and neutral wedges.

The photomultiplier was calibrated at the National Physical Laboratory, and the nominally neutral filters and wedges were calibrated by comparison with a set of rotating sectors.

The same Ilford neutral density filters, in steps of approximately 0.25 log unit, were also used for the experiments.

MAGGOTS

The Calliphora vomitoria maggots, used in most of the experiments, were sold as 'gentles' for fishing. A sample of each batch was allowed to develop into flies, which were all identified as C. vomitoria.

The C. erythrocephala stock was kindly supplied by Prof. V. B. Wigglesworth.

The C. vomitoria were bred on stable manure, C. erythrocephala on lean beef. In both cases the animals were used after they had left their food, which was no longer visible in the alimentary tract.

METHOD

About forty maggots, dark-adapted for at least 2 hr., were placed in the middle of the bridge, using a wide funnel, in very faint light. A black cloth was spread over the outer box, and the two lights, one at each end of the bridge, were switched on simultaneously. After 10 min., the lights were switched off, and any maggots and pupae left on the bridge were discarded. The maggots in each dish were counted, and the number which had travelled towards the standard light was expressed as a percentage of the total in both dishes. (With the standard light alone, at least 70% travelled away from the light.) Each interference filter was used in combination with a series of neutral density filters, at approx. 0.25 log unit intervals; according to the intensity of this monochromatic light either more or less than half of the maggots went towards the standard light. An intensity was found by interpolation at which the two lights were equally effective, as in Fig. 2. The energy at each wavelength, matched like this to the same standard, is the relative threshold on an equal energy basis. To get the relative quantum threshold, the energy needed at each wavelength, \( A \), must be divided by the magnitude of a quantum of energy, which is proportional to \( 1/\lambda \).

The reciprocal of the relative quantum threshold, expressed as a percentage of its maximum, is the percentage quantum sensitivity. This function \( B \), plotted against \( \lambda \), may be considered a first approximation to the absorption spectrum of a hypothetical visual pigment.

RESULTS

In Fig. 3 the relative quantum sensitivity is plotted on a logarithmic base against wavelength. The points (●) refer to C. vomitoria at level A, and the circles (○) at level B. Crosses (×) refer to C. erythrocephala, tested only at level A.

The mean difference between the results at levels A and B for C. vomitoria was 1.04 log units, and this has been allowed for in plotting the curves.

The results at level B, (○) and (×), are derived from between four and ten groups of maggots, as in Fig. 2, which gives an accuracy of about ±0.1 log unit. In order to
find the maximum more exactly for *C. vomitoria* at level *A* at least 15 groups of maggots were used to determine each of the points around 500 mμ, and 32 groups for the wavelength 499 mμ which was taken as 100% (2.0 on the logarithmic scale). The three sets of results are, within experimental accuracy, the same.

The lower level of illumination, level *B*, was used in order to extend the wavelength range (362–640 mμ). At level *A* it was restricted (from 402 to 602 mμ) by the energy of the monochromatic source, but this level had the advantage that the maggots could be used when their response to light was not at its strongest.

Fig. 4 shows the percentage quantum sensitivity for *C. vomitoria* plotted against wavelength. As before (●) represents results at level *A*, supplemented at lower and higher wavelengths by results at level *B*, shown as circles (○).

The bell-shaped curve is characteristic of visual pigments of the rhodopsin type, otherwise known as visual purple; assuming it to be due to a single pigment, it would be best fitted by a visual pigment with a maximum at 504 mμ. The absorption curve of such a hypothetical pigment is drawn (Dartnall, 1953).

The effect of the epithelium covering the light-sensitive cells is not known. The whole maggot is creamy white, so the most likely effect is to reduce the sensitivity to the violet end of the spectrum a little, by scattering. Bolwig does not describe any specialized structure to concentrate the light in *Musca domestica* maggots.

It was of interest to know the level of the relative threshold above the absolute threshold, and this was found for one wavelength. About 400 maggots of *C. vomitoria* were divided into eight groups on the last day before pupating, and were dark adapted.

The filter of wavelength 442 mμ was used, with 1, 2, 3, 4, 4.25, 4.5, 4.75 or 5 log units of neutral density filters. There was no opposing standard light, but otherwise the apparatus was the same as in the main experiments.
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Fig. 3. The relative quantum sensitivity as a function of wavelength. The points (●) refer to C. vomitoria at level A, the circles (○) at level B. Crosses (×) refer to C. erythrocephala at level A. (Level A is equivalent to about 0.01 f.c., level B to 0.001 f.c.).

Fig. 4. The percentage quantum sensitivity for C. vomitoria as a function of wavelength. ● represents mean results at level A, ○ at level B. The line is the absorption curve for a hypothetical visual purple, with a maximum at 504 mμ (Dartnall, 1953).

In Fig. 5, the percentage of each group of maggots collected at the end of the bridge away from the light is plotted against the neutral density filter used. A blank experiment, in darkness, was included. The maggots were left for several hours and the experiment repeated. Both results are shown. The absolute threshold is about 4.0 log units.
below level $A$, i.e. the maggots would just respond to a level of illumination of the order of $10^{-6}$ f.c., i.e. of about $10^{-5}$ lumens/m.$^2$. This is only one log unit more than the minimum intensity needed by man under dark-adapted conditions (Denton & Pirenne, 1954), with a natural pupil of about 0.5 cm.$^2$ (Le Grand, 1948). Now, if man and maggot required the same quantity of light energy at threshold, the levels of illumination at the respective thresholds would be inversely proportional to the areas of the eye pupil in man, and of the total light-sensitive region of the maggot. The difference of one log unit, found experimentally, would on this basis lead to the conclusion that the light-sensitive region of the maggot was one-tenth of man's pupil area, i.e. 0.05 cm.$^2$. This is impossibly large, compared with the size of a maggot, and it is therefore more likely that the high sensitivity is due to some other cause, such as pigment concentration.

![Diagram](image)

Fig. 5. Determination of the absolute threshold of *C. vomitoria* for 442 m.$\mu$; below this level, equal numbers of maggots travel towards the light and away from it. The intensity is governed by the neutral density filter shown in the abscissa. The levels of the relative thresholds are shown as $A$ and $B$.

A direct determination of the author's own absolute threshold of vision, after 45 min. of dark adaptation, confirmed this remarkable efficiency of the maggot, area for area. An artificial pupil of area 2.5 mm.$^2$ was set up at the position of the middle of the bridge, and neutral density filters were added until the standard light at level $A$ was only just visible. At this level the intensity was only half a log unit less than at the absolute threshold for the maggot. Corrected to a pupil area of 0.5 cm.$^2$, this threshold is of the same order as that found by other workers.

**DISCUSSION**

**Discussion of the method**

Bolwig describes the trial-and-error progression of a maggot, which appears to be superimposed on a stronger or weaker drive to wander about at random.

Maggots nearer pupation respond more consistently to light than younger larvae.
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For example, the same light which made 70% travel away, 2 days before pupation, caused 97% to travel away on the last day. In each case the maggots had rested undisturbed in the dark overnight. When maggots which had travelled to the light were gathered up, rested in the dark and tested separately, they divided in the same ratio as before; the group which had travelled away from the light did the same. This suggests that the photonegative behaviour is superimposed on random wandering, rather than that any of the maggots were photopositive.

The finding that older larvae are more responsive to light does not agree with Patten (1916). From a teleological point of view, it is in the interest of the maggots to leave the shelter of the food and disperse, before finding a dark corner to pupate. Bolwig attributes the mechanism of the more accurate orientation of older larvae, relative to the light, to the increasing shielding of the light-sensitive organs from light coming from behind; he says that younger larvae soon become tired and stop responding to light, as was also found in the present work.

The only effect of this lower response on the relative threshold determination is to make the graph of the percentage travelling away from the monochromatic light (e.g. Fig. 2) slope less steeply—it does not change the point of crossing the 50% line. Mast’s work on blowfly maggots was a relative threshold, while Bolwig’s threshold for the housefly maggot suffers the disadvantage of being an absolute threshold.

Certain precautions were taken with a knowledge of the habits of maggots. If they were damp from their food, they were mixed with dry bran before dark adaptation, since a smooth vertical surface presents no obstacle to a wet maggot. The bridge was cleaned with a damp cloth between experiments to remove the trails of the previous group, which maggots tend to follow, and the bridge was levelled with a spirit-level to ensure symmetry.

The cooling fan alone, without the lights, was found to have no effect.

Patten (1914) found that maggots of C. erythrocephala responded equally to a steady light and to a light interrupted 30 times a second, provided that the total quantity of light per second was the same. Since the Bunsen-Roscoe law is thus obeyed, it can make no difference whether 50 c./s. alternating or direct current is used for the incandescent stimulus lamps.

Comparison of present results with previous spectral sensitivity curves

In order to compare the present results for Calliphora larvae with the findings of other workers on muscid larvae and flies, the line of Fig. 5 is redrawn in each part of Figs. 6 and 7, extended to 362 and 640 mμ.

First, attention must be drawn to the simple nature of the maggot’s spectral sensitivity curve—there is no sign of any maximum away from 504 mμ, either in the ultraviolet or red parts of the spectrum.

Where other authors give the percentage quantum sensitivity, or the data from which it may be calculated, this is shown in parts (a) to (d) of Fig. 6 and Fig. 7(a) to (c). Fig. 6(a), ●, shows the results of Mast (1917) for unidentified fleshfly maggots, at levels 7 and 20 m. candles, i.e. of the order of 1 f.c., for wavelengths between 422 and 625 mμ. The standard white light was at right angles to the monochromatic light, which was adjusted in intensity until the maggots set themselves midway between
the two. The maximum is at 504 mμ, the same as for the present work, but the curve is narrower.

Fig. 6(a), ○, is the absolute quantum sensitivity for the housefly maggot for wavelengths between 405 and 700 mμ, drawn from Bolwig (1946). The criterion here was the ability of maggots to re-orient themselves when the paper on which they were on

was turned through a right angle. The maggots were not all of the same age, described as 'second and third instar larvae', which may have influenced the absolute threshold method. (The peak at 520 mμ is sharp compared with other spectral sensitivity curves.) Again, there is no return of sensitivity at the red end of the spectrum; the ultra-violet was not investigated.

In Fig. 6(b) we come to the spectral sensitivity of adult flies, this time from

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![Graph showing spectral sensitivity for muscid flies and larvae.](image)

**Fig. 6.** Percentage quantum sensitivities found by other workers for muscid flies and larvae. The present results for *Calliphora* larvae are repeated in each diagram (thick line). (a) Maggots; ○, Mast, blowfly; O, Bolwig, housefly. (b) Schneider, *C. erythrocephala*. Adult (optokinetic). (c) Walther & Dodt, *C. erythrocephala*. Adult (electrophysiological). (d) Donner & Kriszat. Adult fly (electrophysiological).
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Schneider (1956), the only behavioural results for which we have the data in this form. This is an optokinetic method for C. erythrocephala, at a very low level of intensity, in the human scotopic region. The fly was glued to a glass capillary at the centre of a glass cylinder, outside which turned a concentric cylinder with vertical black stripes, illuminated by monochromatic light of wavelength between 425 and 570 m. When the fly had enough light to see the stripes, it attempted to follow them. The maximum sensitivity was at 480 m.

Walther & Dodt (1959) used an electrophysiological method, and their results are shown in Fig. 6(c), for wavelengths between 290 and 675 m. This curve is the mean result for 24 C. erythrocephala flies, all from the same stock. The criterion here was a constant height of on-effect of the electroretinogram (e.r.g.) in response to 40 msec. flashes of light every 30 sec., for the intact fly. These workers found that the relative height of the secondary maximum at 630 m was dependent on intensity, while the ultra-violet peak did not change with intensity in a regular way.

Donner & Kriszt (1949) also used the on-effect for the intact fly as an index of threshold between 440 and 640 m. The curve shown as Fig. 6(a) is for an individual fly which showed the peak at 500 m most clearly. For others the sensitivity was still rising at the violet end of their available spectrum. They found no apparent differences between the species Musca domestica, Lucilia caesar, Calliphora vomitoria and Pollenia rudis, and do not identify the fly to which this diagram refers. Adaptation increased the relative sensitivity to the violet end of the spectrum (420–40 m), the effect being greatest for green, then red, and then violet adapting lights.

Cameron (1939) found that houseflies were attracted by 366 m more than by any other wavelength. Weiss, Soraci & McCoy (1941), also using a behavioural method for houseflies, found a maximum of response to an equal energy spectrum at 490 m, a minimum at 460 m, and the response was still rising at 360 m. Granit (1947, p. 297) mentions an electrophysiological experiment, in which the eye of the housefly was found to be most sensitive to 490 m, sensitivity falling off rapidly on the long-wave side of the maximum. Granit extracted a 'very light-resistant carrot-coloured pigment' from the eye of the housefly. The only pigment bleached by light which has so far been found in a fly was extracted by Bowness & Wolken (1959) from housefly heads and had maximum absorption at 437 m.

The work of Autrum (1955), using the on-effect of the e.r.g. as an index of sensitivity, may provide a key to this diversity. Autrum uses the isolated head of C. erythrocephala and determines the magnitude of electrical responses at each wavelength for an equal-quantum spectrum. He gives the results at a series of quantum levels and, by reploting the response against quantum level, it is possible to find the relative quantum sensitivity at an arbitrary mV response level by interpolation. This has been done for three individual flies, at three levels of response, in increasing order, represented by •, ○, and × in Fig. 7. Fig 7(a) and (b) refer to two wild-type C. erythrocephala, and 7(c) to a white-apricot mutant of the same species. In Fig. 7(a) the graph at the lowest intensity, •, is of the same type as Fig. 6(c), and increasing intensity changes the wavelength of the peak around 500 m to about 530 m, at the same time increasing the relative height of a peak at about 630 m. 7(b) tells a similar tale, even more dramatically, as the peak in the red completely dwarfs the rest at the highest intensity.
Fig. 7(c) for the mutant form has only one maximum, around 515 mμ; and, again, the relative sensitivity at the shorter wavelengths decreases with increasing intensity. It is clear that the same preparation can give more than one relative spectral sensitivity curve, according to intensity, and that there may be more than one ‘Purkinje’ type of sensitivity change.

![Graphs showing spectral sensitivity curves for different C. erythrocephala forms](image)

Fig. 7. Percentage quantum sensitivities for three adult C. erythrocephala, each at three levels of electrophysiological response, calculated from Autrum, 1955. The present results for Calliphora larvae are repeated in each diagram (thick line). (a) C. erythrocephala (wild). On effect: •, 1 mV.; O, 2 mV.; x, 3 mV. (b) C. erythrocephala (wild). On effect: •, 1 mV.; O, 2 mV.; x, 3 mV. (c) C. erythrocephala (white-apricot mutant). On effect: •, 3 mV.; O, 8 mV.; x, 10 mV.

It seems possible that an electrode picks up the electrical activity of different types of nervous element from one preparation to another. (Though Walther & Dott (1959) say that this effect is small compared with that found in the eye of the cockroach, Periplaneta americana.) Again, more than one retinal element may contribute, in different proportions. Autrum & Stumpf (1953) found that individual C. erythrocephala preparations, at high levels of illumination, gave response maxima at either 540 or 630 mμ, or else at both wavelengths. (In some cases there was evidence for wavelength discrimination, using a flicker method.)

The high sensitivity in the ultra-violet, maximal at 340 mμ (Walther & Dott, 1959), varied from one specimen of C. erythrocephala to another (even between flies of the same stock and age) compared with the maximum near 500 mμ. Reducing the intensity of the stimulus always changed the relative sensitivity to red, but the ultra-violet sensitivity did not always change in the same direction.
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Inspection of Figs. 6 and 7 shows that all these muscid flies have a maximum of sensitivity near 500 m\(\mu\) which is especially prominent at low levels of illumination. This may well be a continuance from the visual mechanism of the larval state, most sensitive to 504 m\(\mu\). No light-sensitive pigment has yet been found to account for this; the atypical pigment found in the housefly by Bowness & Wolken (1959), with its maximum absorption at 437 m\(\mu\), is not a likely candidate. The form of the spectral sensitivity curve of the maggot would suggest a visual purple (or rhodopsin) and the low absolute threshold leads to the idea that such a pigment might be present in measurable concentration.

**SUMMARY**

1. The relative spectral sensitivity of larvae of *Calliphora vomitoria* and *C. erythrocephala* has been determined, using the maggot's natural tendency to travel towards the weaker of two opposing lights.

2. The response to light at each wavelength between 402 and 602 m\(\mu\) was the same for the two species, within \(\pm 0.1\) log unit, and the results are well fitted by the bell-shaped curve characteristic of a (hypothetical) visual purple, maximal at 504 m\(\mu\).

3. Reduction of the intensity of the white standard light by one log unit did not change the shape of the curve, and the extended wavelength range, between 362 and 640 m\(\mu\), shows no sign of a subsidiary maximum of sensitivity. The levels of illumination were \(10^{-2}\) and \(10^{-3}\) f.c., and the absolute threshold was found to be about \(10^{-6}\) f.c.

4. The spectral sensitivity found here is compared with the results of other workers for muscid flies and larvae. It is concluded that one of the independent maxima of sensitivity found in the flies is a continuance from the larval state.

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**REFERENCES**


