ORIENTATION BY OPPOSED BEAMS OF LIGHT

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I

From the elementary postulate that in phototropic orientation the turning movements cease when excitation is made sensibly equivalent upon the two sides of a symmetrical organism, equations have been derived (Crozier, 1925–28; Mitchell and Crozier, 1927–28) which describe properties of the oriented position under the influence of two sources of light. With a moving organism the situation is most susceptible to useful analysis when beams of parallel rays are concerned (Mitchell and Crozier, 1927–28), since then an oriented position is assumed in definite relationship to the axes of the beams. With beams opposed at 180°,

$$\tan \theta = (\cot H/2) \frac{(I_1 - I_2)}{(I_1 + I_2)}, \tag{1}$$

where intensity $I_1 > I_2$ and, for a negatively phototropic animal, θ is the angle of orientation away from I_1; the angle H, loosely termed a "head angle," is the average effective angle between the bilaterally disposed photoreceptive surfaces (Crozier, 1925–28). The magnitude of H must be expected to change if the amplitude of side-to-side movements of the anterior end of the body, or if the random or periodic frequency of such movements, depends upon the illumination or other conditions (*e.g.*, temperature, or concurrent geotropic excitation); it need not correspond to any obvious feature of the structure of the organism (Crozier, 1925–28).

It was pointed out that certain interesting comparisons might be made by contrasting values of H obtained from measurements of θ with two beams of light directly opposed with similar data secured when the beams cross more acutely, say at 90°. For the latter case,

$$\tan \theta = \frac{I_2 \tan H + I_1}{I_1 \tan H + I_2} \tag{2}$$

(*cf.* Mitchell and Crozier, 1927–28). If H were strictly constant, it should appear nearly identical for the two cases (unless complicated by effects of refraction).

Experiments were made with larval blow flies of two species, *Calliphora erythrocephala*, 4 days after emergence and 7 mm. to 9 mm. in

TABLE I

Mean angles of orientation for larvae of *Calliphora* under the influence of two beams of light crossing at 90°. Two series of measurements, six larvae used in each series, six observations on each larva at each intensity.

I_1	I_2	θ Mean	θ P.E.	H
millilamberts	*millilamberts*			
3781	3560	50.86°	± 0.31°	57.5°
	3260	59.56	0.14	58.3
	3008	64.98	0.15	55.3
	2752	69.47	0.08	51.9
	2207	80.33	0.25	49.3
	1910	86.16	0.13	50.5
	1801	88.85	0.13	49.5
	1621	89.22	0.13	45.3
3897	3599	51.22°	± 0.93°	49.4°
	3210	58.74	1.4	46.7
	2995	65.06	1.3	50.4
	2599	72.21	1.2	47.5
	2151	79.81	1.1	44.9
	1898	86.92	0.45	47.9
	1755	87.95	0.32	45.7
	1609	89.03	0.20	43.4

length, and a species of *Lucillia* of the same age but 6 mm. to 8 mm. in length. The first was used by Patten (1914); for larvae of the size he employed, H = 85° under the particular conditions of excitation (Crozier, 1925–28). We used smaller larvae, our chief point being to compare values of H with lights opposed and crossing at 90°, and to compare values of H for two morphologically different larvae. Larvae of *Lucillia* are more sharply pointed at the anterior end. We examined the orientation both with beams opposed at 180° and crossing at 90°. The computed values of H need not be expected to be the same for the two situations, since if the photoreceptors are located beneath the surface of the larva the refraction of incident light will differ significantly. It was expected that variation in H might be correlated with intensity of illumination, or with θ.

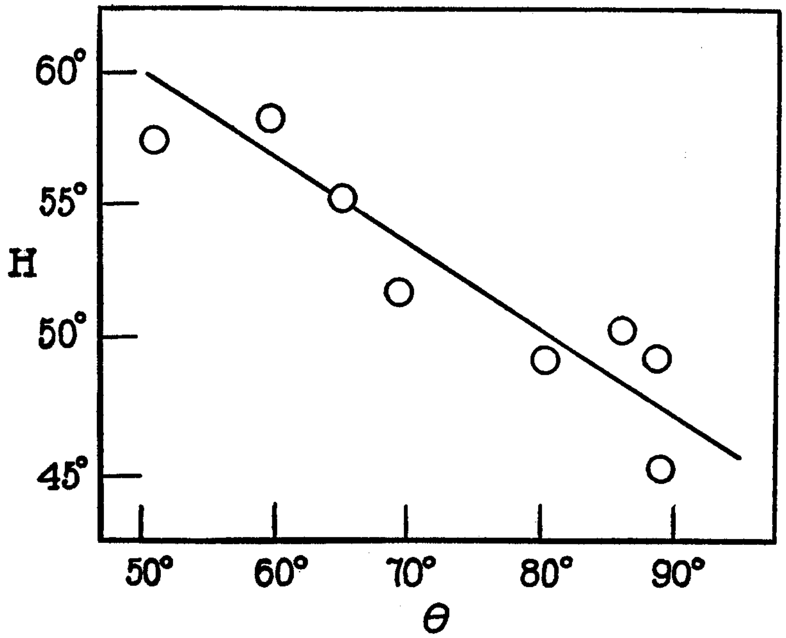

FIG. 1

From two similar electric bulbs, within housings, light was allowed to fall upon a square platform on which the larvae crept. Trails were recorded by placing a drop of methylene blue at the posterior end of the maggot. The lights were mounted upon tracks of an optical bench; in a series of measurements one lamp was moved to different distances from the observation platform. The sources of light were slightly above the level of this platform, to obviate shading of the larva's anterior end at higher angles of orientation. At the position occupied by a larva the illuminations from the two sources were measured with a Macbeth illuminometer. The shape of the larva changes during its development, in a way which presumably affects H; consequently no exact agreement could be expected between successive series of determinations. The values of θ were read from the trails, to the nearest half degree.

TABLE II

Orientation angles for *Calliphora* larvae of size corresponding to those used in Table I, but with beams of light directly opposed; five larvae, six readings on each.

I_1	I_2	θ Mean		θ P.E.	H
millilamberts	*millilamberts*				
3972	3765	3.45°	±	0.31°	60.9°
	3107	8.11		0.65	81.4
	2777	12.00		0.73	80.1
	2474	17.35		0.73	73.6
	2001	26.21		0.85	67.7
	1763	35.42		0.56	57.0
	1407	38.51		1.1	62.1
	1100	43.60		0.67	60.8

TABLE III

Orientation angles for *Lucillia* larvae, with beams of light crossing at 90°; five larvae, six readings on each.

I_1	I_2	θ Mean		θ P.E.	H
millilamberts	*millilamberts*				
3019	2960	45.7°	±	0.52°	21.2°
	2443	53.6		0.73	20.7
	2279	56.4		0.65	20.7
	2098	59.7		0.54	21.1
	1580	69.3		0.64	20.6
	1076	78.8		1.06	18.1
	718	86.4		0.53	20.1
	602	87.8		0.39	18.1
	555	88.4		0.30	17.8

II

With *Calliphora* larvae two series of measurements were made (Table I) with light beams crossing at 90°. In each series there is a definite decline of H as θ increases (Fig. 1); that is, as the total illumination $(I_1 + I_2)$ declines. This may be due to the fact that chance movements, especially toward the less intense light, are more frequent. This does not appear in the variability of the orientation angle θ, since the error in θ is perhaps chiefly in the mechanics of its measurement; with a wider range of intensities of illumination (*cf.* Crozier, 1925–28), $P.E._\theta$ and H might each be expected to go through a maximum. In the second series, with slightly younger larvae, H is consistently smaller than in the first set, and $P.E._\theta$ larger. At high magnitudes of θ, however, H tends to agree.

A third series of observations employed lights directly opposed (Table II). Here again H declines as θ increases; the values are consistently above those in Table I (*cf.* Fig. 1).

The anterior end of the larva of *Lucillia* is much more sharply pointed than is that of *Calliphora* larvae of the ages used. This need not be taken to imply that the effective inclination of the photoreceptive surfaces (of the imaginal discs?) is correspondingly acute; and no measurements were made of the character of the side-to-side movements of the anterior end in creeping, which could affect the computed magnitudes of H. Tests were made of orientation with beams of light crossing at 90°. The results are contained in Table III. H again declines as θ increases (or as $[I_1 + I_2]$ decreases (Fig. 1)). With the more sharply pointed *Lucillia* larvae the magnitudes of H are less than half as great as with *Calliphora*; it does not seem probable that this contrast can be due entirely to differences in frequency or extent of random movements of the anterior end; it must rather be ascribed to a real difference in the angular inclination of the receptive surfaces in the larvae of the two species.

III

SUMMARY

Computations of the effective angular inclination (H) of the photoreceptive surfaces of the two sides, based upon measurements of orientation angles under the action of beams of light directly opposed or crossing at right angles, show that with larvae of *Calliphora* and of *Lucillia* H declines as the total illumination decreases (*i.e.*, as the

angle of orientation away from the more intense light increases). *H* is greater with the two lights opposed at 180°; this may be due to the difference in refraction. For the more sharply pointed larvae of *Lucillia, H* is less than half as great as in *Calliphora*.

CITATIONS

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