Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.
THE REACTIONS OF THE POMACE FLY \textit{(Drosophila ampelophila Loew)} TO LIGHT, GRAVITY, AND MECHANICAL STIMULATION.

FREDERIC W. CARPENTER.

The observations which this paper records were made on the movements of the common pomace or little fruit fly, \textit{Drosophila ampelophila} Loew. Insects of this species can be collected in abundance in the autumn, and a culture can easily be maintained in the laboratory all winter if it is kept supplied with decaying fruit such as bananas or apples. The eggs are laid in this material, which later is used by the larvae as food.

When a large cylindrical glass vessel containing a stock culture of these flies was placed on a table near a window, it was noticed that the flies accumulated in the greatest numbers on the upper part of the side of the vessel nearest the window. This indicated that they were positively phototropic to ordinary daylight, and probably negatively geotropic, although it seemed possible that their position near the top of the vessel might have been due to the fact that, owing to its position near the bottom of the window, the vessel was illuminated more brightly above than below. It was also observed that when the vessel was exposed to direct sunlight the flies, after a time, tended to accumulate, not on the surfaces toward or away from the window, but in intermediate positions on the two sides. Here the majority remained quiet in the regions of least illumination. A similar observation was made by Loeb ('93) on planarians, which
gradually came to rest in the darker portions of a shallow cylindrical glass vessel placed before a window. The large majority of the flies resting thus on the vertical sides of the vessel had their long axes parallel to the light rays, and their heads turned away from the source of light. Parker (1903) has pointed out that the mourning-cloak butterfly, coming to rest in bright sunlight, also places itself with the head away from the sun. The position assumed by the flies under these conditions might have led to the supposition that they had become negatively phototropic through continued exposure to an intensity of light higher than that to which they were accustomed. Such reversals have been observed for barnacle larvae by Groom und Loeb (1900), for Hydra by Wilson (1901), for Polygordius larvae by Loeb (1903), for Limax by Frandsen (1901), for copepods by Parker (1902) and for earthworms by Adams (1903). However, it was found that upon slightly turning the vessel on the table nearly every fly flew instantly toward the window, thus giving marked evidence of positive phototropism.

The experiments about to be described were undertaken with a view to obtaining some definite quantitative statements as to the influences of light and gravity on the movements of the organisms; and most particularly was it desired to test the responses of the flies to a range of high intensities of light. For valuable advice and aid in devising the apparatus and conducting the experiments the writer is indebted to Professor G. H. Parker, under whose supervision the work was carried on.

Apparatus.—In all of the operations the flies were confined in a cylindrical glass vessel measuring 15 cm. in length and 5 cm. in diameter, and closed at both ends by glass caps. Around the outside of the vessel were placed five small rubber bands at equal distances apart, the cylinder being thus divided into six sections each 2.5 cm. long. This subdivision of the vessel by surface markings enabled the observer to record the position of the contained fly at any moment with considerable precision.

In some of the experiments a dark box of convenient size was used, a sectional plan of which is given in the accompanying figure. This box was lined throughout with black cloth. In the center of each end wall was fixed an incandescent electric-light
bulb (L.), which projected into the interior. A determination of the amount of light given off from the ends of these bulbs showed each to have a candle power of approximately 5. The lighting of both these bulbs could be controlled from the outside by means of keys. A window let into one side of the box gave access to the interior when desired. This window could be closed by a tight-fitting shutter. When the dark box was used the glass cylinder (V.), containing the flies, was placed within, midway between the free ends of the two electric-light bulbs, its axis coinciding with the straight line connecting these. The distance from either end of the cylinder to the adjacent electric light filament was 7 cm. Between each bulb and the cylinder was inserted, as a heat screen, a glass vessel (W.), filled with water, and having flat, vertical sides 3 cm. apart. Both the glass cylinder and the heat screens rested on strips of wood painted black; and these supports could be so arranged that the box, with cylinder and heat screens in place, could be used in either a horizontal or a vertical position.

Kinetic Effect of Mechanical Stimulation.—If in ordinary daylight a fly be placed in the glass cylinder, and this be held vertically, the fly will seek the top. If now the vessel be turned upside down the fly, finding itself at the bottom, will creep upward again to the top within considerably less, as a rule, than
one minute. In order to ascertain the behavior, under similar conditions, of flies deprived of light, both when allowed to remain quiet and when mechanically stimulated, the following experiment was undertaken, using the glass cylinder, but not the dark box described above.¹

Two or three flies, the largest number easily worked with at one time, were put into the cylinder, and while exposed to daylight allowed to pass to its top section, whereupon it was quickly covered in such a way as to exclude all light, and the ends immediately reversed, the section containing the flies being thus made the bottom one. After having been left undisturbed for two minutes the cylinder was uncovered, and the positions of the flies on the sides of the vessel recorded. When they had again reached the top the vessel was placed in the dark again by steps similar to those just described, viz., with the flies in the bottom section. At the end of one minute, however, the whole apparatus was this time revolved on the table top with friction for forty seconds so that the flies were mechanically agitated. Then after twenty seconds of quiet—making in all two minutes in darkness—the cover was removed, and the positions of the flies recorded as before. Periods of quiet in the dark were thus made to alternate with periods involving jarring until five readings for each set of flies had been made. Table I gives the combined records for three females and two males, the figures indicating the number of flies discovered in the sections of the cylinder at the end of two minutes in darkness. Section No. 1 is the uppermost, section No. 6 the lowest.

The table shows that the flies allowed to remain undisturbed were found in 16 instances in the lower half of the cylinder, and in 9 in the upper half, only 2 of these being in the top section; while those flies which were mechanically stimulated were distributed 10 in the lower half and 15 in the upper half, 7 of the latter number being in the top section.

¹ It might be mentioned here that throughout the observations male and female flies showed no consistent differences in their reactions.
No. 459.]  

**REACTIONS OF POMACE FLY.**

Table I.

Distribution of five flies in a vertically placed glass cylinder after two minutes in darkness: the flies at the outset occupied the bottom section of the vessel, No. 6.

<table>
<thead>
<tr>
<th>Sections of cylinder</th>
<th>Numbers of trials</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Without mechanical stimulation.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>6</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>With mechanical stimulation.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td></td>
<td>2</td>
</tr>
</tbody>
</table>

Apparently, then, mechanical stimulation tends to induce the locomotion which results in this upward migration, or, in other words, it has a kinetic effect on the organisms. The direction of the movement indicates a negative response to gravity, a reaction which is more strikingly demonstrated in a succeeding experiment. The lesser degree of activity shown by the flies allowed to remain quietly in the darkness recalls the experiment of Loeb ('90) with plant lice, in which continued confinement in a dark chamber brought on a kind of “dark rigor” (“Dunkelstarre”).

**Kinetic Effect of Light.**—To test the possible kinetic influence of light the following experiment was tried. The glass cylinder, containing a single fly, was placed in a vertical position in the
dark box, with an incandescent electric-light bulb at either end. The lower light only was at first turned on, and the fly thus attracted into the lower section. Then the window of the box was closed, the light turned out, and the fly left for one minute in darkness. At the end of this period both the upper and lower lights were turned on simultaneously, and at the expiration of another minute the window was opened and the position of the fly noted. Five readings were taken in this manner for each of six flies, three males and three females. When the results were combined (see Table II) it was seen that, out of a total of 30 readings, the flies had been detected 19 times in the upper half of the cylinder, no less than 16 of these observations being for the topmost section. In 11 cases the flies had remained below the middle of the cylinder.

*Table II.*

*Distribution of six flies in a vertically placed glass cylinder after one minute's exposure to equal illumination above and below: the flies at the outset occupied the bottom section of the vessel, No. 6.*

<table>
<thead>
<tr>
<th>Sections of cylinder</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>2</td>
<td>5</td>
<td>4</td>
<td>3</td>
<td>16</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>5</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>6</td>
<td>2</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>3</td>
<td>9</td>
</tr>
</tbody>
</table>

When this distribution is compared with that for flies left undisturbed in darkness for an equal length of time (Table I), it would appear that light acts as a stimulant to locomotion; and the rather striking efficiency of light in this respect is attested by the comparatively large number of flies found in the uppermost section of the cylinder.

*Directive Effect of Light.*—Experiments to demonstrate the directive effect of light of moderate intensity may be thought to
have been scarcely necessary since under natural conditions Drosophila gives such unquestionable evidence of positive pho-
totropism. However, in order to obtain a more detailed ex-
pression of this, and to make the observations more complete,
the glass cylinder, again containing a single fly, was placed hori-
zontally in the dark box, and the lights on the right and left
were alternately turned on and off. By this arrangement the
influence of the light was brought to bear on the insect at right
angles to the influence of gravity, which could not, therefore,
affect the results. The window in the side of the dark box
was left open in order that the movements of the fly might be
watched. At the beginning of the experiment, when the insect
was in the section of the cylinder the farthest to the left, the
right light only was turned on. The fly would then creep
toward the right along the sides of the cylinder. The time of
the excursion from the line bounding the last section on the left
to the one bounding the last section on the right was taken with
a stop watch. As soon as the fly had crossed the last line on
the right, the light at that end of the box was turned off, and
the left light turned on. This change in the direction of the
illumination was followed by a progression to the left on the part
of the fly, an active insect setting out on the return excursion
within an average time of about 10 seconds. The progress of
the fly toward the left was also timed by the watch. Thus, by
reversing the lights, the animal could be made to travel back
and forth in accordance with the changes in the direction of
the illumination. Flying responses occasionally took place, but,
since these were difficult to time, they were not taken into
account. Moreover, by neglecting these the records were kept
homogeneous in that they were made for creeping excursions
only. Individual insects differed considerably in the degree of
activity they displayed, and often the same insect would respond
less promptly at one time than at another. On those occasions
when the kinetic influence of the light seemed for some reason
to be partially inhibited, recourse was had to mechanical stim-
ulation to bring the animal into a more active state. This was
effected by removing the glass cylinder from the dark box and
shaking it. Flies thus treated usually reacted more readily to
the light rays for some time after.
In all, four flies, two males and two females, were used in this set of experiments. Each fly was sent five times in each direction. The average time for twenty creeping excursions toward the light from left to right, a distance of 10 cm., was 7.65 sec.; from right to left, 7.71 sec. The average rate in either direction was accordingly about the same, 1.3 cm. per sec. That Drosophila possesses the character of positive phototropism is obvious.

Directive Effect of Gravity.—By arranging the apparatus used in the phototropic experiment just described so that the glass cylinder had a vertical position, it was possible to test the directive effect of gravity on flies stimulated to action by light. The incandescent lamps were now situated one at the upper and one at the lower end of the cylinder, and alternately turned on and off. By means of a stop watch, time records of excursions along the vessel were taken as before. Not all the flies tested responded readily to the light, and preliminary mechanical stimulation produced by shaking the cylinder was sometimes resorted to. Finally two active male insects were found, for each of which five readings were obtained for each direction. The average time for ten creeping excursions toward the light from the bottom to the top of the cylinder through a distance of 10 cm. was 6.2 sec., or at a rate of 1.61 cm. per sec.; from the top to the bottom, 44 sec., or at a rate of 0.23 cm. per sec. The flies crept upward quickly and continuously, and at a rate slightly more rapid than that of flies in the cylinder placed horizontally. In their course downward they frequently stopped for short intervals.

The response to gravity accordingly appears to be a negative one, as was indicated by the behavior of the insects when mechanically stimulated in the dark. In the rapid upward excursions positive phototropism and negative geotropism coincided. In the slow downward ones these two influences were opposed, and although the directive influence of the light proved the stronger, the retarding effect of the opposed influence of gravity was apparent in the strikingly reduced rate of progression.

It happened occasionally that an insect would fly through a
portion of its excursion and alight on the vertical side of the cylinder. When this occurred the fly came to rest with its head uppermost, no matter whether its flight had been directed upward or downward. This orientation of the body on alighting may have been due to negative geotropism.

. Effect of Increased Intensities of Light.—In order to subject the flies to light of different intensities use was made of an arc light suspended at one end of a dark room with dead black walls. The glass cylinder containing a single fly was placed horizontally on a small movable table, one end of the cylinder being directed toward the light. The movements of the fly were observed while the end of the cylinder through which the rays fell was at four different distances from the arc light, *viz.*, 800 cm., 300 cm., 80 cm., 40 cm. The candle power of the arc light used was approximately 64. Between the cylinder and the light a rectangular glass vessel containing 3500 cc. of water was interposed as a heat screen. The front and back walls of this vessel were 7 cm. apart.

At each of the four positions the responses of the fly were timed as follows. A small opaque screen was set up between the arc light and the cylinder, and at the opposite end of the cylinder an incandescent lamp was turned on. The fly, attracted by the light of the lamp, crept toward it. At the moment the insect reached the middle of the cylinder the screen obscuring the arc light was removed, the incandescent light extinguished, and the stop watch started. The fly, headed away from the arc light, usually stopped momentarily when suddenly exposed in this manner to the light from behind, and then resuming its course moved on until the opposite (dark) end of the cylinder was reached. Here it turned and hastened toward the illuminated end, either by creeping, or by flying, or by both creeping and flying. With the cylinder close to the arc light the fly sometimes turned about immediately upon the removal of the screen. When the fly crossed the boundary line of the section nearest the arc light the watch was stopped and the time recorded. At distances of 800 and 300 cm. a large majority of the responses were of the creeping kind. At positions nearer the light the insect often flew through a part of the distance —
sometimes through the entire distance. Since it was impossible to obtain pure creeping responses in all cases, those involving both creeping and flying were taken into account. Pure flying responses were not timed.

Observations were made on four flies, two males and two females, and the average time of twenty responses (five for each fly) at each of the four distances from the arc light was obtained. At 800 cm. and 300 cm. and even at 80 cm. the results did not materially differ, the average times of the responses at these three positions being respectively, 18 sec., 18 sec., 16.7 sec. At 40 cm. there was a marked increase in the rapidity of the movements of the flies, the average time of the responses being 7.4 sec.

The behavior of a fly under continued exposure to the highest intensity of light available for these experiments seemed to be of considerable interest. The apparatus used was the same as for the experiments last described, except that an arc light of greater candle power (250 c. p. approx.) was used. The procedure was also unchanged, the insect being brought up from a distance of 300 cm. to 80 cm. and finally to 40 cm. from the light. For each of the first two positions time records for five excursions were obtained, although those for 80 cm. required patient manipulation and many repetitions of the excursions, so numerous did the flying responses become. At 40 cm. the behavior of the fly was such that a full set of five readings could not be taken. Under the influence of the intense light the insect became extremely active, flying and leaping about spasmodically in all directions, and giving little or no evidence of directive responses. That is to say, the directive influence of the light was no longer effective enough to cause the fly to make excursions back and forth along the cylinder in accordance with the position of the illumination. While the fly was in this condition of great muscular activity, the screening off of the arc light and the turning on of the incandescent lamp, were followed by less activity on the part of the animal, but not by a progression toward the illuminated end of the vessel. The directive influence seemed to be for the time inhibited.

It appears, then, that continued exposure to a high intensity
of light produces very rapid locomotor movements, but while the kinetic effect of the light is thus increased, its orienting effect may be strikingly diminished. Throughout the experiments with high intensities there was no evidence of a change from positive to negative phototropism even under the influence of the highest intensity employed, that of a 250 c. p. arc light at a distance of 40 cm.

Discussion of Results.—In the preceding pages it has been found convenient to distinguish between two factors in the effect of light on Drosophila, a kinetic factor and a directive one. These two factors undoubtedly give rise to different kinds of responses, yet they are so closely related that it may be well to lay some stress on their interdependence. The directive effect of light manifests itself only in connection with a kinetic influence sufficient to induce locomotion. The insects while at rest do not regularly lie with their heads directed toward the source of illumination; in fact, those flies of the stock culture already referred to, which, after continued exposure to direct sunlight, came to rest in the least brightly illuminated portions of the vessel, were found with their heads turned away from the window. In the experiments with incandescent lights the turning on of one of the lamps was rarely if ever followed by mere orientation on the part of the fly, i. e., simply an adjustment of the body in such a manner that its long axis became parallel with the light rays and that both eyes received an equal amount of light,—a condition of symmetrical stimulation which Loeb ('97) has maintained to be the essential factor of orientation. While the muscle reflexes necessary to put the insect in this position were usually forthcoming under such stimulation, these movements proved to be initiatory locomotor movements, being continuous with the series of locomotor reflexes which followed. When, on account of light-fatigue or other causes, the insect ceased moving about, no satisfactory evidence of orientation either to light or to gravity could be adduced from the position the animal assumed.

In the case of one fly subjected to the influence of a very high intensity of light, a reaction was obtained which involved only the kinetic factor. This fly while stimulated to great activity
did not appear longer to respond to the directive influence. Its movements were hap-hazard, not guided by the direction of the light, as if the organism, in its state of extreme excitement, had lost for a time its tendency to place itself when in motion under conditions of symmetrical stimulation. This violent kinetic effect of very intense light has been observed for several lower organisms by Pearl and Cole (1902). The conditions of their experiments did not permit them to note the effect on orientation. Long exposure produced a paralyzing effect, so that the movements became more and more slow as the stimulus continued to act. No insects were tested by them.

The experiments with the 64 c. p. arc light made it clear that when the intensity is increased by lessening the distance of the light from 80 cm. to 40 cm. there is a marked increase in the rapidity of true phototropic responses. This result in the case of Drosophila is certainly not due merely to more precise orientation, as was suggested by Davenport (1907) to explain the increase in the rate at which Daphnia traveled under strong light. It is interesting to note that Yerkes (1900), experimenting on the same organism (Daphnia), concluded that while the increase in rate depended chiefly upon precision and quickness of orientation, there was also evidence of a quickening of the swimming motions.

It was stated at the beginning of this paper that when the insects are exposed in a large cylindrical glass vessel, to direct sunlight from a window, many of them eventually come to rest on the sides of the vessel which are least illuminated. Their heads are in this instance directed away from the source of light. When disturbed by the vessel's being turned about they show positive phototropic responses by flying toward the light. This apparent negative orientation while at rest is not due, therefore, to a reversal of the directive influence of the light owing to continued exposure to a higher intensity.

It seems probable that the behavior of the flies under these conditions is the result of the following causes. When first exposed to the strong kinetic influence of bright sunlight Drosophila becomes very active. Its flying and creeping movements toward the light are limited by the wall of the vessel, and the
continued locomotor reflexes bring it into other regions. It may by accident reach the vertical surfaces of the vessel intermediate between the surface nearest and the one farthest from the window. Here the kinetic influence of the light, owing to decreased intensity, is least. The fatigued fly may still, however, be stimulated sufficiently to cause it to creep or at least to turn about. If it chances to place itself with the head directed away from the window, the reduced light stimulus received by the eyes may be inadequate to call forth further muscle reflexes, and the fly remains quiet in this position. Jarring the insect, or turning the vessel about so that more light enters the eyes, may increase the kinetic stimulation to such an extent that renewed movements are induced.

In Drosophila just as light causes locomotion, so mechanical stimulation seems to bring about progressive movements. From the nature of the case this stimulus was very roughly applied in the foregoing experiments, there being no effort to limit its application to one side of the body with a view to detecting its directive effect, if any, under such conditions. On the other hand, an allied form of stimulus, the pull of gravity, directs the movements of the organism, although it does not appear to induce them. A condition of symmetrical stimulation is undoubtedly brought about when, on a vertical surface, the fly places its long axis parallel to the direction of the lines of the earth's attraction. This pull of gravity on the materials which make up the animal's body differs more in degree than in kind from the impact of surrounding objects to which the animal is subjected when mechanical stimulation is applied. If the attraction of gravity and mechanical stimulation are regarded, then, as closely allied forms of stimuli, their two effects upon the organism admit of an almost exact comparison with the two effects of light. When left quietly in darkness, Drosophila gives little evidence of a tendency either to orient itself, or to move about. Thus gravity alone seems insufficient to induce either of these responses. When, however, the insect is mechanically stimulated, locomotor movements do occur, and in connection with them the directive influence of gravity becomes effective. The animal orients itself with its head away from
the center of the earth, and, responding to the kinetic influence of mechanical stimulation, moves upward. The general result is a progression in a definite direction, precisely such as is obtained when a light is placed at one end of a horizontal glass cylinder containing the insect.

Summary of Results.—1. Mechanical stimulation has a kinetic effect upon Drosophila, since it induces locomotion.

2. Gravity has a directive effect upon the active insect, which is negatively geotropic, that is, the insect moves away from the center of the earth.

3. Light has both a kinetic and a directive effect. The insect moves toward the source of light, being positively phototropic. The directive effect is apparent only when the kinetic stimulus is sufficient to induce locomotion.

4. The exposure of Drosophila to light of high intensity is accompanied by an increase in the kinetic effect. Under the influence of the highest intensity used, that of a 250 c. p. arc light at 40 cm., the muscle reflexes of an insect become very rapid and violent, and the directive influence of the light seems inhibited. There is no indication of a reversal of the directive influence from positive to negative.

5. After continued exposure to direct sunlight in a large cylindrical glass vessel many insects come to rest in the least brightly illuminated regions and with their heads away from the source of light. This is not an indication of negative phototropism. The fatigued insects remain quiet in this position because it is the one in which the least light enters the eyes, and in which, as a consequence, the kinetic stimulus is least.
BIBLIOGRAPHY.


