REACTIONS OF DAPHNIA TO SIMULTANEOUS LIGHT AND ELECTRICAL STIMULI.*

BY J. A. ROBERTSON.

(From the Department of Zoology and Comparative Anatomy, Oxford.)

CONTENTS

1. Introduction .................................................. 357
2. Apparatus ..................................................... 357
3. Material ........................................................ 358
4. Quantitative Experiments .................................... 359
5. Conclusions .................................................... 369
6. Summary ....................................................... 372
7. References ..................................................... 372

1. Introduction.

Light and electrical current are the two most easily controlled stimuli suitable for use in studying the behaviour of animals under experimental conditions; they are both easily varied in intensity and constant in direction.

Patten’s well-known experiments upon the reactions of the Blow-fly larva to two lights suggested that there might be an animal which would move toward or away from two stimuli of dissimilar nature, in a direction which would be the resultant of their different effectiveness. Such an experiment has not, to my knowledge, previously been attempted, nor have I found any mention of an experiment relating to the modifying effect of electrical current on phototropism.

For his courtesy in permitting me to work in the Department of Comparative Anatomy, Oxford, during vacation, my thanks are due to the Linacre Professor of Zoology. I also wish to thank Mr J. S. Huxley for much helpful advice and encouragement given me upon the work described below.

2. Apparatus.

A long board, with two 100 volt 40 watt Ediswan Fullolite lamps provided with two switches, one at either end, was used for providing the light. A container was made of plate glass 15 cm. square. It was placed on the centre of the board half-way
J. A. Robertson

between the two lights. Two nickel electrodes 14.8 and 14.7 cm. (15 cm. approx.) long were fitted into the dish along the sides through which the light did not enter. The current and light thus passed through the dish at right angles. The electrodes were connected in series with a reversal key, variable U-tube copper-sulphate resistance, ammeter, resistance lamp, and the terminals of the electrical fittings of the bench upon which the apparatus was set up. The voltage was in the

neighbourhood of 100 volts. The resistance lamp did not light up and so could have no photic effect. The dish was filled with tap-water for the experiments, and the height of water having been taken, it was easy to find the effective area of the electrodes.


It was necessary to find aquatic animals for this experiment. 

Corixa proved unsatisfactory, for though strongly positively phototropic, the galvanotropic reaction (Anodic) too early destroyed the phototropism and the animals were altogether too active.
Reactions of Daphnia

*Daphnia* was experimented upon with better results. In a first qualitative series, six cultures were tried. All were strongly photopositive, and, when subjected to light and a current of 0.08 amps., two of the cultures showed a decided resultant reaction, gathering in the lighted kathode corner. 0.08 amps. was the lowest current strength at which this reaction took place. The four cultures in which no resultant effect was observed all contained a far greater proportion of small than large specimens, and this failure seemed possibly due to some difference in the reactions of small sized animals. No negativation of positive *Daphnia* occurred, but after the first few trials with one culture that showed the resultant reaction, this wore off and photopositivism retained complete control of the situation. This change may be due to sensory fatigue induced by the continuous current. The resultant reaction in those cultures that showed it was sufficiently definite to encourage further work.

4. Quantitative Experiments.

These experiments were all performed on *Daphnia*. For the proper understanding of the results, meanings of the letters and terms used are here explained.

When the distribution of the specimens is given in the tables, the *first sign or term indicates the majority*, another bracketed term with a qualifying adjective denotes the presence of a minority. Size of the minority is indicated in decreasing value by the words “many,” “several,” “some,” “a few.”

The first quantitative experiment was relatively unsuccessful, for the reason that the *Daphnia* differed, in their behaviour, from those employed earlier. They were throughout this series prevalently photonegative. These *Daphnia* and the earlier cultures were collected in different places, and the former somewhat later in the year (July instead of May and June).

These photonegative *Daphnia*, especially the larger specimens, were, moreover, stunned or rendered quiescent and motionless by a current of 0.08 amps. (and even less), which was the lowest strength responded to in the earlier experiments.
J. A. Robertson

For economy of space I have summarised all save three tables, and the original notes upon them are reviewed in each conclusion; but all data are available to those interested.

Experiment 1, 16/7/24—Summary of Table.—Five cultures were examined (a 1 to a 5); water-temperature 19° to 19.25° C; heights of water in the dish 2.1 to 2.4 cm. (length of electrodes given above); amperage 0.068 to 0.094 amps. (with one exception of 0.03 amps.). The reaction of the Daphnia was almost uniformly + K (resultant reaction).

On reversal of both light and current direction in four of the cultures little save quiescence was observed (some were + K, fewer +). In two cases the course followed by the Daphnia was roughly diagonal, in one indeterminate.

![Diagram of Dish with Key to Distributive Terms](image)

**Notes on Positivation.**—Current strengths of 0.08 amps. gave the most definite results but appeared to inhibit activity to a visible extent, causing the Daphnia to become quiescent. A current of 0.06 amps. had perhaps less definite directive effect, but the inhibition was still present.

Before exposure to current all cultures were photonegative. 1 and 2 were photopositive after exposure for a time at least. 3 was positivated to a less extent; in 4 photonegativism was changed to photopositivism by exposure to so low a current as 0.03 amps. They became negative again after one minute's exposure to light alone. On application of the current they became kathodic and evenly distributed, and on release photopositive, showing a negative tendency again in about two minutes.

In 5 the Daphnia were photonegative. When they were crossing to the dark side of the dish after reversal of light direction alone, a current of 0.03 amps. was turned on; they returned from the half-way line, which they had reached,
Reactions of Daphnia
to the lighted side they had just left. On cessation of the current they continued
their interrupted negative course. It seems that the photonegative Daphnia
are positivated by electrical current, for a time at least.

In culture 5, subsequent to the reversal in direction of light and current,
the current alone was reversed. The majority assumed a + K (resultant)
position, taking their course along the lighted side.

After various exposures to current these Daphnia, which were originally
photonegative, had become photopositive, and the majority remained so for
five minutes when exposed to light alone.

**Conclusion.**—All cultures showed the resultant reaction at first, although
there were many quiescent specimens. Positivation of negative cultures occurred
markedly in all during the passage of the current, but in most the positivism
remained for a short time only after cessation of the current. The reversal
of light and current directions was unsuccessful in eliciting a definite response,
owing to the inhibitory effect of the current strengths used, resulting in quiescence.

**Experiment 2, 17/7/24.** (Repetition of Experiment 1.) **Summary of Table.**—
Five cultures were used (b 1 to b 5); water-temperature 18.5° to 19.5° C.;
height of water 2.1 to 2.5 cm.; current 0.04 to 0.06 amps. The reaction of
the small specimens was – or – K (photonegative alone or resultant). The
larger animals were + K in every case. There was a varying minority of
quiescent individuals. On reversal of light and current direction the small
Daphnia took up a – A position and the large took up a + K position as
a rule, though some took up a + and some a K position. Many of both,
however, were quiescent and evenly distributed. The course taken by the
Daphnia was indeterminate or vaguely diagonal.

**Notes on Positivation, etc.**—A fresh collection caught the previous day was
used. The average size was smaller than in the last collection. The individuals
used in the experiments were taken from the darker side of the jar.

**Conclusion.**—These were negative cultures with a tendency to early and
transitory positivism. When exposed to currents of about 0.05 amps. the
large Daphnia assumed a resultant + K position, while the small ones were
mainly photonegative (–) or slightly – K. On simultaneous reversal of current
and light directions the small took up a resultant – A position in every case,
while the large were somewhat vaguely + K, many of the latter being rendered
quiescent by current reversal, a state of affairs which obscured the seemingly
diagonal nature of their course. Positivation occurred in the larger, but not
in the smaller specimens, during the current's passage; on reversal of light,
direction, and subsequent application of current a marked and striking separation
of the sizes occurred.

The positive individuals became photonegative after a short time. The
immediacy of the positivation on application of the current, and of negativation
when it ceases, inclines me to the view that the former effect is the result
rather of the current itself upon the animals than the effect of increased
hydrogen -ion concentration (due to the current's passage), as has been suggested.

**Experiment 3.**—To find the effect of light and electrical current incident
upon Daphnia at right angles, and to discover the response to a change of light
### Experiment 3.

**Table of Tropic Responses.**

<table>
<thead>
<tr>
<th>Culture</th>
<th>Temp. of Water</th>
<th>Height of Water</th>
<th>Amperage</th>
<th>Reaction</th>
<th>Reversal</th>
<th>2nd Reaction</th>
<th>Course</th>
</tr>
</thead>
<tbody>
<tr>
<td>c 1.</td>
<td>18.5°C</td>
<td>2.1 cm</td>
<td>0.04</td>
<td>Large, chiefly + K.</td>
<td>L</td>
<td>Large, chiefly + K.</td>
<td>Chiefly along or parallel to cathode.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(2) Small, chiefly -.</td>
<td></td>
<td>(2) Small, chiefly - to K.</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(3) Some quiescent.</td>
<td></td>
<td>(3) Many to some quiescent and evenly distributed.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>c 2.</td>
<td>18.5°C</td>
<td>2.1 cm</td>
<td>0.058</td>
<td>Large + K.</td>
<td>L</td>
<td>Large, chiefly + K.</td>
<td>Large along cathode. Small indeterminate.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(2) Small - A.</td>
<td></td>
<td>(2) Small, chiefly - A.</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(3) Some quiescent and diffuse.</td>
<td></td>
<td>(3) Many quiescent and diffuse.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>c 3.</td>
<td>18.5°C</td>
<td>2.3 cm</td>
<td>0.04</td>
<td>Large (few in numbers) + K.</td>
<td>L</td>
<td>Large, chiefly K to + K.</td>
<td>Large along cathode. Small fan-wise from corner.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(2) Small (numerous) - A.</td>
<td></td>
<td>(2) Small - A and -.</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(3) Some quiescent.</td>
<td></td>
<td>(3) Many quiescent.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>c 4.</td>
<td>18.25°C</td>
<td>2.4 cm</td>
<td>0.03 at first</td>
<td>Large +.</td>
<td>L</td>
<td>Large + K.</td>
<td>Large vaguely along cathode. Small fan-wise.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(2) Large + K.</td>
<td></td>
<td>(2) Small - A.</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Small - A.</td>
<td></td>
<td>(3) Many diffuse or quiescent.</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Reactions of Daphnia
direction with constant current direction. Procedure as in Experiment 2. The cultures were taken from the dark side of the jar containing the collection caught on 16th July. Four cultures were tested.

Notes on Positivation.—c 1. Before the current most were negative, though some had been at first photopositive. The large Daphnia were positive after treatment with, and cessation of, the current, but soon became negative. On light-reversal and application of the current, retrogression occurred as in the last experiment, but was not so clear owing to the number of (permanently negative) small individuals. Most were soon negative (but many were + and diffuse) on cessation of current, and on reapplication of the current (about 0.05 amps.) the large took up a + K, the small a –, position.

c 2. Before treatment the majority were first positive and then negative. After cessation of the current negativation soon set in. The retrogressive reaction was not so clear-cut as before. In this culture the majority, save the very small individuals, appeared positive in the current, but on its cessation were diffuse after an interval of three minutes; in fact, negativism was not so marked as usual, either before or after the current's passage.

c 3. Nearly all were positive at first, later some became negative, but by no means all, and though the negative specimens were perhaps in the majority, there were many diffuse. On release of the current the majority became negative. Retrogression is very vague, though a check occurs when the current is applied, the large specimens becoming positive or quiescent, and the smaller ones continuing negative.

c 4. At first some were positive, but later the majority were negative with some positive and diffuse specimens. On cessation of the current the large ones were at first positive, and while some remained so, or were diffuse, the majority were negative. Retrogression occurred in some individuals, the smaller ones continuing their negative course. During the passage of the current the largest number of individuals were positive, but later became diffuse with a tendency to negativism.

Conclusion.—The large specimens showed the resultant reaction + K, before and after reversal of light direction alone. The small ones were photonegative (−) throughout, with a tendency to a resultant effect (− A). The course taken by the larger specimens was parallel to and along the kathode; the smaller spread fanwise from the corner, in some cases. There was a tendency to very early photopositivism which was soon supplanted by negative response to light. During the current's passage the large were mainly positive, but they became negative again on its cessation. The small animals were photonegative throughout. The retrogressive reaction was not so well marked as in Experiment 2.

Experiment 4, 18/7/24.—To find the effect of light and electrical current incident upon Daphnia at right angles, and to discover the response to a change of current direction, the light direction remaining constant.

Procedure as in Experiments 2 and 3.
The cultures were taken from the dark side of the collection caught on 16th July.
Summary of Table.—Six cultures (d1 to d6); water temperature 16.75° to 17°C.; height of water 2.1 to 2.5 cm.; current 0.04 to 0.068 amps. (in d6, 0.08 to 0.09 amps.). The reaction in the large animals was the assumption of a + K or + position (in the highest current many were quiescent).

The small were — as a whole, some appeared to be diffuse, a few − K or − A, and there was a slight tendency to positivism. On reversal of current direction alone the large were + to + K but many were quiescent. The small Daphnia were — and diffuse or − A, with the exception of culture d6, in which they were +. In two cultures (d1 and d2) many of both sizes were diffuse. On reversal of current the course taken by the large animals, when they started to move, was in most cases distinctly along the lighted side; in two cultures small positive and small diffuse specimens each became negative and moved across the dish.

Conclusion.—The large animals showed a rather obscured resultant effect (+ to ± K). The small were negative or diffuse, likewise somewhat obscurely. On reversal of the current direction the large specimens took up a rather vague resultant position, as before, and began by moving along the lighted side. This movement showed a resultant reaction beyond doubt, but the later stages were clouded by the annoying prevalence of quiescence. There is a tendency to early positivism in these cultures, which soon gives place to negativism, and this is the photic response of the majority. The large are positivated by the current, but the small are not, and their difference is very marked. The large specimens remained photopositive for a longer time than heretofore in cultures d1, d4, and d5. There was a distinct tendency to positivation in the small specimens. Retrogression was not well marked in some cases.

The whole experiment was far from clear, but the movement of the large individuals along the lighted side, on reversal of the current direction, showed the resultant effect sufficiently well to redeem it.

Experiment 5, 18/7/24. — To find the reactions of Daphnia to an electrical current, and their response to reversal of its direction. The cultures were taken from the collection caught on 16th July. This experiment was performed in darkness so long as the current was flowing. The reactions of the Daphnia to light, before and after the passage of the current, were observed, as well as their galvanotropic reactions.

Summary of Tables.—Five cultures (e1 to e5) were used; water temperature 17° to 17.25°C.; height of water 2.15 to 2.7 cm.; current consistently 0.06 amps. The reaction of the large Daphnia to current alone was kathodic (K) in every case, with a varying number of quiescent individuals. The small animals were diffuse with a tendency to gather at K. On reversal of the current most of the larger animals again took up a K position, while some were diffuse or diffusely quiescent. The small were always diffuse. The course taken (in the dark), on reversal of the current direction, was (as far as could be seen) straight across the dish in two cultures that were watched.

(N.B.—“Diffuse” distribution, in the reaction after reversal, does not include the anodic region.)
Reactions of Daphnia

Conclusion.—The large were kathodic and the small diffuse in their distribution. Trials of phototropic reactions before and after passage of the current (but not during it) showed that all were photonegative before, and that the larger specimens were photopositive directly afterwards but later became diffuse. The small were diffuse, like the large ones, at the end, but were never, as a whole, markedly photopositive.

Experiment 6.

Table of Tropic Responses.

<table>
<thead>
<tr>
<th>Culture</th>
<th>Temp. of Water</th>
<th>Height of Water</th>
<th>Photic Reaction before Passage of Current</th>
<th>Amperage</th>
<th>Reaction</th>
<th>Photic Reaction immediately after Cessation of Current</th>
</tr>
</thead>
<tbody>
<tr>
<td>f 1</td>
<td>17-25°C</td>
<td>2-2 cm</td>
<td>+, −, and indifferent.</td>
<td>0-006</td>
<td>+, −, and indifferent.</td>
<td>+, −, and indifferent.</td>
</tr>
<tr>
<td>f 2</td>
<td>17-15°C</td>
<td>2-2 cm</td>
<td>−, to indifferent (and a few +).</td>
<td>0-015</td>
<td>− to indifferent (and a few +).</td>
<td>− to indifferent (and a few +).</td>
</tr>
<tr>
<td>f 3</td>
<td>17°C</td>
<td>2-2 cm</td>
<td>+, −, and indifferent.</td>
<td>0-025</td>
<td>+ to +K and indifferent (some −).</td>
<td>+, −, and indifferent later rather more −.</td>
</tr>
<tr>
<td>f 4</td>
<td>16-8°C</td>
<td>2-2 cm</td>
<td>Chiefly − (some + and indifferent).</td>
<td>0-035</td>
<td>+ K to + (some, the largest specimens, diffusely quiescent).</td>
<td>+ at first, soon became −.</td>
</tr>
<tr>
<td>f 5</td>
<td>16-8°C</td>
<td>2-2 cm</td>
<td>Chiefly − (some + and indifferent).</td>
<td>0-045</td>
<td>+ K to + (some K, several diffusely quiescent).</td>
<td>Great majority strongly + at first. Then slowly became −.</td>
</tr>
</tbody>
</table>

Experiment 6, 21/7/24.—To find the threshold value of the electrical current for the resultant and positivating phenomena in Daphnia, the light intensity remaining constant.

The cultures were taken from the dark side of the collection caught on 16th July. As many of the Daphnia were dead, these cultures were weak, but the average size of the individuals was large.

General Notes.—f 1. No effect of the current was noticeable. There were some positive, some negative individuals, and some going from light to dark side and back (which are termed indifferent in order to differentiate them from the diffuse individuals that swim in an aimless manner about the dish, or those in which the to and fro motion was not noticed).

f 2. No effect of the current was noticeable. In this culture the indifferent individuals appeared to remain at the negative side longer than at the positive side in their to and fro movement, producing a preponderance of negative individuals over positive.

f 3. Again many indifferent individuals were present. The current seemed to have some resultant and positivating effect during its passage, but the latter soon disappeared on the current's cessation.

f 4. Before the current was turned on, most were at first positive, but later most were negative. To and fro movement occurred (some indifferent individuals were present). A most distinct resultant and positivating effect
J. A. Robertson

was observed during passage of the current. Positivation did not, however, last long after the current's cessation, some individuals soon became negative and finally a stable "-, some + and indifferent" condition was reached.

f 5. A distinct resultant and positivating effect was observed; positivation remained longer after cessation of the current than before. The culture was chiefly negative before treatment with the current, chiefly positive just after its cessation, and finally "+, -, and indifferent."

Conclusion.—The resultant effect begins rather vaguely at 0.025 amps., becoming definite at 0.035 amps. Positivation also begins at 0.025 amps., but disappears immediately on cessation of current; at 0.045 amps. the positivation lasted longer and seemed more permanent.

Experiment 7. 21/7/24. (A repetition of Experiment 6, using the same culture.) Summary of Table.—The same five cultures as in Experiment 6 (f 1 to f 5) were used; water temperature 17° to 17.5° C.; height of water uniformly 2.2 cm. The photic reaction, before the current was turned on, was prevalently negative, with some positive and indifferent. The current was varied between 0.01 amps. and 0.05 amps. by equal amounts of 0.01 amps.

Positivation seems to appear at 0.02 amps., but is incomplete. Resultant (+ K) reaction appears at 0.03 amps. in the large specimens, and continues in higher current strengths. Photic reaction immediately after cessation of the current is - (some + and indifferent) up to 0.04 amps. when positivation appears to become more permanent, but signs of this appear at 0.03 amps.

Conclusion.—These cultures were those used in Experiment 6. Positivation was first clearly seen at 0.02 amps., but was of short duration on cessation of the current. The resultant phenomenon appeared at 0.03 amps. in the large specimens, positivation being more distinct at this current strength but not permanent on its cessation. The resultant was very marked at 0.04 amps. Positivation became more permanent at 0.05 amps. "To and fro movement" occurred throughout most of this experiment, except in cases of strong positivism.

Experiment 8, 23/7/24.—To find the threshold value for galvanotropic reaction, and the threshold value of the current for positivation of photonegative Daphnia.

A fresh collection, caught on 23rd July (the same day) was used. This collection was taken from the same pond as the last, was photonegative, and in all noticeable reactions similar to that of 16th July. The cultures were taken in this, and all subsequent experiments, from the dark side of the jar.

The current was turned on in the dark.

Summary of Table.—Five cultures (g 1 to g 5) were used; water temperature 17.25° to 17.5° C.; height of water, in each case, 2.2 cm. The photic reaction of the Daphnia, before the current was applied, was negative, a varying minority being positive or indifferent. There was an early and transitory positive tendency in g 2 and g 4. The current was varied by equal increments of 0.01 amps. from 0.005 amps. (actually 0.007 amps.) to 0.045 amps. The kathodic galvanotropism first occurred at 0.025 amps., and continued in the higher currents. The small Daphnia appeared diffuse almost throughout, and the large were
Reactions of Daphnia

diffuse up to 0.025 amps. Photic reaction immediately upon cessation of the current showed a distinct positive tendency in most cultures, but this was followed, shortly in some cases, by prevailing negativism with a varying number + and indifferent.

**Conclusion.**—The galvanotropic threshold appeared to be at 0.025 amps., where kathodic reaction first occurred; at 0.035 amps. the larger individuals were definitely kathodic, and the smaller were unaffected and diffuse. A positivation effect, which was transitory in nature, appeared from the first (at 0.007 amps.).

**Experiment 9, 23/7/24.** (A repetition of Experiment 8, with cultures from the same collection.) **Summary of Table.**—Five cultures (h 1 to h 5) were used; water temperature 17.25° to 17.6° C.; height of water 2.2 cm. Photic reaction prior to application of the current was “− (some + and indifferent)” in each case, usually after transitory positivism. The current was varied from 0.01 amps. and 0.05 amps. by equal amounts of 0.01 amps. Kathodic galvanotropism occurred in a current of 0.3 amps. and over; the small were mainly diffuse throughout, and the large were also diffuse up to 0.03 amps., few, however, were near the anode. Photic reaction immediately after cessation of the current was positive in numerous cases, but later the great majority became negative, with a varying number positive and indifferent.

**Conclusion.**—The kathodic reaction was seen clearly at 0.03 amps., while positivation appeared, it seemed, from the first (0.01 amps.).

In both Experiments 8 and 9 the positivation apparently due to low currents (0.007, 0.01, 0.015 amps.) may have been due to the re-illumination of the cultures after some minutes in darkness (during passage of the current); for in many cases the cultures showed a transitory tendency to positivism when first illuminated, prior to treatment with the current.

**Experiment 10, 24/7/24.**—A repetition of Experiment 6 to test whether the positivation by a low current of some individuals in the culture is due to that current and lasts as long as the current flows, or whether the positivism is induced by momentary darkening (after the phototropic sign of the Daphnia has been tested, and before light and current are switched on together as in Experiment 7), or by the interpolation of a fairly considerable dark period (as in Experiments 8 and 9 during passage of the current) and subsequent illumination. If the latter be the true explanation the positivism should not last throughout the passage of the current, but if the former is true the positivism should remain as long as does the current. Many of the cultures used in Experiments 7, 8, and 9 showed a distinct photopositive tendency prior to treatment with the current, which later gave place to negativism.

The cultures were taken from the collection caught on 23rd July.

**Summary of Table.**—Five cultures (i 1 to i 5) were used; water temperature 16.5° to 16.75° C.; height of water 2.2 cm. The photic reaction of the Daphnia, before experiment with the current, was negative in the majority with a varying minority of positive and indifferent individuals, following on a distinct but transient positivism in all cultures. The amperage was varied, by equal amounts of 0.01 amps., between 0.005 amps. (actually 0.007 amps.) and 0.045 amps.
J. A. Robertson

The reaction up to 0.025 amps was "- (some + and indifferent)"; at this, resultant reaction (+ K) began among the majority of the large animals, and continued in the higher currents. The small were, however, - or - A. Some of the large were positive, kathodic, quiescent. Several of both sizes were indifferent or diffuse at 0.25 amps.

Photic reaction, after cessation of the current, showed transitory positivism in the large specimens at and beyond 0.035 amps. (small, negative throughout); otherwise most were negative.

Conclusion.—The resultant reaction and positivation effect appear together at 0.025 amps. in the larger specimens, but both are clearer at 0.035 amps.

The positivation lasts as long as the current flows, and it therefore seems probable that re-illumination after a period of darkness is responsible for photopositivism, after treatment with low currents, in Experiments 8 and 9.

Experiment 11.

Table of Tropic Responses.

<table>
<thead>
<tr>
<th>Culture</th>
<th>Temp. of Water</th>
<th>Height of Water</th>
<th>Photic Reaction before Current</th>
<th>Amperage</th>
<th>Reaction</th>
<th>Photic Reaction after Current</th>
</tr>
</thead>
<tbody>
<tr>
<td>j 1</td>
<td>17-25° C.</td>
<td>2-2 cm.</td>
<td>+ and - at first, later - (many + and indifferent).</td>
<td>0.005</td>
<td>- (some + and indifferent).</td>
<td>- (many + and indifferent).</td>
</tr>
<tr>
<td>j 2</td>
<td>16-9° C.</td>
<td>2-2 cm.</td>
<td>- in great majority (some + and indifferent).</td>
<td>0.015</td>
<td>- (some + and indifferent).</td>
<td>- (some + and indifferent).</td>
</tr>
<tr>
<td>j 3</td>
<td>17-25° C.</td>
<td>2-2 cm.</td>
<td>+ and - at first, later - (some + and indifferent).</td>
<td>0.025</td>
<td>(1) Large + K to K (some -). (2) Small -.</td>
<td>Large + at first, later Total distribution - (some + and indifferent).</td>
</tr>
<tr>
<td>j 4</td>
<td>16-75° C.</td>
<td>2-2 cm.</td>
<td>+ and - at first, later - (several + and indifferent).</td>
<td>0.035</td>
<td>(1) Large + K (2) Small - (some few + and diffused).</td>
<td>Large + at first, very soon became -. Total distribution - (several + and indifferent).</td>
</tr>
<tr>
<td>j 5</td>
<td>16-75° C.</td>
<td>2-2 cm.</td>
<td>Some + at first, later - (a few + and indifferent).</td>
<td>0.045</td>
<td>(1) Large + K to K (some quiescent) (2) Small - A.</td>
<td>Large + at first, later became -. Total distribution - (some + and indifferent).</td>
</tr>
</tbody>
</table>

Experiment 11, 24/7/24.—To discover whether lowering the intensity of illumination will in any way affect (lower) the threshold value of the electrical current for the resultant reaction and positivating effect.

The cultures were taken from the collection caught on 23rd July.

The dish was removed to double its previous distance from one of the lights, reducing the intensity of illumination by 4. The procedure was the same as that in Experiments 6, 7, and 10.

Conclusion.—The resultant reaction, together with positivation, first appears
Reactions of Daphnia

in the large specimens at 0.025 amps. as before. Both reactions are well marked at 0.035 amps.

It appears that there is no lowering of the threshold value of the electrical current for resultant or positivation effects consequent on reducing the intensity of illumination by 4.

Experiment 12, 25/7/24. (A repetition of Experiment 11. The cultures were taken from the collection caught on 23rd July.) Summary of Table.—Five cultures were used (k 1 to k 5); water temperature 16.25° to 16.75° C.; height of water 2.2 cm. The photic reaction, prior to passage of the current, was negative in the majority with a varying minority of + and indifferent specimens. An early and transitory positive tendency appeared in k 4 and k 5. The current was varied between 0.01 and 0.05 amps. by equal amounts of 0.01 amps. Up to 0.03 amps. the Daphnia remained negative, but at this point the large ones took up a (+ K) resultant position, and this effect remained in higher currents; there was a distinct tendency to be cathodic only, and a minority were quiescent in most cultures. The small animals were "- A to - ." Photic reaction after cessation of the current showed a positive tendency of varying duration, from 0.03 amps. onwards, in the large individuals (in k 5 this was permanent). The final reaction was usually - (some + and indifferent). Conclusion.—Resultant reaction and positivation occur at 0.03 amps. for the first time, among the larger specimens. Positivation seemed more permanent after cessation of a current of 0.25 amps. than after other current strengths.

As in Experiment 11, no lowering of the threshold value of the current, due to decreasing the intensity of illumination, was observable.

5. General Conclusions.

In all the later experiments Daphnia was decidedly photonegative, although in the early qualitative trials the cultures used were positive.

Experiment 5 has shown beyond doubt that Daphnia give a kathodic reaction to a current of 0.06 amps. It is remarkable that this reaction is shown by the large specimens only, the small being apparently unaffected. It is also noteworthy that most other animals are anodic (Palaemonetes, Amblystoma, Corixa). The photopositive Daphnia used in the qualitative experiments would not give a resultant reaction to a current of less than 0.08 amps., but such a current induced quiescence in the negative cultures used later, as indeed did currents of as low value as 0.05 and 0.06 amps.

The large individuals, in all experiments (save 5, 8, and 9, which were trials of electric current alone) showed a resultant reaction to light and electrical stimuli incident at right angles. They went to the lighted and kathodic corner of the dish (+ K).
J. A. Robertson

This reaction was not always as clear as could be wished, but the Daphnia used were not easy material, in that they were probably influenced as to their behaviour by many conditions which were difficult to foretell or eliminate (such as temperature and oxygenation of the tap-water used, and the amount of disturbance caused by transferring them to the experimental dish, as well as internal conditions). On the whole the resultant reaction showed itself well and consistently. The small specimens were, as a rule, photonegative throughout the experiments, but not infrequently these too showed a tendency to resultant reaction. They gathered in the dark and anodic corner (−A) in Experiments 2, 3, 10, 12, and 4 to a less extent. In Experiment 2, however, a gathering also occurred at −K. This (−A) resultant was not as consistent in its appearance as that shown by the larger animals, and is therefore more open to doubt.

The course taken on reversal of both light and current, in Experiment 2, was diagonal; in experiment 3 on reversal of light direction alone the large specimens took a course along the kathode, while in Experiment 4 they began to react to change of current direction alone by moving along the lighted side. In Experiments 2 and 4, but especially in Experiment 2, their movement on reversal of current direction was much hindered by the quiescent influence of the current. Yet, on the whole, their position on reversal of current and light direction, whether separately or together, was again the resultant +K.

Another effect of the current upon the reactions of Daphnia to light is of great importance for the resultant reaction. The large animals are, throughout this series of experiments, rendered photopositive by the passage of a current, making the resultant reaction +K rather than −K in sign. This positivation does not as a rule extend to the small specimens, which retain the culture's primary negativism. The positivated individuals remain in this condition as long as the current flows, but on its cessation they usually return to a photonegative state within a short time. Exceptions are usually found among cultures which have been subjected to one of the higher current strengths. As stated in the conclusions to Experiment 2, the immediacy of positivation and of
Reactions of Daphnia

negativation, on "making" and "breaking" the current, inclines me to the view that the current has an electrical, rather than an indirect, chemical effect (through altering the pH) in thus changing the sign of photic reaction in negative Daphnia.

In Experiments 6, 7, and 10 the threshold value of the current for the resultant and positivating reactions just described, was found to be 0.025, 0.03, and 0.025 amps, respectively, though positivation occurred in Experiment 7 at 0.02 amps. The light intensity was that used in the earlier experiments.

The threshold value of the current for galvanotropic reaction was tested in Experiments 8 and 9, as was this value for positivation by the current of negative Daphnia. The galvanotropic threshold was found to be 0.025 and 0.03 amps, respectively, in Experiments 8 and 9, when kathodic reaction occurred. When the Daphnia were illuminated after being exposed to currents of 0.007 and 0.01 amps, in the dark, they were transitorily photopositive. They had, however, been first positive and finally negative before treatment with the current, in several cases. It is therefore probable, as seen in Experiments 9 and 10, that this positivism is due to reillumination after a period of darkness, rather than to the positivating effects of such low currents. The electrical threshold of the positivating effect is, for the reasons there given, not well shown by those experiments (Experiments 8 and 9).

If the galvanotrophic threshold is between 0.025 and 0.03 amps, we should expect no lowering of the electrical threshold for resultant and positivating phenomena due to reduction of the light intensity, for this is the minimum current that elicits a response by itself. In Experiments 11 and 12 this lowering of the electrical threshold was attempted, the light intensity being reduced by 4. Thus the current has its, apparently full, tropic influence when at its minimum effective intensity, and the value of the minimum current that produces the resultant reaction is not in any way related to the strength of the other directive stimulus (light). This state of affairs would not be in agreement with Patten's experiments on the Blow-fly larva with two lights at right angles. In his experiments the minimum
values of the two light-intensitites that produce a resultant reaction are interrelated; for if one light is strong it will require a higher minimum intensity from the other light to produce any noticeable resultant reaction, than it would were the first light weaker. It appears to be substantiated, so far as these experiments go, that the minimum current-strength necessary to produce a resultant reaction is not relative to the strength of the other stimulus, as in Patten's experiments, but is an absolute minimum, i.e. that for reaction to the current alone.


Experiments were carried out with Daphnia to see whether the phototropism and galvanotropism which they exhibit would, when the animals were exposed simultaneously to light and to electric current at right angles to each other, induce a resultant reaction such as occurs in many phototropic animals when exposed to two sources of light simultaneously.

Considering the rather difficult nature of the material (consequent on the number of small specimens present, the prevalence of quiescence or inhibition, and the all too frequent modifiability and variability of behaviour among some individuals in the cultures), the following results may, I think, be seen sufficiently clearly: A resultant reaction in the large specimens, doubtfully in the small ones; positivation, by the current, of the photonegative large specimens, but not of the small animals; kathodic galvanotropism in the large, but not in the small individuals. The threshold value of the current, for galvanotropic reaction alone, and for resultant reaction and positivation, has been found; and finally the latter threshold value has been shown to be independent of the light intensity. The current threshold for resultant reaction, with the light intensities tried, is seen to be the same as that for kathodic galvanotropism alone.

7. References.