ON RHEOTROPISM. I.—RHEOTROPISM IN FISHES.

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THE usual theory regarding the mechanism of stimulation of organisms in currents of water or air is set forth in the following excerpts from the literature. Rädli, in his book on "Untersuchungen über den Phototropismus der Tiere," says concerning the ephemeridae: "They react very sharply to a gentle current of air, turning the head toward the air current, but without leaving the place in which they are floating. The air current acts by exerting pressure on the body surface of the animals and evidently tends to draw the body into the direction taken by it. On the contrary, the fluttering wings strive to lift the body upward and forward. The points of application of this force, lifting the body, and the force of the air current need be only very slightly separated; and a force-couple will result, that will rotate the body until the two forces, the muscle force and the force of the air current, draw the body in opposite directions.

"It is easy to pass from the rheotropism of the ephemeridae to other analogous phenomena of rheotropism. It will everywhere be found that the pressure of the air current acts as one force and contraction of the muscles as the other."

Verworn in his "General Physiology" classes rheotropism, stereotropism, and geotropism together under the collective title barotaxis, since he believes that all alike are responses to pressure. "A second form of barotaxis," he says, "in which the stimulus is produced, not as in thigmotaxis by contact with a solid body, but by a gentle current of slowly flowing water, is rheotaxis, which was discovered by Schleicher and carefully investigated by Stahl ('84). This is the peculiarity belonging to certain organisms, of taking toward flowing water a direction of motion opposed to the direction of the current. Since these organisms thus turn toward a pressure-stimulus, rheotaxis is merely a special form of positive barotaxis."
Wheeler\textsuperscript{1} has named the orientation of flying animals in the wind anemotropism, and thus expresses himself regarding the cause of the phenomenon: "It requires but a moment's consideration to see that anemotropism is only a special form of rheotropism. . . . The only difference lies in the fact that the insect reacts to a gaseous, the fish and myxomycete to a liquid current. In both cases the organism naturally assumes the position in which the pressure exerted on its surface is symmetrically distributed and can be overcome by a perfectly symmetrical action of the musculature of the right and left halves of the body."

It is noticeable that all these authors consider rheotropism a reaction to pressure. The pressure of the wind or water acting against one side of an animal is assumed to be a stimulus like light or migrating ions, leading to one-sided activity of such a kind that the animal at length receives the stimulus uniformly on both sides. Then a uniform activity of its symmetrically arranged contractile elements carries it forward in the stream. This is the general theory of the tropisms.

To us who stand on the earth, the pressure of the wind or water is a very real thing. But if we were floating in a fluid medium, it is doubtful if uniform currents would be known to us. To the aeronaut the earth seems to slip along beneath. All is still, and he feels no wind because his balloon has the same velocity as the air. In the dark he cannot tell whether he is moving or not. In a fog one has no sensation of being borne along by the tide. In other words, as is well known, we have no organ for the recognition of uniform motion, nor can we imagine how such an organ could act. Stimulation implies a change of relation between organism and environment. But if both in all their parts are moving at the same velocity, their relations do not change and the conditions for stimulation are wanting.

Or, look at the matter in a little different light: a fish swims forward in quiet water with a velocity of ten feet a second. Of course the head of the fish sustains a certain pressure or resistance. Now, suppose the fish to be in a uniform current having a velocity of ten feet per second. To hold its place in the stream the fish must put forth the same effort as would carry it forward ten feet per second in quiet water, and the pressure exerted on its head must

\textsuperscript{1} \textit{Wheeler} : Archiv für Entwickelungsmechanik, 1899, viii, p. 373.
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be the same as if it were swimming at the same rate in a quiet lake. How can this pressure orient the fish in one case and not in the other?

Or, let us imagine the fish at rest in calm water. Its body sustains a hydrostatic pressure proportional to its depth below the surface. Now, imagine the fish at rest (i.e., inactive) in a deep and uniform stream of water. It is carried along with the same velocity as the water. Its body is also sustaining hydrostatic pressure and no other; and if it is at the same depth as the other fish, this pressure is equal on the two fish. How can the pressure serve to orient in one case and not in the other? No fish or bird would advocate a pressure theory of rheotropism. But it came naturally enough from man, who stands upon the earth and has that as a reference point for every motion of water or air. To man the wind makes itself known as a pressure. But to the bird above the earth it must express itself in an apparent motion of the ground; and only when the bird attempts to keep its position with reference to the non-moving objects on the ground, does it begin to feel the pressure of the air current, and then only so much pressure as if it were flying in calm air with the same effort. Pressure results from orientation; it does not produce it.

It will be understood that in all these considerations I have in mind currents of uniform velocity. Gusty winds and irregular currents will need separate discussion.

It comes to this: Motion is a relative conception. It implies objects at rest as well as objects moving. We do not know that anything moves unless ourselves or other things are at rest. We are moving through space at a rate of hundreds of thousands of miles a day in the orbit of the earth around the sun. But all our ordinary reference points are going at the same rate; as a result, it took man unknown centuries to discover that he is always moving in this way. He never has any sensation of it. It is equally absurd to imagine a fish in the Gulf Stream to be stimulated and oriented by a uniform forward motion of the water. Whether orientation be a simple reflex or a conscious process, points of reference — i.e., points relatively at rest — are necessary.

It was considerations like the foregoing which led me to believe that rheotropism is not a response to the current in the simple way that writers have assumed, but rather a response to relative motion. Bodies which do not move must be as important in bringing about
stimulation as those which do move,—indeed, more important in some cases. In the case of the fish in the stream, the bottom and banks evidently constitute a large part of the stationary environment. If these are of importance in determining the rheotropic responses, one thinks naturally first of the eyes as the organs through which the stimulation might take place. Furthermore, if rheotropism is a response to relative motion, we might expect the fish to be oriented as well if the water should stand still and the bottom should move (with reference to us and the fish), as in the usual case where the water moves and the bottom stands still. This turns out to be true.

**Experiment 1.**—An aquarium with a glass bottom was so supported that the bottom was freely accessible. Close along the bottom, beneath the glass, could be drawn a long piece of white cloth with black stripes painted across it. This would give the impression of a moving bottom. Fish (Fundulus) placed in the aquarium oriented themselves with the head in the direction of the moving bottom and swam along with it to the end of the aquarium. Reversing the movement of the bottom reversed the orientation and movement of the fish.

This experiment is striking enough to convince any one that orientation may come through the eye, and under conditions where no pressure changes occur. But not every fish responds (especially if we use adults); and we might think, therefore, that the eye, as part of the reflex arc, plays but a small part in rheotropism. It is to be noted, however, that the conditions are very artificial. The bottom is unnatural, the sides do not move, and the fish are disturbed by the presence of the observer.

It might seem at first glance, too, that the animals should move in the opposite direction to the moving bottom. But that is not the correct view, for in an ordinary current the fish tends to be borne downstream away from fixed points in the environment. In other words, we may say the bottom appears to be moving upstream, and the fish moves with the moving bottom.

**Experiment 2.**—A cylindrical glass dish about 12 cms. deep and 30 cms. across was supported from above by wires so as to remain stationary. Around this was placed a galvanized iron cylindrical dish about 18 cms. deep and 40 cms. diameter, supported from below so that it could be rotated about the common vertical axis of the two dishes and around the inner, stationary dish. The bottom of the rotating dish was covered with gravel, and some small seaweeds were attached to the sides. The inner vessel
and the space between the two were filled with water. A beaker of dark liquid was set in the middle of the inner cylinder, so that the fish could see only one side of the rotating cylinder at a time. Thus a circular pathway was formed in which the fish were placed. On turning the outside dish the fish moved round and round inside the stationary dish, and in the same direction as the moving environment.

Reversing the motion reversed the orientation.

With many species of young fish the experiment succeeds with clock-like regularity. With older fish, especially Fundulus, efforts to escape and to hide mar the result. Individual adults may perform well, but there are many exceptions. It is to be noted in this experiment also, however, that not all of the environment moves. As we shall see, cutaneous sensations, as touching the non-moving glass bottom, would tend to correct the illusion of a current. Fundulus, too, seem to learn quickly that they are being deceived. But by a modification of the experiment, suggested by Dr. Garrey, the importance of the optical stimulus even in the adult fish may be uniformly demonstrated. If one by stirring with the hand sets up a real current in the circular path occupied by the fish, they respond to it. Now, by rotating the outside dish opposite to the current, one may intensify the rheotropic response. By rotating it in the same direction as the current, one can annihilate the orientation.

Experiment 3. — The inner, stationary dish was removed, and the fish placed in the outer dish, the beaker being placed in the centre as before. In this case, even better than before, the fish went round and round, keeping with the moving bottom. Reversing the latter reversed the fish.

In this experiment, through friction between the container and the water, currents in the latter are actually set up. They are in the same direction as the rotating cylinder, and slower than the latter. Now, if it were the current per se which orients the animal, they ought to turn and go against the current in the cylinder. On the contrary, they move with the moving optical field, and therefore with and faster than the current. If, after revolving the cylinder several times and getting up a considerable current, the cylinder is suddenly stopped, the fish are borne on a short distance with the current, then turn and face it. But here the current does no more than passively carry the fish past the fixed points of the environment, and therefore create a relative motion of the latter opposite to that it had before (and this effect can be abolished or intensified by proper move-
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ments of the cylinder). This, it seems to me, is all the current in the case of fish usually does. On placing fish in water I have noted repeatedly that they are first borne downstream a short distance, then turn and swim up. The stimulus is the moving or apparently moving optical field, and the current is only indirectly responsible.

This impression is very strongly borne upon the observer if young fish and shrimps (Palemonetes) are placed in the turn-table at the same time. On rotating the latter two sets of circulating organisms are seen. The fish swim round and round in the direction of the motion of the environment. The shrimps swim opposite to this, and therefore against the true current which the revolving cylinder sets up. On stopping the cylinder the fish turn, and both kinds of animals now face the current. I am not yet entirely ready to discuss the rheotropism of Palemonetes. (I hope to take up the rheotropism of the insects, crustacea, protozoa, etc., in a future paper.) But it appears in this experiment that there are two types of stimulation bringing about a rheotropic response, and in the fish apparently the optical type is the stronger. This is satisfactorily substantiated to my mind by the next experiment.

Experiment 4.—In a long bottle of about ten litres' capacity were placed some young fish, and the bottle entirely filled with water and corked. The bottle was submerged and held by wires lengthwise in the large open-air basin at the Fish Commission, near a wall covered with algae. Moving the bottle toward my right, the fish all crowded to the left-hand end. Moving the bottle toward the left, the fish all rushed to the right, and crowded up into the very neck of the bottle in dozens. Nothing could be more beautiful than the machine-like regularity with which a school of silver-side minnows responded. To make it still more striking, I buoyed up the bottle, and placed it in a shallow tide-stream. As I released it, and it started to float off downstream, every fish hastened to the upstream end of the bottle. Stopping the bottle, they swam about in all directions. Letting it go again, they were instantly oriented and swam to the up end. Pulling the bottle upstream against the current, they went to the downstream end.

This experiment seems to shut out all possibility of pressure effects in the orientation of these fish.

Finally, I will describe an experiment which is the simplest and yet perhaps the most convincing of all. It surely approaches natural conditions more closely than the others, unless it be the fourth experiment.
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Experiment 5. — A box about 1.25 metres long, 50 cms. wide, and 35 cms. deep was made with board sides and bottom, but ends of coarse wire netting. The bottom was covered with gravel, and the sides with fucus and sea lettuce. The box was weighted so that its edge would be barely above water. The box was held lengthwise in a strong tide-stream. The Fundulus in it were beautifully oriented. Now the box was released and allowed to float away. Instantly the fish lost their orientation.

"But," one is inclined to say, "there is now no current in the box." That is true in the sense that both box and water now have the same velocity relative to the observer. But the focus of the idea is this: the relation (pressure, for example) between the water and the fish has not changed at any moment. If the orientation depended on some peculiar power on the fishes' part of responding to motion of water, they ought still to be oriented, for the motion of the water has not stopped nor changed. It was the stimulus of the box, of the fixed environment, which really caused the orientation. The current only tended to carry the fish passively away.

If we place the box in quiet water, the fish are of course unoriented. If we begin to draw the box through the water, immediately every fish swims in the direction of the motion of the box. Here again it looks as if we had a current through the box, but it is the latter which moves; the water stands still. The orientation cannot be due, therefore, to pressure, because the pressure relations have remained unchanged. Blind fish placed in the box do not respond as long as their bodies are in contact with water only.

I am therefore convinced that with the fishes experimented with (Fundulus, Scup, Stickleback, Butterfish) orientation in currents of fairly uniform velocity is usually an optical reflex. The current does not directly stimulate. Indirectly it does, by tending to move the fish away from the fixed points of its environment.

It remains to be determined whether the fish possesses other means of orientation besides that through the eyes. First, we may ask whether fish can orient themselves in the dark.

Experiment 6. — A trough was arranged with darkened labyrinths at each end, so that a current of water could be passed through it without admitting light. Some Fundulus were placed in it, and the box tightly closed. On suddenly admitting light, the fish were always found oriented and on the bottom.
Experiment 7. — Several Fundulus were blinded by enucleation. These fish, when put in the trough, through which a not too strong current was kept up, could be seen to swim about more or less at random until they touched the bottom; then they turned their heads against the current. Blind fish stay most of the time on the bottom. If fine sand is sprinkled over the bottom of the aquarium, the fish frequently drag themselves through with sufficient force to leave lines marking the contact of the ventral and anal fins with the bottom.

Experiment 8. — Some blind Fundulus were placed in the strong tideway leading into the Eel Pond. In this the water rushes with more or less eddy and irregularity. The fish, while up from the bottom, would occasionally head up. But on the whole they swam about irregularly (being carried steadily downstream) until they touched bottom. The instant they touched, they headed upstream. This was very striking; even slight and momentary contact with a spear of eel-grass or a tuft of sea lettuce gave the necessary stimulation and reference point, and the animal instantly oriented itself. Very quickly, however, it would be borne by the current away from its contact with the vegetation or other fixed object and would lose its orientation. Such fish were invariably carried out to sea.

It therefore appears that cutaneous sensations are able to effect orientation. But here again the solid, unmoving environment is what stimulates rather than the current itself.

The case is the same exactly as orientation through the optical reflex. Doubtless the two methods of stimulation are closely correlated and ordinarily act together. These observations make clear also why the fish in some of my turn-table experiments were able, by contact with the non-moving bottom, to correct the false optical impression of a current.

Dr. Parker¹ has shown that the lateral line nerves are not concerned in rheotropism, but rather the general cutaneous nerves. My experiments would suggest the probability that the ventral surface is especially concerned, since the fins and general surface of that side would touch solid objects most frequently. But I have made no experiments along this line.

There remains one other, at first sight, apparently different type of stimulation which may cause orientation of fishes in running water.

¹ Personally communicated.
Experiment 9. — A blind fish placed in a trough where water is gushing rather violently, for example, through a small hole, or through a glass tube, may orient itself without contact with solids and strive hard to swim against the stream.

This we might call a true rheotropism, as contrasted with the other forms which have been described. But I am convinced that the methods of stimulation are fundamentally alike. The condition in the trough is this: a high velocity in the middle, just where the stream enters, a less velocity next to the central stream, and even a negative velocity or back flow further to the sides of the trough. This relatively slower movement of part of the water is the essential element for stimulation, just as the relatively slower — i.e., non-moving — bottom is the essential thing in the visual form of orientation. The fish could be seen to vary from side to side and to turn the tail and fins strongly, either into the more rapid water on one side or the slower stream on the other.

If one wishes in this case to attribute stimulation to differences in pressure, it is perhaps correct to do so. But the theory must be quite different from the gross mechanical one of Rádl. It must involve the idea of higher pressure on one part than on the other, through differences in velocity of the water striking the two parts. Through these differences of pressure orientation may be effected. It seems to me, however, rather more likely that the sliding contact between fish and water in the gushing stream is the stimulus, just as the sliding contact between fish and solids is able to effect orientation. Indeed, rheotropism in so far as it is a response to cutaneous stimulation has close relations with stereotropism.

Orientation of this kind would not be possible in a current of uniform velocity, for example, a wide and deep river. In shallow, swift streams it might in certain forms play an important part. It would be interesting, for example, to test trout as to the respective parts played by the optic and cutaneous nerves in orientation. Indeed, I saw indications that the sticklebacks were more sensitive to variations in the velocity of the water than Fundulus. Blind individuals of the former species were more easily oriented by a gushing stream when not in contact with the bottom. In all the fish with which I have experimented, however, I am convinced that the visual form of stimulation is by far the more important. Blind fish were not able to hold their places in streams where the normal ones were regularly found, and where there were visible differences in velocity. Even
by staying near the bottom they could not sufficiently and continu-
ously orient themselves to prevent being borne down the stream. I
could not attribute their failure to hold their places to muscular weak-
ness, for they would swim against powerful streams in the laboratory,
provided strong differences of velocity were produced in close prox-
imity; and they remained alive for days. Moreover, the turn-table
experiments already mentioned made clear that fish follow the mov-
ing visual field in preference to running against the coexistent and
slower current,—a current amply able, however, to orient them, as
could be seen by stopping the rotation. In a current formed by the
rotation of a dish, evidently the swifter-moving layers would be those
close to the bottom and walls of the cylinder. Next these would be
slower and slower layers. Probably the shrimps which went against
the current were oriented by these small differences of velocity,
but the differences were not sufficient to orient the Fundulus, nor even,
apparently, to render orientation through the eyes less precise.

A very good way of investigating rheotropism is that employed by
Devitz.1 Into a circular dish a stream of water from a rubber tube is
introduced tangentially. Thus a current round and round the dish —
an endless stream — is produced. The velocity varies, being greatest
just where the water enters, and zero at the centre of the dish. On
one occasion I had in such a dish two blind Fundulus, one of which
persistently remained on the sandy bottom; the other, up in the
water. With the former a series of trials was made, in the following
way: the fish, having come to rest on a somewhat elevated central
portion of the dish, was stimulated by means of a glass rod and caused
to swim off toward the periphery and thus into the current. The
record of a series of such trials follows:—

1st trial. — Swam radially, touched bottom, headed upstream.
2d trial. — Swam radially, touched bottom, headed upstream.
3rd trial. — Swam radially, touched bottom, headed upstream.
4th trial. — Swam radially a short distance, turned downstream, swam once
and a-half around, touched bottom, headed upstream.
5th trial. — Swam radially, touched bottom, headed upstream.
6th trial. — Swam radially, touched nose to side of dish, headed upstream.
7th trial. — Swam radially, touched bottom, headed upstream.
8th trial. — Swam radially, turned upstream, and sank to bottom.
9th trial. — Swam radially, touched bottom, headed upstream.

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10th trial. — Swam radially, touched bottom, headed upstream.
11th trial. — Swam radially, touched bottom, headed upstream.
12th trial. — Swam radially, touched side of dish, headed upstream.
13th trial. — Swam downstream half around, touched bottom, headed upstream.
14th trial. — Swam radially, touched bottom, headed upstream.
15th trial. — Swam radially, touched bottom, headed upstream.

Meanwhile, and for hours after, the other fish remained up in the water, occasionally touching the side and heading upstream for a moment, or partially orienting itself where the water current entered, but on the whole without orientation, and borne round and round the dish by the current. This fish was in good condition, and quite as active as the other specimen.

It may be well to point out here a relation which exists between rheotropism and the familiar behavior of animals on a turn-table. When revolved on an ordinary open turn-table, many animals run around in the direction opposite to the turning. In animals which do not have semicircular canals — insects, crustaceans — and in vertebrates whose eighth nerves have been severed, I have shown 1 that this compensatory motion is an eye reflex, and that it may be produced either by rotating the animal or the environment. The animal tends to follow the real or apparent movement of the surroundings. This is the case with a fish in a current of water. In my turn-table experiments with fish already described, the environment practically entire moved round, and the fish moved with it. Centrifugal force and semicircular canals were not concerned, for the water in which the fish were swimming was at rest, especially when an inner stationary dish was used. In streams where there is a real or apparent motion of the surroundings in a straight line, we may consider that we have a wheel of infinite diameter and therefore no centrifugal force. But the phenomenon remains the same, and I think we are justified in classifying rheotropic responses among compensatory motions. This must be true, it seems to me, whether the stimulus to orientation be optical or cutaneous.

The probable part played by rheotropism in the migration of fish may be worthy a moment's discussion. In wide and deep streams, where the velocity is fairly uniform, it seems that fish would only be oriented by sight of or contact with the bottom. Only in rushing

1 Lyon: This journal, 1899, iii, p. 86.
torrents would the difference in velocity of closely adjacent parts of the stream be sufficient to orient. It is to be noted further that an explanation of orientation, although a sufficient explanation for migration in the case of the other tropisms (the only additional factor being ordinary forward locomotion), does not in the case of rheotropism explain migration. For here we have to do with a force which, unlike light, heat, or electricity, tends actually to transport the organisms passively from one place to another. Whether the fish stays in one place in the stream, goes upstream or downstream, depends on whether its activity (i.e., velocity of swimming) equals, is greater, or is less than the current. In tide-streams fish ordinarily merely hold their places. Going upstream involves, beside orientation, a greater activity than that required to keep a place in the stream or retain a given optical field. What the stimulus to this increased activity is, we do not know.

**Summary and Conclusions.**

1. In the fish examined the primary cause of orientation in streams of some uniformity of motion is an optical reflex, a tendency on the part of the animals to follow the field of vision. The current tends to carry the fish downstream and therefore to cause a relative, opposite motion of the environment. To keep the same visual field, the fish moves against the stream. The essential element of stimulation is the environment, not the current. Any relative motion between the fish and its solid surroundings will stimulate and orient. The current is responsible for the orientation only in that it causes such relative motion between the fish and the bottom or banks of the stream.

2. Contact between the fish and stationary objects may lead to orientation. The conditions here are the same as in the preceding paragraph, the current playing only the passive part of sweeping the fish against objects on the bottom.

3. In violent streams where considerable differences of velocity exist in adjacent parts, the fish may be oriented without sight of or contact with solid objects. But here again relative velocities constitute the essential elements of stimulation. If part of the water moves, and that next to it is relatively at rest, the fish may respond just as it does to contact with solids.
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4. In other organisms, also, it is believed that the rheotropic response must be brought about by one or more of the three methods of stimulation found in fishes.

5. Rheotropism in fishes is a form of compensatory motion.

6. Rheotropism explains the orientation, but not the migration of fishes.