BIOLOGICAL BULLETIN

STUDIES ON THE CORRELATION BETWEEN META-BOLIC GRADIENTS, ELECTRICAL GRADIENTS, AND GALVANOTAXIS. I.

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I. INTRODUCTION.

Several years ago, while investigating the physiology of regeneration in oligochætes with the aid of the susceptibility method, the idea occurred to the senior author that there was a remarkable similarity between the susceptibility differences and bioelectric differences. The points of similarity noticed were the following:

1. Any injured region or surface is more susceptible to toxic agents than uninjured regions. It has long been known that injured regions are electronegative (galvanometrically[1]) to uninjured ones.

2. Increase in activity increases the susceptibility and, as is well known, induces an electronegativity (galv.).

3. There is a susceptibility gradient along the axes of organisms, such that in general the anterior end is the most susceptible and the susceptibility decreases along the principal axis. It was known at that time for a few animals that there is also an electrical gradient along the axis, the anterior end being the most negative

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[1] It has unfortunately become customary to refer to the bioelectric currents with regard to the direction in which they run in the galvanometer, which is of course the reverse of the direction in the organism. In order to avoid any possibility of confusion with respect to the direction of the current, the abbreviation " galv." in parenthesis will be employed to indicate the direction of the current through the galvanometer, and the abbreviation " int." to indicate the direction of the current through the animal. In all of the tables the designations negative and positive refer to the direction of current with respect to the galvanometer.

(galv.) and the negativity diminishing along the antero-posterior axis.

4. In the oligochætes the susceptibility gradient was found to be of a characteristic kind (Hyman, '16; Hyman and Galigher, '21). Both anterior and posterior ends are the most susceptible and the susceptibility decreases from both ends toward the middle. It is a very suggestive fact that the electrical gradient in oligochætes is in agreement with this susceptibility gradient. As first shown by Morgan and Dimon ('04), the anterior and posterior ends of the earthworm are electronegative (galv.) to the middle. This re-markable agreement between the electrical and susceptibility gradi-ents indicates strongly that they have a common physiological basis.

From a consideration of the facts mentioned above the senior author was led to believe that the bioelectric currents are due to the same factors which are responsible for the susceptibility differ-ences. The susceptibility differences are known to be correlated with metabolic differences. Organisms or parts of organisms which are highly susceptible to toxic agents have a higher metabolic rate than those which are less susceptible. Susceptibility is in-creased by factors which are known to increase metabolic rate and decreased by those which lower metabolic rate.

It thus appears that the bioelectric currents are correlated with differences in the rate of chemical activity at different levels or in different parts of an organism or tissue, probably chiefly with differences in the rate of oxidation. In general, any region of increased chemical activity becomes *ipso facto* electronegative (galv.) to any region of lower chemical activity. Injury increases the rate of chemical change (cf. Tashiro, '17) and the injured area develops an electronegativity (galv.). Activity of muscle, nerve, gland, etc., is generally accompanied by an increased rate of respiratory exchange; hence is also characterized by the appear-ance of an electronegativity. When the differences in rate of chemical change are temporary, the accompanying bioelectric cur-rents are also temporary, as in the case of the current of action; when the differences are permanent, the bioelectric current is like-wise permanent, as in the case of the electrical gradient which exists along the axes of organisms.

While it appears probable that differences in the rate of oxida-

tion are generally responsible for the origin of potential differences in organisms, this need not necessarily be the case. Other chemical reactions could also give rise to potential differences, and in such cases the direction of the resulting current might be different. That is to say, where an oxidative reaction is the cause of the current, the region of higher rate becomes electropositive (int.), since oxidation consists in the assumption of positive charges (or the loss of negative charges). On the other hand, if some other chemical reaction were concerned, the direction in which the current would pass naturally would depend on the nature of the reaction, and could not be predicted until the reaction involved were known. It is very likely that in some organismic activities a bioelectric current would be produced in which the region of highest rate of activity or region of stimulation would be electropositive (galv.) to less active or unstimulated regions. It is also, of course, possible that differences, not only in the rate, but also in the kind of chemical reaction at different regions, may give rise to potential differences, in which case again the direction of the current will depend upon the reactions involved.

Our general point of view, then, is that potential differences in living things usually originate in metabolic processes, probably chiefly the oxidative processes, since oxidation-reduction reactions give rise to currents identical as to direction with those occurring in organisms. Such currents could arise either through the presence of an oxidation process at one point accompanied by a reduction process elsewhere or through a difference in the rate of the oxidation-reduction process at different regions, giving rise to a concentration chain. Although we are unable in the present state of our knowledge to decide between these two possibilities, it seems more probable that the potential differences are due to the second of the two suggestions, since in the organism the oxidation process is not, as far as we know, separated from the reduction process. Differences in the concentrations of ions at different regions would therefore seem to be the usual sources of the potential differences; such concentration differences arise through differences in the rate of reaction.

The point of view presented here that the bioelectric currents are chemical in origin has been held by a number of physiologists.

It seems to have originated with Hermann, who, in 1867, formulated it with a clarity and simplicity which scarcely permit of any addition. As the publication in question is not readily obtainable, it seems worth while to quote Hermann's views *verbatim*. Hermann based his conceptions on his discovery ('67a) that the chemical processes in muscle contraction and muscle rigor are identical. He postulates that these chemical processes consist chiefly of a splitting, designated by him as Spaltung, of chemical substances previously present in the muscle. On this basis he proceeds to develop his views concerning the origin of the muscle and nerve currents as follows ('67b):

"Wir nehmen also an, dass die Muskelsubstanz in der Ruhe in beständiger langsamer Spaltung begriffen ist, und dass die Muskelreize die Spaltung momentan sehr bedeutend beschleunigen (p. 4). . . . Durch das Anlegen eines Querschnitts beschleunigen wir also den im unverletzten Muskel äusserst langsam verlaufenden Spaltungsprocess local in hohem Grade (p. 5). . . . Aus Analogie und theoretischen Gründen ist es sehr wahrscheinlich dass die in schnellerer Spaltung begriffenen Muskeltheile sich negativ verhalten gegen solche welche in langsamerer Spaltung begriffen sind (p. 6). . . . Jede beliebige Stelle eines Muskels wird durch Erwärmung negativ gegen die übrige Muskelsubstanz (p. 9). . . . Von zwei beliebigen Muskelschichten verhält sich die in schnellerer Spaltung begriffene negativ gegen die andere, und zwar so stärker je grösser der Unterschied ihre Spaltungsgeschwindigkeiten ist (p. 22). . . . Der Muskelstrom muss ferner zunehmen durch Einflüsse welche dem vom Querschnitt her vorschreitenden Spaltungsprocess begünstigen, namentlich durch erhöhte Temperatur (p. 23). . . . Während der Contraction, die wir uns zunächst, der Einfachheit halber, gleichzeitig alle Theile des Muskels ergreifend denken, ist nach dem in Eingange Gesagten im ganzen Muskel eine Beschleunigung des Spaltungsprocesses vorhanden. In den bereits erstarrten Theilen des Muskels (*i.e.*, the cut surface) fehlt diese Beschleunigung. In den übrigen ist sie um so geringer, je grösser ihre Spaltungsgeschwindigkeit bereits in der Ruhe ist (p. 31). . . . Der polarisirende Strom beschleunigt jenseits der Electroden die Spaltung in der catelectrotonisirten und verlangsamt sie in der anelectrotonisirten Strecke. Diese Einflüsse nehmen mit zuneh-

mender Entfernung von den Electroden ab (p. 38). . . . Der polarisirende Strom wirkt also an jeder Nervenstelle auf die Geschwindigkeit des Spaltungsprocesses und auf die Erregbarkeit in gleichem Sinne (p. 45). . . . Das erregter Zustand nichts ist als schnellerer chemischen Process, also Erregung nichts als der Act der Beschleunigung (p. 45). . . . Die Erregbarkeit einer Nervenstelle hängt ab von der Geschwindigkeit des Spaltungsprocesses in derselben. Die Erregung einer Nervenstelle beruht auf einer plötzlichen Beschleunigung des Spaltungsprocesses in derselben. Die Leitung der Erregung im Nerven beruht auf der Fortpflanzung einer plötzlichen Spaltungsbeschleunigung längs des Nerven (p. 46). . . . Der Muskel enthält eine Substanz welche langsam spontan sich spaltet in (unter anderen) Kohlensäure, ein fixe Säure und Myosin; letzteres tritt in gallertiger Lösung auf und wird erst unter Verkurzung fest nachdem es zu einer grossen Concentration gelangt ist. Der Nerv enthält ebenfalls eine unter Säurebildung sich spaltende Substanz, welche aber kein dem Myosin entsprechendes Zerfallproduct liefert. Der Spaltung kann durch gewisse Umstände (Wärme, in Nerven Catelectrotonus) beschleunigt, durch ander (Kälte, im Nerven Anelectrotonus) verlangsamt werden. Je grösser die Spaltungsgeschwindigkeit voreits ist, um so geringer ist der Einfluss beschleunigender Einwirkungen auf die Geschwindigkeit. Jedes in schnellerer Spaltung begriffene Muskel- oder Nerventheilchen wirkt beschleunigend auf den langsameren Spaltungsprocess im Nachbartheilchen, um so energischer, je grösser der Unterschied in beider Geschwindigkeit ist. Jedes in schnellerer Spaltung begriffene Teilchen verhält sich negativ electrisch gegen ein in langsamerer Spaltung begriffenes. Diese Ströme bilden die Umkehrung der Wirkung des Stromes auf die Spaltungsgeschwindigkeit (p. 63).

From these excerpts it is evident that Hermann at that time regarded stimulation as an acceleration of metabolic rate and considered that any such acceleration is accompanied by the development of an electronegativity (galv.). This view is identical with that advanced in this paper and discussed in more detail in a previous publication (Hyman, '18). Subsequently, however, Hermann abandoned these conceptions, regarding them as " incomplete," and developed his alteration theory. The alteration theory,

however, is not really a theory of the cause of the bioelectric currents, but merely a statement of the general laws of these currents.[2] The principal terms of the alteration theory are: that the uninjured resting muscle or nerve is isoelectric; that all potential differences arising in muscle or nerve are due to physiological alterations of their substance; that any injured place or any stimulated place becomes electronegative (galv.) to intact or resting regions; and that the electronegativity is the consequence of the injury or stimulation (cf. Hermann, '79, p. 235). These statements are now, of course, accepted facts of electrophysiology. An explanation of the source of the potential differences due to injury and stimulation was not included in the alteration theory, and Hermann (l.c., p. 240) was at this later period disinclined to consider the possibility of a chemical origin of the bioelectric currents.

A viewpoint very similar to the early conceptions of Hermann quoted above was, however, soon developed by Hering. This viewpoint is suggested in a publication by Hering in 1879, in which (p. 242) he proposes the possibility that "an der Stellen wo der Strom die contractile Substanz der Einselfaser betritt oder verlässt, eine chemische Alteration dieser Substanz stattfinden kann, welche in übrigen durchflossenen Strecke nicht statthat." Hering presented his conception of the metabolic origin of the bioelectric currents in 1888. In this paper Hering expresses the belief that all of the functions of living matter are metabolic—*i.e.*, chemical—in nature, either, in general, assimilatory or dissimilatory, and that alterations of chemical function are responsible for the bioelectric currents. Some typical quotations may be given (pp. 250–251): ". . . nearly twenty years ago . . . the prevailing conception of the facts of general nerve physiology was strictly physical. I had,

[2] The alteration theory may be considered as a theory as concerns the current of injury which it regards as due to alterations at the cut surface rather than to the exposure of a previously existing negativity at the cut surface. This latter point of view is presented by Bernstein ('12) and the question may be regarded as still open. However, alterations undoubtedly occur at the cut surface, due to the cutting, and it is rather more than likely that such alterations play a rôle in the current of injury, even though Hermann's crucial experiment, supposed to show that a measurable interval elapses between the cutting and the full development of the electronegativity, be discarded because of inadequate technic.

therefore, to insist . . . that these functions were essentially chem-
ical, and that the intrinsic chemical nature of the vital processes
must not be overlooked in favor of their physical symptoms. . . .
Hermann's weighty dictum of the isoelectricity of uninjured 'rest-
ing' nerve or muscle signifies to me that such a tissue develops
no current that can be led off externally, *so long as its metabolism—
i.e., internal chemical function—is equal in all parts. Every dis-
turbance of this equilibrium sets up currents that can be led off.*
Alteration of chemical function in any part of a living continuum
may, however, be expressed, not merely in its becoming *negative,*
but equally in its becoming *positive* to unaltered parts.   Hence, if
we are to characterize the point differing in chemical function
from the rest of the substance, as (relatively) altered, we must, in
my opinion, *distinguish between a (relatively) positive and a
(relatively) negative alteration.*   And it is not altered chemical
composition, but altered chemical function, which may lead to
altered composition, that characterizes this change. . . . If all
parts of a living continuum are in equilibrium or alter at the same
rapidity, ascending or descending,[3] there will be no current to lead
off.   Every difference in rate or direction of alteration, however,
produces a current that can be led off.   *We may, accordingly, con-
ceive of all the different rates of positive and negative alteration
as forming a series of such a character that the most rapid ascend-
ing alteration forms the upper—i.e., positive—the most rapid
descending alteration the lower—i.e., negative—end of the series.*
If two parts of a living continuum, which differ in chemical func-
tion, are joined by an external circuit, there will, *cæteris paribus,*
be a stronger current in proportion as the distance between the
two points connected in circuit is greater in the above series, and
the positive current will always flow through the external circuit
from the point nearest the positive end of the series to that nearest
the negative end.   *This is the universal law of all physiological
currents in nerve and muscle."* [4]

[3] By the term "ascending" Hering means assimilatory metabolic change,
and by "descending," dissimilatory metabolic change.

[4] The quotation is taken from the English translation in *Brain* with a
few changes which follow the translation in Biedermann's " Electro-physiol-
ogy."   Italics of the original are preserved.

Biedermann ('96), a pupil of Hering's, adopts the latter's viewpoint, designating it as the Hermann-Hering theory. Biedermann likewise refers "all electromotive activities of living matter to chemical changes of the substance." Further details will be found in the volume cited, p. 351 ff.

Waller has long been an exponent of the theory of the metabolic origin of the bioelectric currents, which he designates as "blaze" currents because they are conceived of as due to sudden accelerations of normal chemical processes. This viewpoint appears clearly in his Lectures on Animal Electricity ('97), in which publication the following statements appear (Waller uses the terms positive and negative with reference to the tissue, not to the galvanometer—*i.e.*, the reverse of the usual usage) : "Active matter is electropositive (int.) to inactive matter; more active matter is electropositive to less active matter; matter that is by any means stirred up to greater activity is rendered electropositive to undisturbed matter; matter whose action is lowered is electronegative to matter whose action is normal." Waller further goes on to say that any more active spot "where more chemical action is going on" is electropositive (int.) to a less active spot "where less chemical action is going on." A similar statement is made in his Signs of Life ('03), pp. 84–85: "A lump of protoplasm at rest and homogenous throughout is isoelectric throughout; let it be acted upon by its environment, any point of its surface is chemically more active" and becomes electropositive to "any point of its mass." If the mass becomes chemically more active than the surface, then the mass becomes electropositive to the surface.

In 1903 Mathews discovered the electric gradient along the axis of certain hydroids. This was the first case in which a correlation between potential differences and the principal axis was established for animals. Mathews suggested that the potential differences are due to metabolic differences, and that such potential differences may control polarity. Mathews's present views concerning the relation between the bioelectric currents and metabolic processes, according to personal conversation with him, coincide with those presented in this paper. Mathews's student Tashiro ('17) also favors the conception that "chemical changes underlie and produce the electrical changes" (l.c., p. 102).

Recently R. S. Lillie ('17, '19, '22, and others) in a number of interesting and suggestive papers has been inclined to attribute the origin of potential differences in organisms, particularly of the current of action, to local chemical change, which concerns chiefly the limiting membrane. This conception is added to Lillie's former views of the rôle of depolarization of the surface membrane in the causation of the current of action. Thus Lillie says ('22, p. 17) : "Apparently any rapid local decrease of surface polarization (sufficient in range) causes stimulation in the typical irritable system such as muscle and nerve. This purely physical change, however, is merely the precursor or determinant of the local stimulation reaction; it is not the reaction itself. The latter is a physiological process dependent, like all such processes, on chemical reactions." Lillie is also further of the opinion that bioelectric circuits may be oxidation-reduction circuits.

The conception set forth in this paper, that potential differences in organisms originate in differences in metabolic rate, has been mentioned briefly in several publications from this laboratory— e.g., Child, '15, pp. 63–64, and '21a, pp. 44–46. The senior author has also published a preliminary general paper (Hyman, '18) in which her views are more fully set forth than in the present paper and to which the reader is referred for further details.

The preceding pages attempt to give some account of the development of one idea concerning the origin of the bioelectric currents. The consideration of other suggestions concerning these currents involves the working over of a large literature and is deferred for the present. It may, however, be stated that there are two other principal suggestions as to the causation of these currents. One of them may be referred to as the concentration-cell theory and the other as the membrane-depolarization theory. These two ideas are more or less intermingled and most investigators who have supported the concentration-cell theory have postulated membranes to bring about the concentration differences. The idea that the bioelectric currents arise from concentration chains has been ably discussed by Bernstein, '02, '12; also by Cremer ('06), where earlier references will be found. Bernstein's analysis shows that there are three types of chemical chains setting free electricity: those in which the electric energy decreases

with rise of temperature, those in which it does not alter with change of temperature, and those in which it increases with rise of temperature, so that the chain cools in giving rise to a current. The concentration cells belong to the third class. In concentration chains, also, the increase in electric energy with rise of temperature is proportional to the absolute temperature. It appears that the bioelectric currents possess these properties, so far as tested—*i.e.,* the potential difference increases with rise of temperature and the increase is approximately proportional to the rise; further in at least one case, that of the electric organ of the torpedo (Bernstein and Tschermak, '06), the circuit cools during the discharge, although only a few thousandths of a degree.[5]

The concentration-cell theory can be included in the metabolic rate theory advanced in this paper. For differences in metabolic rate lead to differences in the concentration of ions, which thus become the sources of potential differences. This view was presented above (p. 315). That the electromotive force is proportional to the absolute temperature need not greatly concern us, since this is also not infrequently the case where chemical reactions are obviously involved (cf. Bayliss, '15, pp. 42–43).[6]

The membrane-depolarization theory is closely related to the concentration-cell theory, in that its adherents suppose the concentration differences to arise through the presence of semipermeable membranes in living organisms. This matter is discussed by Bernstein ('02, '12), Cremer ('06), Brünings ('03), R. S. Lillie ('11, '13), and others. The chief tenets of this theory are: that the cell membranes are semipermeable membranes, which are permeable only to certain ions, chiefly, in the opinion of most authors, positively charged ions; that the cations pass through the mem-

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[5] If the production of electromotive energy in organisms is an endothermic reaction, as Bernstein maintains, this may account for the lack of heat production in a stimulated nerve.

[6] It is rather amusing to note that whereas on p. 42 Bayliss severely criticises the idea that the temperature coefficient furnishes reliable information concerning the chemical or physical nature of a biological process and mentions some cases where chemical reactions are obviously involved in which the velocity is a linear function of temperature, on p. 644 he rejects the possibility that the bioelectrc currents are due to chemical reactions on the grounds that the electromotive force is proportional to the absolute temperature.

brane, leaving the anions behind; that consequently the membrane is the seat of a polarization, being positively charged externally, negatively charged internally; that upon stimulation the membrane becomes more permeable at the locus of stimulation, letting anions through; and that consequently the membrane is depolarized at the place of stimulation, becoming temporarily negative. The difficulties in the way of this conception have been pointed out by Keith Lucas ('12), and one of its former chief adherents, R. S. Lillie, has been recently strongly inclined to a chemical point of view. While the current of action is readily accounted for on the basis of the membrane-depolarization theory, it seems to us that it is more difficult to account for the current of injury and almost impossible to explain on this basis the permanent differences of potential which exist along the axes of many organisms. To get such a gradation of potential it is necessary to assume the existence of a gradation in concentration of ions along surface and interior. A difference in concentration of similarly charged ions along the axis could scarcely be brought about by the properties of the membrane; the membrane is either permeable or impermeable to a class of ions. Such concentration differences must be due to differences in the speed of production of such ions at different levels. This differential speed of production of ions with reference to level is exactly what we suggest to exist, and if it exists the assumption of membranes is unnecessary. The membrane-depolarization theory also states that the current of injury is due to the exposure of the (presumably) negatively charged interior of the tissue at the injured surface, thus producing a negativity at the cut surface. But it has long been known that the negativity due to injury is present not only at the cut surface, but also exists along the uninjured external surface, decreasing with distance from the site of injury. This is readily explained on our point of view which regards injury as a form of stimulation, accompanied by increased metabolic rate, and transmitted with a decrement to adjacent regions, as are other forms of stimulation.

So numerous are the possible sources of potential differences that it is probable that such differences in organisms are due in different instances to different factors or to a combination of factors. All that we wish to emphasize here is that certain very

definite bioelectric currents, such as the current of injury, the current of action, and particularly the permanent currents which exist along the axes of the simpler organisms, are associated with metabolic differences and probably result from such metabolic differences. These metabolic differences are chiefly quantitative in nature—*i.e.*, differences of rate.

It further seems probable that these axial differences in the rate of chemical change in organisms are responsible for the phenomenon of galvanotaxis. Owing to the differences in concentration of ions at different levels, the organism is electrically polarized and hence will be expected to respond in a definite way when placed in an electric current. This matter has already been discussed by the senior author ('18).[7] The anterior ends of most of the lower and simpler animals are positively charged (int.) ; hence it will be expected that when placed in a current the anterior end will be directed toward the cathode. Such is the case in such organisms. In a few cases, described below, we have found that the anterior end is negatively charged (int.) ; such organisms orient with anterior ends toward the anode. In some flatworms, and in annelids generally, both anterior and posterior ends are positively charged (int.) ; such animals bend in a U-shape, with the two ends of the body directed toward the cathode. It thus appears that the internal charge, in many animals at least, determines their galvanotactic response. A suggestion to this effect was previously made by Coehn and Barratt ('05), but was incomplete, as these authors did not take cognizance of the fact, at that time but recently discovered, that there is a graded difference of potential along the axis.

One of the prevailing theories of galvanotaxis is that adopted by Loeb and discussed by him in his book on forced movements ('18). This theory assumes that the galvanotactic orientation is due to the direct action of the current on ciliary or muscular elements or on the nerve cells that control the muscles. While such action of the current may play a rôle in galvanotaxis, and may control the galvanotactic response in some animals, it seems inade-

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[7] In this paper near the top of the second column on page 523 the statement that oligochætes in a current travel to the anode should read "travel to the cathode."

quate to account for the facts in the majority of cases.   The be-
havior of the cilia in galvanotaxis has been carefully investigated
by Ludloff ('95), Pearl ('oo), Wallengren ('02, '03), Statkewitsch
('05), and others, and the galvanotactic response has been assigned
in most cases to the direct action of the current on the cilia.   But,
according to Statkewitsch ('05), *Paramecium* under optimum con-
ditions responds to the current with very little change of the cilia
from their normal behavior.   Bancroft ('06) found that exposure
to various salt solutions renders *Paramecium,* which is normally
cathodic, anodic, and some solutions destroy the galvanotropism of
this ciliate.   Dale ('oi) found that *Opalina,* usually described as
exhibiting anodic galvanotropism, is cathodic in slightly acid media
and anodic in slightly alkaline media; the same dependence of the
response on the medium is likewise true of other parasitic ciliates
of the frog.   The behavior of the cilia is the same in either reac-
tion.   According to Terry ('06) and Bancroft ('07), *Volvox* is
cathodic in the light and becomes anodic after being kept in the
dark.   When cathodic, the orientation is brought about by the in-
hibition of the flagella on the cathodal side; when anodic, by their
inhibition on the anodal side.   It thus appears that in *Protozoa*
the galvanotactic response is determined chiefly by the internal
condition, presumably ionic, of the organism, and not by the direct
effect of the current on the cilia.   Similar reversals have been
noted by us in multicellular animals as the result of environmental
conditions or prolonged exposure to the current and appear to be
due to internal physiological changes and not to the action of the
current on the neuro-muscular mechanism.

Since the inception of the ideas recorded above it has been our
purpose to collect further data on the correlation between metabolic
differences, electrical differences, and the galvanotactic response in
animals.   We hope to test in as many forms as possible the meta-
bolic gradient along the axis, the potential differences along the
axis, and the galvanotactic behavior.   For the last three or four
years this work has been carried on whenever opportunity has
afforded.   It seems desirable, owing to the time which has elapsed
since the presentation of the preliminary paper (Hyman, '18), to
record the principal data which have accumulated since that publi-
cation.   To present these data and to point out the correlation

between the three phenomena in question is the object of the present paper.

II. Methods.

The metabolic gradients have been tested by various methods, chiefly the susceptibility to various toxic solutions and to dyes, and the capacity to reduce potassium permanganate. Wherever practical, direct determinations of the respiratory rate at different levels have also been made. For a general discussion of metabolic gradients and of the susceptibility method see Child ('20) and of the permanganate method Child ('19a).

The potential differences have been tested by galvanometers of the D'Arsonval type, put out by the Leeds and Northrup Company. The one which has been used for most of the work is a small portable galvanometer having a resistance of 310 ohms and a sensitivity of 73 megohms (1 volt through a resistance of 73 megohms gives a swing of 1 division of the scale). During the summer of 1919, while being used by Hyman at Friday Harbor, the suspension of this instrument broke and another instrument having a spring suspension was borrowed; the sensitivity of this instrument was not recorded, but it was slightly more sensitive than ours. Part of the data on the medusæ and *Nereis* and all of the data on ctenophores was obtained with this second instrument. Non-polarizable electrodes of the zinc-zinc sulphate type were used, their tips packed with kaolin and terminating in rolls of hard filter paper, frequently changed, soaked in the medium in which the animal to be tested lives. It is necessary to renew these electrodes frequently, as they are apt to develop potential differences. These can be eliminated by running a compensating current through them as was done in part of the work. Usually the difference between the electrodes was eliminated by reversing the animal on the electrodes. In the case of sessile animals the electrodes were clamped in position and the animal placed across their tips; in motile animals the electrodes were held in the hands by means of burette clamps and placed on the animal in the desired position. It is not an easy matter to work with active animals. Usually at least two readings were taken on each individual for each position of the electrodes. The readings recorded in the

table represent divisions of the scale of the galvanometer; where the differences were small, movements of the indicator of less than one division are recorded as .5. Freshly collected material was nearly always used for the galvanometer tests.

Direct current for the galvanotaxis tests was obtained from a number of cells in series or from a 110-volt direct-current generator. Metal electrodes were used, owing to the high resistance of non-polarizable electrodes. The voltage was regulated with a variable resistance shunted across the line in such a way that any voltage from zero to the maximum could be obtained simply by moving a sliding contact. When testing an animal, the slide was placed at the zero end of the resistance, the animal introduced into the testing dish, and the potential gradually increased to a strength which would evoke a definite response. Strong currents or prolonged exposure to the current often alters the galvanotactic response. The records kept were not sufficiently complete to enable us to calculate the current density in the galvanotaxis experiments with any degree of accuracy, as we did not regard such data as significant for the purpose of this investigation.

III. SPONGES.

The work on sponges recorded here was done by Hyman at Woods Hole in the summer of 1919.

1. *Metabolic Gradients.*—Potassium permanganate was used for the study of the metabolic differences along the axis of two simple sponges, *Grantia* and *Leucosolenia*. Potassium permanganate is reduced by protoplasm, giving a brown stain, and the rate of appearance of this stain, as well as the depth of its color, is a rough measure of metabolic differences, since regions of higher metabolic rate reduce the permanganate more rapidly (see further Child, '19*a*). In applying this method to simple sponges it is preferable, owing to the thickness of the animal, to make a median longitudinal section and watch the appearance of the brown color along the cut surface. This was done in the case of *Grantia*, while entire individuals were tested in the case of *Leucosolenia*. In many individuals of *Leucosolenia* and *Grantia* which were tested in potassium permanganate a slight but evident gradation of staining power was noted along the axis, the oral or oscular end staining

first and more deeply, and the depth of color diminishing along the axis. The staining gradient was most marked in medium-sized individuals, practically absent in large or small individuals; the latter, however, stain more deeply than larger individuals. Child has also noted a staining gradient in potassium permanganate in a *Grantia*-like sponge at Friday Harbor.

From these observations it may be concluded that there is a metabolic gradient along the axis of these simple sponges, the oscular end having the greatest metabolic activity and this activity decreasing along the axis.

2. *The Electrical Gradient.*—Numerous tests of the potential difference along the axis of *Leucosolenia* and *Grantia* showed that in the great majority of individuals the oscular end is electro-negative (galv.) to the basal end. In some cases, usually in small or very large individuals, there was no potential difference along the axis; in a few cases the potential difference was reversed, the oscular end being positive (galv.). The results are given in Table I. The potential differences are rather small.

Certain facts not presentable in the table were also noted. In large specimens there is likely to be a greater potential difference between the oscular end and the middle of the sponge than between the oscular and basal ends, indicating some degree of physiological independence of the basal region in such large specimens. There is usually no potential difference between lateral branches (*Leuco-solenia*) and the main osculum—*i.e.,* the buds are also negative (galv.). Freshly cut cross-sections (*Grantia*) are markedly nega-tive (galv.), being often negative even to the oscular end; this is, of course, merely an example of the current of injury.

In these sponges, then, is found the usual correspondence be-tween metabolic rate and electric potential, the region of highest metabolic rate being electronegative (galv.).

IV. HYDROIDS.

The work on the electrical gradients of hydroids was done by Hyman at Woods Hole in the summer of 1919, with the exception of the data on *Obelia borealis,* which were obtained by Bellamy in 1918 at Friday Harbor.

1. *The Metabolic Gradient.*—The metabolic gradients of several

common hydrozoan hydroids have been studied by Child ('19*b*, '21*b*) by means of various toxic solutions, dyes, and potassium permanganate, and have been confirmed by Hyman on the same

TABLE I.

ELECTRIC GRADIENT OF *Leucosolenia* AND *Grantia*. NEGATIVE AND POSITIVE AS IN THE GALVANOMETER.

	Leucosolenia.				*Grantia.*		
No.	Oscular End.	Basal End.	Readings.	No.	Oscular End.	Basal End.	Readings.
1	−	+	.5, 0	1	−	+	.5, 1
2	−	+	1, .5	2	−	+	.5, .5
3	−	+	.5, .5	3	−	+	.5, .5
4	−	+	.5, 1	4	+	−	1
5	−	+	.5, 0	5	−	+	.5, .5
6	No potential diff.			6	−	+	.5, 1
7	−	+	.5	7	No potential diff.		
8	−	+	1, 0	8	No potential diff.		
9	−	+	2, 1	9	−	+	1
10	−	+	.5, .5, 1	10	−	+	1, .5
11	−	+	1.5, 1.5	11	−	+	.5
12	−	+	1.5, .5	12	−	+	1.5, .5
13	−	+	1, 1	13	−	+	1, .5
14	−	+	1, 1.5, 1	14	−	+	1, 1
15	−	+	1.5	15	−	+	2
16	+	−	.5, 0	16	−	+	1.5, 1
17	−	+	1	17	−	+	1, 2, 2
18	−	+	1, 1	18	−	+	1.5
19	−	+	1, 1	19	−	+	2, 1
20	+	−	1.5, 1.5	20	−	+	0, 1
21	−	+	.0, .5, 1	21	−	+	3.5, 3.5
22	−	+	1, 1	22	−	+	1
23	−	+	.5, 1.5	23	−	+	1
24	−	+	1, .5	24	−	+	1, 1
25	No potential diff.			25	−	+	1.5
26	−	+	1, .5	26	−	+	1, 2
27	−	+	.5	27	−	+	2, 1
28	−	+	1.5	28	−	+	2, 1.5
29	−	+	.5, 1.5	29	−	+	.5, 0
30	No potential diff.			30	−	+	.5
31	+	−	1, 1	31	−	+	1.5, 2
32	−	+	.5, .5	32	−	+	1, 1
33	−	+	.5, .5	33	−	+	2.5, 2
34	−	+	1, 0, .5	34	−	+	2, 2
35	−	+	1.5, 1	35	−	+	1, 2
36	−	+	1, .5	36	−	+	1
37	−	+	1.5, 2				
38	−	+	1				
39	+	−	.5				

and other species. The gradients are the same in all of the species studied. The hydranths are more susceptible and have greater reducing power than the stems. The gradient in each hydranth

proceeds from the distal to the proximal ends of the tentacles, and from the oral to the aboral end of the body of the hydranth; in stems the gradient is likewise apico-basal. In the colony as a whole and in each branch the susceptibility and reducing power are, in general, highest in the terminal hydranths and decrease basipetally among the hydranths and growing tips. In general, then, metabolism is carried on more rapidly in the distal portions of individuals, colonies, and branches and decreases basipetally.

2. *The Electrical Gradient.*—The electrical gradient of the hydroids was discovered by Mathews ('03) for *Tubularia, Pennaria,* and *Campanularia.* He found that the distal portions are electronegative (galv.) to proximal portions. This result has been confirmed by us for the same and other genera and species. The forms tested were: *Tubularia crocea, Pennaria tiarella, Obelia geniculata, Obelia borealis, Eudendrium ramosum,* and *Schizotricha (Plumularia) tenella.* The results are presented in Tables II. and III.

Tubularia crocea.—The data upon this species have been published in another connection (Hyman, '20). Hydranths are negative (galv.) to stems, distal levels of the stem are negative to proximal levels, except at the regions of branching, which are usually negative to levels immediately distal to them.

Obelia geniculata.—This species forms a small unbranched colony, 1–2 cm. in height, consisting of a simple stem bearing lateral hydranths alternately arranged, and growing by the formation of a new bud at the apical end. In making the galvanometric tests the entire colony was removed from the substratum and placed across the electrodes. The electrical differences recorded in Table II., therefore, concern the apical and basal regions of the colony; the former is almost invariably negative (galv.) to the latter.

Schizotricha tenella.—This species forms a delicate plume-like branching colony, 3–5 cm. in length. Entire colonies were placed across the electrodes; the electrical differences recorded in Table II. are, therefore, those between the apical and basal levels of the colony; the former is negative (galv.) to the latter.

Eudendrium ramosum.—The colonies of this species are large, bushy, and much branched, with hydranths considerably larger than those of the preceding two species. Most of the tests re-

corded in Table 2 were made upon branches of the colonies; the apical regions of such branches are negative (galv.) to the basal

TABLE II.

ELECTRIC GRADIENT OF *Obelia geniculata, Schizotricha tenella,* AND *Eudendrium ramosum.*

Negative and positive refer to direction through the galvanometer. Readings are divisions of the scale of the galvanometer. Ap., apical; bs, basal; rd., galvanometer readings.

	Obelia.				Schizotricha.				Eudendrium.		
No.	Ap.	Bs.	Rd.	No.	Ap.	Bs.	Rd.	No.	Ap.	Bs.	Rd.
1	—	+	2, 0	1	—	+	2, .5	1	—	+	.5, .5
2	—	+	.5, 1	2	—	+	1.5, 1	2	—	+	1, 1
3	—	+	1.5, 1	3	—	+	.5, .5	3	—	+	.5, 1
4	—	+	2, 1.5	4	—	+	.5, .5	4	—	+	.5, 1
5	—	+	1.5, 1	5	—	+	.5, .5	5	—	+	1.5, 1.5
6	—	+	.5, .5	6	—	+	1, .5	6	—	+	1.5, 1.5
7	—	+	1, 1	7	—	+	.5, .5	7	—	+	2, 1.5
8	No pot. diff.			8	—	+	1, 1	8	—	+	1.5, 1.5
9	—	+	.5, 1	9	—	+	1.5, 1.5	9	—	+	1.5, 1.5
10	—	+	.5, 1	10	—	+	1.5	10	—	+	1.5, 1.5
11	—	+	.5, 1	11	—	+	.5	11	—	+	1, 1
12	—	+	1, 1	12	—	+	1.5	12	—	+	.5, 1
13	—	+	1, 0	13	—	+	1.5, 1	13	—	+	.5, .5
14	—	+	1.5, 2	14	—	+	.5	14	—	+	.5, 1.5
15	—	+	.5, .5	15	—	+	1, .5	15	—	+	.5, .5
16	—	+	1, 1	16	—	+	.5	16	—	+	1, 1
17	—	+	1.5, 1.5	17	—	+	1.5, 1	17	—	+	1.5, 1.5
18	—	+	.5, 1	18	—	+	1	18	—	+	1, 1
19	—	+	1.5, 1.5	19	—	+	1.5	19	—	+	2, 2
20	—	+	.5, 1					20	—	+	.5, .5
21	—	+	.5, .5					21	—	+	1, 1.5
								22	—	+	1, 1
								23	—	+	.5, .5
								24	—	+	.5, .5
								25	—	+	2, 2

levels. In Nos. 3, 10, 15, and 21 a short piece was removed from the apical end of the main axis of the colony, and the potential difference between the apical and basal ends of this piece tested; the former is again negative (galv.) to the latter. In Nos. 24 and 25 the terminal zooid of the colony was compared with one of the lateral zooids, the two being connected by a strip of filter paper soaked in sea-water; the former is negative (galv.) to the latter, as was found also in *Obelia borealis.*

Pennaria tiarella.—This species forms large, open, branching colonies. Most of the data in the table were obtained by com-

paring the apical and basal ends of branches or terminal portions of the main axis; the apical end is negative to the basal end and the p.d. is greater along the distal part of the main axis than along the proximal part, and greater along the distal part of the main axis than along lateral branches. Thus No. 3 in Table III. gives

TABLE III.

ELECTRIC GRADIENT OF *Pennaria tiarella* AND *Obelia borealis*. Symbols as in Table II.

	Pennaria.				Obelia borealis.		
No.	Ap.	Bs.	Rd.	No.	Ap.	Bs.	Rd.
1	−	+	2.5, 2	1	−	+	1, 1.5, 1, .5
2	−	+	3.5, 2	2	−	+	2, 2, 2.5, 2
3	−	+	2, 1	3	−	+	1, 1, 1, 1
4	−	+	.5, .5	4	−	+	2, 2, 2, 2
5	−	+	1, .5	5	−	+	2, 2, 2, 2
6	−	+	2.5, 2.5	6	−	+	2.5, 2, 2.5, 2
7	−	+	1, .5	7	−	+	.5, .5, .5
8	−	+	.5	8	−	+	.5, .5, .5
9	−	+	1, 1.5	9	−	+	.5, .5, .5
10	−	+	.5	10	−	+	1, .5, 1, 1
11	No potent. diff.			11	−	+	2, 2, 2, 1.5
12	−	+	.5	12	−	+	2.5, 2.5, 2, 2
13	−	+	1.5, 1.5	13	−	+	2.5, 2.5, 2.5
14	−	+	2.5, 2.5	14	−	+	2, 2, 2, 2
15	−	+	.5, 1	15	−	+	2, 2, 2, 2
16	−	+	.5, .5	16	−	+	2.5, 2.5, 2
17	−	+	.5, 1	17	−	+	1.5, 1.5, 1.5, 2
18	−	+	1, 1				
19	−	+	1.5, 1.5				
20	−	+	1.5				
21	−	+	.5, .5				
22	−	+	2.5, 3				
23	−	+	1.5, 1.5				
24	−	+	1.5, 2				
25	No potent. diff.						
26	−	+	1.5, 1				
27	−	+	.5, 0				
28	No potent. diff.						

the potential difference between the terminal hydranth and the stem proximal to it; Nos. 4 and 5 give the difference along lateral branches of the same colony. No. 6 is the main axis of a colony; Nos. 7 and 8 lateral branches of the same colony. Nos. 9, 10, and 11 give the potential differences along a distal 10-mm. piece, middle 10-mm. piece, and a basal 10-mm. piece, respectively, of a colony. No. 14 gives the potential difference between the apical and basal regions of a large colony; Nos. 17 and 18 of distal branches of

the same colony; No. 16 of a proximal branch of the same colony; and No. 19 of the distal part of the main axis and No. 21 of the proximal part. Nos. 25, 26, and 28 are old portions of the colony with many medusæ buds; such parts show little or no apico-basal potential difference.

Obelia borealis.—This is a large much-branched colonial hydroid common at Friday Harbor. Apical levels of entire colonies are electronegative (galv.) to basal levels, as in Nos. 1 to 6 in Table III.; apical levels are negative to basal levels of branches, as in Nos. 11 to 17 in Table III.; and the main apical hydranth is negative to the apical hydranth of lateral branches, as in Nos. 7 to 10.

From these data on several species it is clear that in the colonial hydroids, in general, apical levels of the colony are electronegative (galv.) to basal levels, both as regards hydranths and stems. The electrical gradient is steeper in apical regions and slight or lacking in basal regions. These results correspond with the metabolic gradients, regions or parts of higher metabolic rate being negative to those of lower rate.

3. *Galvanotaxis.*—The slight motility of the colonial hydroids precludes the practicability of determining their galvanotactic response. Experiments were, however, tried on *Pennaria.* Branches were placed at right angles to the direction of the current. It was noted that the larger and more vigorous hydranths in such branches, usually the main or lateral apical hydranths, turned the manubrium toward the cathode during the passage of the current. When the current was reversed the manubrium was turned to the new cathode. The animals fatigue rapidly, however, and soon fail to respond; as already stated, only the largest hydranths respond. This behavior, as far as it goes, corresponds with the theory of galvanotaxis outlined above—*i.e.,* that part of the animal having the highest metabolic rate and an internal positivity is directed toward the cathode.

V. HYDROMEDUSÆ.

1. *The Metabolic Gradient.*—The gradients of these medusæ in toxic solutions, dyes, and potassium permanganate have been determined by Child ('21b). In all species tested the manubrium and margin, including the tentacles, are the most susceptible and

have the greatest reducing power of any parts of the animal; the subumbrellar ectoderm ranks next in activity; the exumbrellar ectoderm is the least active part of the animal. McClendon ('17) found that the greater part of the oxygen consumption of *Cassiopea* is due to the manubrium, and that the subumbrellar surface (minus the manubrium) consumes much more oxygen than the exumbrellar surface plus the mesogloea.

2. *The Electrical Gradient.*—The potential differences tested in several species of hydrozoan medusæ correspond completely to the metabolic differences. The distal end of the manubrium is the most negative part of the animal, the margin, including the tentacles, is usually next, the subumbrellar surface next, while the exumbrellar surface is positive to all parts of the animal.

The forms tested were *Gonionemus murbachii* by Hyman at Woods Hole in 1919, *Æquoria victoria* and *Mitrocoma discoidea* by Bellamy in 1918 and by Hyman in 1920 at Friday Harbor, and *Stomotoca atra* by Hyman in 1920 at Friday Harbor. The results are given in Table IV. In *Gonionemus* the manubrium was found

TABLE IV.

ELECTRICAL DIFFERENCES BETWEEN MANUBRIUM, SUBUMBRELLA, EXUMBRELLA, AND MARGIN OF THE BELL IN FOUR SPECIES OF HYDROZOAN MEDUSÆ.

Only two points can, of course, be compared at one time. Man., manubrium; sub., subumbrella; ex., exumbrella; mar., margin; rd., galvanometer readings. Negative and positive refer to direction in the galvanometer.

	Gonionemus.						Stomotoca.				
No.	Man.	Sub.	Ex.	Mar.	Rd.	No.	Man.	Sub.	Ex.	Mar.	Rd.
1			+	−	2.5	1	−		+		1, 1, 1.5
	−		+	.	11, 4				+	−	1.5, 1.5
2			+	−	5	2	−		+		4, 4, 1.5
	−		+		2, 1.5				+	−	1.5, 0
3			+	−	2, 1.5, 2	3	−		+		1.5, 1, 1
	−			+	3, 2.5				+	−	1, .5
	−	+			1.5	4	−		+		1.5, 1, 1.5
			+	−	1, 1				+	−	1, 1
4	−		+		4.5, 2.5	5	−		+		1.5, 2, 2.5
5			+	−	1, 1				+	−	1.5, 2, .5
	−		+		1, 1	6	−		+		1, 1.5, .5
6			+	−	2.5, 3				+	−	1, .5
	−		+		2, 2	7	−		+		1, 1, 2
	−			+	1, 2	8	−		+		4, 3, 2.5
7			+	−	11, 13				+	−	.5, 1
8	−		+		2, 2.5	9	−		+		1.5, 1.5
									+	−	1, 0
						10	−		+		2.5, 1.5, 1.5
									+	−	1, 1.5, 0

TABLE IV—*Continued.*

Æquorea.

No.					Values
1	−	+			2.5, 2, 5
		+		−	.5, 1.5, 2
		−	+		1, 2.5, 1.5
2	−	+			.5, 1.5, 2
		−		+	5, 1.5
		−	+		4, 1, 1
3	−	+			1, .5, .5
		−		+	0, 1, .5
		−	+		2, 2, 1
4	−	+			2, 1.5, .5
		+		−	.5, .5, 1
		−	+		1.5, 1, 1.5
5	−	+			2, .5, 2
		+		−	1.5, 1, 1
		−	+		2.5, 1.5, 2
6	−	+			.5, 1, .5
		−		+	.5, .5, 0
		−	+		2, 3, 1.5
7		−	+		.5, 1
		−	+		1, 1
	−	+			2, 1.5, 1.5
8	−	+			1.5
9	−	+			.5, .5, 0
		−	+		1.5, 1, 1
10		+		−	.5, .5
		−	+		.5, 1
11	−			+	9, 4, 8
12	−			+	4, 3, 5, 4
		−	+		7, 7, 2, 6
13	−			+	8, 9, 3, 3
		−	+		5, 6, 5, 3
14		−	+		14, 13, 14
		−	+		6, 6, 6, 4
		−	+		6, 4, 4, 3

Mitrocoma.

No.					Values
1	−	+			7, 6, 9
	−		+		1, 1.5, 2
		+		−	.5, 2.5, 1
2	−	+			14, 7, 4
	−		+		4, 5, 4
3	−	+			6, 3
		+		−	1, 2, .5
	−		+		2.5, 1, .5
4	−	+			2, 2, .5
		+		−	.5, .5, 0
	−		+		3, 3
5	−	+			3, 6, 7
		+		−	1, .5, .5
	−		+		7, 6
6	−	+			10, 6, 5
		+		−	1, 1, 1
7	−	+			9, 4, 2
	−		+		3, 3, 3
		+		−	1, 1
8	−	+			8, 4, 3
	−		+		6, 6
		+		−	1, 1
9	−	+			4, 3, 6
		+		−	.5, 1.5, 1
	−		+		2.5, 1
10	−	+			12, 12
	−		+		11, 6
		+		−	1, .5, 0
			+	−	2, 2
11	−			+	8, 6, 7, 5
12	−			+	4, 8
13	−			+	8, 12, 10, 13
14	−			+	10, 10, 9, 6
15	−			+	8, 12, 10, 13

invariably negative (galv.) to all other parts and the margin negative to the subumbrella and exumbrella. In *Stomotoca* the manubrium and the margin were invariably negative to the exumbrella, and it can be inferred from the table that the manubrium is negative to the margin; the small size and tall bell-shape of this species did not permit the testing of the subumbrellar surface. In *Æquorea* the electric conditions are somewhat dependent upon the sexual condition. This medusa has numerous radial canals which bear the gonads on their subumbrellar surfaces, as is the case in all of the Leptomedusæ; the canals are so numerous that it is impossible to avoid touching the gonads on applying the electrodes to the subumbrellar surface. In sexually ripe individuals the negativity of the subumbrellar surface is increased and it may be negative

(galv.) to manubrium and margin. In Table IV. the potential difference recorded between manubrium and subumbrella is that between the distal border of the manubrium and a point on the subumbrellar surface near the base of the manubrium; the former is negative (galv.) to the latter. Comparisons between margin and subumbrella were taken on the middle of the subumbrellar surface; in four cases (1, 4, 5, 10) the margin is negative, in four cases (2, 3, 6, 7) the subumbrella is negative, due to the presence of ripe gonads. In all cases tested in *Æquorea* the exumbrella is positive (galv.) to all other parts, and the margin is positive to the manubrium. *Mitrocoma* shows the same relations as the other medusæ: manubrium negative to margin, subumbrella, and exumbrella; margin negative to subumbrella; subumbrella negative to exumbrella.

3. *Galvanotaxis.*—We were unable to find any definite galvanotactic response in the medusæ noted above, except the general tendency for the tentacles to direct themselves toward the cathode. Probably the optimum strength of current was not found. Bancroft ('04) noted a precise response to the current in the medusa *Polyorchis.* In this form the manubrium and tentacles were directed toward the cathode, thus corresponding with the expectation on the basis of our theory, as these parts of the animal are the most positive (int.) regions.

VI. Ctenophores.

1. *The Metabolic Gradient.*—The existence of a gradient along the plate rows of ctenophores may be inferred from the fact that the wave which passes along the plates originates usually at the aboral pole and sweeps toward the oral pole. Child ('17) also found a susceptibility gradient along the plate rows from the aboral to the oral pole. This gradient, however, is readily reversible, at least temporarily.

2. *The Electrical Gradient.*—Tests were made by Hyman in 1920 on a small spherical ctenophore common at Friday Harbor, which is probably *Pleurobrachia;* a few specimens of *Beroe* were also available. The data on *Pleurobrachia* are given in Table V. In 14 cases out of 20 the aboral pole was negative (galv.) to the oral pole; in 3 cases the oral pole was negative, and in 3 cases the

gradient reversed while it was being tested, the aboral pole being first positive and then negative in Nos. 3 and 18 and first negative and then positive in No. 7. In six tests on *Beroe* the aboral pole was negative to the oral in three cases, was negative on first readings and then became positive in two cases, and in one case there was no definite potential difference between the two poles. It was pointed out above that physiological reversal of the wave in the plate rows is common.

3. *Galvanotaxis.*—No definite response to current was found in *Pleurobrachia,* nor to our knowledge has the matter been tested by others.

VII. FLATWORMS.

Definite tests of forms belonging to this group were made by Hyman on *Planaria maculata* at Woods Hole in 1919 and on an unidentified polyclad turbellarian at Friday Harbor in 1920.

1. *The Metabolic Gradient.*—This has been studied by members of this laboratory for several species. The anterior end has the highest metabolic rate and this rate decreases along the axis to the level of the main fission plane, beyond which it increases again. It has also been found that the carbon dioxide production (Robbins and Child, '20) and the oxygen consumption (Hyman, '23) are higher for anterior than for posterior levels of the first zooid. In *Planaria maculata,* tested with potassium cyanide, the following condition was found: The disintegration begins at the anterior end and progresses posteriorly along the margins of the head and the ventral surface; it then begins at the posterior end and progresses forwards; the two waves of disintegration meet at about the middle of the worm. There is thus in this species a "double" gradient, from the two ends of the body toward the middle. The high susceptibility of the posterior end is probably due largely to the use of this end as an adhesive organ, less to the presence of a second zooid there. Very small worms possessed the same susceptibility gradient as large worms. The susceptibility gradient of the polyclad was not tested, owing to scarcity of material.

2. *The Electrical Gradient.*—The data on the metabolic gradient would lead us to expect that the anterior end of *Planaria maculata* will be negative (galv.) to other levels of the body. This was

found to be the case as shown in Table V. in the great majority of cases. The small size of the worm did not permit the testing

TABLE V.

ELECTRICAL DIFFERENCES BETWEEN ABORAL AND ORAL POLES OF THE CTENO-PHORE *Pleurobrachia*, ANTERIOR AND POSTERIOR LEVELS OF *Planaria maculata*, AND ANTERIOR, MIDDLE, AND POSTERIOR LEVELS AND MARGINS OF A POLYCLAD.

Ab., aboral; or., oral; ant., anterior; mid., middle; post., posterior; mar., margin; rd., galvanometer readings. Reversed, reversed during test. Negative and positive refer to direction in the galvanometer.

	Pleurobrachia.				Planaria.				Polyclad.				
No.	Ab.	Or.	Rd.	No.	Ant.	Post.	Rd.	No.	Ant.	Mid.	Post.	Mar.	Rd.
1	−	+	1, .5, .5	1	−	+	1, .5	1	−	+			.5, 1, 2, 1
2	−	+	1.5, 1, 1	2	no p. d.					+	−		1, 1.5, 1.5
3	reversed			3	no p. d.					+		−	4, 2.5, 2
4	−	+	0, .5, 0, .5	4	−	+	.5, .5	2	−	+			1.5, .5, 2, 3
5	−	+	.5, .5, .5	5	−	+	1, 1			+	−		1.5, 2, 2
6	−	+	.5, .5, .5	6	−	+	.5, .5			+		−	2, 2, 2.5
7	reversed			7	−	+	1, .5	3	−	+			2.5, 2, 2
8	−	+	.5, .5, .5	8	no p. d.					−	+		.5, .5, 1
9	−	+	.5, .5, 1.5	9	−	+	.5, 0			+		−	.5, .5, .5
10	−	+	.5, 1.5, .5	10	−	+	1.5, 1	4	−	+			1.5, 3, 2
11	+	−	1, .5, 0	11	+	−	1, 1			re-versed			
12	−	+	.5, 0, .5	12	−	+	1, 1			+		−	.5, 0, .5
13	−	+	.5, .5, .5	13	indefinite			5	−	+			1, 1.5, 1
14	−	+	.5, .5, .5	14	−	+	1, 1.5			+	−		1, .5, 1
15	−	+	1, .5, .5	15	−	+	.5, .5	6	−	+			1, 2, 1.5
16	+	−	1, .5, .5	16	−	+	1, .5			−	+		1.5, 1,.5
17	+	−	1.5, 1.5, 1	17	no p. d.			7	−	+			.5, .5
18	reversed			18	−	+	.5, .5						
19	−	+	.5, 2.5, .5	19	−	+	1, 1						
20	−	+	1.5, .5, 1	20	−	+	1, 1						

of more specific regions of the body; it is possible merely to place the electrodes on general anterior and posterior levels. The lack of potential difference in Nos. 2, 3, 8, and 17 is probably due to the circumstance that in these individuals the susceptibility of the posterior end was practically equal to that of the anterior end.

Of the polyclad mentioned above only seven specimens were available. In all of these the anterior end was negative (galv.) to the middle; in most of them the posterior end was also negative to the middle (this reversed while being tested in No. 4), and in the four cases in which the matter was tested the margins were negative to the middle (Table V.).

3. *Galvanotaxis.*—When placed in the electric current, *Planaria maculata* orients in a very definite manner. The animal curves into a U-form, lying upon one side, anterior and posterior ends and likewise ventral surface being directed toward the cathode, middle and dorsal surface directed toward the anode. Twenty specimens were tested, all of which exhibited essentially the same behavior. The cathodic orientation of the anterior end is more marked than that of the posterior end, and the former is generally in advance of the latter. The animals often assume the posture in question at intervals, hold it for a short time, and between such postures wander about the pan without showing any definite orientation to the current; in other cases the posture was held as long as the current passed. It is evident that there is a remarkable correspondence between the galvanotactic orientation of this species and the double metabolic gradient described above. The electrical gradient, in as far as the data go, also corresponds.

The orientation of the polyclad in the current was very similar to that of *Planaria maculata*. After some preliminary contortions, all of the specimens tested turned their anterior ends toward the cathode, often assuming a U-shaped posture. If the animal is facing the cathode when the current is made, it remains in that position, and may curve the tail under the body so that the posterior end of the tail faces the cathode. If the animal is facing the anode when the current is made, it curves its anterior end under the body so that head, tail, and ventral surface face the cathode. If placed at right angles to the current, the head turns to face the cathode. The animals did not usually travel in the current; the margins of the body were kept in constant undulating movements; the animals were obviously much more stimulated when facing the anode than when facing the cathode.

VIII.   ANNELIDS.

1. *The Metabolic Gradient.*—The gradient of the chætopod annelids has been described by Hyman ('16) and Hyman and Galigher ('21). The gradient is of the double type, the metabolic rate being high at anterior and posterior ends and decreasing from both ends to the middle region. Tests of the oxygen consumption of pieces from different levels show that posterior pieces consume

the most oxygen, anterior pieces next, and middle pieces least (Hyman and Galigher, '21).

2. *The Electrical Gradient.*—It was found by Morgan and Dimon ('04) that in two species of earthworm, *Lumbricus terrestris* and *Helodrilus (Allolobophora) fœtida,* the anterior and posterior ends are, in general, electronegative (galv.) to the middle. This result was verified by Bellamy on *Helodrilus caliginosus.* Other oligochætes have not as yet been tested.

Among the polychætes experiments have been performed chiefly on *Nereis, Nereis virens* on the Atlantic coast by Hyman in 1919 and *Nereis virens* and *Nereis vexillosa* at Friday Harbor by Bellamy in 1918 and Hyman in 1920. It was found that the electrical conditions are highly dependent on the freshness of the animals. It appears that in both species the two ends are negative (galv.) to the middle in very freshly collected animals, but the data are not as yet conclusive. It is certain, however, that when the animals have been kept in the laboratory, if only for a few hours, the gradient is reversed, and the anterior end is always and the posterior end usually positive (galv.) to the middle. Table VI. gives data on the electrical conditions in laboratory animals of both species.

3. *Galvanotaxis.*—The galvanotactic response of oligochætes and leeches was tested by Blasius and Schweizer ('93) for the leech, *Branchiobdella,* and *Lumbricus,* and by Nagel ('95) for the leech, *Lumbricus,* and *Tubifex.* These authors found that all of these forms are definitely cathodic, turning their anterior ends toward the cathode, and usually crawling toward the cathode. The matter was investigated in more detail by Moore and Kellogg ('18) for *Lumbricus terrestris.* They noted that this species bends into a U-shape when placed in the current with anterior and posterior ends directed toward the cathode, middle toward the anode, and crawls toward the cathode maintaining this posture. Bellamy found the same behavior in *Helodrilus caliginosus.* Hyman has tested the behavior in the current of *Dero limosa* and *Lumbriculus inconstans.* Both are markedly cathodic. The former instantaneously places itself with longitudinal axis parallel to the current, head to the cathode, and crawls rapidly to the cathode. *Lumbriculus* assumes the same posture as *Dero,* except that the posterior

end is generally curved toward the cathode, the attitude being, therefore, similar to that of the earthworms.

In *Nereis* the galvanotactic behavior is, like the electrical gradient, dependent upon the freshness of the individuals. It appears, although this has not been conclusively established, that very freshly collected animals are cathodic; they bend their bodies into a U-shape, with anterior and posterior ends directed toward the cathode. Animals which have been kept in the laboratory (and probably also sexually ripe animals) are anodic. They assume the U-position, but with anterior and posterior ends directed toward the anode, and middle toward the cathode. All of the individuals recorded in Table VI., of which the anterior ends are negatively charged (int.), were found to be anodic.

TABLE VI.

ELECTRICAL GRADIENT OF *Nereis virens* AND *Nereis vexillosa* AFTER BEING KEPT IN THE LABORATORY.

Ant., anterior; mid., middle; post., posterior; rd., readings on galvanometer. Negative and positive refer to direction through the galvanometer.

Nereis vexillosa.

No.	Ant.	Mid.	Post.	Rd.
1	+	−		5, 6
		+	−	10, 8, 13
2	+	−		15, 9, 13, 12
		−	+	7, 16, 16
		+	−	31, 25, 14, 13
		−	+	5, 0, 3
		−	+	9, 7
		+	−	5, 5, 6, 7
		−	+	4, 5
3	+	−		4
		−	+	7, 4, 5, 5, 6
4	+	−		12, 8, 7
		−	+	2, 2
5	+	−		6, 9, 3
		−	+	2, 2
6	+	−		5, 6
		−	+	2, 1, 3
7	+	−		5, 5
8	+	−		4, 3
9	+	−		8, 7, 4, 5
		+	−	4, 2, 2
10	+	--		4
		+	−	4, 7
11	+	−		5, 4
		−	+	2
12	+	−		8, 8, 6
		+	−	5, 2

Nereis virens.

No.	Ant.	Mid.	Post.	Rd.
1	+	−		7, 5
2	+	−		3, 3
3	+	−		6, 6, 10
		−	+	1, 1
4	+	−		2, 6
5	+	−		6, 6
		+	−	1, 2
6	+	−		3, 3
		+	−	5, 7
7	+	−		4, 7
8	+		−	10, 9
		+	−	6
9	+	−		4, 3
10	+	−		3, 5
11	+	−		2, 3, 6
		−	+	8, 8

There is thus in oligochætes a remarkable correspondence between the double gradient, the electrical gradient, and galvanotaxis. The U-attitude assumed in the current is consistent with the double respiratory gradient and double electrical gradient found in these forms. Particularly striking is the cathodic orientation of those forms of which the anterior end is positively charged (int.) and the anodic orientation of those of which the anterior end is negatively charged (int.).

IX. TADPOLES.

Although some fragmentary data have been obtained on other vertebrate young, we shall confine our discussion for the present to frog tadpoles.

1. *The Metabolic Gradient.*—This has not been determined for tadpoles, but from the condition in earlier stages of the frog (Bellamy, '19) and in other vertebrate embryos it is probable that the posterior end has the highest metabolic rate of any part.

2. *The Electrical Gradient.*—Hyde ('04) tested the potential differences along the axis of toad (?) tadpoles and states that there is a permanent difference along the axis "in a direction from the tail to the head of the embryo."[8] The meaning of this is not very clear, but from the usage throughout the paper it appears that Hyde means that the tail is negative (galv.) to the head. This was also found to be the case by Bellamy in frog tadpoles. The data are given in Table VII. In nearly all cases the head was found to be positive (galv.) to body and tail.

3. *Galvanotaxis.*—It has been known since 1885, when Hermann discovered the fact, that frog tadpoles are anodic—*i.e.,* when placed in a current, they turn their anterior ends toward the anode, tails to the cathode, bodies in line with the current. This statement we have verified. This orientation in the current corresponds completely with the electrical differences of potential found in the

[8] In a previous paper (Hyman, '18) it was erroneously stated that Miss Hyde had determined that the anterior end of vertebrate embryos is negative to the posterior end. She found a permanent difference of potential along one axis of the blastoderm but was unable to determine the direction of the current with reference to the future embryo, owing to the young stages with which she worked, except in the case of the tadpoles, where her meaning is not clear.

same lot of tadpoles.   No doubt the age of the tadpoles is a factor
in the response, as both the electrical gradient and the galvano-
tactic response were found by Bellamy to be irregular in older
tadpoles.

TABLE VII.

ELECTRICAL GRADIENT OF FROG TADPOLES.

Negative and positive refer to direction of the current through the
galvanometer.

No.	Head.	Body.	Tail.	Readings.
1	—		+	12
	+		—	50, 35
2	+		—	13, 12, 2, 3
	+		—	29, 9, 2
	+		—	25, 11, 9
	+		—	25
3	—		+	7, 7, 7, 9
	+		—	5, 6, 5, 6
4	+		—	7, 3, 4, 3
	+		—	10, 10
5	+		—	3, 3, 2, 2
	+		—	11, 10, 12
6	+		—	6, 10, 10, 8, 9
	+	—		6, 7, 12, 8, 7
		+	—	7, 7, 8
		+	—	6, 6, 7
7	+		—	3, 7, 6, 6, 5, 6, 5, 5
	+		—	8, 8, 8, 11, 9
	+	—		15, 11, 13, 12

X.   SUMMARY.

1. The idea is advanced that differences of potential in organ-
isms, particularly the permanent differences which exist along the
main axis of animals, are due to differences in metabolic rate at
different regions, the region of highest metabolic rate being the
most negative in the external circuit, most positive in the internal
circuit.   It is further suggested that internal potential differences
account for the galvanotactic response, in many animals at least.
Data are presented in various groups of animals to show the corre-
lation between metabolic differences, electrical differences, and
galvanotactic orientation.

2. In the sponges, *Leucoselenia* and *Grantia,* the oscular end
has usually a higher metabolic rate than, and is electronegative
(galv.) to, the basal end.

3. In the colonial hydroids tested the apical hydranths and levels

of colonies have a higher metabolic rate than, and are electro-negative (galv.) to, basal hydranths and levels. In the one species tested the apical end of the hydranth is cathodic.

4. In the hydromedusæ tested the metabolic rate and electro-negativity (galv.) are greatest in the manubrium, next in the tentaculate margin, next in the subumbrellar surface, and least in the exumbrella. So far as tested, manubrium and tentacles are cathodic.

5. In the ctenophore, *Pleurobrachia*, the metabolic rate and the electronegativity (galv.) are highest at the aboral pole and decrease toward the oral pole. No galvanotactic response was obtained.

6. In *Planaria maculata* anterior and posterior ends have a higher metabolic rate than the middle; the anterior end is electro-negative (galv.) to posterior levels. In a current a U-shape is assumed with anterior and posterior ends directed toward the cathode, middle toward the anode. In a polyclad worm anterior and posterior ends and margins were found to be electronegative (galv.) to the middle regions; the galvanotactic response was simi-lar to that of *Planaria*.

7. In annelids anterior and posterior ends have a higher meta-bolic rate than the middle and are electronegative (galv.) to it. In *Nereis*, after being kept in the laboratory, anterior and posterior ends are electropositive (galv.) to the middle. When placed in the current, all oligochætes tested turn their anterior ends toward the cathode, and the larger forms also bend their posterior ends toward the cathode, the body assuming a U-shaped posture. *Nereis*, in which the two ends are positive (galv.), assumes the same posture, but with the ends facing the anode.

8. In frog tadpoles the posterior end has the highest metabolic rate and is electronegative (galv.) to anterior levels. In a current they orient with posterior end directed toward the cathode, ante-rior end toward the anode.

9. It thus appears that so far as our tests have proceeded that regions of higher metabolic rate are externally negative, internally positive, to regions of lower metabolic rate, and that when placed in a current animals direct those parts positively (int.) charged toward the cathode and those parts negatively (int.) charged to-ward the anode.

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