SCIENCE

Friday, April 14, 1916

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THE BASIS OF PHYSIOLOGICAL INDIVIDUALITY IN ORGANISMS[1]

The world of living things exists in the form of what we call in every-day language individuals. We must first inquire whether this word "individual," as applied to organisms or their constituent parts, has any real scientific value. Etymologically the word means something which is undivided or can not be divided, that is, it implies the existence of a unity of some sort. But divisibility is as truly a characteristic of the organic individual as indivisibility, for new individuals arise by processes of reproduction from parts of those previously existing.

How then do we recognize an organic individual? The answer is not difficult, though in certain cases it may be difficult to determine whether a particular organic entity is an individual or not. It is a certain unity and order in behavior in the broadest sense which characterizes the individual, either living or non-living. In the organic individual, whether it is a whole organism or part of it, this orderly behavior consists in a certain orderly arrangement of parts in space and a certain orderly sequence of events in time. The problem of organic or physiological individuality is then the problem of the nature of this unity and order.

Many attempts at the solution of this problem have been made. The so-called vitalistic and neo-vitalistic theories postu-

[1] Read at a joint symposium of the American Society of Zoologists and Section F of the American Association for the Advancement of Science, Columbus, Ohio, December 30, 1915.

late the existence of a non-mechanistic principle which controls and orders the physico-chemical activities. These theories have at least the merit of recognizing and meeting squarely the real problem, but while the present state of our knowledge does not permit a complete demonstration of their falsity, they are intellectually unsatisfying in many respects and particularly in view of the rapid progress of scientific method in its attack upon the problems of life.

The theories which postulate a multitude of distinct specific entities as the basis of the organism are properly speaking not theories of organic individuality at all, for they ignore the real problem. They are merely hypotheses of what we may call the metamicroscopic anatomy of the individual. The real problem of the unity and order remains not only unsolved, but its solution is placed at least beyond the present range of scientific method. Logical analysis of these theories shows clearly that their implications are fundamentally teleological and anthropomorphic. In fact so far as they are regarded as solutions of the problem they are really vitalistic theories in disguise.

In this connection let us consider for a moment the chromosome. Granting for the sake of argument the correctness of the assumptions of certain schools of scientists concerning the spatial localization of factors in particular chromosomes, it is evident that the so-called chromosome maps are nothing more than imaginary pictures of the metamicroscopic anatomy of the chromosome. If these spatially localized entities exist, they are merely anatomical characters of the organism and, as in the case of other anatomical characters, their existence, orderly arrangement and behavior remain to be accounted for. The essential problem of the unity and order of the individual is not only unsolved, but ignored, except by implication, in these hypotheses.

Concerning all the various theories of organization which in one form or another have enjoyed wide acceptance among zoologists the same objection may be made. Granting the correctness of any one of them, the postulated organization is essentially anatomical and its orderly integration remains to be accounted for. Let me make it clear that I have no quarrel with the facts along this line, so far as they are or may in the future be demonstrated to be facts. I maintain merely that they are essentially anatomical facts and as such constitute simply another step in the formulation of the real problem, not an advance toward its solution.

The rapid development within recent years of our knowledge concerning apparently specific chemical correlations between different organs or parts has led many to assert that the fundamental type of physiological correlation in the organism is of this chemical transportative character. Concerning these views I need only point out that the existence of orderly chemical correlation between parts assumes the existence and orderly arrangement of differences of some kind, in other words, of an organization of some sort. Undoubtedly chemical correlation is a factor of very great importance in determining the character of events in the organic individual, but the individual must exist as an order of some sort before orderly chemical correlation is possible. Evidently chemical correlation does not give us the solution of the problem.

The organism has often been compared to a crystal. Leaving out of consideration the fact that there is no optical or other evidence for the crystalline character of protoplasm in general, it seems to me that these hypotheses ignore one very fundamental difference between the organism and the crystal. The unity and order of the organism are fundamentally dynamic and associated with chemical change, and when the characteristic chemical changes cease the unity and order disappear, except in so far as the anatomical record of dynamic activity may persist for a longer or shorter time. The unity and order in the crystal are static and when chemical change begins they disappear.

In this brief survey I have endeavored to bring out the fact that our biological theories of the individual, so far as they are not avowedly vitalistic or dualistic, are largely static and anatomical in fact or in implication, rather than dynamic. They are, in short, hypothetical descriptions of the machine supposed to be at work or else they tacitly assume a machine at work, but concerning the agents or processes which construct the machine and control its operation they tell us nothing. A machine which runs in a definite orderly way must be constructed according to a definite orderly plan and with the orderly employment of energy, and its operation must be controlled. In short, we must either become vitalists and admit the existence of entelechy or some other non-mechanistic principle, or else we must find some sort of dynamic unity and order as the basis of the morphological and physiological unity and order apparent to common observation. We have been trying to conceive an organic machine ready-made which shall operate in such a way as to satisfy the facts of biological observation and experiment. I believe that the essential problem is the problem of the construction and control of the organic machine. If we can gain some insight into the nature of the constructive and controlling processes we shall reach a more adequate conception of the individual than if we merely attempt to imagine a ready-made machine or individual which will satisfy the demands of observed fact. In other words, an adequate mechanistic theory of the organic individual, if such a theory is possible, must be stated in dynamic terms. It must deal primarily with processes, not structures, and with changes, not with static entities.

During the last fifteen years I have been chiefly engaged in studying and analyzing experimentally the processes of individuation in the lower animals, and this work has led me to certain conclusions concerning the nature of physiological individuality which I wish to present briefly. It has been very generally assumed by biologists that the basis of physiological individuality is inherent in protoplasm and dependent on some sort of self-determined organization. The barrenness of our theories of individuality is, I believe, the result of this view. I shall attempt to show that the physiological individual originates in the final analysis, not in a self-determined inherent organization, but in a relation between protoplasm and its environment. There are, of course, many kinds and degrees of individuality in protoplasm, both chemical and physical, such for example as atoms, molecules of the most various degrees of complexity, colloid particles, crystals, mechanical individuals such as fibrillæ resulting from strain, nuclei, cells, etc., but the integration of any or all of these into a physiological individual with a definite orderly behavior in both space and time can not conceivably be self-determined. We must either accept Driesch's entelechy or some other vitalistic principle or we must seek for the integrating factor in the relation between living protoplasm and its environment.

In what aspect of this relation can we hope to find such an integrating factor? I believe that it exists before our very eyes in one of the most characteristic features of environmental relation, namely in spatial quantitative differences in the action of external factors on protoplasm. A brief consideration of a simple case will serve to make the point clear.

Let us begin with a mass of protoplasm, or a cell mass which is undifferentiated, *i. e.*, in which no morphological differences and no localized quantitative or qualitative differences in the metabolic reaction beyond those characteristic of protoplasm or cells in their simplest terms are present. Such a protoplasmic or cell aggregate may include individualities of various kinds, as I have already pointed out, but it is not integrated into a physiological individuality, as a whole, nor does it possess any inherent capacity for such integration.

If now such an aggregate is subjected to the differential action of environment by permitting an exciting factor, a stimulus, to act upon some point of its surface the first result is an increase in dynamic activity in the region immediately affected. It is a familiar fact of physiology that the dynamic effect of such a local excitation does not remain limited to the region directly affected by the external exciting factor. The local excitation is followed by the spreading or transmission through the protoplasm or over its limiting surfaces from the point immediately affected, of some sort of dynamic change, which itself acts as an exciting factor. For present purposes the fact of transmission, rather than the nature of the transmitted change concerns us.

Secondly, we know that in protoplasm in general such transmitted excitations decrease in energy, intensity, or in our present ignorance we may say in physiological effectiveness, with increasing distance from the point of origin, so that at a greater or less distance they become inappreciable or ineffective. This range or limit of effectiveness depends, of course, on various factors, the degree or intensity of the original excitation, the capacity of the protoplasm for transmitting excitations, etc. The case is analogous in certain respects to the spreading of a wave in water, air or any other physical medium from the point of disturbance.

Since a decrement in effectiveness occurs in transmission, the degree of excitation associated with it will be greatest at the point of origin and will decrease with increasing distance from this point. That is to say, a gradient in excitation appears in which the point of original excitation by the external factor constitutes the region of highest rate, intensity, or effectiveness. Such a dynamic gradient represents, I believe, the simplest form and the starting point of physiological integration in living protoplasm.

If the action of the external factor is of short duration this dynamic gradient usually exists for only a short time and leaves little or no appreciable persistent change in the protoplasmic substratum. If, however, the action of the external factor is sufficiently long continued or sufficiently often repeated, the protoplasmic changes sooner or later become more or less evident and more or less persistent. These changes are fundamentally changes in irritability, in the capacity of the protoplasm to react, and since these changes are in general proportional to the rate or intensity of dynamic activity in the protoplasm the dynamic gradient may produce in the protoplasm an irritability gradient. The differences in irritability at different levels are more or less persistent, and when once established tend in general to become intensified up to a certain point. In short, a dynamic or metabolic gradient arising as the result of local excitation by an external factor may become the starting point of a persistent or permanent and primarily quantitative order in the living protoplasm, and such an order as this represents, I believe, a physiological axis or the physiological individual in its simplest form. The first order of this kind to arise in a given mass of protoplasm becomes the chief, polar, or major axis, and other similar orders established later determine minor axes, *i. e.,* the symmetry.

We now turn to the question of the nature of physiological relation or correlation in such an order as this. The fundamental relation must be one of dominance and subordination. The region of highest irritability or rate of reaction must dominate all regions of lower rate within the effective range of the excitations transmitted from it because to any stimulation of the system it reacts more rapidly or more intensely than other regions, and its greater irritability determines that it shall react to some conditions which are not effective in other regions. Consequently the excitations transmitted from this region of highest rate are more effective in determining the general metabolic rate at other levels of the gradient than the changes transmitted from any other region. The region of highest irritability or rate of reaction in such a gradient is then a physiologically dominant region, because it is the chief factor in maintaining the gradient after it is established and so in determining the general metabolic rate at each level. This dominant region of the gradient is relatively independent of other regions while they are relatively subordinate to it. In general any level of the gradient is dominated by higher levels and in the absence of these higher levels itself dominates lower levels.

The region of highest rate of reaction in the chief or major gradient becomes in development the apical region or head of the individual and a definite localization and course of development along the major axis occurs, and the localization of organs with respect to the minor gradients is also definite and characteristic. The orderly specialization and differentiation in such an individual results from the differences, primarily quantitative, which exist at different levels of the gradient.

These conclusions are based on many different lines of evidence which can be referred to only very briefly: First, a gradient in metabolic rate in which the region of highest rate becomes the apical region of the individual has been demonstrated as a characteristic feature of the major axis in animals, at least during the earlier stages of development. There is also much evidence to show that the minor axes are represented by similar gradients. The physiological individuals examined thus far include the amœba pseudopodium and various other protozoa, celenterates, flatworms, echinoderms, annelids, fishes, amphibia and birds, in all more than fifty species. Among the plants various species of axiate algæ have also been examined and a similar gradient with its region of highest rate at the apical end of the axis has been found in all. In many cases these dynamic gradients are readily distinguishable before any visible morphological differences along the axes exist.

Moreover, the very general existence of developmental gradients along the axes in both animals and plants constitutes very strong evidence for the existence of metabolic gradients, even where these have not been directly demonstrated. As regards the major axis of the animal, the so-called law of antero-posterior development is essentially a statement of the fact that morphogenic development begins or proceeds most rapidly in that region which becomes the apical or anterior end of the animal, and in minor axes definite developmental gradients also exist. In the axiate plants essentially similar relations are found. The development of the individual proceeds from the apical end, the growing tip of the axis. In axiate organs and parts also metabolic gradients and developmental gradients correspond, so far as observation goes at present. In processes of experimental reproduction or reconstitution in pieces of the lower animals the same relations between metabolic gradients, axes and the course of development have been found to exist as in embryonic development.

Second, experimental teratogeny affords evidence of great value concerning axial metabolic gradients and even makes it possible to demonstrate their existence in certain cases where other means are technically unavailable or unsatisfactory. The method of experiment along this line depends upon the fact that the degree of susceptibility of living protoplasm to at least many, perhaps to all, agents commonly characterized as depressant or inhibitory, is very definitely related to the rate of metabolism together with the correlated protoplasmic conditions. This relation is briefly as follows: to a high intensity of action of agents and conditions, which kills without permitting the protoplasm to adapt or acclimate itself, the susceptibility varies in general directly with general metabolic rate. The higher the rate the earlier death occurs, and *vice versa.* To a low intensity of action which permits the protoplasm to adapt or acclimate itself to some extent, the susceptibility in the long run varies in general inversely with the metabolic rate, because, the higher the rate, the greater the capacity for, and rate of acclimation. We see these relations more or less clearly in the susceptibility of young and old organisms to various external conditions. To extreme conditions the young with their higher metabolic rate are more susceptible than the old. Medical practise in the administration of drugs to children and adults recognizes this difference in susceptibility, though so far as I know it has never been formulated in general terms. On the other hand, the young organism adapts or acclimates itself more readily and rapidly than the old to conditions which are not too extreme to permit acclimation. There is a large body of evidence in support of these conclusions concerning susceptibility which can not be considered here.

The point to which I wish to call attention is the relation between susceptibility and metabolic rate on the one hand and developmental control and experimental teratogeny on the other. If the major axis of the animal egg, or embryo, is primarily a metabolic gradient with the highest rate in the apical region, we should expect this gradient to appear as a susceptibility gradient to various external factors. This I have found to be the case. By subjecting, for example, the unfertilized egg or the embryo of the sea urchin in various early stages to rather extreme action of various agents and conditions it is possible to obtain a gradient in inhibition of development in which the apical region is most inhibited, the basal least. On the other hand, with agents or conditions whose action permits some degree of adaptation or acclimation, the apical region, though at first most inhibited, is in the long run least inhibited, the basal most, because the apical region possesses greater capacity for acclimation than the basal. By this means two opposite types of teratological larvæ are obtained, the one with apical region most inhibited and therefore disproportionately small and retarded in development, the other with the apical region least inhibited and therefore disproportionately large and advanced in development. Between the two ends of the axis the degree of inhibition differs with the level in the gradient. Similar differences in degree of inhibition along the axes of symmetry are also present in such cases. In this way the whole shape, proportions, and degree of development of different parts can be modified and controlled to a high degree and in two opposite directions. Similar results have been obtained with other forms. Moreover, at least most cases of experimental teratogeny resulting from the action of chemical agents and general environmental conditions, as well as many teratological forms observed in nature can be readily interpreted on this basis. Experimental teratogeny then affords, on the one hand, a valuable check on other means for demonstrating axial gradients, and, on the other, finds a simple interpretation, at least as regards many of its features, on the basis of the general conception of metabolic gradients.

Third, it is possible in some of the lower animals to eliminate the original axes in isolated pieces by means of narcotics, and then to establish a new axis in a different direction by subjecting the pieces to a gradient in external conditions. The shorter the piece, the less marked the original polarity and the more readily new polarities arise in response to the differential action of external factors. Very short fractions of the axis may be completely apolar in their behavior. This fact indicates that physiological polarity is not, as often assumed, a property of the protoplasmic molecule, but rather a function of protoplasmic mass, as it must be if it is fundamentally a metabolic gradient.

Fourth, it has been possible to demonstrate experimentally for certain of the lower animals that a relation of dominance and subordination exists along the major axis. The apical region dominates all other levels of lower metabolic rate within the range of its influence, and in the absence of the apical region the highest level of the gradient present dominates all levels below it and within its range. The apical region itself, however, is to a high degree independent of other levels of the axis. In the reconstitution of pieces it is capable of developing, at least to a very advanced stage, and in the lower animals, apparently completely in the entire absence of other parts. The development of hydranths or apical portions of hydranths from short pieces of *Tubularia* stem, which has been described by various authors, is an example. Other levels of the body, however, never arise in reconstitution except in connection with more apical or anterior levels, though an apical end need not be present to determine their formation. In axiate plants the relations are essentially identical as regards the major axis. The dominance of the apical region, the growing tip of plants, over other levels has long been recognized by botanists. Moreover, in plants the apical region may arise in the absence of other parts, and the development of other parts takes place basipetally from it.

In the experimental reproduction of various simple animals, I have found that when the metabolic rate in the apical region is decreased, organs along the axis arise nearer to the apical end and to each other, while increase in metabolic rate of the apical region determines their localization farther away from it and from each other. If the localization of these organs is determined by a certain position in the axial gradient this relation between localization and metabolic rate in the apical region is easy to understand, for when the rate is low the gradient is shorter and the dynamic conditions for a particular organ arise nearer the apical end, while a high metabolic rate means a longer metabolic gradient and the localization of these conditions at a greater distance.

The relation of the central nervous system to the axial metabolic gradients is a point of particular interest. The apical or cephalic part of the nervous system develops from the apical region of the major axis which is, at least primarily, the region of highest rate in the whole body and the postcephalic portions develop in or near the region of highest rate in the symmetry gradients, the median ventral region in the bilateral invertebrates, the median dorsal region in the vertebrates.

If the organic individual consists primarily of a number of qualitatively different entities between which chemical transportative correlation exists, it is difficult to understand why it should transform itself during development into an individual which is dominated by a nervous system, in which transmitted changes instead of transported substances are the means of correlation. From this point of view the nervous system seems to arise from nowhere and out of nothing as an added superior system which integrates the previously existing mosaic of entities or qualities into an individual. From the dynamic viewpoint, according to which a physiological axis is primarily a metabolic gradient, the appearance, localization, course of development and functional dominance of the central nervous system are the natural and necessary consequences of the relations of dominance and subordination which have existed in the axial gradients from the beginning. The central nervous system is in fact merely the final morphological and physiological expression of dynamic relations which constitute the first step in individuation.

Brief mention of some other cases of functional dominance in relation to metabolic gradients is perhaps of interest. Mayer has shown that in the medusa *Cassiopea* that particular one of the marginal nerve centers which has the most rapid rhythm initiates the wave of muscular contraction and for the time being sets the pace for the others. Dominance here is of course only temporary. In the vertebrate heart the sinus region is dominant and initiates the beat. Dr. Hyman has been able to demonstrate that in the tubular embryonic heart an axial metabolic gradient exists and the region of highest rate in this gradient develops into the sinus. Tashiro has recently shown that a metabolic gradient exists in the neuron and that conduction of impulses is normally down this gradient.

Fifth, the localization of, and the conditions determining, various processes of agamic reproduction of new individuals from parts of those previously existing afford valuable evidence in support of the dynamic conception of the individual. Since the transmitted changes in protoplasm undergo a decrement in effectiveness with increasing distance from the point of origin, their range of effectiveness, in other words the range of dominance, is spatially limited. This range may vary with different conditions, metabolic rate in the dominant region, intensity of transmitted excitation, conductivity of protoplasm, interference with other transmitted excitations, etc. The range of dominance in a particular axis in a specific protoplasm under given conditions represents the physiological maximum of size which the individual can attain in that dimension under those conditions and remain physiologically an individual. Any part which comes for any reason to lie outside the range of dominance is thereby physiologically isolated and no longer physiologically a part of the individual. In most plants and lower animals such physiological isolation of a part, like physical isolation, is usually followed by more or less dedifferentiation and rejuvenescence and then by reproduction of a new individual. In agamic reproduction in general such physiological isolation is a fundamental factor. Physiological isolation may occur in consequence of continued growth in size or length of the body to such an extent that some part becomes physiologically isolated. Second, it may also occur in consequence of decrease in metabolic rate in the dominant region, thus decreasing the range of dominance, until finally the limit of dominance is less than the length of body along the axis concerned. Third, physiological isolation may also result from a decrease in conductivity in the path of transmission, thus decreasing the range of effectiveness of the transmitted excitation, or in extreme cases blocking it. And finally, physiological isolation may result from the local action of an exciting factor on a subordinate part, increasing its metabolic rate to such an extent that it becomes independent of, or insusceptible to the dynamic changes transmitted from the dominant region. The best proof of the correctness and adequacy of this conception lies in the fact that experimental determination and control of physiological isolation and reproduction are possible, either in plants or animals, in all these ways. To mention only one case, in many plants and in various simple animals we can induce agamic reproduction, not only by inducing growth in size, but by inhibiting or removing the apical dominant region.

In order that the physiologically isolated part may give rise to a new individual it must either retain to some degree in its protoplasm the axial gradient or gradients determined in it while it was still physiologically a part of the parent individual, or else new gradients must be determined in it by the differential action of external factors. We find both these possibilities realized in nature and in experiment. In short, the phenomena of agamic reproduction in both plants and animals afford very strong evidence in support of this conception of the organic individual.

Gametic reproduction differs from agamic, first, in that the gametes are more highly differentiated, physiologically older cells than those concerned in agamic reproduction and require in most cases the special conditions of fertilization to initiate the process of reproduction and rejuvenescence; second, in that the isolation of these cells from the parent body in multicellular forms is not directly connected with the range of dominance in the individual, but seems to be rather a process of elimination or extrusion of cells which, so far as the parent body is concerned, have completed their life-cycle, are approaching death and have no further rôle to play as physiological parts of the body and are got rid of like other inactive waste material.

One or two other points require brief consideration. I have endeavored to make it clear that the physiological integration of protoplasmic parts or of cells into an individual with a definite characteristic orderly behavior in space and time is not self-determined by some sort of organization inherent in the protoplasm, nor by some non-mechanistic integrating principle such as Driesch's entelechy, but in the final analysis by the relation of the protoplasm or cells concerned to the environment, primarily the external environment, though in the individuation of parts of an organism the intra-individual environment may be the effective factor. In fact, physiological individuality is fundamentally the result of interrelation between living protoplasm and its environment. The fact that morphological and physiological order in development and evolution are primarily superficial, as for example in the protozoa and in most plant cells where only the superficial layers of the protoplasm show a definite persistent morphology receives a simple interpretation from this point of view, while from any other standpoint it is difficult to find a reason for this superficial appearance of order. The superficial origin of the nervous system in development is perhaps the most notable case in point.

It is not necessary, however, to assume that every organic individual arises directly through the differential action of environmental factors. When the metabolic gradients with their associated protoplasmic conditions are once determined in a mass of protoplasm or cells they or their protoplasmic substratum may persist for many generations through division or other reproductive processes. In other cases factors in the intra-individual environment may determine the gradient or gradients in certain parts. The polarity of the egg, for example, shows in most cases in both animals and plants a definite relation to the point of attachment of the growing egg cell to the parent body, and there is good reason to believe that the differential action of the egg's environment in the organism determines its polarity. In some cases, however, this polarity, if present, is apparently eliminated and a new polarity established by external factors acting after isolation, as for example in the egg of the alga *Fucus*, where the axis of the egg and so of the plant is apparently determined by incident light, or in its absence by other differential relations to external conditions. Evidently a physiological axis may be inherited through one or more generations after it is once established, or it may be determined *de novo* in each reproduction. Experiment demonstrates that even in many cases where it is inherited in nature we can eliminate it and determine the establishment of a new axis by the differential action of external conditions.

Considering for a moment another point, the question may be raised whether a mere gradient in rate of metabolism with its correlate of protoplasmic condition is adequate to account for the differentiation that arises along an axis in development. To those who have been accustomed to postulate a great number of qualitatively different entities as the starting point of the organic individual such a conception may seem to be almost ridiculously inadequate. The facts, however, are these. We can produce experimentally morphological differences which are clearly qualitative through the action of external factors, such, for example, as temperature, which act on metabolism primarily in a purely quantitative way. Moreover, it is clear from various lines of evidence that the character of the substances which accumulate in a particular protoplasm as components of its structural substratum is very closely associated with metabolic rate. When the rate is high only certain substances produced in the course of the metabolic reactions and which are relatively stable under these conditions can accumulate as a structural substratum, while other substances are broken down and eliminated. With a lower metabolic rate some of these other substances do not break down so readily and therefore they also may accumulate and so on. Take the simple case of the accumulation of fat in a cell. We know that a low metabolic rate favors fat accumulation and a higher rate may lead to its disappearance. But we can not doubt that after the accumulation of fat in a cell has begun, the presence of the fat alters the metabolic processes occurring in that cell: its appearance in the cell is associated with a certain metabolic rate, but once present it may alter not merely the rate, but the kind of metabolism which occurs. Various factors indicate also that differences in metabolic rate may determine the production of different substances. On the basis of these and other lines of evidence, I believe that we are fully justified in maintaining that purely quantitative dynamic differences, *i. e.,* differences in metabolic rate may and do serve as the starting point of very great qualitative differences, both in structural constitution and character of metabolic reaction. In short, both physiological and biochemical facts support the view that a metabolic gradient is adequate to account for the beginning of differentiation along a physiological axis, and the burden of proof must rest on those who maintain that it is not. Of course the character of the qualitative differences which arise from the quantitative, must depend on the specific constitution of the protoplasm concerned.

It is evident that as soon as orderly differences arise chemical transportative correlation between the different parts must play a very important rôle in determining the character and course of further developmental changes, but it is also evident that such chemical correlation can not exist until differences exist nor can it be orderly or definite in character unless the differences on which its existence depends are orderly and definite. The conception which I have presented is an attempt to show how these orderly differences arise and make possible chemical correlation.

To sum up, physiological individuality depends fundamentally and from the beginning on the transmission of dynamic excitations and not upon the transportation of substances. Transportative correlation, while of great importance, is a secondary factor, playing a rôle in determining the course and character of development, but not in determining the existence of an individuality. And, furthermore, the facts indicate that a definite orderly transmissive correlation can originate only in a region of relatively high metabolic rate determined in the final analysis by factors external to the protoplasm concerned. Transmission from such a region of high rate determines a metabolic gradient together with its protoplasmic correlates, and so constitutes a physiological axis, a physiological individuality in its simplest form.

In conclusion I wish to point out the fundamental similarity from this point of view between the physiological and the social individual. The organism has often been compared to an ordered community of human beings or a state, but in these comparisons the question as to the factor or factors which determine the orderly character of the organism has usually been ignored. In the social individual it is authority or government which integrates the human units into an orderly whole. I have attempted to show that an authority or government of a simple dynamic kind is the primary integrating factor in the physiological individual. There are, moreover, certain rather fundamental similarities which are more than far-fetched fanciful analogies between government in the organism and in the social individual.

In its simple primitive forms, such as tribe, clan, etc., the social individual is integrated by the authority of a dominant person or perhaps of a group and this authority consists fundamentally in what we call brute force, which is something not very different from high metabolic rate in the organism. The dominance of the ruling personality depends, not upon the transportation of material from him to other members of the community, but upon the transmission of personal influence, and the size of the primitive social individual depends on the extent to which he is able to make this influence felt, *i. e.,* on his personal authority, the degree of his dominance and the means available for its transmission. The border regions of this social individual are but little under his influence and may become physiologically isolated in the same way that parts of the organism become physiologically isolated, either by growth in size of the whole so that the dominant personality can not longer control the outlying portions, by a decrease in his dominance as the result of advancing age, illness or other conditions, by obstacles to transmission of his authority, or finally in consequence of local conditions which make the particular group of persons more or less independent of or less receptive to the original authority. As in the organism, any of these conditions may result in the reproduction of a new orderly individuality like the old or different from it according to the character of the isolated group and the environmental conditions. The only condition necessary for this sort of reproduction in the physiologically isolated part of the social individual is the existence or development of a new dominant personality and neither an isolated part of an organism nor a group of human beings can exist for any great length of time in a natural environment without the appearance of differences of this sort between component parts.

I have maintained that the orderly physiological individual can not arise on a basis of chemical transportative correlation and we can see very readily that the state can not arise on a basis of barter and exchange or commerce. When once different individualities are established the character of material exchange may be an important factor in determining their further course of development, but the social individual originates in authority and its transmission, not in the exchange of substance.

The evolutionary development and differentiation of the social individual also parallels the evolutionary and individual development of the animal organisms. Specialization and differentiation of different parts occur as the result of local commercial or other conditions, and the means of transmission and transportation also develop, so that the physiological limit of size increases to an indefinite degree and physiological isolation of parts is much less likely to occur. The governmental authority and the means for its transmission develop into a complex machine comparable to the nervous system of the animal.

In fact we can even find a parallel in the organism to the approach toward democracy with advancing evolution of the state. The simple organism and the earlier stages of development of the higher forms are fundamentally of the primitive monarchical type. The dominant region is wholly or to a large extent independent of other parts, but dominates them. As organic evolution and development proceed, however, we find sooner or later that the development of the dominant region, the cephalic central nervous system, begins to be influenced by subordinate parts. This influence may result either from transmission or transportation. In certain reflexes in the higher organisms there is something very similar to the delegation of authority by the people to the government. We might say that in the evolution and development of the organism as in that of the state, government becomes more and more a representative government.

These similarities, I am tempted to say these fundamental identities, between the physiological and the social individual are based on the fundamental nature of living things. This close parallelism between those two dynamic individualities seems to me to constitute in itself evidence of great importance for the conception of the physiological individual which I have tried to present.

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THE BASIS OF INDIVIDUALITY IN ORGANISMS FROM THE STANDPOINT OF CYTOLOGY AND EMBRYOLOGY[1]

I

AN individual in the broadest sense is any animate or inanimate thing which is regarded as a unit. In this sense the electron, atom, molecule, crystal, biophore, determiner, chromomere, chromosome, nucleus, centrosome, cell, organ, system, person, corm, state, species, etc., are individuals. In all but the simplest units individuality involves organization, that is differentiation into parts and integration into a single whole. A fundamental property of any unit is its separateness or separableness, from other units, and yet no unit is completely independent. Biological units are separate in both structure and function from other units and yet they are related to others and these relations may be of such a sort that they constitute units of a higher order. Organic individuality of whatever order is dependent upon separateness of structure, of growth and of division. But while all vital units are separate or separable, they vary greatly in independence from the parts of a cell which are incapable of independent life to cells and to persons which are capable by themselves of maintaining life processes. The failure to distinguish between separateness and independence has been a fruitful source of misunderstandings in biological controversies.

[1] Read at a joint symposium of the American Society of Zoologists and Section F of the American Association for the Advancement of Science, Columbus, Ohio, December 30, 1915.

An organic individual then is any unit capable of manifesting the properties of life. The simplest and most fundamental properties of life are: (1) Metabolism, especially assimilation and growth, and (2) Reproduction by division. Every vital unit manifests both of these properties from the ultra-microscopical units of living matter to its more complex aggregates. To these two properties there is usually if not invariably added (3) sensitivity or the capacity of responding to stimuli, frequently in a beneficial or adaptive way. An organic individual then is capable of assimilation, growth and division and it may be irritable or sensitive. This definition can not be made more specific, for individuality is not a hard and fast thing. There are all degrees of organic individuality from the simplest and smallest units of living matter to the largest and most complex. As applied to human beings and their organization into society, the word "individuality" has come to have a metaphysical and mystical significance and not infrequently this mysticism has been extended to all forms of individuality.

1. *Individuality of Ultra-microscopic Units of Living Matter.*—Long ago Brücke (1861) maintained that protoplasm must be composed of ultra-microscopic units capable of assimilation, growth and division and these units he called "the smallest living parts." Many students of the subject since that time have postulated similar units; such as the "physiological units" of Spencer, the "gemmules" of Darwin, the "plasomes" of Wiesner, the "pangenes" of de Vries, the "idioblasts" of O. Hertwig, the "biophores" and "determinants" of Weismann, and the "factors," "determiners" and "genes" of many students of heredity. Recent studies of Men-