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PHYSIOLOGICAL COROLLARIES OF THE EQUILIBRIUM THEORY OF NERVOUS ACTION AND CONTROL.

By C. L. HERRICK.

Opportunity has afforded incidentally in connection with previous articles in this journal to point out the suggestions from anatomy in favor of a theory of nervous action based on the fundamental conception that the differentia of the various forms of nervous action consist in differences in the form of resistance and the reaction thereto, or, in other words, that nerve action partakes of the nature of equilibrium. It may now be permitted to offer fresh illustrations of the application of this principle. In the first place, however, we may note that in no department of physical science is it so plain as in neurology that we are dealing wholly with dynamic elements. While it is true that in the structure of the brain we have to do with morphological details of marvelous complexity and the descriptive side of our work is concerned with the varying outlines, sizes, and combinations of cells, fibres, etc., and the still more recondite structures within the cell and their dendrites, yet it is always obvious that these morphological peculiarities are but the expressions of inner forces and their responses to others from without. Thus it may even be doubted whether such a body as a centrosome or, at any rate, a centrosphere exists as a material element. Authors have been content to interpret the "asters" as the visual evidence of differential attraction in the cytoplasm.

It is possible to go farther and admit that all the structures with which the cytologist (and so the physiologist) has to deal are the visual interpretations of dynamic processes. This is more apparent to the neurologist than to the crystallographer

because the former grows accustomed to observe the close correlation between structural differences and conscious experience whose dynamic nature it is impossible to doubt. There can be no more doubt that the morphological peculiarities of nervous or other tissue are the expression of the equilibrated forces of growth and other functions than that the form and polariscopic qualities of a crystal represent molecular reactions. It is also apparent that the concept of matter in either case helps not at all in the explanation of these forces and that the attribute of materiality is to be determined on independent grounds. Not to discuss the ontological question at this time, it may simply be said that in our use of the morphological terms it is only with the reservation that they are convenient expressions to define the constant elements in our experience of dynamic forms. There are many advantages in this more direct interpretation of vital phenomena, for by the interpolation of imaginary material elements between the objective force and the subjective experience one loses sight of the constant dynamism—a dynamism which does not make necessary a fresh explanation of each new expression of force; for the existence of force may be regarded as self-evident when we recall that activity is the sole element of experience, and its varying forms are, in a sense, the algebraic expressions for interactions. The whole question of trophism is robbed of most of its difficulties if we think of structure as not a thing dissimilar from function, but consider both as different expressions of similar forces.

It would seem that especially in the sphere of embryology we should be ready for the abandonment of the fruitless search for material grounds for persistence of type. The theory of pangens is one illustration out of many of the absurdities to which a materialist construction is driven. The observed conformity to type observed in each of the thousand plants which may arise by minute subdivision of a moss, for example, shows how hopeless is the attempt to base on any specific material the capacity for heredity, no matter how eked out by the doctrine of latency. Correspondence in mode is the condition of identity implied by a dynamic theory, and the heterogeneity ex-

pressed in the forces of the body of a man may be expressed in the terms of the forces of a spermatozoan equally well. The assimilative power necessary when we assume that repeated nucleary division takes place without reduction of the chromatin is certainly dynamic and why should this dynamic determinant be limited to some material element? Does not the body preserve its integrity in spite of the flux of its materials? Why should not the actual material of the nucleoplasm be in a similar flux while retaining its form, i. e., its dynamic attributes?

From this point of view the coordination of parts through the nervous system becomes only a special instance of a coordination in the entire organism. It is true that even the unexpected wealth of fibrous ramification in the nervous end-organs revealed by the various applications of the Golgi method is still insufficient to explain the perfect co-adjustment of part with part in nutritive and trophic equilibrium—in fact, *any* conceivable completeness of nervous *continua* would leave something to be explained, for, in the last analysis, the processes are intracellular or even cytoplasmic. Even if we should grant that unsuspected imperfections in our present methods deprive us of the power of detecting the anastomoses between neurocytes in the same circuit, yet the most perfect conceivable continuity would still leave an appeal lying to protoplasmic transmission. A forthcoming paper will afford illustrations of what is here referred to. In the skin of many (probably all) amphibia and reptiles (*Axolotl* and *Phrynosoma*) there exists about the cells of Leydig a very complete and beautiful protoplasmic reticulum in such a way that each large cell is completely enveloped, while the meshes commingle and pass from cell to cell. This reticulum arises from certain nucleated protoblasts which are devoid of cell wall and whose naked protoplasm fills in interstices between the larger cells. This reticulum is not an artifact for it is found by the use of widely different reagents and is most complete when the fixation of the protoplasmic structure is most perfect, and in some cases of applications of chromosmic + platinic chloride + alcohol solutions this perfec-

tion leaves little to be desired. Ordinary hardening processes do not reveal the structure as a rule. It may be that the protoplasm is a delicate film which is thicker in certain parts than in others but the relation to the intercellular nuclei is certain. These are entirely distinct from the chromatophores. Bethe's methylene blue process reveals the farther fact that nerve fibers, which lose the sheaths after passing through the corium, end in knob-like tuberosities in proximity to these nuclei, though whether they penetrate the protoplasm or simply spread out upon it remains, from the nature of the method, uncertain. These nerve-fibers when stained with picro-carmin or fuchsin, in contrast to haematoxylin nucleary stains, seem to blend with the protoplasm and it is difficult to decide which appearance is nearer the truth. Such close contiguity between a naked fiber and a naked protoblast is too vaguely different from continuity to require physiological separation, however important the distinction may appear morphologically.

Here we have an illustration of a condition, which I believe is more general than we now can demonstrate, in which a nervous end-organ is so connected with a meshwork of vast extent as to suggest a very extensive somatic influence of a nature similar to nervous reaction over vast tissue areas.

We venture to suggest that there is no such sharp distinction between nervous functioning and the intracellular processes of the ordinary non-nervous cell as our present terminology and usage suggest. It is certain that in the differentiation of function the cells of the body at large do not give up all of their heritage of nervous or nerve-like power. Students of histogenesis may have been puzzled, as the writer has, to account for the fact that a very remarkable degree of coordinated trophic power is exhibited by the embryonic body prior to the development of nerve tracts and end-organs. The phenomena of nervous deficiency in anencephalic monsters is equally inexplicable from the standpoint of rigid limitation of coordinating power to the nervous system. In the sponges and Coelenterata it is plain that the coordination necessary to individual existence and perpetuation of specific characters is possible with no cen-

tral nervous system. There is a form of vital equilibrium so resident in the general system as to give rise to much the same phenomena of nervous unity as in the case of higher animals. It is not at all necessary to suppose that the cells of the body of higher animals have lost this power during the differentiation of the central system; it would be more probable that the central system should be superadded.

There are a number of classes of cells which seem to be, in the nature of the case, freed from all direct nervous control. The chromatophores of the Amphibia, to which the writer has devoted some study, seem in some cases not to be in a direct way associated with a definite nervous supply.¹ They are, indeed, literary migratory, though the scope and range of movement remains to be worked out. Two things may be quite positively stated; first, that these cells are to some extent independent of fixed nervous influence, and, second, that they are very really under indirect nervous control. Experiments tried in my laboratory many years ago showed that, in young cat fish, section of a branch of one of the cranial nerves destroyed the very marked adaptive power for the injured side. A fish, originally black, when placed in an aquarium with yellow bottom invariably changed to the color of the environment unless the mutilation described prevented it.

The observations of G. H. Parker on photometric changes in retinal pigment cells of *Palæmonetes* are interesting in this connection in showing that exposure to light causes actual changes in form and a segregation of the pigment of these cells. He finds that section of the nerve or severing the eye stalk from the body does not wholly prevent the reaction. This is an illustration of a reaction exceedingly resembling a true nervous response.

The embryonic tissues of all animals possess this coordinating sensitiveness and trophic interaction to a high degree. In the extreme case afforded by the blood corpuscles and lymphocytes it seems perfectly plain that there can be no direct

¹ Methylene blue seems to show connections in some instances.

nervous relation and yet he would be a bold physiologist who would venture to deny that there is a most subtle and powerful coordination between the stationary tissues and the free corpuscles. One may talk of chemotropism or vital susceptibility, but such terms express merely the fact that the corpuscles, like other cells, are coordinated with the rest of the body and bear both its specific and individual impress. The mysteries of serum therapy only increase our confidence in such an intimate relation.

It, then, may be supposed that the circuit of nervous action in any part of the body passes through a variety of smaller somatic circuits and that the spheres of the two forms of activity overlap so that the return nerve current bears the influence of this interaction. The nervous equilibrium is only a central specialized part of a vital equilibrium embracing all the activities of the body. The wandering cell, even though not in direct continuity with a nerve fiber, nevertheless may be said to act in a "nervous field" and so is not beyond the sphere of coordination, while, on the other hand, the results of changes in the extra-nervous mechanism of the body all have their effect upon the central system. In the same way we may explain the effect of the sum of organic and total or somatic stimuli upon temperament and disposition.

The processes of nutrition may be said to be common to protoplasm quite irrespective of nervous control, but the trophic influence of the latter is well authenticated and it may be assumed that no nervous action takes place without having its effect on growth. From the above it may be gathered that the ground of the mutual reaction may be sought in the fundamental similarity of the two processes, or rather the close relation between the processes of waste and repair lying at the foundation of both. It is necessary to suppose, accordingly, that the central nervous system is continually affected by the vital phenomena of the body at large as truly as the vascular system is under the control of the nervous system.

As a striking result of this effect of the somatic or extra-neural processes, one may take the phenomena connected with

the restoration of mutilations. When the newt's foot is amputated, under favorable circumstances the organ is quickly reproduced and the parts so restored differ in no obvious way from the old organ removed. What is the power which causes such a miraculous change? Does it take place because a simulacrum of the missing limb exists in the soul and the new body develops to correspond? With due allowance for use of terms, we reply, "yes, such a simulacrum does exist." The form of the central equilibrium has been determined by constant reactions between the member and the central system and when the member is lost the equilibrium so established is still in force and the nervous stimuli which but lately served to supply tone to the limb now operate upon the stump. Intense irritation results and the tendency is to influence growth at the point of injury.¹ This growth is under the directive control of the nerve just as we know the normal growth constantly to be. If the nerve of the limb be injured beyond repair monstrous growth results. It may be assumed that in case the leg were amputated and the nerve destroyed in the stump above, that the efforts at restoration might be abortive or result in monstrosities. It would be well to test this matter experimentally. It is believed that the application of the ideas indicated in this paper to the higher spheres of nervous activity will prove fruitful.

Another application of the same principle is found in the processes connected with the regeneration of severed nerves. It is a well authenticated fact that, in the case of section of a peripheral nerve, the nuclei of the sheath of Schwann pass to the centre of the lumen and form the protoplasmic prota of the segments of the new nerve—a process wholly unintelligible if we agree with Kölliker in regarding the sheath nuclei as derived from non-nervous connective tissue corpuscles, but not so remarkable if the abundant evidence be accepted that these nuclei are but the diverted nuclei of the cells which formed the nerve

¹ The assumption that irritation may produce proliferation is supported by the pathological karyokinesis in case of local irritation; see also processes connected with development of spermatozooids, etc.

originally by proliferation and moniliform condescence.¹ We here have an instance where the protoplasm of the cells has become specialized and the nuclei switched out of the circuit and apparently related to the process of forming the cell wall. But, in spite of the specialization implied in the production of an organ for nervous conveyance alone, it appears that the early nature of the cells is dormant rather than lost, so that in the case of injury and the consequent degeneration of the myelin and axis cylinder, the nuclei, with the small portion of less specialized protoplasm associated, return to the embryonic state and repeat the process of neuro-proliferation, after which the new channel is organized from the center outward and the nuclei return to their parietal position. It is more than probable that a similar rejuvenescence is possible in the case of other tissues also.

We have many instances of the same kind of differentiation within the cell. Take as an illustration the formation of glands in the skin of the frog, where a follicle is formed and then the several component cells are fused, the outlines being lost, and only the small nuclei which remain in the thin parietal layer of less altered protoplasm remain to indicate that the gland is really polycellular. It would be interesting in this case to institute experiments on the possibility of rejuvenescence of such cells.

In the application of the neural equilibrium theory to problems of heredity it would seem that there is a large and profitable field. Without attempting details in this direction, it may be pointed out that this point of approach renders unnecessary a vast deal of the most profitless theorizing in reference to heredity. If the neural and somatic forms of reaction are not absolutely unlike, but on the contrary are parts of a common vital type of energy (or rather force) and if it be admitted that the processes of nutrition may be and are influenced by the

¹ The nuclei of the ending of the motor nerve on the muscle offer interesting collateral evidence. See the article by Dr. Huber in the last number of this Journal

neural equilibrium, it follows that the germ is also situated in the field of these equilibrated forces and its composition, i. e. its own force formula, would be the resultant of the reaction of the existing (ontogenetic) formula as modifying the earlier (phylogenetic) force formula. Instead, then, of searching for "ids," "bioplasts," "gemmales," or the like we may feel assured that, in a much more complete and integrated form, the entire life of the organism will have its effect on the germ. This confidence will not cause us to pay less attention to the structural appearance of the cell and, in particular, the germ cells, but will prevent loss of valuable effort in the invention of sterile theories and prepare the way for a dynamic interpretation of these phenomena.

It may be noted in this connection that S. Ramon y Cajal has apparently suggested, by implication at least, some of the grounds for the equilibrium theory in his suggestive article in the *Archiv f. Anatomie u. Physiologie*, 1895. He says: "Die Phänomen der vorerwähnten lawinenartigen Leitung, sowie die geringe Zahl der sensorischen Elemente (Zapfen der Fovea centralis, akustische Zellen u. s. w.) welche alle die zahlreichen Eindrücke, für welche unsere Sinne empfänglich sind, aufnehmen müssen, zwingen zu der Annahme dass jede Sinneszelle, sowie jede subordinierte Gruppe von Pyramidenzellen des Gehirns successiv an der Production verschiedener Bilder sich betheiligen. Vom anatomisch-physiologischen Standpunkt aus, wird eine Wahrnehmung von einander, zu derselben Empfindungsquantität gehörigen, durch die Zahl und die betreffende Lage der corticalen in Erregung gesetzten Pyramidengruppen unterscheiden." It would seem to be evident from the above that not only the exact impression to be perceived is not produced by the organ of sense (since it would then be divided into a large number of parts in being transferred to the larger number of pyramid cells) but also that inasmuch as the same cells may be participants in different percepts the physiological basis for the latter must be the particular formula of these permutations in a given case and thus a simple impression must be

of the nature of an equilibrium constructed from the interactions of the cells implicated.

In conclusion, it may be noticed that the ideas advocated above have a very interesting bearing on the problem of the origin of variation. The theory of the competition of parts has taken strong hold of modern biology because it is becoming more and more evident that the sphere of natural selection must be greatly restricted and some appeal must be made to forces residing within the organism. Even Weismann in his extreme advocacy of natural selection has been forced to yield a large place to the effects of inner coordinations. We suggest that the nature of these coordinations is rendered much more intelligible by conceiving of all these vital-nutritive processes as equilibrated forces. If for any reason, a given part or tissue of the body is in the least exaggerated, its part in this complex coordination is increased and, accordingly, its reflex influence on the organism as a whole, or its nerve centers, will be increased and its quantum of the centrifugal currents will also be increased, so that the tendency will manifestly be for the newly created variation to go on increasing indefinitely until checked. The next generation will inherit this tendency and we should find that, in the absence of restraint, there would be the constant likelihood of the appearances of strange monstrosities with apparently unaccountable exaggerations of horn or spine. It requires very little familiarity with paleontology to discover that its records abound with cases in which no possible serviceability would account for the absurd burlesques which have been produced and only the comparative familiarity of existing types blinds us to the same fact. While not denying that there is a large element of useful adaptation in all cases (otherwise they would never have been preserved), yet it will be admitted that a very considerable proportion of the peculiarities and often the deeper seated characters have no such explanation. We should not be surprised at this, for it is apparent that the slightest variation not directly hurtful will tend to perpetuate itself. It may be said that all unnecessary parts will be eliminated as sapping the nutrition of the body at large. This is an

abuse of a teleological principle for it is not to be assumed that the body is reasoning from present causes to distant effects. If an eye ceases to be used it is atrophied, not because it is no longer useful and is therefore a cumberer of the ground, but because, the function having ceased, it is actually participating less in the equilibrium than formerly and also less than other organs. But a newly formed wart on the skin may be absolutely useless, yet, like a corn, it may be the seat of irritative processes which stimulate nutrition. It is then not the ideal utility but the degree of participation in the vital equilibrium which is the primary determinant. It is necessary to seek no farther for the source of variation and it is not surprising, when we consider the infinite possibilities for the increased vital activity of one group of cells over another that natural mimicry has found at hand all the necessary variations upon which it is to work, though we must not hope to find in their number and variety the complete explanations of the imitations produced.

University of New Mexico, Feb. 20th, 1898.