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THE EVOLUTION OF HOMEOSTASIS

The Phylogenetic Development of the Regulation of Bodily and Mental Activities by the Autonomic Nervous System

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(*Read April 22, 1954*)

"Πάντα ῥεῖ"—"Man is like a fountain, always the same form, but never the same water." (Heraklitus of Ephesus 544–484 B.C. This expresses succinctly the constant change which is necessary to maintain entity in the life of every biological species and individual. As the French physiologist Charles Richet (1900) remarked: "By an apparent contradiction it [the living being] maintains its stability only if it is excitable and capable of modifying itself according to external stimuli and adjusting its response to the stimulation. In a sense, it is stable, because it is modifiable."

This is the point of constancy in all physiological systems toward which every physical and chemical change is aimed. Each environmental change of whatever nature, be it one of temperature or ion concentration, is a challenge to the organism. The mechanisms by which it adjusts have been termed by the distinguished physiologist Walter B. Cannon (1939), as "homeostasis."

Let me give an example: The manufacturers of thermometers mark their instruments at 98.6° Fahrenheit, because they feel confident that this is the mean body temperature of every healthy person. This constancy is quite remarkable in view of all the factors acting from within and without which can alter body temperature. To begin with, the pituitary and particularly the thyroid glands determine the basic amount of heat production. To this a variable quantity of heat is added according to whatever muscular work is performed. Maintenance of bodily temperature is complicated further by the variations in the temperature around us. Nevertheless, the body does manage to keep its temperature oscillating around 98.6° Fahrenheit with surprising accuracy. The escape of surplus heat is permitted by relaxing the skin vessels to allow the blood to cool, by sweating and in more extreme moments by panting. Conversely, when the body temperature falls, the skin vessels contract to prevent further loss of heat, perspiration is at a minimum, adrenin is set free to liberate sugar for burning, and we start to shiver to replenish the deficit of heat. Except for shivering, this delicate shift of body temperature into one direction or the other is mediated through the *sympathetic division* of the autonomic nervous system.

And so we find in those animals which are threatened with moments of extreme emergency, not only by heat or cold, but also when facing an enemy, the homeostatic mechanisms of the sympathetic nervous system are thrown into sudden and complete activity. This profuse sympathetic discharge, the dilated pupil, rapid heart, deepened respiration, color change of the skin, sweating, and dry mouth, is characteristic of a frightened animal. All the resources of the body are mobilized for combat or for flight.

It is clear that energies which were expended during moments of stress must be replenished. In fact, energies must be stored away to stand ready for an emergency. This phase of conservation falls largely under the domain of the other division of the autonomic nervous system, the *parasympathetic*, which protects the eye from excessive light, slows the heart beat and rate of respiration, but activates the assimilation of energies by inducing the secretion of the salivary glands, liver, pancreas, and by promoting the function of the digestive apparatus. Clearly, there must also be proper homeostatic balance between the activity of the parasympathetic, the accumulator of reserves, and that of the sympathetic, the spender of energies. If the body spends too much, it goes bankrupt. If it is too thrifty, incapable or afraid to spend, it will be overwhelmed by an enemy, be it another organism, extremes of temperature, or an excess of material retained in the body, whether salt or sugar. Adequate spending, therefore, helps to free the body from the restrictions of environment and upholds the constancy of the *milieu intérieure*.

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But there is evolution in this story too. The simpler forms of life are subjected to relatively lesser changes in environment, or at least to fewer challenges from without. But the degree of efficiency of homeostatic mechanisms may be as adequate for the simpler organisms in their relatively restricted environment, as for the higher forms in their expanding and more complex world. The amphibian must keep close to its pond, for it cannot maintain the needed constancy of bodily fluid or temperature. Reptiles have learned to safeguard their fluid matrix and are, therefore, not restricted to the neighborhood of rivers and lakes, but as for maintaining the optimum body temperature, snakes and lizards must either bask in the sun or seek the shade as shown recently by Bogert (1949: 3).

And so there must be differences in bodily regulations, in fishes which inhabit the sea, in "cold and warm-blooded" animals, in birds which do not black out when quickly taking to high altitudes or diving rapidly down to the ground to catch their prey, or can run in hot deserts with great speed without fainting, but can die with fright as observed in a zoo, when an ostrich dropped dead upon a boy throwing a few peanuts at the animal.

There must be differences in homeostatic mechanisms in various members of the same species, those living in arctic regions and others which have to cope with hot climates, or between home-bound animals and their cousins which undertake far flung voyages during their periodic migration.

With this thought in mind, during the past several years a search has been made for neurological differences which may run parallel or even underlie evolutionary patterns of homeostasis. It has not been possible to explore all the varieties of mechanisms which uphold the constancy of the *milieu intérieure* as Claude Bernard (1879) conceived it.

This study, therefore, has concentrated on the nervous regulators, recognizing the close interrelationship between these and the chemical and endocrinological forces which operate equally in establishing equilibrium. A detailed investigation has been made of the autonomic nerves, both sympathetic and parasympathetic, in representative vertebrate species such as the *Amphioxus lanceolatus,* Cyclostomata, fishes both Elasmobranchii and Teleostei, the tailless amphibian, domestic fowl, Rhesus monkey, and man.

The intricate details, some of which are not yet unravelled, will be omitted in this account, but, throughout, the growing complexity of autonomic nerves becomes evident in passing from their simple arrangement in primitive chordates to highly integrated nerve plexuses, intimately linked with the expanding forebrain as seen in mammals and in man.

Some prominent features in this study may serve to illustrate this evolution (fig. 1). The individual segments of the neural axis give off on either side a dorsal and a ventral root to skeletal muscle and skin. Each of these nerve roots may carry with it autonomic fibers which are then referred to as dorsal or ventral outflow. The most striking feature morphologically in the evolution of the autonomic nerves is the initial preponderance of the dorsal outflow which shifts gradually in favor of a ventral outflow.[1] At first, all autonomic nerves emerge in a segmental fashion through all dorsal roots as seen in the amphioxus. Subsequently, in the cyclostomata (myxine glutinosa), the dorsal outflow is restricted to the head as the vagus nerve (Brandt, 1922: 65). While this remains, autonomic nerves grow out in a segmental fashion through the ventral roots. Thus, in some sharks, this ventral outflow is confined to the head as pupillary motor nerve, and to a variable number of segments of the trunk. In the more specialized bony fish, the segmental arrangement of the ventral autonomic outflow becomes blurred except for the most anterior and posterior levels. Here, the autonomic nerves of succeeding levels and their branches connect with each other to form the sympathetic trunk and the intricate nerve plexuses which extend into the head and pelvic regions (Young, 1931: 74; 1933: 75).

The principle of this plan, found in teleostean fish, is retained by higher forms, although a further specialization in the anatomy of the autonomic nervous system takes place as one advances from the frog to man. For example, as soon as animals emerge from aquatic life to an existence on the dry land, the ventral outflow is augmented to furnish the innervation of the glands to the head and the nerves to the pelvic organs, particularly to the sphincters of the genito-urinary, and rectal passages, become more distinct. And the anatomy of the sympathetic trunk becomes more complex, apparently, by changes affecting the shape of the vertebral column due to modifica-

[1] Weber suspected this shift already in 1817 and Goodrich (1927) noticed a similar phenomenon in embryological development.

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tion of posture and locomotion. When animals like alligators begin to lift their heads from the ground and subsequently develop a neck, the simple anterior sympathetic trunk, present in the fish and amphibian, becomes a double cervical sympathetic trunk and when the upright posture is assumed, the regularity in the arrangement of the lumbar sympathetic trunk is lost, which is particularly conspicuous in man.

Functionally, the available evidence indicates that in the beginning all autonomic nerve activity is directed towards accumulation and storage of reserves. Only later, some autonomic nerves became gradually concerned with spending of energies.

In particular then, the dorsal and the two extreme limits of the ventral autonomic outflow retain the function of conservation and are then called parasympathetic nerves.

The ventral autonomic outflow of the trunk region, inconspicuous as it is at the outset, either does not operate at all, or if it does, it also serves accumulation of energies. However, as the ventral autonomic nerves grow, they are put more and more into the service of spending energies and are then called the sympathetic nervous system, thereby becoming the antagonist of the parasympathetic.

Thus, for example, it is generally agreed that the vagus nerve exerts a powerful inhibitory in-

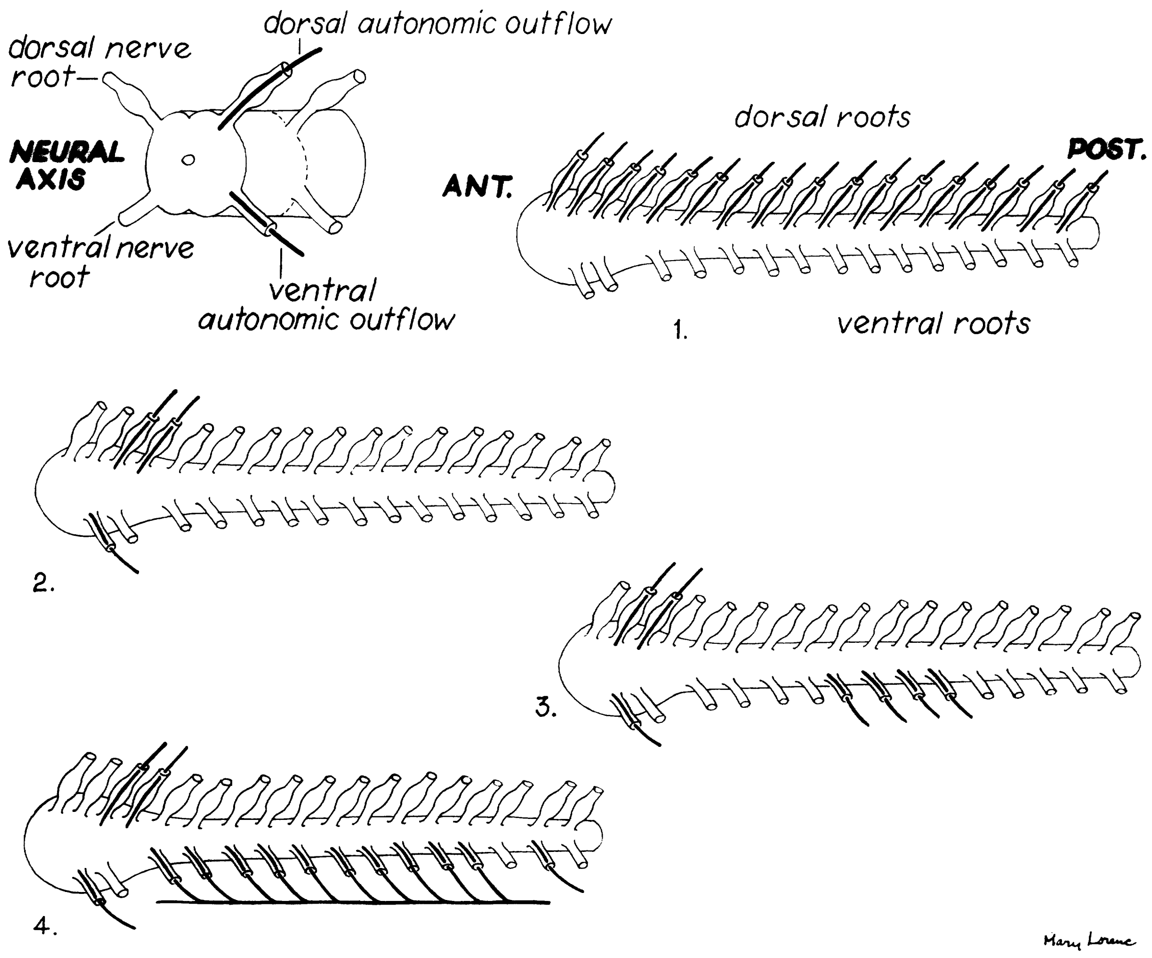

FIG. 1. Diagram illustrating four stages of the phylogenetic development of the outflow of autonomic nerves: Stage 1: All autonomic nerves emerge through dorsal spinal roots. Stage 2: Autonomic outflow is restricted to the anterior end as vagus nerve complex, added by a ventral outflow, the pupillary motor nerve. Stage 3: Anterior outflow remains as in Stage 2 and is augmented by a segmental ventral outflow in the trunk. Stage 4: Dorsal outflow is unchanged; more segments are added to the ventral outflow which, except for the extreme anterior and posterior levels, become connected, forming the sympathetic trunk.

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fluence upon the fish heart; whereas the sympathetic, the accelerator of cardiac activity in mammals, has little or no control upon the heart beat of selachians and teleosts.

Electrical stimulation of the vagus nerve produces powerful contraction of the air bladder in fishes and secretion of oxygen into this organ (Bohr, 1894: 15). Sympathetic activity upon the air bladder causes only slight decrease of secretion of gases, if any at all.

The motility of the mammalian gut is promoted by vagal and inhibited by sympathetic nerve activity. But in fishes, both nerves induce contraction of the intestinal wall.

Hence, it is true that morphology precedes function and that the capacity of mobilizing and spending energies for the purpose of freeing the organism of its environment, is a comparatively late acquisition in the evolution of autonomic nerves. The earlier developed pathways appear more firmly entrenched in that they have a better defined direction, particularly to vital organs. The effect of removal of the phylogenetically older parasympathetic is obvious and permanent and, if performed to great extent, is incompatible with life. On the other hand, even total sympathectomy is tolerated well with imperceptible sequelae, provided the subject is not put to extreme stress.

Now, early in the history of homeostasis, new means for adjustment came into being by modification of already existing tools. As the environment became more complex, new challenges to the organism were met by new responses operating through older mechanisms. Organs serving the function of touch, for example, were modified to serve the sense of bodily balance, and subsequently became adapted in the development of the sense of hearing. The swim bladder helps certain fishes to rise to the surface or drop to the bottom of the sea. Later, the swim bladder became changed to an organ of respiration,[2] the lung, and in warm-blooded animals it also serves as a temperature regulator, especially in birds, by the development of air-sacs which act as air-conditioners.

As we proceed along the phylogenetical scale it is the nervous system which attains increasing importance in the development of new adjustment mechanisms, apparently because of its plasticity, versatility, and faculty of integrating peripheral function. Using the same pre-existing effectors, a greater ability of adaptation to the environment was brought into existence by the nervous system owing to change of the function of areas of the brain. For example, thermoregulation of birds and mammals most likely developed from an already operating vasomotor regulation, as suggested by Prosser (1950).

If we are then to perfect our own homeostasis, we must expect to attain further adaptation through the nervous system. As Le Gros Clark (1951) puts it:

> The human brain has not appreciably changed in its size for about 200,000 years. There seems to be no evidence that man's brain is undergoing any further evolutionary expansion, or that it is even likely to do so. But it may well be argued that there are still tremendous opportunities for us to make evolutionary advances by learning how to make much fuller use of the brain with which we have already been equipped.

The autonomic nervous system is no exception. The sympathetic discharge, which was formerly a response to temperature changes in the environment, was adapted as a mechanism by which an organism could meet any emergency or threat to its existence. The sympathetic nervous system, formerly concerned with the maintenance of body temperature, now became, with the adrenal glands, the means by which the animal was prepared for "fight or flight."

New challenges have arisen for man in his associations with his fellow creatures. Man is endowed with a will, the power of speech and an intellect capable of amazing achievements, which, among all living beings, gave him the highest freedom from the limits of his surroundings. Yet, he has not acquired sufficient ability to live with other members of human society for mutual benefit, perhaps because he is still confused about powerful forces in himself, such as love and hate, aggression and fear, guiding him in his relation to his fellow man.

It is true, man has recognized early the necessity of curbing actions which may impinge harmfully upon others. Therefore, he established legal and ethical codes, most of which play upon man's fear of punishment and craving for gratification and recognition. Thus originated the sense of right and wrong, honesty and dishonesty, of good and bad. However, the effectiveness of existing devices which govern social conduct between individuals, groups and nations, is still limited. They do not promise to ensure the com-

[2] This view is contested by Romer.

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plete and final answer to the challenge of social life.

This is illustrated once more in our scientific age. No doubt, the results of scientific endeavor have brought unforeseen improvement to human life.

But scientific discoveries have also turned against man and threaten social equilibrium to a point where many believe in the possibility of self-extinction of the human race. A number of contemporaries stated the difficulties which confront man and offered various suggestions for the solution of social understanding. Most of these recommendations are based on existing principles of social conduct and aim at greater uniformity of legal rules, to fulfil the material needs of everyone and to encourage further scientific discoveries (United Nations, 1947; Huxley, J., 1944; Russell, B., 1953; Northrop, F. S. C., 1947, 1952).

Obviously, the creation of a single law valid all over the globe is desirable and the necessity of providing food, clothes, shelter, and medical care is beyond dispute. But social equilibrium can hardly be obtained through harnessing of new powers, developing means of speedier transportation and communication, or producing additional labor-saving devices, unless man acquires a better ability of utilizing his discoveries to his advantage and benefit. Man's rapidly developing intellect has created an environment in which human interdependence has grown extremely intricate, but the evolution of the motivation of his behavior which has to deal with this complex world, apparently, has been lagging behind. Man has been able to master space, disease, hunger, and to a large extent the elements of nature, but thus far he has not yet learned to cope with the restrictions of his fellow man, with whom he must live side by side.

And so, in human society, countless situations occur which are not limited to threats against man's materialistic existence, but may be such that he interprets them as a threat to his accepted principles and values, as a danger to his "Ego." Here is surely a challenge, "new" in terms of the age of biological life. This is a new kind of threat, no longer necessarily to one's life, but to one's beliefs and sense of values, to one's ideology and ambitions. To this new challenge man reacts with old instincts and emotions and calls into response old mechanisms. We speak of "resentment," "anger," "urge for power," and "increased nervous tension." The autonomic nervous system is again brought into play and, though the response is modified and to a large extent inhibited, it is nevertheless essentially similar to the response to a simple change in environmental temperature. The body is being prepared for what? For "fight or flight" against a new set of values, for one's own ambitions, to maintain one's personality.

Yes, the response is excessive and misdirected. In modern society its manifestations are seen in the rising death rate from heart disease and cerebral hemorrhage, and in the prevalence of peptic ulcer and high blood pressure; it is seen in the increasing incidence of mental breakdown and suicide as well as in the difficulty which man encounters in his attempts to abolish war.

These phenomena, of course, are not due to a single factor, but they do serve to illustrate once more the evolutionary development of homeostasis.

The response is excessive, but the evolution of the appropriate adjustments to such new challenges, the evolution of an adequate balance of instincts and emotions, which appear as "self-centered" and "altruistic" behavior, has perhaps not yet been completed.

Therefore, when seeking for a solution of this problem one has to enter the borderland of psychology and physiology; once more one is confronted with the problem of reaching the barrier of "mind and body" of which we are still disappointingly ignorant. Nevertheless, it has been possible to influence "mind," at least temporarily by pharmacological drugs, shutting off "consciousness" through anesthesia, abolishing "awakeness" and feeling of pain by hypnotics and analgetics or bringing about "euphoria" or "depression of mood" through other agents. Pavlov's "conditioned reflexes" (1927) have been employed in training children, advertising, and, more recently, have been labeled as "brainwashing" in extracting false confessions. Surgical procedures on the forebrain can cause changes in "personality" inasmuch as "aggressive" individuals have become more "amicable."

However, one can hardly expect to attain peace and harmony merely by taking pills, nor is it likely to find an individual wise enough to be entrusted with the task of conditioning mankind according to a uniform scheme; even if such a person existed, society would scarcely accept such means of obtaining social adjustment, because the trend of man's evolution seems to be directed

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towards the enhancement of the freedom of individuals, rather than towards the creation of automatons, notwithstanding recent events which might indicate the opposite. For obvious reasons, neither is brain surgery a desirable method for social adjustment.

Therefore, the problem of "how" to obtain a more adequate social adjustment through alteration of psychological states, must remain unanswered, at least until such time when a more concrete and accurate knowledge of the neurological basis of the various aspects of "mind" such as "consciousness," "thought," "reason," "memory," "instincts," and "emotions" has been made available.

In spite of Sherrington's (1951) pessimistic view, recent advances in the anatomy and physiology of the nervous system permit us to cast at least a few glances towards the barrier of "mind and body" (Adrian, 1947; Eccles, 1953; Lashley, 1950: 4; Penfield, 1947: 134; Penfield and Jasper, 1954).

"Consciousness" seems to be associated with high level activity of the cerebral cortex and diencephalon as revealed by the electroencephalogram. Concepts of a spatio-temporal pattern of neuronal activity and reorganization of neuronal associations of the cerebral cortex were formed to account for "memory" and the "uniqueness of percepts." These observations, puzzling as they are at the present time, still raise the hope that the gulf between "mind and matter" may be narrowed, and perhaps eventually bridged.

The autonomic nervous system provides another possible approach to the "mind-brain" problem. The significance of the response of autonomic nerves has evolved gradually from a regulator of bodily activities to an important, and extremely sensitive, mediator of emotions. To quote from Shakespeare's *Othello:*

> Give me your hand. This hand is moist, my lady.
> ....
> Hot, hot and moist. This hand of yours requires
> A sequester from liberty, fasting prayer,
> Much castigation, exercise devout;
> For here's a young and sweating devil here
> That commonly rebels.

And, as we persevere in comparative studies of the anatomy and physiology of the nervous system and attempt to correlate the result of these investigations with psychological phenomena in animals and man, we may attain a better comprehension of "what we are" by discovering "from where we came" and some day find ways of modifying our motivations and responses towards "social homeostasis."

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