Biological Order and Brain Organization

Selected Works of W. R. Hess

Edited by K. Akert

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Preface

The centennial of his birthday (17 March 1881) prompted the publication of the *Selected Works* of Walter Rudolf Hess. Although English translation of several of his monographs have appeared, none of his original papers has ever been published in the English language. During his scientific career, Hess made pioneering contributions in the field of hemodynamics, pyhsiological optics, oculomotor diagnostics, regulation of circulation, respiration and temperature, and finally on the somatomotor, visceral, and emotional functions of the diencephalon. His concepts concerning *organization and order in physiology* and his views on the important role of the vegetative nervous system in regulating the activity of the central nervous system are of great interest to science and medicine and were in many respects far in advance of his time. These concepts continue a line of thought which was upheld by such famous physiologists as Xavier Bichat, Claude Bernard, and Walter B. Cannon. Indeed, Walter Rudolf Hess has become one of the rare figures in the recent history of physiology willing to carry out an *integrative* analysis of bodily functions and to search for the basic principles of regulation and interaction between regulatory systems. In fact, he anticipated such ideas in biology as feedback control and servomechanisms long before these notions evolved in the field of engineering and electronics. In analyzing the organizational aspects of biomotricity in the central nervous system, he touched upon such concepts on the psychic level which are of considerable value to us today. He soon realized that his approach could bring him near the brink of teleology. This dilemma was most productive in that it forced him to clarify issues such as order and economy as the guiding principles of the functional organization of living organisms.

His concept of vegetative regulation led Hess to postulate that the vegetative innervation of internal organs has its functional and morphological counterpart in the brain. At that time there were few reliable data to confirm the view that the central nervous system and especially the cerebral cortex are innervated by a terminal network of unmyelinated fibers emanating from

brain stem neurons which secrete aminergic transmitter substances (see Chapt. 9, p. 155). Yet, Hess' neurophysiologic and neuropharmacologic experiments gave strong indication that the *Leistungsbereitschaft* of higher centers is subject to a regulatory control which resembles in every respect that exerted in the periphery by the *vegetative nervous system.*[1] The analysis beginning in 1962 with the histochemical method of Falck and Hillårp more than justified Hess' notion.

The two most important concrete problems concerned *sleep* and *motor organization*, the former as a paradigm of vegetative regulation and the latter as a paradigm of the animal (somatic sensorimotor) system. A thorough conceptual and experimental analysis of these two problems remained the themes of his life. It seems most significant that as a former ophthalmologist he would always return to eye functions to clarify the relevant problems.

The present selection is naturally somewhat arbitrary. It was our intention to expose the breadth of Hess' interest, and for this reason we have included papers which deal not only with "Brain and Behavior," but also with many other topics which occupied Hess' mind on his long march, such as Neurohumoral (Acetylcholine) Transmission at the Motor Endplate, Hering-Breuer Reflexes in Respiratory Control, Stereovision, and Hemodynamics. The thread that winds through his seemingly heterogeneous topics is the concept of "Biological Order" on the one hand, and that of the *Leistungs- und Erfolgsbezogene Physiologie*, on the other. Hess became aware of the role of biological order in his early work on hemodynamics, and he later recognized the same principle as the governing factor in motor coordination, psychic functions, and even in the behavior of human society.

The translation of his work was not an easy task. Hess himself was conscious of his heavy and rather involved German style and characterized this uneasiness when he mentioned his "constant struggle against a recalcitrant pen" in his autobiographical sketch (p. 309). Also, certain expressions which are important to his thinking are quite difficult to translate, because no equivalent terms are found in the English language. We quote two examples: *Leistungsbereitschaft* (readiness of performance) and *Leistungsfähigkeit* (ability to accomplish work). Led by the conviction that a compromise between the reader's comfort and the translator's conscience was inevitable – at least to some extent and in certain instances – we decided to translate the difficult passages in a liberal way. Fortunately, I was aided in this pro-

1 "Vegetative nervous system" is a term found mostly in the German literature and is preferable to the English expression "autonomic nervous system." "Autonomic" implies independence from higher and voluntary influences and is thus only partially correct. "Vegetative" refers to the functional goal

ject by competent and enthusiastic translators: Dr. Michael Bornstein, Miss Verena Bucher, Prof. Rudolf M. Hess and his wife Dr. Silvia Hess, Dr. Philip Levin, and Mr. Gilbert P. Michel, to all of whom I am deeply indebted. The translated manuscript went through at least three stages of revision and involved many vigorous discussions about the meaning of the original German text and the best way of expressing it in English. My colleagues and friends G. Baumgartner, H. R. Lüscher, and G. M. Yasargil were particularly involved at this stage. The final responsibility, especially for inadequacies which have undoubtedly remained in the text, rests with the editor. I was especially fortunate in being able to enlist the help of Hess' former staff member, Miss Verena Bucher, in this project. She was the morphological collaborator of Hess from 1929 until his retirement, and he credited her contribution by naming her as the coauthor of important original publications. Another former staff member, Max Jenny, head technican of Hess from 1926 until his retirement, generously offered his help by searching for the original illustrations (most of which had been prepared by himself) in the archives of the Physiology Department. This was all the more important because it allowed us to obtain in nearly all instances the highest possible fidelity in reproduction, especially of the halftone illustrations.

The most significant encouragement for this enterprise came from Hess' widow, Mrs. Louise Hess-Sandmeier, who kindly agreed to it and, at the age of 94, took an active and lively interest in the translator's work.

I wish to extend my thanks especially to my secretaries, Mrs. Hedi Hauser and Miss Barbara Meili for their most dedicated collaboration. The preparation of the final manuscript was aided by a videocomputer kindly put at our disposal by my friend, Dr. Alexander Guttmann, of Zurich. The bibliography was prepared by Mrs. Ruzena Biehal, librarian of the Physiological Institute, who suggested our undertaking this work and to whom we owe the first professionally prepared list of bibliographical references of Walter Rudolf Hess.

Finally, I would like to acknowledge the cooperation of the publishers: American Journal of Physiology (Bethesda), Johann Ambrosius Barth (Leipzig), S. Karger AG (Basel), Orell-Fuessli Verlag (Zurich), B. Schwabe (Basel), Schulthess Polygraphischer Verlag AG (Zurich), Springer-Verlag (Heidelberg). The University of Chicago Press (Chicago), and Churchill Livingstone (Edinburgh), who generously granted the copyright and the translation rights of the original articles which appeared in their journals.

A special word of thanks is due to Prof. Richard Jung, Freiburg im Breisgau, who assisted in the selection of the articles.

The translations would not have been possible without the financial aid that was kindly provided by grants from the pharmaceutical houses of

Sandoz, F. Hoffmann-La Roche, and Ciba-Geigy, Basel, as well as from the Zürcher Hochschulverein. We would like to express our sincere thanks to these institutions. Last but not least, the technical skills and generous assistance provided by Springer-Verlag, Heidelberg, are gratefully acknowledged.

Zurich, February 1981 KONRAD AKERT

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Chapter 1

Biological Order and Human Society*

W.R. Hess

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The topic of "war and peace" raises a wealth of questions which are related to the problem of *organization.* In fact, organization, in war as in peace, plays a unique and, in many respects, decisive role. Thus, the physiologist, for whom the *central problem of life* resides in the order governing the world of living organisms, is prompted to study human society from the point of view of biological organization. The first obvious question is whether there is any relation between the workings of the human organism and the principles underlying supraindividual systems of the human community. Two different facts should be remembered in this context.

In war and in peace, the acting and suffering element is *man* with all his needs and aspirations, his feelings and moods, his abilities and failings. The fact that these distinctly physiological characteristics also find expression when man lives or acts in a community means that the community has its roots, within certain bounds at least, in the physiological sphere and, hence, has a biological aspect. Furthermore, in the broader field of comparative physiology, supraindividual organizations, i.e., the formation of "states,"

* Hess, W.R.: Kollektive Ordnung in biologischem Aspekt. In: Festschrift Max Huber (Late President of the International Red Cross) – Vom Krieg und Frieden, pp. 151–172. Zürich: Schulthess 1944

are encountered, thereby confirming that collectivity is a general biological phenomenon. The decisive factor here is that the individual is integrated into a society according to definite laws and performs his functions within the framework of a larger unit.

Prerequisite of successful action is the adjustment of individual capacities to common achievements, established in the strive for preservation of the self and of the species. It necessarily follows that the individual is dependent on the whole, a relation which implies a certain contradiction. To overcome this inconsistency, forces which ensure coherence and deliberate cooperation must come into play.

An Example

Speaking of the queen bee in the bee colony implies the concept of the ruling of a central power and – considering the 100-million-year-old history, according to experts – the acknowledgment that the principle of collective order stood the test of time. It is most remarkable that the unique position of the queen bee is expressed in only one single productive achievement: she alone is capable of reproduction and hence is responsible for preserving the line of future generations. In other respects the queen bee is a helpless creature, in no way comparable to the workers and their invaluable abilities. It is also a fact that she does not regulate important activities of the bee colony. However, she fulfills a task of organization in which she is irreplaceable, in spite of individual qualities which, where they do not concern the reproductive sphere, are poorly developed. She keeps the swarm of workers together. A colony without a queen is restless and disorderly, and it easily falls prey to the rapacious appetites of neighboring colonies. It is only by virtue of the cohesive force emanating from the queen bee that the superior qualities of the worker can be concentrated in successful action and come into play, for example, in the delicate organization of food forage, brood care, heating, protection, and defense, as well as tasks of hygiene within the colony. This supraindividual organism is further distinguished by the bond between the individual and the whole which is developed to such a degree that all activity is carried out in *harmonious cooperation*, and rivalries are eliminated by conflict-resolving organizational measures. As a direct consequence, however, the individual has thus lost all freedom and merely functions as an instrument of the whole; his existence has become so dependent on the collective that he is unable to survive by himself for any length of time. Serving the collective has become the exclusive purpose of this life. The behavior of the individual bee is in keeping with these strong ties as soon as the colony is threatened. An extraordinary, active readiness for defense action is constantly present – action which in-

cludes the sacrifice of the individual life. The mode of fighting is organized in such a manner that the loss of its defensive instrument must cause the bee to perish. It is remarkable that the same eagerness to do battle and make sacrifices for the state is also seen in aggression against another colony. Militancy for the sake of preserving and developing collectivity is even more pronounced in certain species of ants which organize veritable predatory incursions and wage "wars."

In the context of the general topic, these remarks could be understood as indicating a direct parallel to human behavior. Although such a comparison is not far fetched, we would like to emphasize the disapproval of this way of thinking, which is rooted in the phenomenology of collective life. Accordingly, the willingness of the individual to make sacrifices on behalf of the collective should not be qualified anthropocentrically by the criteria of "good" and "evil." Objective evidence is available but for a certain form and degree of bonding between the individual and the collective, including some indications as to effects upon the parts, the whole and the environment. It marks ways and means to project biological principles onto the level of human collective life, an approach which will stand up to scientific criticism. This involves an abstraction of the facts inherent in collective life itself and of its underlying principles of organization. Both together constitute the essence of a *biological theory of order*.

Two Spheres

For any organism there is an inside and an outside. The physiologist is particularly aware of this fact when studying the phenomena of regulation. He observes how a group of organs is used to create and maintain inner conditions in such a way that every element of the collectivity – the cell in the cell state – encounters the necessary prerequisites not only for subsistence but also for carrying out certain functions.

This includes the supply of oxygen and nutrients essential for life and the removal of carbonic acid and of other waste products formed in the tissues. The entire complex of functions designed to regulate inner conditions is governed by a single organ known as the vegetative nervous system. It has its own mode of operation and functional laws and is largely – but not completely – independent. Still other aspects appear when we consider the human body as an *individual unit*. Its functional targets now lie in the environment: activities undertaken to acquire food, to protect the body (in the widest sense), and to propagate the race lead to interaction with the environment. Muscles are put to work for this purpose while the sensory organs give direction. The activities having such a specific purpose are organized by a control organ of particular characteristics and subject to partic-

ular laws: the so-called animal nervous system. Depending on the direction taken by the effects of the two regulatory organs, we speak of an internal or external front or, if you will, "ministry." Fundamentally, the facts are always the same.

Whereas the separation of the two systems was stressed so far in view of the separate target spheres of the regulatory functions, the equally important interrelations must now be emphasized. Here too, an invariable reciprocity exists for every form of collective life. To take an example from physiology, nourishment of the constituent elements of body tissue is only possible if the individual as a whole successfully strives for food. Expenditure of energy, needed for this purpose, in turn depends on sufficient nourishment of muscle tissue by means of internal regulation (including circulation with its well-balanced transport and distribution functions). These interrelations are largely *automatic*, i.e., they play freely. On the one hand, consumption of nutritive material in the tissues induces a feeling of hunger and searching for food. On the other, physical exertion increases those products of metabolism which activate respiration and circulation. This circular concatenation of functions is supplemented by a direct connection of the two regulatory systems, the vegetative and animal nervous system, thus refining their harmonization, especially regarding the temporal aspect.

Two Phases

The body, its organs, and their functional elements, the cells, alternate between phases of *work* and *rest*. In work, energy is generated (by the muscles), or specific substances are produced (by the glands). Rest is apparently defined by a negative criterion: the *absence* of activity. However, the true state of affairs is somewhat different. Rest too has its positive aspect. Expenditure of energy and of substances in the active phase is compensated by supplementary processes. In earlier times, physiology spoke of an assimilatory and a dissimilatory phase. Construction and decomposition were thus set against each other. Today we know that this antithesis does not reach the heart of the matter. "Decomposition" is not a function. It is more accurate to speak of a phase of activity and a phase of restitution, thereby stressing the *productive nature* of rest. The two phases are inextricably linked. Every activity requires the expenditure of nutritive substances and accordingly limits the time during which the activity can still be carried out. At the same pace, restitutive processes take on urgency in order to prevent exhaustion and its catastrophic consequences. Building up new reserves ensures proficiency in the future. Ready reserves are thus identical with potential activity.

Even though the interlinked phases are strictly separated as to functional aim and orientation, their timing may overlap and become intertwined. However, in the periodic alternation of waking and sleeping, there does exist a clear distinction with regard to time.

The quantitative relations between activity (and consumption) and restitution can be represented as a profit and loss account for the matter and energy metabolism of our body. The balance yields the material basis of existence and further development, since all organic life is aimed at outgrowing the level of mere subsistence. A powerful drive for expansion is a feature inherent to all forms of life, expressed in the fact that the species' laws of order are imprinted on assimilated matter and on the energy bound to it. Growth and propagation are named as primary phenomena of life, and they are realized by a surplus-producing metabolism. Of course, the extent to which the vital drive for expansion can be deployed is dependent on the environment, in particular on the presence of other systems which are asserting themselves and their further development.

An interesting insight into these conditions is gained when, due to particular circumstances, the account shows a deficit which eventually turns into an emergency situation. First and foremost, the situation of stress acts as a stimulus for increased efforts to acquire food. If external circumstances are so unfavorable that the effort fails, the organism turns to other tactics. As soon as the reserves are exhausted, it starts to live on its own substance, which normally is required in carrying on active life. Naturally, this gives the signal for the rapidly accelerating loss of performance. Yet the body is exploiting this one last chance to defer final collapse, death from hunger, and to pull through to a possibly better time. It is remarkable that even in the emergency preceding collapse there is no disorganization. On the contrary. The way the body confronts hunger is characterized by typically prospective measures. It might be supposed that organs continually under stress in times of hunger would be quickly worn out. In reality, however, the organs that sacrifice their substance for the whole are those which remain inactive in the crisis. For example, even after a long period of hunger, the heart muscle has lost very little weight, whereas the skeletal muscles have lost a great deal. The central nervous system too is spared to a large degree. In the course of these economy measures, unequal organs are not treated equally; rather, substance is consumed in keeping with *the organ's value*. The criterion is its importance for the preservation of the whole. This stretches the period of endurance, thereby increasing the chances of survival until conditions have improved. The success of such an emergency organization far exceeds all expectations. Not a few people believe they are "starving" if they have to miss one meal. In fact, man can survive for a long time, depending, of course, on his constitution and the strain which he is undergoing. If the body is at rest, periods of hunger of 2 months and, under

certain circumstances up to 3 months, have been confirmed. Conditions of relative hunger can be endured for years, of course not without a loss of performance and a gradual decrease in physical and psychic resistance. A similar evaluation of individuals or groups of individuals has been adopted in food rationing in the context of the supraindividual collectivity of our people. However, insofar as it is based on professional categories, rationing employs exclusively causal and not prospective criteria. Nonetheless, there are cases where prospective argumentation does come into play: pregnant women and young people. Here, the higher insight of prospective organization agrees with human feelings. The link of the individual element to the collectivity is not strong enough. Otherwise, there is in this respect an enormous quantitative difference between man as an individual and man as a member of the community. With increasing emergency, however, other forces intervene, which, more and more, shift the weight on the unit as a part of the whole. A glance at those countries waging war confirms the experience that with suitable organization the capacity for endurance of the whole exceeds by far what would ever be expected, judging from peace-time conditions.

Principle of Efficiency and Economy

A direct consequence of the transition from individual to collective life is the onset of a process of differentiation. In its most elementary form it is expressed in the spatial relations of the parts within the whole. At a higher level, an increasing inner differentiation of the individual elements enables them to perform specific achievements. Here is the place to define the concept of efficiency (*Leistungsfähigkeit*). Physiology usually speaks of function. It is of utmost importance for the organism that its functioning is successful, that it produces a result from which the organism benefits in some way or other. However, performance, in the physiological sense, has its full value only when realized in a certain time span. Performance is the decisive factor which, in terms of quality and quantity, positively influences the organism's prospects for existence and "rewards" it with easier conditions of life. If efficiency is the fundamental prerequisite for survival, the second condition is the more or less complete realization of the principle of economy. The optimal physiological achievement is carried out with the minimum expenditure of matter and energy. An impressive example is the peculiar arrangement of the trabecula in the head of the femur, discovered in 1867 by a Zurich anatomist (H. Meyer) in collaboration with a professor at the Polytechnical College (Culmann). The requisite load-bearing capacity of this supportive apparatus is achieved by a system of inner braces in such a manner that there is a minimum expenditure of supportive substance.