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The General Nature of Biological Explanations

In dealing with objects of our research whose explanation from the standpoint of present-day sciences is insufficient, greater scientific clarity is achieved by fully realizing what cannot be explained than by stealing a march on science with suppositions. We cannot reach farther than to understand what can be understood and realize what we cannot understand. (*The Autobiography of Berzelius*.)[1]

Physics and Biology

The degree of satisfaction that a biologist derives from his explanations depends not only on their completeness and neatness and the terms in which they are couched but also on the preferences and interests of the person. There are those whose appreciation is reserved for mathematical, physical, or chemical explanations, all of which signify that an attempt has been made to incorporate new results or conclusions with a structure of known rules and relations, the great edifice of those sciences. Others are more interested in trying to expand their science by developing a structure of a different kind, one that is exclusively biological, concerned with interpretations of a very different order, aimed at understanding organisms in relation to their environment. All of us are in the end fated to beat our heads against a wall. The sign on it is *ignorabimus*, "we shall never know." My point is merely that the structure of the wall we find in our way also depends on the head that beats it.

Physics at this impenetrable barrier, starting as all sciences from the contents of our sensory messages, has overcome their narrow limits with the aid of the mathematical instrument. In doing so, it has lost in pictorial directness while gaining in precision. Physics cannot explain the magnitudes of the two great and all-important constants, the quantum (h) and the velocity of light (c). It does not understand the nature of gravitational and magnetic forces, to mention but a few examples. The triumphal progress of physics depends on understanding the relations between mathematically defined concepts and units. With their aid it has created an understandable world when faced with the challenge of harmonizing science and reality.

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It is not my intention to deal at any length with the nature of physicochemical explanations. The physicists and chemists have provided us with a host of learned treatises and popular writings. One point I want to emphasize—because it is equally valid for physiology—is that the insight laid down in the concepts and formulas of modern physics in the end is subject to the rigorous test of applicability. The most famous example is Einstein's equation relating energy and mass, $E = mc^2$, which led to the design of atomic piles and of the atomic bomb.

Berzelius's remark implies that one is obliged to arrive at an understanding of what is meant by speaking of explanations. This means to be able to define the terms in which one expresses one's insight. Berzelius—at the beginning of the last century—knew only physicochemical explanations, and what the word meant to him is clear. It signified causalities (relations) found by experimentation, the broad royal road of natural science of the day. Now, after 150 years, many new biological sciences have arisen: physiology, genetics, psychology, and many others. At one time or another many of them have raised hopes of novel kinds of explanations revolutionizing our understanding of living things. A great humanist such as Ernest Renan thought that the then new science of physiology would provide answers to the question of the essence of life, and the many expectations based on the concept of evolution, from Spencer onward, hardly require any further comments. At the moment the geneticists are in the limelight; among them there are those who think that they know the secrets of evolutionary development well enough—"wie es eigentlich gewesen ist"*—to be ready to undertake controlling the fu-

*The well-known postulate of Mommsen that history should explain "what it really was like."

ture of our species despite the fact that all leading workers in this field admit that the course of evolution is unpredictable.

The physicochemical line of approach is often unassailable and also plays a major part in biology. Crick has stated this standpoint in the following manner: "Eventually one may hope to have the whole of biology 'explained' in terms of the level below it, and so on right down to the atomic level. . . . So far everything we have found can be 'explained' without effort in terms of the standard bonds of chemistry—the homopolar chemical bond, the van der Waal attraction between non-bonded atoms, the all-important hydrogen bonds, and so on."[2]

Crick has put the word "explained" within quotation marks, but what is it he has said, with or without them? Essentially that he, like most of us, has been educated to employ the explanatory chemical or physical terms current in his field of research, and that he, again like most of us, can reach far down into the microworld by using them. When following the physicochemical approach in biology we are "walking in our mother's street"—to use a Swedish expression. We get the replies to our questions in terms we have been taught to employ and regard as correct. No quotation marks are needed for the word explanation. Everything is in order and all of us agree on principles.

Some of us may feel a little apprehensive of extravagant claims based on the notion that the "molecular" mode of questioning necessarily is the one most important and most likely to reveal more than any other approach to biological problems. The student of the central nervous system, for instance, is faced with many fundamental questions at a very different level of interpretation. This is what I shall deal with in these essays.

Quite generally it can be said that the gain in knowledge, as one penetrates into the microworld, is accompanied by losses at other levels of understanding. For example, twenty years of experimentation have provided us with important and quite detailed knowledge about the chemical and physical events at single contact points between neurons, the synapses; the new facts concern the mode of transmission of nerve impulses from one neuron to the next. Yet all these very important facts represent but a minute fraction of the knowledge we need to understand how one makes a gesture with the hand or interprets a complex visual image.

This situation in biology is commonly understood and in recent years often emphasized, especially by Paul Weiss, who in several books has pointed out the one-sidedness of what is often called a "reductionist" attitude to biology.[3] Weiss has given numerous well-chosen examples of the significance of hierarchical order at the cellular level (see also Hughlings Jackson).[4] This problem turns up with different aspects to physicists among our contemporaries. One way of stating the physicist view is that "complex aggregates of matter generate their own new laws" (Philip Anderson),[5] and Platt[6] has listed the new properties that follow with an increase of complexity of molecules forming lengthening polyatomic chains. Or one might point out that in deriving the gas law by statistical considerations based on the movements of molecules possessing three degrees of freedom, it is not only unknown but also utterly irrelevant how an individual molecule actually has behaved. There is a pragmatic side to science teaching us what can be safely left out. And so it follows that the "machinery" operating nervous transmission at a synapse, while always required to do its job, may or may not turn out to be of much interest for attempts at understanding our upright stance, communication, or visual imagery.

It is in the macroworld of hierarchically organized systems that the biologist must find another set of independent explanations, try to understand what he wants to explain, and explain what he thinks he has understood. There are those who believe that the science called "cybernetics" provides us with the theoretical structure needed for understanding the central nervous system. I shall deal with this assumption in Chapter 10 and explain why I refuse to become a proselyte to this creed, though acknowledging its usefulness along with other approaches to the physiology of nervous events.

Purposiveness in Evolution

In looking for principles, one should begin with some references to what is known about the evolution of beings who have to eat, reproduce, defend themselves, and communicate—things that no physicist need be concerned about. In this field of inquiry one known general principle has universal validity, the idea of natural selection producing adaptations to these challenges of the environment. So important is this principle that by its aid the incisive discovery of the code by which genes are reduplicated, for which Crick, Watson, and Wilkins received the Nobel Prize in 1962, is elevated to a higher level of significance than it could have reached as an isolated discovery.[7] As it is, the mechanism plays a fundamental role in the structural totality of evolutionary theory as a stable factor in the stochastic game Nature keeps playing with our some 40,000 genes.

Zoologists prefer the term "directiveness" in speaking of evolution. They hesitate to use the term "purposiveness" because they feel that "purpose" implies "striving after a future goal retained as some kind of image or idea" (Pantin).[8] Mayr proposes the term "teleonomic purposiveness" (after Pittendrigh) to underline the basic contention of the synthetic evolutionary theory that purposeful adaptations are produced by natural selection operating in a population on the phenotype to test the genetic supply.[9] Recently Monod has used the term "teleonomie."[10] I am quite satisfied with "purposiveness" because, as we shall see, many nervous acts definitely have a purpose but otherwise vary in nature from automatism to definite conscious awareness of what is supposed to be achieved. In considering the central nervous system, the essential point is not that one need be aware of the goal but that the act as such is purposive. The classic term is "teleological interpretation" and I intend to stick to it. It means the kind of interpretation in which "why" is a relevant question alongside the "how" of classic natural science.[11] I shall return to a differentiation of this concept from its evolutionary counterpart in Chapter 2.

Darwin began his analysis of the material collected on his journey in the *Beagle* by studying how skillful breeders produced new strains of animals and plants by selection.[12] In these efforts the purpose of the selecting was more or less clearly defined. When later he understood that Nature did something similar by natural selection, this, too, served a purpose, that of producing and retaining traits favorable for survival. In this century we have seen Mendel's rediscovered experimental approach to heredity lead to a definition of the gene, to experimental demonstrations of mutation, recombination, and other processes within the gene pool of a population as a basis for the emergence of novelty, and to the mathematical development of population genetics as a kind of explanation of how purposiveness is achieved. No doubt a key has been found to one of the many doors locking the entry into full understanding of how useful novelties are stamped in. The evolutionary theory offers the outsider a curious Janus face: on the one hand chance is blind in creating mutations; on the other the test for survival of a trait is its purposive adaptation to the environment. By this it is related to and tested in the outside world. As stated, the mechanism of testing is exerted on the phenotype that is embodying the net result of interacting genetic instructions. Because these are polygenetically determined in the sense that genes influence several "characters," it is difficult to reach final conclusions with specific applications.

However, let us take one thing at a time and consider purposiveness as a scientific explanation of an adaptation. One of the oldest and best known examples is industrial melanism, the augmentation of dark relative to light varieties of some species of moths in the sooty districts of Birmingham and Manchester.[13] Against the black trees the light moths have fallen an easy prey to the birds while the dark ones have had a better chance of survival. This development in the moths has been followed since 1850. I am told by experts that recent control of air pollution has led to reappearance of the light forms. This classic example fits the theory: the gene concerned can produce dark and light varieties of moths. At least in one species the dark varieties are believed to be more vigorous; the light ones in normal circumstances compensate by their protective coloring. Then, as *deus ex machina*, enters man and debases the value of the camouflage of the light moths by removing its purpose. The dark variety of the gene now provides the better match to the environment. The dark moths survive because of their double fitness: they are better fitted or adapted to the environment and produce more numerous offspring (fitness in the genetic sense).

Before anything was known about the genome as the substrate of heredity, an observer of the moths in their environment could invoke natural selection by itself as an explanation of *why* the light forms disappeared. Knowledge of the Mendelian gene was required to explain *how* the mechanism of the color shift operated. On the other hand, without the initial why question there would have been no real understanding of what had happened.

We shall find the latter type of teleological explanation permeating the explanations of responses of the central nervous system. This structure, after all, is Nature's greatest invention for enabling organisms to deal competently with their environment. We cannot imagine a nervous system without a purpose, much as we tend to neglect purposiveness when studying the hardware of chemical and physical events that are the means of realizing this goal. "Purpose" in our present context, like natural selection in evolution, is neither chemical nor physical. It is a point of view, like relativity or quantum mechanics. Such ideas belong to the architecture of understanding rather than to the analyzable material of the edifice of experimental science. They explain something and they have practical consequences. Because "purposiveness" belongs to a category of thinking that deals with biological organisms in their relation to the environment, it is by definition part of the domain of biology.

If we decide to switch from why questions to how questions, we move into the realm of purely causal explanations. These are often usefully predictive. If we know a causal chain $a - b$ we also know that b presupposes a. The universal appeal of rigid causal or statistically valid explanations stems largely from the fact that predictability is essential for control and thus for technical developments. Teleological explanations are often held to be unscientific because they so easily fail to be usefully predictive. I shall take up this question in Chapter 2. In the last instance our attitude to these problems also depends on how one wants to define "scientific understanding." I would think it unjustified to call the synthetic theory of evolution unscientific because of its very obvious deficiencies when it comes to prediction. It embodies deep insight into Nature's secrets and will live with us into the future.

On the other hand, the explanatory value of such a general notion as purposiveness in natural selection should not be overemphasized. Many developments cannot be satisfactorily understood on these lines. Even in the case of melanism, it is not known how a gene capable of producing two colorings has turned up, so to speak, in anticipation of changes in the luminosity of the environment. We can, of course, invent a teleological explanation for it, but even in this science of hindsight there is a limit beyond which it is better to admit that we simply do not know. Geneticists admit this by speaking of "open" genetic instructions, polymorphism, and polygenetically determined characters.[14] Another limit is set by the elements of chance and time, which together have played their roles in environments whose nature we can but vaguely conceive by interpreting geological and paleontological evidence. In addition there must be fundamental unknown factors, some of which will be discovered in due course. The relatively new gene multiplication process is likely to become very important.

There is a serendipitous trait in Nature (open instructions!). Something is begun somewhere in the phylum and after some millions of years is found to be useful for something else. Lucretius (in Chapter 4, *De rerum natura*) pointed out that the tasting tongue preceded speech. The dog uses it for removing superfluous heat from the body. Even in monkeys and apes control of the tongue by mechanisms in the brain has not yet led to the elaboration of speech—excluded also for purely anatomical reasons. These are difficulties, which make one suspect that positive factors concerned with labeling, marking, or "stamping-in" are neglected in evolutionary theory. Such difficulties are well illustrated by what is thought about the transformations of the acousticolateral organ in the evolution of hearing. And with this example I am embarking on my main theme, the central nervous system.[15]

Tufts of hair (cilia) on the skin of very primitive fish are mechanoreceptors likely to respond to vibration. At an early stage these ciliated organs are found enclosed in the lateral line, a kind of tube running superficially enough to be often visible. It extends from the tail to the head. Within the lateral line the cilia still occur in groups, but their free ends are now stuck into a gelatinous mass forming a cupula that swings with the movement of the fluid inside the canal. The cilia are of two kinds, kinocilia and stereocilia. In the lateral canal they still possess vibratory sensitivity, but now the location of the larger and thicker kinocilia toward the head or the tail end of each group provides the fish with directional sensitivity to the flow of fluid in the canal, which can be shown by recording from their nerve fibers. There is excitation, that is, discharge of impulses, when the fluid moves toward a kinocilium and inhibition of the impulse flow to movement of that kinocilium in the opposite direction. We must further assume that there has been parallel development of sense organs, sensory nerves, and projections of these nerves to the fish's brain to make these structural transformations useful.

Another step in the evolution of the acousticolateral organ has taken place in fish. The canals on the head have in part migrated into the bony structure, where they have bent round to form three semicircular organs ending in an ampulla. The canals are found to be orientated in the three planes of space. All kinocilia are now in the ampulla, still with their free ends stuck into a gelatinous cupula. The whole system is closed so that the fluid, set in motion by acceleration, will bend the swing-door cupula. Movement toward the ampulla is excitatory; away from it, inhibitory. Thus has been created a sense organ, the familiar vestibularis, responding to angular acceleration in the three planes. This structure is retained in all vertebrates from fish upward; basically it regulates postural movements.

Other portions of the lateral line have formed closed sacs, known in fish as sacculus, utriculus, and lagena. The cupula there has changed into a membrane loaded with crystals, the large conglomerates easily seen in fish called "otoliths." The loaded membrane touching the hairs responds to gravity and so records the position of the head. The cilia have retained their original sensitivity to vibration.

Sacculus and utriculus are carried over to terrestrial animals with only slight modifications, but the third sac, the lagena, begins to wind itself into a spiral in snakes. This line of development is completed in birds and mammals, and the structure is now helical. We know it well as the cochlea, containing the organ of hearing, still employing the principle of hair cells touching a membrane, but it rides on another membrane, the basilaris, which the sound waves influence through the well-known structures of the ear. The lateral line has become superfluous on land, but the vibratory sensitivity of the original tufts of hair is now utilized to place the world of sound at our disposal. This they do at the extraordinary sensitivity for vibratory amplitudes of the order of the diameter of the hydrogen atom.

Again, all this would have been useless without a parallel development of the structures in the brain dealing with the interpretation of these highly differentiated messages. And again we must admit that though all these developments are obviously purposive in their coordination, there is no real understanding of how they have been labeled for interconnection and timed to develop with some degree of synchronization. At this level of precise questioning the synthetic evolutionary theory delivers its answers in the form of postulates.

Even purposiveness begins to look questionable when we think of musicality and musical creativity as the end product of the development of the tufts of hair on the skin of a primitive fish. There is no explanation of the talent that made possible the creation of the Ninth Symphony or the *Marriage of Figaro*. Why has musical creativity turned up at such high levels of excellence? A possible answer is that this talent has proved harmless in the process of natural selection and so has escaped annihilation. We can, of course, supplement this with a number of postulates such as that musicality is polygenetically determined in happy symbiosis with some more useful characters. But in the absence of an unequivocal genetical explanation of musicality, one is obliged to confess to a great deal of ignorance because musical creativity is but one of many similar apparently useless talents. This underlines the words of Berzelius: "We cannot reach farther than to understand what can be understood and realize what we cannot understand."

Thus, to sum up, a teleological explanation facilitates understanding of the origin or existence of some evolutionary changes (adaptations). There are others, indeed, some of the most significant ones, whose interpretation cannot be significantly advanced by teleological arguments. It seems likely that purposiveness has played its role whichever evolutionary change is under consideration, but at a certain level of complexity application of this principle is of little avail to the inquiring mind. We are forced to begin with a large blank check on chance.

The Biological Approach

Purely biological understanding in the sense that the explanations arrived at employ neither physics nor chemistry can lead to insights as penetrating as those of the latter sciences. For biology, medicine may play the role that engineering plays for physics and chemistry, that of providing a touchstone for the conclusions drawn. A case in point is the role of the *Anopheles* mosquito in the transmission of malaria.[16] Another example is the cure of contagious disease. For some 200 years immunology has had triumph after triumph, curing such diseases despite its ignorance about the chemical mechanisms involved. A number of gifted people by accurate experimentation established the rules governing the defense reactions of the body and tested them in experimental and medical praxis. A chemical solution of the problem of specificity of antibodies has been reached today, but Jenner, Pasteur, Behring, Ehrlich, and many others did well without it; they gave the science of immunology its form and content and discovered the specificities of the antibodies that present-day immunochemistry is engaged in explaining (the 1972 Nobel Prize in medicine given to Gerald Edelman and Rodney Porter).[17] The same may be said about the many discoveries concerning the action of hormones. Their effects regarded as rules based on accurate observations were mostly described by purely physiological experimentation long before it became possible to isolate them chemically. In both examples discovery and understanding belonged to the realm of pure biology. The ultimate chemical work of isolating and purifying hormones was then taken over by the chemist who, without the insight acquired by biological experimentation directed by physiologists with their why questions, would never have realized that there was a problem to which he could contribute by his particular methods.

It is quite typical of experimental biology at its best that it creates basic concepts of its own, such as that of a mechanism in some small lymph cells capable of developing highly specific antibodies, and that it then proceeds to close in on the subject by whatever methods are available. Any odd observation may serve as a starting point. The Western world first learned in 1722 from Lady Mary Wortley Montagu[18] of the inoculation against smallpox at the court of the Turkish sultan, long before Jenner started vaccination at the end of that century. The next great development, bacteriology, found its major tool in the microscope. And then followed microchemistry and electron microscopy, leading to isolation and crystallization of virus particles and to the discovery of the role of the gamma globulins in antigen formation.

However, it is not my intention to discuss immunology beyond using it as one example of a conceptual independence in biology capable of standing tests of application as rigorous as that of saving the threatened lives of intricate mammalian organisms including man. Similar issues are raised by the physiology of the hormones. In both cases the responses observed are purposive, but, so to speak, purposive as a matter of course without the teleological viewpoint necessarily much in evidence in the experimental analyses. The questions—like those in physics and chemistry—have dealt with how rather than with why certain experimental observations should be interconnected. In the case of the melanism of the moths, the why of this change of pigmentation proved to be an essential link in its interpretation. Some examples will show that the latter type of teleological understanding plays a similarly creative role in experimental studies of the nervous system, the organ par excellence for dealing purposively with the environment.

Particularly instructive from this point of view are the findings by von Frisch on the compass of the honeybee.[19] In neurological research we often enter the nervous system by way of a sense organ, just as von Frisch did when he showed that the eye of the bee is sensitive to polarized light. We have been taught that light is a wave motion traveling at high velocity in a straight line. Uninterfered with, the waves have no specific orientation around the beam but swing in all directions. By a Nicol prism or a polarizing film the waves can be forced to oscillate in a single plane and the light is then said to be polarized in that, for instance, vertical or horizontal plane. Our eyes do not recognize this. But if a second polarizing prism or film is inserted as a detector into the light beam, it will let through all the light, whose plane of polarization coincides with that of the first polarizer, and nothing at all if turned to polarize at right angles to the latter. Thus an eye can detect the degree of polarization of a light beam by transforming it into degrees of brightness.

The eye of the bee consists of a large number of units, each of which is radially surrounded by eight sensory cells. These cells are differentially polarized to be detectors of different planes of polarization. Because sunlight reflected from the blue sky is naturally polarized, the bee has at its disposal a map of the sky by which to adjust its angle of flight. Only part of the sky must be visible. By defining the nature of the sensory instrument used by the bee for orientation, von Frisch had solved a characteristic biological how problem. The next step would have been an intricate piece of neurophysiological analysis: how does the animal manage to keep the angle of flight constant relative to the visual image selected? General solutions of this problem could be suggested, but von Frisch's intuition took him on another course.

The bees were marked and could be observed through the vertical glass wall of an observation hive. There he saw the returning bees execute a special kind of patterned dance (*Schwänzeltanz*) in two semicircles whose common diagonal always was danced in the same direction, which indicated the direction of the source of honey to other inmates of the hive. The speed at which this pattern was danced indicated the distance to the source. At 100 m the straight, diagonal portion of the ring dance was repeated 9 to 10 times in 15 minutes, at 1,000 m 4 to 5 times and at 5,000 m only twice in 15 minutes. Needless to say, this is only one cue among others based on color sensitivity and smell. Most interesting is the fact that the dance often was carried out at the vertical plane of the hive so that the learning bees had to transpose this message of information to their own horizontal plane of operation.

Much has been left out in this schematic presentation of the solution of a problem of orientation and communication in an insect. But what has been said should illustrate a very high level of purposive behavior, based on the properties of a measuring instrument (a sense organ) and a cellular organization (a brain) of modest bulk compared with our own, yet capable of inventing and understanding a difficult piece of geodetic geometry, of applying it in the service of communication, and of operating a motor apparatus to its specifications. Questions of how and why have been characteristically intermingled in this work. How is it that the bee can respond to what looks like being a reaction to polarized light? Why do some bees dance in this curious fashion on the wall of the hive? What is its purpose?

The why question is tabooed in physical science but here again it is shown to be decisive in experimental biology, which after all deals with beings that—as I said—have to eat, reproduce, and defend themselves by purposive responses to such challenges. For these reasons replies to why questions may often elevate a trivial observation to the rank of an important scientific generalization. In the present case the *Schwänzeltanz* might well have become one of the innumerable forgotten contributions to the roomy shelf of curios in biology had not von Frisch attempted to unmask its purpose. This made his work a fascinating study of the general problem of communication.

Elsewhere I have given other examples illustrating my thesis. For instance, when rods and cones were discovered in the vertebrate retina, had it not become evident that rods dominated in retinas of night animals and cones in those of daylight animals (Schultze, 1871),[20] this discovery would have remained an observation of but limited consequence. Instead, understanding of its meaning (why) made it a cornerstone in a large body of biological research dealing with the adaptation of the eye to light and darkness, rod vision and cone vision, and the rod-free central fovea of the human retina.

"Getting used to the dark," asked Craik, "is it physics, chemistry, or physiology?"[21] One could add psychology to the rest. The reply is that it is one of the many problems of a biological science that by nature is eclectic and has solutions at several levels of understanding. We have seen that there are replies to Craik's question at the level of anatomy, including its microscopic approaches. It strikes us as a photochemical problem when we realize (with Boll and Kühne in the last century) that the rods contain a highly light-sensitive pigment, rhodopsin, for vision at dawn and dusk.[22] Its spectral distribution of sensitivity is known and has been measured several times. This requires a photocell and introduces a little quantum physics because light is absorbed in quanta within the pigment. There are purely chemical problems involved in the process of bleaching of rhodopsin by light and its regeneration in the dark. The physiologist traces the curve of its spectral sensitivity by electrical recording of the magnitude of messages at several cell stations on the way to the brain. Finally the psychologist, employing a conscious "photocell," measures the same curve as a distribution of perceived spectral brightness, using, for instance, the absolute threshold of vision as his index.

It is interesting that the photochemist, the physiologist, and the psychologist all really do obtain the same curve representing the spectral distribution of sensitivity of rhodopsin. When by the middle of the last century psychophysics was developed as a science, scientists used to speak of "psychophysical parallelism." Although this is well represented by the present case, it is not generally demonstrable because sensory information mostly reaches the perceptual stage in a highly edited version. For this reason the old term has gone out of fashion. Physiologists are nowadays more interested in the mechanisms of editing than in the cases for which real parallelism can be found. When it is as well documented as rhodopsin, it is also a perfect example of a biological explanation that is complete in itself, combining in its tripartite way replies to questions from the physical, physiological, and psychological sciences. This synthetic statement means that something fundamental has been understood. From this knowledge as a *point d'appui*, one can go on "vertically" (Weaver)[23] to greater depths of insight into the special mechanisms underlying the light sensitivity of the rods (photochemical, chemical, neural, organizational).

The original question of why there are rods and cones in the retina ramified into several directions that in one way or another are concerned with the differences between daylight and night vision. I shall only mention the fact that rods and cones are connected to vertical and transverse layers of neurons in the retina, which as a structure may be regarded as an outlying little nervous center of its own. The message dispatched to the visual cortical areas in the brain is therefore highly organized, and in getting used to the dark a neural reorganization takes place, slowing down differentiation velocity of its responses by making the retina more capable of summing up the effect of quantum catches within larger excitatory units than those employed in daylight. Many hundred rods may be connected to the same nerve fiber and in addition interconnected in the retina.

This example is our first encounter with the fundamental problem of organization in the neurosciences. I shall return to it with more attention to detail in different connections. This particular problem presented itself in terms of anatomy and physiology with repercussions in psychology. Physics and chemistry have provided important tools in its analysis, but the final understanding we seek is couched in different terms and teleological points of view are an essential part of it.

In his books Paul Weiss refers to specificity and organization as two major unsolved problems in biology.[3] The former was exemplified with immunology in which today science is closer to a solution than anywhere else. We shall encounter both problems also in the physiology of the nervous system. Weiss discusses organization from the standpoint of cell biology, whereas I will consider it in relation to our endeavor to understand the mode of operation of the central nervous system.

Concluding Remarks

Inasmuch as science is the art of acquiring knowledge in such a manner that coherent structures of understanding can be erected on the basis of a critical evaluation of evidence, the biological sciences can point to many achievements of the first order. One often encounters the implicit notion that the ultimate aim of biology must be to explain its findings in terms of physics or chemistry. By discussing relevant examples, I have tried to show that such explanations indeed are important but may be so without ever touching fundamental questions concerning living organisms in their relation to the environment. Impulses, for instance, are alike in all sensory nerve fibers and their genesis is reasonably well understood in physicochemical terms, yet this knowledge does not help us very much to understand their different effects on the senses.

Biology is, as I have emphasized, an eclectic science, aided in seeking structural knowledge by results at different levels of understanding. Anatomy is always in the background, providing keys of its own for understanding organized responses discovered by physiological work. The machinery may be satisfactorily understood as a physiological entity, yet the elements of which it is composed need be and often can be described individually by, say, chemistry and microscopical anatomy joining forces. In this way structures of biological knowledge are created, such as systems of hormones holding the secretion of one another in check by neural secretory or vascular mechanisms. There are hormones whose individual chemical composition and enzymatic control of specific activities are known in great detail. A hormone may in addition have definite psychological effects on the emotional state of an animal. Whatever contributes to the understanding of such organized systems or structures, most of which have to deal with a repertoire of many tasks, parallel and in series, also contributes to the completion of the biological explanation, whereas any one of the partial explanations may be of only modest interest as an isolated fact. In this way biology with its different levels of understanding ultimately emerges as a synthetic science trying to create coherent structural knowledge by interpreting the integrated effects of interacting components.