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.

# 2
# Purpose, Chance, and Causality

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Every science that is a science will always have to develop its own peculiar and powerful methods of inference and methods of organizing and structuring its field. It cannot abdicate the search for its own rules and its own symbolic representations of its own empirical conclusions, just on the prospect that, with infinitely elaborate computations and great mathematical insight to pluck out the results, it might some day be quantitatively derivable from some more fundamental discipline. (*J. R. Platt,* Properties of large molecules that go beyond the properties of their chemical subgroups, *J. Theoret. Biol.,* [1961]: 342–358.)

From now on I shall not be concerned with the teleological (or teleonomic) explanations of the adaptations which natural selection is supposed to have created in the manner briefly alluded to in the previous chapter. Knowledge and hypotheses in this field have been well summarized in an array of books and papers (Waddington, Mayr, Dobzhansky).[24] Because no better explanation is available than the synthetic theory of the geneticists, I am resigned to an attitude of mild scepticism as to the completeness of its coverage of matters requiring explanations. Admiring their efforts, I shall regard adaptations as established facts and proceed to consider a different aspect of teleology, one we meet in the central nervous system.

In this field the essential questions of physiologists and psychologists tend to concern a related, yet different concept, that of *adaptability*. This is the glorious climax of evolution: to have created a purposive brain with an incredible degree of adaptability as yet by no means fully explored. The concept of adaptation refers to something else; animals are adapted to heat or cold, to respond to polarized light, to swim, to fly, or to feed on grass, but adaptability shows how perfectly and within what limits the various adaptations operate. Many physiological mechanisms have been drawn into the service of adaptability and these have, partly at least, been the subject of study. We shall be concerned with the manner in which adaptability is organized by the neurons and their synaptic network, how it is reflected in cognition, voluntary movement, sensory interpretation, and posture—in short, with the whole machinery as it serves us in our purposive interactions with the environment. The term purposiveness now acquires a different connotation, liberated as it is from the kind of teleonomic



directiveness produced by natural selection modifying a genetic code of instructions.

In the previous chapter it was pointed out that why questions could lead us to discovering adaptations which otherwise might have gone undiscovered or have been regarded as irrelevant curiosities. Such questions also play a role for adaptabilities, but in studying them we go a step further and unashamedly mix how questions with why questions, realizing that mechanisms serving adaptability never can be dissociated from the purpose to which they are adjusted. For this, some relations between purpose, chance, and causality need to be considered.

**Purpose, Causality, and Chance**

The perfect instrument for realizing adaptability is obviously consciousness, but a large number of automatic adjustments to the environment are also eminently purposeful, and their unexpected consequences may fill us with wonder or even surprise. An example will be given in Chapter 3.

In all cases purposiveness implies anticipation of preferred alternatives in dealing with environmental variables. Clearly, therefore, teleological operations aim at becoming predictive, which is another way of stating that they depend on an evaluation of environmental causes. Everything cannot be predicted in detail, but the brain has chosen a heuristic solution out of this dilemma. It has developed an incredibly large number of possible ways of responding purposively to the environmental variables. The final choice between them is left dependent on prevailing circumstances. More often than not the choice is a wholly automatic process.

This may seem surprising, but the best analogy there is to brain function is obtained from a comparison with the immune system (Jerne, 1973)[25] and uses a similar procedure. The small B-lymphocytes (cells), rather than specializing on certain common diseases, generate an extraordinary number of antibodies. Specialization would have led to a fixed rather than an adaptable adaptation. The latter goal is achieved by the existence of random chemical specificities for pattern recognition, enough to match antibodies to most of the inimical epitopes (small patches on the surface of a protein molecule) that are likely to occur. These fits are remembered by the system, and we know them as immunities for the agents that provoked them (when these attacks referred to diagnosed diseases). In this manner the immune system responds adequately to an enormous variety of signals it learns from experience and remembers the lessons taught by foreign agents. The analogy with it can be carried still further: antibodies may cause excitation or inhibition and the cells of the immunosystem both receive and transmit signals.

If this analogy with the immune system is to be valid, there must be comparable elements of chance by multiplication of possibilities in the brain or else we would actually be the mechanical automaton that Descartes would have made us, had he not rescued the situation by letting in the spirit (*l'ame*).[26] "We may consider the brain as consisting of a multitude of small units, each with its particular morphological (and presumably functional) features. These units collaborate by way of an immensely rich, complicated and differentiated network of connections, which are very precisely and specifically organized. The anatomical possibilities for (more or less direct) cooperation between various parts of the brain must be almost unlimited" (Brodal,



1975).[27] In addition, there are widely distributed mutable and hence adaptable connections. The important point is that an extreme precision of wiring, based on somatotopic (localized point-to-point) connections, is responsible for inherited fixed effects, while their very large number in combination with the mutable or plastic connections give chance a chance (see Chapter 3). The central nervous system uses the principles of convergence and divergence. Convergence means that fibers from different sites form contacts (synapses) on the same cell; divergence, that the outgoing fibers of one cell spread in different directions to other cells. At the synapse the incoming or afferent message is transmitted to the next cell by means of an intervening chemical process.[28]

If we could insert a large number of microelectrodes into individual cells in different regions of the brain and have their impulses influence a scintillation counter, we would then see an erratic display of bright flashes representing spontaneous activity. It would not be quite like watching the irregular scintillations from cosmic rays, because between some of the flashes from different sites definite temporal correlations could be established by statistical analysis. But this idealized experiment nevertheless illustrates the natural variations of excitability that occur in an organ containing billions of cells connected by convergent and divergent fibers.

Convergence also implies that if one volley of impulses is incapable of discharging a cell, it may yet have been capable of influencing its membrane in the direction of increased excitability. The cell would then be ready to discharge to a subsequent subthreshold array of impulses from elsewhere. This kind of variable excitability expresses itself also in the fluctuations of size and frequency of membrane potentials recordable from the surface of the brain or even from the scalp (the electroencephalogram of Berger).[28]

I have simplified reasoning by merely mentioning excitation, but inhibitory pathways are just as important though often more localized in their distribution. The impulses do not differ in the two cases. They are messages. The excitatory or inhibitory effect is determined by the subsynaptic membrane site on which they project.[29]

The cellular organization of the brain, faced with Nature's capriciousness, as displayed against a background of basic predictability, has thus solved the problem of adaptability anatomically by an immense multiplication of possibilities on the one hand and strictly somatotopic relationships on the other. The former principle is reminiscent of the apparent wastefulness of plants (and animals) in producing seed (sperms, eggs); the latter, of maintaining genetically fixed relationships calculated to safeguard reproducible causal relations with the environment. The waste is apparent only, because in reality economy is reestablished by the capacity for learning, which gradually cements new associations into blocks of instructions. These, too, are teleologically logical (causal) with respect to the environment and thus replace chance with heavily weighted probabilities. For example, the Pavlov dogs learn to salivate to a tone if during the training period a teleological motivation is introduced in the form of anticipation of a reward (reinforcement). Overlapping or redundant projections will be discussed in Chapter 4.

## Practical Teleology

Occasionally one meets with the opinion that teleological



and causal reasoning are diametrically opposed attitudes. Such a view can be upheld only by neglecting the decisive causal role of the environment in modeling the purposive neural demands and responses. Clearly it is often possible and even desirable to neglect purposiveness in studying established neural events from the physicochemical point of view. It may well happen that the purpose for a time disappears into midair like the grin of the Cheshire cat. However, if one then tries to stick the pieces of an explanation together but does it in a teleologically illogical manner, the cat again materializes, now grinning derisively at the bungler who is missing the point. We are in fact dealing with two ways—the why and the how—of approaching the same neural event. These are "by no means mutually exclusive. They supplement one another and blend well" (Granit).[30]

Physiologists brought up to study precise mechanism in purely mechanistic terms tend to be cautious in applying teleological reasoning, while ethologists, used to watching animals, do so freely. It is not much of an exaggeration to call their science "applied teleology."

Writing as a physiologist, my experience is that teleological explanations are serviceable in two specific situations: one is in the planning of an experimental approach, when often a sound idea about the purpose of a mechanism can be very rewarding (see Chapter 3). Many examples can be found in the field of hormonal interaction. Another situation arises when an adaptable neural event, electrophysiological or behavioral, is sufficiently well analyzed to make it possible to predict that its purpose would either be well or badly realized by one or several of a number of alternative hypotheses or models. In actual practice this amounts to a choice between teleologically logical and illogical alternatives or, in less sophisticated language, a choice between what makes sense and what doesn't. A simple example: if the skin of a dog is stimulated by an electrical "bite" until the animal starts a scratch reflex, its leg will be found to reach for the site actually bitten. To assume that the dog would search for the irritating bite in a very different place would be teleologically illogical. Much experience and insight is needed for making sensible use of teleological ideas in analyzing highly complex neural responses.

## Complexity of Causes

The fact that purposiveness relates an event causally to the environment by no means implies that we would be able to unravel all causal chains involved. The statistical element previously discussed and past experience as retained in memory may prevent us from arriving at the level of causal insight that characterizes many physical or chemical results of experimentation. This need not worry us too much. Also, statistical explanations in physics can be based on a negligible causal insight into the details of the mechanisms described. Why then should we neurobiologists be expected to do so much better with the, say, 10 or 14 billion cells of the brain? Sommerhoff has made an interesting synthesis of purposiveness and causality, however, without making the particular distinction between established adaptations and adaptabilities that is so important in the study of the central nervous system.[31] But his general trend of argument agrees with the attitude adopted here, one that I believe should be acceptable to most physiologists. Sommerhoff developed his theses mathematically at the hand of an example, the servomechanism by which a gun is made to follow its movable target. As to the role of mathematics, I refer to my introductory quotation (Platt).[6]



Study of the brain is still in an early phase and hardly in need of much mathematics.

One should remember, too, that "Nature rings her many changes on a few simple themes. The same expressions serve for different order of phenomena. The swing of a pendulum, the flow of a current, the attractions of a magnet, the shock of a blow, have their analogues in a fluctuation of trade, a wave of prosperity, a blow to credit, a tide in the affairs of men" (d'Arcy Thompson).[32] Therefore much remains to be understood behind the façade of an equation. Physiological knowledge also serves medicine, and the physician as a rule is more in need of precise information on physicochemical agents involved than in the mathematics of some fraction of the total operation.

## Knowledge of Results

Of the many different mechanisms drawn into the service of adaptability, one is particularly important for dealing with the unexpected, and this is the process of checking and correcting manipulation of objects by the returning "knowledge of results" studied so much by the psychologists (Annett).[33] It is familiar from the eye and hand combination that makes man superior in adaptability to all competing species on this globe.

Knowledge of results is incorporated in the scientific concept of feedback, which is essential for the understanding of biological processes at all levels from enzymatic regulation in unicellular organisms to hormonal and nervous control of the mechanisms physiologists deal with in the laboratory or physicians in the hospital. The corrective negative feedback of engineering science is now so well known from innumerable servomechanisms that it tends to be forgotten that feedback control really is one of Nature's major inventions, familiar to physiologists long before it was conceptualized by Wiener (1947) within the framework of cybernetics, the science of regulation.[34] Some examples will be given to illustrate the two main tasks of negative feedback in nervous regulation (1) to counteract the effect of unknown or unforeseeable variables in the environment, thus serving adapatability by error detection and correction, and (2) to stabilize any process that otherwise might overshoot its intended effect within the living organism and so antagonize its own purpose.

In moving about, for example, we commonly encounter unforeseeable changes of loading of our muscles that respond by changes of tension and extension. Both effects are recorded by appropriate sense organs (measuring instruments) in the tendons and the muscles and reported upward in the nervous system. Extension, by the shortest route through the spinal cord, produces a reflex contraction or shortening of the muscle, the so-called stretch reflex (Liddell and Sherrington).[35] Tension similarly generates a reflex slackening (or inhibition) of the contraction. Hence, in both cases the effects, fed back to the motor executive cells in the spinal cord, oppose the muscular process by which they were elicited. Thus the feedback has a negative sign. In both cases it counteracts unforeseen variables and stabilizes muscular action around a useful degree of contraction. Further neural refinement of this mechanism will be discussed in subsequent chapters.

Other negative feedback mechanisms stabilize the discharge of the motor cells of the spinal cord, and one is of great general interest. The outgoing axon (motor fiber) from each of a number of these cells, the motoneurons, sends a recurrent fiber back into the spinal cord where it



branches to intermediate internuncial cells that inhibit the firing of the motoneurons. This inhibitory effect is not strong enough to stop a well-supported discharge, but it prevents the firing rate from reaching high values unsuitable for the contractile properties of the muscle fibers for which the axons are destined. The technical term for this governing mechanism of negative feedback is "recurrent inhibition." Recurrent fibers exist in virtually all nuclei of the central nervous system (Cajal)[36] and so negative feedback emerges as one of the fundamental instruments for regulating the discharge rate by itself. Quantitative studies in terms of firing rates of individual motoneurons have shown that the amount of inhibition is directly proportional to the frequency of the outgoing impulses of a firing cell.[37] By this negative feedback mechanism, strongly supported cells firing at fast rates throw out or suppress the action of feebly firing neighbors.

Nervous inhibition by recurrent fibers is one of Nature's oldest inventions and, like all its ancient discoveries, it is used for a variety of purposes. It has been found by Hartline in the retina of the horseshoe crab (*Limulus*), in which a discharging cell regulates its own firing rate and that of its neighbors by a direct inhibition whose effect is proportional to its own discharge rate and to the distance from the cell on which the inhibition is exerted. Hartline and Ratliff have analyzed the properties of this system quantitatively and shown how it sharpens the retinal image by contrast.[38] Fossils tell us that the horseshoe crab found its final shape some 500 million years ago. In mammals most recurrent mechanisms have become more elaborated. The returning branches act indirectly, through an internuncial cell, which is subject to convergent influences from elsewhere, with the result that the negative feedback can be thrown in or out or be finely modulated in excitability in response to other requirements, a step up in the degree of adaptability.

### Immanent Teleology

This concept has been discredited by a taint of vitalism suggesting knowledge of ultimate causes. Vitalism has been dead for over half a century (although one still finds authors engaged in heaping diatribes on its carcass.) But a condescending attitude to "immanens" as such can hardly be justified. We are after all accustomed to many immanent or ultimate properties of matter that are unexplained. There is immanent gravity and immanent magnetism; why not then immanent purposiveness in the biological realm of knowledge? There is no need for the biologist to hedge from speaking of an immanent teleology in the world being studied. It is but a way of stating that one is dealing with biological processes from this highly pertinent point of view.

## 3
## Exploring Adaptabilities

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The dog not only walks but it walks to greet its master. In a word the component from the roof-brain alters the character of the motor act from one of generality of purpose to one of narrowed and specific purpose fitting a specific occasion. The change is just as if the motor act had suddenly become correlated with the finite mind of the moment. (C. S. Sherrington in *Man on His Nature.* London: Macmillan, 1941.)