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V. Epistemological Aspects

In Defense of Teleology

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Teleological and Causal Explanations

The bad reputation teleological thinking enjoys in many circles may perhaps be traceable to its metaphysical history. As a young man with some interest in philosophy I was taught that there are two metaphysical variants of teleology, the transcendental form which saw in it a divine law, and the immanent form which regarded purposiveness as one of Nature's inherent principles of design. I daresay that many scientists would have been willing to accept immanent teleology on its merits had it not been for the fact that it failed to provide a causal explanation and thus had no predictive value. The current scientific explanation is based on a causal relation between events A and B of such a nature that, knowing A one can predict that B will occur.

It so happened that all the great discoveries and the general progress in science came to be dependent on experiments developing causal connexions between observations. The success was obvious, and so purposiveness could be safely neglected. On the basis of the experimental work, laws and principles crystallized into a structure that was recognized all over the world as the real nucleus of scientific knowledge.

Before going any further it is useful to realize that we ourselves as observers have a share in causal reasoning. Our own limitations are part of the picture. This conclusion forces itself upon us in our confrontation with the micro-world of quantum mechanics. According to the uncertainty principle the act of measuring introduces a disturbance increasing in magnitude the more accurate we try to be in observing an event. It often becomes necessary for us to be satisfied with a statistical rule as an expression of a causal connexion that we can understand only as an average of a large number of micro-events.

At this point I want to state explicitly that I intend to speak in my capacity as an experimenter and neurophysiologist, not as a philosopher. I do not try to provide an answer to the question whether Nature is causal or not, but I want to discuss the ways in which we arrive at scientific knowledge. Thus, in the present case, if we cannot trace the causality of the micro-world by carrying accuracy to its very limit, we take refuge in the trick of multiplying our observations until a causal connexion, pleasing to our sense of order, is either willing to appear or is definitely out of the question.

For the experimenter the important point is not that he needs penetrate the causality which connects the micro-event A with the micro-event B. He may or may not succeed in doing it. His real problem is to find out in what way it is possible to find a causal connexion between events within his particular domain of research.

Similarly, when later on I shall speak about observations which are accessible to, or even in need of, a teleological explanation, it is not my intention to resurrect immanent teleology. It is not a question of whether Nature is designed on teleological principles or not, but only of whether, and to what an extent, we can obtain scientific knowledge by teleological reasoning. In the end, the aim of our work is to create sensible structures of knowledge, scientific insight. I shall try to show that in experimental biology knowledge of a causal connexion may remain a trivial statement unless or until it leads to teleological insight of the kind we accept as a real contribution to the understanding of something. In doing so I hope to be able to show that biological insight often appears as a blending of causal experimentation with teleological hypotheses.

It is not difficult to prove that teleological thinking may be very useful. We can, for instance, assume that a sensible purpose is served by a differentiation of the retina and the rest of the eye for the kind of life an animal is leading, whether it moves about in daylight or at night. This teleological idea runs through a very large experimental literature and has led to a systematic search for differentiations that could be explained as adaptations to either kind of visual life. Taking up only the retinal end of the organs of sight, we know that animals living much in the daylight have millions of cones as receptors while night animals have few cones and many millions of rods. This fact has emanated from the work directed by a teleological point of view but the whole technical apparatus of verification is based on the principle of causation. We may not be able to predict precisely what other developments night vision has required but very shrewd hypotheses have been made by people with the gift of biological imagination in their mental equipment.

However, it is just as interesting to turn the roasting-jack round and assume that some histologist, hunting for something to do, had decided to study the retinal receptors. He may have had no other object in view than that of delivering a scientific paper for a thesis or he may have been legitimately curious. By pure serendipity or by systematic work he could have discovered that there were retinas dominated by cones and others dominated by rods. He may have left behind him a number of observations on various types of eye or produced some interesting classification such as in STRINDBERG'S well known parody: buttons with one hole, buttons with two holes etc. and then buttons without one hole, without two holes etc. Then the scientific world would have been left with one of the many inexplicable curiosities of Natures, the kind of observations that in the physiology of last century often were called 'phenomena', Panum's phenomenon, Purkinje's phenomenon etc. Today we do not use the word 'phenomenon' in this sense. It has to be something really phenomenal, like the Loch Ness monster, for instance, before we are willing to use such a word. I do not know the secret inner workings of MAX SCHULTZE'S (1871) mind when he made the discovery of which I have been speaking, but I believe most people would be willing to admit that the relative dominance of rods or cones became interesting and respectable the moment it was understood teleologically in terms of vision in daylight or in the dark. This teleological lead was stimulating and also valuable, because it inspired much experimentation to elucidate the organization and function of the two types of retinas, the existence of rhodopsin in the rods and its photochemistry, the rod-free fovea, the electrophysiological differences between rod and cone eyes, the organiza-

tion and the convergence of rods with regard to the ganglion cells from which the optic nerve fibers originate, as well as a host of psychophysical observations collected in the duplicity theory.

Teleology and Experimentation

1. Psychophysical Example

From the point of view of teleology psychophysics is a most interesting case. The experimental material gathered by psychophysicists in the field of vision within a span of a hundred years—FECHNER's *Elemente der Psychophysik* appeared in 1862—is probably larger than that collected for any other sense organ, and, I would say, boundless. Some of these papers are still alive in the sense that their results have been integrated under a teleological viewpoint which is easily defined: it is that the purpose of the eye is to distinguish one thing from another—for the benefit of the organism. The eye does it by contrast, by wavelength, by parallax, by the velocity of a movement etc. Unless a contribution to the psychophysics of vision has had something valuable to add to the understanding of some such purpose of vision, it is very likely to be forgotten, because, as such, psychophysics is basically a method only, employing units borrowed from physical science. It will be realized that in the case of my examples the actual experiments have been devoted to the elucidation of causal connexions in the ordinary way of natural science. The teleological point of view has merely served to explain why scientists have performed them, a desire in the background for a 'why' to supplement the neutral scientific 'how'.

2. Reflexes and Recurrent Inhibition

I shall now choose some examples from neurophysiology in which the teleological viewpoint comes a little closer to the type of experiment performed, sometimes close enough to be actually formulated, sometimes to suggest experiments serving to expose in a very direct manner the difficulties of teleological interpretation. The simplest example is the nociceptive reflex whose very name explains that the purpose of this reflex is to protect the body from noxious agents. Knowing that, we really know more than we do when we state that flexor muscles contract when strong stimuli are applied to the skin or when we pinch the toes of a spinal animal. SHERRINGTON's standpoint in these matters was perfectly clear: "Physiology pursues analysis of the reactions of the body considered as physical and chemical events; but, further, it aims at giving reasoned accounts of the acts of an organism in respect of their purpose and use to the organism qua organism" (from DENNY-BROWN, 1939, p. 374). This is integrative physiology, and it represents an insight with a value of its own. The reflexology of SHERRINGTON's time was actually closer to teleology than many of today's neurophysiological approaches. "Every reflex", SHERRINGTON said, "is in its own measure an integral reaction, and is purposive in that it bears some biological purport for its organism. Every reflex can therefore be regarded from the point of view of what may be called its 'aim'. The glimpse at the aim of a reflex is to gain hints for further experimentation on it" (DENNY-BROWN, p. 375). These remarks he supplemented

(SHERRINGTON, 1906, p. 239) with a warning: "the assignment of a particular purpose to a particular reflex is often difficult and hazardous".

The difficulties may be illustrated in a preliminary way by a reference to the Swedish eighteenth century poet, HENRIK KELLGREN, who wrote a long poem on *The late Mr. Simpleton (Salig Dumbom)*: Mr. SIMPLETON wondered why it was that big rivers so often found their way to places where there were big cities.

Within the physiology of the central nervous system we have nowadays other leading concepts alongside the reflex and I shall take an example which seems to me of particular interest, namely recurrent inhibition. Some motoneurons respond with a reduction of their firing rate when surrounding motoneurons are active. This effect is carried by recurrent collaterals which leave the axons of the inhibiting motoneurons in order to re-enter the spinal cord and excite a special set of so-called RENSHAW cells which in their turn inhibit a number of adjacent motoneurons. The evidence for these statements is due to ECCLES, FATT and KOKETSU (1954). The inhibitions as such had been demonstrated by the late BIRDSEY RENSHAW in 1941 and 1946. The work leading to the clarification of this recurrent circuit was a typical scientific experiment employing causalities in the usual way. It need not be reviewed in the present connexion. I believe it is a correct interpretation of the attitudes of a large number of my colleagues in neurophysiology when I maintain that most of us feel that, interesting as these facts are, our knowledge is in an unsatisfactory state if we cannot understand what use the organism makes of this negative feedback mechanism. Not knowing that, we can of course study the properties of this circuit as a physico-chemical proposition and thus, for the time being, put the teleological question of its purpose aside. But there it remains, clamouring for an answer. The purpose is not as easily defined as when dealing with the special senses whose very names indicate their role for the organism.

One way of approaching this fundamental problem is to study the distribution of recurrent inhibition among the motoneurons. ECCLES and his colleagues (ECCLES, ECCLES, IGGO and ITO, 1961) and my laboratory (GRANIT, PASCOE and STEG, 1957) have done this and two of the results are of particular interest. One is the finding that the probability of recurrent inhibition between two motoneurons is a function of their proximity in the spinal cord, the other our observation that it is particularly strong with respect to the tonic extensor cells, many phasic motoneurons lacking it altogether. (Recurrent collaterals, are in fact, not present in the case of all motoneurons.) As to the first result, it might be pointed out that the motor nuclei in the spinal cord are elongated structures lying like sardines in a box and so 'proximity in the spinal cord' means that recurrent inhibition may interconnect motoneurons which do not necessarily belong to synergists at the same joint. It is a more general process.

Our work pointed to one definite functional aspect of recurrent inhibition when it was found to be directed towards the small tonically firing extensor motoneurons. We kept them in a state of tonic activity and so could observe directly how their firing rates were reduced by recurrent inhibition, which therefore could be interpreted as a feedback mechanism with the purpose of stabilizing the discharge rate of tonic motoneurons. Later on it was shown by PHILLIPS (1959) that recurrent inhibition in the motor cortex acted in the opposite direction, the small cells inhibiting the large ones. We have no clear understanding of the reason for this difference but I mention it in order to emphasize the difficulties of teleological explanations.

We (GRANIT, PASCOE and STEG, 1957) did in fact raise the next question of why, in particular, tonic firing required to be stabilized and answered it by pointing to the powerful excitatory input from the excitatory afferents of muscle spindles that ECCLES, ECCLES and LUNDBERG (1957) had found to be a property of the small tonic motoneurones. Our assumption was that the spindle input had to be held in check by this extra corrective of a negative feedback on the output side, automatic and elegant, attacking in proportion to firing rate the spike generation at the cell membrane (GRANIT and RENKIN, 1961). This assumption was at the same time a kind of confession that our real interest was teleological understanding of the functional role of the recurrent circuit in the body. In pursuing this aim one of the first tasks became to study just how firing was handled by the feedback mechanism but I shall not go very far into these details. The most important result that emerged was that such problems really were amenable to quantitative treatment, because a tonic cell could be kept firing at different rates and it could be experimentally subjected to recurrent inhibition of variable or constant frequency of stimulation.

The outcome of these experiments (GRANIT and RENKIN, 1961) was that the recurrent effect on the inhibited cell was proportional to the firing rate of the latter, as one would expect from a negative feedback mechanism, and that a constant recurrent inhibition always removed the same number of impulses from the inhibited cell, independent of the firing rate of the latter. The second result implies algebraical addition of excitatory and inhibitory influences, but this conclusion is as such beside the point. We are now interested only in the teleological implications of these findings.

If one imagines a background of constant recurrent inhibition acting upon tonically firing motoneurones, the effect counted in per cent will be very much greater on motoneurones badly excited and just about able to keep going at low frequencies. They will simply be thrown out of action and not be able to keep interfering with the muscular contraction engendered by their more powerful partners. Again, if one considers the whole assembly of cells engaged in maintaining a contraction, those that fire at high rates will inhibit the ones firing at low rates far more than the latter can inhibit in return.

Teleology of Recurrent Inhibition and of the Negative Feedback

With these consequences of our results I think one is entitled to formulate a teleological conclusion along the following lines: the recurrent inhibition of the tonically firing motoneurones is an accessory mechanism of stabilization of their discharge rate ensuring that only those motoneurones which are well supported by excitatory synaptic action are kept going while those less well supported are thrown out of action.

Is this now the whole story? Let me quote from my book on SHERRINGTON (GRANIT, 1966): "It is possible to suggest other answers. And they may all contain an element of truth. Most mechanisms in the nervous system have various tasks to perform and we can but humbly admit our ignorance when trying to make sense out of the masterpieces of biological engineering involved in motor control. It is hard enough to unravel some major features of design" (p. 158). Also in this particular

case I could go on to suggest a number of other possible roles of recurrent inhibition on the motoneurons. But what I have said should suffice to illustrate a principle.

This is the principle that I promised to illustrate, namely that biological insight often appears as a blending of causal experimentation with teleological hypotheses. The work I have referred to was actually undertaken in order to elucidate the role of this particular mechanism of negative feedback in the organism 'qua organism', as SHERRINGTON said. It makes use of physical methods and of causal reasoning at every step but its aim is integrative. It tries to elucidate specific interactions in order to realize teleological aims. The world of experimental physiology is loaded with experiments of this general type in which the experimenter has carried out his work in order to understand the functional role of his observations for the living body. I suspect it is quite common, too, to discover, in passing, causal relations which are interesting as such. In my example the algebraical additivity of inhibition and excitation was such a result. Let us call it a 'bonus'.

We could also look upon these experiments as specimens of the action of negative feedback in neurology. Such circuits are well known in physiology, for instance in hormonal regulation and blood pressure control, and often their role is to maintain a steady state. A feedback circuit can be regarded as a teleological proposition and it is generally known that the mathematics of such circuits exclude certain alternatives of response and predict others. For this reason negative feedback is sometimes regarded as the ultimate vindication of immanent teleology. This attitude is very different from mine. To me a mathematical function is the very essence of causal analysis and feedback circuits are no exceptions from this rule. They can obviously serve in integrations but so can any physical or chemical event as such. In both cases is it a question of causal analysis in order to acquire scientific knowledge. Certain advantages accrue from demonstrating a component of negative feedback in a complex event, but the same thing may be said, for instance, about the physics of saltatory conduction or the discovery of a connecting link pushing a chemical compound into the Krebs cycle.

After this digression, let us return to tonic firing as an integrated reaction and discuss its components other than recurrent inhibition. There is, for instance, the fact that these motoneurons are small ones and innervate slowly contracting muscles which produce a modest amount of power but instead have considerable endurance. Histochemistry has shown that the slow, tonic muscle fibers depend on enzymatic reactions requiring oxygen, whereas the muscle fibers producing fast powerful contractions of less endurance can do most of their work on anerobic enzymatic reactions. For physical reasons motoneurone sensitivity to incoming stimuli increases inversely with cell size so that the small tonic motoneurons also tend to be more easily started than the large phasic ones. Most important is the slow firing rate of the tonic motoneurons aided as we have seen by the recurrent inhibition, dependent on firing rate itself as a governor. But the basic control mechanism of firing rate is the after-hyperpolarization, after each impulse, as ECCLES, ECCLES and LUNDBERG (1958) and KERNELL (1966) have shown. This is a process of restoration of membrane potential and it is slower in tonic than in phasic motoneurons. Its duration depends upon the amount of incoming excitation which of course tends to interrupt restoration of membrane potential and create a new discharge. This result is prevented or largely held in check by the low 'gain' of the tonic motoneurons (KERNELL, 1965). By gain

is understood the slope of the curve relating firing rate to stimulating transmembrane current. If this slope has a low value a motoneurone will be insensitive to an increase of synaptic excitatory currents, even though it exhibits a low absolute threshold sensitivity with regard to these currents.

Uses, Limitations and Dangers of the Teleological Approach

Many of these results have been attained without any background desire on the part of the experimenters to understand the full range of the problem of tonic motor control. But inasmuch as they have come from our laboratory, they indeed had that background and since we (GRANIT, HENATSCH and STEG, 1956) put the problem on the market in 1956 and the other results have come after that, it may well be that many of these results are responses to that impetus. It was maintained by us that the evidence reported in our paper necessitated a differentiation between phasic and tonic motoneurons.

The teleological hypothesis is perhaps not predictive in the way of causal hypotheses, but I would certainly have been very surprised, to say the least, if it had turned out that the small tonic motoneurons had been characterized by, say, high gain. This would have shown that there is no "method in the madness". And when you ask, why this would be surprising, the answer is that such an arrangement would have been teleologically illogical.

When one maintains that teleological thinking differs from causal thinking in that you cannot predict B from A, it is true that teleological predictions are not rigorous to that degree. But I like to think that scientific predictions could well be extended to cover the case when the experimenter can foresee that something *cannot* happen, if he knows something else. If the purpose of the scratch reflex be defined teleologically as needed to remove itching from the point or region on the left shoulder which itches, then you can predict that the animal will not scratch the right shoulder. It would serve no sensible purpose.

And now we come to the real issue in teleological prediction: since purposive thinking is concerned with integrations, often with quite extensive interconnections, you can predict properties of the mechanisms by exclusion if your knowledge of the integrated totality is good enough. The more you know about a system and think about it, as an entity, the better you can say what is teleologically illogical in view of the general design of that entity. To some extent you can also make positive predictions in view of what would seem teleologically logical or, in simpler words, what would seem to make common sense. It is all a matter of the amount of biological imagination an experimenter can command. Where this innate faculty comes from no one knows but an important ingredient is certainly—as I have said—inconstant devotion to an integrative problem.

I have tried to give reasons for my conviction that the teleological approach to physiological problems is both creative and, within limits, even predictive, if based on good enough insight. In our science it implies an interest in the living animal and not only in the physical or chemical events which can be demonstrated to occur in certain pieces of tissue. In the case of my example dealing with the experiments on tonic control, we tried to define the properties of an integration employed in postural adjustments of the body. We have now seen that the motoneurone is provided with

many defenses against running wild, such as afterhyperpolarization, recurrent inhibition, and low gain, all serving to maintain slow steady firing rates in muscles likewise adapted to those firing rates. Any one of those regulations can be, and some of them have been, analyzed as purely physico-chemical propositions. And it is a matter of inclination and training which route the individual experimenter will follow. The charm of the integrative route is that you create your concepts as you go along trying to peep behind the curtain. The purely physicochemical approach, which gives access to a world of ready, stabilized knowledge to be applied in a different type of analysis, offers the delights of rigorous precision. The two ways of approach are by no means mutually exclusive. They supplement one another and blend well.

It was pointed out above that teleological thinking can be dangerous but it is, on the whole, harmless to be inspired to action by wrong hypotheses if our criterion in the end is bound to be an experimental verification. Neither is the causal thinking quite as foolproof as one might assume, but we are so used to these dangers and warned against them that they do not, as a rule, create much attention. Here is a case, however, that stirred up a cloud of thunder. Owing to the authority of, chiefly perhaps OTTO MEYERHOF, the observed production of lactic acid was assumed to deliver the energy for the muscle contraction, as seemed reasonable also in view of A. V. HILL's thermoelectrical measurements. Then the late EINAR LUNDSGAARD showed that in a muscle poisoned with iodoacetic acid no lactic acid was produced although it contracted. — I think we can dismiss this particular criticism against teleological thinking as being potentially dangerous with a reference to the constant risks we always have to take in thinking and experimentation.

I realize quite well that there are people who think it quite useless to understand the wider purpose of any physiological process in the body and regard such an aim as an expression of general muddleheadedness. Their attitude is that our science is best developed without it and this may well be true for large domains of physiology. But, like SHERRINGTON, I fail to see how a neurophysiology of disconnected observations could legitimize itself if one strikes such an attitude. The literature would become loaded with factual trivialities, quickly forgotten. The aim of science is, after all, to create knowledge with some structure to it and how could such structures be erected for a control organ like the central nervous system without considering their purpose in the body?

Without having exhausted my theme, but possibly my readers, I think I have said enough in defense of teleology and it merely remains to consider a point that I have been wondering about. What is the difference between *integration*, as a term used by SHERRINGTON, and *teleological understanding*? Not very conspicuous, to be sure. What is the integrative action but the knitting together of cells activated or inhibited across synapses for a common goal? Some emphasis should be bestowed also on the word 'action' in the title of SHERRINGTON's book *Integrative Action of the Nervous System*, if one wants to understand the nature of integration, as conceived by him. These actions were for him in those days reflexes which he explicitly referred to as having a purpose. Tonic control, discussed above, as a specimen of teleological interpretation and experimentation represents a wider synthesis with a greater diversity of elements and processes included in the totality of events, but it would have disturbed no one if I instead had spoken of this synthesis as an integration, or, indeed, as integrated acts or processes. The conceptual boundaries are fleeting and perhaps

not in need of a definition. SHERRINGTON's work is a good example of how well integrative or teleological physiology thrives in a climate of sound causal analysis. It adds to the latter a special distinction, that of arriving at an understanding of integrative action.

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