ADAPTABILITY OF THE NERVOUS SYSTEM IN RELATION TO CHANCE, PURPOSIVENESS, AND CAUSALITY

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IN EVOLUTIONARY THEORY "purposiveness" has been toned down by the attribute "teleonomic" instead of the old term "teleological." The reason for this is that the consensus of opinion in this field holds "purpose" to be apparent only and the direction of evolution to be fundamentally explainable on the basis of mutation and recombination. The novel properties thus created are tested for their viability in the phenotype by natural selection. All this takes place in a population and is necessarily statistical. In this way new adaptations are established.

Neurophysiological science is very much concerned with the act of testing the phenotype. Among its problems falls the study of adaptations, the mechanisms by which the phenotype is upheld. But just as often it is faced with the great problem of adaptability and this is where teleology re-enters the picture. The animal may be adapted to swim, to fly, to feed on grass, etc., but in the testing of the survival value of the phenotype, what matters just as much is the range of adaptability that it can muster, in other words, performance relative to the external world. Purposiveness, so happily done away with in the synthetic theory, is sneaking back into evolutionary science simply because it assumes that survival value has to be assessed by teleological usefulness at the phenotypic level.

It would be difficult to understand the whole existence of evolution of an organism or an organ if the genetic instructions were absolutely rigid. We know they are not. I shall give but one example, the tongue, its fly-catching function in the frog, its role in temperature regulation in the dog, or in speech and taste in man. This serendipitous trait in Nature, to make the best possible use of what is available, we see over and over again in the physiology of the nervous system.

While all of us realize that the conscious brain is the summit of development of adaptability of the living organisms, I propose to approach this subject at a simpler level of analysis. My main question is as follows: can we change a normal response of a single cortical cell or of a number of them by impressing upon them properties which are at cross-purposes with an ingrained purposive adaptation? If so, a high degree of adaptability has been demonstrated in objective terms.

The answer will depend very much upon the age of the animal and still more upon the species, because adaptability of the nervous system increases upwards in the phylum. In a frog, for instance, Sperry found that when he cut the optic nerve and turned the eye round by 180°, the individual nerve fibers grew back into their original sites in the optic tectum so that the animal's tongue went upwards when a fly appeared in the lower part of the visual field. The frog never adapted itself to the reversal of the optical image. But in a related species, the amphibian *Xenopus,* Jacobson and Hunt found that if this operation was carried out early enough, that is between 32 and 40 hours of the animal's life, normal fly-catching reflexes developed. The genetic instructions were open for a while and later became closed, probably by chemical markers. In man, the orthopedists have shown that any muscle or tendon can be transferred to a new site and the patient learn to carry out any desired motion. Even in the monkey, an exchange of flexors and extensors never permitted full re-adaptation, despite two years of training (Sperry).

Recording from single cortical cells in cats and monkeys has occupied brain physiologists for some ten years and some of the results concern adaptability. In the visual area seventeen of the cat, certain cells discovered by Hubel and Wiesel are sensitive to the orientation of stripes or lines used as stimuli and only respond if these are

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presented in the correct orientation for the cell under the electrode. An assembly of such cells represent all orientations in a non-preferential manner. But if young kittens are reared in a vertically or horizontally striped environment, the cortical cells begin to respond preferentially to these directions. Blakemore, who did similar work in England following Hirsch and Spinelli in this country, found that no more than an hour's exposure to such visual experience sufficed to modify the preferred orientation of most units, provided that the experiment was followed by a minimum of two weeks in the dark. But if the kittens had had more than five hours of such abnormal experience, the effect became virtually ineradicable.

There are old psychological experiments by Stratton in this country to show that man adapts to inversion lenses turning the world upside down, and in recent decades he has had numerous followers trying prismatic goggles. But the comparison with the cat is more striking in an experiment by Maffei and Fiorentini in Pisa. It presupposes knowledge of the fact that man has optimal sensitivity for the vertical and horizontal directions. In the present computer age one can show by summing up some 200 repetitions that the evoked potential of the stimulus indicates these two preferential directions by their amplitude. The electrode is placed over the visual area. Maffei and Fiorentini proceeded to investigate what happens when seven adult subjects wore tilting prisms continually for seven days. The prisms produced a tilt of the target of 30° or 40° from the vertical, and the angle between the apparent vertical and the real vertical was measured and compared with their evoked potentials. These served to indicate the degree of perceptual compensation. In all subjects "repurposing" to the tilt occurred in the first hours, and compensation was virtually complete on the second day. The adaptive effects were accompanied by a decrease of the mean difference between the amplitudes of evoked potentials for the vertical and oblique patterns. In this, as in the example of repurposing hand muscles, the adaptability was indicated by operating at cross-purposes with an ingrained adaptation in a manner which could not be imitated by the cat.

Let us consider these results, rather than go on with examples. I shall take up three points of view: (i) the mechanism of compensation; (ii) why man is superior to the cat; and (iii) the general significance of such adaptations in relation to purposiveness, chance, and causality.

(i) Verticality, like most percepts, is a complex affair. If one tilts his head, a vertical stripe remains vertical in spite of the tilted retinal image and the new receptors concerned. Verticality has a kind of relative constancy, like size, velocity of movement, and color. The retinal image of our hands alters continually with distance, but the perceived size is constant. There are clearly definite frameworks of reference, some external but most of them internal. The percept of verticality has important components other than visual ones. There is first and foremost an internal world of reference based on feedback from the organs of balance in the head, from sense organs in the spinal muscles and muscles of the leg, and skin sensations from the soles. The perennial necessity of compensating for gravity sees to it that the experience of verticality is solidly anchored by those feedback impulses in a cellular organization capable of error detection. This is based on the information returning to it.

A permanent distortion of the visual input by prismatic goggles is a non-plausible illusion which goes against the grain of all the other sources of information, in particular against those most directly concerned with the position of the head in relation to gravity. Error detection leads by feedback to error correction in this highly purposive brain of ours. These events produce alterations in the wiring diagram which is wired up with a redundancy, very likely exceeding that of all other mammals. We do not know which particular processes are responsible for the error correction but there is no lack of possible alternatives, to judge by experimental results from adjacent neurophysiological fields.

The axoplasmic flow of chemical material in nerve fibers is well known and intensely studied today. It may serve to cement new connections; the old ones may withdraw in a mechanical sense because of disuse while new ones may expand by use. A synaptic cleft, after all, is no more than a few hundred angstroms; or there may be active inhibition involved in error correction. Even if we do not know what is the explanation, it is one that does not seem to be wholly beyond reach of experimentation. We are quite familiar with alterations by use and disuse recordable by the electron microscope. The new element introduced here is the durable effect of error detection, the permanent or semipermanent nature of the compensation. This may simply be maintained by use.

(ii) In considering a likely explanation of why man is superior to the cat, the enormous expansion of our cortex and the high degree of encephalization, that is, of the shift of final control to the cortex of the brain, suggest themselves as the basic elements in any workable hypothesis.

Beginning with the question of why in early development the genetic instructions are open, later to become closed, I feel much attracted by the hypothesis of Jacobson, which is well founded and capable of an experimental expansion. Instead of us using my terms of open and closed instructions Jacobson speaks of specified and nonspecified cells.

At the developmental stage there is a tendency for neuronal specificity to increase and for connections to become more highly determined. But in this respect different neurons vary a great deal. Jacobson speaks of neurons of class I which originate early in embryonic development. They are large neurons with long axons. They form the primary afferent and efferent neurons of the central nervous system of vertebrates, and their central connections usually have a topographical arrangement. Their connections are specified during early embryonic development, and are invariant and unmodifiable thereafter. Sensory stimulation is not required for their development and there are few, if any, lasting changes following electrical activity of class I neurons. By contrast, class II neurons are interneurons of various kinds, and especially the small neurons with short axons of the Golgi II type. They originate later than class I neurons in any particular part of the nervous system, and the production of class II neurons continues into postnatal life in some parts of the brain. The connectivity of these neurons is more variable than that of class I neurons. Specific kinds of sensory stimulation are required for the full development and maintenance of class II neurons or of their connections. Electrical activity of these neurons may result in changes of long duration. Specification of class II neurons occurs slowly and is contingent on specific kinds of sensory stimulation (Jacobson, p. 333).

The talent for re-purposing against an ingrained purpose is thus not a universal property of all brain cells. It is based on the variable connectivity of the interneurons of the Golgi type II cells which are the large majority of all cells in the cortex. According to Ramón y Cajal their number increases upwards in the phylum. One of the teleonomic or directive purposes of evolution may well be to create an instrument of maximum adaptability. The ultimate controls are drawn into the sphere of action of the small internuncial cells at sites where their number is great enough to be decisive in responding teleologically to experience beyond the stage of ontogenetic development.

It follows that man should be the most adaptable organism in existence. His brain is the relatively largest one in relation to body surface.

(iii) I wish I could do better on degrees of connectivity in this cellular organization that is our cortex. Such figures are difficult to come by, because there is no good technique for measuring what Cragg's average of 30,000 synapses per cell and up to 60,000 per cell for the largest ones really means. Is it an enormous branching of fibers of contact or does it represent a very large number of projecting axons and thus a high degree of connectivity? Agreement of projecting axons and thus a high degree of connectivity? Agreement seems to prevail on the fact that man on an average has larger neurons than lower species and that the space between them is densely packed with interconnections. Our encephalization, meaning the size of our neocortex, is something wherein we surpass all other animals. I quote Stephan: "even the highest nonhuman primates are not characterized by unique outstanding brain size. Only the encephalization of man is higher than that of all other mammals so far investigated" (p. 162).

The figures given for the number of cells in the visual area of man vary from 50 millions per cm^3 to 97 millions per cm^3. In the visual area of the cat Sholl found each cell in the geniculate station below it to branch to 5,000 cortical neurons each of which connected to 4,000 neurons. These were so-called stellate cells. The absolute number of neurons in the cortex of man needs perhaps to be re-estimated. The figures given are, for the whole cortex, from 2.6×10^9 to 14×10^9.

Despite all these variations I think we move on certain grounds when we state that no man-made computer has any connectivity near that order of magnitude. It simply is fabulous and adds an element of futility to the hope of ever solving the riddle of brain function by wiring diagrams, important though they be to help us see some order in the organization.

What the figures show, however, is that the numerous small cells of the Golgi II type with their adaptability or plasticity relative to environmental changes are numerous enough to give chance a chance. At this stage we have to turn to biological analogies to realize that we are up against a trick that Nature has used elsewhere. There are plants producing millions of seeds and in one ejaculation of the rabbit there are said to be 700,000,000 sperm cells. Behind this is, of course, the basic stability of the genetic code, just as in the brain, there are fixed connections by cells of Type I and variable ones of Type II, the latter capable of being influenced by environmental challenges.

The best analogy there is to brain function is provided by a comparison with the immune system (Jerne, 1973). The small B-lymphocytes, 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. Adaptability is achieved by the existence of random chemical specificities for pattern recognition, their number being large enough for matching antibodies to most of the inimical epitopes that are likely to occur. These fits are remembered by the system and we perceive them as immunity for the agents that provoked them, at least when the immunity refers to a diagnosed disease with a name attached to it. In this manner the immune system responds adequately to an enormous variety of signals; it learns from experience and remembers the lessons it has been taught by the foreign agents. The chemical markers concerned in this activity are the immunoglobulins.

The analogy implies that in both cases there are systems making use of chemical specificities and relying on chance for adaptability to environmental challenges. Chance comes in as a multiplication of alternatives. Both systems have other cells for fixed tasks. In brain physiology and anatomy the fixed organizations and the various adaptations that they represent have obviously been in the center of neurophysiological research. But there is now a rising interest in adaptability as such, perhaps more often spoken of as plasticity.

Finally, having seen now how purposiveness and adaptability are, so to speak, partners in an indissoluble marriage between the organism and its environment, what about causality? It is perfectly clear that teleological explanations do not imply that we are casting adrift from causality. The aim of a purposive response is predictive; it assumes that the environment behaves in a predictable manner, and adjusts itself to correct for deviations from the predictable. Thus, inasmuch as the external world is concerned, purposiveness relates to definite causes. The experimenter can relate different purposes to the responses he is engaged in studying, for instance, by varying instructions in a demanded motor act. He may or may not interpret an inherent purpose correctly. Yet never can he escape from the purposive causal relation to the environmental challenge. The teleological explanation that he is seeking or proposing may be put aside while he is studying the mechanism by which it is realized in the organism, but it is nevertheless always there clamoring for an answer.

The limitations we encounter in discussing causal teleology are on the inside of the organism. We do not know the internal causes residing in memory, motivation, and in as yet unknown properties of the nervous system. To these unknown quantities we can add mind or consciousness which, of course, is the supreme instrument for dealing with purposiveness in all its aspects. I have left consciousness outside my talk because I have been interested in seeing to what extent it is possible to get at the "hardware" of purposive responses in relation to definite experimental factors. In other words, I have wanted to find out how far we can go with things accessible to physiological and anatomical approaches. There is no denying that it would have been an easy choice to go for experiments that emphasize the complexity of internal causes, such as for instance those referring to numerous illusions.

Returning finally to evolutionary theory, I would like to point out once more that my reasoning amounts to a study of the act of testing of the phenotype and this everlasting process is an essential component of the synthetic theory of evolution with natural selection as a major factor in progress. I think my analysis has shown that adaptability is a teleological concept. I would not hestitate one moment to speak of an *immanent teleology* in the organic world, the one dealing with organisms that have to eat, to reproduce, to defend themselves. People are afraid of this term because they think it implies accepting a vitalism that in my opinion has been dead for half a century. I would just as happily speak of immanent gravity or immanent magnetism. In all three cases no knowledge about ultimate causes is assumed. On the contrary, the term "immanent" means the very fact that we have no idea about the ultimate nature of, say, the gravitational force, or Planck's constant, magnetism, etc. There are these immanent elements in our world of observations and they have proved to be essential in our scientific superstructure. Similarly immanent teleology belongs to the scientific structure dealing with living organisms in their relation to the environment and we should try to make sense of it. My view has been that trying to understand adaptability, as is done in the present phase of physiological experimentation, is a step in the right direction.

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