Critical Review.

THE NERVOUS SYSTEM IN REACTIONS OF THE HIGHER ANIMALS :

A critical review of recent work on the physiology of the nervous system.

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ATTENTION is now being directed to the concept that human behaviour is determined to a great extent by spatiotemporal relations of the external world. While physicists are tending to consider space and time as fundamental realities of the objective world, physiologists and psychologists are beginning to investigate the part played by space and time factors in reactions of the higher animals. The work of Pavlov on the function of the cerebral cortex, the recent researches of Sherrington on the nervous system, and the investigations of Lashley and of Köhler on animal reactions have in common a widening of our view of reflexes in the higher forms of animal life. Certain points of contact in the work of these investigators are here indicated.

In emphasizing the fact that an animal reacts to a complex environment as a functional whole, Köhler¹ says : " Instead of reacting to local and mutually independent events, the organism reacts to an actual *constellation* of stimuli by a total process which, as a functional whole, is its response to the whole situation."

A constellation or set of stimuli possesses definite spatiotemporal relations, and these are said to enter fundamentally into the reaction of an individual to that set of stimuli. Köhler suggests that in the physiological processes of a reacting individual there are reproduced the relations of the set of stimuli evoking the reaction. Thus to a unit, e.g. a physical object, of the external world there will correspond a *dynamic* unit in the physiological processes of an individual reacting to ('aware of') that object. The relations of the dynamic unit in the physiological processes will be congruent or 'isomorphic' with the relations of the physical object. According to Köhler, this is the basis of the

organization in an individual's sensory field of units corresponding to physical units of the external world. He says²: "Some definite relations among the stimuli as they issue from the physical object, and the preservation of these relations in transmission [to the brain of the reacting individual] seem to be an essential condition for the organisation of [sensory] units corresponding to objects in the outer world." It is possible to trace in recent physiological research considerable support for this conception.

Taking first the work of Pavlov on conditioned reflexes, we find a great amount of experimental work on the reactions of animals to complex objects and events of the external world. Pavlov has found that any agent in nature may be used as a stimulus for a conditioned reflex, provided that the organism possesses the requisite organs for the perception of such an agent. Elaborating this statement, he³ writes as follows: "We can, in the first place, divide up natural agencies into their ultimate component parts as regards their properties as physiological stimuli. . . . On the other hand, the animal may be affected by the sum total of numerous elementary stimuli *acting together as a whole*. For example, in distinguishing facial appearance we take into account simultaneously *form, dimensions, shades, colours*. We behave very much in the same way when making out our direction in a more or less familiar neighbourhood. Such examples of *compound stimuli* can be multiplied indefinitely. . . ." (italics mine).

Here the influence on an organism of the spatial relations of its environment is plainly indicated, as is the fact that a component of the environment, acting as a unit or whole, may initiate a reflex. Pavlov⁴ adds that "innumerable individual fluctuations in the external and internal environment of the organism may, each and all of them, singly or collectively, being reflected in definite changes in the cells of the cerebral cortex, acquire the properties of a conditioned stimulus." The effect of *change* in an organism's environment, as here emphasized, implies that dynamic spatial and temporal relationships of the outer world influence an organism's reactions, and the reflection of these dynamic relationships in the physiological processes of the organism is definitely maintained.

The effect of temporal relations of the environment is described by Pavlov⁵ in dealing with inhibition: "The first point of importance in the establishment of a conditioned inhibition is its dependence on the time relations between the applications of the two stimuli in the inhibitory combination."

As already mentioned, the effect on animals of natural agents with certain mutual relations has been studied experimentally by Pavlov, who has termed these agents 'compound stimuli.' In his laboratory, conditioned reflexes were produced by such signals as the simultaneous combination of a touch and a sound, and also the combination of a light and a musical sound. The extremely interesting discovery was made that while a combination of environmental units could initiate a conditioned reflex, each separate unit of that combination could by itself produce the opposite effect, viz. inhibition of the

conditioned reflex. Here again the effect on an animal of an environmental component is shown to depend on the grouping together in space and time of the various elements of that component. Many kinds of compound stimuli were employed by Pavlov, such as the repetition of a certain stimulus (e.g. a tone), with different intervals of time between the applications of the stimulus, making a certain order of pauses between the repetitions. In other experiments various kinds of stimuli made up the compound (e.g. four different tones of an octave, or different sights and sounds). Then, writes Pavlov⁶, "the next step was the introduction of different modifications of these compound stimuli. In the first case the order of the two pauses between the repetitions of the tone was reversed. . . . In the remaining cases the order in which the different stimuli were applied was changed. . . . These modified compounds were repeatedly applied without reinforcement [by the unconditioned stimulus], but when the stimuli were applied in their original order the compound was always reinforced, with the result that ultimately the original compounds became differentiated from their modifications, which latter finally lost their positive conditioned effect and acquired an inhibitory one." We see here that the order of application of the elements of a natural agent (compound stimulus), that is, the mutual spatiotemporal relations of those elements, determines the response of the organism.

Pavlov's work not only demonstrates experimentally the determining effect on animal reactions of spatiotemporal relations of the environment, but also shows that the same reaction may be produced by similar, but not necessarily identical components of the environment of an animal. Pavlov⁷ expresses this fact as follows:—

"Natural stimuli are in most cases not rigidly constant but range around a particular strength and quality of stimulus in a common group. For example, the hostile sound of any beast of prey serves as a conditioned stimulus to a defence reflex in the animals which it hunts. The defence reflex is brought about independently of variations in pitch, strength and timbre of the sound produced by the animal according to its distance, the tension of its vocal cords and similar factors."

A corollary of this fact (of similar components of the environment producing the same reaction in an animal) is that similar but not necessarily identical spatiotemporal relations of the environment may produce the same reaction.

The theory of conditioned reflexes provides a possible explanation of this fact, by the light which it throws on brain function. When a conditioned reflex is first formed to a certain stimulus, it can be also evoked by allied stimuli—those affecting the same sense of the animal, more or less similar to the first stimulus. This is what Pavlov calls 'generalization of stimuli,' and appears due to an *irradiation of excitation* from a point of the cerebral cortex affected by the first stimulus. Pavlov⁸ gives the following example of irradiation of cortical excitation:—

"If you form a conditioned reflex, for example, to the ticking of a metro.

nome, and then try other sounds, you will find that these other sounds at first also produce the salivary flow. Consequently the stimulation from a certain group of cells irradiates over a large part of the cerebrum, and therefore every other auditory stimulus provokes the secretion of saliva. If you make a conditioned stimulus from a tone of 1,000 vibrations, and afterwards try other tones of various vibrations, all of them have an effect. The same holds true for other conditioned stimuli."

This irradiation of excitation in the cortex has its counterpart in *concentration* of excitation, in which "the irradiated excitation gathers along certain lines and towards certain foci" (of the cortex). When concentration occurs, other (similar) stimuli fail to evoke the conditioned reflex, only one particular stimulus producing it.

Irradiation and concentration of excitation are constantly occurring in the cerebral cortex, with the result that on the one hand an animal reacts in the same way to similar stimuli (with similar spatiotemporal relationships), and on the other hand 'discriminates' between units of the environment by reacting only to one particular stimulus. Irradiation and concentration of cortical inhibition also occur, as the opposite and complementary process to excitation.

Similarities and differences in human behaviour may perhaps be partially and provisionally explained by the process of irradiation and concentration of excitation and inhibition in the cerebral cortex. According as excitation irradiates or concentrates we do or do not react to units of the environment possessing certain relations. As inhibition irradiates, an individual fails to react to stimuli which would otherwise be effective.

The conclusion that similar relations of the environment may produce the same reactions in individuals is reached by K. S. Lashley from his own experimental work on brain function. Lashley⁹ describes this conclusion as follows :—

"In so far as we can define them, 'intelligent' acts are those dealing with relationships rather than with concrete units. Insight consists of the *identification of two systems of elements through common relationships among their parts*. It is, I think, certain that these relationships are not patterns of identical elements, but are, rather, *similar relations subsisting among dissimilar elements*. There is no possibility of reducing association by similarity to the excitation of the same synapses or reflex arcs. A theorem applied to the solution of a problem in geometry may differ in every detail from the statement of the problem and yet be immediately associated because of common spatial relations involved" (*italics mine*).

A neurological basis of reactions to relationships is suggested by Lashley¹⁰ as follows :—

"Neurologically these relationships must be in the nature of *ratios of excitation*, patterns without a fixed anatomical substratum, since the sensory

and motor elements of a situation may change fundamentally without altering its logical significance.

"We seem forced to the conclusion that a final common path may somehow be sensitized to a pattern of excitation so that it will respond to this pattern in whatsoever part of the nervous tissue it may occur. In the simplest cases the relationships forming the basis of reaction seem expressible as *ratios of intensity of excitation*; in others, as *ratios of spatial extent or temporal distribution*" (italics mine).

A comparison regarding the neurological basis of reactions in the higher animals can be drawn between Lashley's concept of ratios of intensity of excitation in the nervous system and Pavlov's theory of irradiation and concentration of cortical excitation. According to Pavlov, the cerebral cortex is a mosaic of areas of excitation and inhibition which are constantly changing as stimuli from the external world affect the cortex. If irradiation and concentration of excitation around focal points of the cortex are constantly taking place, there will surely be ratios of intensity of excitation in the cortex, for example, between the focal point of an irradiating area of excitation and its periphery. The concept of ratios of intensity of excitation (corresponding to relationships among external stimuli) implies the existence of *degrees* of excitation in the nervous system, and references to such are indeed to be found in Pavlov's¹¹ writings. Further research into the nature and function of the nervous system, particularly the cerebral cortex, will no doubt bring to light the physiological processes underlying reaction to spatiotemporal relations of the external world. Meanwhile the known facts point to the importance of dynamic relationships in the distribution of excitation in the central nervous system.

Already there is evidence of processes in the central nervous system other than the mere conduction of nervous impulses. The work of Sherrington and Fulton shows that nerve impulses undergo modifications in the nerve-cells, and that in the nerve-centres summation of states of excitation and inhibition can occur. In his Ferrier Lecture (1929), Sherrington¹² says: "Though trains of impulses are the sole reactions which enter and leave the central nervous system, nervous impulses are not the sole reactions functioning within the system. States of excitement which can sum together and states of inhibition which can sum together, and states which represent the algebraical summation of these two, are among the central reactions." Sherrington and Fulton¹³ conclude from recent experimental work: "It is in nerve-centres that functional study finds evidence of forms of reaction which summate, that, is can add themselves together both in space and in time, which nervous impulses cannot do."

We see here that space and time factors appear as particularly significant, even though as yet but dimly outlined. The above conclusions may be compared with the concept of sets of external stimuli, the relations of which determine an organism's reactions, possibly by the production of corresponding relations in physiological processes of the organism's central nervous system. If, as Sherrington declares, states of excitation (and of inhibition) in the central

nervous system are capable of summation in space and time, then it would appear that in the nervous centres there must be ratios of intensity of excitation, and also definite spatiotemporal relations in the distribution of excitation in those nervous centres. Whether such ratios and spatiotemporal relations are congruent with the relationships of the sets of stimuli of the external world affecting the nervous centres remains to be proved.

It is not only in nerve-centres that space and time factors have recently been shown experimentally to play a highly important part, for the researches of Adrian have demonstrated the significance of a time factor in the transmission of impulse along nerve fibres. Adrian¹⁴ makes the following statement (to which he attaches certain limitations): "Provided there is nothing to distract our attention, the intensity of the sensation at any moment turns out to be proportional to the frequency of the impulses in the sensory nerve-fibre." Furthermore, Adrian has found in his experiments that the effectiveness of a stimulus depends on the rate of change in the environment as well as on its extent. This, he¹⁵ says, "applies to mechanical stimuli as well as to electrical, for a gradually increasing pressure on a nerve is far less effective than a sudden blow . . . it applies also to the sensory nerve-ending under its natural conditions and has an important influence on the nature of the messages which the brain receives from the sensory organs."

It appears then that from nerve-ending to nerve-centre, spatiotemporal relations—rates, ratios, and spatial distribution—of nervous processes underlie the production of an organism's reactions to external stimuli. Also, according to the theory of neurobiotaxis formulated by C. U. Ariëns Kappers, the presence of ratios of excitation in the nervous system influences its development. The co-ordination of all this work is a problem demanding further research and far more knowledge than is at present available concerning nervous function, particularly of the cerebral cortex. Recent neurological work has gone beyond the stage of regarding man as a reflex automaton of *fixed* nervous paths, working *only* through a series of impulses conducted along those paths. It has been shown that conduction of impulses is not the only process that occurs in the central nervous system. The main problems now awaiting solution include what modifications nerve-cells impose on nerve impulses, what is the nature of excitation and of inhibition in nerve-centres, and what are the forms taken by central states of excitation and central states of inhibition in their summation. Pavlov has indicated the *general* movement of states of cortical excitation and inhibition—their constant irradiation and concentration around various focal points of the cortex. We have now to discover something of the nature of those states, and the particular kinds of movement that they take. This may make possible some degree of definition of dynamic spatiotemporal relations in the nervous system, in far greater detail than can be made at present. It is not beyond the bounds of possibility that these dynamic inner relations of the nervous system will be found to correspond with the relations of the ever changing environment to which the organism reacts,

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- ⁴ Idem, p. 43.
- ⁵ Idem, p. 69.
- ⁶ Idem, pp. 145, 146.
- ⁷ Idem, p. 113.
- ⁸ PAVLOV, *Lectures on Conditioned Reflexes*, 1928, p. 157.
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- ¹¹ PAVLOV, *Lectures on Conditioned Reflexes*, p. 221.
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