CONDITIONED REFLEXES

AN INVESTIGATION OF

THE PHYSIOLOGICAL ACTIVITY

OF THE

CEREBRAL CORTEX

BY

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TO

THE MEMORY OF

MY SON

VICTOR

IVAN PAVLOV

LECTURE I

The development of the objective method in investigating the physiological activities of the cerebral hemispheres.—Concept of Reflex.—Variety of Reflexes.—Signal-reflexes, the most fundamental physiological characteristic of the hemispheres.

THE cerebral hemispheres stand out as the crowning achievement in the nervous development of the animal kingdom. These structures in the higher animals are of considerable dimensions and exceedingly complex, being made up in man of millions upon millions of cells—centres or foci of nervous activity—varying in size, shape and arrangement, and connected with each other by countless branchings from their individual processes. Such complexity of structure naturally suggests a like complexity of function, which in fact is obvious in the higher animal and in man. Consider the dog, which has been for so many countless ages the servant of man. Think how he may be trained to perform various duties, watching, hunting, etc. We know that this complex behaviour of the animal, undoubtedly involving the highest nervous activity, is mainly associated with the cerebral hemispheres. If we remove the hemispheres in the dog [Goltz[1] and others[2]], the animal becomes not only incapable of performing these duties but also incapable even of looking after itself. It becomes in fact a helpless invalid, and cannot long survive unless it be carefully tended.

In man also the highest nervous activity is dependent upon the structural and functional integrity of the cerebral hemispheres. As soon as these structures become damaged and their functions impaired in any way, so man also becomes an invalid. He can no longer proceed with his normal duties, but has to be kept out of the working world of his fellow men.

In astounding contrast with the unbounded activity of the cerebral hemispheres stands the meagre content of present-day physiological knowledge concerning them. Up to the year 1870,

[1] F. Goltz, "Der Hund ohne Grosshirn," Pflüger's *Archiv*, V. li. p. 570, 1892.

[2] M. Rothmann, "Der Hund ohne Grosshirn." *Neurologisches Centralblatt*, V. xxviii. p. 1045, 1909.

in fact, there was no physiology of the hemispheres; they seemed to be out of reach of the physiologist. In that year the common physiological methods of stimulation and extirpation were first applied to them [Fritsch and Hitzig[1]]. It was found by these workers that stimulation of certain parts of the cortex of the hemispheres (motor cortex) regularly evoked contractions in definite groups of skeletal muscles: extirpation of these parts of the cortex led to disturbances in the normal functioning of the same groups of muscles. Shortly afterwards it was demonstrated [Ferrier,[2] H. Munk[3]] that other areas of the cortex which do not evoke any motor activity in response to stimulation are also functionally differentiated. Extirpation of these areas leads to definite defects in the nervous activity associated with certain receptor organs, such as the retina of the eye, the organ of Corti, and the sensory nerve-endings in the skin. Searching investigations have been made, and still are being made, by numerous workers on this question of localization of function in the cortex. Our knowledge has been increased in precision and filled out in detail, especially as regards the motor area, and has even found useful application in medicine. These investigations, however, did not proceed fundamentally beyond the position established by Fritsch and Hitzig. The important question of the physiological mechanism of the whole higher and complex behaviour of the animal which is—as Goltz showed—dependent upon the cerebral hemispheres, was not touched in any of these investigations and formed no part of the current physiological knowledge.

When therefore we ask the questions: What do those facts which have up to the present been at the disposal of the physiologist explain with regard to the behaviour of the higher animals? What general scheme of the highest nervous activity can they give? or what general rules governing this activity can they help us to formulate?—the modern physiologist finds himself at a loss and can give no satisfactory reply. The problem of the mechanism of this complex structure which is so rich in function has got hidden away in a corner, and this unlimited field, so fertile in possibilities for research, has never been adequately explored.

[1] Fritsch und E. Hitzig, "Ueber die elektrische Erregbarkeit des Grosshirns." *Archiv für (Anatomie und) Physiologie*, p. 300, 1870.

[2] D. Ferrier, *Functions of the Brain*, London, 1876.

[3] H. Munk, *Ueber die Functionen der Grosshirnrinde*, Berlin, 1890 and 1909.

The reason for this is quite simple and clear. These nervous activities have never been regarded from the same point of view as those of other organs, or even other parts of the central nervous system. The activities of the hemispheres have been talked about as some kind of special psychical activity, whose working we feel and apprehend in ourselves, and by analogy suppose to exist in animals. This is an anomaly which has placed the physiologist in an extremely difficult position. On the one hand it would seem that the study of the activities of the cerebral hemispheres, as of the activities of any other part of the organism, should be within the compass of physiology, but on the other hand it happens to have been annexed to the special field of another science—psychology.

What attitude then should the physiologist adopt? Perhaps he should first of all study the methods of this science of psychology, and only afterwards hope to study the physiological mechanism of the hemispheres? This involves a serious difficulty. It is logical that in its analysis of the various activities of living matter physiology should base itself on the more advanced and more exact sciences—physics and chemistry. But if we attempt an approach from this science of psychology to the problem confronting us we shall be building our superstructure on a science which has no claim to exactness as compared even with physiology. In fact it is still open to discussion whether psychology is a natural science, or whether it can be regarded as a science at all.

It is not possible here for me to enter deeply into this question, but I will stay to give one fact which strikes me very forcibly, viz. that even the advocates of psychology do not look upon their science as being in any sense exact. The eminent American psychologist, William James, has in recent years referred to psychology not as a science but as a *hope* of science. Another striking illustration is provided by Wundt, the celebrated philosopher and psychologist, founder of the so-called experimental method in psychology and himself formerly a physiologist. Just before the War (1913), on the occasion of a discussion in Germany as to the advisability of making separate Chairs of Philosophy and Psychology, Wundt opposed the separation, one of his arguments being the impossibility of fixing a common examination schedule in psychology, since every professor had his own special ideas as to what psychology really was. Such testimony seems to show clearly that psychology cannot yet claim the status of an exact science.

If this be the case there is no need for the physiologist to have recourse to psychology. It would be more natural that experimental investigation of the physiological activities of the hemispheres should lay a solid foundation for a future true science of psychology; such a course is more likely to lead to the advancement of this branch of natural science.

The physiologist must thus take his own path, where a trail has already been blazed for him. Three hundred years ago Descartes evolved the idea of the reflex. Starting from the assumption that animals behaved simply as machines, he regarded every activity of the organism as a *necessary* reaction to some external stimulus, the connection between the stimulus and the response being made through a definite nervous path: and this connection, he stated, was the fundamental purpose of the nervous structures in the animal body. This was the basis on which the study of the nervous system was firmly established. In the eighteenth, nineteenth and twentieth centuries the conception of the reflex was used to the full by physiologists. Working at first only on the lower parts of the central nervous system, they came gradually to study more highly developed parts, until quite recently Magnus,[1] continuing the classical investigations of Sherrington[2] upon the spinal reflexes, has succeeded in demonstrating the reflex nature of all the elementary motor activities of the animal organism. Descartes' conception of the reflex was constantly and fruitfully applied in these studies, but its application has stopped short of the cerebral cortex.

It may be hoped that some of the more complex activities of the body, which are made up by a grouping together of the elementary locomotor activities, and which enter into the states referred to in psychological phraseology as "playfulness," "fear," "anger," and so forth, will soon be demonstrated as reflex activities of the subcortical parts of the brain. A bold attempt to apply the idea of the reflex to the activities of the hemispheres was made by the Russian physiologist, I. M. Sechenov, on the basis of the knowledge available in his day of the physiology of the central nervous system. In a pamphlet entitled "Reflexes of the Brain," published in Russian in 1863, he attempted to represent the activities of the cerebral hemispheres as reflex—that is to say, as *determined*.

[1] R. Magnus, *Körperstellung*, Berlin, 1924.

[2] C. S. Sherrington, *The Integrative Action of the Nervous System*, London, 1906.

Thoughts he regarded as reflexes in which the effector path was inhibited, while great outbursts of passion he regarded as exaggerated reflexes with a wide irradiation of excitation. A similar attempt was made more recently by Ch. Richet,[1] who introduced the conception of the psychic reflex, in which the response following on a given stimulus is supposed to be determined by the association of this stimulus with the traces left in the hemispheres by past stimuli. And generally speaking, recent physiology shows a tendency to regard the highest activities of the hemispheres as an association of the new excitations at any given time with traces left by old ones (associative memory, training, education by experience).

All this, however, was mere conjecture. The time was ripe for a transition to the experimental analysis of the subject—an analysis which must be as objective as the analysis in any other branch of natural science. An impetus was given to this transition by the rapidly developing science of comparative physiology, which itself sprang up as a direct result of the Theory of Evolution. In dealing with the lower members of the animal kingdom physiologists were, of necessity, compelled to reject anthropomorphic preconceptions, and to direct all their effort towards the elucidation of the connections between the external stimulus and the resulting response, whether locomotor or other reaction. This led to the development of Loeb's doctrine of Animal Tropisms;[2] to the introduction of a new objective terminology to describe animal reactions [Beer, Bethe and Uexküll[3]]; and finally, it led to the investigation by zoologists, using purely objective methods, of the behaviour of the lower members of the animal kingdom in response to external stimuli—as for example in the classical researches of Jennings.[4]

Under the influence of these new tendencies in biology, which appealed to the practical bent of the American mind, the American School of Psychologists—already interested in the comparative study of psychology—evinced a disposition to subject the highest nervous activities of animals to experimental analysis under various

[1] Ch. Richet, *Réflexes Psychiques. Réflexes Conditionels. Automatisme Mental.* Pavlov's *Jubilee Volume*, Petrograd, 1925.

[2] J. Loeb, *Studies in General Physiology*, Chicago, 1905.

[3] Beer, Bethe und Uexküll, "Vorschläge zu einer objectivirenden Nomenklatur in der Physiologie des Nervensystems," *Biologisches Centralblatt*, V. xix. p. 517, 1899.

[4] H. S. Jennings, *The Behavior of Lower Organisms*, New York, 1906.

specially devised conditions. We may fairly regard the treatise by Thorndyke, *The Animal Intelligence* (1898),[1] as the starting point for systematic investigations of this kind. In these investigations the animal was kept in a box, and food was placed outside the box so that it was visible to the animal. In order to get the food the animal had to open a door, which was fastened by various suitable contrivances in the different experiments. Tables and charts were made showing how quickly and in what manner the animal solved the problems set it. The whole process was understood as being the formation of an association between the visual and tactile stimuli on the one hand and the locomotor apparatus on the other. This method, with its modifications, was subsequently applied by numerous authors to the study of questions relating to the associative ability of various animals.

At about the same time as Thorndyke was engaged on this work, I myself (being then quite ignorant of his researches) was also led to the objective study of the hemispheres, by the following circumstance: In the course of a detailed investigation into the activities of the digestive glands I had to inquire into the so-called psychic secretion of some of the glands, a task which I attempted in conjunction with a collaborator. As a result of this investigation an unqualified conviction of the futility of subjective methods of inquiry was firmly stamped upon my mind. It became clear that the only satisfactory solution of the problem lay in an experimental investigation by strictly objective methods. For this purpose I started to record all the external stimuli falling on the animal at the time its reflex reaction was manifested (in this particular case the secretion of saliva), at the same time recording all changes in the reaction of the animal.

This was the beginning of these investigations, which have gone on now for twenty-five years—years in which numerous fellow-workers on whom I now look back with tender affection have united with mine in this work their hearts and hands. We have of course passed through many stages, and only gradually has the subject been opened up and the difficulties overcome. At first only a few scattered facts were available, but to-day sufficient material has been gathered together to warrant an attempt to present it in a more or less systematized form. At the present time I am in a

[1] E. L. Thorndyke, *The Animal Intelligence, An Experimental Study of the Associative Processes in Animals*, New York, 1898.

position to present you with a physiological interpretation of the activities of the cerebral hemispheres which is, at any rate, more in keeping with the structural and functional complexity of this organ than is the collection of fragmentary, though very important, facts which up to the present have represented all the knowledge of this subject. Work on the lines of purely objective investigation into the highest nervous activities has been conducted in the main in the laboratories under my control, and over a hundred collaborators have taken part. Work on somewhat similar lines to ours has been done by the American psychologists. Up to the present, however, there has been one essential point of difference between the American School and ourselves. Being psychologists, their mode of experimentation, in spite of the fact that they are studying these activities on their external aspect, is mostly psychological—at any rate so far as the arrangement of problems and their analysis and the formulation of results are concerned. Therefore—with the exception of a small group of "behaviourists"—their work cannot be regarded as purely physiological in character. We, having started from physiology, continue to adhere strictly to the physiological point of view, investigating and systematizing the whole subject by physiological methods alone. As regards other physiological laboratories a few only have directed their attention to this subject, and that recently; nor have their investigations extended beyond the limits of a preliminary inquiry.

I shall now turn to the description of our material, first giving as a preliminary an account of the general conception of the reflex, of specific physiological reflexes, and of the so-called "instincts." Our starting point has been Descartes' idea of the nervous reflex. This is a genuine scientific conception, since it implies necessity. It may be summed up as follows: An external or internal stimulus falls on some one or other nervous receptor and gives rise to a nervous impulse; this nervous impulse is transmitted along nerve fibres to the central nervous system, and here, on account of existing nervous connections, it gives rise to a fresh impulse which passes along outgoing nerve fibres to the active organ, where it excites a special activity of the cellular structures. Thus a stimulus appears to be connected of necessity with a definite response, as cause with effect. It seems obvious that the whole activity of the organism should conform to definite laws. If the animal were not in exact correspondence with its environment it would, sooner or later,

cease to exist. To give a biological example: if, instead of being attracted to food, the animal were repelled by it, or if instead of running from fire the animal threw itself into the fire, then it would quickly perish. The animal must respond to changes in the environment in such a manner that its responsive activity is directed towards the preservation of its existence. This conclusion holds also if we consider the living organism in terms of physical and chemical science. Every material system can exist as an entity only so long as its internal forces, attraction, cohesion, etc., balance the external forces acting upon it. This is true for an ordinary stone just as much as for the most complex chemical substances; and its truth should be recognized also for the animal organism. Being a definite circumscribed material system, it can only continue to exist so long as it is in continuous equilibrium with the forces external to it: so soon as this equilibrium is seriously disturbed the organism will cease to exist as the entity it was. Reflexes are the elemental units in the mechanism of perpetual equilibration. Physiologists have studied and are studying at the present time these numerous machine-like, inevitable reactions of the organism—reflexes existing from the very birth of the animal, and due therefore to the inherent organization of the nervous system.

Reflexes, like the driving-belts of machines of human design, may be of two kinds—positive and negative, excitatory and inhibitory. Although the investigation of these reflexes by physiologists has been going on now for a long time, it is as yet not nearly finished. Fresh reflexes are continually being discovered. We are ignorant of the properties of those receptor organs for which the effective stimulus arises inside the organism, and the internal reflexes themselves remain a field unexplored. The paths by which nervous impulses are conducted in the central nervous system are for the most part little known, or not ascertained at all. The mechanism of inhibitions confined within the central nervous system remains quite obscure: we know something only of those inhibitory reflexes which manifest themselves along the inhibitory efferent nerves. Furthermore, the combination and interaction of different reflexes are as yet insufficiently understood. Nevertheless physiologists are succeeding more and more in unravelling the mechanism of these machine-like activities of the organism, and may reasonably be expected to elucidate and control it in the end.

To those reflexes which have long been the subject of physiological investigation, and which concern chiefly the activities of separate organs and tissues, there should be added another group of inborn reflexes. These also take place in the nervous system, and they are the inevitable reactions to perfectly definite stimuli. They have to do with reactions of the organism as a whole, and comprise that general behaviour of the animal which has been termed "instinctive." Since complete agreement as regards the essential affinity of these reactions to the reflex has not yet been attained, we must discuss this question more fully. We owe to the English philosopher, Herbert Spencer, the suggestion that instinctive reactions are reflexes. Ample evidence was later advanced by zoologists, physiologists, and students of comparative psychology in support of this. I propose here to bring together the various arguments in favour of this view. Between the simplest reflex and the instinct we can find numerous stages of transition, and among these we are puzzled to find any line of demarcation. To exemplify this we may take the newly hatched chick. This little creature reacts by pecking to any stimulus that catches the eye, whether it be a real object or only a stain in the surface it is walking upon. In what way shall we say that this differs from the inclining of the head, the closing of the lids, when something flicks past its eyes? We should call this last a defensive reflex, but the first has been termed a feeding instinct: although in pecking nothing but an inclination of the head and a movement of the beak occurs.

It has also been maintained that instincts are more complex than reflexes. There are, however, exceedingly complex reflexes which nobody would term instincts. We may take vomiting as an example. This is very complex and involves the co-ordination of a large number of muscles (both striped and plain) spread over a large area and usually employed in quite different functions of the organism. It involves also a secretory activity on the part of certain glands which is usually evoked for a quite different purpose.

Again, it has been assumed that the long train of actions involved in certain instinctive activities affords a distinctive point of contrast with the reflex, which is regarded as always being built on a simple scale. By way of example we may take the building of a nest, or of dwellings in general, by animals. A chain of incidents is linked together: material is gathered and carried to the site chosen; there it is built up and strengthened. To look upon this as reflex we must

assume that one reflex initiates the next following—or, in other words, we must regard it as a chain-reflex. But this linking up of activities is not peculiar to instincts alone. We are familiar with numerous reflexes which most certainly fuse into chains. Thus, for example, if we stimulate an afferent nerve, *e.g.* the sciatic nerve, a reflex rise of blood pressure occurs; the high pressure in the left ventricle of the heart, and first part of the aorta, serves as the effective stimulus to a second reflex, this time a depressor reflex which has a moderating influence on the first. Again, we may take one of the chain reflexes recently established by Magnus. A cat, even when deprived of its cerebral hemispheres, will in most cases land on its feet when thrown from a height. How is this managed? When the position of the otolithic organ in space is altered a definite reflex is evoked which brings about a contraction of the muscles in the neck, restoring the animal's head to the normal position. This is the first reflex. With the righting of the head a fresh reflex is evoked, and certain muscles of the trunk and limbs are brought into play, restoring the animal to the standing posture. This is the second reflex.

Some, again, object to the identification of instincts with reflexes on this ground: instincts, they say, frequently depend upon the internal state of an organism. For instance, a bird only builds its nest in the mating season. Or, to take a simpler case, when an animal is satiated with eating, then food has no longer any attraction and the animal leaves off eating. Again, the same is true of the sexual impulse. This depends on the age of the organism, and on the state of the reproductive glands; and a considerable influence is exerted by hormones (the products of the glands of internal secretion). But this dependence cannot be claimed as a peculiar property of "instincts." The intensity of any reflex, indeed its very presence, is dependent on the irritability of the centres, which in turn depends constantly on the physical and chemical properties of the blood (automatic stimulation of centres) and on the interaction of reflexes.

Last of all, it is sometimes held that whereas reflexes determine only the activities of single organs and tissues, instincts involve the activity of the organism as a whole. We now know, however, from the recent investigations of Magnus and de Kleijn, that standing, walking and the maintenance of postural balance in general, are all nothing but reflexes.

It follows from all this that instincts and reflexes are alike the inevitable responses of the organism to internal and external stimuli, and therefore we have no need to call them by two different terms. Reflex has the better claim of the two, in that it has been used from the very beginning with a strictly scientific connotation.

The aggregate of reflexes constitutes the foundation of the nervous activities both of men and of animals. It is therefore of great importance to study in detail all the fundamental reflexes of the organism. Up to the present, unfortunately, this is far from being accomplished, especially, as I have mentioned before, in the case of those reflexes which have been known vaguely as "instincts." Our knowledge of these latter is very limited and fragmentary. Their classification under such headings as "alimentary," "defensive," "sexual," "parental" and "social" instincts, is thoroughly inadequate. Under each of these heads is assembled often a large number of individual reflexes. Some of these are quite unidentified; some are confused with others; and many are still only partially appreciated. I can demonstrate from my own experience to what extent the subject remains inchoate and full of gaps. In the course of the researches which I shall presently explain, we were completely at a loss on one occasion to find any cause for the peculiar behaviour of an animal. It was evidently a very tractable dog, which soon became very friendly with us. We started off with a very simple experiment. The dog was placed in a stand with loose loops round its legs, but so as to be quite comfortable and free to move a pace or two. Nothing more was done except to present the animal repeatedly with food at intervals of some minutes. It stood quietly enough at first, and ate quite readily, but as time went on it became excited and struggled to get out of the stand, scratching at the floor, gnawing the supports, and so on. This ceaseless muscular exertion was accompanied by breathlessness and continuous salivation, which persisted at every experiment during several weeks, the animal getting worse and worse until it was no longer fitted for our researches. For a long time we remained puzzled over the unusual behaviour of this animal. We tried out experimentally numerous possible interpretations, but though we had had long experience with a great number of dogs in our laboratories we could not work out a satisfactory solution of this strange behaviour, until it occurred to us at last that it might be the expression of a special *freedom reflex*, and that the dog simply could not remain quiet when it was constrained in the stand.

This reflex was overcome by setting off another against it—the reflex for food. We began to give the dog the whole of its food in the stand. At first the animal ate but little, and lost considerably in weight, but gradually it got to eat more, until at last the whole ration was consumed. At the same time the animal grew quieter during the course of the experiments : the freedom reflex was being inhibited. It is clear that the freedom reflex is one of the most important reflexes, or, if we use a more general term, reactions, of living beings. This reflex has even yet to find its final recognition. In James's writings it is not even enumerated among the special human "instincts." But it is clear that if the animal were not provided with a reflex of protest against boundaries set to its freedom, the smallest obstacle in its path would interfere with the proper fulfilment of its natural functions. Some animals as we all know have this freedom reflex to such a degree that when placed in captivity they refuse all food, sicken and die.

As another example of a reflex which is very much neglected we may refer to what may be called the *investigatory reflex*. I call it the "What-is-it ?" reflex. It is this reflex which brings about the immediate response in man and animals to the slightest changes in the world around them, so that they immediately orientate their appropriate receptor organ in accordance with the perceptible quality in the agent bringing about the change, making full investigation of it. The biological significance of this reflex is obvious. If the animal were not provided with such a reflex its life would hang at every moment by a thread. In man this reflex has been greatly developed with far-reaching results, being represented in its highest form by inquisitiveness—the parent of that scientific method through which we may hope one day to come to a true orientation in knowledge of the world around us.

Still less has been done towards the elucidation of the class of negative or inhibitory reflexes (instincts) which are often evoked by any strong stimulus or even by weak stimuli, if unusual. Animal hypnotism, so-called, belongs to this category.

As the fundamental nervous reactions both of men and of animals are inborn in the form of definite reflexes, I must again emphasize how important it is to compile a complete list comprising all these reflexes with their adequate classification. For, as will be shown later on, all the remaining nervous functions of the animal organism are based upon these reflexes. Now, although the possession of such

reflexes as those just described constitutes the fundamental condition for the natural survival of the animal, they are not in themselves sufficient to ensure a prolonged, stable and normal existence. This can be shown in dogs in which the cerebral hemispheres have been removed. Leaving out of account the internal reflexes, such a dog still retains the fundamental external reflexes. It is attracted by food ; it is repelled by nocuous stimuli ; it exhibits the investigatory reflex, raising its head and pricking up its ears to sound. In addition it exhibits the freedom reflex, offering a powerful resistance to any restraint. Nevertheless it is wholly incapable of looking after itself, and if left to itself will very soon die. Evidently something important is missing in its present nervous make-up. What nervous activities can it have lost ? It is easily seen that, in this dog, the number of stimuli evoking reflex reaction is considerably diminished ; those remaining are of an elemental, generalized nature, and act at a very short range. Consequently the dynamic equilibrium between the inner forces of the animal system and the external forces in its environment has become elemental as compared with the exquisite adaptability of the normal animal, and the simpler balance is obviously inadequate to life.

Let us return now to the simplest reflex from which our investigations started. If food or some rejectable substance finds its way into the mouth, a secretion of saliva is produced. The purpose of this secretion is in the case of food to alter it chemically, in the case of a rejectable substance to dilute and wash it out of the mouth. This is an example of a reflex due to the physical and chemical properties of a substance when it comes into contact with the mucous membrane of the mouth and tongue. But, in addition to this, a similar reflex secretion is evoked when these substances are placed at a distance from the dog and the receptor organs affected are only those of smell and sight. Even the vessel from which the food has been given is sufficient to evoke an alimentary reflex complete in all its details ; and, further, the secretion may be provoked even by the sight of the person who brought the vessel, or by the sound of his footsteps. All these innumerable stimuli falling upon the several finely discriminating distance receptors lose their power for ever as soon as the hemispheres are taken from the animal, and those only which have a direct effect on mouth and tongue still retain their power. The great advantage to the organism of a capacity to react to the former stimuli is evident, for it is in virtue of their action that

food finding its way into the mouth immediately encounters plenty of moistening saliva, and rejectable substances, often nocuous to the mucous membrane, find a layer of protective saliva already in the mouth which rapidly dilutes and washes them out. Even greater is their importance when they evoke the motor component of the complex reflex of nutrition, *i.e.* when they act as stimuli to the reflex of seeking food.

Here is another example—the reflex of self-defence. The strong carnivorous animal preys on weaker animals, and these if they waited to defend themselves until the teeth of the foe were in their flesh would speedily be exterminated. The case takes on a different aspect when the defence reflex is called into play by the sights and sounds of the enemy's approach. Then the prey has a chance to save itself by hiding or by flight.

How can we describe, in general, this difference in the dynamic balance of life between the normal and the decorticated animal? What is the general mechanism and law of this distinction? It is pretty evident that under natural conditions the normal animal must respond not only to stimuli which themselves bring immediate benefit or harm, but also to other physical or chemical agencies—waves of sound, light, and the like—which in themselves only *signal* the approach of these stimuli; though it is not the sight and sound of the beast of prey which is in itself harmful to the smaller animal, but its teeth and claws.

Now although the *signalling stimuli* do play a part in those comparatively simple reflexes we have given as examples, yet this is not the most important point. The essential feature of the highest activity of the central nervous system, with which we are concerned and which in the higher animals most probably belongs entirely to the hemispheres, consists not in the fact that innumerable signalling stimuli do initiate reflex reactions in the animal, but in the fact that under different conditions these same stimuli may initiate quite different reflex reactions; and conversely the same reaction may be initiated by different stimuli.

In the above-mentioned example of the salivary reflex, the signal at one time is one particular vessel, at another time another; under certain conditions one man, under different conditions another—strictly depending upon which vessel had been used in feeding and which man had brought the vessel and given food to the dog. This evidently makes the machine-like responsive activities of the

organism still more precise, and adds to it qualities of yet higher perfection. So infinitely complex, so continuously in flux, are the conditions in the world around, that that complex animal system which is itself in living flux, and that system only, has a chance to establish dynamic equilibrium with the environment. Thus we see that the fundamental and the most general function of the hemispheres is that of reacting to signals presented by innumerable stimuli of interchangeable signification.