Problems in the Physiology of the Cerebral Hemispheres.[1]

THE function of the nervous system is to maintain dynamic equilibrium within the organism and between the organism and its environment. In the latter case the equilibrium is, in the higher animals, extremely complex and is achieved mainly by means of the hemispheres. These continuously analyse and synthesise events occurring in the environment, and in correspondence with its changes establish temporary connexions between events, whether simple or complex, and various activities of the organism, in particular those of the skeleto-muscular system, which is preponderantly concerned in reacting to environmental changes and is likewise itself highly differential and integrative in its response.

At present the physiology of the hemispheres exists only in outline—as a framework consisting of a limited number of known factors, such as excitation and inhibition, their two-directional movement in the form of irradiation and concentration, and their mutual induction. The working out of the innumerable details of their intimate mechanism is a colossal problem of the future. A few of the latest investigations carried out by the author and his co-workers (*i.e.* subsequent to the publication of the author's book, "Conditioned Reflexes") are here summarised.

(1) The development of new temporary connexions between external agencies and definite reactions of the organism (development of conditional reflexes) depends on the coincidence in time of the action of these agencies upon the receptor mechanisms of the organism, with the various activities of the organism evoked either by external stimuli effective since birth, or by external stimuli which have become established as such after birth, or finally by changes in the internal condition of the organism (automatic stimuli). The formation of the connexion is then a physiological law.

In order to become a firmly established, powerful, conditioned stimulus the external stimulus *must* begin to act slightly before the particular activity of the organism, and *may* even cease a few seconds before the beginning of the activity. If, on the other hand, the given activity constantly begins before the stimulus, either no connexion is established, or if any is established it is weak, and survives only for a short time, and the specialised excitatory effect of the stimulus is invariably replaced by general inhibition. The biological significance of this fact is not yet clear. Where the stimulus begins to act before the given activity of the organism and continues during that activity, the reflex tends to increase in strength and stability. The mechanism underlying these phenomena cannot yet be expressed in terms of the general properties of the cortical tissue.

(2) The analysing activity of the nervous system is founded in the first instance on the peripheral receptor organs, which constitute not only a receptive mechanism but also an analysing apparatus of the organism. To the peripheral points of the analyser separate points correspond in the cortex (the primary and simplest cortical mosaic). A good proof of this is that by applying definite external stimuli belonging to the same analyser, for example, different auditory stimuli, it is possible to produce various disturbances or fatigue at different strictly localised cortical points. In this manner a very delicate method is opened up for investigating the construction of the cortical parts of the analysers, and it is possible to distinguish special areas in the cortex corresponding to the different analysers (visual, auditory, etc.) from certain other cortical elements of those analysers, which are dispersed probably over the whole mass of the cortex of the hemispheres. Not only are these dispersed elements incapable of performing any higher synthesis and analysis, but they have a very low degree of vitality, as evidenced by the rapidity of their transition into an inhibitory state under the influence of external stimuli.

(3) The conditions determining the characteristics and the magnitude of the excitatory and the inhibitory effects of conditional stimuli are bewilderingly complex and are only gradually being classified.

It is obvious that the magnitude of the positive effect is directly related to the amount of energy applied to the receptor organ. The phenomenon of summation of weak stimuli comes out clearly. The limit of normal excitability and the optimum strength of stimulation are also definite. In the case of very strong stimuli and of the summation of medium stimuli, the excitatory process rapidly changes into an inhibitory one. Of course the strength of stimulus is a relative quantity, varying greatly with individual differences of nervous system.

Since most probably the points between which the new connexions are established are in the cortex, it follows that the variations in the effect of conditioned stimuli will be dependent on the mutual relation between the different cortical points corresponding to the different conditioned stimuli, and also between the different points of those areas of the hemispheres which are affected by the unconditioned stimulus. For example, the conditioned stimuli based on food and acid respectively, both become connected with the chemical analyser of the hemispheres, and therefore, if in the experiments both sets of conditioned stimuli are used, their effect will be determined not only by the interrelation of the points corresponding to the stimuli, but also by the relation existing between the alimentary and 'acid' points of the chemical analyser.

(4) The accumulation of observations upon the normal and pathological activities of the hemispheres gives grounds for distinguishing various types of nervous system. There is the excitable type, which always displays partial or complete failure when confronted by difficult relations between the excitatory and inhibitory processes, and if the experiments are continued, ends by developing an abnormal and extremely protracted weakening of the inhibitory activity, attended by an exaggerated general excitation. At the other extreme stands the inhibitable type, which very easily becomes subjected to inhibition by stimuli either unusual or slightly stronger than usual, and, when confronted by comparatively difficult relations between the excitatory and inhibitory processes, passes into a state of complete inhibition for prolonged periods of time.

In between can be placed the well-balanced type which, successfully and without any signs of abnormality, establishes in all cases a balance between the opposed nervous processes. This type comprises two varieties of animal, differing greatly from one another in external appearance—the stolid animal, always quiet, and the animal which is lively under ordinary conditions, but becomes drowsy with surprising rapidity under monotonous conditions. The latter variety has some difficulty in obtaining a balance between the two processes. This grouping of the types of nervous system corresponds closely to the ancient classification of temperaments; the excitable type—choleric temperament; the inhibitable type—melancholic; the quiet, balanced type—phlegmatic; the lively balanced type—sanguine.

[1] Abstract of the Croonian Lecture delivered before the Royal Society on May 10, by Prof. I. P. Pavlov, For. Mem. R.S.