CHAPTER XXXIX

THE INHIBITORY TYPE OF NERVOUS SYSTEMS IN THE DOG

(Read before the Psychological Society, Paris, December, 1925, on the occasion of the election of Prof. Pavlov to honorary membership.)

DESCRIPTION OF AN INHIBITORY TYPE OF DOG—EXPERIMENTAL ANALYSIS OF THE EFFECT OF THE LENINGRAD FLOOD ON THIS DOG—PASSIVE DEFENSIVE REFLEX (FEAR) APPEARS—INTERPRETATION OF THE EXPERIMENT—STIMULATORY SUBSTANCES AND FATIGUE—RESEMBLANCE BETWEEN THE PASSIVE DEFENSIVE REFLEX AND INHIBITION—PHOBIAS—ANALOGY OF TEMPERAMENTS (SANGUINE, EQUILIBRATED, MELANCHOLIC) TO PAVLOV'S TYPES OF DOGS—DISCOVERY OF THE SOCIAL REFLEX.

I WISH to express my sincere thanks for the great honour you have shown in giving me this opportunity to address you. In the study of the nervous system physiology and psychology must, I am confident, be sooner or later united in an intimate and friendly work. Now, however, let every one of us try in his own way, to marshal his special resources. The larger the number of approaches, the greater the chances that we shall finally unite and proceed together, each helping the other.

In the study of the activity of the brain in the higher animals (in particular, the dog), I and my collaborators, as you know, have adopted a purely physiological point of view, and the terms and explanations we use are exclusively physiological.

The more we investigate, by our method, the higher nervous activity of dogs, the oftener we come upon considerable and striking differences in the individual qualities of the nervous systems of these animals. These differences, on the one hand, added difficulties to our investigation and often disturbed the complete reproduction of the results in other dogs: on the other hand, they were extremely advantageous, as they strongly emphasised a certain aspect of the nervous activity.

Finally, we have been able to distinguish several definite types of nervous systems. To one of these types, then, I take the liberty to direct your attention. This type of dog is one which judging by his behaviour (especially under new circumstances) every one would call a timid and cowardly animal. He moves cautiously, with tail tucked in, and legs half bent. When we make a sudden movement or slightly raise the voice, the animal draws back his whole body and crouches on the floor. We now have in the laboratory an extreme example of such a type. The dog—a female—was born in the laboratory and has lived there five or six years. Never have we subjected her to anything unpleasant. The only thing required of her was this: we put her periodically on the stand and offered food in the presence of certain signals—our conditioned reflexes. But even up to this time, at the sight of any of us, although constant members of the laboratory staff, she starts, and slinks off as if from dangerous enemies. Such an animal is very useful for work on conditioned reflexes, but not at once. At the beginning it is exceedingly difficult to form conditioned reflexes; the animal resents being placed on the stand, the attaching of the various pieces of apparatus and especially the feeding, etc. But when all this difficulty is at last overcome, the dog acts like a perfect machine. Especially notable is the stability of the inhibitory conditioned reflexes—when conditioned agents call forth not the process of excitation but of inhibition. In dogs of other types, on the contrary, it is the process of inhibition which is the more labile and the more easily destroyed. When on a dog of this type there falls, under the usual experimental conditions, some inconsiderable new stimulus, for example the presence of a stranger outside the door of the experimental chamber, only the negative conditioned reflexes are fully maintained; the positive ones immediately weaken or vanish.

I shall now discuss a dog of this type. My collaborator, Dr. Speransky, performed the experiments. Six positive conditioned reflexes were formed: to a bell, a metronome, a whistle, an increase of the general illumination, to a circle of white paper, and to the appearance of a toy rabbit. Differentiations were formed, *i.e.,* inhibitory stimuli were elaborated to a metronome of another frequency, to the decrease of the illumination, to the shape of a paper square, and to a toy horse. The size of the positive reflexes varied as follows: All the auditory reflexes were one and a half times or twice as great as the optical. The bell occupied first place among the sounds, next came the metronome, and the weakest of all was the whistle. The optical were all of nearly the same size. As has been already stated in general (and this dog worked perfectly), all the described relations could always be reproduced uniformly.

In September of last year (1924) there was in Leningrad a great flood. The dogs were saved only with difficulty and under extreme circumstances. Five to ten days later, when they were returned to their usual kennels, the dog under discussion was, to all appearances, perfectly healthy, but in the experimental room it perplexed us not a little. All the positive conditioned reflexes were completely annihilated; not one drop of saliva flowed, and the dog refused to take food offered in the customary manner. For a long time we could not guess what was the matter. All our first suppositions about the cause of this phenomenon could not be substantiated. Finally we came upon the idea that the strong effect of the scene of the flood still persisted.

Then we adopted the following course. Our experiments with conditioned reflexes are now usually conducted so that the dog remains alone in the experimental chamber, while the experimenter is seated outside the door in another room. From here the various agents are made to act on the dog: by a certain mechanical device the vessel of food is swung under his nose, and here on the outside of the door are registered the results of the experiment. For this dog we altered the circumstances. Dr. Speransky sat quietly inside the room with the dog, but did nothing else, while I, instead of him in the outer room, performed the experiment. The conditioned reflexes, to our great satisfaction, reappeared, and the dog began to take the food. We repeated this experiment (at first rarely and then more often) over a period, and then gradually weakened or modified it by sometimes allowing the dog to remain in the room alone: in this way we restored the animal to his normal condition. Next we tried the effect of a certain component, so to speak, of the inundation, by reproducing it in miniature. Under the door of the experimental chamber we allowed a stream of water to trickle. Perhaps the sound of the running water or its reflection threw the dog into the former pathological state. The conditioned reflexes vanished as before and their restoration had to be brought about by the means employed previously.

Moreover, when the dog had recovered, it was impossible to elicit an effect from the former strongest of all the conditioned stimuli, *viz.*, the bell. It inhibited itself, and afterwards there was inhibition of all the remaining conditioned reflexes. A year elapsed after the flood, and during this time we carefully protected the dog from every kind of extraordinary stimulus. Finally in the autumn (of 1925) we were able to get the old reflex, even to the bell. But after the very first time the reflex began gradually to decrease, although it was employed only once a day; and at last it disappeared entirely. At the same time all the remaining reflexes suffered, now temporarily vanishing, now passing into various hypnotic phases ranging between the waking state and sleep, although in this dog the latter state was never fully attained. During this condition of the animal we again tried two methods in order to restore the normal reflexes. The inhibitory reflexes in this dog were, as has been said, stable to an unusual degree. But concerning the well-inhibited stimuli, we know that they are able by induction to strengthen the process of excitation. Therefore we applied those differentiated stimuli (negative, inhibitory) mentioned above. And we actually saw many times that after this the reflexes reappeared and the dog took the food, although before the reflexes had been absent and the food refused, or in the presence of transitory hypnotic stages, under influence of induction, the phase was transposed toward the normal state.

The other method is only a variation of the one described previously. Into the dog's chamber we introduced not the experimenter in *toto* but only a part of his clothing. This was sufficient to increase markedly the reflexes. As the piece of clothing was not visible to the dog it was evidently the scent of it which acted.

To the experimental facts, which I have purposely kept clear of suppositions, it is necessary to add the following. If we turned our attention to the movements of the dog when the conditioned reflexes had disappeared and he refused to eat, then we saw not the food reaction but the *passive defensive,* according to our terminology, or as it would be called ordinarily, the reaction of *fear.* This is particularly striking when the dog falls into one of the hypnotic stages, or as we call them, *paradoxical, i.e.,* when only weak conditioned stimuli act, but not the strong ones. With optical stimuli (these are in general weak) there is an evident motor-food reaction, while immediately after with auditory (strong) stimuli there is a striking passive-defensive reflex: the animal moves the head uneasily from side to side, crouches with head hung down, and does not make the slightest movement toward the food box. Nevertheless, the animal when outside the experimental room is very lively and greedy.

The animal described, however, is by no means an exception. We have had several dogs of this type, as I mentioned earlier, upon which the flood and its variations had a similar influence.

I shall now pass on to our interpretation of all the above facts.

For us it is perfectly clear that this type must be the opposite of all other types, in which it is frequently impossible to elaborate full inhibitory reflexes, or in which, although they may be well elaborated, they are very unstable and are quickly impaired. This means that in the described type the inhibitory process is predominant, while in all the remaining types the process of excitation either prevails or is in more or less equilibrium with that of inhibition.

How can we approach to the understanding of this type, and of its deeper mechanism? We recognise as the most constant and general law in the physiology of the conditioned reflexes the fact that an isolated conditioned excitation conducted into the cerebral cells inevitably leads, sooner or later, and sometimes astoundingly quickly, to an inhibitory state of the cells and perhaps even to its uttermost degree—to the sleeping state. This fact can best be understood thus: these cells being extremely sensitive and quick to react, rapidly expend their *excitatory substances* under the influence of stimuli, and then there sets in another process, in a certain degree conserving and economic, the process of inhibition. This process cuts short a further functional destruction of the cell, and thereby accelerates the restoration of the expended substances. In favour of this speaks our fatigue after the day's work. It is removed by sleep, which, as I have shown before, is an overspread inhibition. Evidently the same is proved by the striking fact, demonstrated in our laboratory, that after damage of certain parts of the hemispheres, for a long time it is impossible to obtain positive conditioned reflexes from the receptors (sense organs) connected with these parts, their stimulation producing only an inhibitory effect. And when later a positive effect of these stimuli appears, it lasts for only a short time and quickly passes over into inhibition. This is an effect typical of so-called nervous exhaustion. Here should be mentioned an observation which we made during the recent difficult years of my native country when the state of exhaustion which the dogs shared with us caused them to fall quickly into different stages of inhibition, and finally into sleep, under the influence of the conditioned stimuli, so that there was no possibility of carrying on researches with the positive conditioned reflexes.

We may conclude, therefore, that the cortical cells, in the type of dog we have described, possess only a small reserve of the excitatory substances, or that these substances are extraordinarily destructible.

A state of inhibition in the cortical cells may be produced by either very weak or by very strong stimuli; only with stimuli of average strength may the cells continue for a long time in a state of excitation without passing over into different degrees of inhibition. With weak stimuli the process of excitation passes over into inhibition only slowly, but with strong stimuli the change is rapid. These degrees of strength of stimulus are, of course, relative, *i.e.,* a strong stimulus for one type of nervous system may be only of average strength for another type. The great inundation produced inhibition only in the type under discussion, while on the other dogs it had no perceptible influence. A bell did not act as a strong stimulus on the subject under consideration until the neurosis appeared (which can be put in a class with human traumatic neuroses), but after the flood, which caused the neurosis, the bell acted definitely as a strong stimulus—as an inhibitory one. The same may be stated in regard to one of the normal hypnotic phases, the paradoxical, when only the weak stimuli acted positively, and the strong led to inhibition.

Then it is impossible not to be struck with the resemblance between the passive defensive reflex in dogs and the inhibitory process. And our dog, we observed, possessed a nervous system in which the process of inhibition predominated. The constant presence of this passive defensive reflex is a common and constant characteristic of the general behaviour of such dogs. At the height of development of the neurosis with all conditioned stimuli, and afterwards in the paradoxical phase during the action of only the strong stimuli, the passive defensive reaction constantly occurs. A remarkable thing! Even in dogs which do not as a rule manifest the passive defensive reflex this reaction characteristically appears, nevertheless, during the time of the paradoxical phase in the presence of strong conditioned stimuli.

On these grounds, we may, I think, assume that at the basis of normal *fear* (timidity or cowardice) and in particular of the pathological fears (*phobias*), there lies a predominance of the physiological process of inhibition, an expression of the weakness of the cortical cells. In this connection I ask you to recall the aforementioned case of induction, when a purely physiological application temporarily removed the inhibition and with it the passive-defensive reflex.

As I gradually analysed the types of nervous systems of various dogs, it seemed to me that they all fitted in well with the classical description of *temperaments,* in particular with their extreme groups, the *sanguine* and the *melancholic.* The first is the type for which there is continually necessary varying stimuli, and furthermore this type indefatigably seeks such stimuli and is itself under these conditions capable of expressing great energy. With monotonous stimuli, however, it quickly and easily falls into a state of drowsiness and sleep. The melancholic type is the one with which we experimented. You recall the extreme representative of this group described in the beginning of my lecture. Is it not natural to consider this as melancholy and to term it so, when at every step, at every moment, the surrounding medium calls forth in the animal always the same passive-defensive reflex?

Between these extremes stand the variations of the balanced or *equilibrated* type, where both the process of excitation and the process of inhibition are of equal and adequate strength, and they interchange promptly and exactly.

Finally, we have come across in our dogs a definite *social* reflex, operative under the influence of an agent of the social surroundings. Dogs and their wild ancestors, wolves, are herd animals, and man, owing to their ancient, historical association together, represents for them a *"Socius."* Dr. Speransky, who always brought this dog into the experimental room, who played with him, fed him and petted him, represented for him a positive conditioned stimulus, heightening the excitatory tonus of the cortex, and dispersing and overcoming the inhibitory tonus. That Dr. Speransky acted on the dog only as an external synthetic stimulus, consisting chiefly of optical, auditory and olfactory components, was proved by our recent experiment in which the scent alone of Dr. Speransky had the same effect (though, of course, weaker) on the nervous system of the dog as he did himself.

This experiment taken together with other similar experiments, brings us, finally, into the field of social reflexes, which we shall include in the future program of our experiments. It is hardly possible now to doubt that by the help of the method of conditioned reflexes, for the purely physiological investigation of the activity of the cerebral hemispheres, there is opened a limitless region.

CHAPTER XL

A PHYSIOLOGICAL STUDY OF THE TYPES OF NERVOUS SYSTEMS, *i.e.*, OF TEMPERAMENTS

(Delivered before the Pirogov Surgical Society, December, 1927, and rewritten February, 1928, for this volume.)

PHYSIOLOGICAL STUDY OF TEMPERAMENTS RESULTS FROM THE METHOD OF CONDITIONED REFLEXES—ADAPTABILITY—REVIEW OF THE METHOD OF CONDITIONED REFLEXES—THE CONDITIONED AND UNCONDITIONED REFLEXES—REACTIONS FORMERLY KNOWN AS PSYCHICAL CAN NOW BE STUDIED PHYSIOLOGICALLY—SIGNALLING REFLEX—FORMATION OF THE CONDITIONED REFLEXES AND THEIR IMPORTANCE IN THE ANIMAL'S LIFE—THE POSITIVE AND THE NEGATIVE CONDITIONED REFLEXES, EXCITATION AND INHIBITION—OBSERVATION ON DOGS SHOWS THEY FALL INTO THREE GROUPS,—ONE HAVING A PREDOMINANCE OF EXCITATION, THE SECOND OF INHIBITION, AND A THIRD CENTRAL OR EQUILIBRATED GROUP—EXAMPLE OF HOW EXCITATION AND INHIBITION MAY COLLIDE AND PRODUCE NEURASTHENIA—TREATMENT OF DOGS WITH NEUROSES BY REST, AND IN EXCITATORY CASES, BROMIDES AND CALCIUM—THE CENTRAL TYPE UNDER THE SAME EXPERIMENTAL CONDITIONS REMAINS HEALTHY AND EQUILIBRATED—THE CENTRAL, NORMAL GROUP HAS TWO SUB-GROUPS—APPLICATION OF THE ABOVE FACTS TO THE HUMAN FINDS AN ANALOGY IN TEMPERAMENTS, TO THE CLASSIFICATION OF HIPPOCRATES OF CHOLERIC, MELANCHOLIC, SANGUINE, AND PHLEGMATIC—DESCRIPTION OF THESE HUMAN TYPES—EXPLANATION OF NEURASTHENIA AND HYSTERIA IN MAN, AND THEIR ANALOGS IN THE CYCLIC PSYCHOSES AND SCHIZOPHRENIC FORMS OF INSANITY—ISOLATION OF PATHOLOGICAL POINTS IN THE CORTEX OCCURS IN HYSTERIA, AND TO A GREATER EXTENT IN SCHIZOPHRENIA, WHICH IS AN EXTREME DEGREE OF HYSTERIA—THE CONTRIBUTION OF THE LABORATORY IN SOLVING THIS QUESTION.

At this festival, dedicated to the memory of a great Russian physician, as a mark of deference to the talent, scientific services and life of Nicholas Ivanovitch Pirogov, I am permitted to make a report of the experimental work done together with my collaborators, which, though not strictly surgical, has a physiologico-medical significance.

Temperament forms an important part of constitution, and as constitution occupies an obviously important place in the attention of the medical world, my communication will not be untimely.

The physiological study of temperaments is the result of a new method used in the investigation of the higher nervous activity. But as this study has not yet been included in textbooks and in the physiological teaching from which we draw our basic information of the animal organism, it devolves upon me, in order to be better understood, to touch upon a few general points before passing over to the special subject of my communication.

The general characteristic of living substance consists in this, that it responds with its definite specific activity not only to those external stimulations with which connections have existed from the day of birth, but to many other stimulations, connections with which have developed in the course of the individual's life; or in other words, that the living substance possesses the function of adaptability.

For the sake of greater clearness, I shall pass directly to the higher animals. In them specific reactions are known as reflexes, and by means of these reflexes there is established a constant correlation of the organism to the surroundings. This co-ordination is obviously a necessity, for if the organism did not especially conform to the environment, it would indeed cease to exist.

Reflexes are always of two kinds: the constant reflex to a definite stimulus, existing in each animal from the day of birth, and the temporary reflex, formed to the most diverse kinds of stimuli which the organism meets during its life. Concerning the higher animals, for example the dog, to which all our investigations refer, these two sorts of reflexes are applicable to the various parts of the central nervous system. The constant reflexes, those which have always been known as reflexes, are connected with all parts of the central nervous system, even with the cerebral hemispheres. But the hemispheres are especially the seat of formation of temporary connections, of transient relations of the animal to the surrounding world, the organ of conditioned reflexes.

You will know that until recently, until the end of the last century, these provisional relations, the transitory connections of the animal organism with the surroundings, were not even considered physiologically, and they were designated as psychical relations. Recent work has shown, however, that there is no reason whatever to exclude them from the scope of physiological investigation.

From these general statements I now pass over to a series of special facts.

Take some injurious influence, some harmful agent such as fire, which the animal avoids and which burns the animal if he happens within its sphere of action or comes into contact with it. This, of course, is a usual inborn reflex, the work of the lower parts of the central nervous system. But if the animal is guarded by the distance from a red light and the representation of the fire, then this reaction, formed during the life of that animal, will be a temporal connection. This impermanent, acquired reflex may be present in one animal, but in another which has not come into contact with fire, it may be entirely absent.

Consider another kind of stimulation, such as the food reflex, *i.e.*, the seizing of food. First of all, this is a constant reflex and children and new-born animals make special movements to take the food into the mouth. But there is also the response seen when the animal runs toward food at a distance on account of some of its aspects, perhaps a sound which is emitted, as, for example, from small animals serving as food for others. This is also a food reflex, but one which is formed during that individual's life with the help of the cerebral hemispheres. It is a temporary reflex which from the practical point of view might be called a signalling reflex. In such a case the stimulus signals the real object, the actual purpose of the simple inborn reflex.

At present, the investigation of these reflexes has gone far. Here is a common example which we constantly see: You give or show to a dog food. A reaction to this food begins: the dog tries to get it, seizes it in his mouth, saliva begins to flow, etc. In order to call out this same motor and secretory reaction, we can substitute for the food any accidental stimulus, whatever we will, as long as it has with the food a connection in time. If you whistle, or ring a bell, or raise the hand, or scratch the dog—whatever[1] you will—and now give the dog food and repeat this several times, then each one of these stimuli will evoke the same food reaction: the animal will strive toward the stimulus, lick his lips, secrete saliva, etc.,—there will be the same reflex as before.

Obviously it is highly important for the animal under the circumstances of his life to be physiologically connected thus distantly and variedly with the favourable conditions which are necessary for his existence or with the injurious influences which threaten him. If some danger, for example, is signalled by a sound from a distance, then the animal will have time to save himself, etc. It is clear that the higher adaptability of animals, the most delicate equilibrations with the surrounding medium, are unfailingly connected with this kind of temporarily formed reflex. The two kinds of reflexes we are accustomed to designate by two adjectives: the inborn, constant ones we call unconditioned reflexes, but those which are built up on the inborn reflexes during the individual's life, conditioned reflexes.

We connect and disconnect the electric light and the telephone many times every day. It would be inconceivable that in the multitudinous connections of the nervous system, uniting the organism with the surrounding infinite world, this technical principle were not utilised, if this were not also a common physiological occurrence. Theoretically there is no ground for objection; and physiologically this view receives full confirmation. The conditioned reflex is formed and exists under definite conditions and laws, as indeed is true of every other nervous phenomenon.

Let us take still another fact concerning the conditioned reflex. A tone, for example, of 1000 vibrations per second has been made a conditioned food stimulus by means of the usual procedure, *i.e.,* its simul-

[1] Prof. Pavlov has previously qualified this with the statement that the signalling agent must be to a certain extent indifferent, or at least not call out some other too strong reaction.—*Translator.*

taneous application with food. This reflex in which the conditioned stimulus evokes in the cortex a process of excitation is a positive food reaction. Such a reaction we call a positive conditioned reflex. But alongside of the positive conditioned reflex we have the negative, which calls out in the central nervous system not a process of excitation but one of inhibition.

If now after the elaboration of this reflex to a tone of 1000 vibrations per second, I try another tone, differing from the original by an interval of 10 to 15 notes, then the new tone is also effective, but less so in proportion to the extent of its variation from the original tone. Proceeding further, if as previously, I always accompany the original tone with food, and never give food with the other tones, then the latter, which acted at first, by and by completely lose their influence as conditioned food stimuli.

What then! Have they become indifferent? By no means. Instead of showing a positive effect they have taken on an inhibitory one. They call out in the central nervous system a process of inhibition. The proof of this is very simple. You try a tone of 1000 vibrations per second. It produces as always a positive reflex, the food reaction. Now apply one of those tones which have ceased to act. Immediately after this trial, the 1000-vibration tone also temporarily loses its effectiveness. Consequently the new tone has evoked in the central nervous system inhibition, and some time is necessary for the inhibition to pass off. Thus you see that it is possible for these temporary agents to produce in the central nervous system the process of inhibition as well as that of excitation. You can readily see that this is of the greatest importance in our life as well as in the life of animals; it amounts to this, that under any given circumstances and at any moment a certain activity must be manifested, but in another situation, inhibited.

Upon this principle is founded the highest orientations of life. In such a way, a continual and proper balancing of these two processes lays the basis of a normal life for both man and animal. These two opposite processes, it is necessary to add, are coexistent and equally important in the nervous activity.

So much for the preliminary explanation. We can now pass on to the main theme of our report.

In the elaboration of conditioned reflexes, both positive and negative, we observe in dogs enormous differences in the speed of formation of these reflexes, in their stability, and in the degree of absoluteness they attain. In certain animals it is easy to produce positive reflexes, and these reflexes are stable under varying conditions; but in these dogs, it is very difficult to elaborate inhibitory reflexes, and in some animals it is impossible to obtain them in pure and exact form, for the reflex will always contain an element of positive activity. This is the characteristic of one group.

At the other extreme, however, there are animals in which the positive conditioned reflexes are formed with great difficulty, are highly unstable, and become inhibited by the slightest change in the surroundings, *i.e.*, they lose their effectiveness. The inhibitory reflexes, on the other hand, are quickly formed and remain stable.

Thus certain animals are specialists, as it were, in excitation, but failures in inhibition, while others are specialists in inhibition, but weak in excitation. Between these extremes there is a central group which can inhibit well, and at the same time easily form positive conditioned reflexes, and both the positive and negative reflexes remain constant and exact. Consequently all dogs fall into three chief groups: an *excitatory group,* an *inhibitory* group (extreme groups), and a *central* group. In the last, the processes of excitation and inhibition are equilibrated. As conditioned reflexes are referred to the cerebral hemispheres, the peculiarities of the indicated groups concern three kinds of character and the corresponding activities of the cerebral cortex.

But we have an even more convincing proof of the existence of these three types of nervous systems.

If there is a very difficult meeting of the excitatory and inhibitory processes, then there will be a complete change in the relations of these three kinds of central nervous system. I shall describe to you in more detail the means which we usually employ, and which are undoubtedly the highest proof of the adaptability or strength of the nervous system. We apply an apparatus with which we mechanically, by rhythmical tactile stimuli, irritate the skin, for example, every second, and we make this a conditioned stimulus. This stimulus can be differentiated, *i.e.,* the nervous system can be made to respond differently to other frequences of the mechanical stimulus. Let us suppose that instead of 30 irritations in a half minute as formerly, I make 15, then it will come about that when I apply the first stimulus there will appear a positive food reaction, but with the stimulus of 15 per half minute the reaction will be inhibited. The first stimulus (30) is of course always accompanied by food, while the latter (15) is not.

In such a way, two stimuli, differing only slightly from each other, produce in the nervous system two opposite processes. And if these two processes are made to follow one immediately upon the other, to collide, as it were, then very interesting results ensue. Let us say I begin with the stimulus of 15 taps; there is no food reaction. If I now exchange the 15 frequency for the 30, this will be a test of the nervous system which will clearly distinguish the three mentioned types. If the experiment is done with the dog of the excitatory type, standing at the extreme pole of the group, in which there predominates excitation and in which the inhibition is always weak, then the following occurs: either at once or after several repetitions of this procedure the dog becomes ill. He retains only excitatory processes, and all the inhibitory ones disappear almost completely. Such a condition we in our laboratory call *neurasthenia,* and it sometimes lasts for months.

If in a dog standing at the opposite pole to this type, I apply the same procedure, conversely the excitatory processes are weakened, while the inhibitory prevail. This state we think represents *hysteria.*

In both cases the normal relation between excitation and inhibition has disappeared. We call this a nervous breakdown, and these destructions of equilibrium in the nervous system we consider as neuroses. They are real neuroses, one showing a predominance of excitation, the other of inhibition. It is a serious illness, continues months, and is one for which treatment is necessary.

The chief curative measures we apply are interruption of all experimentation, but sometimes we have recourse to additional methods. For dogs of the inhibitory type we have discovered no other cure than to let them rest for five or six months or even more from the experiments. But for the other neuroses we have found bromides and calcium salts very useful; in a week or two the animals return to normal.

Thus it plainly appears that different dogs subjected to the influence of one and the same condition develop diseases of opposite nature.

But besides these extremes there is a *central* type. The same application to the latter type of animal has no effect whatever; they remain healthy.

Now it becomes quite evident that there stand out three well-defined types of nervous systems; the central or equilibrated, and the two extreme types, the excitatory and inhibitory. The extreme types use different sides, as it were, of the nervous system, employing only one-half of its function. We might call them half types. Between them stands the whole type, in which both processes are constantly active and in equilibrium.

The following moreover is interesting. The central type has two forms, externally very divergent one from the other, but judged by our criterion the difference is slight. In one form the various balancings of the opposite nervous processes are accomplished easily, but in the other with some difficulty and just avoiding pathological breakdown. Now if we turn our attention to the general external behaviour of our dogs, we observe the following: The excitatory type in its most characteristic form is made up largely of animals having an aggressive nature. For example, if the master, to whom they are well accustomed and obedient, beats or whips such dogs, they may lose control and bite him.

With members of the extreme inhibitory type it is necessary only to threaten them—raise the hand, shout, etc.—and they will tuck in the tail, crouch, or even urinate. These are what we call cowardly animals.

Regarding the central type, there are two forms: quiet, self-contained, sedate animals, ignoring everything about them; and on the other hand, animals which in the waking state are very lively and active, running here and there, sniffing at everything, etc. But paradoxically the latter animals easily fall asleep. When they are brought into the experimental chamber and put on the stand, just when the surroundings cease to stimulate them, they begin to doze and sleep. This is certainly an astonishing combination of the processes of excitation and inhibition.

Thus all our dogs fall into four definite groups. Two extreme groups of markedly excitatory and inhibitory animals; and two central groups of well balanced, equilibrated animals, but also different—one being quiet and the other exceedingly lively. We may consider this an exact statement.

Now can we apply this to man? And indeed, why not? I do not think it will be an insult to man if it is shown that his nervous system has the same common characteristics as that of the dog. Our education has already proceeded so far that against this view no one will seriously protest. We have a perfect right to use the facts established concerning the dog's nervous system for the human, and there is a close parallel. These types of nervous system are, when existing in people, what we call *temperaments*. Temperament is the most general peculiarity of every person, the most basic essentiality of his nervous system, and the type of nervous system colours all the activity of the individual.

The question of temperaments is an empiricism dating from the observation of human beings by the genius Hippocrates, who, it seems, came closest to the truth. His ancient grouping of temperaments divided them into choleric, melancholic, sanguine, and phlegmatic. This classification, it is true, has been now much elaborated: One says there exist only two temperaments; another three; another six, etc. However, during the course of 2000 years the majority are inclined to recognise four forms. We think that the old view is essentially correct. That some of the latest authors have erred in their opinions, I may mention as an example the following instance of a Russian psychiatrist. He proposed six temperaments—three normal and three pathological. The normal were subdivided into lively, serene, and phlegmatic; and the pathological into choleric, melancholic, and sanguine. It seems strange that the sanguine temperament, for example, should be classified as pathological simply because sanguine people have a vacillating nature.

If one accepts the old grouping of four temperaments then one can not fail to see its analogy to our experimental results in dogs. Our excitatory type is the choleric; and our inhibitory is the melancholic. The two forms of the central type correspond to the phlegmatic and the sanguine temperaments. The melancholic temperament is evidently an inhibitory type of nervous system. To the melancholic, every event of life becomes an inhibitory agent; he believes in nothing, hopes for nothing, in everything he sees only the dark side, and from everything he expects only grievances. The choleric is the pugnacious type, passionate, easily and quickly irritated. But in the golden middle group stand the phlegmatic and sanguine temperaments, well equlibrated and therefore healthy, stable, and real living nervous types no matter how different or contrasted the representatives of these types may seem outwardly.

The *phlegmatic* is self-contained and quiet,—a persistent and steadfast toiler in life. The sanguine is energetic and very productive, but only when his work is interesting, *i.e.*, if there is a constant stimulus. When he has not such a task he becomes bored and slothful, exactly as seen in our sanguine dogs, as we are accustomed to call them. Such animals are extremely lively and active as long as the surroundings stimulate them, but they begin to doze and sleep when they are not stimulated.

We may speculate and consider somewhat further such as touching the clinic of nervous and mental diseases, although our knowledge does not extend beyond that of the textbooks. These clinics draw their material chiefly from the extreme, unstable types or temperaments, as we believe; both forms of the central type remain more or less inviolable before the waves and storms of life's sea. It seems correct to think of the excitatory choleric type as corresponding to the pathological form known as neurasthenia; and the inhibitory melancholic as hysteria, for this is properly an inhibitory disease. And further when these illnesses attain to the degree of the so-called psychoses, may not one think that the two chief groups of constitutional endogenetic forms of insanity—the cyclic psychoses and schizophrenia—are only more marked developments of the same diseases?

The neurasthenic, on the one hand, may accomplish much in life, produce some great work. Many prominent people have been neurasthenics. But together with these periods of intense activity, the neurasthenic also has to live through times of deep depression, during which his abilities are curtailed.

But what about the cyclic psychoses? There is a striking similarity. Before the onset of actual insanity, they either reach states far beyond the normal limits of excitation, or they become plunged in periods of deep depression and melancholy.

On the other hand, our laboratory cases of hysteria, our dogs, evidently have very weak cortical cells easily passing over into various degrees of a chronic inhibitory condition. But the basic features of human hysteria are also a weakness of the cortex. Malingering, suggestibility and emotionality (I take these psychical characteristics of hysteria from the pamphlet *Hysteria and Its Pathogenesis* by L. V. Blumenau) are manifestations of this weakness. A healthy person does not hide behind a cloak of disease to attract sympathy or interest in his illness. Suggestibility obviously has at its basis a readiness of the cortical cells to pass over into inhibition. But emotionality is the predominance of a flood of very complicated unconditioned reflexes (aggressive, passive-defensive, and other functions of the subcortical centres) with weakening of the cortical control.

There is thus basis for considering schizophrenia as an extreme weakness of the cortex, as a marked degree of hysteria. The basic mechanism of suggestibility is destruction of the normal unification of the activity of the whole cortex. Therefore the inevitable conclusion is that it arises in the absence of the usual influences, coming from the other parts of the cortex. But if this is so, then schizophrenia is the highest manifestation of such a mechanism. How may we consider the extreme, general weakness of the cortex, its abnormal and pathological fragility? In our inhibitory, hysterical dogs, by applying the functional difficulties presented by our experiments, we can make completely isolated pathologic points and foci in the cortex; in schizophrenia, in the same manner, under the influence of certain experiences of life, acting perhaps on an already organically pathological condition, gradually and constantly there appear a larger and larger number of such weak points and foci, and by degrees there occurs a breaking up of the cerebral cortex, a splitting up of its normally unified function.

And in consideration of all the above mentioned facts, it seems to me that in this thousand-year-old question of temperaments, the laboratory by virtue of the elementary and simple nature of its experimental objects, has an important and unequivocal contribution to make.

CHAPTER XLI

CERTAIN PROBLEMS IN THE PHYSIOLOGY OF THE CEREBRAL HEMISPHERES

(The following is the Croonian Lecture which was delivered before the Royal Society, May 10, 1928. It was translated into English by G. V. Anrep, and is printed here by the permission of the Royal Society.)

FUNCTION OF THE CENTRAL NERVOUS SYSTEM—CONDITIONED AND UNCONDITIONED REFLEXES—SYNTHESIS—CONDITIONED TRACE REFLEXES, SIGNALS—EXTERNAL INHIBITION AND NEGATIVE INDUCTION ARE THE SAME—EXPLANATION OF THE ORIGIN OF THE CONDITIONED REFLEX—ANALYSIS—APHASIA—VICARIATION OF FUNCTIONS OF THE HEMISPHERES—SUMMATION OF CONDITIONED STIMULI—TYPES OF NERVOUS SYSTEMS (EXCITABLE, INHIBITABLE, AND CENTRAL, THE LATTER BEING FURTHER SUBDIVIDED INTO STOLID AND LIVELY)—THESE TYPES CORRESPOND TO THE HIPPOCRATIC CLASSIFICATION OF TEMPERAMENTS—CONCEPTION OF THE CORTEX AS AN ISOLATED AFFERENT AREA FOR ANALYSIS AND SYNTHESIS; THE SPINAL CORD IS BOTH AFFERENT AND EFFERENT—PLASTICITY OF THE CORTEX IN THE SOLUTION OF DIFFICULT PROBLEMS—EXPERIMENTATION ON THE HIGHER NERVOUS ACTIVITIES OF ANIMALS WILL POINT THE WAY TO SELF-EDUCATION.

It is a great pleasure for me to take this opportunity to offer my hearty thanks to the Fellows of the Royal Society for the help which they gave me during the difficult years through which my country has passed. I wish to thank the Society also for the grant which enabled my last scientific work to be published in English, and for inviting me to deliver the Croonian Lecture.

I believe that physiology has at last reached a stage at which it is possible to give a general outline of the activity of the entire central nervous system, including that of the cortex of the hemispheres, though as yet, of course, without deep analysis or detailed knowledge of this activity. The primary function of the nervous system is obvious. It is continuously to maintain a dynamic equilibrium between the functional units within the self-contained system of the organism and between the organism as a whole and its environment. The pre-eminent function of the lower parts of the central nervous system is to integrate the activities of the separate parts within the organism. The rôle they play in maintaining the higher animal in equilibrium with its environment is only subsidiary, the most delicate adjustments of this equilibrium being pre-eminently the function of the hemispheres.

A clear and definite proof of this is provided by the old and repeated observation on dogs, in which the cerebral cortex has been extirpated. Such dogs remain in flourishing health, and can probably live as long as normal animals, so high is the co-ordination between the various internal activities of the organism. This, however, can happen only if the animal is under the constant care of man, who must bring food to his mouth and shelter him from all sorts of harm; otherwise he must inevitably perish. His powers of adaptation to the environment are very limited. The parts of the nervous system which still remain are insufficient to break up the environment into its elementary units, and to make correlation with its perpetual changes, by establishing temporary connections with the various activities of the organism—for instance, with those of the skeleto-muscular system. The activities of this latter system itself, which is the one chiefly concerned in confronting the environment, now fail to be analysed and synthesised to the same degree as takes place in the presence of the hemispheres. As a result, the dog without hemispheres loses the capacity for fine and precise correlation of each separate act with the separate events occurring outside it.

As a result of these observations it is truly legitimate to distinguish a lower from a higher nervous activity, relating the latter to the hemispheres. An unlimited field opens before the physiologist for investigating the analysing and synthesising aspects of this higher nervous activity of the higher animals, and the mechanism underlying them. This fact of nervous analysis and synthesis has confronted the inquisitive mind of man for a long time. Nervous analysis was the subject of the physiology of the sense organs or receptors of the nervous system, which obviously by their nature also serve the organism as analysers of the environment. The synthesising activity was first formulated by psychologists in the form of the law of association. Thus analysis and synthesis first attracted attention as subjective phenomena. Since then, with the co-operation of many biologists, a method was evolved of strictly objective investigation of these phenomena—a method which can be successfully applied to animals.

The fundamental nervous phenomenon, the use of which renders such an investigation possible, is what I call the *conditioned reflex*. The phenomenon itself was known long before. It is an act of *synthesis* by the hemispheres of the animal. Given that there is a coincidence in time of any external stimulus whatever with some definite activity of the organism, this activity tends to become evoked by that stimulus. I, in co-operation with a great number of co-workers—to whom I send from here warm and sincere greetings—founded on this fact a systematic investigation of the functioning of the hemispheres under both normal and pathological conditions.

We have concerned ourselves mainly with two activities of the organism, namely, its reaction to food and its reaction to substances which are rejected on introduction into the dog's mouth—that is, with the alimentary and with one of the defence reactions—and we connected with these all sorts of stimuli that occurred to us. Food, as a stimulus which acts in its own right from birth, evokes a definite reaction of the animal. The animal takes it into its mouth, masticates and swallows it, and at the same time a secretion of saliva occurs. This reaction we call an *unconditioned reflex.* If, during the act of eating, some sight or sound or touch affects the animal on each of several occasions, we find that these stimuli become signals of food evoking the same movements and the same salivary secretion. In our experiments we measured only the secretory reaction.

During the last twenty-seven years we have collected an immense number of observations, which it would be impossible to describe even in the shortest form; nor is it necessary, since this would merely be a repetition of what has been said in my recent book. I shall therefore restrict myself to those problems in the physiology of the hemispheres concerning which we have obtained new facts since the appearance of the book.

As the foundation of the activities of the hemispheres we recognise the processes of excitation and inhibition, their movement in the form of irradiation and concentration, and their mutual induction. At present we are obliged to refer special cases of the activity of the hemispheres to one or other of these heads, but no doubt this classification will have to be modified and probably simplified.

Before discussing the actual problems of the present lecture, I wish to emphasise one important point. More and more observations are being accumulated which show that the establishment of new nervous connections takes place entirely in the hemispheres. The implication is that not only neutral stimuli—*i.e.,* stimuli which are not connected with any activity of the organism—but unconditioned stimuli also, come into communication with definite points of the cortex, pertaining to the respective stimuli. I cannot discuss the evidence for this statement now, but must proceed to the problems which are our immediate concern.

We now know quite well all the conditions under which the conditioned reflex is necessarily established. It follows, therefore, that its establishment is governed by physiological laws, as definite as those which regulate other phenomena in the nervous system. A full and stable conditioned reflex develops when the stimulus which is to become conditioned slightly precedes that activity (unconditioned reflex) with which it is to be linked. The stimulus may also, without ill-effect, terminate a short time before the activity begins (*conditioned trace reflex*); but if the stimulus is introduced *after* the beginning of the activity, then, although, as our present experiments seem to show, a conditioned reflex may also develop, it is insignificant and evanescent; on continuing the procedure the stimulus, which in this connection we term the *neutral agent,* becomes inhibitory. This fact, which is at present under careful investigation, is sometimes strikingly manifested. If during an experiment we simply repeat short feedings of the animal, not combining them with any external stimulus, no influence is produced either on the general condition of the animal or on the previously established conditioned reflexes. This is shown by tests carried out during the intervals between the feedings. If, on the other hand, some extraneous stimulus is introduced during the actual time of eating, and this is repeated many times, then, after a period varying in different animals, a general inhibition develops: conditioned reflexes weaken conspicuously, and finally disappear completely, the dog even declining food—in fact, there supervenes a hypnotic state. The extraneous stimulus itself, when tested outside the time of feeding, in combination with a positive conditioned stimulus, is found to have become strongly inhibitory. This inhibition can be observed whether the positive stimulus is applied concurrently with the extraneous stimulus or within the period of its after-effect.

Where, under the ordinary method of establishing conditioned reflexes, the conditioned stimulus preceding the neutral stimulus is continued together with it, this, as has been observed from the very beginning of our experiments, never weakens the reflex: on the contrary, this frequently strengthens it.

How are these facts to be understood? From a biological point of view of machine-like reactions of the organism, the interpretation of all these relations does not seem difficult. Since conditioned reflexes play the rôle of *signals,* they must obviously acquire significance only when they precede in time the physiological activity of which they become signals; and since they act on the extraordinarily responsive cells of the cortex, it would be natural to expect that these cells would not be stimulated longer than necessary, and their energy thus dissipated, but that they should be left to recuperate for another phase of activity. (This suggestion has already been made in my book, *Conditioned Reflexes.*) But how should these facts be explained in terms of the general properties of the cortical tissue? How is it that an overlapping in time, given that the neutral stimulus begins to act first, renders this agent an excitatory stimulus, while a similar overlapping when the unconditioned reflex precedes the neutral agent makes the latter an inhibitory stimulus? The following interpretation may be possible.

Negative induction or external inhibition (more and more observations are available to show that these are identical) consists in this, that a stimulation of the cortex at one point leads to inhibition of the rest of the cortex. This would explain how the cells when they are affected by the neutral stimulus, after some definite activity of the cortex has already been started, undergo inhibition: the neutral stimulus, therefore, cannot under these conditions acquire excitatory properties. The mechanism of the development of the conditioned reflex under ordinary conditions can be pictured as follows: the excited state of the cells of the cortex acted on by the neutral agent (when this begins to act first) resists the inhibitory influence of the unconditioned stimulus, and it is only under these conditions that a fusion of the effect of the stimuli takes place, leading to the establishment of a connection between the two points. In other words, the mechanism is based on the confluent irradiation of excitation arising at the two points. This interpretation of the facts, however, leaves many questions unanswered. Why does not the neutral stimulus, when it acts first, evoke inhibition of the points pertaining to the unconditioned stimulus? Why does it not produce the same effect as that produced by the unconditioned stimulus when this operates first?

While it is difficult to answer these questions, one can to some extent understand the position by remembering the relative strength of the stimuli; an unconditioned stimulus is usually much more powerful and more extensive in its effect than the neutral stimulus. There is abundant evidence that the relative strength of stimuli is a factor of the utmost importance in the activity of the cortex. Moreover, as I have already mentioned, even where the unconditioned stimulus precedes the neutral agent, an abortive conditioned reflex may appear. Why then, in this case, do the cells pertaining to the neutral stimulus, which is already on its way to becoming a positive conditioned stimulus, invariably pass into a state of inhibition? A fact of special interest is that, while a neutral stimulus which is introduced at the time of the operation of an unconditioned reflex sooner or later becomes strongly inhibitory, other points of the cortex, which are not stimulated at that time, do not become centres of a strong and protracted inhibition. At the same time, as I have already said, when an established but weak conditioned stimulus overlaps the unconditioned stimulus, its effect becomes, if anything, stronger. The fact that a neutral agent acquires powerful inhibitory properties when it is introduced during the unconditioned reflex (in our experiments on alimentary reflexes) is quite unintelligible from a general biological point of view. It might be suggested that our mode of administration of stimuli is artificial, and that therefore our observations disclose only a sort of pathological exaggeration of a normal mechanism. As against this, however, is the fact that all the temporal combinations of stimuli, which have just been described, frequently occur under normal conditions of life. A satisfactory solution of the problems presented cannot be given without further experimentation.

The second problem with which I propose to occupy your attention relates to the *analysing* function of the hemispheres. It is obvious that the analysis is based, in the first instance, on the peripheral endings of the various afferent nerves. These peripheral apparatus are a collection of special transformers, in which different forms of energy are changed into nervous energy. Each single afferent nerve fibre, running from some definite element of the peripheral receptive field, must be regarded as a conductor to the cortex of some definite element of one or other form of energy. In the cortex a special cell must stand in connection with the fibre, the activity of the cell being related to some definite element of one or another definite form of energy. This interpretation of the structure of the cortex rests on definite experimental indications: as a result of investigation of functional disturbances of the cortical cells, such a fragmentation of cortical functions is revealed as we could never dream of obtaining by any operative procedure. In my recently published lectures an observation was mentioned showing that it is possible to derange a point pertaining to a separate conditioned stimulus, namely, the sound of a metronome, leaving points corresponding to other auditory stimuli undamaged. Succeeding experiments have confirmed that it is similarly possible to create a localised disturbance of the cortex, corresponding to a definite point in the tactile analyser, without impairment of the normal functioning of any other points. The *mosaic* construction of the cortex becomes more and more tangible. The further question, however, immediately arises: How far does this spacial differentiation extend, for instance, in the case of different auditory stimuli? We have started, and are continuing, the following series of experiments.

After having produced impairment localised at the cortical point related to a metronome, we proceeded to produce similar impairment at the point related to a particular tone: the selected tone then also ceased to produce a normal effect. It is interesting that in this case the impairment of function involved, to a certain extent, the rest of the tonic scale, so that the reflexes to other tones, which were not used in the experiments, also lost their normal stability—*i.e.,* they easily underwent inhibition. Reflexes to other auditory stimuli, such as buzzing, hissing or bubbling sounds, remained normal. How can we interpret these results except as indicating a precise localisation of different auditory stimuli in the cellular net of the cortex? The facts which I have mentioned are to some extent analogous to some of the various phenomena observed in *aphasia* in man.

The localised disturbance of the activities of cortical elements can be achieved in two ways. We employ a definite stimulus, which we have reason to believe is related to a definite cortical element, as both excitatory and inhibitory—that is, we develop a differentiation either of frequency of stimulation or of its intensity, and then bring these opposite reflexes into acute *collision* by applying one frequency or intensity immediately after the other: in certain nervous systems a pathological state of the corresponding cortical point results. The same thing happens when an attempt is made to transform a long-established excitatory stimulus into an inhibitory one, and vice versa. In both cases, as illustrated by instances in my book, the disturbance is the result of a difficult encounter between the opposite processes. Moreover, by mere repetition of a conditioned stimulus for a prolonged period it is possible to render the cortical point more or less permanently inhibited. For instance, on repeating an auditory conditioned stimulus day after day many times in each experiment, it finally became null and void, a condition which lasted for some time. Other auditory conditioned stimuli, however, which were only used infrequently or were temporarily disused, remained entirely unaffected.

I will now refer to another point bearing on the structure of the cortical end of the analysers, namely, *vicariation* of functions. We extirpate some definite convolution of one hemisphere: a generalised cutaneous conditioned reflex suffers definite impairment, conditioned reflexes from some points of the skin lose their positive effect, and stimulation of these places now produces inhibition of all other conditioned reflexes when these are evoked simultaneously or after a short interval. The stimulation of these places may even lead to profound sleep in an animal, which up to this point never slept during the experiments—*i.e.*, it leads to an irradiation of inhibition, not only over the cortex, but over the lower parts of the nervous system. Within weeks or months after the extirpation the positive effect of stimulation at these places returns, but is transformed with extreme ease into inhibition. A few repetitions of stimuli in the same experiment may lead to complete inhibition. In these cases there is no evidence of the possibility of stable differentiation, according to the localisation of stimuli at any of the affected places. Some differentiation is obtained fairly rapidly, but the positive effect soon becomes weak and then vanishes.

The same results of extirpation are at present under observation in a dog which was operated on nearly three years ago. This case is specially instructive, because the operation was not followed by any sign of immediate or late complications in the form of convulsions. I previously advanced the conception that, in the cortex, there are, besides the special areas representing the different analysers, certain elements so to speak in reserve which are dispersed over the whole mass of the cortex. I mentioned also that these dispersed elements do not participate in any of the higher synthesis and analysis, functions peculiar to the special areas. As a result of the experiments just described, we are now able to add that the dispersed elements are not even *capable* of reaching the state of functional perfection with which the special areas are endowed.

The next problem in relation to which we have collected new data is that of *fluctuations* in the excitation of the cortical cells, their transition into an inhibitory state, and the *summation* of conditioned stimuli. The positive effect of various conditioned stimuli often undergoes considerable fluctuations in strength, even when the conditions apparently remain constant. As we push our investigation further, the necessity of determining the precise cause of every fluctuation becomes more and more imperative. The following is a typical case of which the significance has only recently been appreciated. For a long time it was impossible to find the cause of the fluctuations of different conditioned reflexes evoked during a particular series of experiments. None of the already recognised causes of fluctuation would explain the case in question. Finally, attention was focused on one of the stimuli as a source of the prevailing disorder in the strength of the reflexes. We began to notice that this stimulus, on being applied first in an experiment, evoked a conspicuously large response, compared with those to other stimuli. If, however, it was repeated in the experiment a second time, its effect was then conspicuously small. Next we noticed that it was just after the application of this stimulus that the irregular fluctuations appeared in the strength of the other conditioned reflexes, and that, in addition, the animal became excited.

All this inclined us to think that the stimulus was a very strong one for the cortical cells of the particular animal: the verification of this supposition was not difficult. It was sufficient to decrease the intensity of the stimulus in order to make the condition of affairs change abruptly. The positive effect of this stimulus diminished somewhat, but it now became considerably more uniform in strength on repetition. Sometimes, even, it did not change at all during the whole of an experiment. The other reflexes also ceased to fluctuate in strength, and the animal quieted down. In order to collect further evidence some of the other stimuli were in turn somewhat increased in strength, and, as a result, the same fluctuations were observed as had been produced by the original strong stimulus. Experiments showing the effects of increased and decreased strength of stimuli can be repeated several times over in the same animal. Having acquired this information, we often, when beginning work with a new animal, tested the strength of various conditioned stimuli. In every separate experiment we repeated the same stimulus several times. In the usual course of things, after several repetitions of a conditioned stimulus in the same experiment, its effect diminishes to some slight extent towards the end of the experiment. The extent of this diminution and the amplitude of the fluctuations during the experiment definitely indicate those stimuli which are excessively strong, and therefore unsuitable for further experiment (unless, of course, the object of the experiment is to test stimuli of excessive strength). In the case of the repetition of excessively strong stimuli the progressive diminution in their effect is very considerable towards the end of the experiment, and during the experiment the fluctuations are remarkably great.

In different animals the agencies which act as extraordinarily strong stimuli may be widely different from one another, as regards their *physical* strength. Every animal, therefore, has a certain limit to what may be called normal excitability, for there is a definite optimal strength of each stimulus. As soon as the individual limit of normal excitability is reached, the corresponding cortical cells become more and more inhibited, and this state is reflected in other cells which are stimulated by other stimuli, with resultant variations in the strength of the reflexes in one direction or another, on account of irradiation or induction. It is therefore obvious that we have constantly to ensure that our conditioned stimuli should remain within the limits of their optimal strength.

In close conjunction with the question of the limits of normal excitability stands that of the summation of conditioned stimuli, which has interested us for a long time, but has hitherto not lent itself to solution or experimentation. As suggested in my lectures, the magnitude of the conditioned reflex is determined, *ceteris paribus,* by the amount of energy transmitted from the stimulus to the cortex. The greater the energy, within certain limits, the greater is the conditioned response. If two weak conditioned stimuli are applied together, their summated effect approximates to that of a strong stimulus. At certain strengths of weak conditioned stimuli an exact arithmetical summation of effect can be observed. If a weak stimulus is combined with a strong, their summated effect is nearly always equal to the effect of the strong one alone. Finally, the summation of two strong stimuli produces an effect which is usually somewhat smaller, and only very seldom greater, than that of either singly. In the variation of the experiment already described, when, in the course of one experiment, a single conditioned stimulus was repeated many times, the following results of summation were observed: first we obtained several curves expressing the fluctuations in the strength of conditioned reflexes for a weak, a medium and an excessively strong stimulus. Next we combined the action of the weak and medium stimuli, and repeated this summated stimulus the same number of times as the separate stimuli: the curve so obtained is identical in type with the curve for the strongest stimulus, exhibiting very considerable variations during the experiment, and ending in a profound diminution during the last few applications.

There are other phenomena concerned in summation. In the first place, it has a certain after-effect. In the case of a single application of a summated stimulus, the after-effect involves the subsequent reflexes in the same experiment—not only those in response to the component stimuli, but also to all others. The after-effect is obvious for several days. Most conspicuous is the inhibitory after-effect left by the summation of strong stimuli. The conception of the limit of normal excitability of cortical cells throws much light on the details of the fact of summation, but there still arises the further and very difficult question of the point where summation takes place. The results of summation of weak conditioned stimuli might naturally be regarded as a fusion of the effect of both weak stimuli in that point of the cortex with which, in all these particular experiments, the conditioned stimuli are brought into relation, *viz.,* the chemical analyser in the cortex. But on the other hand, the summation of the weak conditioned stimulus with the strong, and of the two strong together, definitely points to the cells pertaining to the conditioned stimuli themselves. We have every right to regard the inter-relation of processes in summation as taking place somewhere within the above-mentioned sets of cells, but what is the share of the chemical analyser, and what the share of the cells pertaining to the conditioned stimuli, must be answered by the investigations on which we are now engaged.

When, in the same experiment, we apply alimentary conditioned reflexes in conjunction with the reflexes to acid, the inter-relations become still more involved, because they are complicated by the interactions of the different regions of the chemical analyser itself. The problems thus arising are also under investigation.

Our final problem concerns the types of nervous system. The experimental material, collected from dogs which we used for our observations, is so large that we have a certain basis for defining at least the main types of nervous system. The difference as regards the development and the character of excitatory and inhibitory conditioned reflexes in our animals may be striking. There is one group of dogs in which the positive conditioned reflexes develop with ease, quickly reaching and persistently remaining at their maximum strength, often in spite of various inhibitory influences, *i.e.,* interference from extraneous reflexes. In the case of these animals an attempt has been made to reduce the effect of strong or weak conditioned stimuli by means of unbroken repetition, a method usually very effective for this purpose, but the reflexes remained very steady. The inhibitory reflexes, on the other hand, develop in these animals with great difficulty, and it seems as if the animals' nervous system opposes a barrier to their establishment. Much time must usually be spent in order to establish them firmly, if, indeed, this is possible at all. Some of these dogs fail to develop fully inhibitory reflexes, such, for instance, as those involved in the establishment of absolute discrimination of stimuli. In others fully inhibitory reflexes can be established, but they should not be repeated during a single experiment, or even once a day, otherwise they again lose completeness, and they are very easily disinhibited by extraneous stimuli. This type of animal may be called the *excitable type*.

At the other extreme is the type in which the positive reflexes develop under our conditions very slowly, slowly reach their maximum strength, and are extremely liable to diminish and disappear for considerable periods of time, in the presence of quite insignificant extraneous stimuli. Frequent repetitions of the excitatory reflexes also lead to their diminution and disappearance. The inhibitory reflexes, on the other hand, are developed extraordinarily quickly, and well maintain their strength. This type of animal may be called inhibitable. As regards the cortical cells of these two groups of animal, it may be presumed that in the excitable type the cells are vigorous and richly provided with "excitable substance," while in the *inhibitable type* the cells are weak and poor in that substance. For these weak cells the usual strength of stimuli is super-maximal, and hence leads to inhibition.

In between these two extreme types is the *central type*. This easily acquires both positive and negative conditioned reflexes, which, after development, are stable. Since the normal nervous activity consists in a perpetual equilibration of the two opposing nervous processes, and since in the last type this equilibration is more or less easily achieved, we may call this the "well-balanced" animal. We have at our disposal several criteria for comparing different animals as regards their conditioned activity, and the grouping of animals which I have just indicated finds constant confirmation. Of course, there are several gradations between these primary types. This classification also finds support in the fact that all the characteristic differences become exaggerated under the influence of various prolonged nervous disturbances (experimental neuroses) which develop as the result of excessively strong stimulation, or of unresolvable conflict between the two nervous processes. The balanced type more or less quickly, and at any rate without lasting disturbance, overcomes these difficulties; the extreme types show definite neuro-pathological symptoms differing in the two types. The excitable type entirely loses all capacity for inhibition, and enters a state of strong and continuous excitation, both under the conditions of our laboratory environment and at large; the inhibitable type, on the contrary, loses almost completely the positive conditioned reflexes, and, in response to conditioned stimuli, passes through various phases of the hypnotic state. Treatment is needed in order to restore these animals to the normal—prolonged rest and interruption of the experiment, or pharmaceutical remedies, or both.

It is of interest that the balanced type, as judged by means of our tests, is represented in two groups of animals, varying greatly in their general behaviour—one *stolid* and quiet, peculiarly indifferent to external happenings, but always on the alert; the other extraordinarily *lively* and mobile under ordinary conditions, and showing continual interest in whatever happens around them, but under monotonous conditions—for instance, when left alone in the experimental room—surprisingly apt to fall quickly asleep. These dogs, like the quiet ones, though not so easily, overcome the difficulties presented to them.

It is obvious that these types of nervous system are what is usually defined as "*temperaments.*" Temperament is the most general characteristic of an individual, whether man or animal. It is the most fundamental characteristic of the nervous system, a characteristic which colours and pervades all the activities of every individual. This being so, we cannot fail to see that our types correspond to the ancient classification of temperaments, the choleric and melancholic types being our extremes—excitable and inhibitable; while the phlegmatic and sanguine correspond well to the two forms of balanced type—the quiet and the lively. It seems to me that our classification of temperaments, which is based on the most general properties of the central nervous system, namely, the relations between the two aspects of nervous activity, inhibition and excitation, is the most simple and the most fundamental possible.

Now since, in our experiments with conditioned reflexes, we are concerned with the properties of the hemispheres, we can go a step further and say that temperament is determined mainly by the properties of these. That the facts of temperament are not attributable to special complex peculiarities of the unconditioned reflexes, usually known as instincts or tendencies, is shown by the fact that the unconditioned alimentary reflex may be very intense in extremely inhibitable animals. Complex and special manifestations of unconditioned reflexes, such as the alimentary, the defensive both in its active and passive form, and others, depend of course on the activity of the higher sub-cortical centres, which serve as the basis of the elementary emotions. The sum total of the vital expressions, however, will be mainly dependent on the type of the activity of the cortex, which may be predominantly excitatory or inhibitory, or both in different proportions, and which modifies the sub-cortical activity accordingly.

The conception of the preponderant significance of the fundamental properties of the cortex, as determining temperament, should be accepted as applicable to man.

Having completed this survey of our recent experiments, and of the series of new problems arising therefrom in the physiology of the hemispheres and of the brain generally, I will attempt to draw two general conclusions—one purely physiological, the second more practical and of a certain general application.

If the central nervous system is to be divided into two parts only, the afferent and the efferent, then I would regard the cortex of the hemispheres as constituting an *isolated afferent area.* In this area only does the higher *analysis and synthesis* of the inflowing excitations take place, and it is only from here that ready-made combinations of excitation and inhibition can flow into the efferent areas. In other words, only the afferent part is the active or, so to speak, the creative part, while the efferent is the obedient executive. In the *spinal cord* the afferent and efferent parts are intimately connected: the investigator always carries away the impression of a unified activity of both parts, and is, as I believe, precluded from giving a self-contained description of the peculiarities of the afferent part. For instance, the law of forward conduction of the nervous process is substantiated by experiments demonstrating the uninterrupted progression of the spinal reflex act from start to finish. But is this law valid for a purely afferent organ? In the cortex of the hemispheres we continually observe both progression and regression of the excitatory and inhibitory processes. Is this the result of two-directional conduction along the same paths or, in order to preserve the principle of the law of forward conduction, must we understand that special complicated constructional devices come into play?

Coming to the more practical of the two conclusions which I have mentioned, I am led to it under the influence of persistent impressions, formed over a long series of years devoted to this work. These multitudinous experiments on the activity of the hemispheres reveal the astounding plasticity of this activity. Many problems depending on the nervous function, which may seem for a given brain entirely impossible of solution, nevertheless, by means of gradual presentation and careful method, become in the end satisfactorily solved: and if they are to be solved, the type of nervous system of the individual animal must never be ignored.

I trust that I shall not be thought rash if I express a belief that experiments on the higher nervous activities of animals will yield not a few directional indications for education and self-education in man. I, at any rate, can say, looking back on these experiments, that for myself they have made clear many things, both in myself and in others.

episode and of the facts generally. I will attempt to draw two general conclusions—one purely physiological, the second truly practical, one of a certain general application.

In the cortical analysers we are accustomed to distinguish two parts only, the afferent and the efferent, that I would regard the cortex of the hemispheres as constituting an isolated afferent area? Is this true only that in the higher analysers analysis and synthesis of the inducing excitations take place, and it is only from here that ready-made combinations of excitation and inhibition flow into the efferent areas. In other words, only the afferent part is the active cause to which the efferent part, while the efferent is the obedient executive. In the spinal cord the afferent and efferent parts are intimately connected. The investigators always entertain a concrete impression of a unified activity of both parts, and it and I have been prevented from giving a self-contained description of the peculiarities of the afferent part. For instance, the law of one-sided conduction of the nervous process is substantiated by hypotheses that and after the unconstrained progression of the spinal reflection from back to front. But is this law valid for a purely afferent domain? In the cortex of the hemispheres we continually observe both the progression and regression of the excitatory and inhibitory processes. Is this the result of bi-directional conduction along the same paths or, in order to preserve the principle of the law of forward conduction, must we understand that special complicated anatomical devices come into play?

Coming to the more practical of the two conclusions which I have mentioned, I am led to it under the influence of persistent impressions formed over a long series of years devoted to this work. These [illegible] immediate capacity of this activity. Many problems depending on the nervous function which may seem for a given brain entirely impossible of solution nevertheless by means of gradual preparation and careful methods become in the end satisfactorily solved; and if they are to be solved, the type of nervous system of the individual animal must never be forgotten.

I trust that I shall not be thought naïve if I express a belief that experiments on the higher nervous activities of animals will yield not a few physiological indications for education and self-education in man. I, at any rate, looking back on these experiments, feel that for myself they have made clear many things both in myself and in others.

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