

## CHAPTER XII

### A LABORATORY FOR THE STUDY OF THE ACTIVITY OF THE CENTRAL NERVOUS SYSTEM IN THE HIGHER ANIMALS

(Built on the plans of I. P. Pavlov and E. A. Hanike, with funds received from the Ledenzov Society.)

#### DESCRIPTION OF DIAGRAMS OF THE NEW LABORATORY.

THIS laboratory is a part of the Institute of Experimental Medicine in Leningrad. Its façade is shown in Fig. 4. It has three floors as shown in Fig. 5. The first and third floors are for the experiments on animals, and are shown in Fig. 6, altogether eight working rooms ("a" designates the experimental rooms, and "b" the corridors in which are the electrical and other apparatus). The middle or second floor has the same plan except that its rooms are not so high, and it has not the 4-corner rooms for the dogs. It serves for the arrangement of hydraulic and other apparatus.

The following measures were used to eliminate vibrations and the conduction of sounds into the rooms where the dogs are at work.

1. A moat surrounds the entire building, the upper part of which is filled with straw.

2. The eight working rooms on the first and third floors are separated one from the other by the intermediate floor, and by the cross-shaped corridor.

3. The underpinning of the building, *i.e.*, the beams, are immersed in sand-filled rooms.

4. The windows in the working rooms are small and consist of one piece of the thickest ground glass. The doors from these rooms leading to the staircase are double, iron, hermetically closing, and with special layers impermeable to sounds.<sup>1</sup>

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<sup>1</sup> War and revolution delayed the equipment of this new laboratory, and only in 1925 did the work in this building, with mechanical registration of the salivary reflex, start on the large scale aimed at by Pavlov.—*Translator*.



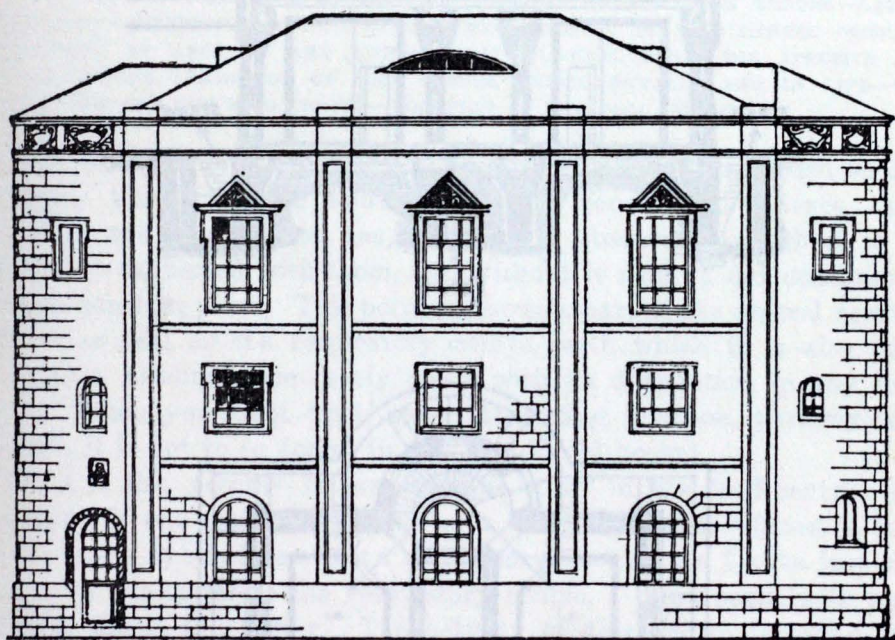


FIG. 4



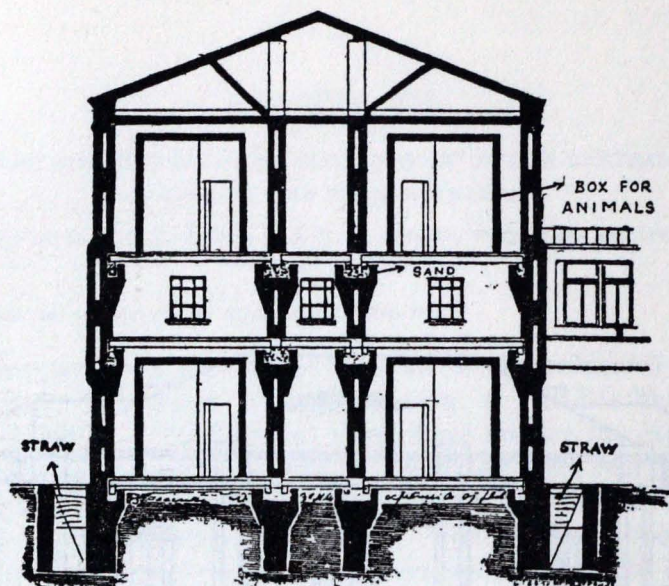


FIG. 5

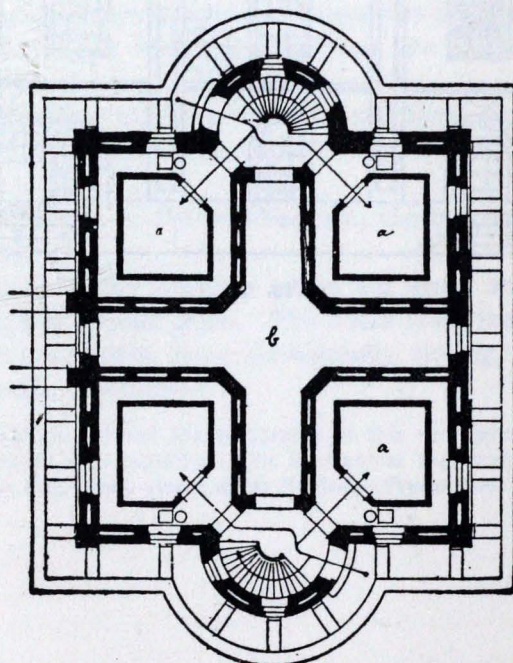


FIG. 6



## CHAPTER XIII

### THE FOOD CENTRE

(Read before the Society of Russian Physicians, and published in *Transactions of the Society of Russian Physicians*, 1910-1911.)

THE ANALOGY BETWEEN THE FOOD CENTRE AND THE RESPIRATORY CENTRE—AUTOMATIC STIMULATION OF FOOD CENTRE BY "FASTING" BLOOD—DELAYED CONDITIONED REFLEX AND DIS-INHIBITION BY DIFFERENT STATES OF THE FOOD CENTRE—LATENT EXCITATION—RECIPROCAL ACTION OF CENTRES—ACTIVITY OF FOOD CENTRE PRODUCES SENSATIONS OF APPETITE AND HUNGER—PHYSIOLOGICAL BASIS FOR APPETITE AND TONICS—REFLEX INHIBITION OF FOOD CENTRE EXPERIMENTALLY AND IN LIFE—THE REFLEX ARC AND THE FOOD CENTRE—LOCATION OF THE FOOD CENTRE.

WITHIN these walls the conditioned salivary reflexes have been spoken of many times. In our knowledge of the conditioned reflexes, there has been one point which has remained in obscurity, though it is indissolubly connected with them, and without it none of our conditioned reflexes can take place. This point concerns a part of the central nervous system as real as the respiratory centre, with which it is also fully analogous, although one rarely meets with its description in any textbook. When you light upon some interesting question, paradoxically enough, it is not to be found in new but in old books!

What is this point? It concerns the study of the food centre. On the basis of our material dealing with the conditioned reflexes, a food centre exists as surely as does a respiratory centre. As I have just said that it is analogous to the respiratory centre, I must begin with some remarks about this latter. The activity of this centre is manifested in the movement of certain skeletal muscles belonging to the thorax. You know that the first impulse for respiration comes from the chemical properties of the blood, overloaded with carbonic acid and other products of metabolism; further, the activity of the centre is conditioned by reflex stimulations from various peripheral organs, particularly from those where breathing occurs—from the lungs. We have an analogous fact relating to the food centre.

How is the activity of the food centre manifested? It is manifested in the exercise of the whole skeletal musculature, when it directs the body of the animal to the nutritive object, and also in the activity of that part of the skeletal musculature which transfers the food from the outside world to the digestive tract. The food centre sets into activity the upper secretory parts of the digestive canal, especially the salivary and gastric glands, simultaneously with the stimulation of certain move-



ments of the skeletal musculature. These two different functions, the secretory and the muscular, are excited by the food centre in a parallel manner, so that by following the activity of one of these functions the experimenter can judge of the activity of the other. Consequently, the work of the salivary glands as studied in the conditioned reflexes is closely connected with the manifestations of the activity of the food centre. By limiting our observations to its secretory activity we lose nothing, but on the other hand we gain in exactness and clearness; for the skeletal muscles serve other masters besides the food centre, and therefore their phenomena are very complicated. The gastric glands are deeply situated, and their activity is not directly and exclusively dependent on this centre but is also conditioned by some other internal stimulations. Only the salivary glands serve as a special representative of the activity of the food centre.

What do we know about this activity? By what is it stimulated, varied and checked? It is clear that the first impulse to the activity of the food centre—by which the animal is set in motion, led to the food, and impelled to take it, by which it secretes saliva and gastric juice—arises from the chemical composition of the blood of the animal which has not eaten for several hours. In such an animal the blood acquires “hungry” properties. This finds a close analogy in the respiratory centre. Just as the respiratory centre regulates the inhalation of oxygen, so the food centre controls the entrance of solid and liquid foodstuffs into the organism. If it is admitted that the chief stimulator of the respiration centre is an internal automatic stimulus, then the same must be accepted in regard to the food centre. Besides the analogy there are facts which support this view.

In general, every centre can be stimulated either automatically or by external stimuli affecting the centripetal nerves in the different peripheral organs. Up to the present time there has been no single testimony to the fact that for the development of the activity of the food centre there is absolutely necessary a reflex stimulus, although this question has been thoroughly studied. Although various nerves leading from the gastro-intestinal tract have been cut, no one has ever seen a disappearance of the positive movement reaction of the animal to food, or, using the usual terminology, a loss of appetite. I, too, have performed many such experiments; I have cut the splanchnic, the vagus, and both pairs of the receptor nerves of the tongue, and the animals felt well, lived long, and took food as normally. We see here the same result as in the case of breathing, after cutting all centripetal nerves, the activity of the centre remains as before.

Consequently, the chemical composition of the blood of a hungry animal is a stimulus for the food centre. This internal automatic



stimulation exists at first in a latent form, and later begins to manifest itself in the movement of the animal toward the food, in salivary secretion, etc. I shall devote some moments to this latent, automatic stimulation, as it has appeared many times in our salivary reflexes. Some experiments of Dr. P. M. Nikiforovsky will illustrate this.

A salivary conditioned reflex was elaborated in a dog, using a light as the conditioned stimulus; in a darkened room a bright flash of light was given before introducing an acid solution into the mouth of the animal. After many repetitions of this combination every flash of the light caused a secretion of saliva. Now the experiments were so altered that the introduction of the acid was delayed for three minutes after the flashing of the light. In such a case there is formed the so-called retarded or *delayed conditioned reflex*, i.e., in the first and second minutes there is no saliva, and only in the third minute, just before the introduction of the acid, does saliva appear.

Analysis of this phenomenon showed that the delay of the salivary reflex developed because of internal inhibition, for during the first two minutes the action of the bright light is inhibited, is delayed by some internal condition.

It can be easily proved that this is really so. The internal inhibition itself may be paralysed or inhibited; in other words, the reflex may be *dis-inhibited*. Every unusual stimulus from the external world may be a paralysing agent of this inhibition, i.e., a dis-inhibiting agent. Thus, if between the flashing of the light and the third minute any stimulus appears, it will inhibit the inhibition, and produce the salivary secretion.

Now, after reminding you of the nature of this *delayed salivary reflex*, I shall cite a fact always observed in this dog. Our dogs are fed usually at 5 P.M. If the experiment with the light is begun at 10 A.M., and the delayed reflex tried, then the salivary secretion begins only during the third minute after the flashing of the light. If the same experiment is made between 3 and 4 P.M., then one does not see the phase of delay, but otherwise there is nothing unusual in the behaviour of the animal, and he conducts himself as he did in the morning. It is clear to us that the latent stimulation of the food centre acts on that centre which is in relation to the acid reflex. We know, however, that between the different centres there is some relation, and that one centre can inhibit another. And as in our case there is during the first and second minute an inhibitory process in the acid centre, the increase of the latent excitation of the food centre paralyses this inhibition, as would any other new stimulus; the increasing latent stimulus dis-inhibits the acid reflex during the first two minutes.

Further I shall give many facts testifying to the existence of this *latent excitation* of the food centre. The question arose, What is the



basis for this latent stimulation? One might think that the stimulation did not reach an intensity sufficient to produce an effect. Certainly this can and must be true, but it hardly answers the question. There is apparently an internal inhibition, which up to a definite moment does not permit the activity of the food centre, as manifested by the secretion of saliva. Several facts substantiate this.

We have before us a dog; there are no manifestations of the activity of the food centre, the dog makes no movements toward the food and secretes no saliva. I introduce into his mouth acid, which certainly is not food, and indeed the motor reaction of the dog is quite different from the food reaction. When the reaction to the acid is ended, the dog begins to make marked motor reactions, particularly toward food, sniffing the air, and prancing on the table, *i.e.*, it is unquiet, and if there is any apparatus near which has been used as a conditioned food stimulus, the dog turns toward it and even licks it, etc. Here we have a positive expression of the activity of the food centre.

Only in this way can I understand that the excited acid centre acts on the food centre, and according to the general law of *reciprocal action* of centres, inhibits it. As the food centre is in a certain degree of inhibition, the inhibiting effect of the acid falls upon this inhibition and inhibits it; the stimulus is freed and the reaction appears. This is the phenomenon of dis-inhibition, with which we meet constantly; it is a striking reality of which we are freshly convinced every day.

Here is another example, from the work of Dr. Kudrin. We have a dog with the posterior parts of the cerebral hemispheres removed. The variation from the normal expresses itself, among other things, in this, that the processes of inhibition are weakened as a usual result of any considerable operation on the cerebrum. If you take a normal dog which has not been fed during the day of the experiment, and begin the séance, giving it meat powder, you get a flow of saliva. After this, there sets in a certain excitation of which I shall speak further. The excitation passes off in about five minutes, the dog becomes quiet, the salivary secretion stops, and some dogs even go to sleep. In the dog upon which we had operated and which had a weakened inhibition, we see the following: As long as the animal is kept without food, it remains quiet, but as soon as it is fed, it is thrown into great excitation; this excited state, with salivary secretion, lasts a long time, sometimes one and a half hours or more. It disappears slowly. An irregular wave-like secretion can be seen, now weaker, now stronger. From physiology we know that if the secretion is wave-like we have to do with a conflict of antagonistic processes; for example, reciprocal action of the pressor and depressor apparatus. If we transfer this conception to our case then we must assume that in the food centre,



when there is a state of latent *excitation*, there is also an element of inhibition.

In order to apply what I have said to human life, I shall add the following: It is clear that the food centre, besides affecting the skeletal musculature and the secretory glands of the first part of the digestive tract, also has another action, with which we, as animal organisms observing ourselves, are also acquainted—it is the production of the sensations of appetite and of hunger. When we speak of appetite in man this is an indisputable fact, but when we refer to the animal world, in order not to indulge in fantastic speculation, we must limit ourselves to registering and comparing the visible phenomena.

Thus is the activity of the food centre represented in our sensations. The fact that the activity of the food centre can be made to manifest itself in dis-inhibition, is observed in human beings; it lies at the basis of therapeutics. If the appetite becomes poor, in order to stimulate it there are often administered not nutritive, but inedible and disagreeably tasting substances; the patient receives something bitter, sour, etc., as a tonic, and the result is the same as that obtained in the dog, when stimulation of the acid centre increases the inhibition of the inhibited food centre, thereby dis-inhibiting it, and causing its energetic activity.

For the respiration centre, there are besides the automatic excitants different reflex stimuli. If both vagus nerves are cut (which bring impulses from the lungs to the respiration centre), then marked and lasting changes in respiration occur. Also in the activity of the food centre, the sensory centripetal nerves play a colossal rôle, especially the taste nerves, the nerves of the chemical receptors in the oral cavity.

Here are some experiments bearing on this. You try in a dog the natural conditioned food reflex, *i.e.*, you let the sight or odour of some food morsel act on the dog for a definite time, say one-half minute, and you note a certain effect—3 to 5 drops of saliva. The amount of secretion can serve as a measure of the irritability of the food centre. After this you let the dog eat, and when it has finished, you see the beginning of an excitation which was not present before; the dog licks with its tongue, sniffs, prances, and begins to whine. If now, immediately after all this is over and the dog is quiet, you repeat the experiment, showing the dog something to eat, you will receive not 3 to 5 drops of saliva, but 10 to 15. With the first feeding you sent reflex impulses into the food centre, and this activity was greatly increased; for the same stimulus produced a much larger secretion.

In our daily life this phenomenon is often seen. It may happen that at the dinner hour there is no appetite and we are indifferent to food, but it is enough to eat one morsel to stimulate the taste nerves, and



an appetite comes immediately. *L'appetit vient en mangeant*. This is evidently an excitation of the food centre through a peripheral reflex stimulus.

But the food centre as well as the respiratory centre is excited not only by these peripheral stimulations (*e.g.*, from the mouth), but is reflexly regulated, both positively and negatively. Every day we see this in our experiments. The following will serve as an illustration: In the beginning of the experiment as I have said I applied the natural conditioned reflex, *i.e.*, showed food to the dog, and received 3 to 5 drops of saliva, and then fed the animal. In the second experiment there was a stronger action, 10 to 15 drops appeared, as a result of joining the stimulation from the mouth to the internal excitation of the food centre. When I repeated this experiment a third time, I received not 10 to 15 drops but 8; in the fourth repetition still less, about 4 drops, and on the fifth trial only 2 to 3 drops. The conditioned reflex gradually disappears, every time I give only a little food, and in the nature of the experiment there arise conditions which inhibit the food centre.

Why is this, and what does it mean? The action certainly starts from the stomach, either from its contact with the food, or from the initial phase of its secretion; in general because food has just entered the stomach. Consequently, in this case there is a reflex inhibition of the food centre. The explanation is clear. When the food has entered the stomach, the food centre must temporarily stop its work until the introduced food is digested. How can it be proved that this is really a reflex from the stomach? The experiments of Dr. Boldirev give an answer. His dog had a fistula of the œsophagus so that the swallowed food did not enter the stomach, and in this case the described inhibition of the conditioned reflex did not develop, and from frequent repetitions of the conditioned reflex, one always received the same amount of saliva.

And who of us is not acquainted with the following fact of our daily life! At a certain time of day you feel the paroxysms of a good appetite, and if you eat only a small amount, the appetite becomes sharper, but after 5 to 10 minutes it completely disappears. Every mother knows this, to her sorrow. Children wait for the dinner hour unwillingly, and beg for something, even though a little, to eat beforehand, but the mother admonishes them with the words, "You will ruin your appetite." And it actually happens that if the child has eaten something earlier, he does not eat at dinner; there has developed a reflex inhibition of the food centre.

It would seem that this is a defect in the organism, but we know of many such cases. And again arises the question, Are these really



imperfections in the animal machine? The entrance of a small amount of food in the stomach temporarily suspends, or at least weakens, the activity of the food centre. There is not much harm in this. If there is a great lack of food material in the organism, then this small amount introduced is quickly digested, and appetite soon returns. The state of affairs might be worse; if the irritability of the food centre began to decrease only when the animal became stuffed with liquid and solid food, there would be, as a consequence, overeating and immoderate overfilling of the stomach.

Thus we see a complete analogy between the respiratory and the food centres. As I have described these analogies, it might seem that they are not so many, but we meet with these facts every day in the laboratory, and we are constantly persuaded that the food centre is a perpetually acting machine just as is the respiratory centre.

Now the question arises, How is this food centre to be described, what are its component parts, and what is its activity? It is certain that it must be counted as a part of the nervous system which regulates the chemical equilibrium of the body. Food must be understood here in a very general way; if a child breaks off and eats a piece of chalk with a sensation of pleasure, it is the work of the food centre.

One must consider this centre as highly complicated and consisting of several parts. Some months ago I expressed the idea that in the central part of the reflex arc, there can be constantly differentiated two halves. This fact is often overlooked. In physiological books there is much written about the centres, but little explained: of what parts do they consist, and do the given cells belong to the centripetal or to the centrifugal nerves? A strange regression has occurred in regard to this. When in the investigation of the spinal cord, knowledge of the reflex arc arose, the view was expressed very clearly that in the central part of the arc there is the central end of the sensory nerve and the beginning of the motor nerve, and this was based on histological findings in the cells of the dorsal and ventral horns. As investigations proceeded and as one penetrated deeper into the central nervous system, he got further and further away from this original and correct conception, and finally did not observe of what cells the given centre was composed. The cells which have been designated as "sensory," I shall, according to the terminology used at present, call receptor cells.

The main point of nervous activity is located, I believe, in the receptor part of the central station; at this point is to be found the impetus for the full development of the central nervous system, realised in the cerebral hemispheres of the brain; for these constitute the basic organ of that most perfect equilibrium with the external world which is incarnate in the higher animal organisms. The centrifugal portion



of the reflex path is purely executive; the same muscles may be employed for a thousand different purposes, and these purposes are determined by the activity of the receptor apparatus; this latter apparatus conditions what functional combinations will be formed by the cells of one or another motor nerve.

I shall return to the food centre. Of what cells does it consist? I state positively that it consists of receptor cells; for they receive different stimulations, from internal as well as reflex stimuli. The nerve centres of the organs in which the activity of the food centre is manifested are, however, simplified to a high degree. In the case of the conditioned reflex we can excite the food reflex through an endless variety of stimuli, and the salivary secretion always proceeds from the same centre, the salivary centre.

As the food centre is a receptor centre it is comprehensible that it must be extremely complicated; like every receiving centre, it performs the most varied reactions; it forces the muscular system to move, now in response to the acid stimulus, now meat, now bread, chalk, etc.; the centre receives the stimulation, and transfers it as an impulse to the executive organ. In short, it is as complicated as is the cortical centre of the optic or auditory nerve.

Where is this centre situated? Physiologists consider the question of topography more indifferently than do pathologists. For physiologists the question of the function and of the activity of the centre is of more importance. That the exact location of a centre is not an easy matter may be seen from the example of the respiratory centre. At first one thought that this centre was in the *medulla oblongata*, and about the size of a pin-head. At present its limits have broadened, it has ascended into the brain, descended into the spinal cord, and no one can exactly define its boundaries. In the same way, one must accept the fact that the food centre is widely spread out. To define exactly its limits is at present impossible. At present we have only a few indisputable facts bearing on the answer to the question.

We must admit that the food centre is situated in more than one part of the central nervous system. Let us recall the pigeon from which the cerebral hemispheres have been removed; he remains motionless for hours, and even though surrounded by mountains of grain, he can not transfer a single one to his mouth. In such a pigeon, however, the activity of the food centre is clearly manifested. Five to seven hours after he has been fed by putting grain into his mouth, he begins to walk, and the more energetically the greater the length of time after feeding. Evidently, this is the activity of the food centre calling out the work of the skeletal musculature. That this is so can be proved by again filling the crop of the bird with grain, whereupon he again



becomes quiet and motionless. From this it follows that a part of the food centre lies lower than the hemispheres. On the other hand, it is also evident that a part lies in the hemispheres, and that the taste centres also are there. Our taste, be it pleasant or disagreeable, undoubtedly represents a nervous stimulation which is reflected in our consciousness. Of course, such a phenomenon can be attributed only to the cerebral hemispheres. The food centre must consist of different scattered cell groups, and in the hemispheres there must be a special large group of such cells. Thus for the solution of this problem we have a certain amount of material at hand, but it is not entirely sufficient. As regards the respiratory centre, however, the state of affairs is not better.

After all I have stated to you it is clear that the food centre is a nervous apparatus for the regulation of the intake of solid and liquid substances necessary for the chemical processes of life. It is just as real and it works just as incessantly as the centre for breathing.



## CHAPTER XIV

### SOME FUNDAMENTAL LAWS OF THE WORK OF THE CEREBRAL HEMISPHERES

(Based on experiments of Drs. N. I. Krasnogorsky and N. A. Rozhansky. Read before the Society of Russian Physicians, and published in *Transactions of the Society of Russian Physicians*, 1910-1911.)

DISCOVERY OF INHIBITION—LAW OF IRRADIATION—TRACE REFLEXES—LAW OF CONCENTRATION—THE SLEEP REFLEX—SLEEP MAY BE CAUSED BY EXPERIMENTAL EXCITATION—CONDITIONED INHIBITION—EXPERIMENT IN WHICH SURROUNDINGS ACT AS CONDITIONED INHIBITOR—EXPERIMENT SHOWING SPEED OF IRRADIATION OF A PROCESS THROUGH THE BRAIN—CONCENTRATION—PRESENT FACTS JUSTIFY OBJECTIVE POSITION TAKEN ON THEORETICAL GROUNDS—FALLACY OF PSYCHOLOGICAL REASONING.

NERVOUS activity consists in general of the phenomena of excitation and inhibition. These are, so to speak, its two halves. I shall not commit a great error if I liken these two phenomena to positive and negative electricity.

The first conception of inhibition in the nervous system belongs to the Weber brothers, and concerns the peripheral nervous system. In 1863, twenty-four years after the discovery of the Webers regarding peripheral inhibition, it was shown that inhibition is a constant phenomenon in the activity of the central nervous system. That was the work of I. M. Setchinov, and the first contribution of Russia to physiology. By the brilliant discovery of the inhibitory centers in reflex activity he laid the cornerstone of Russian physiology. From that time on, central inhibition has attracted much interest and an increasing number of research workers. This inhibition has been established for many kinds of nervous activity, and it may be asserted now that the inhibitory process has the same frequency and importance as the excitatory.

My present report has to do precisely with inhibition, and how it manifests itself in so high a part of the organism as the cerebrum.

As most of you know, the activity of the hemispheres is now being studied by us in an objective way, *i.e.*, without making use of any psychological conception in the analysis of the phenomena, but by comparing only external facts, *viz.*, the phenomena of the external world with the reaction of the animal. The reaction which we use is that of the salivary glands. The conception of the conditioned reflex is the central one in this objective study of the activity of the nervous system. Our conditioned reflex represents a temporary connection between external phenomena and the activity of the organism, in the given case with the activity of



the salivary gland; the usual reflex represents, on the other hand a constant connection. We may not only easily observe the origin of this temporary union, but we may also note that it is a highly sensitive and constantly fluctuating reaction, now stronger, now weaker, now vanishing, so that the study of nervous activity by the objective method is reduced to the study of all the conditions which affect the conditioned reflex. In our case the conditioned salivary reflex is formed by the coincidence of some indifferent phenomenon with the feeding of the animal, or by the introduction of an irritating substance into the mouth. I shall now proceed to add some facts about the physiology of the conditioned reflexes.

I shall give a description of inhibition as it occurs in the activity of the cerebral hemispheres. In previous articles I have already referred to the process of excitation in the brain. The essential feature of this part of nervous activity consists in the fact that when stimulation originates in the hemispheres it must spread and *irradiate* over the cerebrum. We call this the *first law of excitation*.

A mass of facts speaks for this. If you form a conditioned reflex, for example, to the ticking of a metronome, and then try other sounds, you will find that these other sounds at first also produce the salivary flow. Consequently the stimulation from a certain group of cells irradiates over a large part of the cerebrum, and therefore every other auditory stimulus provokes the secretion of saliva. If you make a conditioned stimulus from a tone of 1,000 vibrations, and afterwards try other tones of various vibrations, all of them have an effect. The same holds true for other conditioned stimuli. If you repeatedly combine mechanical stimulation of the skin (pricking) with feeding, finally this pricking calls out every time a secretion of saliva. Now when you subject other parts of the skin to the same pricking, they all cause the salivary secretion. This is because the stimulation has spread over the hemispheres, so that all the points of the skin region of the brain act the same as the first point excited. There is a form of experiment in which we do not connect the activity of the salivary gland with the present stimulus, but with its remains, or *trace*, *i.e.*, we give the stimulus and then allow an interval to elapse after its termination before putting acid into the mouth of the dog, or before feeding it. In the *trace reflexes*, the excitation spreads still further. After forming them to the given stimulus, you will find that saliva flows in response to many different stimuli.

Besides the law of irradiation, there is another law, that of *concentration* of excitation, *i.e.*, the irradiated excitation gathers along certain lines and towards certain foci. This is a fact which is seen in the laboratory every day. If you have formed a conditioned reflex to the



metronome and then repeat this reflex many times, other sounds gradually lose their effect, and at last only the metronome calls out the excitation. And this concentration of the excitation proceeds still further: if you repeat the stimulation with the metronome long enough, it finally happens that only the metronome with the number of strokes you have constantly used will be effective; the dog may react to your stimulation of 100 ticks per minute, but not to one of 96. If in another dog you repeat for many times the mechanical stimulation of the skin at one and the same place, occasionally using it at other places, you will find that the action at these other places becomes less and less and finally disappears, and the former diffused skin irritation becomes concentrated. If you form a conditioned reflex to a tone of a certain strength, then only this one tone, and in the given strength, is effective; tones of greater or of less strength have no action. In these cases of high concentration of the excitation, besides repetition of the given stimulus it is also important to repeat the other neighbouring and related stimuli, but without feeding (*i.e.*, without the corresponding unconditioned reflex).

Now I shall pass over to the study of the other half of the nervous activity, the inhibition process. As you will see from experiments, the same laws that apply to excitation also hold here; inhibition likewise irradiates and concentrates. I shall first speak of sleep, as this state plays an important rôle in experiments with inhibition.

For many years we noticed that our dogs became sleepy; this interrupted our work, for the conditioned reflexes weakened and disappeared. We noticed especially that sleep occurred during thermal stimulation when thermal stimuli were connected with the stimulation of the salivary glands. It proved that thermal stimuli are special producers of sleep, *i.e.*, they condition and cause sleep just as other stimuli call out other activities of the animal. It is interesting that for the production of sleep one may use either warm or cold stimuli, but one must apply them on the same spot on the skin and keep their temperature constant. If you change the spot stimulated or the temperature, the sleep is light and uncertain. On the basis of these experiments we have the right to speak of a *sleep reflex*, and it became obvious to us that the state of sleep is a kind of inhibition of the activity of the hemispheres. Why do we say it is inhibition? Because this state of drowsiness, this sleep reflex, acts on our other conditioned reflexes in exactly the same way as well-known inhibiting agents, in all details as inhibition in general; there is a complete analogy between their actions. I shall bring before you further facts showing that other undoubted cases of inhibition pass over gradually into sleep, evidently on the basis of their mutual relationship.



We now come to other phenomena of inhibition. I form a trace reflex by scratching the skin of the dog for one minute in a definite place, waiting one minute, and then introducing acid into the mouth. Consequently I am undertaking to elaborate a conditioned reflex on the *trace* of the scratching irritation, from what remains of it in the nervous system. After many repetitions, I note the fact that I receive no effect on the scratching; but after I stop the scratching, at the end of another minute, during which I am waiting, the salivary secretion begins; therefore, I have formed a trace reflex out of the remains of the mechanical stimulation which is in the nervous system. But when the experiment lasts longer, there is the following interesting phenomenon: during the scratching, the dog becomes more and more quiet and drowsy and finally falls into deep sleep. If until the moment of the scratching he was awake, then immediately when you begin the scratching he becomes sleepy. The sleep grows deeper and deeper and lasts for an increasing length of time. At last we must abandon our experiments because the dog on the stand is constantly fast asleep. Apparently this is an unaccountable and unexpected process; you repeatedly give the dog acid, which should stimulate him strongly, but instead he sleeps, *i.e.*, the acid becomes a producer of sleep. On the contrary, in the same dog, the same acid reflexes, if they are not present as trace reflexes, *i.e.*, if the conditioned stimulus is given simultaneously with the unconditioned, produce not the slightest sleep.

How is this to be understood? During the scratching we never put the acid into the dog's mouth, consequently the inhibition must develop in this time. This is a peculiar and difficult situation for the nervous system. The inhibitory process must be connected with the presence of the stimulus, but the acid reflex must be excited by the trace of this stimulus. As the inhibition is connected with a strong stimulus, and as the process of excitation is connected with a weak stimulus (the trace stimulation), the inhibition at last prevails and there ensues a diffused effect of this inhibition, which goes over into drowsiness. With the appearance of these phenomena the conditioned reflex itself vanishes.

If you observe these experiments many times, and carefully consider the results, you can find no other more natural explanation for the curious relationship. At first, gentlemen, this explanation may seem artificial, but in the future you will make acquaintance with other facts which will convince you of its truth.<sup>1</sup>

In the next case the relation is simpler. You have formed some conditioned reflex, say, to the ticking of a metronome and this stimulus evokes a constant salivary reaction. Now I add to the metronome an

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<sup>1</sup> The large body of evidence showing that sleep is a state of inhibition is given in chapter xxxii.—*Translator*.



odour, say camphor, and at this moment I do not reinforce the metronome, *i.e.*, I do not feed the dog while the metronome and odour are present. At first the metronome causes a flow of saliva in spite of the effect of the odour. But if we repeat this several times the combination becomes ineffective. The metronome with the odour of camphor does not produce a flow of saliva. Such a state we call *conditioned inhibition*, and the agent which we add to bring it about, we call a *conditioned inhibitor*.

There are some interesting details of conditioned inhibition. I begin my experiments by trying the metronome as a stimulus, and it yields not less than 10 drops. Then I try the combination of the metronome and the camphor, and get no effect. If one to three minutes after I have applied the conditioned inhibitor, I try the metronome alone, it evokes only 1 or 2 drops. What does this mean? It means that the inhibition, which developed in the central nervous system when I applied the camphor and the metronome, has spread out over the large hemispheres and remains thus irradiated; some time must elapse before it disappears. Therefore, if I try the metronome ten to thirty minutes after the combination, then it acts as well as usual.

This fact of conditioned inhibition explained one point for us which for a long time we could not reconcile with our results. When we came across experimental animals which were lively and sprightly and with which we thought the work would proceed quickly and smoothly, we found that in actual use they brought us only despair; on the experimental stand they continually slept, and we could get no kind of conditioned reflex. What is the cause of this? You have a lively animal which loses no opportunity to play, jump around, and lick every person and thing which it sees. You take such an animal and put him on the stand, in a light harness for a support; at first he behaves in the same way as he did when on the ground, and then he tries to get free, pulling and struggling. You combat his efforts, bind his paws, tie his head tighter, etc., and at last you attain your wish—the dog becomes quiet, but at the same time he begins to get drowsy and finally falls into a deep sleep. What does this signify? By vigorous methods you have suppressed, inhibited, the normal reaction of the animal to the external surroundings. In the nervous system of the dog inhibition has arisen, grown stronger, and spread from the motor region over both hemispheres, as sleep. All the surroundings have become transformed into conditioned inhibitory stimuli (inhibitors).

This can be proved as follows: You may gradually reduce the elements of the surroundings, and you will note that at the same time the inhibition becomes gradually less. In the following table from Rozhansky's work, the results of one of his experiments are presented:



## EXPERIMENT OF FEBRUARY 22, 1912 (DOG "KABILL")

<i>Time</i>	<i>Stimulus</i>	<i>Number drops of saliva from parotid fistula during 30 sec.</i>	<i>Remarks</i>
3:50	Metronome	$\frac{1}{2}$	On stand in harness
4:00	"	2	On stand without harness
4:12	"	4	On another table
4:25	"	7	On the floor
4:35	"	3	On new table
4:47	"	0	On stand without harness
4:56	"	0	On stand in harness

You let the dog down on the floor, apply a conditioned stimulus, and receive 7 drops of saliva. If you put the dog back on the table, but without the stand and the harness, 3 drops. On the stand, zero drops.

In the case before you, gentlemen, you see this fact. You call out through the total effect of the surroundings, which acts as a conditioned inhibitor,<sup>2</sup> an inhibition of muscular reaction to the external world, but by inhibiting that you lose the conditioned salivary reflex. Here you have an inhibition which is not limited to those bounds necessary for you, *viz.*, the muscles; the inhibition spreads further and is expressed as a general state of rest of the nervous system. These cases show us that a nervous inhibition called out in a definite place, does not remain in this place, but spreads—irradiates.

Should this not be convincing, we shall present such facts in conclusion as leave no room for doubt, and substantiate the law of which I have spoken. The following experiment has been performed by Krasnogorsky. We have apparatus for pricking the skin fastened at three points on the lower part of the left hind leg; the first on the paw, the second 3 cm. above this, and the third 22 cm. higher. The lowest is ineffective, as this one has never been accompanied by food, and it has ceased to stimulate. The other two have always been accompanied by feeding, and they are therefore positive conditioned stimuli. From former experiments we know that the differentiation of the skin spots is based on the development of inhibition in these places. If pricking at the lowest point has ceased to be effective in provoking a salivary flow, this is because inhibition has developed in this place and prevents stimulation. You can clearly see how the inhibitory process irradiates over a certain distance and you can follow it exactly, and state the distance. When you have applied the lowest stimulus (the inhibitory one) and have received zero drops, and you now try the stimulus at the middle point and another time at the highest point, you see an enormous difference.

<sup>2</sup> This word is used to designate an inhibiting agent. Prof. Pavlov uses the word *tormoz*, meaning "brake."—*Translator*.



If after a certain time following the application of the inactive stimulus, you apply the one lying next to it, it proves to be inhibited, showing that the process of the inhibition has spread to it. If after the same time and under the same conditions you apply the highest one, you find there no inhibition.

In this way you can follow the nervous process and the movement of the inhibitory wave with the eye, and you see that after reaching a certain limit it does not spread further.

Now one can see also with what velocity this inhibition wave spreads in the nervous system and how far it travels. If one and a half minutes after the application of the inactive stimulus, whose inactivity is based on the development of inhibition at this point, you try the effect of the other stimuli, you will see that at the distance of 3 cm. the inhibition is clearly present, but at 22 cm. it is absent. Consequently one and a half minutes after the application of the inactive stimulus, the inhibitory process is not present at the point corresponding to the highest stimulating apparatus. If, however, you try the effect of this uppermost apparatus not one and a half minutes, but only a half minute after the inactive apparatus, you will find that the inhibition is present there; you thus see clearly how the wave of inhibition spreads out over the nervous system, and how it contracts. This fact seems to me an unmistakable illustration of the law of *irradiation* of inhibition; no other explanation can be given.

In conclusion, one is forced to say that inhibition spreads over the hemispheres in the same way as does excitation.

We also have many facts which show that inhibition is concentrated just as is stimulation.

We have, for example, a conditioned reflex (metronome), and a conditioned inhibitor (camphor). If the latter has been applied for only a short while as an inhibitor, and if you try the metronome five to ten minutes after the camphor, the metronome produces no effect. But if you continue the experiments further, *i.e.*, if you always reinforce the metronome by the unconditioned stimulus, but do not thus reinforce the combination of metronome and camphor, you will see how the process of inhibition is more and more concentrated. If now the metronome alone is tried five to ten minutes after the combination, it acts exactly as formerly, giving a full reaction. An apparently similar phenomenon is observed in the following fact. If you have a tone of 1,000 vibrations, and try to make a differentiation of a note varying from it by only one-eighth tone, *i.e.*, you accompany the tone of 1,000 vibrations by feeding, but not that which differs by one-eighth tone—finally these tones are differentiated; the one is effective, the other is not. This differentiation depends upon the inhibition process. If you try the tone of



1,000 vibrations very soon after trying the differentiated one-eighth tone, the former will be inhibited. If a longer time has elapsed after the differentiation, then the inhibition concentrates, *i.e.*, the trial of the differentiated (negative) tone after a short interval has no more an inhibitory effect on the active (positive) tone (1,000).

Similar facts were observed accidentally in other dogs with which we worked. We cannot yet bring these facts into any scheme, we are only observers, but apparently they have to do with the law of irradiation and concentration of inhibition.

Here is a series of dogs. One of them, you notice, has developed a condition of drowsiness which affects all the activity of the cerebrum. Then there is another type.<sup>3</sup> He does not sleep on the experimental stand. Consequently, inhibition did not reach its high point and manifest itself in a general inactivity of the hemispheres. In this dog inhibition is manifested by the inactive state of the muscles; the animal stands there like a statue. The inhibition is not limited to the muscular system, but passes over to the salivary gland. Now the last type of dog: It is lively as long as it remains on the floor. In the stand it does not sleep, but there is a state of muscular rest; it stands as if cut out of wood; however, the inhibition is limited to the muscular system and does not affect the salivary glands, which are strongly excited. In different dogs we have different degrees of irradiation of inhibition, and a certain definite concentration of this inhibition in consequence of one and the same inhibiting influence of our surroundings. The last dog has an ideally elaborated nervous system; inhibition remained at that point where we desired it, affording muscular rest to the dog, but not going any further than that; the salivary reflexes were unaffected and intact.

Even though the last-mentioned facts represent only observed material, their meaning is unmistakable; at one and the same time you see the phenomena of conditioned inhibition, and the phenomena of the definite limitation of this inhibition. The above facts give us reason, I think, to say that inhibition bears the same relation to its basic law as does excitation. Just as excitation at first irradiates and then concentrates, so does inhibition.

These facts offer substantial ground for the belief that excitation and inhibition are two different sides, two manifestations of one and the same process.

This is all, gentlemen, that we wanted to demonstrate and communicate to you. In conclusion I count it as not without interest to tell you of some further and more intimate facts which we collected in our

<sup>3</sup> For several types of dogs, see chapter xvii of Pavlov's book, *Activity of the Cerebral Hemispheres*, and chapter xxxix of this volume.—Translator.



investigations by this new method and which can be understood only much later.

When ten or eleven years ago we started to apply the objective method of studying the nervous activity of the dog, our situation was difficult. We were accustomed, as were others, to represent the dog as willing and thinking. As we were considering the objective point of view, it seemed highly improbable that there could be success. But we made our decisions on theoretical grounds and began working objectively, although on the one hand, the field of investigation appeared infinite, and, on the other hand, there were almost no general facts to begin with. Our position was a hard one; for we had no facts, no basis, to show us that our decision was right. We could only hope to attain to something, but at the same time there was the doubt whether our work would be recognised as worthy of science. Afterwards moments of success gave us courage.

For years we collected many facts. Our assurance began to increase. Still I must admit that doubts also increased, and did not leave me even up until a short time ago, although I did not speak of them. Many times I asked myself the question, Have I taken the right position in considering the facts from only the external aspects, or had I not better return to the old point of view? Such a predicament was repeated and filled my thoughts, but finally the matter became clear. Every time there was an appearance of a new series of facts—and they were difficult ones, almost incomprehensible from our point of view—doubts became greater. Why was this? What was the matter? It is plain enough. Because in these new facts we had not yet found any causal relations, we could not then explain what kinds of connection existed between the phenomena, by what they were conditioned. But when we had explained these connections, when we saw that from a certain cause follows this or that effect, at that self-same moment we felt calm and satisfied.

Why had we formerly, like cowards, returned to the old subjective methods? The secret is simple: because the subjective method is the method of thinking without considering real causes, because psychological reasoning is indeterminate reasoning, recognising phenomena, but knowing not whence they come nor whither they lead. I say, "the dog thought," "the dog wishes," and I feel satisfied by that explanation. But this is fiction. This is no cause for the phenomena. The psychological explanations were fantastic and without basis. Our objective explanation is truly scientific, always based on facts, always seeking for the cause.



## CHAPTER XV

### DESTRUCTION OF THE SKIN ANALYSER

(Read before the Society of Russian Physicians, and published in *Transactions of the Society of Russian Physicians*, 1910-1911.)

EXPERIMENT WITH DOG WITHOUT MOTOR REGION OF BRAIN; CONDITIONED REFLEXES AFTER SUCH AN OPERATION MAY BE NORMAL BUT LACK ADAPTATION BECAUSE OF DESTRUCTION OF SKIN ANALYSER—LOCOMOTOR ACTIVITY A CHAIN OF REFLEXES—MOVEMENT ANALYSER—PSYCHOLOGICAL ANALYSIS OF THE GIVEN CASE LEADS ONLY TO CONFUSION.

OUR report to-day consists mainly in the demonstration of a series of experiments based on observations by Dr. N. M. Saturnov. At first please notice and consider the following phenomena: The dog before you is placed on the floor, and, as you see, remains for a long time in the same position as if his legs were frozen. One, five, ten, or twenty minutes may pass without his changing this attitude. You see the dog moving his head, but his legs very seldom if at all. There must be some special reason for this. The next symptom: I stroke the animal very gently, and he barks and growls. I can keep this up for an hour or more, and a threatening reaction in the form of barking is provoked. And thus again and again for months. Formerly, when the dog was in a normal state, a series of conditioned reflexes was elaborated; skin reflexes of two sorts (thermal and mechanical), and afterwards a sound reflex. The mechanical irritation of the skin was the oldest of these conditioned reflexes; every time pricking was applied to the skin, saliva flowed. Later, we extirpated some parts of the so-called motor region of the cortex, and then this condition now present gradually developed.

Now that we have described and you have seen the behaviour of this dog, we shall inquire into the state of his conditioned reflexes. First, let us try out our conditioned mechanical reflex from the skin, which, as we have said, was present for a year or more before the operation, and which was always exact and unfailing in its action. Dr. Saturnov, who has worked with this animal, will perform the experiments before you.

Now as the skin is pricked you notice that the dog exhibits no movements connected with eating, and no drop of saliva appears. This is a result of the operation; the conditioned skin reflexes have disappeared, in spite of the fact that these were our oldest conditioned reflexes, and that even after the operation mechanical stimulation of the skin was



combined with eating more than 500 times. Thus, the conditioned skin reflex is impossible for this animal. This fact is plainly in accord with the behaviour of the dog we have seen on the floor, as described above. From what we have seen in this dog we might think that his higher nervous activity has been completely destroyed. We shall now see his other characteristics and you will learn that they are quite different.

Before the operation the sound of a bell was connected with the activity of the salivary glands and was their conditioned stimulus. This reflex was quickly restored after operation—after six combinations of the bell with eating. We formed a new sound reflex to a tone of 300 vibrations; on the twentieth combination the saliva appeared, and by the fiftieth trial the reaction had become constant. Consequently, new conditioned reflexes of hearing are easily formed, and the old ones (formed before the operation) readily restored. Here is an experiment illustrating this. You see that the dog is now quiet, and that saliva does not flow spontaneously. The bell begins to ring. The dog moves and looks for food, and 9 drops of saliva appear—clearly a normal reaction. The bell is obviously a conditioned stimulus. This demonstration is so evident that it is not necessary to show you other sound reflexes.

With the same facility a conditioned reflex to the smell of camphor was formed after the operation. This odour *per se* does not provoke saliva, *i.e.*, it is not an unconditioned stimulus for the salivary gland. It acts only when it is brought into temporary connection with the secretion. At the twelfth combination of the camphor with feeding there is a movement of the dog (the food reaction), and on the twenty-second, a salivary reaction is observed. Now we will demonstrate the experiment. In this hermetically sealed bottle there is camphor. We will break the seal during the experiment, and by means of a rubber bulb, diffuse the odour under the nose of the dog. We begin the experiment. The dog stands quietly, and saliva is not flowing. Now we liberate the vapour of the camphor. The dog gives a positive movement reaction (food), and there are 5 drops of saliva. It is evident that the odour of camphor is conditionally connected with the salivary reflex.

These are the facts which we wished to show you to-day. As you can see, they are exact and very clear phenomena. Let us consider them in more detail.

First you note a peculiar behaviour of the animal. The dog does not move spontaneously, but whenever he is touched, he exhibits a threatening reaction, *i.e.*, he snarls, growls, and shows his teeth. If you had seen only this much of his behaviour you would have said that he was maimed or injured. But, on the other hand, when we put him on the table and test his complicated nervous activity by delicate methods, we



find him perfectly normal. How is this to be understood? What has happened? The analysis of this question is rather simple.

Comparing all the facts before you, you will find no difficulty in arriving at an explanation. The strange behaviour must be considered as an absence of the signals which normally come in from the skin. If you observe the animal more closely, you will see that when the dog is forced to move among hard objects which might strike against him, there is a lack of adaptation to the surroundings. The normal activity of the skin analyser has been destroyed.

From the standpoint of our knowledge of conditioned reflexes—the objective method of investigating the activity of the higher nervous system—we conceive of two mechanisms: first, the mechanism of a temporary connection; second, the mechanism of the analyser, *i.e.*, that nervous apparatus which has the task of decomposing the entire complexity of the external world into its elements. Thus we have the ear analyser, the eye analyser, etc. The skin analyser in this dog is destroyed, *viz.*, its central end in the highest part of the central nervous system has been extirpated, and therefore the delicate, exact, and accommodating connection of this analyser with the outer world is absent. Stroking, which normally brings about a reaction of contentment, produces in our dog without the upper end of the skin analyser an opposite reaction—one of defence, issuing from the lower-lying centres. That this is actually so is proved by the disappearance of the skin reflex after operation, and the consequent loss of delicate connections with the external world through the skin analyser. There have remained only the skin reflexes of the lower centres, and these have been constant under varying conditions for several months. We have repeated the experiments hundreds of times, probably a thousand times, and the effect is always the same.

One is inclined to think that the first symptom to which I called your attention, *i.e.*, the position of the dog for some time in an unchanging attitude, is dependent on the same cause. There are data showing that the entire locomotor activity is a chain of reflexes in which the end of one reflex is the beginning of the next; this chain begins with the normal stimulation of the sole of the foot through its contact with the ground, etc. It is natural to suppose that those stimuli which are the initial stimulation for walking are lacking in this dog, and he therefore remains motionless.

The behaviour of this animal can be explained thus: one of the chief stimuli and regulators of movement, *viz.*, the skin, having been greatly restricted in its receptor action by the operation, affects only the lower centres; therefore, the more complicated connections for motion are absent, and only the gross and unrefined ones remain. Everything relating to the higher activities effected through the other analysers remains undis-



turbed; for these analysers are intact. From the nose and the ear you can produce a normal reaction, and differentiation by means of them is unimpaired. For example, the bell had an effect, but another sound (the metronome) did not (differentiation), as the latter had not been accompanied by food. Odours and sounds produced not only the salivary, but also the corresponding movement reaction. If the dog is standing on the floor as usual, and if you now begin to stimulate it by the bell or the odour, moving them from place to place, the dog is set into motion and follows them (as signals of food), behaving as a normal animal.

Besides the aforementioned facts, there is another point of interest. Though this dog has lost the central part of the skin analyser, and has therefore a marked defect, he shows no symptoms of ataxia; he walks easily, scratches energetically, and can even deftly scratch the back of his ear with his hind foot, and can get himself out of difficult situations; if there is any ataxia, it is very slight.

If these are the facts, then we have luckily come upon a case in which the function of the skin analyser is impaired, but not that of the movement analyser. One must now add to those analysers generally referred to as eye, ear, skin, nose and mouth, the *analysers of movement*, which have to do with centripetal stimulations arriving from the motor apparatus—from the muscles, bones, etc. Thus besides these five external analysers, there is a sixth, the delicate internal analyser of the motor apparatus, which every moment must signalise in the nervous system the simultaneous position and tension of all the separate co-ordinating parts engaged in the given movement. For this analyser there is a special place in the brain—the motor region of the cortex. Our dog is interesting because he represents an example of an isolated defect of the skin analyser without impairment of the movement analyser. Further investigation must proceed in this direction—it must examine the individual peculiarities of these two analysers. Such a study will guide us, I think, in the orientation of those peculiarities shown in dogs with destruction of the frontal parts of the brain.

I now ask your attention to the following: Every experiment, like the one shown to-day, gives us the possibility of making a certain test, of comparing the psychological with the objective point of view concerning the observed phenomena. If you consider the given animal psychologically, you will be seriously perplexed. When you see the dog only on the floor you must conclude that he is stupid and inert. Stroke the dog as much as you will, without doing him any harm (we are doing him no harm—we are only feeding him), and yet the animal always reacts as if he wished to attack you. Put upon the table, the same animal becomes clever and normal, as shown by his numerous and



delicate connections with the phenomena of the surrounding world. A sound after being several times repeated and accompanied by feeding, becomes the signal for food, and the same is true with the odour of camphor. Here is an apparent contradiction; at one time the dog is stupid, at another, clever. I come to the same conclusion if I compare the movement of the dog's head and feet. The head moves constantly and makes the customary orienting motions, but the legs are motionless—again a contradiction; judged by his head and neck the animal is normally active, but judged by his legs, he is as if paralysed.

The activity of the animal is conditioned by the corresponding stimulations. In those parts of the animal where the stimulation apparatus remains whole, we see normal and complicated relations; in those parts whose corresponding stimulating signals have been injured, there is always an absence of some of the normal activity.<sup>1</sup> From the nose and the ear there are complex reflexes, but from the skin, only the reflexes of the lower brain centres remain.

This is comprehensible because the central portion of the signalling apparatus of the skin, resident in the hemispheres of the brain, has been destroyed. The peculiar movement phenomena of the head and feet can also be understood. The impulse for locomotor activity, for movement of the feet, is lacking, but it is present for movement of the neck and head; for during the operation the upper part of the brain, corresponding to the lower parts of the body, is destroyed, but not the lower part of the motor region corresponding to the upper part of the body, the head and the neck.

For me it is obvious that the confusion and perplexity arising from consideration of the behaviour of such an animal from the psychological standpoint disappears after the physiological analysis. Ultimately, we may be able to state exactly what is lost in a given animal and what remains.

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<sup>1</sup> This is very strong evidence in favour of the physiological point of view.—*Translator.*



## CHAPTER XVI

### THE PROCESS OF DIFFERENTIATION OF STIMULATIONS IN THE HEMISPHERES OF THE BRAIN

(Based on the experiments of Dr. V. V. Belyakov. Read before the Society of Russian Physicians, and published in *Transactions of the Society of Russian Physicians*, 1911-1912.)

MECHANISMS OF THE ACTION OF THE CENTRAL NERVOUS SYSTEM BASED ON TEMPORARY CONNECTIONS AND ANALYSERS—ANALYSER AND ANALYSIS—DIFFERENTIATION BASED ON INHIBITION—EXPERIMENT SHOWING DIS-INHIBITION AND DIFFERENTIATION—SEAT OF INHIBITION DURING DIFFERENTIATION—COMPARISON OF PHYSIOLOGICAL AND PSYCHOLOGICAL EXPLANATIONS OF THESE EXPERIMENTS SHOW LATTER IS INADEQUATE—PHYSIOLOGY OF THE ANALYSERS; LOCALISATION OF CENTRES.

THE objective study of the higher nervous activity of the animal, the doctrine of conditioned reflexes, has arrived at a conception of two of the chief mechanisms of the central nervous system, *viz.*, the mechanism of *temporary connections* and the mechanism of *analysers*.<sup>1</sup> The present report concerns the physiological rôle and the activity of the analysing mechanisms.

I remind you that by analyser we mean a nervous apparatus consisting of the following parts: a certain peripheral end (eye, ear, etc., commonly called "sense organ"), the corresponding nerve, and finally the brain terminus of this nerve, *i.e.*, the group of cells in which this nerve ends. We have to do with the uppermost part of this nerve, lying within the cerebral hemispheres. This apparatus is rightly called an analyser because its function consists in the decomposition of the complicated external world into its smallest possible integral parts. Its activity may be divided for study into two parts: on one side the limits of analysis are defined, and on the other the mechanism of analysis is investigated. To-day we shall deal with the second part of this problem, *i.e.*, with the mechanism.

In order to explain to you how we represent the mechanism of analysis, I shall give a detailed experiment. We take some agent of the external world acting on one or another analyser, some sound, smell, mechanical stimulus of the skin, etc., and try to bring it into temporary connection with a certain physiological activity, always in our experiments with the activity of the salivary gland. We introduce the given agent into the connection we desire by combining it with the usual physiological stimulus of this organ.

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<sup>1</sup> For definition of "analyser" see chapter ix, footnote 2.—*Translator.*



After some repetitions we attain what we wished; the agent which formerly had no effect on the organ, is now brought into relation with its activity and soon becomes its stimulus. Every time it acts, it awakens the activity of the organ, in our case the secretion of saliva. Now when the combination is formed, if we try other stimuli from the same receptor surface of the body, they act effectively, although they have never before coincided with the activity of the organ. For example, if I have connected a definite tone with the activity of the salivary gland, and then try other tones or sounds, they also are effective. But this is only a stage, a definite phase. If we repeat many times our chosen agent, we notice that our stimulus, which had at first a general character, gradually becomes specific. Formerly, the most diverse tones and noises were effective, then many of these became inactive, and finally the sounds which function as stimuli become fewer and fewer and consist only of those tones closely related to our original tone. We are now convinced that this gradual transition from a diffuse, widely spread excitation to a special, narrowly limited one, this differentiation, comes about owing to the development of an inhibitory process at some point in the nervous system.

What are the grounds for our conviction? It rests upon a basis of constantly repeated facts. They are the following:

I choose, for example, a tone of 1,000 vibrations; this has become a stimulus of the salivary glands, and by means of many repetitions I have brought about a condition in which 1,000 vibrations stimulates, but not a tone even so close as 1,012. Consequently, the field of stimulating sounds has narrowed, and a tone which differs by only 12 vibrations, *i.e.*, one-eighth of a note from the original, does not stimulate. Such differentiation of the stimuli has taken place through the development of an inhibitory process, as I have said, and the proof is as follows: I take a tone of 1,000 vibrations and it calls forth a flow of saliva; then another, of 1,012 vibrations, is applied and there is no saliva; complete differentiation between the two tones has occurred. If immediately after the 1,012 tone, I apply my original one, it is inactive and I must wait some minutes before it becomes effective again.

This is to be understood in the following way: When the differentiated tone is applied, there results an inhibitory process in the nervous system, and if during this time I apply my originally active tone, the inhibitory process suppresses its action. It is necessary for some time to elapse before the tone will be effective, in order that this inhibitory process may disappear in the nervous system. The fact that inhibition develops here is unmistakable.

The process of analysis and the process of differentiation must be presented thus: If our chosen special agent is brought for the first time



into connection with a definite physiological function, then the stimulation called out by this agent, coming to a certain point of the cortex, irradiates or spreads over the corresponding receptor centres; and thus not only the single point in the brain end of the given analyser enters into the definite connection, but the whole analyser or a greater or smaller part of it. And only later, owing to the opposition of the inhibitory process, does the field of influence of the stimulation become smaller until at last an isolated action is obtained. This is the important fact explained by the foregoing experiment.

This is, obviously, only the beginning of the matter, and manifold questions arise. Some of these are answered in the experiments of Belyakov, the protocols of which I shall give. The first experiment shown is as follows: If we are right in saying that differentiation has for its basis the process of inhibition, then we should be able to destroy this differentiation at any moment by destroying the inhibition. Why? Because in the investigation of the complicated nervous activity we constantly encounter the process of *dis-inhibition*.<sup>2</sup> If differentiation is really based on inhibition of all the neighbouring stimuli which were formerly active, it should be possible to dis-inhibit them and to make them again effective. We can show this in the accompanying protocol.

TABLE I

Dog "DOGONYAI," MAY 9, 1911.\*

Time	Conditioned Stimulus	Quantity of Saliva in Drops			
		First $\frac{1}{2}$ minute	Second $\frac{1}{2}$ minute	Third $\frac{1}{2}$ minute	Total
10:58	Trumpet	Dog barking	Dog barking	Very excited	Shivers
10:58.30	$\frac{1}{8}$ tone	6	3	2	11
11: 3.—	$\frac{1}{8}$ "	1	1	1	3
11: 7.—	$\frac{1}{8}$ "	3	1	1	5
11:11.—	$\frac{1}{8}$ "	$1\frac{1}{2}$	$1\frac{1}{2}$	—	3
11:15.—	$\frac{1}{8}$ "	trace	—	—	trace
11:20.—	$\frac{1}{8}$ "	$\frac{1}{2}$	—	—	$\frac{1}{2}$
11:24.—	Original tone	1	Feeding with meat powder		—

These are the results of our experiments on our dog "Dogonyai," in which, during the course of many months, we had elaborated and used a differentiated tone varying from the original by  $\frac{1}{8}$  of a note.

<sup>2</sup> The reader will remember what has been said concerning *dis-inhibition* in footnote 1, chapter viii, and in chapter xi. All the processes of internal inhibition can be dis-inhibited by extra stimuli, and as the process of differentiation is based on internal inhibition, the differentiated (negative) stimuli can also be dis-inhibited, i.e., in the presence of extra stimuli they will manifest an excitatory action instead of the usual inhibitory one.—*Translator*.

\* The trumpet is applied as an unusual and strong stimulus (extra-stimulus);  $\frac{1}{8}$  tone means  $\frac{1}{8}$  note higher pitch than the original tone used as the conditioned stimulus. The  $\frac{1}{8}$  tone is the negative or differentiated tone.



That is, the differentiated tone had no effect in calling out a secretion, while the original promptly stimulated a flow. Now we allowed the sound of another musical instrument to act on the dog—a trumpet with a very shrill sound composed of many overtones. It produced a marked effect on the animal, which began to bark, break loose from the stand and to tremble. When he had become quiet after the sound of the trumpet had ceased, we tried the differentiated (negative) tone 1,012, and there was no trace of differentiation. First, 6 drops were obtained during 30 seconds, exactly the same as received from the original tone (1,000 vibrations), and in the next two consecutive half minutes, 3 and 2 drops respectively, a total of 11 drops. After five minutes we repeated the same tone, and it acted, giving 4 drops in one minute. Four minutes later its action had not entirely ceased. If one examines the last column of the table, showing the total amount of saliva secreted, he sees that it is considerable. It looks as if the differentiated tone acted as a usual stimulus; for on being repeated, its effect was gradually extinguished. This dis-inhibition lasted for 10 to 15 minutes, and there was no trace of differentiation. Of such experiments we have many. Here we have given one which clearly illustrates the fact that the differentiated tone is extinguished just in the same way as is a well elaborated and old conditioned reflex.

And further. If inhibition lies at the basis of the process of differentiation, then it should be possible to reinforce, accumulate, and summate this inhibition. How? By several successive repetitions of the differentiated stimulus. Table II describes such an experiment:

TABLE II  
DOG "KRASAVETS," JUNE 1, 1911 \*

Time	Stimulus	Number drops of saliva for ½ minute from	
		Parotid Gland	Submaxillary Gland
1:45	Positive tone	9	10
1:53	Negative tone	0	0
1:54	Positive tone	8	7
2:10	Positive tone	8	7
2:25	Negative tone	0	0
2:28	Negative tone	0	0
2:31	Negative tone	0	0
2:32	Positive tone	5	3
2:55	Positive tone	10	8

In "Krasavets" a certain tone had been used as a conditioned stimulus. The first row of figures in Table II shows a usual size of the con-

\* Positive tone = the one which has been accompanied by feeding.

Negative tone = the one which has not been accompanied by feeding.



ditioned reflex—9 drops from the parotid and 10 from the submaxillary gland. Now we try the differentiated tone which is about  $\frac{1}{2}$  note lower. It has no action. We apply it once and one minute later repeat the original (*positive*) tone, and we see that if there is any inhibition here it is very small—instead of 9 drops we have 8 and 7. Now we repeat the same differentiated (*negative*)<sup>3</sup> tone three times in succession, *i.e.*, we accumulate the inhibitory action, and we see that the habitual (*positive*) tone applied (as before) at the same interval after the application of the differentiated (*negative*) tone, now becomes sharply decreased, giving 5 and 3 drops instead of 8 and 7. If we allow some time to elapse for the dispersion of this inhibition, and again try the *positive* tone, we see that it has recovered its usual effect—10 and 8 drops. Thus can we say that inhibition, which lies at the basis of differentiation, can be summated by repeating the differentiated (*negative*) stimulus.

Here is another fact following from this. If inhibition lies at the foundation of differentiation, then the more difficult the task of differentiation, the greater will be the inhibition. It is obvious that it is more difficult to distinguish between two tones differing in pitch by only one-eighth of a note than it is to distinguish between two tones differing by two full notes. One may suppose that also the intensity of the inhibition process will vary. The more delicate the differentiation, the stronger will be the inhibition, and vice versa. Here is an experiment:

TABLE III  
Dog "DOGONYAI"

Date	Time	Conditioned Stimulus	Drops of saliva for $\frac{1}{2}$ minute
June 11, 1911	11:25	Positive tone	4
	11:40	$\frac{1}{8}$ Negative tone	0
	10 minutes { 11:44	$\frac{1}{8}$ Negative tone	0
	11:54	Positive tone	1
	12:15	Positive tone	3
July 6, 1911	1:20	Positive tone	5
	1:40	Negative tone	0
	10 minutes { 1:44	Negative tone *	0
	2:54	Positive tone	4
	2:10	Positive tone	4

Under normal conditions we get in the dog "Dogonyai" 4 drops of saliva from the positive tone (1,000 vibrations). Afterward we try

<sup>3</sup> It seems convenient to refer to these two tones as positive and negative, using positive to mean the stimulus which has been accompanied by feeding and produces a flow of saliva, and negative to mean the stimulus applied later, which is not accompanied by feeding and which usually produces no flow of saliva (the differentiated tone.)—*Translator*.

\* The negative tone differs from the positive by two musical steps.



the negative tone (1,012), which does not produce saliva. For two successive trials it gave zero drops. Ten minutes later we try the positive tone again, and it is inhibited. The inhibition of the differentiated tone lasts for some time and is expressed in the decreased effect of the positive tone. Let us compare this experiment with the second (*see* experiment of July 6, 1911, Table III). In the first row, we see a normal size of the conditioned reflex—5 drops. Then we try a differentiated tone, but one which is easily distinguished, *i.e.*, one which differs from the positive tone by two whole notes. This negative tone is repeated twice. After ten minutes we try the positive tone. It has not changed in the least; it gives 4 to 5 drops. Thus we see that a fine differentiation (with the one-eighth, negative, tone), caused an intense inhibition, but a coarse differentiation (the negative tone differing by two notes) did not evoke any marked inhibitory effect.

There arises an interesting question: Where does this inhibition which lies at the basis of the differentiation take place? Naturally one thinks that it develops in the corresponding analyser, *i.e.*, in that place where the stimulations are analysed. But this must be proved. Now I will give an experiment which leads to the conclusion that the inhibition occurs exactly in that analyser to which the given inhibitory stimulus belongs. We tried to dis-inhibit the differentiation by applying various stimuli coming through different analysers, with the results as shown in Table IV.

TABLE IV  
DOG "KRASAVETS"

Date	Time	Conditioned Stimulus *	Quantity saliva in drops for $\frac{1}{2}$ minute from	
			Parotid Gland	Submaxillary Gland
June 24, 1911	1:20	Positive tone	9	11
	1:40	Negative tone		
		plus gramophone	3 + 2	5 + 3
	1:55	Positive tone	10	12
	2:05	Positive tone	12	14
June 25, 1911	2:35	Positive tone	8	10
	2:45	Positive tone	12	13
	3:00	Negative tone	$\frac{1}{2}$	trace
		plus light		
	3:20	Positive tone	10	12
June 28, 1911	3:25	Positive tone	10	12
	3:45	Positive tone	12	13
	70	Negative tone	trace	0
		plus odour of camphor		
	4:00	Positive tone	10	12

\* The negative tone was  $\frac{1}{2}$  note lower than the positive.



The first row in the table shows the usual normal secretion to the positive tone, 9 to 11 drops. Thereafter, together with the negative tone is applied a new stimulus which should produce the orienting reaction of the animal. The stimulus used was the music of a gramophone and it gave a considerable dis-inhibition. Instead of the usual zero which we should expect, the differentiated tone together with the gramophone gives 3 and 2 drops (for each 15 seconds) from the parotid gland, and 5 and 3 drops from the submaxillary. Thus the gramophone dis-inhibits the negative tone. In the following experiment (Table IV, June 25, 1911), we applied a light stimulus as the dis-inhibitor; it had almost no effect. Differentiation remained. The light stimulus has not dis-inhibited—it has not destroyed the differentiation. Finally, in the third experiment (Table IV, June 28), we applied camphor odour as the dis-inhibiting agent. This also had no effect. Thus we used three different stimuli; light, gramophone, and camphor, for the eye, ear, and nose analysers respectively. Our differentiated (negative) tone affects the ear analyser, and the gramophone which affects the same analyser, proves to be a strong dis-inhibiting agent; but the stimuli falling on the eye and nose analysers are without effect. Although the light is only a weak stimulus, the same is not true of the odour. Odours are strong stimuli, but, as you see, the odour did not dis-inhibit our negative tone.

We have other experiments which directly prove that the inhibition takes place in the analyser of the differentiated stimulus. Such an experiment is given in Table V.

TABLE V  
DOG "DOGONYAI"

<i>Date</i>	<i>Time</i>		<i>Conditioned Stimulus *</i>	<i>Quantity saliva for ½ minute</i>
June 2, 1911	11:05	} 10 minutes	½ Negative tone I	0
	11:15		Whirligig	2
			Whirligig	2
June 4, 1911	11:10	} 10 minutes	½ Negative tone I	0
	11:20		Positive tone	1½
	11:40		Positive tone	4
June 14, 1911	10:40	} 1 minute	⅛ Negative tone II	0
	10:44		⅛ Negative tone II	0
	10:45		Whirligig	½
	11:10		Whirligig	3
June 15, 1911	10:55	} 1 minute	⅛ Negative tone II	0
	10:59		⅛ Negative tone II	0
	11:00		Positive tone	trace
	11:40		Positive tone	4

\* Negative tone = that not accompanied by feeding.

Negative tone I = ½ step variation from positive tone.

Negative tone II = ⅛ step variation from positive tone.



Here we compare two conditioned reflexes, one on a tone and the other on a whirling object (whirligig). After the applications of the negative tone there remain in the central nervous system the inhibitory traces the action of which is compared by measuring the size of the reflex to a positive stimulus, a tone (of the same analyser as the negative stimulus, *i.e.*, the ear analyser) with the size of the reflex to a positive stimulus (whirligig) from another analyser (the eye analyser). At first a coarse differentiation was tried out (a half note). This differentiation by "Dogonyai" resulted in a weak inhibition; for in him we had elaborated a much finer differentiation, one on an eighth tone. The effect of the inhibitory traces from the differentiation we tried on a reflex through the eye analyser, *viz.*, on the whirligig. This reflex was not inhibited by the application of the negative tone, but gave the same number of drops as it had given on a previous trial that same day, *i.e.*, 2 drops. Consequently, a weak differentiation (*i.e.*, an insignificant inhibitory process) in the ear analyser under the given conditions (of time) showed no effect on the excitation process in another (eye) analyser. Now turn again to Table IV. The same differentiation ( $\frac{1}{2}$  tone), *i.e.*, the inhibitory process of the same strength and under the same conditions, gave a marked inhibitory effect on a conditioned reflex of the same analyser (ear). On that day the salivary secretion to the positive tone was 4 drops. The application of the coarse differentiation ( $\frac{1}{2}$  tone) gave a zero effect. Ten minutes later the application of the positive tone produced the secretion of  $1\frac{1}{2}$  drops of saliva instead of 4. Thus it is proved that one and the same differentiation, an inhibitory process of one and the same analyser, has an inhibitory effect for reflexes of the same analyser; but for reflexes of other analysers it has no inhibitory action. The location of the inhibition arising from differentiation is, therefore, to be found in the very same analyser as in the one to which the differentiated (negative) stimulus was applied.\*

But as you remember from foregoing reports, the nervous processes in the highest parts of the central nervous system constantly flow, irradiate, and concentrate. This is the reason for believing that the inhibitory process coming from a given analyser, may spread over the entire hemispheres. In order to prove this, instead of a simple differentiation (which demands only a weak inhibitory process) one must use a higher differentiation, or accumulate the differentiated inhibition; for then the

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\* That is, if differentiation has been elaborated for sounds, then the inhibition resulting from the negative sounds affects not all positive conditioned stimuli, but mainly those of the sound analyser; if differentiation has been elaborated between stimuli coming in through the eye analyser, then the inhibition resulting from negative optical stimuli affects principally positive conditioned stimuli of the eye analyser, but not, for instance, sound stimuli.



inhibitory wave is not limited to the given analyser, but embraces the neighbouring and the distant analysers.

In the same dog "Dogonyai," we apply now a higher differentiation, one-eighth tone, and we repeat this. And you see clearly that its action is not limited to the same analyser, but spreads to other analysers. In Table V (June 14) you have an experiment showing the effect of the differentiated inhibition aroused in the ear analyser on the reflex of the eye analyser—on the reflex from the whirligig. After the application of the negative tone the whirligig produces only one-half drop; but if we wait 25 minutes, so that the wave of inhibition has had time to disappear, it gives the full effect—3 drops instead of one-half drop. Obviously, the same thing occurred when both reflexes were in one and the same analyser, *viz.*, in the ear analyser; thus, if the positive tone is tried after the repeated application of the (negative) one-eighth tone, the former has no effect (see Table V, June 15, 1911). If the inhibitory process had attained a certain strength in distant analysers, it is clear that it should have a much greater effect in the analyser where it arose.

Such are the facts which we have established with Dr. Belyakov. From them it is evident that one may advance, *i.e.*, that one may propose very penetrating and profound questions about this mechanism, and may obtain definite answers. We are able not only to establish the fact of the differentiated inhibition, but we can actually direct it into certain paths experimentally, strengthen or weaken it, and find out where it originates.

In reviewing these results, it is interesting to propose a comparative judgment on our objective point of view, a point of view which is maintained without difficulty. You see that I am not merely imagining, that I continually stand on a basis of facts. I control all my propositions by experiment, and in this way I always subject my ideas to the decision of facts. In order to know the power of this objective physiological point of view, I ask you, gentlemen, to try to understand and explain the above-mentioned facts from the psychological point of view. You will see a remarkable difference. Let us take one or two examples. I make a conditioned stimulus from a definite tone. We will imagine, and say that the dog well remembers that this sound is a signal for eating and that it will be followed by eating, and in expectation of this, the dog secretes saliva. Now, when I apply, after this tone, another differing by only one-eighth of a note, the dog cannot distinguish them immediately but confuses them, and consequently secretes saliva. He remembers badly. Thereafter I repeat many times the usual (positive) tone and the unusual (negative) tone, and I bring it about that the dog well remembers that the positive tone is accom-



panied by eating and the negative tone is not accompanied by eating. When I apply the positive tone, the dog secretes saliva and is ready to eat, but when I apply the negative tone he is quiet and does not expect food. Now immediately after the negative tone, I apply the positive, and it has no effect. Why is this? The dog well understands the tones; it remembers which tone is the signal for eating, and which is not for eating. Why does it not secrete saliva now on hearing the positive tone? How can this be explained? And further. I repeat for the second time the negative tone; there is no saliva. This means that the dog remembers that this tone is not followed by eating. I repeat the negative tone the third time with the same result, which proves that he remembers accurately. But why has he forgotten the positive tone? This is impossible to understand when considered psychologically. It is even more incomprehensible that, as shown in the experiment, he is able to recollect the positive tone 15 minutes after the negative one. But from our physiological point of view the matter is simple. If the differentiation is an inhibition, if a repetition of the differentiation is a summation, an accumulation of inhibition, then one must wait a certain length of time for the inhibition to disappear and thereupon the normal relations return.

To examine all psychological conceptions, and to show that in comparison with our objective data, they are crude, empirical and fantastic, and that their properties are an insurmountable obstacle for an analysis of the most delicate phenomena of the highest nervous activity—this is the task that lies before us.

Now I revert to the question of the analysers. We have already collected and systematised facts concerning the activity of the analysers. Further, we have data as to how their activity changes under certain conditions. If we destroy parts of the hemispheres of the brain, which represents a complex of analysers, this destruction is manifested in the way we should expect, judging from the aforementioned facts. If we damage a part of an analyser, this is immediately reflected in its function. The degree of impairment of function is conditioned by the size of the lesion and the time which has passed between the operation and the moment of the observations. These disturbances are, as is known, to a certain degree gradually compensated for, but they never entirely disappear.

Further, there is the task of explaining which disturbances of the functions of the analyser are to be attributed to injury and which to removal of its parts. Certainly this is a far-reaching question and I do not know when it will be solved, but I hope that in the experiments which we have done, we have certain clues to its answer. We have evidence, for example, that the disturbance in differentiation is depend-



ent on a certain distortion and interruption of the normal current of the process of inhibition.

So you see, gentlemen, that the highest activity of the nervous system, the activity of the cerebral hemispheres, their analysing function, can be subjected to a strict physiological investigation with absolutely no aid from the conceptions of psychology. And this analysing function is the chief task of the cerebral hemispheres.

The present report of facts and fragmentary knowledge, humble as it is, gives us, I think, some indications for the solution of those deep secrets concerning the physiological activity of the analysers. One of the phenomena before which we stand in great bewilderment is the fact that after removal of considerable portions of the cerebral hemispheres, you cannot always discover, after a lapse of some time, any defect in the activity of the nervous system. It seems that you are dealing with a precious and extraordinarily important mechanism; but, on the other hand, you destroy and ruin a mass of it, and you see therefrom no consequences. I should like to emphasise that the remarkable compensating ability of the brain demands attention. Thus you see what was stated about the great hemispheres as a whole nearly 100 years ago and then rejected, now stands forth as a living fact relating to their separate parts. The physiology of the brain had its beginning in the observations of the French school, which asserted categorically that in the hemispheres there is no localisation, and that in destruction of the hemispheres, if only a part is left, the conditions return to normal.

These views were entirely abandoned in 1870 when the famous experiments of Fritsch and Hitzig were made, giving a basis for the doctrine of localisation of centres. Then the former views seemed a great mistake; now, however, when we are making a detailed study of the analysers, this abandoned idea comes to light again. When one has removed large parts of the cerebral hemispheres, in the beginning it seems as if the analyser has been annihilated; its action is hardly expressed. But after weeks and months have passed, these injuries have become so compensated for that it is with difficulty that one notices in what way the animal is not normal.

The fact of the existence of a localisation, as regards the great part of the cerebrum, is hardly subject to doubt. But how is it with the localisation inside of separate regions of the brain—this is a difficult and colossal task which confronts physiology. How is it to be explained that a structure can be broken and destroyed, and yet we can see no results of this damage? For the separate analysers apparently one must admit as an undoubted fact that there is some substitution, some compensation of functions. How is this to be understood, what sur-



mises is one to make here? Our conception must, of course, be mechanistic.

Some hope, some approach to this subject is already evident. It is probable that the statement with which I began to-day has significance. I refer to the fact that when the conditioned reflex is just formed it becomes generalised. From this it is apparent that the brain end of an analyser represents a common mass in which all parts are in close connection, and one part can be substituted for another. One may suppose that at the peripheral end of the analyser there is a strict differentiation of the stimulating elements, each element separate and distinguished one from the other; at the same time at the brain end of the analyser there is a connection extending over the whole cerebrum so that all the peripheral stimulations are conducted to every point of the brain. Thus there is the possibility of replacing a great part by a small part of the analyser.

What I have said is not so much a proposal as a presentiment as to how these extremely complex and important questions can be solved. Finally, I should like to give expression to the thought, how far we are from any sort of real conception of the mechanism of the cerebral hemispheres!



## CHAPTER XVII

### SOME PRINCIPLES OF THE ACTIVITY OF THE CENTRAL NERVOUS SYSTEM AS SHOWN FROM THE STUDY OF CONDITIONED REFLEXES; INTERACTION OF CENTRES

(Read in commemoration of I. M. Setchenov, before the Society of Russian Physicians, and published in *Transactions of the Society of Russian Physicians*, 1911-1912.)

WHITE AND GREY MATTER—SETCHENOV'S INHIBITION—GOLTZ'S EXPERIMENT—THE CONDITIONED REFLEX—DESTRUCTIVE (PAIN) STIMULI—FLOW OF ENERGY AND NERVOUS IMPULSES FROM WEAK (PAIN) CENTRE TO STRONG (FOOD) CENTRE—LAW OF CONCENTRATION AND IRRADIATION—ROLE OF PAIN AND FOOD CENTRES IN THE STRUGGLE FOR EXISTENCE—"WARM" AND "COLD" CENTRES AND THEIR RELATION TO THE ACID CENTRE SHOWN BY EXPERIMENT—RELATION OF CENTRES BASED ON IRRADIATION AND CONCENTRATION—INTERRELATION OF MEAT AND SUGAR CENTRES SHOWN BY EXPERIMENT; ITS APPLICATION TO DIETETICS—PHYSIOLOGICAL CONCEPTIONS ARE THOSE OF TIME AND SPACE.

THE extent of our knowledge of the two principal parts of the nervous system—*viz.*, of the peripheral part, the nerve fibres, on the one hand, and on the other hand, of the central part, the grey matter, consisting mainly of nerve cells—differs greatly. In the physiology of the peripheral nervous system there have been established, as is well known, many exact laws relating to both irritability and conductivity. Certainly the nervous process as such remains a mysterious secret; but this applies in equal measure to the central nervous system, for the process in both cases is exactly the same. But, as you know, this process is being energetically attacked by scientific minds and their efforts will probably not be unavailing.

Concerning the central nervous system, the grey substance, the grouping and connections of the cells one with the other, our chief knowledge is limited to topographical data. There are many investigations and many assertions about the location of this or that centre. The facts relating to the chief question, their functions are, however, very poorly elaborated. We know that the essential function of the central nervous system is performed through the so-called reflex activity, *i.e.*, the transference of the stimulation from the centripetal to the centrifugal paths. Our knowledge is certainly too elementary, too general. One can readily understand that after these general statements, there arise at once important questions as to the special path along which the transference of the stimulation occurs and the laws governing this transference. Concerning the activity of the central nervous system, however, our



knowledge is very limited, and one can say that the subject has just begun to be worked upon. During the last ten to twenty years questions of this sort, but relating to the lower parts of the central nervous system, *i.e.*, the spinal cord, have been considered systematically.<sup>1</sup> Such inquiries pertaining to the activity of the highest parts of the central nervous system were begun in my laboratory for the first time by use of physiological and not psychological methods.

At first there might be doubt as to whether such methods really possess advantages for the solution of this question when they are extended from the lower to the higher parts of the central nervous system. If the lower parts are complex, how infinitely more complicated are the higher parts! In spite of this obstacle, there are in the study of the brain certain favourable circumstances, and the most favourable is this: Reflex activity with all its complexity is already complete and fixed when we meet it in the spinal cord. Thus in these pre-formed connections we have no means of seeing how they are established. The physiology of the higher parts of the central nervous system is in quite another position. Here we see the process of formation of the reflex act, and we have the possibility of observing fundamental properties and elementary processes, thanks to which this formation occurs.

In order to explain the matter, permit me to make some comparisons. Take a factory turning out finished articles from raw stuffs. If you know only the materials used and the end products, great wisdom is required to divine what is done in the factory, and to know through what processes these products pass in their elaboration. Such a problem in many cases might forever remain unsolved. It is another matter when you enter this factory and can see how these substances are worked over, into what combinations they enter, and how they pass from one department to another. Then you more or less easily understand the principles. The same holds good for the physiology of the highest sections of the central nervous system. Here before our eyes is formed a reflex act. Its mechanism is thus disclosed and laid bare before us.

The members and guests of our Society are well aware that we have now accumulated a great deal of material relating to the physiology of the normal activity of the higher parts of the central nervous system, material which consists not only of separate facts, but which can be ordered and systematised. To-day I shall make an effort to add new facts to our former generalisations, or, more exactly, to introduce new material so that another series of facts will be embraced, facts which have been obtained not only from a study of the higher parts of the central nervous system but also from investigations of the lower parts, *viz.*, the spinal cord.

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<sup>1</sup> Pavlov refers to the researches of Sherrington and his collaborators.—*Translator.*



One of the chief facts in the activity of the central nervous system is that of a peculiar inhibition, which I shall now consider. As the initiator and promulgator of this conception, we with full justice acknowledge I. M. Setchenov, to whom to-day's meeting is dedicated. It is just fifty years ago since the appearance of his famous work, *The Inhibitory Reflex Centres*. This article and its facts may be counted as the first victory of Russian thought in the realm of physiology, its first independent original contribution to that science.

The fact of inhibition is shown in the following experiment. The speed of reflex action was determined by immersing the hind foot of a frog in an acid solution of known strength, and measuring the time between the beginning of the immersion and the beginning of the responsive reaction, the contraction (the so-called Türk's method). In such frogs the hemispheres had been extirpated, and on the exposed parts, *i.e.*, on the optic thalami, were put crystals of sodium chloride. Under the influence of this chemical stimulus the reflex weakened greatly, as was shown by the longer time between the immersion in the acid and the contraction.

The latter phenomenon can probably be explained thus: the irritability of the lower parts of the central nervous system, *viz.*, of the spinal cord, through which the reflex takes place, is markedly decreased, in consequence of which a greater interval of time must elapse before the stimulation can reach that strength which will produce an effect, the withdrawal of the foot from the acid. This observation must be considered as the starting point for the collection of a large number of other facts relating to the central nervous system.

At about the same time appeared the first reports on the so-called *Quakversuch* of Goltz which consisted in causing a frog from which the cerebrum had been removed to emit croaking sounds by lightly stroking its back. The reflex could be repeated with machine-like regularity. If at the same time one stimulates another point, for example, presses on the foot, the croaking reflex is inhibited.

At present we have a series of similar facts. As an example, I shall take another experiment of Goltz. In experiments on dogs with the spinal cord cut between the thoracic and lumbar vertebræ, he showed that many reflexes in the muscles and genito-urinary system, which occur with mathematical exactness, immediately cease if at the same time some place on the hinder half of the animal is stimulated sufficiently to call out another reflex. The latter reflex inhibits the former. These facts have been proved repeatedly and have been worked out systematically. Here is an example:

The posterior roots of the seventh, eighth, ninth and tenth spinal nerves are exposed in a frog, and the contraction of the gastrocnemius muscle



is registered. When the ninth nerve root is stimulated, this muscle contracts. But if simultaneously other centripetal roots, *viz.*, the seventh or eighth thoracic are irritated, leading to the contraction of other muscles, the reflex contraction of the gastrocnemius weakens or entirely disappears.

In other words, if together with a certain reflex another is produced, the former suffers in strength or is completely destroyed. In the physiology of the conditioned reflexes, *i.e.*, in the influence of such stimuli as are brought into temporary connection with the activity of the salivary glands, we have seen a number of such facts, showing the interaction of two stimuli originating at separate points. If during the time a conditioned stimulus is being tried, another stimulus acts—for example, some new tone, the sight of a new figure, an odour, or some thermal stimulation of the skin, etc., or in fact anything that can evoke a new reflex—then the conditioned reflex weakens and may vanish.

This is one of the most common facts which we meet in studying the function of the central nervous system. Now I shall dwell some moments on the mechanism of this phenomenon. How is it to be explained? What does this fact show to us, what properties or elementary processes? What conception does it bring to us? I should like to emphasise the following situation. Let us take a certain reflex, *i.e.*, there is excitation of a certain point in the central nervous system. If at the same time another reflex is evoked, another point in the central nervous system is stimulated, and the first reflex becomes weaker and may disappear. One may suppose that the exercise of the second reflex withdraws a certain amount of energy into its own centre at the expense of the energy of the first reflex centre; consequently less energy remains in the first reflex centre and its manifestation is weaker, or, if the diversion of energy is considerable, entirely absent. Other explanations can be given, but this one can not be gainsaid, as it corresponds well to the actual facts.

If the foregoing facts are understood in this way, then another phenomenon of the activity of the central nervous system has an identical internal mechanism. This phenomenon is the so-called conditioned reflex, *i.e.*, the temporary connection between a given external stimulus and a certain organ.

How does this phenomenon which we call a conditioned reflex originate? In our experiment we feed the animal or introduce acid into his mouth, and thereby stimulate either the food or the acid receptor centre. From these centres the excitation is conducted to the centres of the corresponding organs; in the case of food, from the food centre to the centres of movement and secretory reactions; or, if we have to do with the acid centre, to the centre of defensive movements (by which the animal rids himself of the acid), and also to the centre of salivary secre-



tion. We have here a certain focus in the central nervous system—a focus of great activity. When such conditions exist, then all other stimulations formerly indifferent that enter at that time the central nervous system, are attracted and conducted to this active focus. If a certain stimulus is often repeated without being accompanied by any kind of effect which is more essential for the organism than the stimulus itself, then this stimulus becomes neutral and indifferent. We are surrounded by a multitude of sounds, sights, etc., but if they call out no specially important stimulations, then we react to them as if they did not exist. If now these neutral stimuli coincide several times with the stimulation of the activity of our centre, then they no longer spread and irradiate over the hemispheres as they did when they were not attracted to a specially excited focus; instead, they open up a persistent narrow path to the active centre, connect with it, and thus the formerly neutral stimuli become definite stimulators of the centre.

If one accepts this explanation, then two important groups of facts may be considered from one and the same point of view. In both cases we see that the excitation flows from one place to another. That this is not fantasy but is really so, is proved by the experiments of Dr. Yero-feyeva. I will consider her results from a new point of view to-day, and I think it will be plain that our conception is strengthened in a high degree by them.

What are our facts? We take a dog with a chronic salivary fistula—our usual laboratory animal for these experiments—and let a strong electric current act on his skin. This, according to the subjective terminology, is a *pain stimulus*; but according to the objective term, a *destructive stimulus*. It is obvious that the answer to such a stimulus is a usual reflex, a *defensive* reaction of the animal; he protects himself with all his might against this stimulus. He tries to break loose from the stand, he bites the stimulating apparatus, etc. The stimulation passes into the centre of the defence reaction; it is expressed in defence movements. If you repeat this experiment for several successive days, the irritability of the animal increases with each repetition, and the defence reflex becomes reinforced. But let us perform this experiment in another way. If you give the dog food during the action of the destructive stimulus (if he will not eat the food, forcibly introduce it into his mouth in order to stimulate the taste cells), you will notice that the defence reaction becomes weaker and weaker, and in the course of time may vanish. This means that you have before you a fact of the first category, an inhibition. The stimulation of the food centre leads to inhibition of the centre for pain reflexes.

If feeding is often repeated simultaneously with the pain stimulus, finally you will not only fail to have the defensive reaction, but, on the



contrary, with the application of the electric current, you will see that the dog develops the food reaction; he turns toward you, looks toward the place from which the food is brought, and saliva flows. The stimulation which entered into the centre for defence reaction, now passes over to the food centre, *i.e.*, the centre which governs the movements and secretions relating to food. This is an illustration of the second group of reflexes; it is a conditioned reflex.

From this example you witness how one phenomenon passes inevitably over into another; and thus their relationship is clearly established. First, as you have seen, the pain centre was inhibited, and then the stimulation was transferred to the food centre. Hence follows the logical conclusion that the processes are essentially one and the same, that there is merely a transference, an alteration of direction, an attraction of energy from one centre to another. And if the new centre is the stronger, as in the given case, all the energy of the first centre passes over to this stronger centre, and the previously active centre becomes entirely quiescent.

Let us go further. What does this mean, that the energy of one centre can be conducted to another? This occurrence can be related to a great group of facts about which I have spoken earlier. One year ago at an anniversary meeting of this society, I discussed the laws of irradiation and concentration of the excitation processes. The law of concentration consists in this, that the excitation is collected and directed to certain points of the nervous system. This law is founded on the following observations. By the method previously described you have made a conditioned reflex from some tone; *i.e.*, you have repeated the tone always at the same time with feeding or with the introduction of acid into the mouth, and at last you have the corresponding reflex and the corresponding secretion. Let us suppose that we have made this reflex from a tone of 800 vibrations per second, and the tone evokes constantly its conditioned reaction. Now we try other tones. And it turns out that they are all effective, though they are very far apart, for example, pitches of 100 and 200 vibrations and even 20,000 to 30,000. This fact—*viz.*, that we have united the food center only with a single stimulus and that the excitation has become generalised—furnishes a direct basis for speaking of a law of irradiation, and for representing the phenomenon thus: the excitation arriving at certain cells of the hemispheres, does not remain exclusively in those cells which it first entered, but overflows, *irradiates*, into the neighbouring cells.

The second half of the experiment is as follows. As you repeat the reflex on 800 vibrations, supporting it by feeding, it becomes more and more specialized, the range of effective tones becomes narrower and narrower, and if you employ your given tone for a long period, you



may reach an extreme grade of specificity.<sup>2</sup> From a tone of 812 vibrations there may be no reflex. The excitation which was at first spread out, irradiated, is now collected and concentrated.

This justified the proposal of the related law of concentration. It is clear that the facts which I mentioned earlier are in perfect correspondence with the law of concentration, and that in the experiments with inhibition and formation of conditioned reflexes, the law of concentration of the excitation, of focusing it at a certain point, is made manifest.

These are our facts; this is what we have already done. It is to be understood that this is only a general formulation, only the beginning. Further, in each of these laws—of irradiation and of concentration—there must be more detailed points established. To work out these details must be the task of future investigations. My laboratory is at present occupied with this problem, as I shall show.

In the experiments of Dr. Yerofeyeva we find facts which prove that the law of concentration under special conditions may be expressed differently, *i.e.*, in different cases it appears in individual forms. As I have shown, the excitation in the centre for defence movements may be diverted to the food centre. This experiment is easily carried out in all animals. If, however, you try to direct this excitation into the acid centre, *i.e.*, if you wish to make from the electric stimulus a conditioned stimulus for the acid centre, you will fail. Hence follows a supplement to the law of concentration: the direction of the stimulation is conditioned by the relative strength of the interacting centres. The food centre is obviously a powerful physiological centre; it is the protector of the individual's existence. It is evident that in comparison with the food centre, the defence centre is of less importance. You know that during the struggle for food the different parts of the body are not especially defended; among animals there are fierce tussles and fights for food in which occur wounds and serious injuries. Thus the destruction of separate parts of the body is a sacrifice to the most important requirement of life, the obtaining and capture of food. It is manifest that the food centre must be considered as the most powerful physiological centre, and therefore we have a clear reason why this centre may attract excitations from other centres. The acid centre certainly has no such importance; its activity is a special one, and it is plain that in comparison with it the defensive centre is of greater

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<sup>2</sup> In later work it proved to be necessary not only to repeat the conditioned stimulus followed by the unconditioned, but also to apply the similar stimuli without the unconditioned reflex in order to bring out the contrast. See chapter xxxi of this book, end of paragraph 10, and the last part of chapter vii in Pavlov's book, *Activity of the Cerebral Hemispheres*, where differential inhibition is discussed.—Translator.



moment; consequently an excitation can not be drawn from the centre of defence into the acid centre. This is in reality the case.

Finally, I can give you experiments which well illustrate the law of irradiation. Experiments with thermal stimulation of the skin have been performed in our laboratory by Dr. P. N. Vassilyev, and the following unexpected fact was observed. For a long time, since the beginning of our studies, conditioned reflexes on thermal stimuli have been developed. Either warming or cooling may be made a conditioned stimulus for the food or for the acid centre. In this respect the thermal stimuli do not differ from others. But in the following respect there is a considerable difference; it is very difficult to obtain simultaneously various conditioned responses from cold and warm stimulations. For example, if you have made from a warm stimulus acting on a certain area of the skin a conditional stimulus for the acid centre, *i.e.*, you obtain the corresponding movement and secretion, and if this is well developed, you may be assured that even though you do not further apply this conditioned stimulus the conditioned reflex will remain intact for weeks and months depending upon how well and how long you developed and reinforced it. In the same way you may form a conditioned reflex from cooling a certain part of the skin and feeding the animal. Such a reflex can also be stable and remain intact for weeks and months. But if you wish to apply these stimuli together during one and the same experiment, then you will encounter insurmountable difficulties. Let us begin the experiment with the cold reflex, and suppose that cold as a stimulus is connected with the food centre. You note the corresponding food reaction; the dog turns toward you, looks for the food, and saliva begins to flow. You repeat this, once, two or three times, and every time you see a uniform reflex. If, after this you try the warm stimulus which is connected with the acid centre, then instead of the motor-acid reaction and the corresponding salivary secretion, you see the same cold reflex, *i.e.*, the food reaction. In other words, the dog confuses the warm-acid reflex with the cold-food reflex. If you begin the experiments in reversed order, you will obtain analogous results, *i.e.*, if you begin with the warm-acid reflex, then the cold-food stimulus will be confused with the warm-acid stimulus.

This phenomenon may be explained by assuming that there is an easy irradiation from the warm to the cold centre, and vice versa. If, for example, you repeat several times the cold stimulus, the thermal nerve cells (cold and warm) become fatigued, and the stimulus becomes generalised; the stimulation overflows and spreads equally over both centres, and if you now pass over to the other thermal stimulus, the reaction is the same as from the first thermal stimulus. No other interpretation, it seems to me, is plausible. It is necessary to admit that both thermal



centres are very close together, that they are intimately interwoven, just as are the warm and cold points of the skin, and hence the phenomenon of irradiation is seen especially clearly; the irradiation readily passes from one centre to another, and to separate them is a matter of great difficulty. It would be interesting to see how quickly this separation could be brought about. At any rate we see here a brilliant example of irradiation.

Further arises the question, what are the relations between the laws of irradiation and of concentration? These laws, it is evident, are of opposite nature. In the first case we have to deal with an overflowing, with a spreading of the excitation in the brain; in the second case, with a grouping, a collection of the excitation around a separate distinct point.

Thus we see that the problem of the interrelations of these two chief laws is of the highest importance for the whole mechanism of the central nervous system. Certainly the solution of the problem is very distant, but, nevertheless, valuable material may be collected. Two investigations in my laboratory give some hints toward a solution. One year ago experiments were completed, showing that different reflexes (food) can be compared with one another (Yegorov). Up to that time only the conditioned acid and the conditioned food reflexes, and consequently the stimuli connected either with the acid or with the food centre, had been set in opposition. In this investigation the first attempt was made to define the mutual effect of the various food reflexes on one another. The examination was made in this way: Certain indifferent stimuli were combined with various kinds of food, one stimulus with cheese, another with milk, a third with bread, a fourth with meat, etc., the influence of one of these reflexes on the others was noted. In these experiments, the fact was brought out, that the stimulations by various food substances is often accompanied by an extremely long-lasting after effect.

In the physiology of the conditioned reflexes we have many instances showing that a stimulation in the form of its *trace* can manifest itself in the central nervous system for a long time after the cause of the stimulation has been removed and its visible effects have ceased. We formerly had to do with traces after ten-minute intervals, and we had not dealt with longer lasting traces. In the experiments of Yegorov the traces (after-effects) were of much longer duration, not only of hours but of days. This coincides with the experience of actual life, when, for example, some taste, especially if unpleasant, is remembered for a long time.

The peculiarity of the facts of which I shall now speak is probably dependent upon a long duration of this *trace* (after-effect). The experiments were done as follows. We have a conditioned reflex, *i.e.*, we have



a certain stimulus connected with feeding, say with meat powder. The conditioned stimulus gives a more or less constant effect. Afterwards another conditioned reflex is elaborated from another stimulus, for example, the eating of sugar. We may for brevity designate these as the "meat reflex" and as the "sugar reflex". What will be the result if I allow one reflex to act during the trace of the other? The following answer was received from the experiments of Dr. Yegorov. If you have a "meat reflex" of a certain size (measured by the number of drops of saliva—one of the effects of the stimulation of the food centre), say 10 drops, and if now you apply the "sugar reflex," and soon afterward try again the "meat reflex," the latter will be markedly decreased. The stimulation of the "sugar centre" (using this expression for the sake of conciseness), *i.e.*, of a group of nerve cells which are stimulated through their corresponding fibres from the peripheral apparatus by sugar, inhibits the "meat centre," *i.e.*, the group of cells which are stimulated by meat in the mouth.

If this experiment is repeated many times, and all the details noted, the highly interesting fact given below is observed. If soon after (five to ten minutes) the application of the conditioned sugar reflex, you apply the conditioned meat reflex, you now receive a fairly large reflex response, 7 to 8, or even 10 drops, *i.e.*, nearly the same quantity as was obtained before the sugar reflex. Only in the next trial will the meat reflex be entirely inhibited. At the third and fourth repetition it slowly regains its strength. On the following day the meat reflex may still be somewhat inhibited, and only on the third day be completely restored.

The existence of this lasting effect of one taste reflex on another is well known in practical life. You know the annoyance of a mother when her children eat something sweet before dinner, because after this they do not want their usual food. Apparently now they do not relish other foods.

I ask your attention especially to the course of this phenomenon. I reiterate that the sugar reflex undoubtedly inhibits the meat reflex, not only for some hours but for some days, and that this inhibition sets in not at once but after some time. Immediately after the sugar reflex the meat reflex gives a nearly normal effect, and only on the second and third repetitions does it become inhibited. This unexpected state of affairs can be explained, I think, in only one way. One must suppose that when the sugar reflex—a reflex of considerable strength—is applied, its influence is not confined to the cells of the sugar centre, but spreads and overflows a large region of the food centre, *i.e.*, the excitation arising from this reflex can be detected in other parts of the food and taste centres. If you use the meat reflex very soon after the sugar reflex, the former is effective; for in the meat centre there *still exists*



the excitation which has spread out from the sugar centre. If, however, a certain time has elapsed after the sugar reflex, according to the law of concentration the excitation has begun to collect in the sugar centre; then to this strong centre the excitation from the meat centre is attracted, and the reflexes proceeding from the meat centre are inhibited.

In the experiments cited we can see the mutual influence and a certain exchange of work by centres acting according to these two laws. In the first phase you have irradiation; the stimulation overflows, covers a large region, and this is the reason why the meat reflex is at first unaffected and exists at the expense of the sugar reflex. Some time later this stimulation of the sugar centre collects, concentrates, and the meat reflex becomes weaker for a long time. That this is really so is shown by the experiments of Dr. A. A. Savitch. If you try the meat reflex twenty-five minutes after the application of the sugar reflex, the former is more or less effective; but if you wait thirty to forty minutes after the sugar reflex, there is a marked weakening of the meat reflex, because during this time the irradiation wave has already contracted and is concentrated at the sugar centre. Consequently, the energy from the meat centre has been diverted also to the sugar centre.

In this way these experiments point to a new wide territory for investigation. The questions before us concern a fundamental point, *viz.*, the mutual relations of two fundamental laws of the central nervous systems, the law of irradiation and the law of concentration.

When you behold a series of such facts, I believe you will arrive at the conception which for me is the only true one. As all the experiments presented show, the study of the reflex mechanism, which forms the basis of the activity of the central nervous system, is here reduced in its essence to a study of space relations, of the definition of the paths along which the excitation at first spreads, and then concentrates. If this is so, then it is comprehensible that a sure probability of mastering the subject in all its extent is given only by conceptions which are characterised by notions of space. This is the reason why it must be perfectly clear that it is impossible by means of psychological conceptions, which essentially are not spatial conceptions, to penetrate into the mechanism of these mutual connections. You must be able, so to say, to point with the finger where the excitation process was at a given moment, and where it has gone. If you conceive of these relations as they are in reality, then you will understand the truth and power of that science which we are vindicating and developing—the science of the conditioned reflexes. It has absolutely excluded from its domain psychological conceptions, and has to do always with only objective facts—facts existing in time and space.



## CHAPTER XVIII

### SUMMARY OF RESULTS OF REMOVAL OF DIFFERENT PARTS OF THE CEREBRAL HEMISPHERES

(Read before the Society of Russian Physicians, and published in *Transactions of the Society of Russian Physicians*, 1912-1913.)

POINT OF VIEW—CONDITIONED REFLEX DEPENDENT UPON THE CEREBRAL HEMISPHERES—HEMISPHERES ARE THE SEAT OF THE CENTRAL END OF THE ANALYSERS—ANALYSER OF MOVEMENT AND SKIN ANALYSER—"MOTOR" CELLS ARE SENSORY—MUNK'S EXPERIMENT; "PSYCHICAL" BLINDNESS—PAVLOV'S ANALYSIS OF THIS—EXPERIMENT WITH DAMAGED EAR ANALYSER—LOCATION AND FUNCTION OF THE ANALYSERS—FUNCTION OF POSTERIOR AND OF FRONTAL LOBES—EXPERIMENTAL DIFFICULTIES IN BRAIN OPERATIONS.

WHEN the question of a subject for to-day's report came up, I thought to myself, what shall I do, take a small part of the subject and discuss the results of a single series of experiments, or review the whole of our work? I decided on the latter; for it seems to me that this will be both instructive for my hearers and not entirely useless for us. It will be of great value to us to consider what we have attained by our labour of many years, to draw some conclusions therefrom, to weigh the results, to contemplate them, to define more clearly our shortcomings, and to set our goal and tasks for the future.

We in my laboratory have now for seven years been occupied with the extirpation of the whole of the hemispheres as well as of their separate parts; for this purpose we have used many scores of dogs, which afforded us exceptionally significant data for the basis of the present survey.

Many years ago we stated our special point of view regarding the highest nervous activity as it is manifested in the highest animals. In the investigation of this activity we rejected subjective psychological conceptions, and chose the external, objective, physiological point of view, *i.e.*, that which the biologist uses in all of his science. From this standpoint, the whole complex nervous activity, which was formerly interpreted as psychical, appeared to us as the expression of two chief mechanisms; first, the mechanism of the formation of temporary connections between the agents of the external world and the action of the organism, *i.e.*, the mechanism of the conditioned reflex; and, second, the mechanism of the analysers, *i.e.*, an apparatus whose purpose it is to analyse the complexity of the external world, to decompose it into its separate elements and moments. All our results up to the present fit into these conceptions. This, of course, does not exclude the pos-



sibility of further development and enlargement of conceptions relating to the subject.

Although our researches on the complicated nervous activity have been carried out on organs of small physiological importance, on the salivary glands, the two mechanisms at work in the cerebral hemispheres are nevertheless clearly manifested in the activity of these glands.

I shall present my material not in chronological order, that is, not in the order in which we came into possession of the facts, but in logical sequence, disposing and grouping the data so as to make clear to you the essence of the matter.

The first question which we must decide here is the question of the relation of the cerebrum to the above mentioned mechanisms—to the mechanism of the formation of conditioned reflexes and to the mechanism of the analysers. The outstanding fact which was constantly manifest to our many collaborators in a large number of dogs was this: that the cerebral hemispheres are the seat of the conditioned reflexes, and that one of their chief functions is the formation of these transitory connections. We have many proofs thereto, although our subject is of such a nature that new evidence may always be of service. Investigators who have extirpated either the whole or a part of the cerebral hemispheres have observed a disappearance either of all of the conditioned reflexes, or of special groups of them, depending upon whether the whole or a part of the hemispheres was removed. Various and exact measures were used in this work, in order to obtain the facts, and the results were always the same. Under certain conditions there was constantly a loss of all or of only some of the conditioned reflexes. Great perseverance was used in this research; many times we tried for years to restore a lost conditioned reflex before we concluded that it could not be established again. With one dog we not only tried to form conditioned food reflexes in the experimental room, but we went so far as to accompany all of his feeding with a certain tone, in order to ascertain whether in this manner it was not possible to form the conditioned reflex again. But once the organ of a given conditioned reflex was annihilated (as by removal), the conditioned reflex never reappeared. After these constantly recurring facts, it must be acknowledged that the hemispheres are, in effect, the organ of the temporary connections, the birthplace of the conditioned reflexes. Certainly one may categorically ask whether these temporary conditioned connections can not be formed also outside the hemispheres, but in my opinion there is no good ground for considering such a question. All the knowledge we have at present brings us inevitably to the conclusion that the temporary connections owe their formation to the cerebral hemispheres, and that they vanish with their removal. But it is conceivable that sometimes under extraordinary conditions, conditioned re-



flexes may be formed outside the hemispheres, in some other part of the brain. In this respect one can not be too positive, because all our classifications and laws are more or less conditional, and are significant only for the given time, under the circumstances of the given method, and within the limits of the given material. Fresh in the minds of us all is a well known example—the indivisibility of the chemical elements, which was considered for a long time as a scientific axiom.

Thus I repeat that in various experiments by many workers the fact was constantly met that the temporary reflexes occurred only in the presence of the whole or a part of the hemispheres. Consequently, we may accept without misgivings the statement that one of the most *essential functions of the hemispheres* is the elaboration of the conditioned reflexes, just as the main work of the *lower parts of the nervous system* is concerned with the simple, or according to our terminology, the unconditioned reflexes.

The second mechanism belonging to the cerebral hemispheres is the mechanism of the so-called *analysers*. In this case we started from the old and well known facts, changing somewhat the conception of them. We designate as analyser that apparatus whose function it is to decompose the complexity of the outer world into its separate elements; for example, the eye analyser consists of the peripheral part of the retina, the optic nerve, and the brain cells in which this nerve ends. The union of all these parts into one functional mechanism called analyser has its justification because physiology at present has no data for an exact division of the work of the analyser as a whole. We can not assert that a certain part of its function is performed by the peripheral section and other parts by the central end.

Thus the cerebral hemispheres, according to our understanding of the matter, consist of a number of analysers; of the eye, ear, skin, nose and mouth analysers. An examination of these analysers brought us to the conclusion that their number must be increased, that besides the above cited ones relating to external phenomena, to the outer world, there must be recognised in the cerebrum special analysers, whose purpose it is to decompose the enormous complexity of the inner phenomena which arise within the organism itself. Certainly not only an analysis of the external world is important for the organism, but of the same value is a *signalling upwards* and analysis of everything happening within the organism itself. Besides the external analysers there must be internal analysers. The most important of these inner analysers is the *analyser of movements*. We know that from all parts of the motor apparatus, from the joints and their surfaces, from the tendons, ligaments, etc., there originate centripetal nerves which signalise every moment the exact details of the act of movement. All these nerves unite



above in the cells of the hemispheres. The most diverse peripheral endings of these nerves, together with the nerves themselves and their terminal cells in the great hemispheres, form a special analyser, which decomposes the motor act with its enormous complexity into a large number of the finest elements, whereby is attained the multiplicity and exactness of our skeletal movements.

Bound up with the conception of such an analyser is a marked interest in the physiology of the brain. In 1870 Fritsch and Hitzig demonstrated, as you know, that an electrical stimulation of a definite part of the cortex in the frontal half of the hemispheres called forth a contraction of certain groups of muscles. This discovery furnished a basis for recognising in these places particular motor centres. But then the problem came up as to how these parts of the hemispheres could be represented. Are they motor centres in the full sense of the word, *i.e.*, cells from which impulses proceed direct to the muscles, or are they merely sensory cells to which peripheral stimulations course and from which they are dispatched into the active motor centres, that is, those centres from which motor nerves go out directly to the muscles? This controversy, begun by Schiff, has not yet ended.

We also were forced to take a part in the decision of this question, and came to the following conclusion. We had been inclined for a long time to assume that those places in the cortex through the stimulation of which certain movements result are aggregations of sensory cells, *viz.*, cerebral endings of centripetal nerves, which go out from the motor apparatus. But how were confirmations of the correctness of this view to be found? Besides the data which had been adduced previously, and which were used by the defenders of this view, we succeeded in finding a new proof, and one seeming to us to be especially convincing.

If the so-called motor region is in reality the analyser of the motor apparatus and is entirely analogous to the other analysers (ear, eye, skin, etc.), then a stimulation brought to the analyser can be directed into any centrifugal path, *i.e.*, this stimulation can be connected with whatever activity we desire; in other words a conditioned reflex may be elaborated from a motor act. This we have succeeded in doing. Dr. Krasnogorsky, using, on the one hand, one of our usual stimuli, acid, and, on the other hand, flexing some joint, formed a temporary connection between the flexion and the work of the salivary gland. The definite movement called out a salivary secretion as well as did the stimuli from the ear, eye, etc. Then the question arose, how true is this interpretation of the given phenomenon; is this actually a reflex of flexion proceeding from the motor act, or a reflex from the skin?

In answer to this question Krasnogorsky succeeded in giving a proof which seems to me to be almost incontestable. When he formed on one



leg a skin reflex, and on the other a flexion reflex, and then removed various parts of the cerebral hemispheres, it was proved that if the sigmoid gyrus was removed, the flexion reflex was lost, but the skin reflex persisted and might be demonstrated. On the contrary, when the gyri coronarius and ectosylvius were extirpated, the skin reflex disappeared and the flexion reflex remained. There was no room for doubting that the skin and the movement analysers are not the same, and that the latter analyser has its location in the motor region of the brain.

After these experiments I think we may speak specifically of the motor or the movement analyser with the same scientific justification as we do of the eye and ear analysers.

It remains for us to explain why movement results from electrical stimulation of those parts of the hemispheres in which are, as some authors assert, the motor centres. The sensory cells of the motor analyser are situated here, according to our opinion, and, consequently, from here in normal life stimulations stream out to the definite motor centres; hence it is conceivable that with such well worn paths, the stimulation of these places by electricity, evokes the usual result, *i.e.*, the impulse passes out from here along the customary ways to the muscles.

Thus from all our experiments we can say that the cerebral hemispheres represent a central station of all analysers, which may serve, either as do the eye and ear analysers for the analysis of the external world, or as the motor analyser, for an analysis of internal events, for example, movement. It is, however, obvious that our knowledge of the analysis of all other internal phenomena taking place through all the remaining internal analysers is much more limited. Besides the motor analyser we have not studied any other analysers of this sort by the method of conditioned reflexes. Undoubtedly, however, such phenomena will eventually enter into the physiology of the conditioned reflexes.

Now let us pass over to a consideration of the function of the analysers. What do they do? As indicated by their name, they have the purpose of decomposing complex phenomena into separate elements. But what do we know more particularly about their uses, and what have the experiments by the method of conditioned reflexes taught us? Here, I think, the objective point of view has served us admirably. General facts concerning the analysers were observed many years ago. The researches of Ferrier and Munk brought out a number of details bearing on the work of the analysers. These facts, however, were interpreted from a confused and unscientific point of view. When Munk removed the occipital and temporal gyri he noticed certain abnormalities of hearing and vision in the operated dog. Such peculiar behaviour of the animal towards the external world he called "psychical blindness" and "psychical deafness." What does this mean? Let us



consider psychical blindness. It means that after extirpation of the occipital parts of the brain, the animal does not lose the ability to see. He avoids objects which are in his way, distinguishes between light and dark, but at the same time he does not recognise his master and the people he formerly knew. The dog fails to react to them; if they exist for the dog, they are only common optical stimuli. Now Munk and others assert that the dog "sees" but does not "understand." But what does this mean—he "understands," "he does not understand"? These words do not express any definite notion of the process and they, too, must be explained and interpreted.

The method of conditioned reflexes, after refusing all psychological conceptions, has brought a solid foundation and understanding to the matter. From the objective point of view, the removal of this or that part of the cerebral hemispheres was considered as a complete or partial destruction of this or that analyser. If the given analyser remained intact, if its brain end was uninjured, then the dog by means of this analyser differentiated separate elementary phenomena as well as their combinations, *i.e.*, the dog behaved normally in this respect. If, however, an analyser was destroyed or damaged in more or less degree, then the dog could not distinguish finely these phenomena of the external world. And this defect of analysis is proportional to the destruction of the analyser. If the analyser is completely destroyed, there is no trace of an analysis, even of the most elementary phenomena. If fragments of the analyser are left, if a part of it is still intact, then the connections between the organism and the environment remain, but in the most general form. Further, the more of the analyser which is saved from destruction, the better and finer its power of analysis. Briefly, if we consider injuries of the analyser as injuries of a mechanism, then it is evident that the more this analysing apparatus is damaged, the poorer its work. Such a conception makes the subject completely clear, and provides a basis for further investigations, while the psychological point of view confronts an insoluble problem, and contributes nothing by the expressions, "the dog understands," "the dog does not understand."

Now let us examine the experiments of Munk from our standpoint. We destroy the occipital parts of the hemispheres, *i.e.*, the brain end of the eye analyser. If after this operation only a minimal part of the analyser is uninjured, the animal can make only coarse analyses, distinguish between light and dark. In such an animal, you cannot elaborate conditioned reflexes to the form of objects, nor to the sight of their movement, but very easily to stimuli of light and dark. If, for instance, you repeatedly stimulate the dog with an intensive light just before feeding him, then later every time this light appears before the



dog, the secretion of saliva begins; this is the work of that portion of the analyser which was left after the operation. This is the reason why Munk's dog did not collide with objects in his path. He distinguished between darkness and light, and passed around objects. In such a restricted way the eye analyser functioned well. But where a fine analysis was required, where it was necessary to distinguish between combinations of light and shade, forms, etc., the analytical ability was insufficient, for the damaged analyser did not function. It is plain why such a dog is unable to recognise his master—because he cannot discriminate between objects. There is no mystery about the matter. Instead of saying that the dog has ceased to "understand," we say that the analyser is damaged, and that it has lost the capacity to form conditioned reflexes on the more delicate and complex visual stimuli. And now we approach the great task of investigating this analyser step by step in order to see how it acts when it is whole and in good order, and what disappears gradually from its ability when we destroy one or another part of it.

We have exact and clear data bearing on this problem. If after our operation, there is left only an insignificant part of the eye analyser, the animal can form conditioned reflexes only to the intensity of light. If less damage is done to the analyser, then you can work out a conditioned reflex to the sight of moving objects, and later also to their form, etc., up to the point of normal activity, these different stages depending upon the extent of injury to the analyser.

The same holds for the ear analyser. If there is much damage, or if its activity is temporarily inhibited, then the animal can distinguish only between silence and sound. For such a dog there is no difference between various sounds. All sounds, noises and tones, whether high or low, are for him the same. The animal reacts only to the intensity of the sound; its detailed properties do not exist. If the destruction of the analyser is less, you can form independent reflexes to noises and musical tones, which signifies that there is some qualitative analysis yet present. If the injury is still less, then there is differentiation between separate tones, and the less the detriment to the analyser, the better is the analysis of tones. With a considerable destruction, the animal differentiates only between great intervals of pitch, for example, between octaves; if the injury is moderate, it differentiates between tones, and finally between fractions of a tone. We have a gradation from complete inability of the analyser up to normal activity.

I shall now present to you the highly interesting experiments of Dr. Babkin. As the dog he worked with lived for three years after removal of the posterior part of the cerebrum, one may consider that the condition became stationary. The dog easily distinguished not



only between noise and sound but between tones of different pitch. To one tone there was a positive conditioned reflex, to another tone, no reflex, and hence in this respect the dog was entirely normal. But he had an irremediable defect; he could not differentiate between difficult sound combinations. Conditioned stimuli were made from a series of ascending tones, *do, re, mi, fa*. After some time the corresponding conditioned reflexes were obtained. But now reverse the order of the tones to *fa, mi, re, do*. A normal dog can distinguish between these combinations, but this one could not make so exact an analysis; try as much as we would, we obtained no differentiation. He had such an injury of his ear analyser that it became unable to perform this task. In close connection with this last phenomenon is an old and well-known fact, to which usually the expressions, he "understands," he "cannot understand," are applied; such dogs cannot recognise their names. The dog in this experiment was named "Ruslan," but after the operation his name produced not the slightest effect, though it was repeated a thousand times. His ear analyser was in such a state that he was incapable of distinguishing between sound combinations. If the dog cannot discriminate the groups of tones, *do, re, mi, fa*, from the same tones in another order (*fa-mi-re-do*), then he certainly cannot recognise his name—for "Ruslan" is a more complicated combination of sounds. Such an analysis is beyond the ability of his damaged ear analyser.

I reiterate that in the investigation of the function of the analysers there is great merit in the method of conditioned reflexes—the objective method. This method has entirely removed all mystery from our subject, rejected all meaningless expressions as "he understands," "he does not understand," and has replaced all these by a clear-cut and productive programme for the study of the analysers.

The problem before the investigator is the exact delimitation of the functions of the analysing apparatus, and the tracing out of all variations in its functions in the cases of destruction of its different parts. From the mass of facts obtained in this way, one may make an attempt to reproduce the structure of the analyser, and to decide of what parts it consists and how these parts mutually interact.

So much for the work of the analysers. Concerning their topography and their arrangement it must be said that an exact localisation, as proposed on the basis of earlier facts, is now unsuitable. As to this point there had been even previously many objections. Our experiments show the formerly established boundaries of the analysers are incorrect. Their limits are much wider; they are not so sharply separated, but are interlaced and interwoven one with another. Certainly it is a difficult task to define exactly how the analysers are distributed in the brain, how and why they are connected with one another.



From the standpoint of the conditioned reflexes the *cerebral hemispheres* appear as a *complex of analysers*, whose functions are: to *decompose* the intricacy of the outer and inner worlds into their separate elements and components, and further to *connect* all these with the manifold activity of the organism.

The next question with which the method of the conditioned salivary reflexes is closely related and which without this method cannot be decided or even strictly defined is this: Is the activity of the hemispheres limited to the mechanism of the formation of temporary connections and the mechanism of the analysers, or must there be recognised some higher mechanism for which at present we have no name? That is a question which is not based on fancy, but arises from experiment. If you cut out all the posterior part of the hemispheres behind the gyrus sigmoideus and along the fissura sylvia, you will have an apparently normal animal. With the help of his nose and skin he will recognise you and the food and all the objects he meets. He will wag his tail when you stroke him, and he will show joy on recognising you by sniffing, etc. But this animal will not react to you if you are at a distance because he does not use his eyes in a normal fashion. If you call him, he will not come. You must conclude that this dog uses his eyes and ears very little, although otherwise he is entirely normal.

But if you remove the frontal parts of the cerebrum along the same line as in the above operation, extirpating the regions which you left in the other dog, you get a completely abnormal animal. He has no correct relations to you, or to other dogs, to his food, or to any part of his environment. It is an entirely demented animal which apparently shows no sign of purposeful behaviour. Thus there is a great difference between the two animals—the one without the hinder, and the other without the frontal half of his cerebral hemispheres. About the first, you would say he is blind and deaf, but otherwise normal; about the latter, that he is an invalid and a helpless idiot.

Such are our facts. An important and pertinent question arises, Is there not something special, some higher function in the frontal parts of the brain as compared with its posterior sections, is there not here concentrated the essential functions of the cerebral hemispheres?

The method of the conditioned salivary reflexes gives a clear and definite answer to this question, such as can be obtained from no other method of research. Is it actually true that an animal without the frontal half of his hemispheres shows none of that higher nervous activity which characterises the normal animal? If you adhere to the former methods, if you observe only the activity of the skeletal muscles, then you will be inclined to answer in the affirmative. But if you turn to the salivary glands with their conditioned reflexes, the matter appears



in an entirely different light. The value of our method depends not only upon the use of the conditioned reflex, but also upon the employment of the salivary gland in this reflex. If you observe the work of the salivary glands in such an operated dog, which seems at first sight to be demented, you will be astonished to see in what degree the complicated nervous relations of these glands are preserved. In the function of the gland you can find not the slightest disturbance. In such a dog (deprived of the frontal part of the hemispheres) you can form temporary connections, inhibit them, and dis-inhibit them. That is, the salivary glands exhibit the whole complexity of relations which is observed in a normal animal. You see plainly that there is an unexpected discrepancy between the activity of the salivary glands and that of the skeletal muscles. Whilst the muscles perform in an abnormal and disorderly manner, the salivary gland functions perfectly.

What does all this signify? First, it is unmistakably clear that in the frontal lobes there are no mechanisms which are dominant for the whole cerebrum. If such mechanisms were present there, then why did not the removal of this part of the brain destroy also all the delicate and complicated functions of the salivary glands? Why does everything proceed as normally with these glands? Obviously we must admit that all the peculiarities which we observed in this dog are phenomena relating to the skeletal musculature. Our task is thus reduced to finding out why the action of the skeletal muscles becomes so disturbed. There is no ground for assuming a general mechanism situated in the frontal lobes. In these lobes there cannot be any important arrangements which condition the highest perfection of nervous activity.

A simple explanation of these disturbances in the work of the skeletal musculature as a whole is this—the activity at every *moment* is dependent upon the skin analyser and the motor analyser. Thanks to these analysers, the movements of the animal are continually co-ordinated and accommodated to the surroundings. In this dog without frontal lobes, both the skin and the motor analysers have been destroyed, and it is natural that the general activity of the skeletal musculature should be impaired. Consequently, we have in the destruction of the frontal lobes only a partial defect (analogous, for example, to the injury of the eye analyser), but not such a general disorganisation as might result from the removal of the influence of some hypothetical higher mechanism of the brain situated in these lobes.

A series of experiments were performed in view of the importance of this question, in collaboration with Drs. Demidov, Saturnov and Kurayev. The experiments were so conducted that the entire frontal lobes, including the olfactory parts, were removed. In such a dog



the conditioned salivary reflexes could be elaborated only from the mouth cavity, the so-called water reflex; if as the unconditioned stimulus, a solution of acid was poured into the mouth, then it happened that the introduction of water, which by itself is without effect on the salivary glands and formerly was indifferent for them, caused a secretion, showing thus the production of a conditioned reflex. But as this water reflex might not be convincing enough to every one, it was necessary to prove in such a dog the existence of other reflexes. Therefore, Saturnov extirpated the frontal lobes but left the olfactory. In this dog there could be formed after the operation a conditioned reflex from the olfactory nerves.

After these experiments we must consider the subject clarified, and come to the final conclusion that a dog without frontal parts of the cerebral hemispheres loses only some special mechanisms, *i.e.*, some of its analysers, but not a general or higher mechanism.

When we thus examine the activity of the brain by the method of the conditioned reflexes, we get an absolutely definite answer. Maintaining our exact facts as a foundation, we can state that the cerebral hemispheres represent an accumulation of analysers, which decompose the activity of the external world into its individual elements and moments, and afterwards connect the phenomena thus analysed with the special activities of the organism.

Can we be satisfied with the results obtained? Without doubt we can, for our experiments afford a starting point for the further successful investigation of the subject. At the same time it is clear that this study has just begun, and its magnitude and difficulties stretch far out into the future. If we would outline the further investigation of this subject we must pay the greatest attention first of all to our present method, the dismemberment of the apparatus under investigation (*i.e.*, the hemispheres) into its component parts. A method inherently combined with infinite difficulties! The more we experiment with extirpations of the brain the more we wonder at the results obtained with this method by former investigators. Owing to the extirpation we never attain a stable condition, it constantly changes. You put your hands on the brain, you touch it with your heavy hands; you have wounded it, and removed certain of its parts. This damage irritates the brain, and the action of the injury lasts for an indefinite time and spreads to uncertain limits. You cannot say when this detrimental effect will end. That such a harmful effect exists, however, is proved by many well known experiments, which it is not necessary to review. Finally, the looked-for moment comes when the irritation from the wound passes. But now appears a new stimulus—the scar. And there are only a few days during which you can work with the certi-



tude that all the observed changes depend only upon the absence of the extirpated portions of the hemispheres. Then the following course of events sets in: At first there appear the phenomena of depression, and you know that it is the effect of the cicatrix. Such a condition continues for some days, and then appears a convulsive attack. After the irritation, after the depression, after the convulsion, there ensues a new period of depression or an entirely special state of the animal. After the convulsion you cannot recognise your dog as the same one you had before; he is much more upset now than he was immediately after the operation. Evidently the scar has not only irritated, but has exerted pressure, drawn and wrenched the tissues, in a word, done damage again.

I must add that this effect of the scarring never ceases, at least I have never seen it end. The affair sometimes lasts for months and years. Convulsions usually begin after one to one and one-half months, and then they recur. We have operated on many scores of dogs, and I can categorically state that not a single one escaped convulsions, and if they were not repeated it was only because the animal died during the first attack.

Try under these discouraging conditions to analyse successfully so complex an activity as that of the brain. Without doubt the contemporary investigator of the cerebrum should above all be scrupulous as to how to adapt his manipulations in relation to this organ. This is a most important question, because under present conditions there are lost an enormous amount of human labour and a multitude of animals. Endeavours have already been made to reduce this waste. A German experimenter, Trendelenburg, has tried local freezing of the brain, and in our laboratory Dr. Orbeli is using the same method. The near future will show us in what degree this procedure will be of avail, and what good it will bring to us.<sup>1</sup>

These are our results, our complaints, and our hopes.

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<sup>1</sup> The difficulties and complications following operations on the hemispheres brought Pavlov almost to despair of this method as a means of physiological investigation. And until now he has not used it systematically for investigation of the physiological mechanisms in the brain, having recourse to it only occasionally. In his other book, *Activity of the Cerebral Hemispheres*, this point of view is expressed even in the titles of the chapters dealing with the experiments on destruction of the hemispheres: chapters xix-xxi are entitled "Pathological Disturbances," etc.—*Translator*.



## CHAPTER XIX

### INTERNAL INHIBITION AS A FUNCTION OF THE CEREBRAL HEMISPHERES

(Article published in the Anniversary Volume of Prof. Ch. Richet, Paris, 1912.)

REVIEW OF THE TWO CHIEF MECHANISMS IN THE HEMISPHERES—DISCUSSION OF THE FORMATION OF THE CONDITIONED REFLEX—EXTINCTION; RETARDATION; DIFFERENTIATION; CONDITIONED INHIBITION: ALL TYPES OF INTERNAL INHIBITION—LAW OF IRRADIATION AND CONCENTRATION—DIFFERENTIATION OF INHIBITION—DIS-INHIBITION—INHIBITION ALWAYS FOLLOWS EXCITATION.

MORE than ten years have passed since I decided to study the complicated nervous relations of higher animals (the dog) to the outer world. Usually these relations were understood and analysed on the basis of an analogy with our own subjective internal world, and considered as psychical. I undertook their objective external investigation just as physiologists study the other functions of the organism. Now for more than ten years I and my collaborators have applied ourselves energetically to this problem. We have collected considerable material on the subject, but it has been published only in Russian in doctors' dissertations or in reports to scientific societies. I refrained from publishing in foreign languages because I intended to advance and systematise our inquiry in order to present reasonable and acceptable physiological conclusions. So it happened that I postponed a complete and systematic review of the attained results, and permitted to be printed only short, generalised communications regarding our investigations. But at present, wishing to express my esteem to one of the creators of contemporary physiology, I ask your attention to a group of phenomena constituting an independent chapter on the subject of conditioned reflexes.

As I explained in my report in Moscow in 1909,<sup>1</sup> we investigate and consider the higher nervous activity of the dog as the work chiefly of two nervous mechanisms: the *mechanism of temporary connections* between external agents and certain activities of the organism, *i.e.*, the mechanism of temporary reflexes, which we call conditioned reflexes in contrast to those better known and recognised reflexes which we designate as unconditioned; and another mechanism, the mechanism of *analysers*, whose function it is to decompose the complexity of the surrounding world into its elements. The analyser consists, according to our scheme, of a receptor surface (for example, the retina), of the

<sup>1</sup> See chapter x of this book.—*Translator.*



corresponding nerves (for example, optic, auditory), and the brain ends of these nerves located at various levels of the central nervous system, including the hemispheres. The work of these two mechanisms embraces a countless number of simple and complicated nervous relations of the animal to the outer world.

In 1910<sup>2</sup> I endeavoured to systematise the phenomena of inhibition which appear in the work of the above-mentioned mechanisms. First, we considered a group of inhibitions which can be easily defined and characterised, and which we termed *external inhibition*. The mechanism of this inhibition is apparently the following: if some other point of the central nervous system is set into activity through the corresponding external or internal stimuli, this causes an immediate diminution or complete disappearance of our conditioned reflex—the conditioned reflex becomes weaker or vanishes.

Besides external inhibition there exists another group of inhibition phenomena whose mechanism is quite different. The conditioned reflex, which is a temporary connection of some external, previously indifferent agent with a certain function of the organism, originates because the action of this indifferent agent on the receptor surface of the animal repeatedly coincides in time with the action of an already existing reflex stimulus of one or another activity. Owing to this coincidence, the indifferent agent becomes a stimulus of the same activity. All our experiments have been done on the salivary gland, which, as you know, reacts to psychical stimulations, using the old terminology, and is consequently in complicated relations to the external world. Food and other stimulating substances entering into the mouth of the animal cause an unconditioned reflex; *a conditioned reflex, however, may be called out by any agent of the external world if it is capable of acting on any receiving surface of the organism*. It is clear that a pre-formed reflex must exist as the basis of this formation of the new reflex. Now, if the conditioned stimulus acts for some time alone, unaccompanied by the unconditioned stimulus with the help of which it was formed, then the action of the conditioned stimulus becomes weaker, or, in other words, is inhibited.

The first clear example of inhibitory action is the phenomenon which we call the extinguishing of the conditioned reflex. If a well elaborated and stable conditioned stimulus be repeatedly applied at short intervals, alone, without being followed by the unconditioned stimulus, then it begins to decrease and gradually becomes inactive. This is not a complete destruction of the conditioned reflex, but only a temporary suspension. That this is so is proved by the spontaneous restoration of the reflex after an interval, unless during this time something acts

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<sup>2</sup> See chapter xi of this book.—*Translator*.



unfavourable to its restoration. That this extinction of the conditioned reflex is not a matter of fatigue is proved by its restoration without the assistance of the unconditioned stimulus. How this reappearance comes about will be referred to on later pages of the present paper.

This *extinguishing* was the first instance of the different kinds of inhibition which we have studied. We have met with other examples, however, since this first one.

If we have established a conditioned reflex by giving an unconditioned stimulus (for example, food) shortly (for example three to five seconds) after the beginning of the action of some indifferent agent, then the indifferent agent becomes a conditioned stimulus, quickly manifesting its effect: now if this conditioned stimulus is applied alone, saliva begins to flow after a few seconds. But let us slightly alter the experimental relations. We systematically join the unconditioned stimulus to the conditioned stimulus three minutes after the beginning of the latter; in this case, the conditioned stimulus soon becomes weak, and disappears for a certain period, and then the following state of affairs sets in: during the first minute, or one and a half to two minutes, there is no effect seen from the conditioned stimulus; its action becomes manifest only at the end of the second minute, at first weakly, then increasing in strength, and attaining its maximum at the moment of the connection with the unconditioned stimulus. Such a conditioned reflex is *delayed*, and the phenomenon itself we call *retardation*. What kind of phenomenon is this? The apparently effective conditioned stimulus remains without action during the beginning of its application. The analysis of this fact showed us that in the case of the delayed reflexes inhibition takes place, because disappearance of this state of inhibition may be brought about immediately by special interference, and the conditioned stimulus will then be as active at the beginning as at the end of its three-minute application.

The third kind of inhibition is manifested during the differentiation of stimuli. Let us elaborate a conditioned stimulus from a tone of some musical instrument of 800 vibrations: finally, we have a stable and considerable action. Now let us apply for the first time the nearest tones; we get at once an effect somewhat proportional to the proximity of the second tone to that which was originally used as the conditioned stimulus. But if you constantly and systematically accompany the original tone of 800 vibrations with the unconditioned stimulus (for example, food), *i.e.*, reinforce your conditioned reflex, as we are accustomed to say, and if you repeat the other neighbouring tones without the unconditioned stimulus, then these neighbouring tones gradually become ineffective.

It is plainly seen that the *differentiation* of these tones is effected through the development of an inhibitory process set up by the neigh-



bouring tones. To prove this, you begin the experiment by trying the tone of 800 vibrations. It shows its usual significant effect. You reinforce it by the unconditioned reflex. After establishing the conditioned reflex you may be sure that subsequent repetitions of the experiment give a uniform result. Instead of the usual experiment, you now apply soon after the first trial (*i.e.*, first for that day) of the tone of 800 vibrations, one of 812 which you have well differentiated, never having given food after it; the action of the latter is null. But now try again your tone of 800 immediately after the negative tone (812) and you will find that this time it has either no action or a very slight one. If, instead of applying the positive conditioned stimulus immediately after the negative, you apply it 15 to 20 minutes later, then it has its usual effect, *i.e.*, produces the same flow of saliva. Consequently, in order to abolish the action of the neighbouring tones, inhibition must arise, and this inhibition only slowly disappears from the hemispheres.

Finally, the last type of inhibition. We take some indifferent agent having no marked effect on the animal and add this to a well elaborated conditioned stimulus, not accompanying this combination of two agents by the unconditioned stimulus (food); the indifferent agent will gradually become an inhibitor of the conditioned stimulus, *i.e.*, the combination of the conditioned stimulus with the indifferent agent is always null, although the conditioned stimulus used alone is as active as before. This phenomenon we call *conditioned inhibition*. Here, too, we have an after effect of the inhibition, just the same as we have described in the case of differentiation of the stimuli.

All these types of inhibition we have united under the term of *internal inhibition*. This group is rather a natural one, because all its members are characterised by the same general, sharp features.

In 1870 the experiments of Fritsch and Hitzig laid the foundation for an exact and successful physiology of the brain, and physiologists made acquaintance with the important and not sufficiently appreciated fact that the stimulation of a certain point of the hemispheres always tends to irradiate quickly: the initial contraction of a definite group of muscles under the influence of a continuous or strong stimulus passes over into tonic convulsions of the whole body. This is a characteristic of the mass of the cerebral hemispheres, of the most reactive and most labile part of the central nervous system.

It is a well known fact, which may be observed with all agents, that when they have just become conditioned stimuli their action, during the first days, is very general, *i.e.*, there now act as conditioned stimuli (calling out the same effect as the original stimulus) all phenomena similar or akin to the elaborated conditioned stimulus. Only by and by, under the influence of definite circumstances, does the conditioned



stimulus become specialised (specific), *i.e.*, the action of all these accessory stimuli, which do not coincide with the conditioned reflex, is obliterated by the process of inhibition, and only the conditioned stimulus remains active. Now it is quite natural to conceive the first effect as a phenomenon due to irradiation.

These considerations and our additional data give us the right to accept the law of *irradiation* and concentration for impulses arriving in the hemispheres; first these excitations spread, and flood the whole cerebrum, and later they collect in certain, definite points.

This law of irradiation and concentration is even more clearly manifest in the process of the internal inhibition than in the process of excitation. Here are some illustrative facts. Suppose that we have several conditioned stimuli connected with the same unconditioned stimulus. According to the method mentioned above, let us extinguish one of these conditioned reflexes. Immediately after, we can see partial or complete extinction of all other conditioned stimuli, even those belonging to other analysers. If you now vary the experiment so that after the extinction of one of the conditioned stimuli, you try the other ones, not at once but after some minutes, you will see that the latter, at this time, operate with full effect, but the one which you have extinguished remains for a long period inhibited. From these cases of extinction one may suppose that the inhibition originates in the analyser to which the extinguished stimulus belongs, whence it irradiates to other analysers; afterwards it disappears from these other analysers first, and concentrates in the initial point (experiments of Horn).

Similar relations are observed in differentiation of inhibition. Let us form a conditioned stimulus from a definite tone and differentiate from it other tones. Suppose that the positive tone is one of 800 vibrations, and that one of 812 vibrations is ineffective (negative). Besides this we prepare several conditioned stimuli from agents affecting other analysers, using the same unconditioned stimulus which was connected with the tone of 800 vibrations. In order to attain a strong inhibition, a fine differentiation was elaborated, and, therefore, after the application of this differentiated (negative) tone, the positive tone of 800 vibrations, as well as the positive stimuli of other analysers, were ineffective. If the differentiation were not so delicate (if the negative tones used were two or three full tones higher or lower), only a weak inhibition is developed, wherefore after application of this negative tone only the positive tone stimulus is directly inhibited, and the positive stimuli of other analysers remain active (experiments of Belyakov).

The same relations are strikingly corroborated in experiments with the skin analyser (work of Krasnogorsky). We apply as a conditioned stimulus the mechanical irritation of the skin. For this purpose we ar-



range on the hind leg of the dog a series of four pricking apparatuses at a certain distance from one another, and we see that the stimulation of these points gives a regular and uniform effect. Now we differentiate from these stimuli the action of a fifth apparatus, placed at the lowest part of the leg, and always unaccompanied by food, *i.e.*, a negative stimulus. The effect of all our stimuli, as I have said before, is measured by the number of drops of saliva. Suppose we get 10 drops during thirty seconds from each of the upper four (positive) conditioned stimuli. Now we apply the fifth and lowest apparatus and receive a null effect—full differentiation. Thirty seconds later we try the action of the four upper apparatuses (positive), and we find that they are all inert. If now the same trial is made one minute after the action of the negative conditioned stimulus, we get quite another result. The following number of drops is received, respectively, taking the apparatuses in order from above downward (the last figure showing the apparatus next to the inactive one): 5, 3, 1, 0; after waiting two minutes, 10, 8, 5, 2; after three to four minutes, 10, 10, 10, 4; and after five to six minutes the normal and equal size of reflexes from all of the four positively acting apparatuses. It is to be understood that all these experiments must be performed under equal conditions, during the course of several days, etc.

From this experiment it is clear that the inhibition, which resulted from the lowest apparatus, irradiated over a great region of the skin analyser, and afterwards gradually concentrated around its point of origin.

The group of internal inhibitions is distinguished by the following highly characteristic features. For the sake of complete clearness I shall give a concrete case. Suppose we have a delayed conditioned reflex, *i.e.*, the conditioned stimulus calling out this reflex does not exercise its effect immediately but only one to two minutes after its beginning, during the third minute of its action. If now during the first ineffective phase of the conditioned stimulus (the first two minutes of its action), there acts on the animal some agent of moderate strength, producing an external inhibition, for example, an agent calling out a slight orienting reflex, saliva will begin to flow immediately; the conditioned stimulus has, now, become effective earlier. Certainly this additional agent *per se* has no relation to the salivary gland, and is incapable of producing a salivary secretion.

As this agent has an inhibiting effect on the same conditioned stimulus during the active phase, we may conclude that during the inactive phase it becomes effective by inhibiting the internal inhibition, and thus freeing the stimulation (experiments of Zavadsky). Such *dis-inhibition* is met with in other cases of internal inhibition.

If we have produced extinction of a conditioned stimulus to a certain



degree, or even to zero, we can at once restore its action, to a greater or less degree, by joining to it an agent from the group of external inhibition (experiments of Zavadsky). In this way one may cause to disappear the inhibition of all kinds of differentiation (experiments of Belyakov), as well as of the conditioned inhibition (experiments of Nikolayev).

As I have said in previous publications, *dis-inhibition* is manifest only under certain conditions, viz., if the *dis-inhibiting* agent is of average strength (not very strong and not too weak). But if this agent is of great intensity it inhibits the conditioned stimulus itself, and consequently there is nothing to be liberated from internal inhibition. It is essential that this agent be of definite strength, neither too powerful, lest it inhibit the stimulus, nor too weak, lest it can not inhibit the internal inhibition. Only under these conditions is there complete dis-inhibition. If our explanation of the facts is accepted, then one must come to the conclusion that the process of internal inhibition is less stable than that of excitation. I do not exclude the possibility of other explanations of what we call "internal inhibition," but I see no serious objection to our understanding of the phenomena. We must admit that at the present time we know altogether nothing of the real nature of internal inhibition.

If you employ a process of internal inhibition which is already present, you can obtain thus a new negative inhibitory conditioned reflex just as you may receive a new positive conditioned reflex with the aid of well elaborated conditioned reflexes (experiments of Volborth). This is done in the following manner: we apply a well established conditioned reflex, and by the method described above, cause its complete extinction. To the extinguished stimulus an agent is added which must be indifferent to the extent that it does not act on the extinguished stimulus, i.e., it should not dis-inhibit it. Such a combination is repeated several times, whereby the indifferent agent receives the potentiality of the conditioned inhibition, i.e., if it is now joined to the active conditioned stimulus which gives a full effect, it weakens this effect; this weakening may be considerable and may lead to the complete disappearance of its action. Consequently, the formerly indifferent agent, which coincided many times with the process of internal inhibition, became connected with the inhibition, and thereupon its application called out this process.

One must notice that the three above-mentioned characteristics of internal inhibition are also properties of the excitatory process. This harmonises well with the view, which occupies an ever larger place in physiology, that *inhibition always follows excitation*, that it is in a certain sense the *reverse side of excitation*.

More and more material must, evidently, be collected in order finally



to give a firm foundation for a more or less proper understanding of the mechanism of the central nervous system.

When many years ago I began to devote my energies to the objective study of the highest parts of the central nervous system, I was continually astonished and impressed by the infinite complexity<sup>a</sup> of the existing relations. But it also seemed to me that the higher sphere of nervous activity, in comparison with the lower parts of the central nervous system, offers to the experimenter many advantages. In the spinal cord we find pre-formed connections; we can not see nor assist in their elaboration, and consequently we do not know what elementary properties and what most general and simple laws, manifesting themselves in the central nervous system, played a part in their formation. It is otherwise with the higher parts. Here we observe the phenomena in unbroken succession, and we continually see the elaboration of new relations and the analysis of stimuli, and thus we have the possibility of watching and learning how these phenomena develop and upon what elements they rest.

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<sup>a</sup> See chapter xxvi, footnote 3.—*Translator.*



## CHAPTER XX

### THE OBJECTIVE STUDY OF THE HIGHEST NERVOUS ACTIVITY OF ANIMALS

(Read before the Society of the Moscow Scientific Institute, March, 1913.)

BEHAVIOUR AND AMERICAN PSYCHOLOGY—PSYCHICAL REACTIONS ARE CONDITIONED REFLEXES—SENSE ORGANS AND ANALYSERS—WAKING AND SLEEPING STATES—THE SLEEP INHIBITION; EXTERNAL INHIBITION; INTERNAL INHIBITION—THE DEFENCE REACTION IS OVERCOME BY THE FOOD REACTION BUT NOT BY THE ACID REACTION—IRRADIATION OF EXCITATION ILLUSTRATED BY EXPERIMENT—PSYCHOLOGICAL EXPLANATIONS HOPELESS—THE AGGRESSIVE REFLEX—EMOTIONS—CONDITIONED STIMULUS MUST PRECEDE THE UNCONDITIONED—INTERACTION OF CENTRES—CONSCIOUSNESS.

IN to-day's illustrious festival of Russian science permit me to call your attention to the work of Russian investigators in one of the most interesting regions of contemporary research. The theme of my report is the objective study of the higher nervous system of animals.

With full justice Charles Darwin must be counted as the founder and instigator of the contemporary comparative study of the higher vital phenomena of animals; for, as is known to every educated person, through his highly original support of the idea of evolution he fertilised the whole mentality of mankind, especially in the field of biology. The hypothesis of the origin of man from animals gave a great impetus to the study of the higher phenomena of animal life. The answer to the question as to how this study should be carried out and the study itself have become the task of the period following Darwin.

Since 1880 more and more frequent have become investigations of the influence of surroundings on the movements of animals, or according to the American terminology, *behaviour*. First the attention of biologists was turned to the lower animals. Simultaneously, with a purely physico-chemical explanation of the external reactions of the animal, as, for example, in the study of tropisms and taxises, there were also attempts at an objective, realistic description and systematisation of the facts which constitute the behaviour of animals, as well as the psychological understanding of the phenomena (these latter more rarely). These studies continually widened, and embraced an ever increasing number of animals all along the zoological ladder. Most of these investigations at present belong to North America, the new home of science. But in American researches on the behaviour of higher animals there is, in my opinion, a gross defect which prevents the success of the work, but which, I have no doubt, will sooner or later be removed. I refer to the application of psychological conceptions and classifications in this es-



entially objective study of the behaviour of animals. Herein lies the cause of the fortuitous and conditional character of their complicated methods, and of the fragmentary and unsystematic character of their results, which have no well planned basis to rest on.

Twelve years ago, I with my collaborators, to whom I send friendly and grateful greetings, decided to study the higher nervous activity of the dog, strictly objectively, absolutely excluding psychological conceptions in the analysis of our material.

The present report, although sketchy, will include a complete review of our work and our conclusions. I shall enumerate our chief facts, show how they may even now be systematised, and what conclusions may be drawn from them.

Definite, constant, and inborn reactions of the higher animals to certain influences of the external world, reactions taking place through the agency of the nervous system, have for a long time been the object of strict physiological investigation, and have been named reflexes. We call these *unconditioned reflexes*. The apparently endlessly complicated, seemingly chaotic (forming and disappearing during the life of the individual), constantly vacillating reactions of the higher organism to the countless and eternally changing influences of the outer world—in short, what are generally called *psychical functions* we recognise also as reflexes, *i.e.*, regulated responses to the external world. As these reactions are dependent upon a multitude of conditions, it appeared logical to us to designate them as conditional, as *conditioned reflexes*.

Numerous and infinitesimal phenomena of the external world become stimuli of the several functions of the organism under only one condition: their action must coincide one or many times with the action of other external agents which call out the activity of the organism, and then these new agents themselves begin to provoke this activity. Food, the chief bond between the animal, the living organism, and the surrounding world, stimulates (through its odour, and its mechanical and chemical effect on the surface of the mouth) the food reaction of the organism—*i.e.*, the approach of the animal to the food, the introduction of it into the mouth, the flow of saliva, etc. If with the action of food on the animal there coincides several times the presence of any indifferent agent, then this latter will call out the food reaction. The same holds true for the remaining activities of the organism, the defensive, the reproductive, etc. These functions begin under the influence of constant as well as of temporary stimuli. In this way these temporary stimuli become signals—the agents of the constant stimuli—and they make much more complex and delicate the relations of the animal to his environment.

But it is clear that the organism must possess mechanisms which



are capable of decomposing the environment into its elements. These it has in the form of the so-called *sense organs*, which, in our objective analysis of life, correspond to the scientific term, *analysers*.

The action of the mechanism through which the temporary connections, or conditioned reflexes are formed, and the more delicate work of the analysers lays the basis of the higher nervous activity. It has its seat in the cerebral hemispheres; the coarser analysis and the unconditioned reflexes being functions of the lower parts of the central nervous system. It is clear that these complex and delicate relations of the animal organism to the outer world are constantly vacillating and changing. We have already become acquainted with three different kinds of inhibition which lead to the weakening or complete disappearance of the conditioned reflexes.

Sleep, or, as we call it, the sleep inhibition, divides the life of the organism into two phases: the *waking* state and the *sleeping* state, or the *externally active* and the *externally passive* state. Under the influence of inner causes and also under certain external stimuli, drowsiness and sleep set in, during which the activity of the higher parts of the central nervous system, as manifested in the conditioned reflexes, is either weakened or entirely disappears. By means of this inhibition an equilibrium is maintained between those parts of the organism which are directly concerned with the external world, an equilibrium between the processes of destruction and of restoration of the reserve material of organs during their states of work and of rest.<sup>1</sup>

The second kind of inhibition, which we call *external inhibition*, is an expression of the concurrence of different outer, as well as of inner, stimuli on the predominant influence in the organism during every separate moment of its existence. This is an inhibition which we meet as often in the lower as in the higher parts of the central nervous system. Every new agent at the outset of its action on the central nervous system enters into a struggle with those other agents operating there; sometimes it weakens the effect of the latter, at other times it routs them completely, and in other cases it retreats and leaves the field to the agents formerly present. Translating this into the language of neurology, we may say in the given case that a strongly excited point of the central nervous system decreases the irritability of all surrounding points.

The third sort of inhibition of the conditioned reflexes, we call *internal inhibition*. This is a rapid loss of the positive effect of the

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<sup>1</sup> Here sleep is considered as a peculiar kind of inhibition. Further investigation proved that sleep is to be regarded as widely irradiated internal inhibition. The chapter, "Inhibition and Sleep—One and the Same Process," contains the whole body of evidence strengthening this view.—*Translator*.



conditioned stimuli when they do not act as true and exact signals and agents of the unconditioned stimuli. This, however, is not a destruction of the conditioned reflex, but only a suspension.

While some agents of the external world can condition the above-described kinds of inhibition, others, on the contrary, may remove an existing inhibition. We thus have the phenomenon of *dis-inhibition*—the freeing of the stimulation from the effect of the inhibition.

This kaleidoscope of the conditioned reflexes, with their fanciful and apparently irregular and incomprehensible course, is in reality exactly determined, *viz.*, through the strength, duration, and direction of the movement of the nervous process in the mass of the great hemispheres. I shall now illustrate this through examples taken from actual experiments. You have before you two kinds of external agents; on the one hand, various substances, edible and inedible, which, introduced into the mouth of a dog, are accompanied by corresponding reactions (certain movements, certain secretions); and on the other hand, an electric current which, directed to one or another point of the skin, calls out also a corresponding reaction of the animal—the *defence* reaction. If you allow both agents to act simultaneously there begins in the central nervous system a conflict. If the electric current is confined only to the skin, and at the same time food is put into the mouth of the dog, the struggle ends with the victory of the nutritive agent, and the electric current, be it ever so strong, becomes the signal, the representative, of food, and a conditioned stimulus for the food centre. The electric stimulus now provokes not a defence, but a food reaction: the animal turns toward the experimenter, makes licking motions, etc., as before eating. The same is observed if the electric current is supplemented by burning and wounding of the skin. In other words you have an actual diversion of the nervous process from the paths of the defensive centre to the paths of the food centre.

But if you take some other combination—the same electric current and the introduction of acid into the mouth—you never succeed in forming a conditioned reflex for the acid from the electric stimulus, no matter how often this combination is repeated. The nervous process aroused by the acid in the mouth is not strong enough to overwhelm the nervous process set up by the action of the electricity on the skin. Let us go further. If you apply the electric current on such parts of the body that it penetrates to the bone, then in spite of your patience, with certain intensities of the current you will never receive a conditioned reflex from the electricity, even taking food as the unconditioned stimulus. Now the nervous process from the electric stimulation is more intense than the nervous process from food. We know subjectively that bone is more sensitive to pain than the skin. The nervous



process is thus despatched in the direction of the most powerful stimulation. It should not be difficult to show the practical meaning of the relations brought out in this experiment: for example, we often see in the struggle of the animal for food that the integrity of the skin is sacrificed. The danger to the existence of the organism in this case is not so great, and the animal prefers the danger involved in the acquiring of food to the safety of his skin. But if the bones are broken, the animal, to preserve himself from total destruction, must neglect for a time the calls of nutrition.

Thus the relative intensity of the nervous processes determines the direction of the nervous impulses, and the connection of the agents with the various activities of the organism. These relations of intensities comprise a large chapter in the physiology of the conditioned reflexes: and the exact definition of the comparative intensity of nervous processes set up by the action of various stimulating agents forms a most important point in the present study of the activity of the cerebral hemispheres.

The latent after-effects of foregoing stimulations at any given moment have enormous significance for the activity of the hemispheres. For this reason it is necessary to make a careful study of the duration of such latent effects. In this direction, too, the physiology of conditioned reflexes furnishes abundant material. For example, the ticking of a metronome, indifferent because it has not been connected with any activity of the organism, has an effect on the conditioned reflexes for some seconds, or even a minute, after its cessation. The introduction of acid into the mouth of the dog alters the conditioned food reflex for 10 to 15 minutes after its application. The eating of sugar can change for several days the conditioned reflex on meat and bread powder. It is a great, though entirely feasible, task to calculate the traces of the stimuli which have previously fallen upon the animal in question.

Not less important is the establishment of a general rule for the movement in the cerebral hemispheres of the nervous processes, excitation as well as inhibition. Forty years ago in the first exact experiments on the hemispheres it was noticed that the stimulation of a certain point on the cortex of the brain, if it be of short duration, calls out a contraction only of a certain group of muscles. If, however, the stimulation lasts for some time, it spreads over to other muscles, indeed over the whole skeletal musculature, leading to convulsions. Obviously, the fact which confronted the physiologist was a characteristic of the brain as a part of the central nervous system, *viz.*, the fact that excitation easily spreads from its original point over a large area of the cerebral cortex, the fact of irradiation of the nervous process



over many groups of nerve cells. This *irradiation* of the excitation is constantly met with in the physiology of the conditioned reflexes.

If you have made some special tone a conditioned stimulus of the food reaction, then not only this tone, but in general all sounds, will call out the same conditioned reflex as that produced by the special tone. Or if you have a conditioned reflex from the pricking or stroking of some particular spot of the skin, then at first in the early part of your work, pricking of all remaining points of the skin also evokes the conditioned reflex. This is a general fact. We must suppose that in all these cases the excitation arriving at a certain point of the cerebral hemispheres spreads and irradiates over the corresponding part of the brain. It is only in this way that all the stimuli of the given category could become connected with a definite activity of the organism.

The fact of irradiation of the nervous process is even more clear and salient in the case of internal inhibition. The following is an experiment remarkably convincing. You arrange on the leg of the dog a series of apparatuses for the mechanical stimulation of the skin. The action of the upper four is accompanied by feeding. After some repetitions, the mechanical stimulation of these four points produces the food reaction; the animal turns toward the operator, makes licking motions, secretes saliva, etc. Due to the process of irradiation, the fifth and lowest apparatus, when for the first time put into action, also calls out a flow of saliva although its action was never accompanied by feeding. But if you repeatedly use it without feeding, you finally reach the point where it produces no visible effect (negative conditioned stimulus). How has this been brought about? It has occurred in consequence of the development of the inhibitory process in the corresponding point of the central nervous system. The proof of this is obvious. If you now apply the fifth (negative conditioned stimulus) apparatus, then for some time afterwards all the upper (positive conditioned stimulus) apparatuses are without effect. The inhibitory process has irradiated from its original point to neighbouring regions of the cerebral hemispheres.<sup>2</sup>

The irradiation of the nervous processes forms thus one of the fundamental phenomena of the activity of the cortex of the brain. Related to this process is its counterpart—the *concentration* and collection of the nervous process in a certain point. To save time I shall demonstrate this new phenomenon with the same experiment. You apply for a long while the action of the lowest apparatus (negative conditioned stimulus). If you try the upper apparatuses after a short interval, they also will be ineffective. The greater the interval of time between the trial of the lowest (negative conditioned stimulus) and of the upper four (posi-

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<sup>2</sup> See also preceding chapter for a description of this experiment.—*Translator.*



tive conditioned stimuli), the more is the inhibition freed, and in strict succession from above downwards, until, when the interim is sufficiently long, there is no inhibition from the application of the lowest of the four apparatuses.<sup>3</sup> Before your eyes the inhibition wave contracts and returns to its starting point, in other words, it concentrates. After many repetitions of the ineffective stimulus, the inhibition concentrates more and more quickly, first during minutes and then during seconds, and, finally, during a hardly perceptible period. In this way the separate phenomena of the nervous activity of the cerebral hemispheres are subject to two general laws (or they may be spoken of as one law)—the law of irradiation and of concentration of the nervous process.

Hence it follows that the pivotal point in the scientific investigation of the activity of the brain lies in the delimitation of the paths along which the nervous process spreads and concentrates—a problem of space relations. This is the reason why from the strictly scientific point of view, it seems to me that the position of psychology as a study of *subjective states* is completely hopeless. Certainly these states for us are a reality of the first order, they give direction to our daily life, they condition the progress of human society. But it is one thing to live according to subjective states, and quite another thing to analyse purely scientifically their mechanism. The more we work with conditioned reflexes, the more we are persuaded how deeply and radically the decomposition of the subjective world into its elements and their grouping by psychologists differ from the analysis and classification of nervous phenomena by physiologists who think in terms of spatial relations.

Partly to give an example of this, partly to show how wide are the boundaries of our investigations and what they include, I shall describe some more experiments.

Our experimental animal seems to be a watchdog, and in addition, one of a nervous temperament. He reacts aggressively to every person who enters the room where, with the experimenter sitting close beside him, he is on the stand. This pugnacity becomes pronounced if the intruder makes some threatening gesture, or if he strikes the dog. In the objective study of the central nervous system, this represents a special reflex, the *offensive reflex*. The internal mechanism of the nervous system of the given dog is revealed in the following experiment. The intruder—the cause of the continued and energetic aggressive reaction of the animal—sits in the place of the experimenter, and puts into

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<sup>3</sup> At first all four skin spots give no effect, then after a greater interval, the uppermost is active but the other three inactive (inhibited); a little later, the upper two active, and the lower two inhibited; then only the lower of the four inhibited, and at last they are all free.—*Translator*.



action a formerly well elaborated conditioned stimulus of the food reflex. Contrary to expectations this stimulus evokes now an enormous effect, much greater than the usual experimenter was ever able to obtain when he performed his experiments on the quiet animal. The dog secretes more saliva than in any of the preceding experiments and eats the food greedily out of the hand of him whom he has just attacked so ferociously and whom he will again attack after the feeding. How can this be explained?

Before answering this question I shall mention other peculiar facts. The object of the dog's animosity—the newcomer—remains in the seat of the regular experimenter, behaves himself faultlessly, making not the slightest movement, not even the most indifferent, and limits his conduct to repetition of the conditioned stimulus accompanied by feeding the dog. Gradually the animal becomes quieter; he still barks but not so fiercely, and after some time becomes entirely calm, although he never turns his eyes away from the new experimenter. The aggressive reaction has apparently become weaker. A most remarkable state of affairs it is that when the conditioned stimulus begins to act again, there is no drop of saliva, and the dog takes the food only five to ten seconds after it is offered and eats it slowly and apathetically. But if the new experimenter stands and behaves more freely, the aggressive reaction recurs and at the same time the food reflex is reinforced. How are these phenomena to be understood?

From the standpoint of our previously known facts, the mechanism of these strange phenomena is no puzzle. When the most pronounced offensive reflex was manifested, the excitation flowed from a certain point in the cerebral hemispheres over a large area, probably over the whole of the hemispheres, embraced many centres, and among them the food centre. All this resulted in a general, extremely heightened activity of the hemispheres. This is the reason why the food stimulus produced such an extraordinary effect. Supposedly, this is the nervous mechanism of what we subjectively call an "*affect*"; what we have seen in our dog must be designated psychologically as the affective state of *anger*. In the weakening of the external stimuli (the movements of the stranger), the reflex gradually diminishes, and the nervous process contracts and concentrates in a certain part of the cerebral hemispheres. When this concentration has reached a certain degree there results an isolation of the centre of the offensive reflex, and there follows, according to the above-mentioned law of conflict of centres, a decrease in the excitability of all the remaining centres, including that for food. This, I think, is a beautiful illustration of the laws of irradiation and concentration of the excitation and of the interaction of these processes.



In conclusion, I shall present one of the latest facts from our laboratory. We have always developed the conditioned reflexes in the following manner. The new agent, with which we had chosen to develop a conditioned reflex, was brought into action, and five to ten seconds or even later the dog was fed. After several recurrences of these combinations, the agent itself called out the food reaction of the animal, became a conditioned stimulus. But when this method was slightly varied, an unexpected result cropped out. If we began with the feeding and then five to ten seconds afterwards added a new agent, then in spite of innumerable combinations, we failed to develop any reflex.

Whether under such circumstances it will be possible to form a conditioned reflex is a problem for further enquiry. But the extraordinary difficulty of its formation is an indisputable fact. What does this mean? Judging again from our known facts, the answer to this is not intricate. When the dog eats, the food centre is in the state of excitation (for this is a very strong centre), and according to the law of the conflict of centres, all the remaining parts of the cerebral hemispheres are in a state of considerably decreased irritability, wherefore the incoming stimulations will be without effect.

Allow me to take this opportunity to express in a few words how we represent physiologically what we call "*consciousness*" and "*conscious.*" Certainly I will not discuss this question from the philosophical point of view, *i.e.*, I shall not touch on the problem of how the brain substance creates subjective phenomena, etc. I shall only endeavour to answer provisionally what kind of physiological phenomena, what sort of nervous processes, proceed in the hemispheres of the brain when we say we are "*conscious*" and speak of our "*conscious*" activity.

From this point of view, *consciousness* appears as a nervous activity of a certain part of the cerebral hemispheres, possessing at the given moment under the present conditions a certain optimal (probably moderate) excitability. At the same time all the remaining parts of the hemispheres are in a state of more or less diminished excitability. In the region of the brain where there is optimal excitability, new conditioned reflexes are easily formed, and differentiation is successfully developed. That area is at the given moment the creative part of the hemispheres. The outlying parts with their decreased irritability are incapable of such performance, and their functions at best concern the previously elaborated reflexes arising in a stereotyped manner in the presence of the corresponding stimuli. The activity of these areas is subjectively described as unconscious, automatic. The area of optimal activity is, of course, not fixed; on the contrary it is perpetually migrating over the whole extent of the hemispheres, being dependent on the relations which exist between the different centres as well as on the



influence of external stimuli. The borders of the region of lowered irritability obviously change in conformity with those of the area of excitation.

If we could look through the skull into the brain of a consciously thinking person, and if the place of optimal excitability were luminous, then we should see playing over the cerebral surface, a bright spot with fantastic, waving borders constantly fluctuating in size and form, surrounded by a darkness more or less deep, covering the rest of the hemispheres.

Let us return to the last experiment. If an external stimulus of moderate strength impinges on the brain of the dog, when at the moment there is no definite, sharply circumscribed focus of excitation, this stimulus conditions the appearance in the hemispheres of a region of increased irritability. If afterwards on the same hemispheres a more significant stimulus acts—for example, a stimulus aroused by food stuffs—which creates a new and more energetic focus of excitation, then there arises between these two foci certain connections. The nervous process, as we have seen, is directed from the area of lesser excitation to that of greater excitation. If, however, the process begins with strong stimulation, as, for example, that called out by feeding, the resulting increase of irritability at a certain point in the cerebral hemispheres is so strong and great, the inhibitory process arising in the other parts is correspondingly so intensive, that all impulses falling at the given moment on this point can not open paths or enter into new connections with any activities of the organism.

I do not argue for the unconditional acceptance of the last hypothesis; it should only show how the objective study of the higher parts of the central nervous system gradually reaches into the realm of the most complicated nervous activity, as far as we can judge from the provisional comparison of our subjective states with facts from the physiology of the conditioned reflexes.

I have finished my communication, but I should like to add what seems to me to be of great importance. Exactly half a century ago, in 1863, was published in Russian the article "Reflexes of the Brain," which presented in clear, precise, and charming form the fundamental idea which we have worked out at the present time. What power of creative thought was necessary under the then existing physiological knowledge of nervous activity to give rise to this idea! After the birth of this idea, it grew and ripened, until in our time, it has become an immense force for directing the contemporary investigation of the brain. Allow me at this 50th anniversary of the "Reflexes of the Brain" to invite your attention to the author, Ivan M. Setchenov, the pride of Russian thought and the father of Russian physiology!