

A NEW CONCEPTION OF THE PHYSIOLOGICAL ARCHITECTURE OF CONDITIONED REFLEX

P. K. ANOKHIN

The present conception has taken shape over a period of more than 30 years as the result of the work of the author and his pupils on the physiology of higher nervous activity.

The conception proposed in this paper eliminates a number of contradictions that have accumulated in the physiology of the conditioned reflex in recent years; it opens new avenues of research in the mechanisms of the conditioned reflex discovered by Pavlov, who revolutionized the study of the behaviour of animals and man.

The generally accepted view of the mechanism of the conditioned reflex rests on Descartes's reflex theory expressed in the concept of the 'reflex arc'. According to this view, the excitation evoked by a conditioned stimulus constitutes the afferent part of the conditioned reflex arc. In the central part of the arc the excitation is transferred from the analyser to the effector part of the reflex and, finally, the excitation reaches the efferent part of the reflex arc where it stimulates some working organ or combination of organs to action.

This classical concept has three characteristic features.

1. In the reflex arc the excitation spreads according to the linear-translational principle: at each successive moment it spreads to new neural elements and never returns to the course already traversed.

2. The reflex arc ends in an adaptive action which, from the point of view of these ideas, forms as an entirely new phenomenon in the path of the linear-translational spread of the conditioned excitation.

3. The formation of the reflex action in the peripheral working apparatuses is conceived as a process *completing* the reflex arc and, consequently, the very adaptive result of the reflex action is not the decisive factor for the dynamic alternation of the processes of excitation and inhibition in the reflex arc.

The conception proposed below does not exclude the reflex as a principle of the organism's activity and its relation to the external environment. The reflex invariably constitutes the nucleus of our new ideas.

However, this nucleus is considerably expanded and supplemented by new links physiologically conceived as components of an integral neurodynamic and *not linear* organization, which we have named the 'functional system'.

The formulation of our concept became possible only when the basic classical method of investigating conditioned reflexes had been supplemented by additional techniques which enabled us to reveal the other aspects of conditioned reactions and their physiological substrate.

The 'secretomotor method', the method of studying conditioned reflexes proposed by us, has been of particular importance in the elaboration of the new concept. Owing to a special design of the stand this method made it possible to record simultaneously the secretory and motor components of the conditioned reflex, the motor component constituting not a mere manifestation of movement towards food but a movement of choice towards one of the two or four feeding troughs connected with the given conditioned stimulus (Fig. 1).

The special design of a two-sided experimental stand made it possible to connect various conditioned stimuli with the different sides of the stand and to compare the secretory and motor components in the most diverse experimental situations.

Since by the classical secretory method this had not been possible on a wide scale, the first experiments conducted in our laboratory with our method revealed new aspects in the physiological architecture of the conditioned reflex (Anokhin, 1932, 1933). All the results of our investigations were published in detail in some of our generalizing papers (Anokhin, 1949, 1955, 1958).

To solve the problem of the physiological architecture of the conditioned reflex we have made extensive use, since 1937, of the electroencephalographic method. A method of recording the EEG in a perfectly natural environment in the study of conditioned reflexes was first used in our laboratory (Laptev, 1941, 1949). Recently these aims have been considerably furthered by the numerous investigations of the physiological peculiarities of the brain stem reticular formation so brilliantly begun in the laboratories of Magoun, Forbes and Moruzzi and later applied to the elaboration of conditioned reflexes in the laboratories of Jasper, Hernández-Péón, Morrell, Gastaut, and our own (Jasper, 1957; Morrell, 1958; Hernández-Péón, 1958; Gastaut, 1957, Ioshii, 1956).

Our conception of the general physiological architecture of the conditioned reflex is best considered fragmentally, so that at the end of this report it may appear before the reader in its totality.

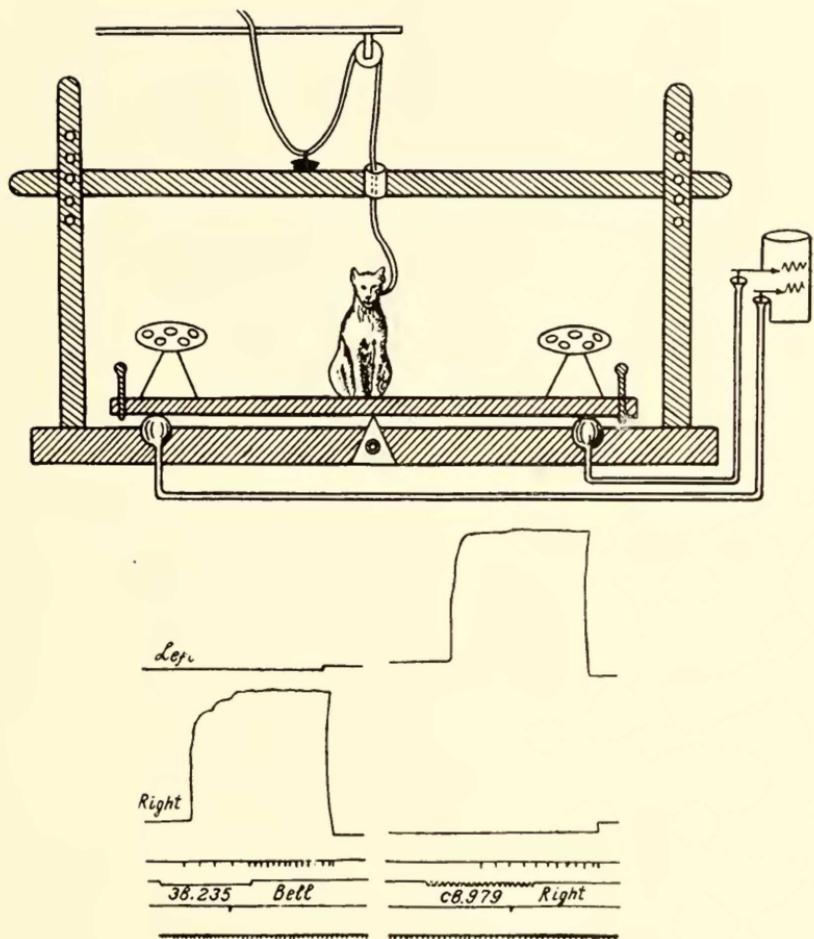


FIG. 1

- A. Two-sided stand with two feeding-troughs making it possible to record simultaneously the secretory and motor components of the conditioned reaction ('Secretomotor method'). Pneumatic transmission.
 B. Sample of kymograph record showing movement to the left (1) and right (2) and the conditioned secretion of saliva in drops.

I. CONCEPT AND MECHANISM OF AFFERENT SYNTHESIS

According to the reflex theory the role of the afferent influences on the central nervous system consists in the fact that the external stimulus usually serves as the *impetus* for the beginning of some reflex action. This

conception ascribes the decisive role to an isolated stimulus, something that has found expression in the evaluation of the conditioned stimulus as a decisive factor in determining the quality and strength of the conditioned reflex effect.

However, one physiological phenomenon which has considerably shaken this widespread idea was described in detail in Pavlov's laboratory. I refer to the phenomenon of the *dynamic pattern* (Pavlov, 1932).

As is well known, a definite and precise sequence of the *selfsame* conditioned stimuli, trained without any alterations over a long period of time, becomes the principal factor determining the quality and strength of the conditioned reactions. Conversely, the role of the *individual* conditioned stimulus is eliminated and the latter serves only as a *non-specific impetus* for the appearance of the conditioned reflex, whereas the quality and nature of the conditioned reaction does not depend on any conditioned stimulus in particular. This stimulus does not even have to be a conditioned stimulus, but may be an entirely new, i.e. indifferent (in Pavlovian terminology) stimulus. Nevertheless, it will evoke the conditioned reaction characteristic of the absent conditioned stimulus which was always used in the former experiments at the given point of the *dynamic pattern* (Pavlov, 1932).

Thus these experiments already revealed that the conditioned reflex, as regards its quality, strength and time of appearance, is a *synthetic result* of the action of the conditioned stimulus and the preceding action of a greater sum of afferent stimuli representing the *conditions of the experiment as a whole*.

A direct EEG analysis of the processes of the cerebral cortex conducted in our laboratory has shown that a sound stimulus, applied at the point of the dynamic pattern where light was always used, causes a desynchronization of cortical electrical activity, although applied at its usual place 15 seconds previously it did not produce such desynchronization (Fig. 2) (Anokhin, 1956). Thus a real sound cannot alter the electrical activity of the cerebral cortex, this activity alternating according to the preceding training of the dynamic pattern.

This dependence of each conditioned reflex on the synthetic nature of the external afferent influences was particularly clearly revealed in a special experiment conducted in our laboratory. The *selfsame conditioned stimulus* (bell) was reinforced by food in the morning and by an electro-cutaneous pain stimulus in the evening (Laptev, 1937). In the end the dog elaborates a perfectly clear differentiation: experimented upon in the morning it responds to the bell with pronounced food reflexes, whereas

in the evening in response to the *same* bell in the *same* chamber the animal shows a pronounced defensive reaction.

In this experiment the difference in the reactions clearly does not depend on the conditioned stimulus which has retained only the *non-specific trigger* action because both reactions emerge only in response to the action

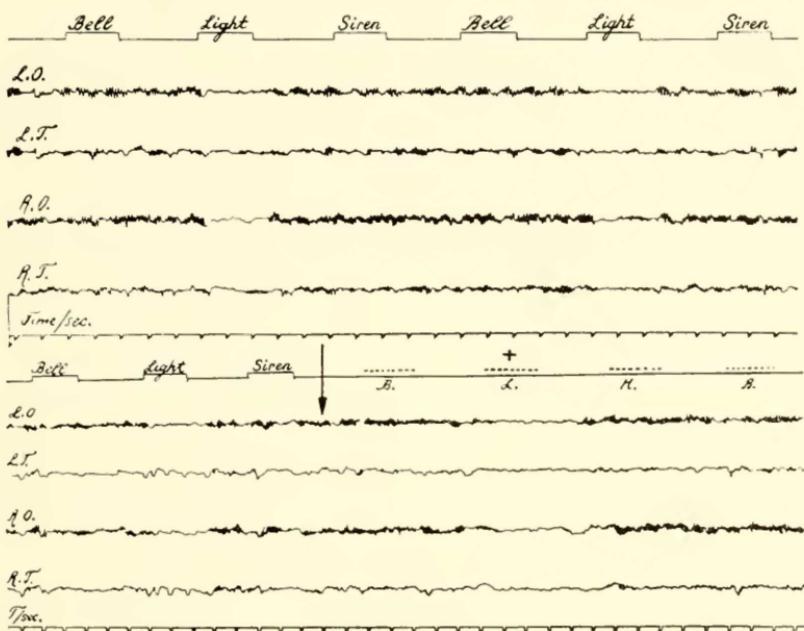


FIG. 2

A. EEG of the dynamic pattern of 'Bell-Light-Siren'. The regular light (+) is suddenly replaced by a bell, but a desynchronization corresponding to the application of light at this place is evident just the same.

B. Application of all the stimuli of the dynamic pattern (↓) is discontinued. Further development of cerebral activity in total conformity with the structure of the pattern can be seen. Complete desynchronization can be seen in place of the absent light (+).

of the bell, whereas in the intervals between the conditioned stimuli the animal sits quietly.

Nor are the conditions of the experiment as a whole a differentiating factor since they are the same in both experiments and only the *time of day*, as one of the components of the conditions of the experiment, is the determining factor.

If we take into consideration the fact that the time of day becomes an

active factor the moment the dog is placed in the stand and the reaction emerges only at the moment the bell comes into play it will become clear that the time of day, being a special stimulus, determines the quality of the reaction because of the creation of a specific *subthreshold* dominant state of the central nervous system (according to Uchomsky) which spreads to the working apparatuses owing to the trigger action of the conditioned stimulus.

The synthetic nature of the relations between the conditioned reflex and the external conditions of the experiment, both as a whole and of its individual components, may also be revealed under the usual conditions. Suffice it to transfer the animal, that until then had responded with good conditioned alimentary reflexes, to other surroundings (for example, a lecture-hall for demonstration to students) and the conditioned stimulus loses its conditioned reflex effect. In this case the synthesis elaborated from the tonic afferent action of the usual experimental situation and the trigger action of the conditioned stimulus is disturbed and the conditioned reflex disappears.

The following question arose in our laboratory: does this process of the synthesis of the situational and trigger afferent influences have any preferable localization in the cerebral cortex?

The experiments of our associate Shumilina, conducted over many years and consisting in extirpation of the frontal lobes in dogs who had conditioned reflexes elaborated in the two-sided stand, have shown that the frontal lobes have a very definite relation to this function of synthesis of the afferent stimulations of different quality. During the experiment all the normal intact animals in the two-sided stand behave rather monotonously, with certain insignificant variations. Since the different conditioned stimuli are reinforced by a single portion of food on the different sides of the stand, the animals elaborate an expedient habit of sitting quietly during the intervals between the conditioned stimuli *in the middle of the stand*.

After removal of the frontal parts (six to eight according to Brodmann) all the intact animals begin to behave in a characteristic way immediately following the operation — they keep running from one feeding trough to the other as long as the experiment lasts. We have named these movements 'pendular' (Fig. 3).

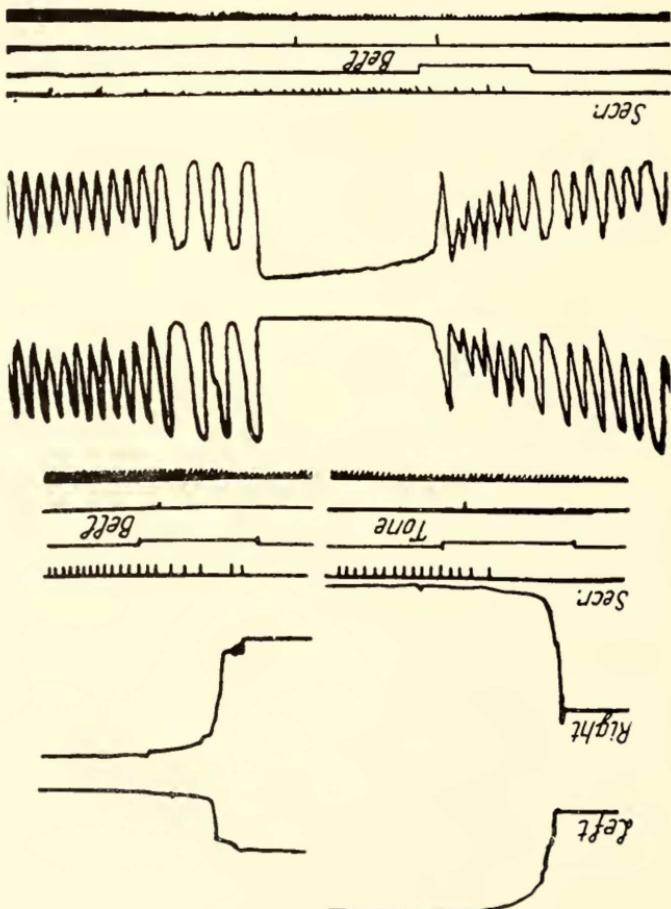
It might be assumed that these movements were one of the forms of 'motor restlessness' described by many authors after they had removed the frontal areas of the animals' brains. However, a direct analysis of the mechanism of these pendulous movements has shown them to be directly

one side of the stand, i.e., set up the conditions of Pavlov's classical method, for example, if we elaborate in the animal conditioned reflexes only to one side of the given experiment.

For example, under the conditions of the different influences suffered by the animal depending on the nature of the afferent influences received by the animal under the conditions of the given experiment.

A. Normal discrimination of the sides of the stand in response to correlative stimuli. Stable movements to the left and right sides and quiet attitude in the middle of the stand during the interval between sounding conditioned stimuli. Stable movements to the left and right sides and removal of the frontal divisions of the cerebral cortex. Steps only after removal of the frontal divisions of the cerebral cortex. Steps only after feeding. Conditioned secretion is the same as before the operation.

FIG. 3



after the removal of the frontal parts of the cerebral cortex this animal behaves perfectly quietly during the intervals between the applications of the conditioned stimuli: *it sits on one side of the stand and performs no pendular movements.*

However, if we feed this quiet animal from the opposite feeding trough but once, it immediately begins to perform the well-known continuous pendulous movements to both sides of the stand.

These experiments suggest that the 'pendular' movements are a direct result of the situation stimulation which includes conditions of alternate choice and behaviour.

Why then does the intact animal sit quietly in the middle of the stand during the intervals between the applications of the conditioned stimuli?

The interest of this phenomenon consists precisely in the fact that the numerous stimulations of the experimental conditions (situational afferentation) affect the nervous system all the time, whereas the conditioned reaction manifests itself only at the moment the conditioned stimulus begins to act (trigger afferentation). At the same time the extreme change in the experimental situation convinces us that the situational stimuli form an organic component part of the afferent integral. Thus it becomes clear that all forms of afferent excitations affecting the animal's nervous system at the given moment undergo a synthetic processing and that *only after this stage* does the efferent complex of working excitations begin to form.

In recent years, neurophysiological studies have convinced us that all the afferent influences on the organism come to the cerebral cortex along two channels: (1) the specific or lemniscus pathway and (2) the non-specific, i.e. the brain stem reticular formation. The latter excitation is an indispensable condition for any interaction and interconnection of specific excitations on the level of the cerebral cortex.

Specially for the physiology of the conditioned reflex this means that any form of association of stimulations acting on the organism simultaneously or successively becomes possible only if the activating effect of the reticular formation has spread to the substrate of the cerebral cortex. The constant mediator between the new external conditions and the associative activity of the cerebral cortex and subcortical structures is the orienting-investigatory reaction of the animal taking place under an uncommonly high activation of the apparatus of the brain stem reticular formation (Hernández-Péón, Shumilina, Havliček).

The physiological and biological purport of the orienting-investigatory reaction was very well revealed by Pavlov himself (Pavlov, 1925). It has now been shown that it occurs under a constant excitation not only of

the cerebral cortex but also under an efferent excitation of the peripheral apparatus of the sense organs (Granit, Dell, Livingston). Owing to the rapid alternation of this efferent stream from one analyser to another the afferent synthesis stage preceding the very conditioned reaction is considerably enriched by afferent impulses, something that determines a finer and more adequate (for the given conditions) formation of effector processes of the conditioned reflex.

Naturally, after the stage of elaboration of the conditioned reaction this primary period of the multifarious efferent influences on the sense organs, increasing the excitability of the latter, is in large measure eliminated, owing to which the apparatus of the very conditioned reflex are simplified during the stage of its complete automation (see Fig. 4).

Electrophysiological studies of the orienting and investigatory reaction have shown that it is able continuously to maintain a high level of excitation in the cerebral cortex and at the same time maintain in an active state the newly formed temporary bonds (Anokhin, 1957; Karazina, 1957). Recently Professor Lindsley published a remarkable paper in which direct stimulation of the brain stem reticular formation demonstrated the tremendous role played by the reticular formation in the discriminative function of the cerebral cortex for rhythmic flashes of light (Lindsley, 1958).

Thus we believe it completely proved that *the power basis for the all-round synthesis of the numerous external and internal, situational and trigger afferent influences on the cerebral cortex is the ascending generalized activation of the brain stem reticular formation.*

The role of the reticular formation in refining afferent analysis also manifests itself in the fact that at this moment an alternate increase in the excitability of various receptor structures at the periphery takes place (Granit, 1957; Dell, 1957; Snyakin, 1958).

All told this makes it absolutely necessary, in analysing conditioned reflex adaptations, to set apart an independent stage of afferent synthesis.

The significance of this stage consists first of all in the fact that before its completion the flow of effector excitations to the functioning organs cannot be formed. The composition of these effector excitations and, consequently, the nature of the adaptive act itself are directly dependent on the way in which this stage of the afferent synthesis is completed.

At this point I must emphasize that the decisive role of the afferent function, as a 'creative' function of the cerebral cortex, was repeatedly indicated by Pavlov (Pavlov, 1928). The proof of this decisive role of the afferent function of the cerebral cortex is, in our opinion, the *afferent*

synthesis stage which, as we shall see below, determines all the subsequent stages in the formation of the behaviour of man and animals.

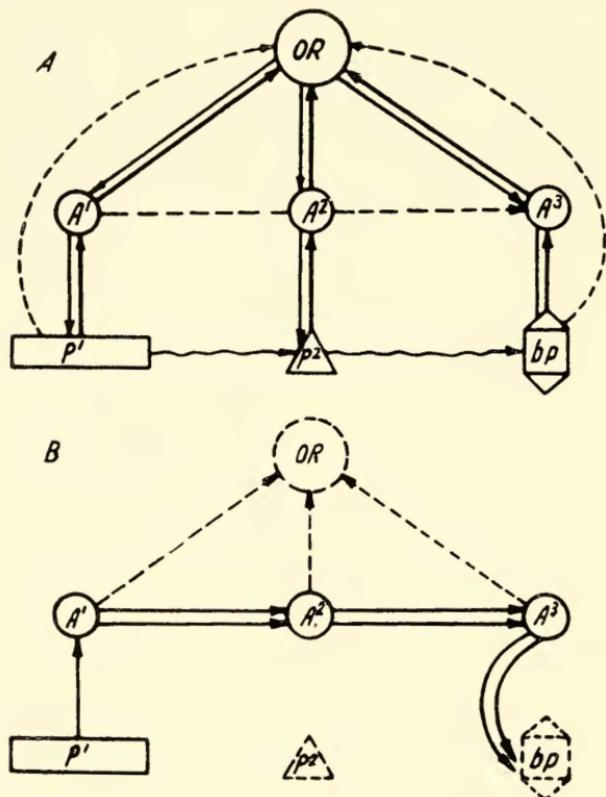


FIG. 4

General scheme illustrating the role of the orienting-investigatory reaction in the formation of the conditioned reaction, i.e. in the establishment of the chain of afferent traces from the stimulus to the acceptor of action.

A. At each stage of the animal's movement towards the reinforcing factor the orienting-investigatory reaction contributes to the production of return afferentation.

B. Final form of bonds. The conditioned signal aids in the almost instant spread of excitations along the afferent traces fixed in the past by means of the orienting-investigatory reaction.

2. SPECIFIC ACTIVATING EFFECT ON THE CEREBRAL CORTEX AND PROCESSES OF AFFERENT SYNTHESIS

The *specific activating* function of the brain stem reticular formation plays a special part in the processes of afferent synthesis (Anokhin, 1958).

There is a widespread opinion that the activating effect of the reticular formation on the cerebral cortex is of a non-specific nature. According to this view, the non-specific influence on the cerebral cortex is always of the

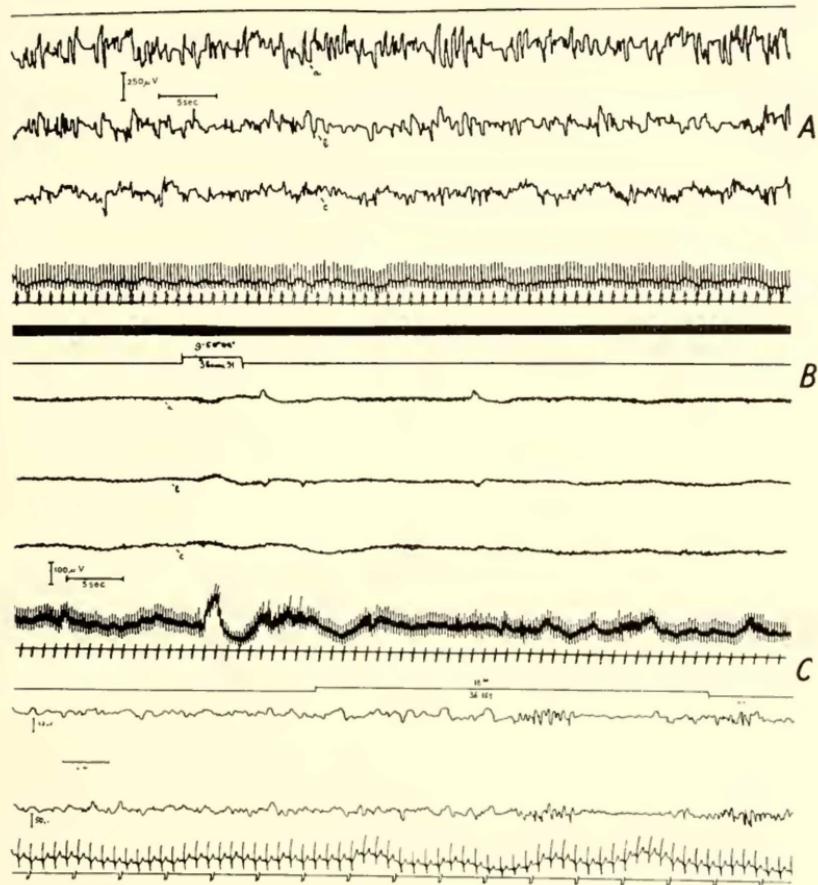


FIG. 5

- A. Normal EEG of the rabbit in an experiment without a pain reinforcement.
- B. EEG of the same rabbit after application of several pain reinforcements during elaboration of a conditioned defensive reflex. Very strong desynchronization of electrical activity can be seen not only at the moment of application of the conditioned stimuli but also during the intervals between them.
- C. After chlorpromazine injection.

same physiological nature regardless of the reactions of the integral organism taking place in the given situation (Moruzzi and Magoun, 1949; Magoun, 1952; Magoun, 1958; *et al.*).

This point of view undoubtedly finds justification in the facilitating effect which develops in the cortical cells for the excitations coming to the cortex along the specific lemniscus system. This conclusion is also favoured by the phenomenon of 'awakening' or desynchronization of the cortical electrical activity which is always of a generalized nature and seems to be independent of the biological quality of the unfolding reactions.

However, along with these remarkable generalizations, our laboratory has obtained facts attesting that the non-specific activating effect of the brain stem reticular formation on the cerebral cortex is *organically connected with the biological specificity of the given conditioned reaction*. It proved possible to block by means of chlorpromazine (aminasine) the activating effect of the reticular formation for the conditioned *defensive* reaction, at the same time retaining the activating effect on the cortex for the *alimentary* reaction, i.e. for a reaction of another biological quality. At this moment the animal can greedily eat the food offered to it (Gavlichek, 1958) (Fig. 5).

Similarly blocking the defensive activation of cortical electrical activity by chlorpromazine fails to eliminate the animal's waking state which, as is well known, is also maintained by the activating effect of the brain stem reticular formation on the cerebral cortex (Fig. 6).

Thus it was demonstrated beyond all doubt that there are several activating influences on the cerebral cortex and that *each of them may be blocked individually because of the different chemical specificity of the nervous substrate on which each of these biologically different reactions occur*.

What is the significance of this varying biological specificity of the activating influences on the cerebral cortex occurring during the afferent synthesis which precedes the formation of the conditioned reaction itself?

In the first place it contributes to the *selective* rise in the excitability ('facilitation') of the neural elements in the cerebral cortex, which in the given animal were historically associated, by the principle of conditioned coupling, with the inborn subcortical reaction of the given biological quality (positive or negative).

Owing to this selective involvement of the cortical elements the mobilization of the numerous cortical systemic connections, which help to complete the stage of afferent synthesis, proceeds much faster and more efficiently.

Our view of the specific, i.e. selective, activating influence of the reticular formation on the cerebral cortex *with the perceptible generalized desynchronization of its electrical activity* fits in with the remarkable experi-

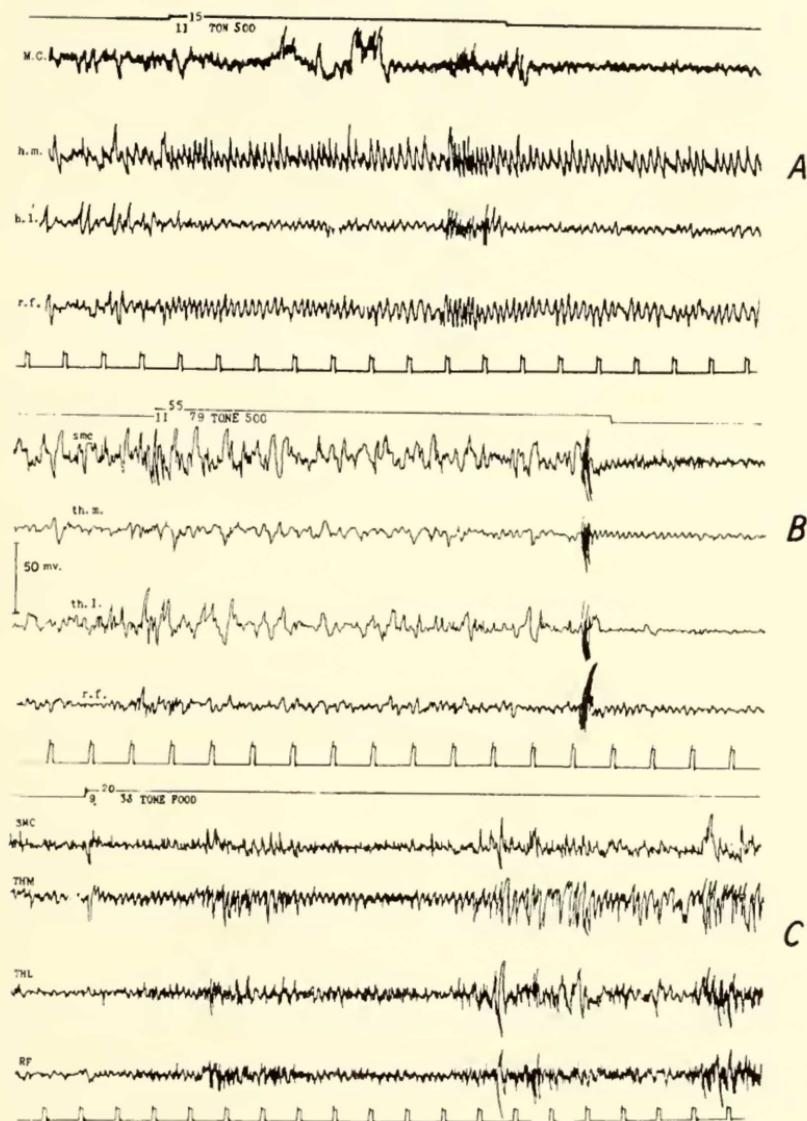


FIG. 6

- Shows the presence in the reticular formation of a specific rhythm of electrical activity (4-6/sec.) corresponding to the animal's defensive state.
- Elimination of the specific reaction by an injection of chlorpromazine. Application of the conditioned defensive stimulus no longer produces the generalized activation of the EEG.
- Cortical and subcortical EEG of the food conditioned stimulus (tone).

stem reticular formation. These influences reach the cerebral cortex in the draws its energy from the ascending activating influences of the brain. This figure shows that theafferent synapses, as a physiological process, conditioned reflex may be represented schematically as in Fig. 8.

This first stage in the formation of the physiological architecture of the cerebral cortex (according to the desynchronization index) has a corrective synthesis.

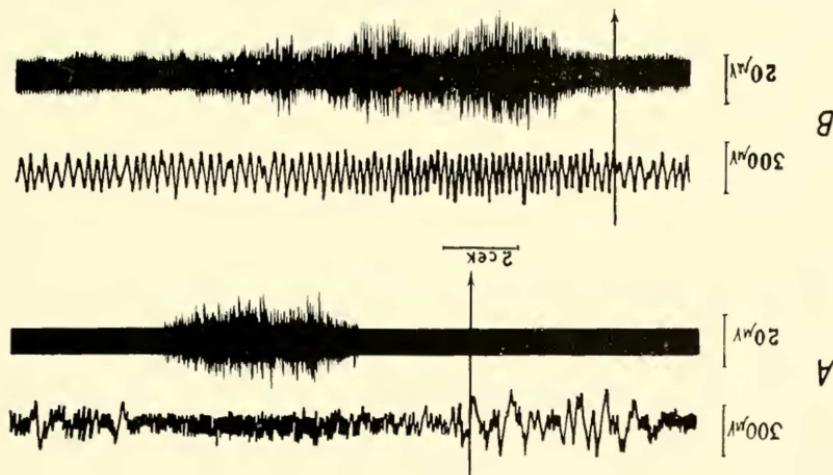
This constitutes the physiological basis for the extrinsically ramified process of cortical bonds. It is just this that constitutes the system of selective excitation of cortical bonds. It is even more evident that synaptic transmission at all but the cellular impulse activity emerges just the same.

A. An even more demonstrative lack of coincidence is revealed by leading off the two indices from the same point of the reticular formation. Here the EEG does not have the usual desynchroniz-

B. The two forms of activity show a certain independence of the cellular impulse between the two forms of activity and impulse activity. The apparent lack of coincidence between the two forms of slow EEG activity and impulse activity, i.e., from the same point of the cerebral cortex, of simultaneous lead-off with the same electrode, i.e., from the same point of the cerebral cortex, of slow EEG activity and impulse activity. Here the EEG does not have the usual desynchroniza-

tion at all but the cellular impulse activity emerges just the same.

FIG. 7.



These authors have shown that, when cortical electrical activity is in a state of generalized desynchronization, the various individual cortical elements are in absolutely different states of activity. Some of them may be excited, others inhibited, while still others may change the form of their activity several times during the entire desynchronized state. These data can be understood only in the sense that each activated state of the

(Jasper, 1957; Kogan, 1958; Polyantsev, 1959) (Fig. 7).

Mechanisms performed by Jasper, Kogan and our own collaborator Polyantsev

form of facilitating influences both at the moment of the action of the external stimulations and, especially, at the moment of the appearance of the orienting-investigatory reaction.

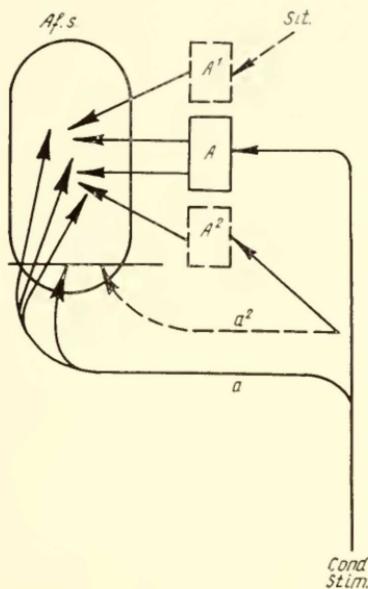


FIG. 8

Schematic representation of the constituent processes of the afferent synthesis stage. The scheme shows the constant activating influence of the brain stem reticular formation on the afferent synthesis. It manifests itself during the action of the experimental situation as a whole and during the episodic action of the conditioned stimulus.

A¹, A². Analysers through which the situation stimuli produce their effect.

a². Collateral action of the same stimuli through the reticular formation.

A. Analyser of the conditioned stimulus.

a. Collateral action of the conditioned stimulus through the reticular formation.

3. PHYSIOLOGICAL MECHANISMS FORMING THE APPARATUS OF THE ACCEPTOR OF ACTION

In this part of our report we shall describe a new mechanism of the conditioned reaction noticed and elaborated in our laboratory. In its physiological essence this mechanism is the end result of the afferent

synthesis stage, like the subsequent formation of the effector apparatus of the conditioned reaction itself. However, it forms, in large measure as an independent, physiological formation and has, as we shall see later, a special *afferent* significance.

In its physiological content this apparatus consists essentially of the afferent excitations which in their totality reflect precisely the sum of afferent excitations that must enter the cerebral cortex only at the end of the reflex action. It follows that the acceptor of action, as an afferent reflection of the results of future action, is a physiological apparatus of so-called 'anticipation'.

The tremendous importance of this apparatus in the behaviour of animals consists primarily in the fact that forming immediately after the end of the afferent synthesis stage *it considerably forestalls the process of formation of the reflex action as well as the completion of this action*.

The acceptor of action makes its appearance so soon after the end of the afferent synthesis that it may be argued that this apparatus is a direct and immediate result of precisely the afferent synthesis stage.

From a psychological point of view this moment, i.e. the end of the afferent synthesis corresponds to the emergence of the 'idea', 'intention' or 'aim' to perform the given action.

I believe it is necessary to observe at this point that the various reports that I have published on the physiological mechanisms of this stage in the development of conditioned reflex actions, have shown that many investigators do not as yet adequately understand that in a psychological sense the emergence of an 'intention' to perform some action *is an absolutely indispensable stage* which antedates the action itself and that, consequently, we, physiologists of the nervous system and higher nervous activity, must strive to analyse the physiological correlates of this 'intention'.

The physiological content of this apparatus consists of the entire past afferent experience of the animal or man concretely related to the given behaviour pattern. Basically it is a certain integration of the afferent impulses which arise from the *results* of some reflex action or act of behaviour.

For example, grasping a pitcher of water is connected with the reception of a series of afferent influences of a varying modality.

Our brain receives specific tactile impulses reflecting the form and mechanical properties of the pitcher, temperature impulses, kinaesthetic impulses suggesting weight and, consequently the fact that the pitcher is filled with water, etc. The impulses also include a visual afferentation suggesting the movement of the hand towards the pitcher.

The aggregate of all these afferent impulses arises only when the pitcher is grasped and, consequently, may be referred to as *afferentation of the results of the action*, in the true sense of these words.

From the morpho-physiological point of view such an aggregate of afferent influences forms in the cerebral cortex and subcortical apparatus a system of strong bonds which, by virtue of a number of repetitions of the given act acquires properties of an organized, integral afferent formation. It is precisely this system of bonds that becomes active owing to the rapid selective spread of excitations at the moment the afferent synthesis stage is being completed and that constitutes the physiological basis of the acceptor of action.

At this point we are consciously leaving out of consideration the aggregate of the internal and external influences which, after the afferent synthesis stage, have, on the whole, conditioned the emergence of the very intention 'to grasp the pitcher'.

It stands to reason that this intention is only a separate stage in a series of other 'intentions' which are finally completed through the stage of a subjective 'quenching of thirst' by a drop in the osmotic blood pressure.

At this point it is important to note that, as soon as the afferent synthesis stage was completed, the cerebral cortex immediately exhibited an active excitation of the entire system of the aforesaid afferent bonds which had become consolidated on the basis of the past experience of the afferent results of the act of grasping the pitcher.

In other words, the afferent apparatus, which we have named the acceptor of action, forms under any action of a conditioned stimulus before this reflex action has occurred and consequently constitutes an absolutely integral part of the cyclic architecture of any conditioned reflex action.

It may be assumed that the anticipatory formation of the acceptor of action has become the decisive factor in the organization of the adaptive behaviour of animals because it eliminates chaos in the choice and elaboration of the individual acts of this behaviour (Fig. 9).

Containing all the *afferent results* of the past reinforcements, i.e. containing at the moment of action of the conditioned stimulation the afferent results only of the future (!) action, the acceptor of action becomes a peculiar control apparatus which establishes a physiological correspondence between the completed action and the initial 'intention' to perform this action.

There are several forms of experimental proof of the existence of such

an afferent apparatus which forestalls the appearance of the conditioned reflex action, as well as its afferent results.

The first and most demonstrative form of experiment consists in the fact that the *experimenter suddenly replaces the quality of the unconditioned alimentary reinforcement*.

In conducting these experiments we reasoned as follows: if the prepared conditioned excitation of the afferent cells in the cortical representation of the unconditioned centre precisely reflects the properties of the *future*

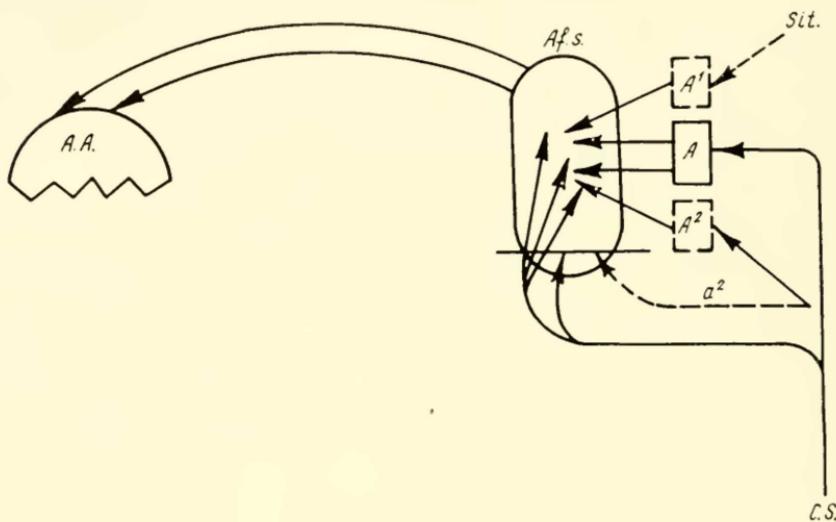


FIG. 9

Stage of formation of the 'acceptor of action' consisting of the afferent traces of past reinforcements. At this stage the reflex action itself has not formed as yet.

return unconditioned excitation and the normally elaborated behaviour of animals is based on this adequacy, the latter must infallibly change if we replace the unconditioned stimulus. Owing to this replacement the anticipatory conditioned excitation in the additional afferent apparatus would be of one quality (on the basis of the former reinforcements) while the real unconditioned stimulus would suddenly (!) be of another quality and, consequently, because of such a combination of the conditions the composition of the nervous impulses of the return afferentation coming to the cerebral cortex from the real unconditioned stimulus would not correspond to the conditioned excitation prepared there. What will the actual behaviour of the animal in this case be?

This idea was applied in our laboratory (Anokhin and Strezh, *Soviet Journal of Physiology*, No. 5, 1933) on the basis of a bilateral alimentary reinforcement allowing these peculiarities of higher nervous activity to be demonstrated.

The experiment was conducted in the following manner. Only two conditioned secretomotor reflexes were elaborated in the animal: to the tone of 'A' with a reinforcement on the right side of the stand and to the tone of 'F' with a reinforcement on the left side. Both reflexes were reinforced by 20 g. of dry bread and were sufficiently well consolidated. After a brief latent period the animal would rush to the corresponding side of the stand and wait there for the unconditioned stimulus. At this stage of the experiments the animal no longer exhibited any erroneous motor reactions.

At the beginning of an experimental day dried meat was placed in one of the plates on the *left side* and thus, against the background of the usual dried-bread reinforcements, the animal was to receive a meat reinforcement to one of the regular stimulations with the tone of 'F'. On the basis of the aforementioned peculiarities of the afferent apparatus of conditioned excitation we must assume that for some brief space of time the new unconditioned stimulations which do not coincide in their visual, olfactory and gustatory qualities with the already emerged conditioned excitation must lead to a lack of coincidence in the two excitations and then to the development of an orienting-investigatory reaction. The latter should be the more strongly pronounced the more the prepared conditioned afferent excitations and the available afferent excitations from the true unconditioned stimulus fail to coincide.

These expectations were justified by experiment. When the unconditioned stimulus is thus replaced it usually gives rise to an orienting-investigatory reaction which, depending on the strength of the stimulatory action of the suddenly used inadequate unconditioned stimulus, either changes to an active alimentary reaction (when bread is replaced by meat) or retards the alimentary reaction and the animal even refuses the food (if the meat is replaced by bread).

The foregoing experiment enabled us to observe both forms of the reaction.

The second form of the experiment aimed at proving the existence of the acceptor of action is based on the peculiarities of the experimental method in the two-sided stand proposed by us (see Fig. 1).

Several conditioned secretomotor reflexes firmly fixed by training are elaborated in the animal. To each of the stimuli used at any given moment

the animal responds with a positive motor alimentary reaction to a feeding-trough either on the right or left side according to the side on which the animal was fed during the application of the given conditioned stimulus.

Let us assume that with a flash of light the dog was always fed from the right-hand trough, whereas with the sound of the tone of 'C' it was given food in the left-hand trough. According to the law of the conditioned reflex, the animal responds to this form of experiment by elaborating precise conditioned motor reactions to the right and left sides of the stand.

As soon as these conditioned reactions are firmly fixed the food is suddenly (!) given to the flash of light on the left rather than on the right side of the stand.

In other words, an operation is performed or, in the terminology of the Pavlovian laboratory, the conditioned reflex is 'reshaped'.

In this form of experiment it is possible to see that the animal frequently fails to take food from the trough on the side that does not correspond to the conditioned signal. For a long time it looks alternately to the right and left feeding-troughs (orienting-investigatory reaction) and begins to eat the food only after a long latent period. Additional investigations of the animal's respiratory component, when the side on which the food reinforcement is made is suddenly changed, show the animal to exhibit an uncommonly pronounced orienting-investigatory reaction with a strongly marked inspiratory tonus in breathing.

The only cause that could be thought of for this pronounced reaction was the *lack of correspondence between the sudden feeding (return afferentation) and the already prepared complex of afferent excitations in the cerebral cortex in accordance with the place of the old and usual feeding* (acceptor of action). The same conclusion is suggested by the fact that both food reinforcements, on the right as well as on the left sides, are essentially of the same significance to the animal, the distances from both feeding-troughs also being the same.

The only remaining cause is the lack of correspondence between the already prepared acceptor of action and the afferent influences emerging when the animal is fed on the inadequate side.

The method of sudden replacement of the reinforcement may be used in most diverse variations, especially in experiments on human adults and children. For example, by showing some dainty to a child and placing this dainty, so that the child sees it, in a 'problem box' from which the child extracts it, it is possible finally to establish adequate correlations between the sight of the dainty and the subsequent reinforcement which occurs

when the child opens the box. However, if a *dainty of another quality* is imperceptibly placed in the box, upon opening the box the child immediately develops a reaction of 'surprise' ('What is it?', according to Pavlov) which occurs with different variations depending on a number of conditions. The child may carefully examine the box from all sides, shake it in the hope of receiving the *expected reinforcement*, etc. It is perfectly clear that all these actions are a direct result of the *lack of correspondence between the fixed afferent excitations in the form of the acceptor of action and the afferent influences coming to the central nervous system from the inadequate appearance of the new dainty when the box is opened.*

The third way of proving the emergence of afferent excitations in the acceptor of action forestalling the formation of the action itself is the electroencephalographic method. As stated previously the systems of afferent excitations forming part of the acceptor of action are mobilized much more rapidly than the effector part of action. At times, a very complex reflex action is formed. It follows that the *ascertainment of the preparatory excitations in the area of the cerebral cortex, which must, in the future, receive the return afferentation from the results of the action*, should become one of the methods of studying the physiological mechanisms of the acceptor of action.

A typical example of the anticipatory spread of excitations over the cerebral cortex is the generally known, so-called, electroencephalographic 'conditioned reflex' which manifests itself when sound and light are combined. As is well known, after a number of such combinations the sound alone causes a desynchronization of the α -rhythm in the occipital area of the cortex *before the appearance of the light*. Here the sound sets off a chain of excitations in the cerebral cortex, which spreading rapidly reaches the elements in the visual cortex that will not receive adequate visual excitation from the periphery until a few seconds later (Jasper, 1937; Livanov, 1937; Karazina, 1957; and many others).

Any acceptor of action for any, even very complex acts of behaviour, is formed absolutely according to the same type. Any act of behaviour is represented in the cortex by the development of an uninterrupted chain of afferent excitations received from the individual stages of this act to the final reinforcing factor inclusive. It is precisely this chain of traces of the past afferent excitations that is a peculiar 'conductor' for the rapid spread of the excitations from the conditioned stimulus to the system of excitations *which is the afferent reflection of the results of the as yet forthcoming action.*

Examples of such a spread of the afferent excitations may now be

obtained from most diverse papers in which the authors themselves did not intend to study precisely this problem.

We may cite data from the work of Jasper who points out that in a number of cases the secretomotor area of the cerebral cortex exhibits a depression of its rhythm much ahead of the real movement of the arm, this desynchronization sometimes appearing in the person tested at the thought of the forthcoming movement alone (Jasper, 1958).

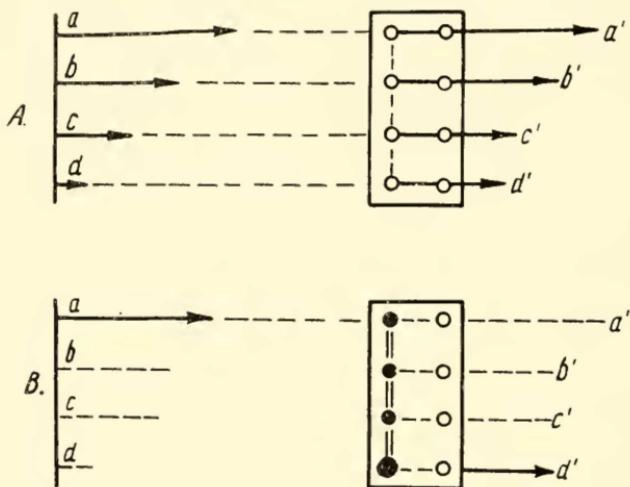


FIG. 10

Schematic representation of the 'anticipatory' spread of excitation and its significance in the formation of the acceptor of action.
A. $a, b, c, d \rightarrow$ successively developing action of the external stimulations of which d is the reinforcement with food. Orienting reactions a', b', c' and d' emerge correspondingly.

B. Correlation of the processes after training. The action of the one initial stimulus a is enough for the process of excitation immediately to spread along the afferent traces to d which is the 'acceptor of action' in this case.

We find indications of similar facts in the studies of Gastaut concerned with depressing the rolandic rhythm (Gastaut, 1957).

In his recent detailed review of the studies of the reticular formation O'Leary also cited data to the effect that the 'idea' of the forthcoming movement alone may lead to a desynchronization of the electrical activity of the cerebral cortex (Fig. 10).

All the data culled from the literature, as well as our own observations, indicate that after the application of a stimulus or the reading of instructions the selective impulse process of excitation, which ensures the

formation of the conditioned reflex, spreads with uncommon speed through all the chains of the past afferent stimulations which reflected the continuity in the development of some act of behaviour. This process of the anticipatory propagation of afferent excitations until the moment the acceptor of action is formed may be shown diagrammatically as in Fig. 9.

4. FORMATION OF THE CONDITIONED REACTION EFFECTOR APPARATUS

The stage of formation of the conditioned reaction effector apparatus is directly dependent on the course or end of the afferent synthesis. The latter is always an integral whole and contains in its composition both somatic and vegetative components (motor component, respiratory component, cardiac component, vascular component, hormonal component, etc.).

The characteristic feature of this effector integration is the fact that each of its functioning peripheral components is harmoniously related to the other components and together they constitute the given act of behaviour or the conditioned reflex.

For example, the respiratory component of the conditioned reflex was subjected to systematic analysis for the first time in our laboratory (Balakhin, 1930-35; Polezhayev, 1952; Makarov, 1958; *et al.*). It was shown to be of an entirely specific character corresponding to the biological quality of the animal's given reaction as a whole. In the defensive conditioned reflex the respiratory component exhibits a high inspiratory tonus and frequent respiratory movements of the thorax.

In a well-fixed alimentary conditioned reflex the respiratory rhythm is, on the contrary, quiet and only at the moment when the conditioned stimulus is applied does the orienting-investigatory reaction temporarily raise the activity of the respiratory component (Fig. 11).

A comparative evaluation of the secretory, motor, respiratory and cardiovascular components of the conditioned reflex shows that they are all harmoniously adapted to the biological significance of the whole reaction. If the reaction requires general activity and tension (as, for example, the conditioned defensive reaction) all the vegetative components, as many as there are, unite into an integrated whole, each of them corresponding to the tasks of the given adaptive act. This means that the intensity of the vegetative components of the conditioned reflex, which provide the entire reaction with power resources, is directly dependent on the degree of the *forthcoming* expenditure of these resources.

This state, revealed particularly clearly as early as 1935 in the studies of

our associate Balakin, was recently confirmed by special forms of experiments.

In our laboratory Dr Kasyanov has shown that the respiratory component of the conditioned reflex is the first conditioned reflex component to form in the effector pathways (Kasyanov, 1950). The cardiovascular complex reaches the effector pathways almost simultaneously with the respiratory component. Gant's studies have shown, however, that the cardiac component of the conditioned reflex appears somewhat ahead of the respiratory component (Gant, 1952).

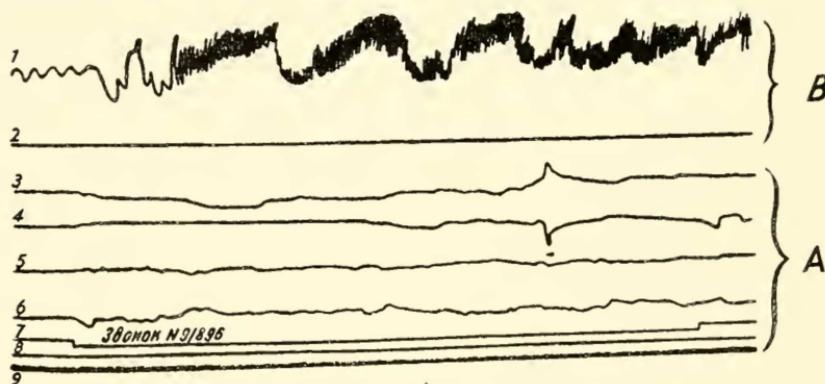


FIG. 11

Dissociation between the generalized and local excitation of the motor apparatus of the dog after bilateral extirpation of the sensorimotor areas of the cerebral cortex. The generalized reaction (A) is on hand, while the local raising of the hind limb is totally absent (B).

The recent studies conducted by Shidlovsky in our laboratory with the aid of up-to-date cardiographic apparatus ('Cardiovar', 'Barovar', etc.) have confirmed our former observations and have shown the respiratory component to reach the effector pathways somewhat ahead of the cardiac component (Shidlovsky, 1959).

It should be noted, however, that these insignificant differences in the appearance of the vegetative excitations in the peripheral organs, where they are detected by suitable apparatus, are of no fundamental importance. They may be due to different lengths of the pathways the excitations must traverse from the centres to corresponding organs, to the number of synapses in these pathways, and, lastly, to the peculiarities of the recording apparatus.

But some aspects of this phenomenon, constant for all types of conditioned reactions, are undoubtedly important. For example, the vegetative

components in general reach the terminal effector components in the form of components of specific qualities (secretion for the alimentary conditioned reaction, movement for the defensive conditioned reaction) before the conditioned reflex reaction manifests itself. The other important aspect of what we call 'vegetative outstripping' consists in the fact that all these components in their totality are of a conditioned reflex nature and reflect precisely the energy requirements of the forthcoming conditioned reflex action.

Shidlovsky devoted a special experiment to this problem. He recorded the cardiovascular components of the conditioned alimentary reaction in two different situations: in one case, the animal had to overcome a small obstacle to get at the food received as reinforcement, thus exerting a muscular effort, while in the other case the food was brought directly to the animal's muzzle. Thus, in the first case, the conditioned signal warned the animal not only of the forthcoming feeding but also of *certain muscular efforts* it had to exert before receiving the food.

In total conformity with these conditions the respiratory and cardiovascular components of the conditioned reaction are vigorously activated in the first case. Conversely, in the second case, the same vegetative components manifest no such changes and deviate but slightly from the level of the resting state (Fig. 12).

All the experiments performed in this direction clearly show that the conditioned reaction, as a manifestation of the integral organism, affects the periphery through very numerous terminal neurones involving most diverse somatic and vegetative components.

An evaluation of the physiological composition of this integral efferent formation should take into account its three physiological peculiarities:

- (a) it is a direct result of the afferent synthesis stage;
- (b) it forms during the entire course of elaboration of the given conditioned reflex (see below);
- (c) it has a vertical physiological architecture, since it infallibly includes cortical and subcortical components.

The last of the foregoing propositions is clearly demonstrated by the very participation of vegetative components in the conditioned reflex. Since these components reflect the integral character of the total reaction and are formed through the terminal pathways of the hypothalamus and the brain stem reticular formation, it is possible to chart the general distribution of the nervous impulses within the entire efferent stream of excitations, including the functioning organs.

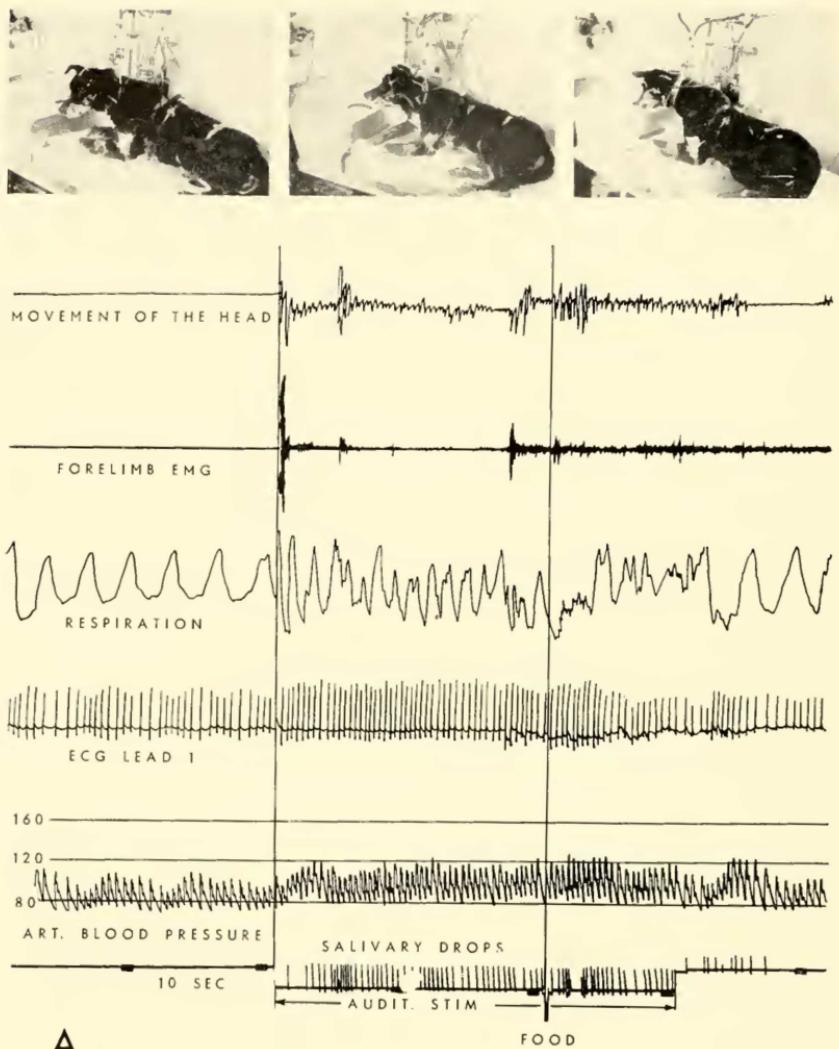


FIG. 12A

Illustration of the dependence of the vegetative components of the conditioned reflex on the forthcoming energy expenditures signalled by the conditioned stimulus.
 A. Reaction to the conditioned stimulus with the animal in close proximity to the food.

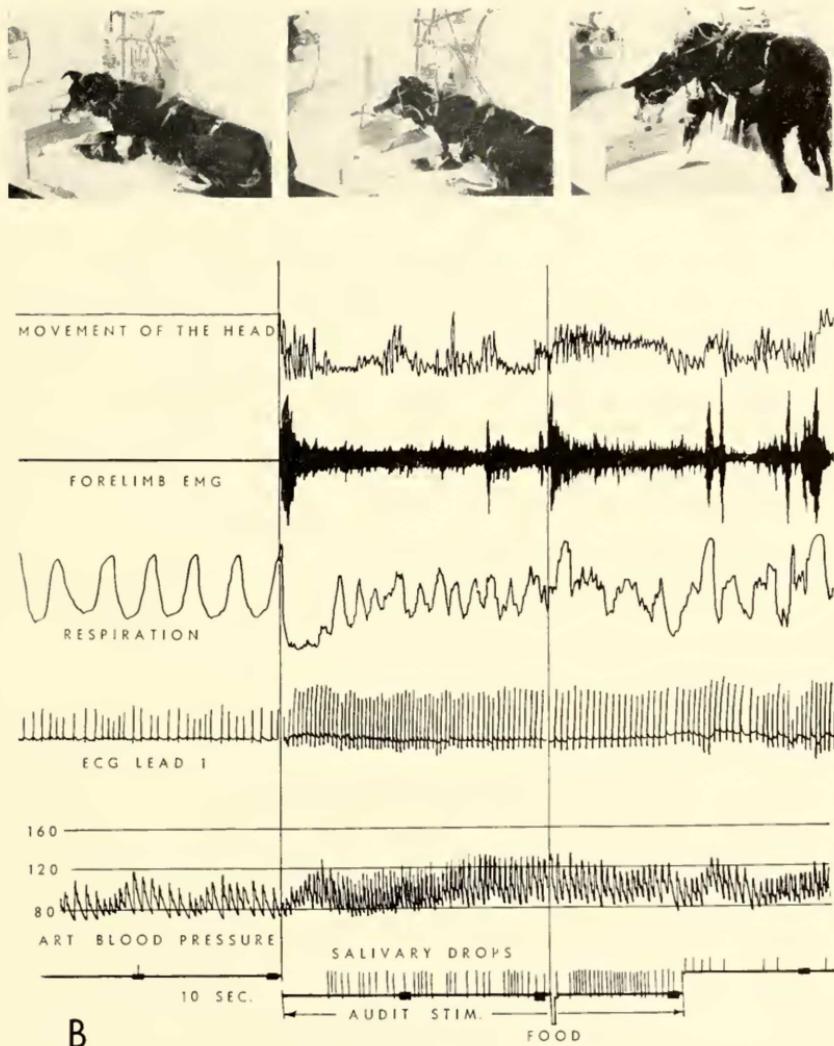


FIG. 12B

B. Reaction to the conditioned stimulus when overcoming a difficulty before taking the food. The latter case shows much greater activity of all the vegetative components of the conditioned reaction.

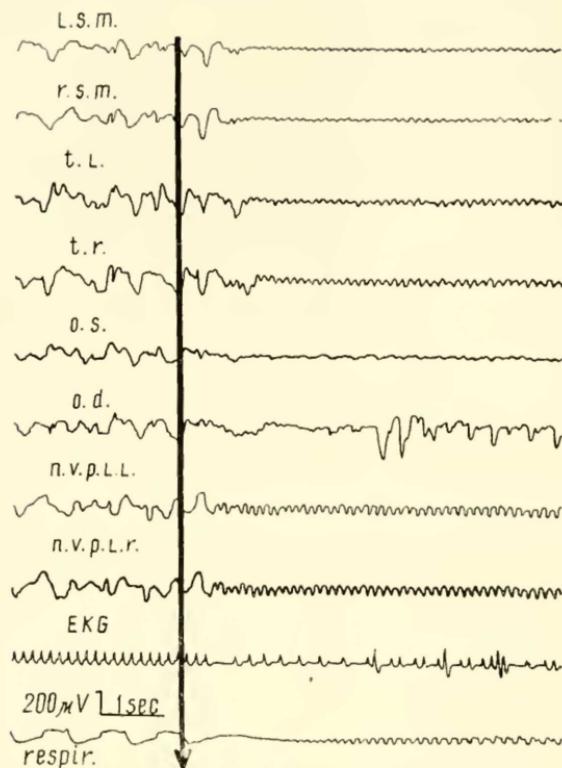


FIG. 12C

C. Confrontation of different components of a response to direct stimulation of the brain stem reticular formation. Abbreviations: l.s.m.—left sensorimotor cortex, r.s.m.—right sensorimotor cortex, t.l.—left temporal cortex, t.r.—right temporal cortex, o.s.—occipitalis sinistra, o.d.—occipitalis dextra, n.v.p.l.l.—n. ventralis posterior lateralis, left, n.v.p.l.r.—n. ventralis posterior lateralis, right, EKG, resp.—respiration.

The latest data on the representation of vegetative functions in the cerebral cortex once more emphasize the importance of precisely the vertical plan in the structure of the effector complex of excitations in the conditioned reflex. I am referring primarily to Papez's view of the 'visceral cortex' and to the studies of a number of other authors directed towards the same aspect of the subject (Papez, 1958; Maclean, 1954; Bard, 1948; Green, 1958; Adey, 1958).

On the basis of authentic facts indicating representation of vegetative

functions in the limbic, orbital, gyrus cinguli and other parts of the cerebral cortex it might be assumed that the whole effector part of the conditioned reflex, including the vegetative components is elaborated in some form at the level of the cerebral cortex.

However, the manifestation of the vegetative components during the first fractions of a second in the action of the conditioned stimulus warrants the assumption that this first reaction of the well-fixed conditioned reflex forms at the level of the subcortical apparatus.

With this question we closely approach the problem of localization of conditioned reflex coupling. On the basis of electroencephalographic experiments Fessard, Gastaut and Yoshii reached the conclusion that the coupling of the conditioned bond occurred primarily in the area of the reticular formation and that only later, already as a vertical 'projection', did the conditioned reflex process become cortical (Fessard and Gastaut, 1958; Gastaut, 1958). The very rapid changes in the respiratory component, revealed in our experiments, also seem to indicate this localization of the process of coupling of conditioned bonds. This seems the more probable since the brain stem reticular formation, which receives along collaterals the afferent impulses from the lemniscus-conditioned excitations, contains all the fractions of the respiratory and cardiovascular centres.

Moreover, the unconditioned excitations also come to the reticular formation. Thus all favourable conditions for the coupling function seem to be set up in the area of the brain stem reticular formation whose neural elements have extensive possibilities for the convergence of afferent excitations (Moruzzi, 1956; Amassian, 1958; Fessard, 1958). Nevertheless, considering the particular role of the orienting-investigatory reaction in the formation of the conditioned reflex, it is difficult to agree with the idea of a primary subcortical coupling of the conditioned bond (Anokhin, 1957; Anokhin, 1958).

The question of the composition of the effector complex of the conditioned reaction came particularly clearly to the fore in our experiments during the studies of the conditioned motor reflex. In this case we are referring to the local motor-defensive conditioned reflex reinforced by electric current and manifesting itself in lifting the hind limb.

In our laboratory it was established long ago that this 'local' reflex, its seeming simplicity and 'localness' notwithstanding, is a result of extraordinarily complexly integrated effector excitations selectively propagated to the peripheral motor apparatus according to very definite stages in the formation of the conditioned reaction. It was found that, before the

animal lifts its corresponding limb in response to the conditioned stimulus signalling pain stimulation, the excitations are rapidly redistributed along the axial musculature of its body. Owing to this rapid process, the animal assumes a new posture with new relations between the points of support and the centre of gravity, enabling it to raise the corresponding limb (Shunilina, 1939).

An electromyographic analysis of the antagonistic muscles in the different limbs of animals and man made it possible to show that this excitation, which we have named 'positional excitation', very rapidly reaches the extensors of the limbs, and the entire body shifts to three points of support within several fractions of a second before the limb previously stimulated by electric current is raised (Shumilina, 1949; Kasyanov, 1950).

In this interesting phenomenon we thought it possible to analyse the composition of the effector complex of excitations in so commonplace a conditioned motor act as the jerking away of the hind limb.

For the physiologist interested in higher nervous activity and animal behaviour this phenomenon of the dual nature of excitations in the motor conditioned reflex is important because both the first and second stages are clearly of a conditioned reflex character despite their different central localization. As a matter of fact, the rapid redistribution of the tonic tensions in the axial musculature of the body and the proximal parts of the limbs is not 'diffuse' in the ordinary physiological sense. This positional excitation is distributed over very definite motor neurones which shape the animal's posture precisely corresponding to the *future* raising of one of the limbs. From the biomechanical point of view we know very well that, if it had not been for this preliminary phase of shift of the centre of gravity in accordance with the basic points of support, the dog would fall, in attempting to raise the hind limb, as a bronze statuette falls when one of its legs is broken.

A conditioned motor reflex may be elaborated for any of the dog's four limbs by reinforcing it with electric current, and in each individual case the positional excitation will be distributed over the body segments anew, i.e. depending on the limb which will be lifted within several fractions of a second after the application of the conditioned stimulus. This fact is the best proof that both stages in the development of motor excitations are of a conditioned reflex nature.

At the same time we know very well that the central localization of both excitations is not the same. Whereas the positional excitation forms at the level of subcortical centres, especially in the neural elements of the

reticular formation (Magoun, 1952; Moruzzi, 1956, *et al.*), the local limb lifting, i.e. the local conditioned motor act is effected by the pyramidal tract and has a definite cortical localization.

The question is: how do both these organic components integrate in the animal's integral conditioned motor act? We endeavoured to answer this question by means of a number of variations of conditioned reflex experiments.

In order to trace the very fact of the shift in the centre of the body's gravity during the stage of formation of the positional excitation we

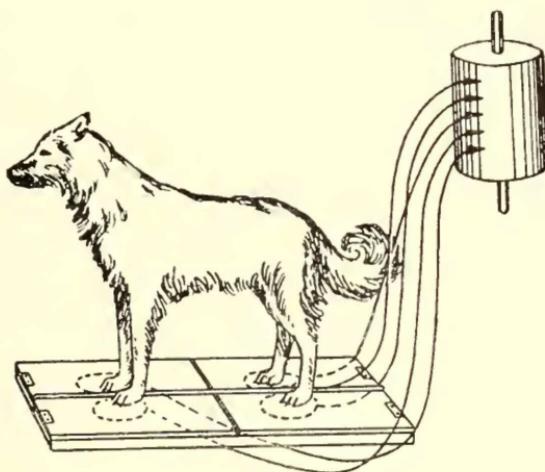


FIG. 13

Stand designed with four separately recorded stages. In addition to recording the spread of positional excitation this stand permits of recording the secretion of saliva and the vegetative components.

designed a stand by means of which we could record the pressure exerted by each of the four limbs (Fig. 13). The experiment showed that the moment the conditioned stimulus was applied there was a rapid and rather complex redistribution of muscular efforts, which could be easily recorded kymographically and electromyographically (Koryakin, 1958). It also showed that, if the conditioned motor defensive act was effected, say, by the right hind limb, the lifting of the paw was always preceded by an uncommonly stable complex of relations in the excitations of the brain stem. Now, if both sensomotor areas of the cerebral cortex are removed, an interesting dissociation between the positional and local

stages of the conditioned motor reaction are observed. Whereas in response to the conditioned stimulus the positional complex is retained in total conformity with its former nature, the local motor act is completely absent. This selective injury to the local component of the conditioned motor act indicates that positional excitations are really of a subcortical origin. (Fig. 14).

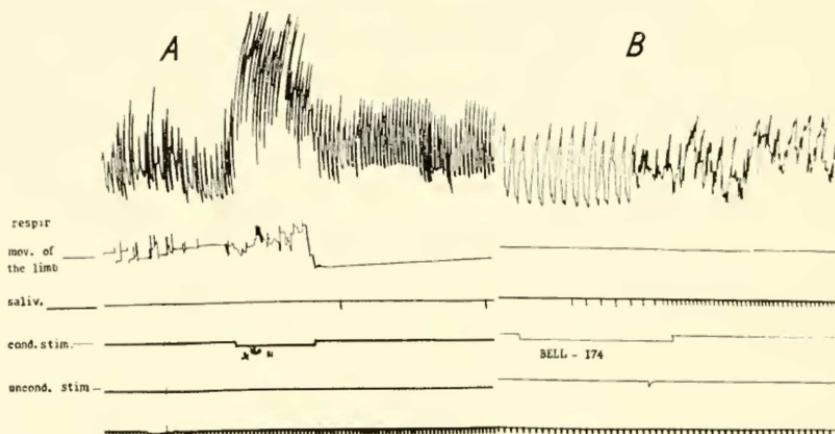


FIG. 14

Comparison of the respiratory component of two conditioned reactions — defensive (A) and alimentary (B).

The question of how a clearly subcortical complex of excitations could acquire a conditioned reflex nature cannot be dealt with at present, since it would lead us away from the subject under consideration. Here it is important only to note that our various experiments with the orienting-investigatory reaction have convinced us that the *conditioned reflex nature of the subcortical reactions is not primary*. It becomes such only after the active interference of cortical control at the stage of the very strong orientating reflex (Anokhin, 1949; Livingston, 1958; Hernández-Péón, 1958, 1959; *et al.*) (Fig. 15).

I presume that this part of my report illustrates sufficiently clearly two propositions: (1) the intricate complex of the effector excitations of the conditioned reflex is always very extensive and includes the cortex, as well as subcortical apparatus, and (2) this complex can be understood only by assuming the existence of a stage of synthesis of all the afferent influences affecting the animal at the given moment.

5. RETURN AFFERENTATION OF THE RESULTS OF CONDITIONED REFLEX ACTION

The conception of 'return afferentation' had developed in our laboratory long before the cybernetic trend of thinking led to the formulation of the 'feedback' idea, now being transferred into neurophysiology and proposed for the self-regulating technical systems.

Studying the problem of compensation of organic functions after the production of cross anastomoses we came to the conclusion that the creation of any new functional system of the organism in place of a

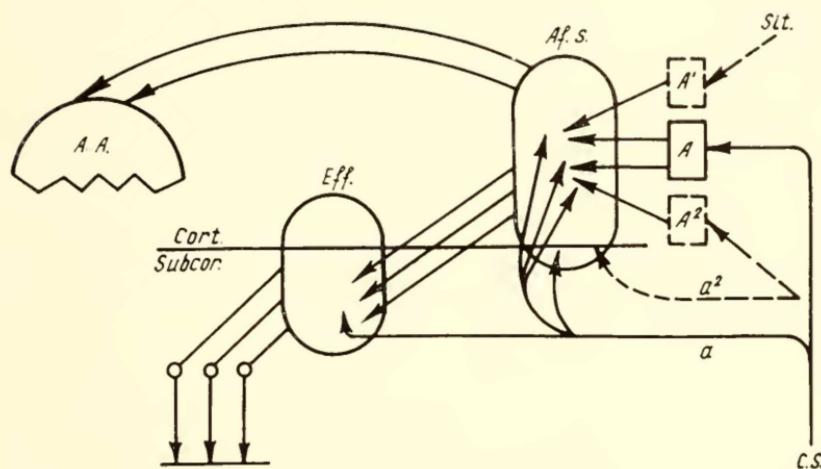


FIG. 15

Further development of the conditioned reflex architecture. Integrated effector excitations reach the functioning organs, and formation of the adaptive action.

previous system that has been abolished required constant interference of return afferent impulses from the results of the performed action themselves.

The physiological meaning of return afferentation consists in the reflection in minutest afferent impulses of the minutest details of the results of a given action. These results may direct the information to the central nervous system through the most diverse receptor apparatus. However, this afferentation as a whole constitutes a peculiar integral which reflects in the stream of afferent impulses the aggregate results of the given reflex action (Anokhin, 1935; Anokhin and Ivanov, 1933). Since it is directed back to the central nervous system to the neural formations just activated we found it most convenient to name it the 'return afferentation'.

In the existing literature afferent impulses of this type are ascribed mainly to proprioceptive formations. At this point I want to stress the fact that this conception has nothing in common with that of return afferentation. Proprioceptive signalling is also of a return nature, but it regulates the trend of the very action in the sense of its biomechanical characteristics. Proprioceptive signalling will never be able to inform the brain of the results of the adaptive effect obtained by means of the given movement. As a matter of fact, we cannot assay by means of a proprioceptor whether we have grasped a knife or fork, although the impulses of a tactile nature, suggesting that the hand has touched the object and the visual impulses fixing the moment of grasping the object, by means of return afferent impulses together ensure exhaustive information of the fact that the movement has ended in a certain positive result.

Here we approach the most critical point of the physiological architecture of the conditional reflex from which all the new adaptive acts, yielding more perfect results of action, begin. We shall ask the question in the following manner: where is the return afferentation of the results of the action directed to, what apparatus of the central nervous system perceives it and, so to speak, 'assays' the correspondence of the result achieved with the result of the afferent synthesis performed by it earlier?

The experiments and considerations discussed above, as regards the formation of the afferent apparatus of the acceptor of action, have led us to the conclusion that the meeting of the excitations of the acceptor of action and of the return afferentation from the results of the performed action is the moment at which the organism is always informed of the satisfactory precision of the act of behaviour that has taken place. It is precisely at the point where these two excitations — the excitation of the acceptor of action and the stream of return afferentations from the results of the action — meet that, in our opinion, the necessary condition for any co-ordinated and regulated relation of the animal and man to the external environment lies. Only when these two streams of excitation exactly coincide do the effector excitations cease to reach the functioning apparatus and is the given behaviour stage in the chain of individual reflex actions completed (Fig. 16).

Conversely, if the streams of return afferentations entering the brain along different analysers fail to coincide with the system of excitations, which has formed at the end of the afferent synthesis and is the apparatus of the acceptor of action, this lack of coincidence immediately involves other reactions, primarily, the orienting-investigatory reaction. By its very essence the orienting-investigatory reaction leads to an accumulation

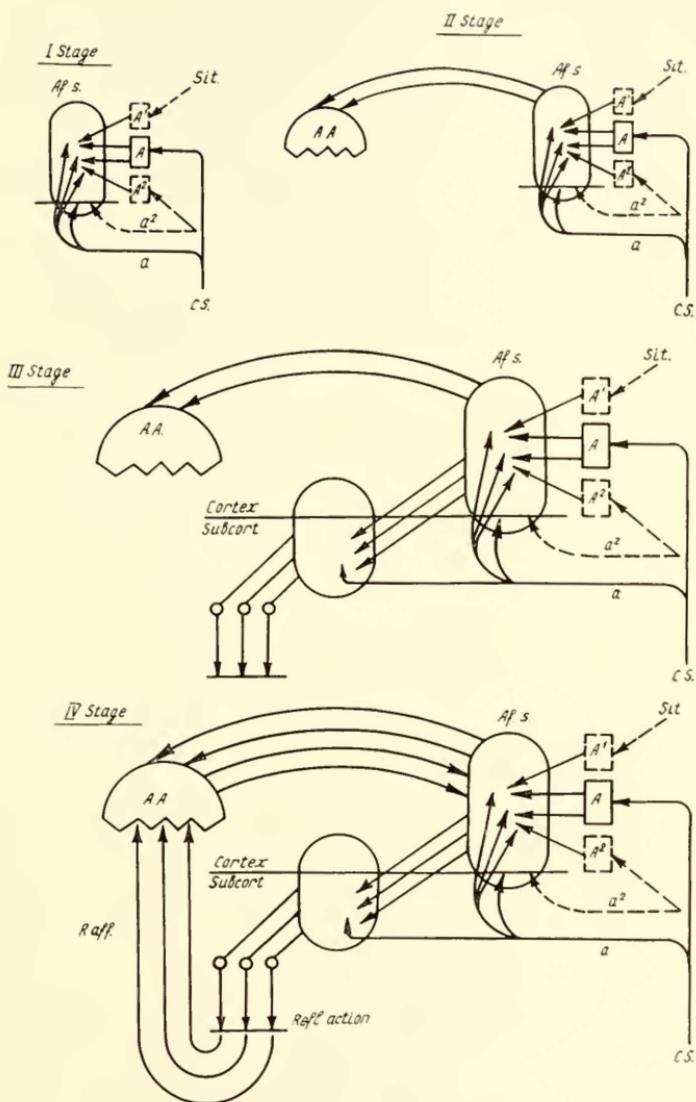


FIG. 16
Completion of the conditioned reflex physiological architecture. The figure shows the successive stages in the development of the architecture.

of new afferentations from the external environment, to a repetition of the afferent synthesis stage already at a new level and, lastly, to the formation of new effector complexes. On their part, these latter lead to some new act of behaviour and thus determine streams of new return afferent impulses which usually correspond in larger measure to the established acceptor of action. In any act of behaviour this cyclic process, beginning with the afferent synthesis stage and ending in the confrontation of the return afferentations and the excitations of the acceptor of action, continues until

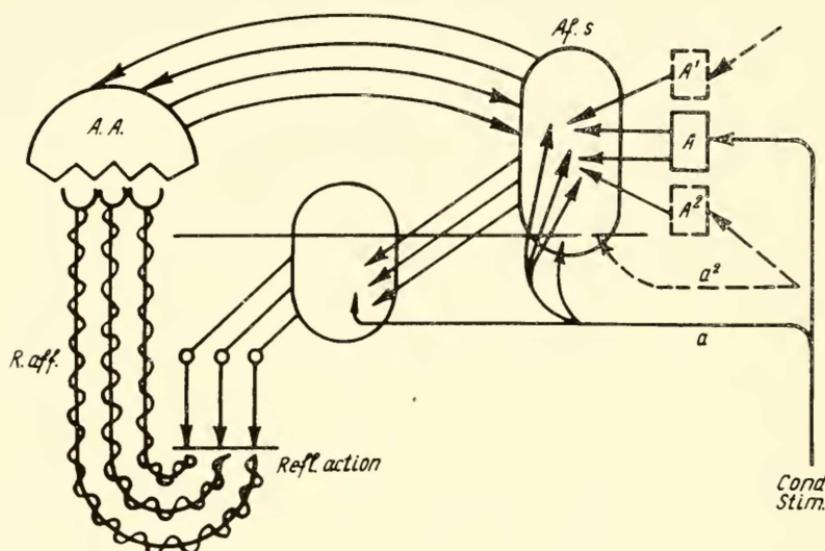


FIG. 17

Example of lack of correspondence between the acceptor of action and the return afferentation 'Discordance'.

both excitations fully coincide. In human behaviour, which, in our opinion, unfolds, even in its higher forms, according to the foregoing physiological architecture of the conditioned reflex, this final moment may be formulated as a 'coincidence of the results of action with the initial intention'. It is in this that the definite significance of the conception proposed by us for the physiological understanding of a number of phenomena of a psychological nature lies.

An analysis of most of the experimental situations, especially conducted in the way of the integral behaviour of the animal by the 'free runs'

method, shows that very many forms of behaviour are elaborated according to the aforesaid physiological architecture of the conditioned reflex (Fig. 16). The diagram shows the completion of the whole stream of excitations, which arose as a result of the afferent synthesis and of determined and particular adaptive effect. Practically every act in the life of man develops according to this architecture. Both as regards erroneous actions and the initial period of learning new actions, the only criterion of the correctness of the action is, in our opinion, the coincidence of the assigned excitations with the stream of the return afferent impulses which bring information of the results of the action performed at the given moment. This is particularly well seen in cases in which some erroneous act is performed. How do we detect the errors of an action if the latter has ended 'safely' from the point of view of all the demands made on it by the classical reflex theory? Everything seems to be on hand here: the stimulus, the central apparatus, as it is usually understood, and, lastly, the reflex action. By means of what additional apparatus then does man or the animal discover that the action they have performed is inadequate or erroneous? (Fig. 17).

The physiological architecture of the conditioned reflex proposed by us, like that of any 'voluntary action', offers a sufficiently objectively grounded answer to all these questions. At the same time it offers a real basis for a further scientifically objective analysis of the complex behaviour reactions of man and the animals.

CONCLUSION

The concept discussed above is an attempt to unify some of the available information on the physiology of the central nervous system and to combine it with the facts obtained in direct studies of the neurophysiological mechanisms of the conditioned reflex.

It is but natural that, with such a synthesis of the vast number of facts, we had to introduce several new conceptions which correspond to certain mechanisms discovered by us.

To begin with these conceptions include that of the *afferent synthesis*. The absence of stress on this stage of the complex treatment of all the multiform and numerous afferent influences on the organism by the central nervous system rendered unintelligible the very process of formation of the *efferent* complex of excitations, always of an integrative nature, i.e. always harmoniously combining the functioning components of the whole conditioned reaction.

To be sure, on the basis of what mechanisms does the given combination, rather than any other out of the millions of possible combinations of excitations developing in the cellular elements of the central nervous system, become integrated?

On the basis of what mechanisms is a very definite end effect of adaptation chosen and fixed out of the many probable end effects of adaptation, this end effect being precisely the one which exactly corresponds to the aggregate of the afferent influences affecting the organism at the given moment?

We have become convinced that the key to the solution of these problems lies in the extremely fine and multiform processes of accumulation of afferent information from the external and internal environments of animals and man. This is followed by a dynamic interaction and synthesis of this afferent information and, on the basis of these processes, one of the most intimate processes of any form of conditioned behaviour — the formation of the complex integrations of the effector apparatus. This process truly deserves the picturesque designation given to it at one time by our teacher Pavlov who named the afferent function of the brain the 'creative' function.

We see that it is indeed 'creative' if we take into account the enormous number of qualitatively heterogeneous afferent stimulations acting on the organism at each given moment and if we add to this that for man it infallibly ends in what may be psychologically termed the formation of the 'intention' of action.

Many physiological factors contribute to this remarkable process. Here we may include the rule of *convergence* of heterogeneous afferent stimulations in the selfsame element of the stem reticular formation (Fessard, 1958; Moruzzi, 1958; Amassian, 1958), the activating effect of this system on the cortical level of elaboration of the afferent signals (Moruzzi and Magoun, 1949), the integrating action of the frontal divisions of the cerebral cortex on this synthetic process (Shumilina, 1944; Anokhin, 1949) and, lastly, the controlling action of the cerebral cortex on all the subcortical and spinal entering elements for the afferent impulses (Anokhin, 1949; Livingston, 1958). All the above, put together, serves the highest synthesis — the formation of the conditioned bond!

Application of the term 'creative' to this process does not exclude the fact that all its details, as well as the process as a whole, are structurally and physiologically determined and, consequently, may become the subject of a strictly objective scientific analysis.

This latter proposition is illustrated by the fact that it is precisely the

physiological methods of research that enabled us to discover the existence of a special apparatus — the acceptor of action. As may be observed it co-ordinates behaviour during the second stage of the conditioned reflex, i.e. during the formation of the efferent act and the emergence of the return afferentation on the adaptive results of this act.

The entire architecture of the whole conditioned reflex offered for your consideration shows that this physiological analysis may be continued. It shows how living nature in the long evolutionary process mastered the *future* and fixed in material forms — structural and dynamic — the possibility of the animal's adaptation to *forthcoming events* in the external environment.

The conditioned reflex is the expression of the higher adaptation formulated by Pavlov in the *principle of signalling*, i.e. the possibility of adaptation of the animal and man to future events by just the *remote signal* of these forthcoming events alone.

Of course, it would be wrong to assume that the foregoing material exhausts the entire content of the physiological architecture of the conditioned reflex. The material presented is undoubtedly only the beginning of its study. However, it is important that its features be outlined precisely as those of an *integral physiological architecture* and for us it serves as the point of departure for further analysis.

Making a positive evaluation of our concepts of the physiological architecture of the conditioned reflex in one of his recent works, Alfred Fessard expresses the opinion that a further fine neurophysiological elaboration of the 'main points' of this general architecture will make an essential contribution to the development of these concepts (Fessard, 1958).

We fully agree with this opinion and, as may be judged from the foregoing material, we are doing all we can to concretize physiologically the various aspects of this general architecture.

We also think it possible that further analysis and accumulation of facts in the study of the neurophysiological bases of the conditioned reflex may make us change some of our present-day views and form new concepts concerning the concrete physiological mechanisms. This is the essence of scientific progress.

We believe, however, that any study of the intimate processes of the conditioned reflex by means of analytical and very fine methods and techniques may prove much more successful if it is correlated with the general physiological architecture of the conditioned reflex. And it is just this that prompted us to make this general architecture of the conditioned reflex, as we conceive it today, the subject of discussion.

GROUP DISCUSSION

OLDS. I would like to address myself to the remarks on the reticular formation and its differentiation. We also found differentiation in the reticular formation based on the dichotomy between the aversive and approach behaviour. We find that stimulation in the dorsal medial tegmentum produces escape. Stimulation in the ventral lateral tegmentum produces approach of the self-stimulation variety — in between there are overlaps.

First — the type of electrical activity which Dr Anokhin showed as typical of aversive stimulation did not appear in the ventral lateral placements but did appear in dorsal medial placements. The type of electrical activity which he showed as characteristic of alimentary stimulation did appear in the ventral lateral placements, but not in the dorsal-medial placements. My question is whether the electrodes used by Professor Anokhin were in the same parts of the reticular formation or in different parts.

My second question is: We have applied chlorpromazine and we have obtained results which are superficially in conflict with Dr Anokhin's results and we have checked our data. This is it: Chlorpromazine inhibits the self-stimulation response *totally* in the rat at 2 mg. per kilogramme — a dose which has very little effect on the escape reaction produced by stimulation of the dorso-medial tegmentum. This is different from Nепробамат and Nembutal which inhibit the escape reaction and have little effect on the self-stimulation response.

ANOKHIN. I suppose that the difference here is to be found in the specific localization of the stimulation. A given reaction may be induced from different points of the functional system; it can be provoked by natural stimuli, as by electrical ones. Yet, if electric stimulation is applied to a given spot of the reticular formation which is on the excitation pathway, after synapses which have been made sensitive to chlorpromazine, it may happen that the drug will have no blocking effect on the animal's defence reaction, which had been induced by direct excitation.

GRASTYÁN. I am in perfect agreement with Professor Anokhin about the conception of the functional specificity of reticular activating influences. I think we also obtained in our own experiments evidence confirming this supposition: we found that the stimulation of different points in the reticular formation in the hypothalamus had always a specific influence in the sense that it activated only certain behavioural acts, but inhibited others, antagonistic to those of the activated ones. The only point with which I do not agree is the interpretation of the electrical activity recorded in the reticular formation. I cannot believe that it represents a specific activity of the reticular formation (I refer to the 4-6 cycles per second activity see *slides 6 and 7*). It must be recorded very close to the substantia nigra centralis in the mesencephalon and in my opinion it reflects a special projected activity of the rhinencephalon to the brain stem (hippocampus, entorhinal cortex). It was shown by Dr Adey that abundant connections exist between these two areas. Moreover I have seen this activity to appear in the same point of the reticular formation in both alimentary and defensive conditioned reflexes; thus in my opinion it could not be regarded as representative of a specific function of this reticular subcentre.

ANOKHIN. I can give Dr Grastyán the following answer: Comparison of the slow rhythms of the reticular formations of the hippocampus and of the different

regions of the cerebral cortex shows that the specific slow rhythm of 4-7 per second occurs as a general rule in connection with direct painful stimuli of either the sciatic nerve or the skin of the foot. With other forms of stimuli, for instance, stimuli due to food, one does not get this rhythm. As has been shown by simultaneous recordings of EEG and of nervous impulses of individual nerve cells from one and the same point of the brain, the main characteristic of this rhythm is its persistence and its regularity.

As soon as the rhythm changes even for a fraction of a second, the cell impulses disappear or diminish.

We believe that this rhythm originates in the reticular formation and after a very short time (0, 1-0, 3 seconds) spreads to the corresponding region of the cortex, the parietal and the visual region. I suppose that our disagreements with Dr Grastyán are basically due to the fact that under normal experimental conditions our laboratory animals are always under some painful influence or in a state of fear. A specific rhythm can always appear on the electroencephalogram according to the degree of fear. In normal animals, which are awake, it is very difficult to suppress this rhythm and it can be achieved only after working several months with a pleasant food reinforcement. It may be that all these conditions were fulfilled in Dr Grastyán's experiments.

I think that in the future we also shall endeavour to bring about conditions under which this rhythm appears more often.

GALAMBOS. The data from Dr Grastyán's experiments resemble ours closely. I am not sure, however, that the term 'conditioned response' should be applied to these data. Choice of term is of course merely a matter of definition, and since a stimulus followed by a reinforcement here yields a changed brain response, the brain event fits the usual definition for a CR. We view the electrical event, however, as more probably indicating an elementary process in a chain of processes, that, when completed, yield learning. The phenomenon in question probably indicates that the brain is being prepared for the specific change that will occur and is not the signal of the actual change itself.