ACTA NEUROBIOL. EXP. 1974, 34: 15-31

Lecture delivered at Symposium "Brain and Behavior"
held in Jabłonna near Warszawa
July 1972

CONDITIONAL REFLEX THEORY AND MOTIVATIONAL BEHAVIOR

E. A. ASRATYAN

Institute of Higher Nervous Activity and Neurophysiology
Moscow, USSR

Abstract. Motivational behavior is explained in the light of reflex theory by reference to: (i) Pavlov's concept of nerve center as an assembly of structures possessing the same function, (ii) Sherrington's and Magnus' ideas about the hierarchical structure of the nervous system, (iii) author's notion about the multistage arc of the unconditioned reflex, i.e., an arc with many branches in its central path, each passing through the main integrative levels of the central nervous system, (iv) experimental facts of this laboratory and particularly concerning bidirectional conditioned connections. It is assumed that motivational behavior elicited by endogenous and exogenous factors through hereditary mechanisms may be regarded as a manifestation of complex inborn reflexes, in which the main branch is located in the limbic system. The cortical branch makes it possible to elaborate particular conditioned reflexes. Physiological mechanisms of so-called purposive movements in motivational behavior is regarded as the activity of backward conditioned connections, leading from the unconditioned reflex centers to the centers controlling motor effectors.

Advances of modern neurophysiology and experimental psychology, particularly the fruitful results of experiments concerned with the functional study of various brain centers, using both traditional and modern methods and procedures, have led to contradictory views concerning the Pavlovian doctrine of higher nervous activity. On the one hand, a large body of well founded and reliable data obtained in these studies has lent strong support to the neurophysiological bases of Pavlov's doctrine with respect to its three main components: conditioned reflex activity of the cerebral cortex, complex unconditioned reflex activity of the subcortex, and the diverse interactions between them. On the other hand, these data have provided a basis for enhancing various trends and tendencies opposed to this doctrine as a whole, or to some of its theses. This concerns, in particular, the Pavlovian understanding of the physiological mechanisms of complex innate forms of neural activity, known as instincts, drives, etc. The rich and varied body of pertinent experimental evidence provided by the studies of behavioral responses of animals under natural or nearly natural conditions, or in chronic experiments using microelectrophysiological procedures, has been employed by ecologists, experimental psychologists and neurophysiologists for the development of a multitude of theories and hypotheses, under the general name of motivational theories. It would not be an exaggeration to say that in the system of brain sciences, motivation is today one of the most pressing problems, holding a central place in contemporary studies by experimental psychologists and neurophysiologists. This is confirmed by many conferences and symposia, numerous monographs and collections of papers devoted to this subject, not to speak of a host of publications in special and general periodicals.

While it is not my intention to give a critical survey (even in a brief form) of the current status of studies on this problem, it is necessary to note certain points of particular pertinence to the subject under discussion. In particular, many authors hold the view that the key principle of purposive actions and of motivational behavior of animals consist in diverse kinds of drives which are supposedly not determined by external factors and which express certain essential requirements of the organism and species. These drives are determined by changes in the functional state and activity of the limbic structures of the brain, primarily by the hypothalamic region, under the influence of a variety of endogenous, neurohumoral factors. It is believed that the so-salled purposive movements elicited by these drives are not reflexes and that the environmental factors play only an ancillary role.

There are also trends, however, developed in the last few years, which assign to environmental factors and learning processes a much more important role in motivational responses, whereas the endogenous neurohumoral factors are supposed to create only a special readiness of the organism ("central motivational state", according to Morgan, 31) to respond to the action of adequate environmental stimuli. This point is based on the results of experiments of several investigators (13, 28, 32, 33, 38, 47) who suggest that endogenous factors or artificial stimulation of the hypothalamus or other neural structures elicit adequate motivational behavior in the form of variable integrative actions of an adaptive character. These are manifested only in the presence of an adequate object or subject in the environment (food, water, enemy, etc.). Noteworthy in this respect are the results of recent experiments by Valenstein (47) and his colleagues which have demonstrated that electrical stimulation of the same hypothalamic structures in rats may elicit alternatively either drinking, or eating, or wood gnawing, depending on the presence of an adequate external object. Such shifting from sexual to alimentary behavior and vice versa has been observed by Caggiula (11) and Gallistel (19). These views are supported by results of two kinds of experiments. Several studies have shown that in the case of motivational, behavioral responses elicited by artificial stimulation of certain limbic structures, the animals usually make use of previously conditioned or learned forms of movement, adequate to the particular situation. It has also been found that a state of drive and motivational behavior may be generated in a conditioned reflex manner, under the effect of factors of the experimental situation or of certain external stimuli (7–9, 12, 14, 18, 21–23, 29, 30, 46). Hence the terms "secondary" or "acquired drives", "conditioned incentive motivation" etc. have been proposed.

Both with regard to the experimental and, particularly, theoretical considerations, there are still many uncertainties and contradictions in this problem of considerable interest for the biology, psychology and neurophysiology of today. Views and opinions of various students disagree over a wide range, not only with regard to the more or less fundamental factors of motivational behavior, but also with regard to the definitions of the concepts of motivation and drive themselves and their relation to the concepts of instinct and emotion. Many neurophysiologists are used to indulge in speculations or mere psychological descriptions of their views on a given subject, which are often presented as a physiological interpretation. Although, in recent years, there has been a noticeable increase of research in which much attention is given to the neurophysiological mechanisms of motivational behavior and the great importance of its organization is attached to learning and environmental factors, it is noteworthy that some adherents to this research trend (e.g., 49) lay stress on the formation of so-called operant behavior, which is traditionally regarded by them as non-reflex in nature. Beritov (6) ascribes the leading role in behavioral acts to so-called image-guided behavior, which he considered as non-conditioned reflex in nature. Anokhin (1) interprets motivational behavior in the light of hypotheses about a functional system in which one can hardly find even a place for the conditioned reflex. Konorski (25) divides reflexes into two separate and independent groups — drive and consumatory — with corresponding, unique neural substrates. However, there is every reason to believe that it is the present-day dynamic and monistic reflex theory with its distinct and strict scientific principles that is capable of elucidating this very important and fairly complicated problem of modern neurophysiology and experimental psychology, and of opening up most favorable perspectives for its further development. In this context Pavlov's (35) concept about neural centers is noteworthy. He considered a neural center to be a system or assembly of central structures in different parts of the central nervous system, closely interconnected both anatomically and functionally, constituting a single set and providing for the performance and regulation of certain functions of the organism.

When many years ago (2, 3), on the basis of experimental facts obtained in this laboratory, I proposed a new notion of the structure of the unconditioned reflex (Fig. 1), I was guided by the above concept of Pavlov

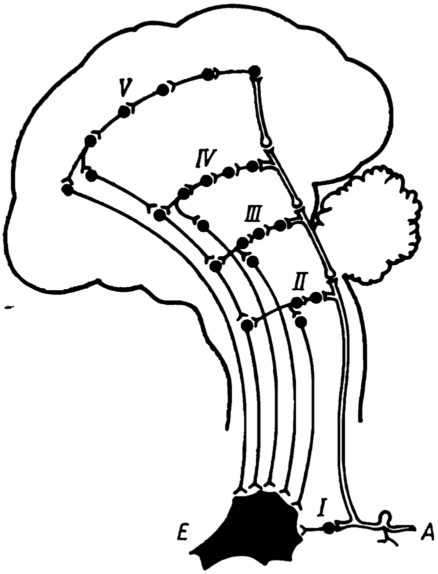

Fig. 1. Scheme illustrating the uncoditional reflex arc I–V, branches of the central part of the reflex arc at different levels of central nervous system; A, afferent neurons; E, efferent neurons.

and by analogous ideas of Sherrington (41) and Magnus (27) concerning the characteristics of the different levels of integrative activity of the central nervous system. Without going into details I shall limit this text to a few remarks. According to these ideas, the central part of the unconditioned reflex passes not through a single level of the central nervous system, but through many branches, each passing through its main parts: spinal cord, medulla, hypothalamus, thalamus, cortex (Fig. 1*I–V*). Judging by the available data, each of these branches has specific functional properties; by its participation in the accomplishment of an unconditioned reflex it imparts a definite functional character and a definite level of perfection to this reflex. It must be assumed that the special significance of each of these branches is different for all sorts of unconditioned reflexes, varying according to their kind, type, complexity, and other characteristics. Every reflex — alimentary, defensive, orienting, sexual, circulatory, respiratory, etc. — has its specific representation at various levels of the central nervous system, but the main branch for each of them may be located in a particular part of this system. For instance, the main branches of the circulatory and respiratory reflex arcs are located in the bulbar level (*II*) while the main branches of the alimentary, defensive, sexual and other reflex arcs are located at the hypothalamic level (*III*). The cortical branches make it possible to elaborate particular conditioned reflexes on the basis of corresponding unconditioned reflexes. There must be great variability in the degree of activity of each individual branch of the arc and its specific participation in the accomplishment of the reflex, depending on current local and non-local changes in the functional state of the central nervous system under the influence of different endogenous and exogenous factors. From the above point of view, innate motivation could be considered as a manifestation of vitally important complex inborn reflexes, in which the main branch of the arc is located in the hypothalamic region.

Thus, in the light of the reflex theory and in particular of the above mentioned ideas of Pavlov, Sherrington, Magnus and others, concerning the complex functional architecture of inborn reflexes and different levels of integrative activity of the central nervous system, it is possible to interpret satisfactorily the main facts of motivational behavior, without recourse to illusory forms of neural activity of non-reflexive nature.

To an even higher degree this concerns conditioned reflex theory. Being a major achievement of natural sciences in this century, this theory continues to develop along the main course delineated by its founder, despite various opponents who continue in explicit and implicit attacks. The joint efforts of many of Pavlov's pupils, who have remained loyal to this basic idea, have considerably improved the conditioned reflex theory in a number of respects, its basic propositions having been substantiated and others modified or even discarded.

In this context and with the intention of elucidating some aspects of motivational behavior in the light of the conditioned reflex theory, I would like to discuss here the possibility of altering somewhat the concept of the functional architecture of conditioned connections. It is known, that the views of Pavlov himself on this point underwent considerable changes as the conditioned reflex theory developed. Subsequently, some of his pupils and followers (1, 4, 25, 26, 34, 45, 48, 49, 51) and others have also advanced some new ideas. It is not my intention to review these ideas and underlying facts, but I shall instead discuss only the question of the bidirectionality of conditioned connections and its role; considering mainly evidence from our laboratory.

A most characteristic feature of contemporary conditioned reflex theory is the concept of a bidirectional conditioned connection with reciprocal conductivity. Although the idea of the bidirectionality of associative connections is rather old in psychology, its strict experimental verification has been accomplished only in this century. Beritov (5) was the first to introduce it into the physiology of conditioned reflexes on the basis of facts obtained mainly in the Pavlovian laboratories. After that, Pavlov himself also assumed the existence of bidirectional conditioned connections, by which he explained the formation of motor alimentary conditioned reflexes. It should, however, be noted that there is a fundamental difference in the initial interpretation of this problem between Beritov (5) and Pavlov (35). According to Beritov, connections running from the center of a conditional stimulus to the center of the unconditional stimulus are involved in the performance of a conditioned reflex, while backward connections produce a diametrically opposite result, namely extinction, differentiation and delay of conditioned reflexes, which were regarded by Pavlov as manifestations of internal inhibition. On the one hand, according to Pavlov's view, the direct and backward conditioned connections carry out similar functions in principle. For instance, with regard to the above mentioned motor conditioned reflexes, he maintained that a movement of the paw via activation of a direct conditioned connection elicited an alimentary reflex, while the alimentary reflex via activation of the backward conditioned connection brought about the movement of the paw. Furthermore, he held that such bidirectional conditioned connections were established between kinesthetic cortical cells and those of the cortical terminations of all other analysers to become the physiological basis of voluntary movements.

More recent experimental and theoretical studies on the physiology of bidirectional conditioned connections carried out, on the one hand, by Beritov (5) in collaboration with Bregadze (10), Dzhavrishvili (16) and others and, on the other hand, by Kupalov (26), Federov (17), Skipin (45), Voronin (49), Wyrwicka (50), Dostalek (15) and many others, are sufficiently well known that they need not be recapitulated. It seems appropriate however, to mention certain points emerging from these studies which are of special interest to the subject under discussion. First, the basic facts on the bidirectional conditioned connection obtained mainly in our laboratory by use of the mechanographic recording of reflexes during their occurrence, have been confirmed by a number of experimenters who used modern electrophysiological methods, including microelectrophysiological ones. For instance Rabinovich (37), Shulgovsky and

Kotlyar (43), Shulgina (42) and others, have carried out experiments in which changes in neuronal activity of the cortical points of the signal and reinforcing stimuli were recorded. After the elaboration of an appropriate conditioned reflex the presentation of each of these stimuli evoked a change in neuronal activity not only in the corresponding cortical point, but also in that of the paired stimulus. Although the majority of these authors do not say explicitly how these facts are related to the question of bidirectional conditioned connections, such a relationship appears to be quite obvious. In this relation our co-worker Borukaev (unpublished data) has obtained the following interesting results. Rhythmic clicks were presented to dogs throughout the test period at two different frequencies in each half of the test. In that part of the test in which clicks followed one another at one second intervals, the dogs were not subjected to any other stimulation. In the other half of the test, however, in which the interclick intervals were half a second, the dogs were trained in defensive motor conditioned reflexes to a bell and to light by periodic combinations of the latter signals with electrical stimulation of the right forepaw. The EEG of the auditory cortical area, as well as the mechanogram and EMG were recorded (Fig. 2). When, for one reason or another, a motor de-

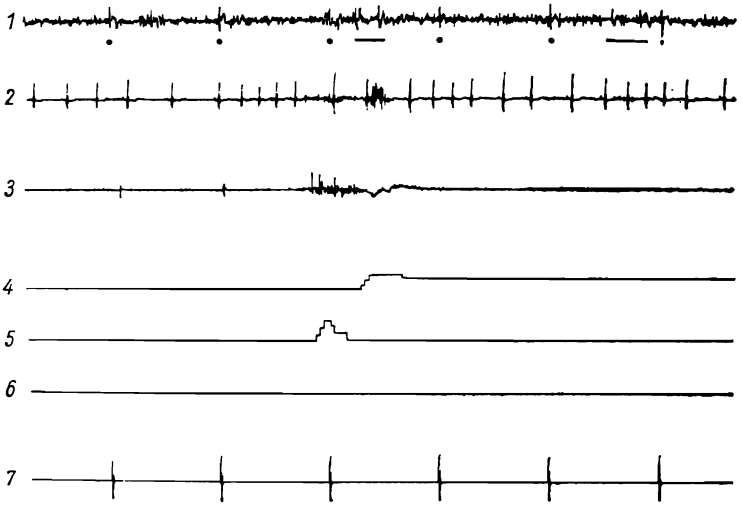

Fig. 2. Appearance of additional potentials similar to evoked potentials to clicks (marked by lines on line *1*), in "spontaneous" manifestation of the defensive reflex in an appropriate situation. *1*, electrocorticogram of the auditory cortical area with evoked potentials to clicks; *2*, electrocardiogram; *3*, electromyogram of extensors of the right ("conditioned") forepaw; *4*, mechanogram of the right forepaw; *5*, mechanogram of the left forepaw; *6*, mark of electrocutaneous stimulation; *7*, clicks (1 Hz).

fensive reflex was present (line 3), then between the potentials evoked by clicks in the auditory cortex additional potentials (line 1), appeared similar to those evoked in the sensorimotor area. It seemed to us that the only structural basis for such a phenomenon could be a backward conditioned connection between the sensorimotor and auditory cortical areas. The experiments by our co-workers Merzhanova and Samoilova (unpublished data), in which a food-procuring reflex of the paw was elaborated in response to electric stimulation of the medial thalamic nuclei, have produced the following result: thalamic stimulation elicited in the cortical representation of the paw potentials characteristic for the conditioned reflex, while tests with food presentation without pre-stimulation of the thalamus also altered the electrical activity of the cortical point of the paw in the form of appearance of high-amplitude and high-frequency discharges in the EEG followed by an occurrence of the food-procuring reflex (Fig. 3). Analogous or similar results were obtained earlier by Jasper and Shagass (24), Dostalek (15) and others.

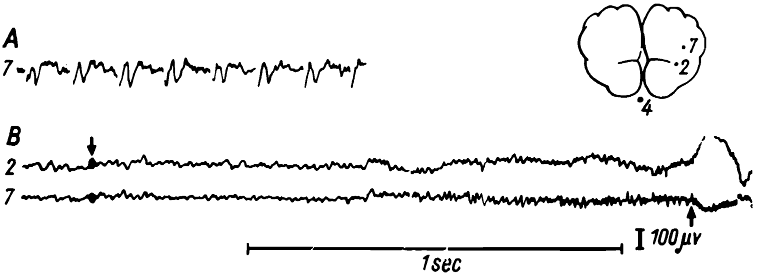

Fig. 3. Electrophysiological manifestation of bidirectional conditioned connections. *A*, pattern of recruiting potentials in a stabilized CR in the sensory point of the cortical representation of the forepaw. *B*, appearance of high-amplitude and high-frequency EEG activity in cortical points 2 and 7 of the same paw. Upper, trace, EEG from the motor point; lower trace, EEG from the sensory point. Arrow above, food delivery; arrow below, forepaw movement. Calibration: 100 μv, 1 sec.

Secondly, the evidence obtained in our laboratory and also that reported by others warrants the conclusion that activation of a backward conditioned connection may result not only in a conditioned reflex reproduction of the reflex to the preceding stimulus, but may also be limited to an increase of excitability of the central structures corresponding to this latter stimulus. There are some reasons to postulate that a direct conditioned connection also has both properties, namely reproduction of the response to a reinforcing stimulus and to the conditional stimulus, as well as the increase of excitability of central representation of the latter stimulus.

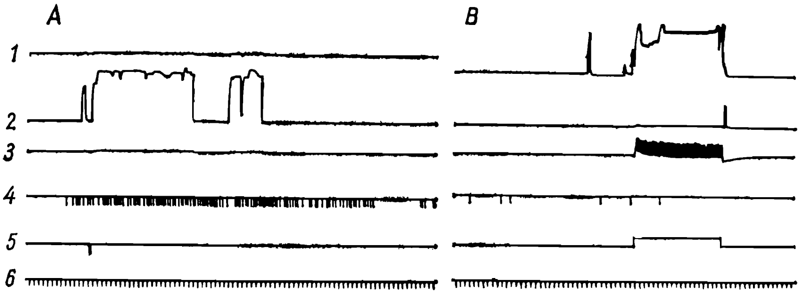

Fig. 4. Specificity of the backward connections in food and water CRs. Flexion of right forepaw in food motivation (*A*) and flexion of the left paw in water motivation (*B*). *1*, mechanogram of the left limb; *2*, that of the right limb; *3*, swallowing movements during drinking (in *B*); *4*, salivation; *5*, food (in *A*) or water presentation (in *B*); *6*, time in seconds.

Thirdly, as evidenced by results obtained by Pankratov (34) and his colleagues and by facts of our laboratory, well-formed backward conditioned connections exhibit considerable specificity. Thus, for example, if flexion of one forepaw provided the dog with food and flexion of the other provided it with water, then, after the respective instrumental conditioned

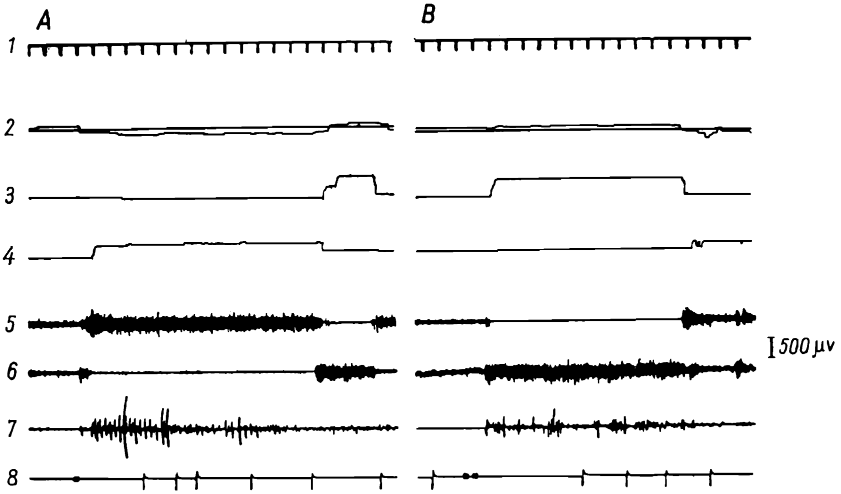

Fig. 5. Specificity of backward connections in two different alimentary CRs *A*, eating from left food-bowl causes flexion of left forepaw; *B*, eating from right food-bowl causes flexion of right paw. *1*, time in sec; *2*, head position in horizontal plane relative to middle position between the feeders; *3*, mechanogram of movements of right forepaw; *4*, of left forepaw; *5*, EMG wrist extensor of the right forepaw; *6*, of left forepaw; *7*, masticatory movements; *8*, salivation and food presentation (single dot for left feeder and two for right).

reflexes having been elaborated, each kind of motivational excitation entailed flexion of the adequate paw (Popova, this Symposium, 36) (Fig. 4). If flexion of a paw provided the dog with food from the left food-bowl, while flexion of the other paw also provided it with food from the right food-bowl, then after the elaboration of appropriate instrumental reflexes, food presented from each of the food-bowls entailed flexion of the adequate paw (Kolotygina, unpublished data) (Fig. 5). A similar specificity of backward conditioned connections has been shown by Struchkov and Davydova (unpublished data) in experiments in which dogs were allowed to move freely in the room during the tests. During food intake from the right food-box, a tone of 1,000 Hz was presented, while during eating from the left food-box, situated 5 m from the right one, a tone of 300 Hz was presented. After repeated combinations each of these acoustic stimuli, when presented separately, made the dog run to the appropriate food-box (Fig. 6 and 7).

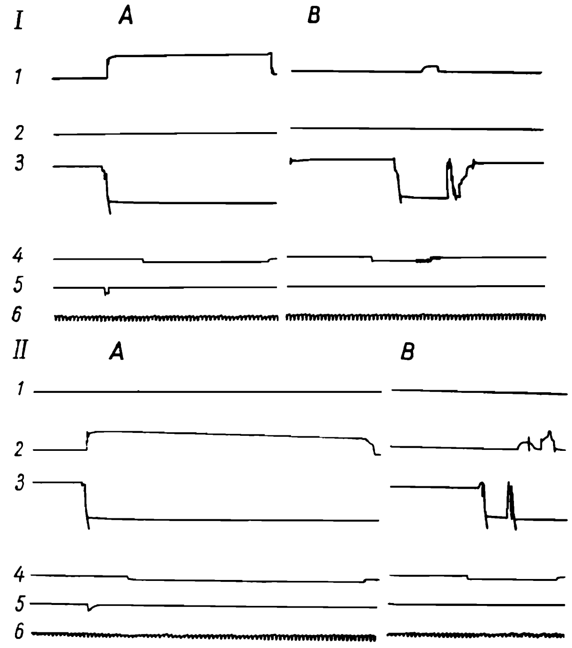

Fig. 6. Specificity of backward connections in selection experiments. *I*: *A*, during eating from the right feeder a tone of 1000 Hz is presented; *B*, running to the right feeder during the tone of 1000 Hz. *II*: *A*, during eating from the left feeder a tone of 300 Hz is presented. *B*, tone of 300 Hz elicits running of the dog to the left feeder. *1*, presence of the dog at right feeder; at left feeder; *3*, at starting platform; *4*, tone; *5*, food-presentation; *6*, time in sec.

Finally, although bidirectional conditioned connections are formed in all sorts of CRs, they are particularly well manifested in instrumental conditioned reflexes. It is noteworthy that Pavlov advanced his idea on bidirectional conditioned connections on the basis of analysis of experimental evidence relating precisely to that variety of CRs. Carefull and comprehensive analysis of the primary and secondary, alimentary and defensive instrumental CRs in dogs, performed with colleagues co-workers in this Laboratory has led to the conclusion that the cortical point of the secondary signal is connected with each reflex in a dual manner — directly to each of them and indirectly, i.e. via each to the other. Moreover, the pathway from the representation of the CS via that of the biologically important UR to that of the instrumental movement is formed earlier, is more stable, and plays a more important role than the direct pathway from the representation of the CS to that of the instrumental movement. On the basis of such evidence, schemes have been presented for these two kinds of reflexes. Since these schemes will be used here to validate some theoretical propositions, they are reproduced in Fig. 8, in

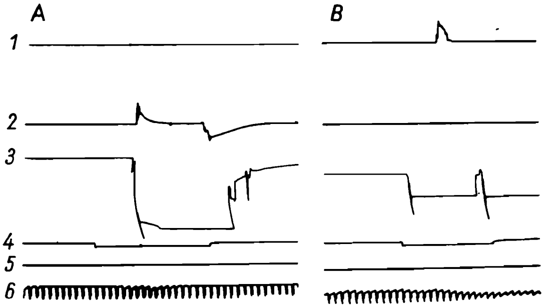

Fig. 7. Similar experiments on another dog. *A*, tone 300 Hz elicits running to right food-box. *B*, a tone of 1000 Hz elicits running to left food-box. Denotation as in Fig. 7.

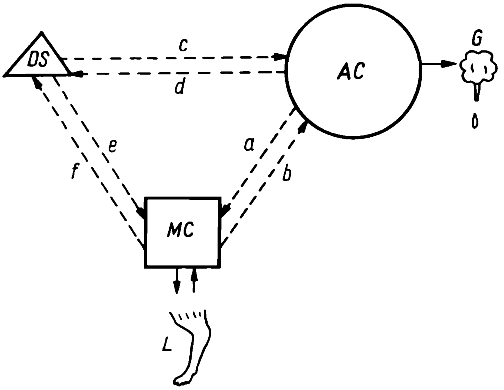

Fig. 8. Schematic representation of the arc of instrumental CR. DS, distant signal; AC, alimentary center; MC, motor center; G, salivary gland; broken lines from *a* to *f*, direct and backward conditioned connections.

a somewhat generalized form. In the case of increased excitability of the alimentary center (AC) a selected local movement of a given leg (L) may be evoked in several ways — by activation of primary direct connection (*a*) between alimentary and motor cortical points, by activation of the indirect pathway ($a + c$) from distant or secondary conditional stimuli (DS) to the motor cortical point (MC), by activation of direct connection between the same points (*e*).

It appears that the above concept on bidirectional conditioned connections, which I regard as a further development and substantiation of Pavlov's ideas, represents one of the most characteristic features of the current stage of development of his theory. Although it is not yet possible to say exactly how and to what an extent this concept may expand that theory, it seems obvious that it will play a dominant role in the study of motivational behavior. In order to illustrate this point I shall discuss one of the complex and still unresolved problems concerning motivation.

The problem is as follows. It is generally considered that selection and performance of an adequate response called purposive action, in the form of a definite set of specialized motor acts, is one of the most important characteristics of motivational behavior. But what is the mechanism of these purposive movements, how do the motivational agents select and elicit appropriate movements? This question has not yet been answered in any meaningful way.

In my opinion the most satisfactory and well substantiated answer to this question can be given on the basis of the bidirectional conditioned connections. The instrumental CR is regarded by many, and not without reason, as a model of motivational behavior. However, because these authors do not yet have a distinct notion of the physiological mechanisms of the instrumental movement itself, this model cannot elucidate the physiological mechanisms of complex purposive movements in motivational behavior. Since, according to the Pavlovian idea which underlies our studies, an instrumental response is regarded as the result of activation of the backward conditioned connection from the cortical point of an US to the cortical representation of the respective motor organ, there is a real possibility for a more complete and effective utilization of this model in attempting to answer the question of selection and performance of acquired or purposive movements in motivational behavior.

If, following Sechenov's and Pavlov's concepts, one will regard complex behavioral motor responses as integrated sequences of simpler motor acts, then it would be reasonable to assume that the set of purposive movements in motivational behavior is determined mainly by the activation of the system of backward connections from the cortical representation of the complex UR (in other words drive or motivational center) to the cortical representation of the motor organs taking part in an integrated chain of CRs of the second, third, and higher orders. Extraneous stimuli of different modalities coinciding with the above movements and becoming conditioned signals may orient the animal to the probable location of the object looked for, via the direct conditioned connections to the cortical points of these movements. Such an explanation is equally applicable to those cases where a central motivational state is created by neurohumoral factors, as well as to those where this state arises, or is enhanced under the action of environmental factors, including conditional stimuli. If, in the presence of increased excitability of the neural substrate of some complex UR (Fig. 9*AC*), a definite sequence of movements (M_1, M_2, M_3) is performed, accompanied by the action of certain stimuli (S_1, S_2, S_3), and if this series is followed by finding an adequate, biologically significant object or event, then the combination of these stimuli and movements becomes a complex CS. When a CR established to such a multi-component stimulus with multi-chain conditioned connections becomes sufficiently stable and specialized owing to repetition of the situation and increased excitability of neural structures of the UR then it acquires the ability to reproduce the appropriate chain of movements, via the backward conditioned connections. Here accompanying conditional stimuli may also play an even more important role than in the case of unitary instrumental CRs by way of activation of direct connections to the appropriate motor points. This is especially important because central motivational structures through conditioned connections activate the cortical representation of motor organs and simultaneously enhance the excitability of central structures of these conditional stimuli via the mediation of backward conditioned connection to them.

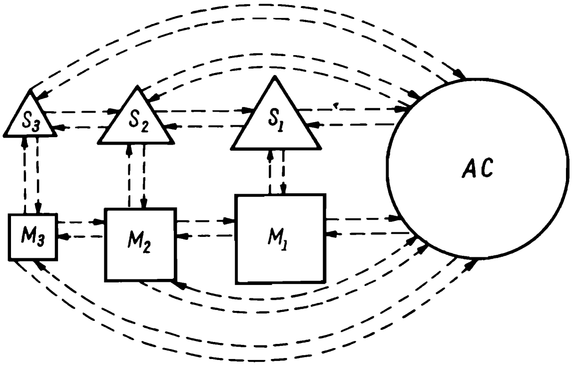

Fig. 9. Schematic representation of the formation and perfomance of alimentary motivational behavioral acts. For explanation see text.

Although this concept is so far purely hypothetical it deserves close attention, because it allows elucidation of the important problem of physiological mechanisms of so-called purposive motivational behavior. Moreover, it seems that on the basis of this concept it is possible to explain at least the most important data related to motivational behavior. Without going into details it should be stressed that this explanation refers not only to complex motor CRs such as situational or sequential responses studied in detail by Kupalov (26), Konorski (25), Voronin (49), Gotsiridze (20), Shustin (44) and others, but also to the so-called image-guided behavior and to various kinds of motivational behavioral reactions, which are allegedly non-reflex in nature. As noted several years ago, this concept enables one to explain satisfactorily the complex forms of behavioral reactions in primates, which are based, according to Pavlov, on a special type of association. These differ from ordinary CRs by the fact that a connection is established not accidentally between concurrent events, but between those phenomena which are connected by cause-and-effect relationships in natural life, and fixed by the organism during its activity and interaction with environmental factors. I have proposed the term "causal CR" for this type of association. Pavlov, in analysing the physiological mechanism of these associations, limited himself mainly to their reflex nature. While sharing his point of view in general, it seems necessary to point out a particularly important role of the bidirectional conditioned connection in this type of association. It is gratifying to note that the recently published monograph by Schastny (39) discussed in a similar way the interesting facts obtained in his comparative studies on primates.

Pavlov assigned a dual role to complex URs called also instincts, drives, etc. On the one hand they play a virtually independent role, but on the other hand they form a basis for the elaboration of a great variety of CRs. He repeatedly stressed the importance of their extensive study and classification. Considerable advances made in this line have confirmed the validity of this view and of his fundamental proposition on the reflex nature of the more complex behavioral reactions mostly known in modern science as motivational. It may be no matter of principle for neurophysiology that this subject has been invaded by non-physiological terms and concepts, such as motivation, emotion, etc. The important thing is that by manipulating these terms and studying their physiological mechanisms, the neurophysiologist must stand on firm ground of his science and adhere to its strict principles. It is on this road that my colleagues and I firmly stand both in experimental and theoretical studies of the highly important problem of motivation, namely the role of bidirectional conditioned connections in the performance of so-called purposive motor responses in motivational behavior.

REFERENCES

1. ANOKHIN, P. K. 1968. Biologia i neurophysiologia uslovnogo reflexa. Izdat. Meditsina, Moscow. 547 p.
2. ASRATYAN, E. A. 1955. New data about unconditioned and conditioned reflexes (in Russian). Zh. Vyssh. Nerv. Deyat. 5: 480–491.
3. ASRATYAN, E. A. 1965. Compensatory adaptations, reflex activity and the brain. Pergamon Press, Oxford. 194 p.
4. BELENKOV, N. Y. 1965. Uslovnyĭ reflex i podkorkovye obrazovaniya mozga. Izdat. Meditsina, Moscow. 300 p.
5. BERITOV, I. S. 1932. Individual'no priobretennaya deyatel'nost' nervnoĭ sistemy. Gosizdat, Tiflis. 470 p.
6. BERITOV, I. S. 1961. Nervnye mechanismy povedeniya vysshikh pozvonochnykh zhivotnykh. Izdat. AN SSSR, Moscow. 355 p.
7. BINDRA, D. 1969. The interrelated mechanisms of reinforcement and motivation, and the nature of their influence on response. Nebraska Symp. on Motivation, 17: 1–33.
8. BOLLES, R. C. 1963. Effect of food deprivation upon the rat's behavior in its home cage. J. Comp. Physiol. Psychol. 56: 456–460.
9. BRADY J. V. 1968. Potentiating operations. Neurosci. Res. Progr. Bull. 6: 19–21.
10. BREGADZE A. N. 1937. Elaboration of individual reaction to complicated count in dogs (in Russian). Tr. Inst. Fiziol. 3: 415–430.
11. CAGGIULA, A. R. 1970. Analysis of the copulation-reward properties of posterior hypothalamic stimulation in rats. J. Comp. Physiol. Psychol. 70: 399–412.
12. CAMPBELL, B. A. 1960. Effects of water deprivation on random activity. J. Comp. Physiol. Psychol. 53: 240–241.
13. COONS E. E. 1963. Motivational correlates of eating elicited by electrical stimulation in the hypothalamic feeding area. Ph. D. Thesis. Yale University.
14. DELGADO, M. R. 1971. Mozg i soznanie. Izdat. Mir, Moscow. 263 p.
15. DOSTALEK C. 1964. Rückläufige Bedingte Verbindungen. Verlag Czech. Akad. Wiss., Praha. 105 p.
16. DZHAVRISHVILI, T. D. 1956. On bidirectional temporary connections (in Russian). Trudy Inst. im. Beritashvili 10: 163–187.
17. FEDOROV, V. K. 1955. Fiziologicheskie osobenosti dvigatel'nogo analizatora sobaki. Izdat. Meditsina, Leningrad. 120 p.
18. FINGER, F. W., REID, L. S. and WEASNER, M. H. 1960. Activity changes as a function of reinforcement under low drive. J. Comp. Physiol. Psychol. 53: 385–387.
19. GALLISTEL, C. R. 1969. Self-stimulation: failure of pretrial stimulation to affect rats electrode preference. J. Comp. Physiol. Psychol. 69: 722–729.
20. GOTSIRIDZE, A. M. 1965. Ordinal conditioned reflexes to cessation of stimulation (in Russian). Zh. Vyssh. Nerv. Deyat. 15: 982–986.
21. GROSSMAN, S. P. 1968. Drive centers and drive state. Neurosci. Res. Progr. Bull. 6: 50–57.
22. HOLST, E. von and SAINT PAUL, U. 1963. On the functional organization of drives. Anim. Behav. 11: 1–20.
23. HULL, C. L. Behavior postulates and corollaries. Psychol. Rev. 57: 173–180.
24. JASPER, H. H. and SHAGASS, C. 1941. Conditioning of the occipital alpha-rhythm in man. J. Exp. Psychol. 28: 373–388.

25. KONORSKI, J. 1967. Integrative activity of the brain. Univ. Chicago Press. Chicago. 531 p.
26. KUPALOV, P. S. 1949. On the mechanisms of the processes of conditioned excitation (in Russian). Fiziol. Zh. SSSR, 35: 582–591.
27. MAGNUS, R. 1924. Körperstellung. J. Springer, Berlin. 740 p.
28. MENDELSON, J. 1966. The role of hunger in T-maze learning for food by rats. J. Comp. Physiol. Psychol. 62: 341–353.
29. MILLER, N. E. 1957. Experiments on motivation. Science 126: 1271–1278.
30. MILLER, N. E. 1968. The relationship between drive and learning. Neurosci. Res. Progr. Bull. 6: 58–62.
31. MORGAN, C. T. 1950. Physiological psychology. McGraw Hill Book Co., New York, 609 p.
32. MORGANE, P. J. and JACOBS, 1969. Hunger and satiety. Word Rev. Nut. Diet. 10: 100–213.
33. NISSEN, N. W. 1954. The nature of drive as an innate determinant of behavioral organization. Nebraska Symp. on Motivation 2: 281–320.
34. PANKRATOV, M. A. 1955. Functional method study of localizations in cerebral cortex (in Russian). Uch. Zap. Gos. Pedagog. Inst. Gertsena (Leningrad) 108: 27–43.
35. PAVLOV, I. P. 1949. Polnoe sobranie trudov. Vol. III. Izdat. AN SSSR, Moscow.
36. POPOVA, A. 1974. The effect of exercise on the selective display of instrumental reaction. Acta Neurobiol. Exp. 34: 93–97.
37. RABINOVICH, M. Ya. 1963. Electrical responses of different layers of the cerebral cortex during acquisition of conditioned reflexes (in Russian). Ph. D. Thesis. Inst. Vyssh. Nerv. Deyat. Neurofiziol. Moscow.
38. ROBERTS, W. W. 1968. Central nervous system: species-specific behavior and drive. Neurosci. Res. Progr. Bull. 6: 37–44.
39. SCHASTNY, A. I. 1971. Slozhnye formy povedeniya antropoidov. Izdat. Nauka, Leningrad. 186 p.
40. SECHENOV, J. M. 1935. Izbranye trudy. Izdat. Inst. Exp. Med., Moscow. 389 p.
41. SHERRINGTON, C. S. 1906. The integrative action of the nervous system. C. Scribner's, New York. 433 p.
42. SHULGINA, G. I. 1968. Reaction of cortical units in the rabbit at early stages of defensive conditioning to stimuli of different modalities (in Russian). Zh. Vyssh. Nerv. Deyat. 18: 565–573.
43. SHULGOVSKI V. V. and KOTLYAR B. I. 1968. Dynamics of unit activity of the visual and motor cortex in the process of formation of a conditioned defensive dominant (in Russian). Zh. Vyssh. Nerv. Deyat. 18: 799–806.
44. SHUSTIN, N. A. 1959. Fiziologia lobnykh doleï golovnogo mozga. Medgiz, Moscow. 222 p.
45. SKIPIN, G. V. 1947. O mechanizme obrazovaniya uslovnykh pishchevykh refleksov. Sovetskaya Nauka, Moscow. 139 p.
46. TEITELBAUM, P. 1968. Can studies of feeding centers provide a model for drive? Neurosci. Res. Progr. Bull. 6: 45–49.
47. VALENSTEIN, E. S. 1970. Stability and plasticity of motivation systems. *In* G. C. Quarton, T. Melnechuk, F. O. Schmitt (ed.), The neurosciences. Rockefeller Univ. Press, New York, 1068 p.
48. VATSURO, E. G. 1967. Uslovnye refleksy na specificheskie pishchevye razdrazhiteli. Osobaya forma vremenoï svyazi. Izdat. Meditsina, Leningrad. 204 p.

49. VORONIN, L. G. 1952. Analiz i sintez slozhnykh razdrazhiteleï u vysshikh zhivotnikh. Medgiz, Leningrad. 200 p.
50. WYRWICKA, W. 1966. The role of the alimentary center in motor conditioned reflexes. *In* E. A. Asratyan (ed.), Nervnye mechanismy dvigatel'noï deyatel'nosti. Izdat. Nauka, Moscow, p. 346–351.
51. ZELENY, G. P., VISOTSKY, N., DOBROTINA, G., IRZHANSKAYA, K., MEDYAKOV, F., NAUMOV, S., POLTYREV, S. and TUNTSOVA E. 1937. Forms and means of forming associated reflex (in Russian). Trans. Biochem. Pharmacol., Tbilisi, p. 165–171.

Received 7 July 1972

E. A. ASRATYAN, Institute of Higher Nervous Activity and Neurophysiology, Academy of Sciences of the USSR, 48 Pyatnitskaya, Moscow, USSR.