

INTERACTION OF BRAIN MACROSTRUCTURES IN THE BEHAVIOR ORGANIZATION PROCESS

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The degree of functional specialization of the brain structures which participate in the behavior of the higher mammals remains a subject of intense discussion, in which two extremel points of view have been defined. The concepts of McLean [30], who has rigidly confined certain forms of behavior to strictly defined brain formations, may serve as an example of one of these points of view. Another leading investigator of the limbic system, Isaacson [26], maintains a diametrically opposite viewpoint. According to Isaacson, there "do not exist single anatomical formations for single behavioral functions, as there do not exist single behavioral functional which can be confined to anatomical brain formations". Some authors seek a way out of this theoretical cul-de-sac, which has been engendered by the extreme contradictoriness of the experimental facts, in the quasiholographic principle of the distribution of functions, a contemporary version of classical equipotentialism.

It occurs to me that Wilkies, who in her report at the Seventh International Congress on Scientific Logic at Salzburg (1983) came to the conclusion that the lack of success in imposing mental and behavioral functional on local brain structures is governed by an inadequate choice of the functions themselves (see [7]; emphasis added, P. S.), is much closer to the truth. After all, the structure and function of the brain were formed in the channel of a single evolutionary process, under the influence of the very same factors, much as the formation of the structure and functions of the human hand, the larynx, capable of articular speech, or the skeleton, suited to erect gait, took place. It is another matter that we not infrequently try to ascribe to the brain operations which are appropriated more from technical and logical schemata than from the true history of its biological and socio-cultural development.

The data of neuropsychology also attest to the specificity of the functions of brain macrostructures: Tsvetkova writes, "The functional systems of the brain, which are complex dynamic formations resting on the operation of individual (sometimes located far from one another territorially) brain segments, each of which fulfills its specific role by bringing to the operation of whole functional system its specific contribution, are the material substrate, the psychophysiological base of the higher psychological functions" [19, p. 52].

In defining behavior as the form of life activity which changes the probability and duration of contact with an external object which is capable of satisfying a need existing in the organism, we have attempted to "lay on" to the structural-functional "canvas" of the real brain the dynamics of two factors which have decisive significance for the organization of behavior: the presence of needs which are actual at the given moment, and the assessment of the possibility of their satisfaction through interaction with the external environment [16].

The experimental facts obtained in our laboratory, and equally those drawn from the literature, have shown that the functions of the four brain formations, whose conjoint activity carries out an assessment of signals arriving from the external environment and determines the choice of the corresponding reactions, agree precisely with such a conception of the organization of behavior. We have in mind the hypothalamus, the nuclei of the amygdaloid complex, the hippocampus, and the anterior divisions of the neocortex.

Since structures associated with the actualization of needs and with the emergence of the emotions have been found in the hypothalamus, it can be said that the hypothalamus

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at a minimum participates twice, both in the earlier stages of the organization of behavior, and at its latest stages, when the somatic and vegetative components of the externally realizable behavioral act are formed. According to the data of Mikhailova and Kuliev, obtained in our laboratory, there are two types of neurons in the lateral hypothalamus of rats. The activity of neurons of the first type reaches a maximum at an intensity of electric current stimulation which elicits the motivational effects of food, drink, gnawing, etc., and depends on the degree of deprivation of food (drink). The activity of neurons of the second type is maximal at an intensity of current capable of eliciting a reaction of self-stimulation, and in a significant proportion of these neurons, does not depend on the state of motivation. The data obtained indicate that motivations and emotions are associated with various cellular elements of the hypothalamus, and possess relative independence.

Although the hypothalamus is, as it were, among the "sources" of the behavioral act, its activity is secondary in relation to the need-motivational mechanisms of the underlying divisions of the brain, and represents a relatively high level of integration. Neurons have been found in the monkey hypothalamus which react to the sight only of water, or only of food. The latent period of the neurons which react to the sight of food is 150-200 msec, while the latent period of the neurons which react to the ingestion of food is 300 msec [42]. Visual information about food reaches the hypothalamus via the temporal cortex and the amygdala [41].

The degree of hunger arousal has proven to be the decisive factor for the involvement of the structures of the hypothalamus in the learning process and in the reaction to external objects. Pavlov precisely defined the initiating role of this arousal in the food-procuring behavior of animals: "It is perfectly clear that the first impetus (emphasis added, P. S.) toward the activity of this alimentary center, which compels the animal to move, to get food, to secrete saliva and gastric juice, comes from the chemical composition blood of an animal which has not eaten for several hours, whose blood is gradually rendered "hungry" [9, p. 148]. Neurons responding to the sight and smell of food, to the sight of a syringe with glucose, or to a nut-shell, were found only in the lateral hypothalamus of hungry monkeys, and the administration of glucose reduced the reactions of the neurons to these natural food stimuli [21]. Hypothalamic neurons sensitive to the administration of glucose are involved in food-procuring behavior: their activity sharply increased in monkeys for 2-0.8 sec before pressing a bar to get food [35], and was suppressed at the time of pressing. Neurons insensitive to the administration of glucose, on the contrary, increased their activity during the performance of the motor reactions. This makes it possible to regard the neurons of the first type as belonging to the system which excites and motivates behavior. It is more appropriate to associate the neurons of the second type with the performance of the motor act, with the anticipation of imminent reinforcement, and with the emotions [20]. It is felt that the neurons of the lateral hypothalamus mainly participate in the discrimination of food and non-food objects, and in the initiation of food-procuring behavior [38]. A portion of the glucose-sensitive neurons alter their impulse activity in response to the conditioning signal; the majority, to reinforcement by food [20].

In comparison with the hypothalamus, the functions of the second brain formation, concerned with the discharge of the "motivational" nuclei of the amygdaloid complex, depend to an even greater degree on factors of the external environment and of the available situation for the satisfaction of present needs. The regulation of body mass, the need for food and water, the reactions to the level of blood glucose and to the duration of alimentary deprivation are not altered after damage to the amygdala. Its preservation is more important for appetite, for the distinction between palatable and non-palatable, new and familiar food, i.e., for response to exteroceptive alimentary stimuli, including during the period following brief alimentary deprivation, when metabolic shifts have still not arisen within the organism [48]. Rats with destruction of the basolateral nucleus of the amygdala lose the ability to avoid the utilization of a solution which is unpalatable for intact rats [42]. The preeminent association of the function of the amygdala with external, and not with internal motivating stimuli agrees well with the features of its morphological associations. The amygdala forms powerful pathways to the hypothalamus, and weaker ones from it, together with well-developed pathways from the frontal and temporal zones of the neocortex. As distinct from the ancient afferent input from the side of the brain-stem through the posterior nuclei of the thalamus, the pathway through the cortex evolves parallel with the development of the neocortex [6]. The neurons of the amygdala which respond to the pre-

sentation to a monkey of the face of another monkey or a person have a more prolonged latent period (110-220 msec) than analogous neurons in the temporal cortex (90-140 msec), and respond to the presentation of different faces more selectively [28]. In the system which codes and extracts emotionally significant information, which includes the prefrontal cortex, the amygdala, and the mediodorsal thalamus, it is the amygdala precisely which has the leading role [46].

Gloor [24], in summarizing the available data on the functions of the amygdala and its role in the organization of behavior, concludes that "the main effect elicited by damage to the amygdala can be described as disruption of the motivational mechanism, which makes it possible in the norm to select behavior acquired in the given situation." The amygdala is required for the re-structuring of behavior in accordance with the changed conditions of reinforcement. In accepting this conclusion, it is necessary to specify that the amygdala is relatively indifferent to the probability of reinforcement, to its informational component. Pigareva [12] developed alimentary conditioned reflexes (CR) in rats after bilateral destruction of the amygdalas. It was found that the rate of development of the reflexes in these animals did not differ from the analogous indices in intact rats, with neither high (100% and 50%) nor low (25%) probability of reinforcement. Only a probability of 33%, for which case the appearance of the maximal emotional tension is characteristic, is accompanied by some slowing of the process of CR formation.

Bilateral destruction of the amygdalas does not prevent the development of either alimentary or defensive CRs in rats. According to the data of Russell and Thompson [43], the amygdala does not play a substantial role in the development of the nictitating membrane CR to tone in rabbits. However, the picture changes radically in the case of the competition of co-existing motivations, when the singling out of the dominating need relevant to priority satisfaction becomes necessary. The development of conditioned reflex switching of heterogeneous reflexes by the method of É. A. Asratyan, in which one and the same signal (sound, in Pigareva's experiments) is reinforced by food in the morning, but by painful stimulation in the evening, may serve as a good experimental model in this situation. Bilateral destruction of the amygdalas did not permit the achievement of switching over the course of 40 days. The development of switching was found to be possible only with the combination of weak painful stimulation with high alimentary excitability, or, on the contrary, with the combination of brief alimentary deprivation with strong painful reinforcement of the defensive reflex.

The many defects of conditioned reflex activity and natural behavior which arise after damage to the amygdala can be explained precisely by the competition of motivations. Thus, the conclusion that the amygdala belongs to the system of structures which determine behavior choice, can be accepted with the specification that the amygdala participates in this choice by "weighing" the competing emotions engendered by competing needs. The amygdala is involved in the process of behavior organization at the comparatively late stages in this process, when the actualized needs are already compared with the prospect of their satisfaction, and are transformed into the corresponding emotional states.

The prediction of the probability of need satisfaction (probability of reinforcement) is achieved with the participation of the preeminently "informational" brain structures, the hippocampus and the anterior divisions of the neocortex. Generalizing the experimental data, as numerous as they are contradictory, the majority of authors conclude that the hippocampus mediates not one of the functions, but accomplishes the processing of the information necessary for the fulfillment of many functions [47]. The hippocampus is critically necessary for the formation of conditioned associations between stimuli which are substantially dispersed in time [40]. It is supposed that the "working" (recent, intermediate) memory is the chief function of the hippocampus, independent of whether it is a matter of spatial or temporal material [37], and that these functions are similar in man and the higher animals [44].

The hippocampus is involved in learning in its earliest stages. It should be noted that destruction of the dorsal and ventral hippocampi in rats does not disrupt their capacity for learning and even facilitates the development of conditioned reflex switching. In Pigareva's experiments [12], after 10 days of unsuccessful attempts to develop switching of defensive and alimentary CRs in rats, bilateral hippocampectomy led in the course of two weeks to the formation of stable conditioned reflex switching. The most glaring defect of the hippocampectomized animals was found to be their sensitivity to situations

with low probability of reinforcement of conditioned signals. According to Pigareva's [12] data, with a probability of reinforcement of alimentary CRs of 100% and 50%, even though the hippocampectomized rats lag behind intact rats, they nonetheless cope with their task. The development of CRs at a probability of 33% and 25% was found unattainable for them. The dropping out of reactions to signals with low probability of reinforcement leads to the fact that hippocampectomized rats exceed control rats in distinguishing signals with different reinforcement probabilities, a particular case of this being the facilitation of conditioned reflex switching in these animals.

As it is a structure in which motivational arousal from the posterior and anterolateral hypothalamus is compared with information arriving from the external environment (through the septum), as well as with the traces of previously accumulated experience (through the temporal cortex), the hippocampus evidently fulfills a dual function. Firstly, it plays the role of an input filter of information which is or is not relevant in long-term memory [5]. Secondly, the hippocampus participates in the extraction of traces from memory under the influence of motivational arousal for utilization in the organization of on-going behavior [25]. Teylor and Di Scenna [49] attempted to unite these two functions of the hippocampus within the framework of a single theoretical model, according to which "indexes" are maintained in the hippocampus of various cortical zones, in whose modules are fixed earlier acquired experience. The authors compare the role of these cortical modules with the letters of the alphabet of the natural languages. We should emphasize that traces can be extracted from memory independent of external stimuli, and can afford selective expectation of stimuli by the mechanism of tonic conditioned feed-back [3].

In the opinion of Batuev [4], motivational arousal spread from the limbic system to the frontal, and particularly the parietal, cortex information regarding the external environment reaches the associative systems of the neocortex through the associative nuclei of the thalamus, and by a transcortical pathway from the sensory projection zones. On the basis of the information received, and of engrams extracted from memory, the frontal cortex constructs a probabilistic prognosis, while the thalamoparietal system provides selective attention to the significant factors of the external environment and to the leading links of the imminent motor act. In other words, the parietal cortex effects the confinement of the motor reaction to the spatial organization of the external world.

The decisive significance of the anterior divisions of the neocortex for the prognostication of the probability of imminent events has been established in rats, cats, dogs, monkeys, and man. It must be emphasized that in contrast to the hippocampus, whose preservation is necessary for the support of reactions to signals with low reinforcement probability, the frontal cortex is important for the organization of behavior in response to signals of highly probable events. After removal of the frontal divisions of the neocortex in rats and dogs, the significance of frequently and rarely reinforced conditioned signals become, as it were, equal: all the signals become effective to the same degree [2, 13].

According to the data of Meerson [8], in man, not only the frontal, but also posterior, primarily the anterior temporal, divisions of the cortex, participate in probabilistic prognostication, with the left cerebral hemisphere discriminating highly probable events and fixing the regularity of the appearance of signals, and the right appraising the indefiniteness of the milieu and predicting slightly probable events.

Pigareva [13] followed the dynamics of the development of alimentary CRs in rats with various reinforcements before and after the destruction of the anterior divisions of the neocortex. It was found that the process of formation of CRs slows down with the high probability of reinforcement, and speeds up with low probability. In other words, signals with different probabilities of reinforcement by food become identically effective. This results is all the more interesting in that, judging by the data in the literature, the frontal regions of the cerebral cortex of rats do not differ with respect to their basic functions from the frontal cortex of the higher vertebrates, including the primates [27]. The preeminent relationship of the dorsolateral divisions of the frontal cortex to the "informational" system of the brain formations, and of the mediobasal divisions to the "motivational" system, agrees well with the anatomical associations of these two parts of the frontal neocortex: the dorsal portion with the hippocampus, and the ventral, with the amygdala [33]. Motivating influences reach the frontal cortex from the lateral hypothalamus [17, 39]. The neurons which react to the absence of reinforcement during the accomplishment of instrumental reactions, are localized in the medioventral zones of the prefrontal cortex of monkeys

[34]. Thus, the anterior divisions of the neocortex are found to be implicated also in the programmed behavioral act, and in the assessment of its results. "Limbic" memory must be distinguished as the active extraction of information necessary for the satisfaction of a need, and as the phenomenon of recall which is limited by the choice of a familiar stimulus from those presented. The latter mechanism is not undergone until the memory is stored in the temporal cortex [29].

In completing this review of the functions of the anterior divisions of the neocortex, the hippocampus, amygdala, and hypothalamus, we conclude that the interaction of these four structures is found to be necessary and sufficient for the organization of behavior in the system of coordinates: "needs-probability of their satisfaction in the external environment." All the remaining brain formations, whether the sensory systems, the mechanisms of constructing movements (pyramidal and extrapyramidal), or the systems of regulating the level of wakefulness and the vegetative functions, play an actuating or auxiliary role. With regard to the other structures of the limbic system, the septum is so closely associated with the hippocampus that the majority of investigators prefer to speak of a single septo-hippocampal system. The central gray substance is specifically associated with the assessment of the aversiveness of stimuli, with the organization of the avoidance reactions, such as with the stimulation of the medial hypothalamus [45]. The nonspecific thalamus serves as the site of convergence of the sensory and motivational impulses [22]; its significance does not go beyond the functions of transmission and relay. In other words, it is precisely the above-enumerated four structures which determine to which external stimuli and with what behavioral reaction at each given moment the living organism will respond.

According to the opinion of Mogenson, et al. [31], the association of the limbic system with motor system is accomplished through the ventral division of the tegmentum of the midbrain and projections of the adjacent globus pallidus. With this the dorsocaudal portion of the globus pallidus is directly linked with the planning and execution of movement, while the ventrorostral portion is directly linked with the transmission of motivational information to the motor system [36]. With regard to the coordinative activity of the "decision making" structures, the thought of Ukhtomskii, that "the coordination of the physiological apparatuses in the order of their nervous interrelationship is an obligatory process and does not presume the interference of any supplementary, special 'coordinating center'" [18, p. 127] is entirely germane.

Having successively considered the functional specialization of the individual brain structures, let us try to represent the dynamics of their interaction as a whole (Fig. 1).

The schema generalizes the factual material obtained primarily in the investigation of food-procuring, drinking, sexual, and similar types of behavior. The involvement of brain structures in the process of the organization of defensive behavior has its own peculiarities, as follows from the studies of Adrianov [1], Popova [14], et al.

Internal (metabolism) and external (pain, smell, etc.) excitatory unconditioned stimuli activate the motivational structures of the hypothalamus, which in their turn activate the hippocampus, the amygdala, and the anterior division of the neocortex. Due to the hippocampus, a wide circle of external stimuli enhances the dominant state characteristic for the generalization stage of the CR [10]. In the case of the coincidence of these stimuli with the effect of the reinforcing unconditioned stimuli, the hippocampus proves to be the first meeting place of the combined afferentations. With the appearance in the motivational brain structures of a dominant state diagnosable according to the features described by Ukhtomskii, of one to a maximum of two combinations of an external stimulus with the cessation of the dominant, this is sufficient for the formation of a firm two-way temporal association [11]. If this stimulus elicits a motor reaction, the re-appearance of the dominant state leads to the realization of a reaction discontinuing the given state, which one can regard as a truly voluntary movement, i.e., determined by the internal state of the animal. The enumerated experimental facts prompted Palygina to separate out a special class of endogenous CRs, distinct from the classical and from the instrumental.

In the formation of the behavioral act, as the result of the conjoint activity of the hippocampus and the frontal cortex those external stimuli or their engrams are selected which were previously accompanied by the satisfaction of the given need.

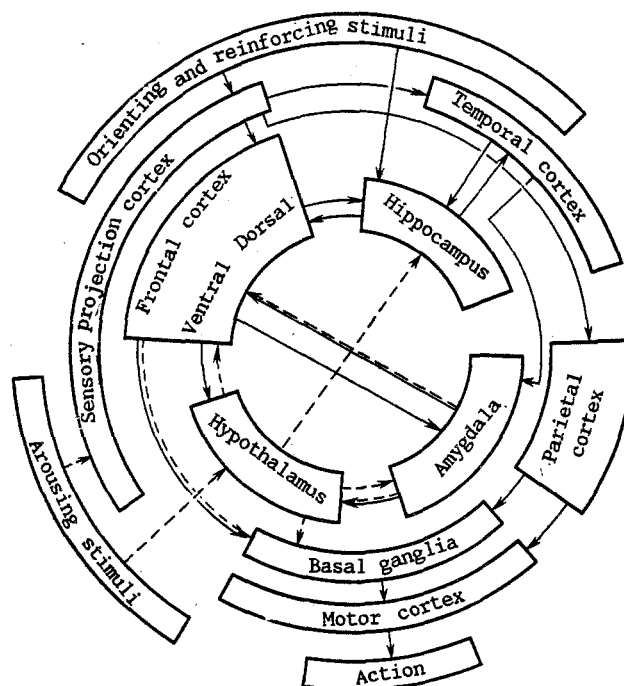


Fig. 1. Schema of the sequential and parallel involvements of the brain structures in the organization of the behavior act. Solid lines) "informational" (emotionally neutral) afferentation; interrupted lines) motivational influences; double lines) emotionally colored afferentation. Explanation in text.

Through a comparison of the motivational excitation with the present stimuli and engrams extracted from memory with the participation of the temporal cortex, emotional coloring of such stimuli and engrams forms in the amygdala, which leads to the singling out of a dominating motivation relevant to priority satisfaction.

The program of action taking shape in the frontal cortex reaches the basal ganglia, where, through interaction with the parietal cortex, it is "inscribed" in the spatial coordinates of the imminent action. Recording of evoked potentials has shown that at the stage of the formation of the CR the parietal cortex is associated primarily with the cortical representatives of the sensory system, and as stabilization occurs, with the motor cortex [15]. Changes in neuronal activity of the corpus striatum, the globus pallidus, and the substantia nigra precede movements, and arise in response to external sensory stimuli only in those cases in which these stimuli and movements have behavioral significance [23]. The authors conclude that the initiation of motor acts is mediated by the activity of the basal ganglia, and the frontal cortex associated with them. From the fronto-striatal system, excitation reaches the effector organs which realize the goal-directed behavior through the motor cortex.

Naturally, the depicted schema of events, which play out sequentially and in parallel in the higher divisions of the brain, is general in character, and requires future refinement and experimental confirmation in application to various mammalian species. In addition, it offers the possibility of examining the integrative activity of the brain as a whole and does not contradict the available factual data and anatomically traced associations between structures. We can treat this activity without leaving physiological soil and without recourse to concepts borrowed from other fields of knowledge, such as "aim", "modelling of the external world," "decision making", and the like.

LITERATURE CITED

1. O. S. Adrianov, "The structural-functional bases in complex forms of higher nervous activity," *Zh. Vyssh. Nervn. Deyat.*, 36, 2, 265 (1986).

2. L. N. Andreev, "On the question of the mechanism of hyperactivity in lobectomized and caudatectomized animals," *Zh. Vyssh. Nervn. Deyat.*, 19, 6, 1082 (1969).
3. É. A. Asratyan, "The two-way connection as a general neurophysiological principle," *Zh. Vyssh. Nervn. Deyat.*, 31, 1, 3 (1981).
4. A. S. Batuev, *The Higher Integrative Systems of the Brain* [in Russian], Nauka, Leningrad (1981).
5. O. S. Vinogradova, *The Hippocampus and Memory* [in Russian], Nauka, Moscow (1975).
6. O. S. Gonchar, *The Organization of Afferent Inputs in the Amygdaloid Complex of the Cat*, Abstract of Dissertation for the Degree of Doctor of Biological Sciences, Kiev (1984).
7. V. Zh. Kelle, I. Z. Naletov and E. N. Sokolov, "The philosophical bases of psychology and the social sciences," *Vopr. Filos.*, 2, 34 (1984).
8. Ya. A. Meerson, "On the role of the left and right cerebral hemispheres in the processes of probabilistic prognostication," *Fiziol. Cheloveka*, 12, 5, 723 (1986).
9. I. P. Pavlov, *Complete Collected Works* [in Russian], Vol. 3, Book 1, Izd. AN SSSR, Moscow, Leningrad (1951).
10. R. A. Palygina, "The dominant and the conditioned reflex at the stage of generalization," *Zh. Vyssh. Nervn. Deyat.*, 23, 4, 687 (1973).
11. R. A. Palygina, "The dominant and its significance in the behavior of an animal," *Usp. Fiziol. Nauk*, 13, 2, 31 (1982).
12. M. L. Pigareva, *The Limbic Switching Mechanisms (Hippocampus and Amygdala)* [in Russian], Nauka, Moscow (1978).
13. M. L. Pigareva, *The Experimental Neuropsychology of the Emotions*, Abstract of Dissertation for the Degree of Doctor of Biological Sciences, Institute of Molecular Genetics of the USSR Academy of Science, Moscow (1983).
14. N. S. Popova, *Systemic Analysis of Intercentral Integration* [in Russian], Meditsina, Moscow (1983).
15. N. S. Popova, G. N. Gneushev, and V. I. Derevyagin, "Evoked potentials of brain structures during the formation of the avoidance reactions," *Zh. Vyssh. Nervn. Deyat.*, 32, 1, 10 (1982).
16. P. V. Simonov, "Need-information organization of brain activity," *Zh. Vyssh. Nervn. Deyat.*, 29, 3, 467 (1979).
17. K. V. Sudakov, *Biological Motivations* [in Russian], Meditsina, Moscow (1971).
18. A. A. Ukhtomskii, *Outline of the Physiology of the Nervous System*, Collected Works [in Russian], Vol. 4, Izd. AN SSSR, Moscow, Leningrad (1954).
19. L. S. Tsvetkova, "The psychological potentials of man and problems of training," *Kommunist.*, 11, 49 (1986).
20. S. Aou and Y. Oomura, "Behavioral significance of monkey hypothalamic glucose-sensitive neurons," *Brain Res.*, 302, 1, 69 (1984).
21. M. Burton, E. Rolls, and F. Mora, "Effect of hunger on responses of neurons in the lateral hypothalamus to the sight and taste of food," *Exp. Neurol.*, 51, 3, 668 (1976).
22. K. Casey and J. Keene, "Unit analysis of the awake animal," in: *Brain Unit Activity during Behavior*, S. Thomas, Springfield (1973), p. 115.
23. E. Evarts, M. Kimura, R. Wurtz, and O. Nikosaka, "Behavioral correlates of activity in basal ganglia neurons," *Trends Neurosci.*, 7, 11, 447 (1984).
24. P. Gloor, "Amygdala," in: *Handbook of Physiology. Neurophysiology*, Vol. 2, Amer. Physiol. Soc., Washington, D.C. (1960), p. 1395.
25. R. Hirsh, "The hippocampus and contextual retrieval of information from memory: a theory," *Behav. Biol.*, 12, 4, 421 (1974).
26. R. Isaacson, "Limbic system contributions to goal-directed behavior," in: *Neural Mechanisms of Goal-Directed Behavior and Learning*, Acad. Press, N.Y. (1980), p. 409.
27. B. Kolb, "Functions of the frontal cortex of the rat: a comparative review," *Brain Res.*, 8, 1, 65 (1984).
28. C. Leonard, E. Rolls, F. Wilson and G. Baylis, "Neurons in the amygdala of the monkey with responses selective for faces," *Behav. Brain Res.*, 15, 2, 159 (1985).
29. B. Malamut, R. Saunders and M. Mishkin, "Monkeys with combined amygdala-hippocampal lesions succeed in object discrimination learning despite 24-hour intertrial intervals," *Behav. Neurosci.*, 98, 5, 759 (1984).
30. P. McLean, "The limbic brain relation to the psychoses," in: *Physiological Correlates of Emotion*, Acad. Press. London (1970), p. 129.

31. G. Mogenson, D. Jones and Yim Chi Yiu, "From motivation to action: functional interface between the limbic system and the motor system," *Prog. Neurobiol.*, 14, 2-3, 69 (1980).
32. F. Mora, E. Rolls and M. Burton, "Modulation during learning of the responses of neurons in the lateral hypothalamus to the sight of food," *Exp. Neurol.*, 53, 2, 508 (1976).
33. W. Nauta, "Neural associations of the frontal cortex," *Acta Neurol.*, 32, 125 (1972).
34. H. Niki, "Reward-related and error-related neurons in the primate frontal cortex," in: *Learning and Memory Drugs Reinforced*, Elsevier, Amsterdam (1982), p. 22.
35. H. Nishino, T. Ono, K. Sasaki and K. Muramoto, "Characteristics of glucose-sensitive neurons in monkey feeding center," *J. Physiol. Soc. Jpn.*, 41, 8-9, 316 (1979).
36. H. Nishino, T. Ono, K. Muramoto, et al., "Movement and non-movement related pallidal unit activity during bar press feeding behavior in the monkey," *Behav. Brain Res.*, 15, 1, 27 (1985).
37. D. Olton, J. Becker, and G. Handelman, "Hippocampus, space, and memory," *Behav. Brain Sci.*, 2, 313 (1979).
38. T. Ono, "Responses of lateral hypothalamus and amygdala to food and non-food stimuli," in: *Integrative Control Function of the Brain*, Vol. 3, Elsevier, Tokyo-Amsterdam (1981), p. 323.
39. Y. Oomura and M. Takigama, "Input-output organization between the frontal cortex and the lateral hypothalamus," in: *Mechanisms in Transmission of Signals for Conscious Behavior*, Elsevier, Amsterdam (1976), p. 163.
40. J. Rawlins, "Associations across time: the hippocampus as a temporary memory store," *Behav. Brain Sci.*, 3, 3, 479 (1985).
41. E. Rolls, "The neurophysiology of feeding," *Int. J. Obesity*, 8, Suppl. No. 1, 139 (1984).
42. B. Rolls and E. Rolls, *Thirst*, Cambridge University Press, Cambridge (1982).
43. R. Russell and R. Thompson, "Amygdaloid unit activity during classical conditioning of the nictitating membrane response in rabbit," *Physiol. Behav.*, 32, 4, 527 (1984).
44. U. Saghal, "Functions of the hippocampal system," *Trends Neurosci.*, 3, 5, 116 (1980).
45. G. Sander, P. Schmitt, and P. Karli, "Effect of medial hypothalamic stimulation inducing both escape and approach of in rat mesencephalon," *Physiol. Behav.*, 29, 2, 269 (1982).
46. M. Sarter and H. Markowitsch, "Involvement of the amygdala in learning and memory: a critical review, with emphasis on anatomical relations," *Behav. Neurosci.*, 99, 2, 342 (1985).
47. N. Schmajuk, "Psychological theories of hippocampal function," *Physiol. Psychol.*, 12, 3, 166 (1984).
48. Th. Schoenfeld and W. Hamilton, "Disruption of appetite but not hunger or satiety following small lesion in the amygdala of rats," *J. Comp. Physiol. Psychol.*, 95, 4, 565 (1981).
49. T. Teylor and P. Di Scenna, "The hippocampal memory indexing theory," *Behav Neurosci.*, 100, 2, 147 (1986).