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BRAIN MECHANISMS OF EMOTIONS

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At the 23rd International Congress of Physiological Sciences (Tokyo, 1965) the results of experiment led us to the conclusion that emotions were determined by the actual need and estimation of probability (possibility) of its satisfaction. Low probability of need satisfaction leads to negative emotions actively minimized by the subject. Increased probability of satisfaction, as compared to the earlier forecast, generates positive emotions which the subject tries to maximize, that is, to enhance, to prolong, to repeat. We named our concept the Need-Informational Theory of Emotions. According to this theory, motivation, emotion, and estimation of probability have different neuromorphological substrates. Activation through the hypothalamic motivatiogenic structures of the frontal parts of the neocortex orients the behavior to signals with a high probability of their reinforcement. At the same time the hippocampus is necessary for reactions to signals of low probability events, which are typical for the emotionally excited brain. By comparison of motivational excitation with available stimuli or their engrams, the amygdala selects a dominant motivation, destined to be satisfied in the first instance. In the cases of classical conditioning and escape reaction the reinforcement was related to involvement of the negative emotion's hypothalamic neurons, while in the course of avoidance reaction the positive emotion's neurons were involved. The role of the left and right frontal neocortex in the appearance of positive or negative emotions depends on these informational (cognitive) functions.

William James – the author of one of the first physiological theories of emotions more than a century ago – published a paper with a most remarkable title: "What is emotion?" [5]. Nevertheless, a hundred years after this question was formulated, we can find in the textbook *The Physiology of Man* the following revelation: "Despite the fact that each of us knows what emotions are, it is impossible to give the emotional state a precise scientific definition... At the present time there is no generally accepted scientific theory of emotions, nor any precise data concerning which centers emotions arise in, how they arise, or what their nervous substrate is" [15].

At the 23rd International Congress of Physiological Sciences (Tokyo, 1965), the results of psychophysiological experiments led me to conclude that human emotions were determined by some actual need and the estimation of the probability (possibility) of its satisfaction on the basis of phylo- and ontogenetic experience [16, 18]. The individual makes this estimation involuntarily (sometimes unconsciously) comparing information on the means and time that are predictably necessary for satisfaction of this need with the information at hand. A low probability of goal achievement leads to the negative emotions (fear, alarm, fury, grief, etc.) which are actively minimized by the subject. An increased probability of satisfaction, as compared to an earlier prognosis, generates positive emotions of pleasure, joy, and encouragement, which the subject tries to maximize, i.e., to intensify, continue, repeat. Attaching great importance to the estimation of the probability of need satisfaction in the genesis of emotions. I called this concept the "Need-Informational Theory of Emotions" [17].

In its most general form, the rule for the genesis of emotion may be presented as a structural formula:

$$E = f[-N(In - Ia)]$$

where E is emotion, its degree, quality, and sign; N is the power and quality of the actual need in the broadest sense of the word. For humans, it is not only vital needs like hunger, thirst, sex, but also diverse social and ideal (spiritual) needs including

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TABLE 1. Relationship between Motivating and Rewarding Stimulation of Lateral Hypothalamus

Behavior	Strength of current (mA)
Exploratory	0.05-0.01
Eating, drinking, gnawing, etc.	0.1-0.25
Consummatory behavior and self-stimulation	0.25-0.35
Self-stimulation	0.35-0.5

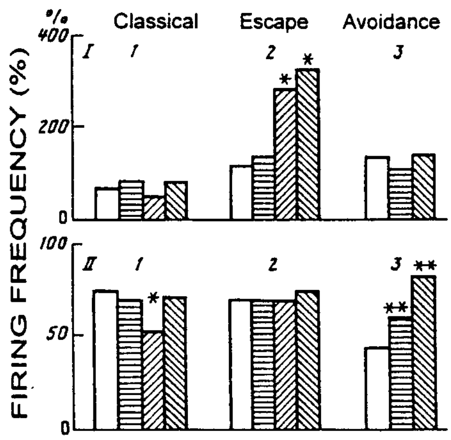

Fig. 1. Changes in spike frequency of lateral hypothalamus neurons during defensive CR.

the most complicated and haughty ones. ($In - Ia$) is the estimation of the probability (possibility) of need satisfaction on the basis of phylo- and ontogenetic individual experience. In – information about the means and time prognostically necessary for satisfaction of the need. Ia – information about the means and time available to the subject at a given moment. The term "information" refers to its pragmatic meaning, which can be determined as the change in probability of goal achievement.

The results of neurophysiological experiments show that needs, motivation, and emotions have different morphological substrate. Thus, upon stimulation of the areas of self-stimulation in the lateral hypothalamus by a gradually increasing electric current, the behavioral reactions of rats occur always in the same sequence. Weak stimulation elicits a generalized searching behavior that is not addressed to the objects in the chamber – food, water, lever for self-stimulation. The current increase elicits eating, drinking, gnawing behaviors. Further current increase elicits self-stimulation behavior with related motivational effects, and at the next stage – only self-stimulation takes place (Table 1).

In the zones of self-stimulation of the lateral preoptic area and lateral hypothalamus, neurons were recorded which specifically changed their activity in motivational and emotionally-positive states elicited by electric and natural stimuli and by change in the level of alimentary and water motivations. Neurons of the 2nd type (reinforcing), which were maximally activated during stimulation by the current eliciting self-stimulation, were also activated at satiation. Motivational and emotionally positive behaviors oppose each other and elicit reciprocal changes in the activity of the first and second types of neurons.

In the experiments of our collaborators N. G. Mikhailova and M. I. Zaichenko it was shown that neurons of these two types participate in a different way in the realization of classical and operant defensive conditioned reflexes in rats, in which the conditioned signal (light) correlated with the emotionally negative intracerebral stimulation of the dorsolateral tegmentum [7].

Figure 1 demonstrates changes in impulse activity of motivational (upper panel) and positively reinforcing (lower panel) neurons of the lateral hypothalamus during realization of conditioned defensive reflexes: classical, escape, and avoidance. The

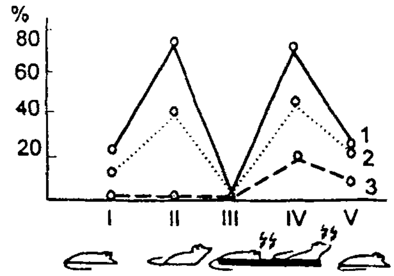

Fig. 2. Percentage of significant changes in coherence of electrical activity in the rat brain at different steps of self-stimulation. 1) Emotionally positive point of the hypothalamus – motor region of the neocorex; 2) emotionally negative point – motor neocortex; 3) motor neocortex – visual neocortex.

columns show the frequency of discharges 5 s before the conditioned stimulus, during the action of light, during combined light and current, and after switching off the stimuli. It can be seen that realization of classical conditioned reflex and reaction of escape were accompanied by intensification of activity in motivational neurons and suppression of spiking in the reinforcing ones.

Only a well-elaborated avoidance reaction, when the rat was not punished by electric current, led to an increase in activity in positively reinforcing neurons.

These data allow us to answer the question frequently discussed in the literature: What serves as a reinforcement in operant defensive reflexes? In the case of classical reflexes and reactions of escape, the emotionally negative state of fear serves as a reinforcement. Successful accomplishment of avoidance reaction involves a mechanism of positive emotions in the process of behavioral decision.

I have already noted above that the influence of emotions on behavior is determined by the animal's attitude to its emotional state, and is dominated by the principle of maximization of positive emotions and minimization of negative ones. This principle is accomplished via the influence of motivationally-emotional hypothalamic structures on the informational (cognitive) and motor-organizing neocortical areas, which is confirmed by analysis of the spatial synchronization of electrical activity in brain structures during self-stimulation in rats by a weak constant current [13]. Figure 2 shows the percentage of cases in which a significant coherence ($p < 0.05$) was observed in the alpha- and theta-frequency ranges when the potentials in the following brain structures were compared: 1) the emotionally positive point of the hypothalamus – the motor region of the cortex; 2) the emotionally negative point of the hypothalamus – the motor region of the cortex; 3) the motor cortex and the visual cortex. The analysis was carried out in the following behavioral states: I) calm state of the animal; II) immediately before pressing the lever; III) while pressing the lever; IV) the period of leaving the lever; V) after leaving the lever. In examining the graph, one can clearly observe that immediately before the lever pressing there is a sharp rise (by a factor of more than 3) in the percentage of cases in which there is a statistically significant coherent electrical activity in the emotionally positive point of the hypothalamus and the motor region of the cortex.

This increase in coherence demonstrates the readiness of nervous pathways for the spread of excitation along three channels of conditioned connections: from the initially stimulated emotionally positive point to the motor cortex and to the visual cortex, and also between the visual analyzer which receives the conditioned signal of future reinforcement (the sight of the lever, its location in the chamber, etc.) and the motor cortex, since it is the view of the lever which will direct the movement of the animal initiated by the trace arousal of the emotionally positive region.

While the rat is on the lever, the coherence decreases, and the animal receives reinforcement and becomes totally passive. Immediately before the rat leaves the lever, there is for the first time an increase in the coherence of the negative point and the motor region of the cortex: the excitation in the negative structures is ready for transformation into the motor reaction of avoidance. After the animal leaves the lever, the percentage of cases in which there is a statistically significant increase in coherence returns to its original value. Only traces of the emotionally negative state can still be seen on comparison of the electrical activity in the negative point with the motor region of the cortex.

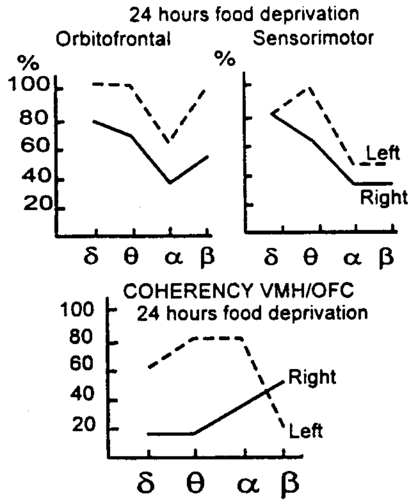

Fig. 3. Changes in spectral content after 24 hours food deprivation.

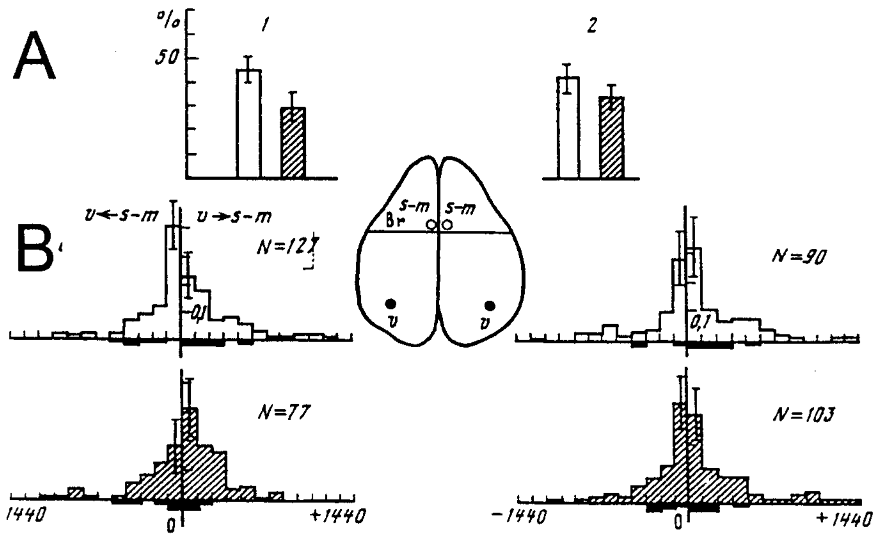

Fig. 4. Neocortical neurons with correlating activity in hungry and satiated rabbits.

R. A. Pavlygina and Yu. V. Lyubimova in their investigations [11, 12] have shown that the motivational influences of the hypothalamus on the neocortex are asymmetrical. In Fig. 3 (upper panel) are presented summated data showing a statistically significant decrease in values of spectral functions of electrical activity in the orbitofrontal and sensorimotor cortical regions of the right (solid line) and left (dashed line) hemispheres after 24 hours food deprivation of rabbits. The asymmetry is expressed not only in the prevailing activation of the left hemisphere but also in the intensification of interactions in the left hemisphere. The lower panel in Fig. 3 demonstrates a statistically significant increase in estimations of coherency in potentials in the ventromedial hypothalamus and the orbitofrontal cortex in the right (solid line) and left (dashed line) hemispheres of the rabbit in the state of hunger after 24 hours deprivation.

Interhemispheric asymmetry during natural alimentary motivation is revealed also by recording the spiking of individual neurons of the visual and sensorimotor regions of the rabbits' neocortex and by investigating interaction of these neurons [8].

In Fig. 4 the neural data are presented for the left (1) and right (2) hemispheres of the neocortex in hungry (open columns) and satiated (shaded columns) rabbits. In A the percentage of pairs of correlatively working neurons is shown. In B the probability of appearance of peaks (positive values) and gaps (negative values) in the corresponding bins of the cross-correlation histograms is shown (abscissa – time in ms; ordinate – probability). N is the number of histograms of cross-correlation. In the inset the location of the recording electrodes is shown.

TABLE 2. Effect of Amygdala Destruction on the Development of Conditioned Reflex Switching in Rats

Strength of current (mA)	Duration of food deprivation			
	one day		three days	
	groups of rats			
	intact	operated	intact	operated
0.4	4(0)	5(0)	8(2)	8(5)
0.6	5(2)	5(0)	8(4)	8(4)
0.8	5(3)	5(0)	5(5)	5(0)
1.0	5(4)	5(0)	5(3)	5(0)
1.2	7(5)	7(4)	6(4)	6(1)
1.4	8(3)	8(5)	6(3)	6(0)

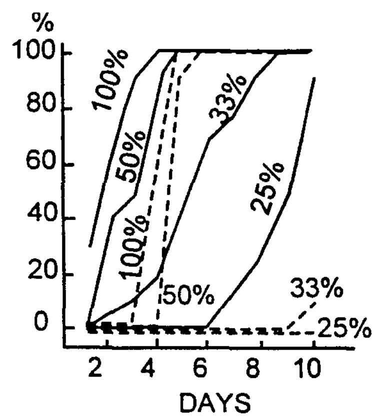

Fig. 5. Percentage of correct CR in control and hippocampectomized rats in conditions of different probability of reinforcement.

Judging by the neural impulsation, the left hemispheric cortex is more active in hungry rabbits and the right hemispheric cortex – in satiated ones. The most pronounced differences were observed in the neurons of frontal regions, and the least pronounced – in the sensorimotor neurons.

All the recent data suggest that the hypothalamus is the key structure for realization of the most ancient ***reinforcing function*** of emotions which serves for the solution of the universal behavioral task of maximization-minimization of the given emotional state and is expressed in behavior as approach or avoidance.

In comparison with the hypothalamus, the consumption of food and water and the response to blood glucose level during food deprivation are essentially unaltered after the amygdala lesions.

According to M. L. Pigareva [14], bilateral destruction of the amygdala does not prevent the development of either alimentary or defensive conditioned reflexes in rats. However, the picture changes radically in the case of competition between coexisting motivations, when it becomes essential to distinguish the dominant need for immediate satisfaction.

A good experimental model of such a situation is the elaboration of conditioned switching of heterogeneous conditioned reflexes by E. A. Asratyan's method [1] when the same conditioned signal (tone) in the morning is reinforced by food and in the evening – by noxious shock.

Judging from the percentage of correct defensive and feeding conditioned reactions, destruction of the amygdala in rats results in failure to achieve switching for a period of 40 days. Nevertheless, the solution of such a behavioral task is possible in the case of artificial creation of a sufficient imbalance between competing motivations and corresponding emotions: between hunger and fear.

The figures in Table 2 show the number of rats in each group, and the figures in brackets show the number of animals in which the conditioned switching was elaborated in 60 days (criteria of elaboration were three sessions in succession, in each a 100% fulfillment of either alimentary or defensive conditioned reflexes). The amygdalectomized rats managed to fulfill this task if a strong noxious stimulation is paired with 24 hours food deprivation, or, vice versa, a weak painful stimulation is applied against the background of hunger after a three-day deprivation. In other words, the amygdala plays a crucial role in the realization of ***trans-switching the behavior function*** of emotions, in the choice of motivation, which corresponds not only to one or another need, but to the external conditions of its satisfaction in the given context and at the very moment. The amygdala is involved in the process of behavior organization at comparatively late stages, when the actualized needs are already being compared with the possibility of their satisfaction and being transformed into the corresponding emotions.

As for the prediction of the probability of satisfying a need (probability of reinforcement), it is realized by the "informational" brain structures – the hippocampus and the frontal regions of the neocortex. The most striking defect in hippocampectomized animals turns out to be their sensitivity to situations with low probability of reinforcement of conditioned signals. When the probability of reinforcement of alimentary conditioned reflexes is 100% or 50%, the hippocampectomized rats (dashed lines) are less advanced than the intact ones (solid lines), but still realize the task (Fig. 5). The elaboration of conditioned reflexes when the probability of reinforcement is 33% to 25% turns out to be beyond their abilities. In the above-mentioned experiments with conditioned switching, the probability of reinforcement by food or tone is high in the morning tests and low in the evening ones, while the probability of reinforcement of the same tone by noxious stimulation is reciprocal.

As a result of ignoring the low probability of reinforcement by hippocampectomized rats after ten days of unsuccessful attempts to elaborate switching of defensive and alimentary conditioned reflexes in normal rats, bilateral hippocampectomy in two weeks led to formation of the stable conditioned switching in the same animals. Bilateral hippocampectomy not only facilitates elaboration of conditioned switching, but also eliminates signs of emotional tension in these animals, which was observed by recording the heart rate.

The property of the hippocampus to react to signals of low-probability events allows us to consider it a key structure for realization of the ***compensatory*** function of emotions, which helps to substitute for the lack of information. This function is manifested not only in the hypermobilization of the vegetative shifts (increased heart rate, rise in blood pressure, release of hormones into the blood, etc.), which generally exceed the actual needs of the organism. The appearance of emotional tension is accompanied by a switching to behaviors different from those that are characteristic of the calm state, the use of mechanisms of evaluation of external signals and responses to these signals based on A. Ukhtomsky's principle of the dominant. It is not an accident that a student of Pavlov, the psychiatrist V. Osipov, called "emotional" the first stage of formation of a conditioned reflex: the stage of generalization, the behavioral, electrophysiological, and neuroanatomical characteristics of which show similarity to the manifestation of Ukhtomsky's dominant [9, 10]. An emotionally aroused brain reacts to a wide range of signals presumed to be significant, the actual significance of which, correspondence or lack of correspondence to reality, will become clear only later in the process of conditioned reflex stabilization.

In the process of consolidation, a conditioned reflex is accompanied by a fall in emotional tension and a simultaneous shift from a dominant (generalized) reaction to strictly selective reactions to the conditioned signal; then the emergence of emotions leads to secondary generalization. The growth of emotional tension widens the variety of engrams retrievable from memory; and on the other hand, it lowers the criteria for "decision-making" when these engrams are compared with the present stimuli. The greater the anxiety, the more often the subject responds to a neutral stimulus as if it were an aversive one.

A hypothetical dominant reaction is advantageous only in conditions of pragmatic uncertainty. Information deficit is replaced by exploratory behavior, perfection of skills, and the mobilization of engrams held in the memory. The compensatory significance of negative emotions consists in their ***substitutional*** role. As for positive emotions, their compensatory function is realized via their effects on the need that initiates the behavior. In a difficult situation, when there is a low probability that a goal will be achieved, even a small success (increase in probability) will generate a positive emotion that strengthens the need according to a rule that follows from the formula of emotions.

In distinction to the hippocampus, the second "informational" brain structure – the frontal neocortex – orients the behavior towards signals of high-probability events. Figure 6 shows the percentage of motor alimentary conditioned reactions in intact rats in conditions of different probabilities of reinforcement. The abscissa shows days of tests. It can be seen that elaboration of conditioned reflex is retarded when the probability of reinforcement is low.

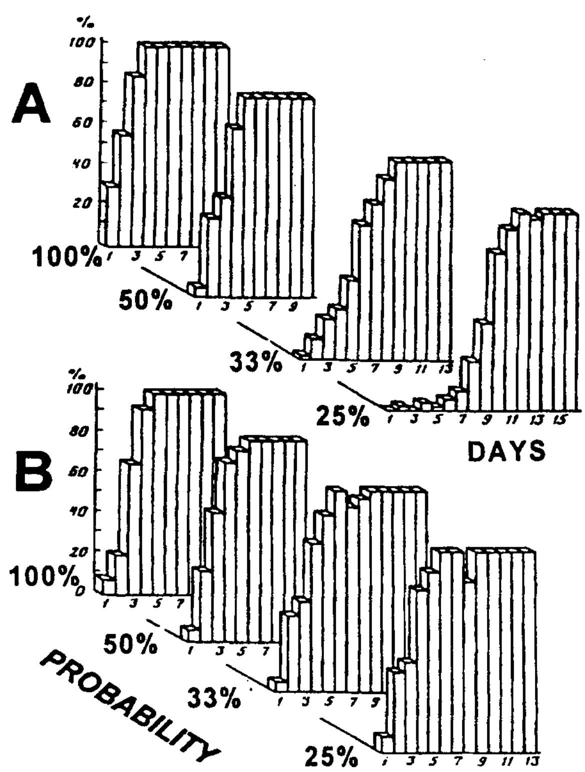

Fig. 6. Percentage of CR in control rats (A) and after destruction of frontal cortex (B) in conditions of different reinforcement probability.

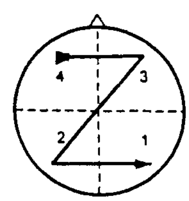

Fig. 7. Elaboration of conditioned reflex evokes shift of maximal activation focus.

Destruction of the frontal cortex eliminates the effect of low probability of reinforcement. In other words, signals with different probabilities of being reinforced with food become equally effective after frontal cortex ablation. This result is especially interesting since, judging by the available data, the frontal regions of the rat's brain cortex do not differ in their essential functions from the frontal cortex of higher vertebrates, including primates [6].

In discussing the influence of the hypothalamus on the neocortex, I have already mentioned the functional asymmetry of the left and right frontal brain regions. The analysis of the brain electrical activity in humans, dogs, and rats showed that upon repeated fulfillment of the same tasks and in the process of elaboration of classical conditioned reflex, the zone of higher activation shifts from the anterior parts of the left hemisphere to the anterior and then to the posterior areas of the right one (Fig. 7). In other words, the factor of novelty is significant in a discussion of the problem of lateralization of emotions [21].

The intensity of emotional tension, irrespective of its sign, is often related to the activity of the temporoparietal regions of the right hemisphere [3, 4]. In contrast to the connections of the left hemisphere with the reticular and brainstem regions, that region has well-developed connections with diencephalic structures. It determines the expression of emotional tension in changes in vegetative functions manifested by changes in the skin-galvanic reflex, heart rate, blood pressure, cortisone secretion, etc. The significant role of the temporal cortex of the right hemisphere in the realization of emotional reactions is revealed in animals as well [2]. Concerning the sign (positive or negative) of emotions, Heller and Davidson suggested that it is determined by the ratio between the activities of the left (LFC) and right (RFC) regions of the frontal cortex.

V. Heller [4] presented this rule as two inequalities:

$$\text{LFC} > \text{RFC} - \text{positive emotions;}$$

$$\text{RFC} < \text{LFC} - \text{negative emotions.}$$

In the above-mentioned papers there is still no answer to the question what determines the specificity of the left and right frontal cortex in the genesis of positive and negative emotions. It would be too simplistic to suggest that the "centers" of the corresponding emotions are localized in these two brain structures. According to the "Need-Informational Theory of Emotions," positive emotions arise when the available information exceeds a prognostically necessary one, and negative – when the necessary one is greater than the available.

The comparison of these inequalities with that proposed by Heller (see above) suggests that RFC preferentially deals with pragmatic information, required for satisfaction of need, i.e., earlier experience stored in memory, whereas LFC processes the most recent and currently available information. Taking into account the specificity of informational (cognitive) functions, which are realized by the left and right frontal neocortex, allows us to interpret the lateralization of positive and negative emotions and the role of these brain structures in the genesis of emotional states [20].

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