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APPROACH TO THE STUDY OF NEUROPHYSIOLOGICAL MECHANISM OF FOOD MOTIVATION

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The present article estimates depolarization-polarization processes in the nerve tissue of afferent systems, including visceral ones, according to the changes of the direct current (DC) potential level. Food motivation is formed and satisfied concurrently with changes in the neocortex direct current potential level and a number of cerebral brain limbic structures in rats. Lateral hypothalamic nucleus, basolateral amygdala area, and auditory cortex in hungry rats have a more negative DC potential shift than in satisfied animals, while a reverse relation is observed in the ventromedial hypothalamic nucleus. The results obtained are considered an indication of polarization shifts in the mechanism of motivated and emotional behavior. An idea of the determining role of polarization processes in the mechanism of motivated and emotional behavior is developed.

Keywords DC potential, food behavior, food motivation, neurophysiology of motivation and emotions, polarization processes in nervous system

The necessity to search for new approaches to the problem of the nervous mechanism of motivations and emotions is accounted for by the fact that most of the existing theories (MacLean, 1970, 1989; Simonov, 1987) have not been experimentally confirmed. To date, accumulated data indicate that the nervous substratum of a great

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number of motivations can be closely related to sensory systems. Thus, most biological motivations aimed at homeostasis maintenance (hunger, thirst, etc.) are presumably formed in the interior of the visceral analyzer (Mayer, 1953; Vasylevskaya, 1971; Lakomkin & Myagkov, 1975; Zambrzhitsky, 1989). In particular, food motivation is related to the systems receiving and analyzing information on the level of nutrients in the internal environment of the organism and in the digestive tract (Mayer, 1962; Oomura, 1989; Zambrzhitsky, 1989). Thus, food motivation results from integration of the afferent information, such as chemo- and mechano-sensitive visceral systems.

According to our concept (Murik, 1995a, 1995b, 1997, 1998, 2000, 2001), neurophysiological mechanisms of motivations and emotions are closely related to each other and are connected with changes of the functional state of afferent (i.e., sensory) neurons. The assessment of the biological significance of stimuli is possible by the change in the functional state of neurons constituting the sensory pattern. As an unfavorable functional state of neurons, which generate nervous model of stimulant, their long-term depolarization resulting in the inhibition of excitability by cathode or parabiotic principle is considered.

The depolarization decrease in the excitability of sensory neurons can be the basis of the subjective sensation of the perception system of stimuli as a negative emotion. On the other hand, the reason of the purposeful behavior is aimed at elimination of this functional state.

On the basis of this approach, during food motivation formation, the focus of depolarized neurons, being in an adverse functional state or close to such, should be localized in the system receiving and assessing the nutrient level in the internal environment of the organism and in the digestive tract. Lateral and ventromedial hypothalamic nuclei closely related to prefrontal and limbic cerebral cortex areas belong to the visceral analyzer assessing the nutrient level (Zambrzhitsky, 1989). Most probably, the functional state of neurons of these structures primarily determines the subjective sensation of hunger and satiety perception.

It is a great challenge to investigate objectively the role of polarization processes in the food motivation mechanism from the

methodological point of view. The most accurate way in this case would be multichannel microelectrode recording of membrane potential fluctuations of neurons of the food center in a chronic experiment. However, there might be simpler indirect approaches. The investigation of the DC potential level of the cerebral brain is, in our opinion, one of them. Up until now, the problem of the origin of the DC potential and its shifts has remained unsolved. However, the majority of researchers believe that the DC potential level reflects the functional state of the nerve tissue (Shvets, 1966; Ponomareva & Fokin, 2000). Rusinov (1969) thinks of the DC potential level as an electrographic expression of membrane potential stationary change (neuron polarization). A number of works (O'Leary & Goldring, 1964; Starobinets, 1967; Roytback, 1971) show that activation processes in the nervous system produce the DC potential negative shift of the structures under examination in relation to a neutral (zero, indifferent) point, which might be presented by the inner liquid medium of cerebral ventricles or blood vessels, or organism areas of low electric activity. In particular, it was recorded many times that the transition from sleep to awakening associated with central nervous system activation caused a negative shift in the DC potential level of the cerebral cortex hemispheres (Starobinets, 1967). The DC potential negative shift was observed during formation of stable cortex neuron depolarization produced by KCl (Kuznetsova, 1963) or ischemia (Koroleva & Vinogradova, 2000). The DC potential negative shift also occurs under the action of a cathode, which is known to depolarize the neuron membrane (Shvets, 1972b).

It can be concluded that the negative shift in the DC potential level follows depolarization of the membrane of neurons, which can be in different functional states. At a certain stage the depolarization processes are related to the activation of neuron activity (as during awakening), while during deep and long-term polarization (under the effect of KC1 or the cathode of heavy current; Shvets, 1972a), the DC potential negative shift coincides with neuron activity depression.

Hence, we believe that the DC potential level can be used for assessment of polarization processes in the nerve tissue. The DC potential negative shift apparently reflects the development of depolarization of the nerve cells.

The aim of the present research was to study the polarization processes in neuron populations more or less related to food behavior organization (lateral and ventromedial hypothalamus nuclei, amygdala, anterior thalamus nuclei, hippocampus) and not directly related to it (auditory cortex) by recording and analyzing the DC potential level.

METHODS

The experiments were carried out with 53 nonpedigreed white rats. Nonpolarizable chlorinated silver electrodes of 0.25-mm diameter were used for DC potential removal. Two series of tests were performed. In the first series (n = 23), the electrodes were implanted into the lateral hypothalamus nuclear (LHN), basolateral area of amygdala complex, hippocampus, and auditory cortex following the stereotaxic method (Pellegrino et al., 1979). In the second series (n = 30), the electrodes were inserted into the ventromedial hypothalamus nucleus (VHN), frontal nuclear (n.AV) of thalamus (FNT), and as in the first series, into the basolateral amygdala media and auditory cortex. The tests were followed by the morphological control of localization of electrode ends.

An indifferent chlorine-silver nonpolarizable electrode was fixed in the nasal cranium bone. The DC potential was recorded with a 4-channel direct current amplifier with an analogue digital transformer to accumulate the data for further computer processing.

The DC potential was recorded in a chronic experiment in the animals after 2 days of food deprivation, in the process of meeting food need and in the state of food satiation. The potential record-ing time was 40–60 min, with 60 s periods and 1–2 min intervals. The results were processed with the Microsoft Excel program. The reliability of diversities was assessed according to nonparametric and parametric criteria for dependent samplings: sign criterion, Wilcoxon test and Student t-test.

RESULTS

The analysis of the data recorded showed the difference of voltage between nasal cranium bones and structures under the examination;

the value and sign of this difference varied from –5,500 μV to +10,000 μV and was individual for each rat. However, in most cases the structures examined were positively charged in relation to frontal bones. Negative potential was often recorded in limbic structures, in FTN in particular.

Figure 1 shows an average DC potential level value for 3–4 min observed in the examined structures of hungry animals before meeting food need, during meeting food need, and after satiation. It is obvious that hungry animals have more negative DC potential level (in all cases $p < .001$) in the LHN, amygdala, and auditory cortex, and a more positive DC potential level ($p < .01$) in the VTN than satiated animals. For all of this, no reliable DC potential level difference was observed in the hippocampus and FTN. There is only some tendency toward DC potential positive shift in the FTN of hungry rats. The most significant DC potential level difference was recorded in the LHN (460 μV on the average) and in the VHN (about 410 μV) in satisfied animals as compared to hungry ones.

Figure 1 also shows that the process of meeting food need was accompanied by the DC potential positive shift in the LHN ($p < .05$), in the amygdala ($p < .001$), and by DC potential negative shift in the neocortex ($p < .05$) and in the VHN ($p < .05$). The greatest potential changes were observed in the amygdala (about 310 μV) and in the VHN (370 μV). There was no DC potential change recorded in the FTN during food consumption. At the same time, a tendency toward DC potential positive shift was observed in the hippocampus.

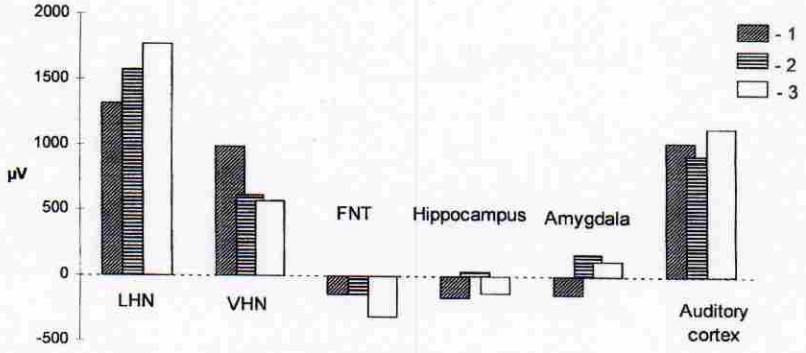

FIGURE 1. The DC potential shift of hungry rats (1), in the period of food need satisfaction (2), and after food satiation (3). Other designations are explained in the text.

An individual analysis of food behavior in rats showed that the DC potential level reduction (a negative shift) in the lateral hypothalamus preceded the activation of the food consumption process; thus, when the food was available in the cage, the rat began to move, sniffed around the litter, found the food, and began to eat it (Figure 2).

Food need being met, further LHN positive shift was observed ($p < .001$). In the amygdala, the DC potential positive shift was kept after satiation as compared to hungry animals ($p < .001$); however, it reduced slightly in comparison with that during food consumption. In the auditory cortex, the satiation resulted in the change of the DC potential negative shift processes observed under food need meeting for the DC potential positive shift. As a result, the DC potential level became reliably more positive not only in comparison with the food need meeting period ($p < .001$), but also in comparison with the state of hunger ($p < .01$). In the VHN the DC potential negative shift observed during food need meeting increased under food satiation ($p < .01$). In the hippocampus and FTN there were no reliable DC potential deviations under food satiation, as compared to the food need meeting period. However, a tendency was observed toward DC potential negative shift found in the FTN at the same period.

Hence, the formation of food motivation and its satisfaction

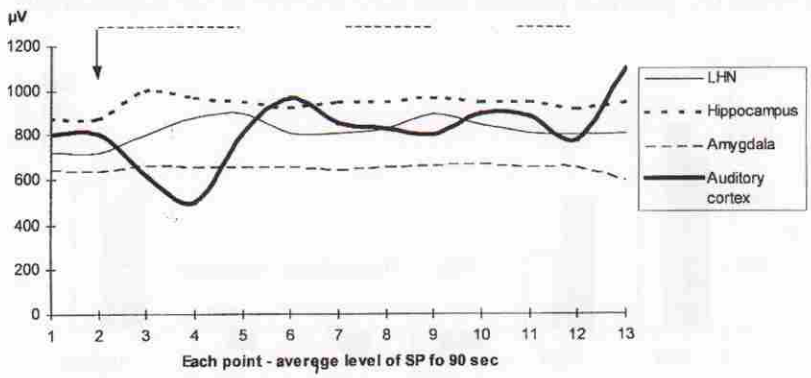

FIGURE 2. The example of the DC potential in rats during food needs satisfaction. The arrow indicates the beginning of feeding, and the dotted line shows periods of eating.

affected the DC potential of a number of cerebral brain structures studied. In most cases (LHN, amygdala, and auditory cortex), more DC potential negative shift was observed in hungry animals under food motivation than in satiated ones. A reverse dependence was found only in the VHN; thus, hungry animals had more DC potential positive shift than satiated ones. In the amygdala, the greatest DC potential positive shift was recorded in rats during food consumption. The process of food consumption was accompanied by the DC potential negative shift in the auditory cortex.

DISCUSSION

The results obtained indicate that food motivation is formed and satisfied concurrently with the DC potential changes in the cerebral brain. As mentioned in the introduction, the DC potential can reflect the processes of polarization and depolarization in the nervous tissue. Both relatively low depolarization of the neuron membrane followed by the development of the activation processes in the nervous system (as in passing from sleep to awakening [Starobinets, 1967]) and relatively long-term and significant depolarization associated with the inhibition of neuroactivity (as in the cases of potassium spreading depression [Kuznetsova, 1963], long-term cathode impact [Shvets, 1972a], or hypoxia [Yanvareva & Kuzmina, 1985]) are expressed in the DC potential negative shift. It must be added to the data the fact that the inhibition of neurons affected by ethereal narcosis being a parabiotic factor and depolarizing nerve cells also causes the DC potential negative shift (Starobinets, 1967).

According to some opinions, glia affects the DC potential level (Ranson & Goldring, 1973). The main mechanism in this case is attributed to the adsorption of ions [K+] by glial cells resulting in the change of their membrane potential. Physiological change of extracellular [K+] can widely vary under various functional states (from 3 to 60 mM) (Futamachi et al., 1974; Fisher et al., 1976). However, in the intact brain the appearance of potassium in the extracellular medium must be preceded by its release from neurons, which is only possible if the nerve cells are first depolarized themselves. In other words, the negative shift of the DC potential is

impossible in any case without the processes of depolarization in the nerve cells or in the neuroglial complex.

The DC potential positive shift is evidently connected with the processes opposite to those of depolarization, namely, with repolarization and hyperpolarization of the membrane of nervous tissue cells. Thus, the DC potential level of the cortex becomes positive during falling asleep (Starobinets, 1967) and under the effect of direct current anode (Shvets, 1972a, 1972b). In the latter case, as is well known, the hyperpolarized shifts of the membrane potential are observed. The level of the DC potential of the cerebral brain also becomes positive followed by adenosine injection (Poltavchenco & Grigoriev, 1989). At the cellular level, adenosine and its analogues cause hyperpolarization of the membrane (Shefner & Chiui, 1986) and inhibition of neuroactivity (Kostopoulos & Phillis, 1977; Stone, 1982; Shefner & Chiui, 1986). The DC potential positive shift is also observed in the period of activation of epileptic attacks (Kambrova, 1981), which may be accounted for by the exaltation of excitability similar to the anode type.

In functional terms, the processes of repolarization and hyperpolarization can be related to the enhancement of excitability (as in the case of membrane recovery from the state of deep depolarization (parabiosis) (Golikov & Kopylov, 1985), or during relatively long depolarization (similar to anode exaltation [Voronin 1966; Khodorov, 1969]). On the other hand, it can be related to its decrease (e.g., during repolarization caused by removing of the membrane potential from the critical depolarization level or in the period of hyperpolarized inhibition; Shefner & Chini, 1986).

Thus, both negative and positive shifts of the DC potential of one or more structures can be accompanied by differently directed changes of the functional state of their neurons. One can be more or less confident only regarding the character of the polarization. Negative and positive shifts of the DC potential presumably reflect depolarized, repolarized, and hyperpolarized processes in the nervous tissue, respectively. Apparently, relatively short-term and slight negative shifts of the DC potential caused by low depolarization of the membrane potential will follow the nerve processes coinciding with an increase in excitability and activation of nervous activity, whereas long-term and high negative shift of the DC potential will coincide with its depression observed, for example, during potassium spread-

ing depression or under intense and long-term cathode effect. The processes accompanied either by a decline of excitability (sleepy inhibition, adenosine effect) or by its exaltation (as in the case of epilepsy [Kamborova, 1981]) can develop in the nervous tissue during DC potential positive shift caused by the polarization of the membrane. However, regardless of the pathology, and extreme or injury effects, the DC potential negative shifts following natural behavior of animals evidently reflect the activation, whereas the positive changes reflect the inhibition in the nervous system.

The DC potential shifts observed in the work during food motivation make it possible to describe the proceeding processes of polarization-depolarization with a certain degree of approximation. The greatest negative shift of the DC potential registered in the state of hunger in the LHN indicates, in our opinion, that a rather deep center of depolarization is formed here at this period. Presumably, with hunger becoming more intense a number of neurons of this nucleus transfer from the initial state of the increased excitability and activity to the state corresponding to the cathode depression. In our opinion, the formation of such a center is subjectively perceived as a negative emotion of hunger.

The hypoxia, which is known to cause depolarization of neurons (Yanvareva, 1985), is accompanied by a two-phase reaction: by initial higher frequency of action potentials with a successive lower frequency and a block of cathode depression type or parabiosis type (Yanvareva & Kuzmina, 1985). We suggest that the processes occurring in the center of food motivation are similar to those taking place during the formation of nutrients deficit in the organism.

Judging by the DC potential shifts in other structures, the center of depolarization is not confined to the hunger center, but also involves both the structures directly related to the food center, the amygdala (Zambrzhitsky, 1989), and those indirectly related to it, the auditory cortex. In our opinion, motivated and excitation depolarizing the neurons of these brain structures increases initially their excitability, thus contributing to organization of the adaptive behavior by actualization of the inborn and acquired individual sensation. However, even in this case, the prolonged depolarization can result in the depression of the excitability, which subjectively will be expressed in the intensification of hunger.

As shown in our experiments, in the state of hunger the VHN

remains in a relatively inhibited state, which can be inferred from the DC potential positive shift at this period. According to our data, the intake of nutrients in the organism activates this nucleus and at the same time inhibits the LHN. Thus, the motivation depolarization center is gradually reduced. During food consumption, the processes of inhibition are also observed in the amygdala. It is in this nucleus that the greatest positivation of the DC potential was found during food consumption. Presumably, not only repolarization, but also hyperpolarization processes associated in this case (Murik, 1995, 1996, 1997, 1998, 1999, 2000, 2001) with the appearance of positive taste sensation accompanying food consumption proceed here at this period. The literature provides data showing that the amygdala is very important in discerning tasty and unpleasant foods (Wood, 1958; Bakuradze, 1975; Mershanova et al., 1999). As such, amygdala complex neurons frequently respond inhibitory to biologically significant stimuli (Ben-Ary et al., 1974). The positive DC potential shift of the auditory cortex after food satiation obviously reflects general inhibition of the neocortex observed in this period.

Thus, the process of food need satisfaction is primarily accompanied by the development of the inhibition processes in the nervous system. The mechanism of inhibition can be associated both with the repolarized and hyperpolarized shifts of the neurons membrane potential, which can be inferred from the DC potential positive shift in this period.

The literature also provides data that directly or indirectly show a possibility of the development of the polarization processes in the case of motivated or emotionally colored behavior, with positive emotions being most often accompanied by inhibition processes. Thus, it was observed that the positive emotions appearing in the process of satisfaction of biological needs, such as hunger or thirst, are accompanied by synchronization of slow electric activity in the neocortex (Clemente et al., 1964; Buchwald et al., 1967). The cortex electric activity is synchronized in doe-rabbits immediately after coupling (Sawyer & Kawakami, 1959). The visceral stimulation (inflation of the balloon in the small intestine) of low intensity causes hypersynchronization of an electroencephalogram in the cat, as in the case of low visceral stimulation of the human uterine neck (Adam et al., 1978). Under positive nourishment, the DC potential positive

shift is developed in the new cortex, the same as during development of a sleepy state (Marczynski & York, 1969). The negative shift in the brain DC potential is observed under negative emotions related to the orientation response (Starobinets, 1967). The same author found that nightmares were accompanied by the DC potential negative shift. A widely generalized negative shift in the DC potential level was also observed in the cortex during motional orientation response of awake rabbits (Shvets-Teheta-Guryi, 1983).

Therefore, the results obtained and the analysis of the data available show that the neurophysiological basis of food motivation can be related to the phenomena of polarization in the nervous system. It is in conformity with our conception (Murik, 1995, 1996, 1997, 1998, 1999, 2000, 2001) that the mechanism of the formation of motivations, and the resulting emotions, is closely related to the sensory processes, and is a reflection of the biological significance of stimuli through the change of the functional state of the neurons involved in these processes.

CONCLUSIONS

1. The formation of food motivation is formed and satisfied concurrently with the DC potential shift in the rat brain.
2. In the state of hunger, a more negative shift of the DC potential was observed in the LHN, basolateral area of amygdala, and auditory cortex, while a more positive one, in the VHN, compared to satiated animals.
3. The process of satisfaction of food need was associated with a positive shift of the DC potential in the LHN, amygdala, and a negative shift in auditory cortex and VHN.
4. The analysis of the recorded DC potential and literature data makes it possible to conclude that the food motivation formation and the process of food need satisfaction are accompanied by polarization changes in the nervous brain tissue of rats.

Evidently, in the system of structures associated with the assessment of the level of nutrient substrates in the organism, during the formation of food motivation, the depolarization locus formed is

felt subjectively as a sense of hunger. The reduction of this locus associated with food intake and satisfaction of food need will be accompanied by appearance of positive emotions.

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