System Organization of Alimentary Behavior in the Newborn and the Developing Cat

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This review deals with the structural, behavioral, and EEG correlates of searching for food and food intake. Data were collected on freely behaving kittens of 1 to 60 days of age with chronically implanted electrodes. The 1st manifestations of hunger involve activation of limbic-reticular structures and electroencephalographic (EEG) activity consisting of fast oscillations of 30-40-60 cps, correlated with general behavioral arousal as manifested by motor restlessness and vocal reactions. The more specific behavior form of hunger–feeding motivation–involves structures that include the motor and parietal cortex, amygdala, and medial hypothalamus; the EEG activity consists of high-amplitude, slow waves of 3-6 or 6-8 cps; and the behavioral correlate is purposeful search for the mother's teat or food. Satiation is associated with activity of the synchronizing structures in the forebrain and lower brain stem, as well as in the relay nuclei that transmit the sensory flow from oral afferents; EEG activity consists of regular rhythms of 10-14 and 2-4 cps; and the behavioral correlate is the act of feeding.

The growing interest in the mechanisms of the whole brain inevitably leads to the study of system organization of behavior, especially in work with waking animals. This is also fostered by the increased knowledge about structures whose functional properties are connected with integral behavioral patterns. We remember the time when interest flared up in the reticular formation (Magoun, 1950); in the limbic structures, the anatomic bases for motivation and emotion (Adey, 1961; Leontovich, 1968; Miller, 1957); and in the synchronizing structures which ensure active regulation of sleep and wakefulness (Clemente & Sterman, 1963; Moruzzi, 1964). However, these structures that regulate integral behavior were not always studied in actual connection with the corresponding behavioral patterns. The studies were most commonly conducted in acute preparations involving anesthetized or otherwise immobilized animals. On the other hand, studies on freely behaving animals have denoted little attention to a deep analysis of the structural bases of behavior and were, often, casual

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and incomplete. Our laboratory, over a period of many years, has been elaborating a functional system theory that, by its integrative properties, facilitates the resolution of certain of the foregoing contradictions. The functional system, the self-regulating organization with feedback sensory mechanism (Anokhin, 1935, 1961, 1964, 1968, 1974), is a complex of dynamic interactions that form between the various structural and functional patterns of the organism in order to obtain a particular useful or adaptive result.

From the point of view of functional system theory the final aim of studying the activating, synchronizing, and other structures of the brain is to establish their role in the integrative processes of the whole organism and to discover the relations that form between them in natural adaptive forms of behavior (Anokhin, 1933, 1948). The present review pertains to data on the system organization of the cat's alimentary behavior, the most important functional system of the organism with a strictly circumscribed effector manifestation and fairly definite structural composition. The data were obtained on awake, freely behaving kittens in the first 2 months of life. The data characterize the selective involvement of various cerebral structures in realizing the patterns of the search for food and the act of feeding. They include the electroencephalographic (EEG) changes recorded at various levels of the neuraxis, from the medulla to the cortex. The methods have been described in detail in Shuleikina (1964, 1968, 1970a, 1971).

EEG Patterns of Food Search Intake

The natural feeding behavior of the kitten comprises 2 clearly manifested inborn reactions: search for the mother's teat and sucking (Fig. 1A). Finding and grasping the food with subsequent lapping or chewing are added to these reactions after the 3rd week of life.

In newborn animals the feeding reactions are a form of behavior unequalled as regards degree of activity. This is a purposive action at birth: the newborn kitten begins to crawl "in search of its mother" even before it has managed to dry. It will find its mother as a result of crawling. Poking its muzzle into her hair it performs characteristic movements with its head nuzzling in the region of her teats, all 4 limbs either helping it to advance or tensing to maintain its balance. The grasping of the teat is the culminating point in the series of food-obtaining movements and signifies a transition to the act of feeding. This transition is realized instantly; it is reflex in nature and is triggered by the receptors of the mouth. Most commonly the kitten lies still and, placing the teat along its tongue which forms a groove, begins to suck, making 1-2 movements per sec. In cases of considerable feeding motivation, the kitten is observed to move its forelimbs and to massage the mother's teat. This is often accompanied by a characteristic vocal reaction from the kitten.

Thus, in a newborn animal food-obtaining is an extraordinarily active inborn form of behavior that is particularly impressive because, on the whole, the newborn kitten is a helpless creature, the orienting, playing, and active-defensive forms of behavior being practically absent. Even the acts of urination and defecation are not performed spontaneously, but are reflexive in response to the stimuli applied by the mother in the region of the sphincters.

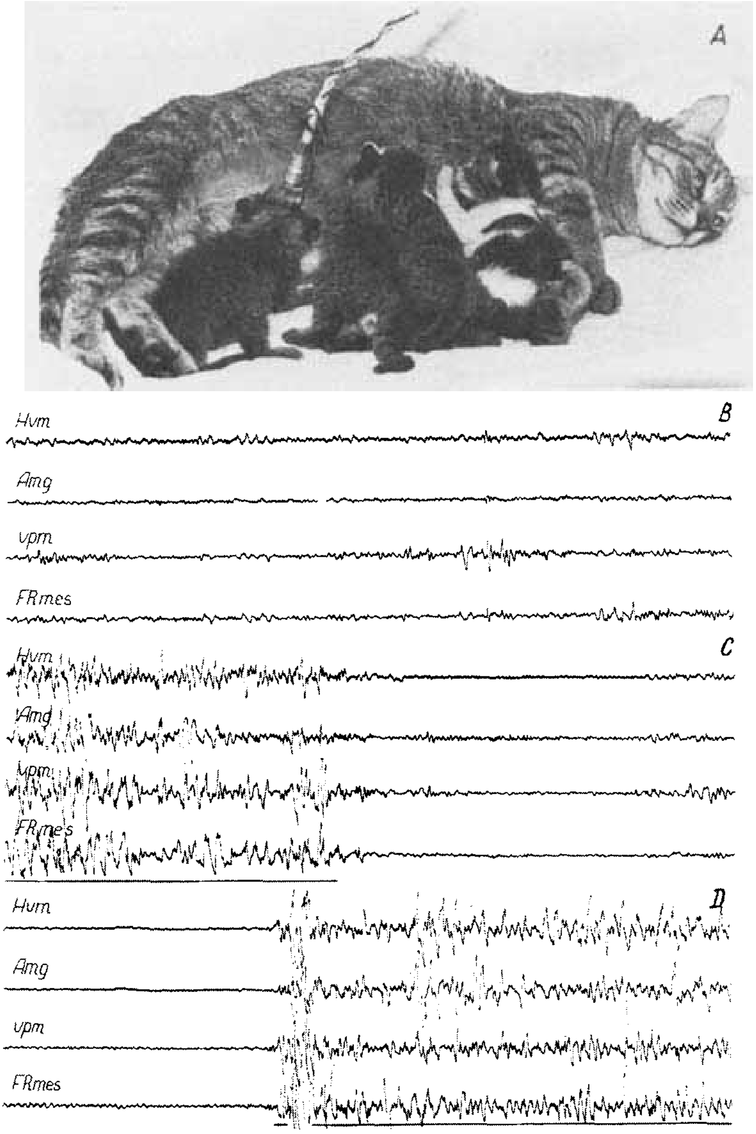


Fig. 1. EEG correlates of the young kitten's alimentary behavior. (A) General conditions of the experiment during search for the mother's teat and sucking. (B) Background EEG outside alimentary reactions. (C, D) EEG changes during search and sucking. Period of search underlined. Age of kitten: 3 days. Calibration: 50 μV/sec. Latin designations here and below: AL–Amygdala, pars lateralis, Amg–Amygdala; CC–Corpus callosum; Cd–nucleus (n.) caudatus; CM–centrum medianum; FRmes–formation reticularis mesencephali; GC–substantia grisea centralis; GP–globus pallidus; Ha–n. anterior hypothalami; Hdm–n. dorsomedialis hypothalami; Hpv–n. periventricularis hypothalami; Hvm–n. ventromedialis hypothalami; Hid–hippocampus dorsalis; Hiv–hippocampus ventralis; HL–area hypothalamica lateralis; Mot–cortex regio praecoronalis; ng–n. magnocellularis medullae oblongatae; nV–n. nervi trigemini (V); n.tr.s.–n. tractus solitarius; nv–n. reticularis ventralis medullae oblongatae; Orb–cortex regio orbitalis; PAmg–cortex regio periamygdalaris; Par–cortex regio parietalis; R–n. reticularis thalami; RP–formatio reticularis pontis; RPc–n. reticularis pontis caudalis; RPo–n. reticularis pontis oralis; Sens–cortex regio postcoronalis; va–n. ventralis anterior thalami; vpm–n. ventralis posteromedialis thalami.

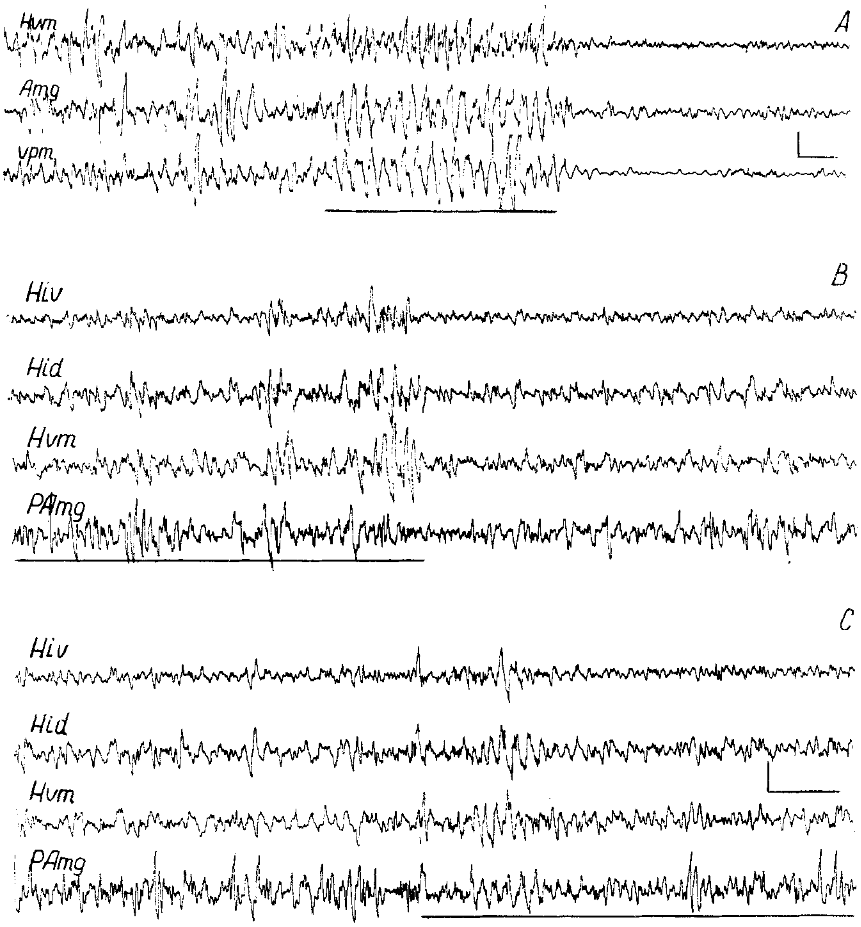


Fig. 2. EEG of older kittens during search and sucking. Periods of search (B, C) and teat grasping (A) underlined. Age of animals: 18 (A) and 30 (B,C) days. Calibration: 50 μV/sec.

In dealing with the characteristics of EEG patterns, we should first of all remember that, according to the published data, the general EEG of newborn animals awake but at rest and during natural or pharmacological sleep is a low-amplitude activity of a comparatively narrow frequency range (Fig. 1B; see also Blozowski, 1970; Farber, 1969; Golubeva, 1971; Marley & Key, 1963; Myslivec̆ek, 1970, Nikitina, 1971; Schwartze, 1973; Shimizu & Himwich, 1968; Shuleikina, 1970a). According to our observations, the food-obtaining behavior of the kitten (the crawling toward teat with nuzzling) reveals an entirely different EEG, which in a number of characteristics approaches the parameters of the adult cat. In the beginning of the search for the teat (Fig. 1 C,D), the amplitude of the initial potentials sharply rises, increasing from 30-50 to 100-150 μV. The frequency range noticeably extends, high-amplitude slow waves 3-6 and 8-10 per sec becoming the dominant rhythms. At the moment the teat is grasped these waves become particularly regular (Fig. 2A), after which in the beginning of sucking a sharp drop in the amplitude of the potentials with a tendency toward their synchronization is observed. During sucking low-amplitude activity is recorded again, but in a number of structures regular rhythms of 2-4 or 10-20 per sec are observed (Fig. 3). Such phenomena have been traced in all age groups and are, in a general way, maintained in cases of the newborn kitten's search for the mother's teat and sucking, as well as in those of 1- to 2-month-old kitten's food-finding reactions with subsequent lapping or chewing. Compared with the newborn the slow "searching" waves recorded in older animals approached a minimum rate and amplitude but are of a less generalized manner and at a lower level of the feeding motivation (sated animal). All of this is accompanied by a general activation of the background rhythms, owing to which the decrease in the potentials at the search-feeding borderline in older animals is less strongly pronounced (Fig. 2 B,C). Nevertheless, the general regularities of the change in types of rhythms during food-obtaining and feeding are maintained, enabling us to appraise them as EEG correlates of feeding behavior, as a whole, regardless of the animal's age. They have been corroborated by EEG-related phenomena obtained for feeding reactions in adult animals (Adey, 1961; Buchwald, Horvath, Myers, & Wakefield, 1964; Grandstaff, 1969; Rosen & Marczynski, 1967; Roth, Sterman, & Clemente, 1967; Shumilina, 1961; Sterman, Kanauss, Lehmann, & Clemente, 1965; Sterman, Wyrwicka, & Roth, 1969; Wyrwicka, 1964; Wyrwicka, & Sterman, 1968).

System Distribution of Activatory Processes During Feeding Behavior

Our 1st studies have shown that both in food-obtaining and feeding the processes of activation spread over the brain selectively. During the search for food high-amplitude slow waves were recorded at all the studied levels, from the medulla to the cortex. Moreover, structures were distinguished where the aforesaid waves were recorded

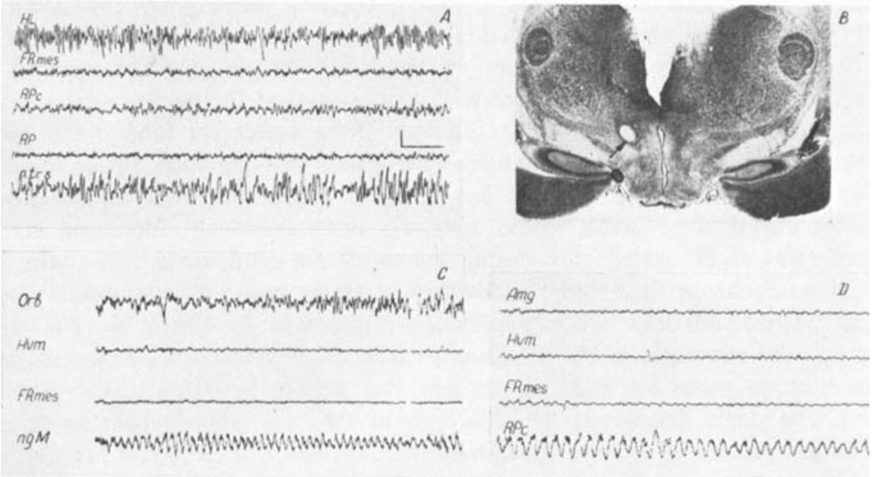


Fig. 3. Selective EEG synchronization during food intake observed in n.tr.s. and HL (A, B). Orb. and ng. (C), and RPc (D). (B) Electrode localization in HL. Age of animals: 30 days. Calibration 1 μV/sec.

the most clearly and constantly. These structures include the motor and parietal cortex, the amygdala, and a group of medial nuclei of the hypothalamus: ventromedial, dorsomedial, periventricular, and anterior. Later structures were discovered where high-amplitude slow waves were not always recorded during the search for food and where the initial background rhythms were retained. This finding suggested that during the search for food such structures are not activated. The structures turned out to be the orbital cortex, ventral posteromedial nucleus of the thalamus (Fig. 4A), lateral hypothalamus (Fig. 4B), and ventral reticular nucleus of the medulla oblongata (Fig. 4C).

The studies of the spread of rhythms that accompany the food intake have shown that these types of activity also spread over the brain selectively. Thus a synchronization of 10-20 per sec was most clearly manifested in the group of structures consisting of the orbital cortex, the ventral posteromedial nucleus of the thalamus, the lateral hypothalamus, and the nucleus of the solitary tract (Fig. 3A,B,C). Regular slow activity of 2-4 per sec was also recorded during food intake in the giant cell nucleus of the medulla oblongata, the caudal reticular nucleus of the pons (Fig. 3C,D), the sensory nucleus of the trigeminal nerve, the central grey matter of the mesencephalon, the medial center of thalamus, and the dorsal hippocampus. The characteristic feature of these structures is that, unlike those of the preceding group that were not activated during the search, these structures were activated during the search for food. In the latter group high-amplitude show waves of 3-6 and 8-10 per sec appeared.

Lastly, structures were revealed in which during feeding neither synchronization of electrical activity nor any other changes in the EEG except low-voltage irregular rhythms characteristic of the initial "nonfeeding" background were observed. These rhythms warranted the conclusion that the structures are not activated in the process of feeding. They are the motor cortex, the amygdala, and medial hypothalamus, that is, the structures that are the most active during the search for food.

The foregoing correlations are represented in Figure 5. It shows the distribution of the types of EEG characteristic of the process of feeding: synchronization of 10-20 per sec; slow sinusoid oscillations of 2-4 per sec; and low-voltage irregular activity characteristic of the rhythms of the initial "nonfeeding" background. The diagram also shows the activity of these structures against the background of obtaining food. Thus, the studies of EEG correlates of the search for food and the act of feeding in the various cerebral structures have shown that the EEG during the search for food and during feeding really has different expressions, and the processes of activation during these states spread over the brain selectively. Moreover, some of the structures are activated only during the search for food, some only during feeding, and some change their initial background rhythms during the two distinct feeding reaction. These relations are schematically represented in Figure 6. The double line shows the structures of the 1st group, which are activated only during the search (high-amplitude waves 3-6 and 6-8 per sec) and are not activated in the process of feeding. The single line shows the structures of the 2nd group, which are activated only in the process of feeding (synchronization of 10-20 per sec) and are not active during the search. The gray line shows the structures of the 3rd group, which are active in both forms of feeding behavior–the search for food and the feeding. High-

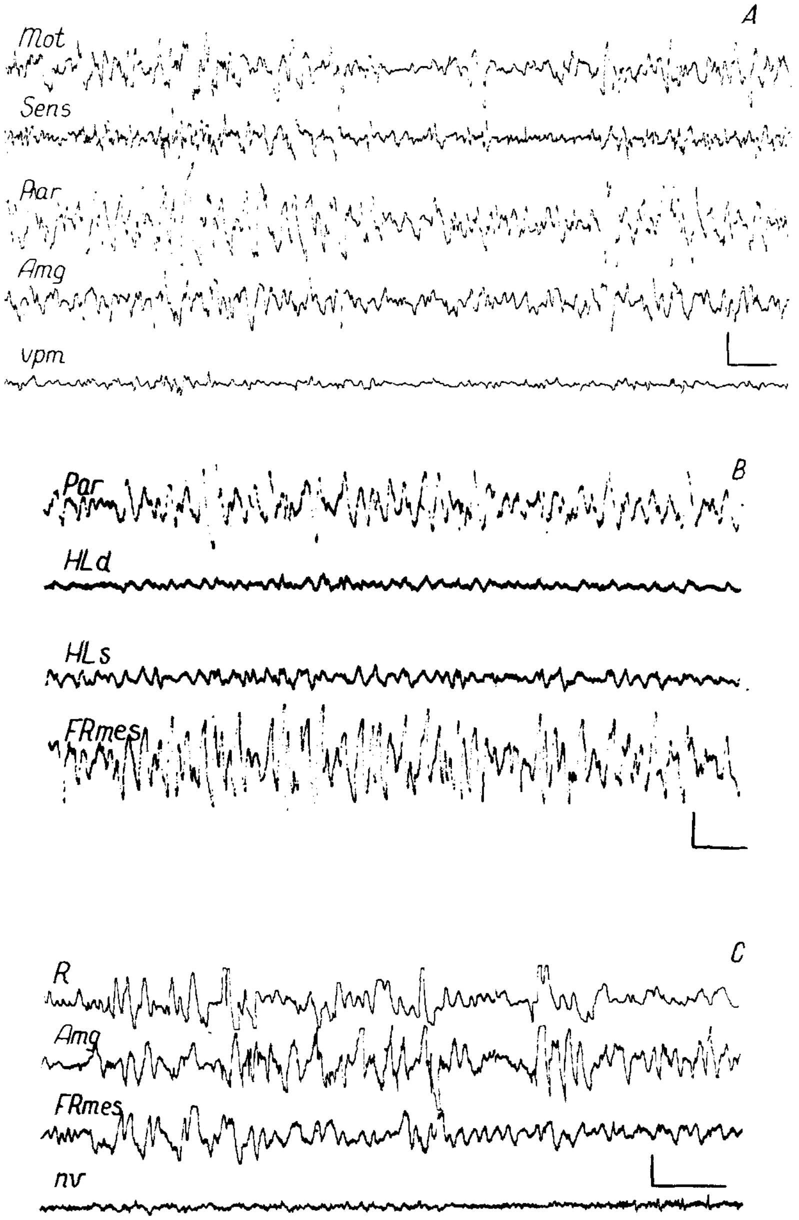


Fig. 4. Absence of high-amplitude slow waves during the search for food in vpm (A), HL (B) and nv. (C).

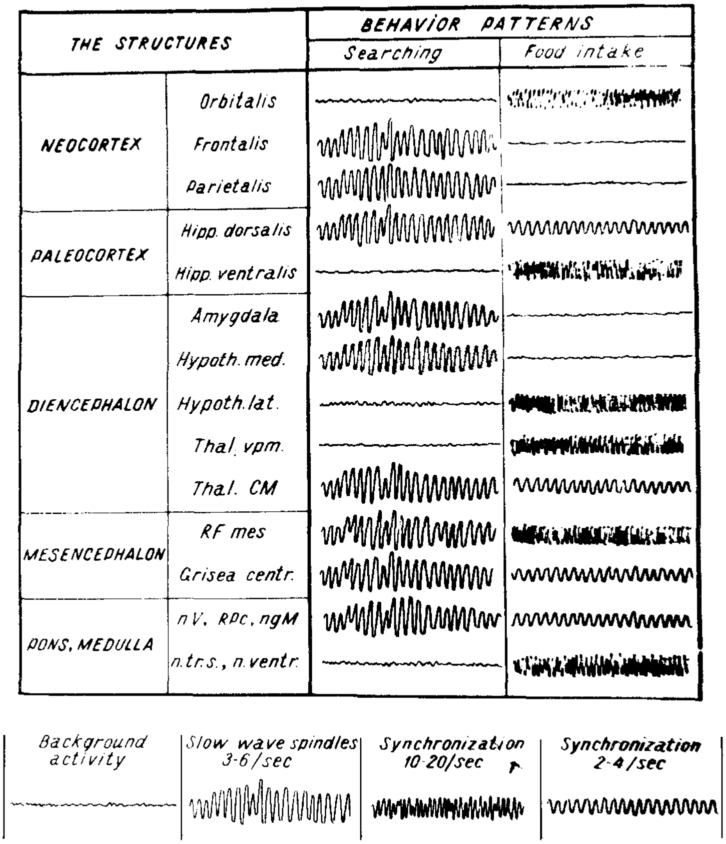
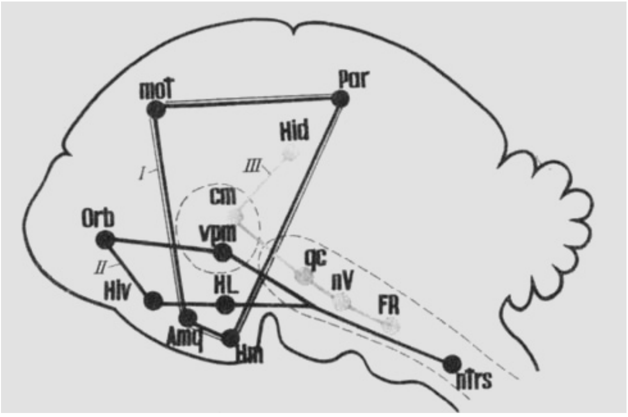

THE STRUCTURES
BEHAVIOR PATTERNS
Searching
Food intake
NEOCORTEX
Orbitalis
Frontalis
Parietalis
PALEOCORTEX
Hipp. dorsalis
Hipp. ventralis
DIENCEPHALON
Amygdala
Hypoth. med.
Hypoth. lat.
Thal. vpm.
Thal. CM
MESENCEPHALON
RF mes
Grisea centr.
PONS, MEDULLA
n V, RPc, ngM
n. tr. s., n. ventr.
Background activity
Slow wave spindles 3-6/sec
Synchronization 10-20/sec
Synchronization 2-4/sec

Fig. 5. Diagram of distribution of the main types of EEG patterns observed during the search for food and food intake in the various brain structures.


moT
Par
Hid
III
I
cm
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gc
nV
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HL
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nTrs

Fig. 6. Three groups of structures organized in the kitten's brain during the search for food and food intake. Double line: structures of the searching cycle (Group 1). Single line: structures of the food intake cycle (Group 2). Gray line shows the limbic brain stem system activated in both alimentary reactions (Group 3).

amplitude slow waves 3-6 and 6-8 per sec were recorded in these structures during the search, and sinusoid waves 2-4 per sec during feeding.

Our schematic representation raises the question of the nature of the noted phenomena, primarily, the common properties of the structures belonging to each of the 3 distinct groups. Published studies have shown that the structures of the 1st group–the amygdala, medial hypothalamus, and motor cortex–are really concerned with the reactions of searching for food, many of them having direct fiber interconnections (Adrianov & Molodkina, 1971; Bakuradze, Asatiani, Dateshidze, Nikolayeva, & Salukvadze, 1971; Bell, 1971; Fonberg, 1969; Glick & Greenstein, 1973; Grossman, 1966; Konorski, 1962; Lewinska, 1967; Miller, 1957; Rolls & Rolls, 1973; Rosen, 1968; Shugalev, 1970; Shumilina, 1961; Stevenson, 1969). The 2nd group consists of the structures that are closely connected with the food intake. Thus, the orbital cortex and lateral hypothalamus are known as the cortical and hypothalmic representations of the feeding center (Adrianov, Shuleikina, & Kovalenko, 1968; Anand, 1971; Delgado & Anand, 1953; Nutzubidze, 1962; Teitelbaum, 1971; Valenstein, Cox, & Kakolewski, 1968), whereas the nucleus of the solitary tract, ventral posteromedian nucleus of the thalamus, and orbital cortex represent a successive chain of relays along which the afferent flow proceeds from the receptors of the tongue and perioral zone (Appelberg & Landgren, 1958; Darian-Smith, 1966; Durinyan, 1965; Norgren & Leonard, 1971). Note that the areas where the synchronization of 10-20 sec is manifested during feeding are the dorsolateral region of the lateral hypothalamus and the nucleus of the solitary tract, which, as is well known, are regarded as synchronizing systems of the forebrain (Clemente & Sterman, 1963; Sterman et al., 1965) and the lower brain stem (Moruzzi, 1964). Thus, the aforesaid synchronizing structures take part not only in the formation of sleep phenomena, as was formerly indicated in the literature, but also play an essential role in processes of satiation. Moreover, within the limits of the organization of feeding behavior both groups of structures are functionally united.

Of considerable interest is the question of the functional unity of structures of the 3rd group distinguished by us and activated during the search for food and during feeding. The facts attesting to the participation of the given structures in feeding behavior were obtained mainly from the hippocampus (Adey, 1961; Brown, 1968; Gralewitz & Strumillo, 1971; Grastyan, Karmos, Vereczkey, & Kellenyi, 1966; Routtenberg, 1968; Shumilina, 1961). Moreover, Adey confirmed that activation of the hippocampus is observed both in searching situations and during feeding. The published literature contains no direct information on the participation of the central medial nucleus of the thalamus, the central grey matter, and pontomedullary structures in the feeding reactions. Remember, however, that this group forms part of Nauta's limbic-midbrain circuit (1960) in which, after Jouvet's studies (1967), the underlying reticular nuclei are also included. These structures presumably ensure the functions of the organism connected with maintenance of homeostasis (Bell, 1971; Leontovich, 1968; MacLean, 1958; Morgane, 1969), in light of which the participation of the given structures in the functional feeding system discovered by us may be considered natural. This point of view is confirmed in the following material, which shows that the group of structures under discussion is the most active in disturbance of homeostasis under conditions of physiologic hunger.

Sensory Mechanisms of Feeding Behavior

The foregoing facts demonstrate the integral work of the brain and the processes of activation against the background of the kitten's main feeding reactions: the search for food and the feeding. These initial electrophysiologic phenomena denote EEG correlates of feeding reactions under conditions of the animal's natural behavior. These correlations give rise to the question of the sensory processes underlying the given complex dynamics of the phenomena. In the 1st place, our attention was attracted by the sharp decrease in the amplitude of potentials corresponding to the moment of grasping the food and transition to sucking movements. This decrease agreed very well with our belief that the replacement from grasping the nipple to sucking was of a reflex nature and was triggered by signals from receptors of the perioral zone and the tongue (Shuleikina, 1966, 1975). On the basis of these presumed relations, experiments were done on the kitten that had as their aim the study of the conduction of the afferent stream from the tongue and of investigating the changes in behavior and the EEG in cases where the oral receptors were artificially disconnected by means of anesthesia.

Unconditioned and Conditioned Signs of Food

Studies of the sensory mechanisms of feeding behavior in growing animals rest primarily on a purely ontogenic peculiarity of the problem. An adult organism recognizes the source of food by a complexly organized afferent integration composed of visual, auditory, olfactory, tactile, and gustatory signals. Clearly, a newborn animal cannot obtain food by so intricate a sensory complex if only because of the immaturity of various sensory components. What are the signs by means of which the newborn finds and recognizes food? Which sensory signals inform the animal of the results? Which of these parameters are inborn signs of food and which become signals in the process of training? From the point of view of the functional systems theory the answers to these questions reveal the inborn and acquired parameters of the "afferent synthesis" and the "acceptor of the results of action" (Anokhin, 1948, 1968).

Published data and our own observations (Rayevsky, Chernikov, Shuleikina, & Diyachkova, 1975; Rosenblatt, 1972; Shuleikina, 1966; Uzdavini & Shepeleva, 1966) warrant the conclusion that the inborn signs of the source of food (mother) in newborn mammals are determined by tactile and temperature receptors stimulated by warm fur. Any object that possesses these properties is regarded as a sign of the mother and causes a search. In the beginning the olfactory signals of the kitten do not participate in recognizing the mother (Uzhdavini & Shepeleva, 1966). The same may be said of visual and auditory reception.

The inborn signs of the food itself are programmed in mammals by tactile and gustatory receptors that signal the presence of milk. At this time the entrance of food into the esophagus and stomach plays no role. The newborn infant sucks not only the teat but any object put in its mouth and develops equally vigorous sucking movements whenever the entrance of milk is stopped (sucking a baby nipple). At the same time, the sucking movements are inhibited if the teat is smeared with a foreign substance or if a sour or bitter liquid enters through the nipple (Jensen, 1932; Shuleikina, 1966, 1971). Thus the inborn program of the signs of expected food in mammals includes tactile, thermal, and gustatory signals that are provided by the warm fur surface and presence of the teat secreting a liquid with the properties of milk. The primary significance of tactile and gustatory afferent stimulation is supported by the electrophysiologic data obtained in our laboratory by Chernikov (1972). By the methods of evoked potentials and recording of the unit activity in the medullary relay nuclei and the cortical projections, he showed in kittens that the gustatory and tactile conduction from the tongue are the earliest to mature. The finer discriminative tactile capabilities mature later.

The inborn signals of the signs of food begin to become overgrown with conditioned reflex signals the moment the organism makes its appearance in the world. This process develops, in the main, along 2 lines. First, the range of possible food signals extends in connection with the formation of distance receptors (olfaction, vision, hearing). Second, the executive apparatus of feeding reactions becomes more differentiated and economical. These processes operate against the background of new sensory reorganizations with an increase, in the 1st place, in the number of parameters of the goals and the results of action. Thus, in addition to the tactile and temperature signals, the odor of the mother also becomes a sign. Note that the infant animal's reactions to the odor of the mother are elaborated earlier than to the odor of milk (Uzhdavini & Shepeleva, 1966).

The reactions of preference for "its own" teat served as a fine model for studying the sensory mechanisms of alimentary learning. Rosenblatt (1972) has shown that the kitten learns to recognize "its own" teat by the sum of 3 sensory components, namely, the tactile, olfactory, and kinesthetic. If the tactile information is altered by shaving the hair around the teat, the kitten learns to find the teat by its odor. If the teat and the surrounding surface are deprived of the odor, the kitten will begin to find the teat in 1-2 days by tactile signals. Lastly, if the tactile and olfactory signs of the teat are deliberately altered under conditions of feeding by an artificial mother, where reactions of preference also develop, the kitten will still learn to find the way to it by kinesthetic signals.

EEG Synchronization as a Correlate of a Sensory Flow from Oral Afferents

Thus, as a result of alimentary learning, new food parameters are formed, 1st, through maturation of distance receptors and, 2nd, through extension and complication of the sum of signals forming the inborn program. Because a considerable role in this complex sensory integration is played by oral receptors, we wished to determine the EEG changes in the relay nuclei that effect the sensory conduction from the tongue under conditions of their natural functioning.

We observed a synchronization of electrical activity and a common rhythm with a frequency of 10-20 cps for all structures against the background of the rhythmic feeding movements (sucking, chewing, and lapping) in all links of the afferent flow from the tongue to the nucleus of the solitary tract, the ventral posteromedian nucleus of the thalamus, the lateral hypothalamus, and the orbital cortex (Fig. 3 A, C). The unity of electrical processes discovered for these structures enabled us to mark them as a separate (2nd) group of structures activated in the feeding process (shown in Fig. 6 by the single line).

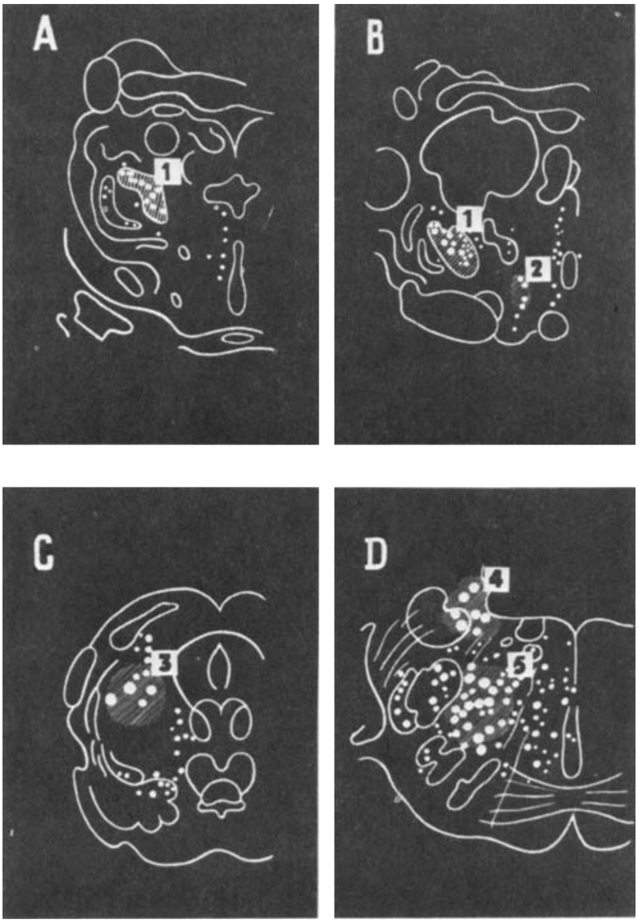


Fig. 7. Topography of brain stem neurons responding to trigeminal stimulation (Berry et al., 1956) and mapping of 10-20 /sec EEG synchronization recorded during food intake (Shuleikina, 1971). Neurons marked by white dots; regions of EEG records shaded. Designations of structures: (1) vpm; (2) HL; (3) FRmes; (4) n.tr.s.; (5) nv.

The phenomenon of synchronization may be appraised as a manifestation of the unity of these structures that share in the conduction of sensory streams from the perioral zone and tongue in the process of feeding. This may be confirmed by the following comparisons: Berry, Anderson, & Brooks (1956) investigated regions in which they could discover neurons responding to stimulation of the trigeminal nerve of the cat. By means of recording the impulse activity of separate units they traced the ascending tract formed by trigeminal afferents. The results of the study are shown in Figure 7. The white dots indicate the neurons responding to trigeminal stimulation, the larger diameter corresponding to the units that had a shorter latent period. The same diagram contains our data on distribution of the regions in which were recorded the synchronized rhythms (10-20 cps) under conditions of the kitten's natural state in the process of feeding. The diagram also shows that all the areas where we discovered the synchronization of 10-20 per sec coincided with the zones where, according to Berry et al., the neurons responding to trigeminal stimulation with the shortest latency are located.

Exclusion of Oral Afferents

The foregoing data indicate that the information from trigeminal afferents constitutes an important link in the sensory processes of feeding behavior. Consequently, we wished to learn how a cessation of this sensory stream would influence the feeding reactions. A series of experiments was performed for this purpose on a kitten with exclusion of the perioral zone and tongue by anesthesia (application of a tampon soaked in a 2% cocaine solution to the tongue or lips for 1-2 min).

The local exclusion of the receptors of the tongue resulted in a sharp activation of the food-obtaining behavior. The kitten began to dig in the mother's fur with a frenzy and continued its incessant search for a long period of time. The capacity for the oriented search was retained, the 3-45 day-old kittens searching only in the region of the teats but losing in a number of cases its striving for the preferred teat. After grasping the teat the kitten did not calm down, but moved about restlessly, sucked with interruptions, and often broke away and resumed its search. The local exclusion of the perioral zone (lips) also resulted in a sharp increase in food-obtaining activity. Moreover, the orientation of the search was disturbed. The kitten began to search for the teat all over the cat's body, including the back and head. The ability to grasp the teat disappeared and, despite the long search and proximate location of the teat, the kitten did not grasp it and was unable to start sucking.

Because the studies on an intact animal revealed clear EEG changes in the chain of the searching-grasping-sucking reactions, we began tracing the changes that occurred under the influence of anesthesia, the EEG that corresponded to the search and sucking, and, what was the most important, whether or not the decrease in the amplitudes of the potentials continued during the grasping of the teat and the transition to sucking movements. This series of experiments was carried out under anesthesia of the tongue because under perioral anesthesia sucking, as was stated, failed to take place.

The following is a typical case recorded in a 45-day-old well-fed kitten with a fairly weak initial EEG manifestation of the searching reaction (Fig. 8A). During the 1st seconds after application of cocaine the search became increasingly more intense and the structures conducting the impulses from the tongue (orbital cortex, thalamus, and ventral reticular nucleus of the medulla oblongata adjoining the nucleus of the tractus solitarius) exhibited epileptoid activity (Fig. 8B,D). After several minutes of a continuous search all leads began to record a high-amplitude slow "searching" activity (Fig. 8C). If the kitten managed to grasp the teat during the 1st phase of anesthesia, the ability to suck remained unchanged (Fig. 9A). At this time the EEG in the lateral hypothalamus, the ventral posteromedial nucleus of the thalamus, and mesencephalic reticular formation still exhibited the regular waves characteristic of feeding. As the anesthesia became deeper in the case of continued sucking, the synchronization diminished and eventually disappeared (last, in the lateral hypothalmus [Fig. 9B]). At the same time slow, high-amplitude waves with which we heretofore associated only with the recordings during the search behavior began to appear in the EEG singly or in groups. Finally, at the stage of the

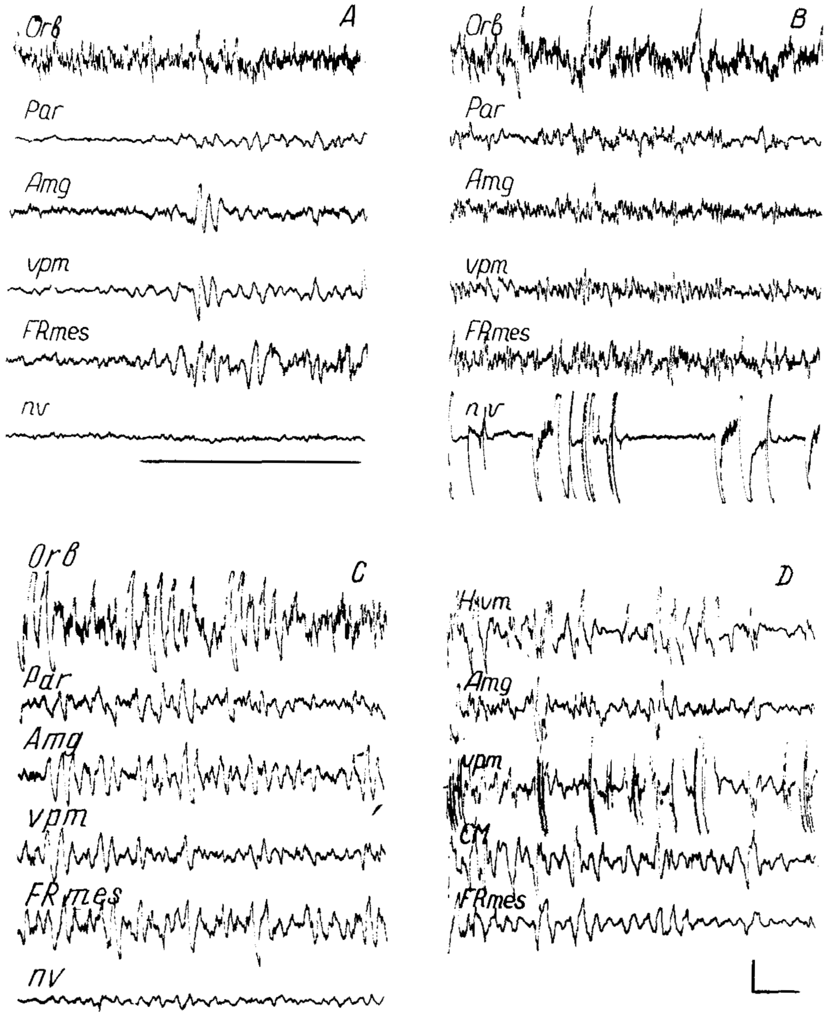


Fig. 8. EEG patterns accompanying the search for food, tongue anesthetized. (A) Before anesthesia (search underlined). (B–D) Successive records of the searching reaction against background of developing anesthesia. Age of animals: 45 (A–C) and 3 (D) days. Calibration: 50 μV/sec.

maximum effect of anesthesia when generalized searching waves were observed in the highest degree in the EEG during the search, if the teat was grasped the subsequent sucking exhibited no change in the amplitude of the potentials characteristic of the transition from the search to sucking and the EEG continued to be one of high voltage (Fig. 9C,D). In this stage the sucking did not last long. Receiving no return information on grasping and the course of sucking, the kitten often broke away, searched, grasped again, became restless, lost the teat, and resumed the search. At this time a continuous stream of high-voltage slow searching rhythms was recorded in the EEG.

Morphological Substrate and EEG Correlates of Feeding Behavior in Hunger

So far the exposition of the main phenomena has dealt with the behavior and EEG under conditions of a natural feeding regime with moderate fluctuations of appetite. However, the observations conducted earlier on adult animals (Anokhin & Sudakov, 1971; Sudakov, 1965, 1971) showed that the most important factor of the functional system of feeding is the dominant motivation manifested in the highest degree in the state of hunger. Below are observations pertaining to the nature of these states in the developing kitten.

The behavior of a kitten deprived of food for 24 hr has specific features. Signs of general arousal are manifested in continuous motor restlessness, a decrease in or an absence of sleep, and frequent vocal reactions with purposeful food-related behavior

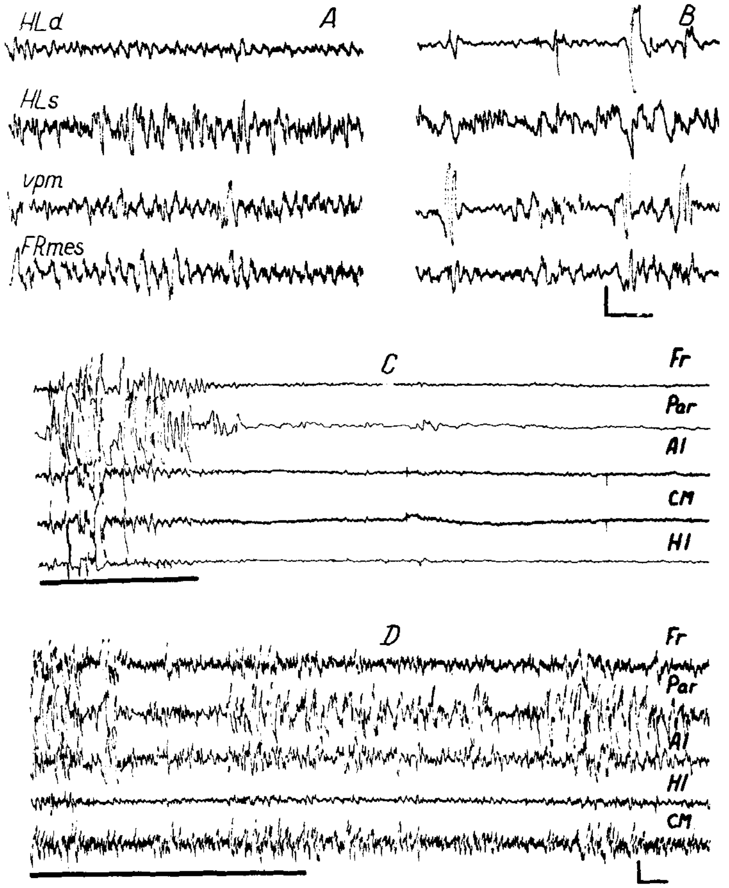


Fig. 9. EEG patterns accompanying food intake, tongue anesthetized. Sucking (A) and transition from search to sucking (C) before anesthesia. Sucking (B) and transition from search to sucking (D) during development of anesthesia. Periods of search underlined. Age of animals: 30 (A, B) and 15 (C, D) days. Calibration: 50 μV/sec.

increasing simultaneously. In older animals this deprivation is manifested in sniffing at the room and searching for the feeding trough; in younger animals it is exhibited by a maximum purposefulness of the search for the teat with subsequent particularly "greedy" sucking.

The background EEG corresponding to the hunger state has the following peculiarities: First, the frequency spectrum shifts in the direction of rapid rhythms (30-40 per sec), in the beginning unaccompanied by an increase in their amplitude (Fig. 10A,B). As the duration of hunger increases, these rapid rhythms decrease in amplitude and

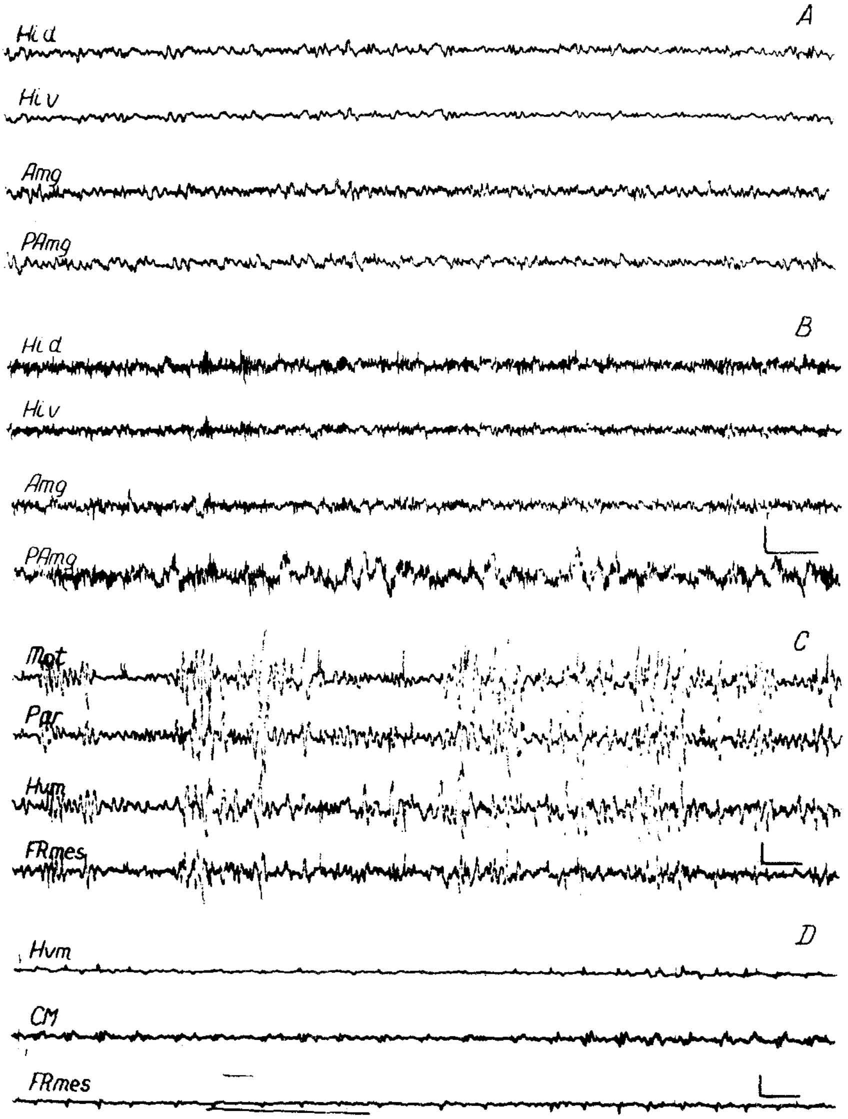


Fig. 10. Main changes in background EEG appearing of food-deprived animals outside alimentary reactions. (A) Satiated animal; (B, C) after 1 day of hunger; (D) after 2 days of hunger. Age of animals: 30 days. Calibration: 50 μV/sec.

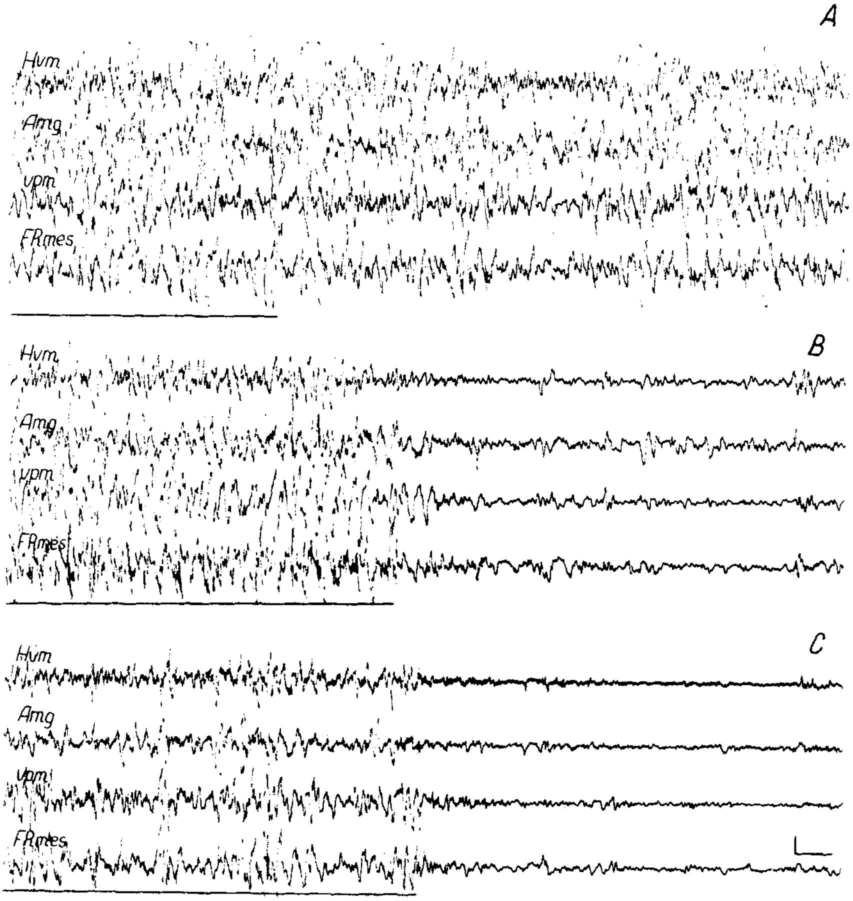


Fig. 11. (A) EEG during search and sucking in hunger. (B, C) Subsequent phases of satiation. Periods of search underlined in all cases. Age of kitten: 5 days. Calibration: 50 μV/sec.

are replaced by desynchronization (Fig. 10D). The 3rd kind of EEG are slow, high-amplitude waves, which in the undeprived animals are recorded only during the search. Under conditions of hunger these waves usually acquire a higher frequency (8-10 per sec) and can be discovered not only during food-obtaining but also in the background rhythms outside search for mother's teat or sucking (Fig. 10C).

Still clearer changes in the EEG are observed, however, during feeding reactions (Fig. 11). Thus during the search for the teat the slow high-amplitude waves noticeably increase in amplitude and acquire a still higher frequency of up to 10-12 oscillations per sec. During the transition to sucking, lapping, or chewing movements, no drop in the amplitude of the potentials occurs, and in the 1st minutes of feeding the same high-amplitude activity is recorded on the EEG as during the search (Fig. 11A). Between the 5th and 8th minutes of continuous feeding comes a stage in which, if sucking is interrupted, the transition from searching to sucking begins to be accompanied by a drop in the amplitude of the potentials (Fig. 11B,C), and a synchronization appears in the corresponding structures of the brain. These EEG dynamics are observed against the background of a successive subsidence of rapid hunger rhythms that are at first superimposed on slow activity and then gradually disappear.

We assumed that the rapid rhythms and slow, high-amplitude waves were associated with different cerebral structures and reflect different components of the feeding activation in hunger (Shuleikina, 1970a, 1971). To elucidate this question, we had to study 1st, and in greater detail, the conditions under which both types of rhythms emerge and are distributed over the different cerebral structures. We remembered that rapid rhythms in the state of hunger were described in numerous studies on adult animals (Dumenko, 1972; Freeman, 1962; Hockman, 1964; Shumilina, 1961; Sudakov, 1971; Wyrwicka, 1964). Thus, the presence of these rhythms in both adult cats and kittens indicates, 1st, that the mechanisms of hunger activation are already formed at the moment of birth and, 2nd, that rapid rhythms are really EEG correlates of hunger. Our studies of the spread of high-frequency activity over the different structures of the kitten's brain showed that these rhythms are most constantly and clearly manifested in the dorsal hippocampus and in the central grey matter of the mesencephalon and pontomedullary reticular nuclei (Fig. 12A-D). In hunger lasting 2 days the activation of these structures increases still more and assumes a tonic character. In such cases we observed a "continuous" desynchronization in the EEG that persisted in the background EEG as well as in the search for food and in the act of feeding (12E).

Phenomena of selective hunger activation studied in detail in an adult animal showed interaction between the hypothalamus and the cortex (Sudakov, 1963, 1971). In our experiments on kittens we have described a new group of structures not previously studied for their participation in the formation of hunger. As was pointed out above, these structures form part of the Nauta-Jouvet limbic-brain stem circuit and, according to a number of authors, ensure the constancy of homeostasis. The selective activation of these structures in hunger corroborates this proposition. In cases of a kitten's moderate hunger that did not exceed 24 hr, high-frequency

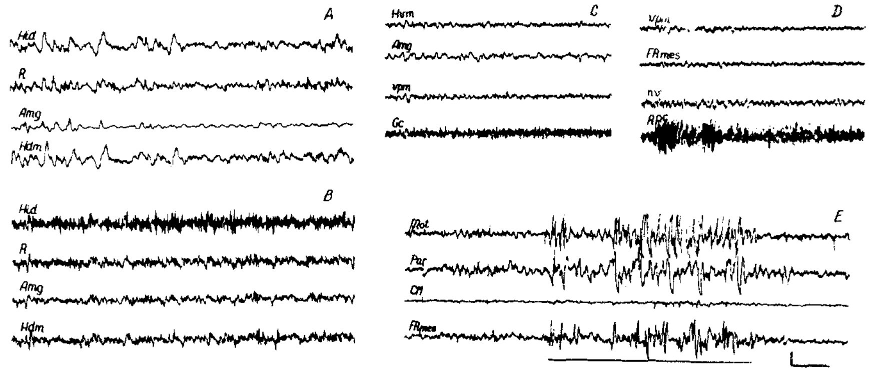


Fig. 12. Predominant manifestation of high-frequency activity in the limbic-reticular structures during hunger. (A) Background rhythms in satiated animals. (B–E) Rhythms in food-deprived animals. Age of animals: 40 (A, B), 18 (C), 25 (D), and 8 (E) days. Calibration: 50 μV/sec.

activity 1st appeared in these structures before it was recorded in other cerebral structures, including the hypothalamus. A comparative study of the involvement of the limbic reticular formation in the activation of hunger showed that the EEG of the changes differed and manifested themselves to the greatest extent in the pontomedullary nuclei. Studies of the topography of the medullary zone warranted the conclusion that the structures embrace the medullar giant cell nucleus and the lower 3rd of the caudal reticular nucleus of the pons (Shuleikina, 1971).

Recognizing that the given reticular nuclei belong to the activating mechanisms of the brain (Anand, 1971; Brodal, 1960; Jouvet, 1967; Morgane, 1969), we assumed that the selective activation of the limbic reticular formations is effected in hunger from a common focus, namely, the pontomedullary nuclei. Recognizing, also, that the hypothalamus is the most important source of ascending activating influences in hunger (Anokhin, 1962, 1968; Anokhin & Sudakov, 1971; Shuleikina, 1970a, b; Sudakov, 1963, 1965, 1971), we wondered about the relation of the feeding centers of the hypothalamus to the origin of the rhythms of the limbic reticular system recorded in hunger. In the experiments with destruction of the medial (Fig. 13A,B) and lateral (Fig. 13C,D) areas of the hypothalamus we showed that the high-frequency activity of the limbic reticular formations persists in both types of destruction. Recalling, further, that in the hungry, intact animal high-frequency activity can be recorded in the limbic reticular structures from the earliest stages of hunger when no EEG changes are observed in the other structures, including the feeding centers of the hypothalamus, we conclude that in feeding excitation the activity of the structures of the limbic reticular system is an independent process with respect to the hypothalamus.

Thus, the behavior of an animal compelled to perform a very important adaptive pattern in relation to factors of the external environment has as its 1st component a general emotional reaction, which makes possible the appraisal of the usefulness or harm of the current influence, and the consolidation and strengthening of the subsequent adaptive effect (Anokhin, 1962, 1968). The group of old cerebral structures, including the archipaleocortex, nonspecific nuclei of the thalamus, central grey matter, and pontomedullary reticular nuclei, may be considered the morphological substrate of this 1st, initial stage (general arousal: Dell, 1958; vigilance behavior: Morgane, 1969). The activation formed by these structures arises with the 1st signs of hunger and accompanies the more specific forms of behavior: the purposeful search for food and its consumption. The feeding nuclei of the hypothalamus, as well as the structures of the thalamus and neopallium, are the structural substrate of this 2nd, motivational component of feeding behavior. The following part of this review deals with these mechanisms.

Feeding Motivations and the Hypothalmus

EEG Correlates of Feeding Motivation

One of the most important aspects of the problem of motivation is the question of its objective correlates–behavioral, structural, and electrophysiological. The fewest facts have as yet been obtained on EEG correlates of motivational excitation.

An attempt was made in our laboratory to distinguish some of these correlated by investigating the nature and conditions of appearance of high-voltage, slow waves with a frequency of 3-6 and 8-10 per sec, first discovered in the reactions of searching for food (Fig. 1C,D).

The experiments on older animals that were offered tidbits serve as a demonstrative example of the manifestation of slow high-amplitude waves. Because the kittens were not food deprived beforehand, we maintained that the hunger excitation proper was at a fairly low level. This was also evidenced by the absence of high-frequency "hunger" activity (Fig. 14A,C,D). However, if such an animal was offered tidbits, it grasped them greedily. A clear burst of slow waves was obtained

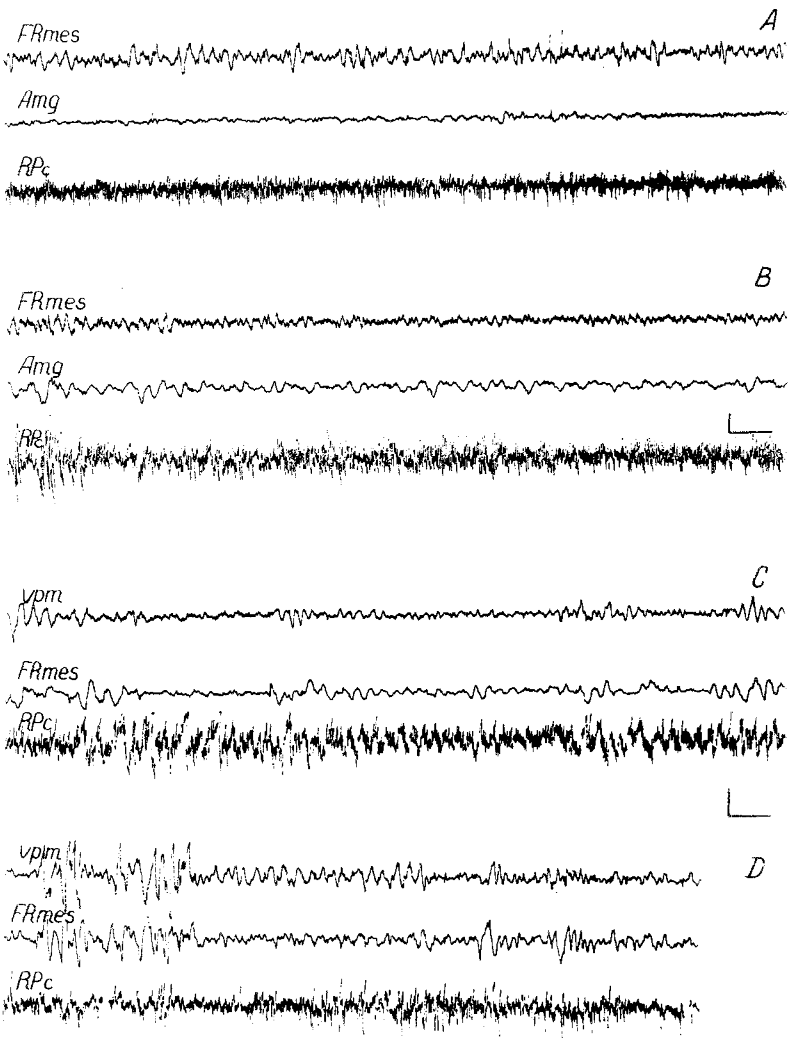


Fig. 13. High-frequency activity of the caudal reticular nucleus of the pons in a food-deprived animals before (A, C) and after destruction of the ventromedial (B) and lateral (D) hypothalamus. Age of animals: 18 (A, B) and 8 (C, D) days. Calibration: 50 μV/sec.

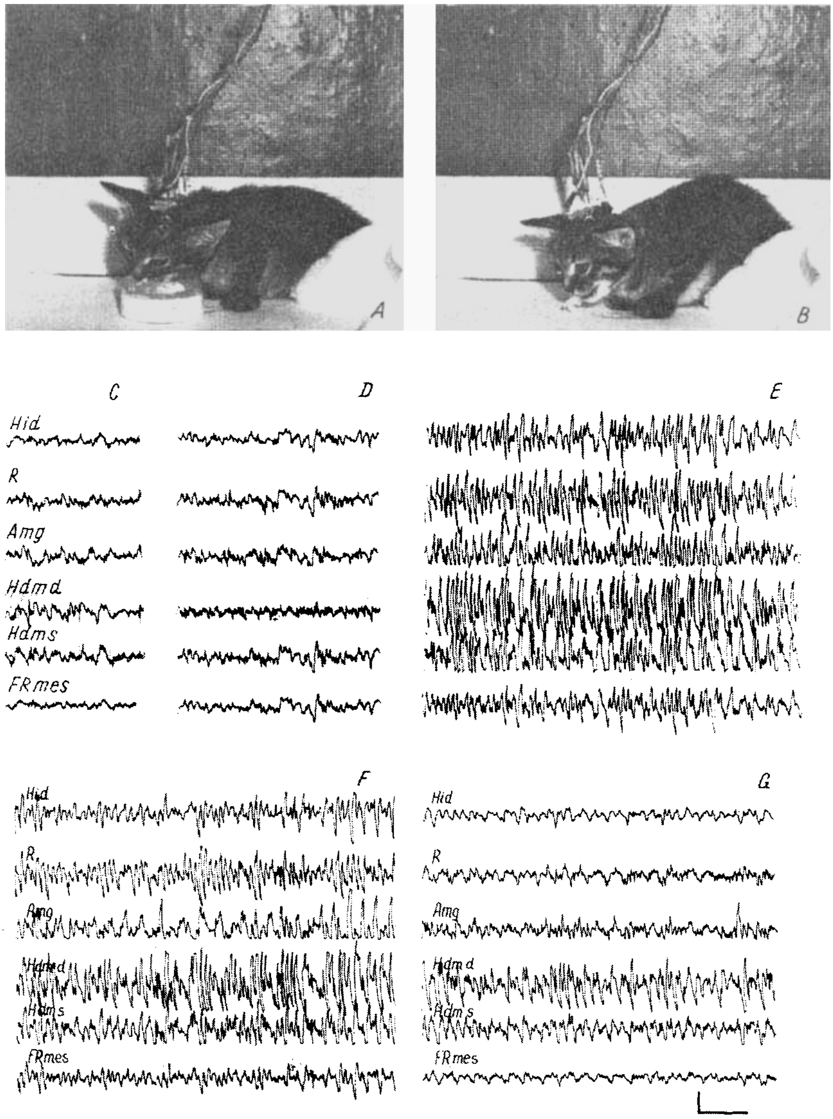


Fig. 14. Animal's behavior (A, B) and EEG dynamics (C–G) at different levels of feeding motivation. (C) background EEG; (A, D) lapping milk; (B, E) sniffing at meat and beginning of its consumption; (F, G) subsequent phases of meat consumption. Age of kitten: 45 days. Calibration: 50 μV/sec.

in the EEG appearing when the animal sniffed at the food and at the beginning of feeding (Fig. 14B,E) and was followed by a subsidence of these rhythms to the point of their complete disappearance (Fig. 14F,G). Because the foregoing EEG was not recorded in a hungry animal and the rapid-frequency component of feeding excitation was absent, we concluded that the evolution of slow high-amplitude waves reflects the dynamics of motivational excitation alone, when the hunger excitation proper is stable. This is predicated on the assumption that the aforesaid high-amplitude waves are EEG correlates of feeding motivation. Such slow waves have been described by authors who worked with feeding reactions in adult animals. The waves appear during increased motivation when the animal is in a state of "goal-directed behavior," that is, when it approaches the pedal or spring of the feeding trough in response to a conditioned stimulus, or otherwise orients itself as though to move (Buchwald et al., 1964; Grastyan et al., 1966; Pickenhain & Klingberg, 1967; Roth et al., 1967; Shumilina, 1961; Sterman et al., 1969; Storm van Leeuwan & Lopes da Silva, 1969; Wyrwycka & Sterman, 1968).

Participation of Medial Hypothalmus in Formation of Feeding Motivation

We noticed that the given waves, which successively subsided with the decrease in motivation, were the last to disappear in the medial hypothalamus (Fig. 14F,G) and, in a number of cases of increased motivational excitation, were the 1st to appear. We suspected, therefore, a direct connection between the activity of the nuclei of the medial hypothalamus and the marked motivational EEG of the waves. In order to verify this conclusion we performed experiments with destruction and stimulation of the medial nuclei of the hypothalamus. The experiments showed that in cases of destruction of the ventromedial, dorsomedial, anterior, or periventricular nuclei (2-3 mA, 10-15 sec) the animals retain their ability to search for food and to eat. However, the motivational component of feeding behavior is appreciably suppressed. Even after 1-2 days of hunger the operated kittens search for food as if they were sated, without their usual purposefulness. They searched for the mother's teat not only on the belly, but also on the back and other parts of the body, and were often easily diverted from their search. These animals fully retained the entire complex of emotional affective hunger reactions: they moved about incessantly, fidgeted, and did not sleep and the level of their vocal reactions rose sharply. This dissociation of behavior clearly coincided with the changes in the bioelectrical rhythms: the high-amplitude, slow, motivation waves either disappeared or diminished in rate and amplitude in the operated animals nor were they observed in either the background rhythms or during the search or feeding. However, the high-frequency activity characteristic of the state of hunger was retained (Fig. 15).

In the experiments with stimulation of the medial nuclei of the hypothalamus behavioral patterns of 2 types were reproduced, namely, rage-type reactions (in the study they were appraised as reactions of "struggle for food") and searching reactions (increased sniffing, turning of the head from side to side, general searching movements). On stimulation of medial nuclei (5-20 V, 10 and 100 Hz) we observed an EEG desynchronization of slow high-amplitude rhythms similar to the high-amplitude waves obtained during natural feeding behavior. These findings are corroborated in the literature where experiments with stimulation of similar structures in adult animals have been described (Grastyan et al., 1966; Gromova, Tkachenko, & Provodina, 1965; Sollertinskaya, 1964). Thus, the experiments with destruction and stimulation of the medial hypothalamus warrant the conclusion that this structure has something to do with the formation of the feeding motivation and may be one of the sources of origin of the slow high-amplitude waves that reflect motivational excitation. However, the opinion that the medial hypothalamus is the satiation center and

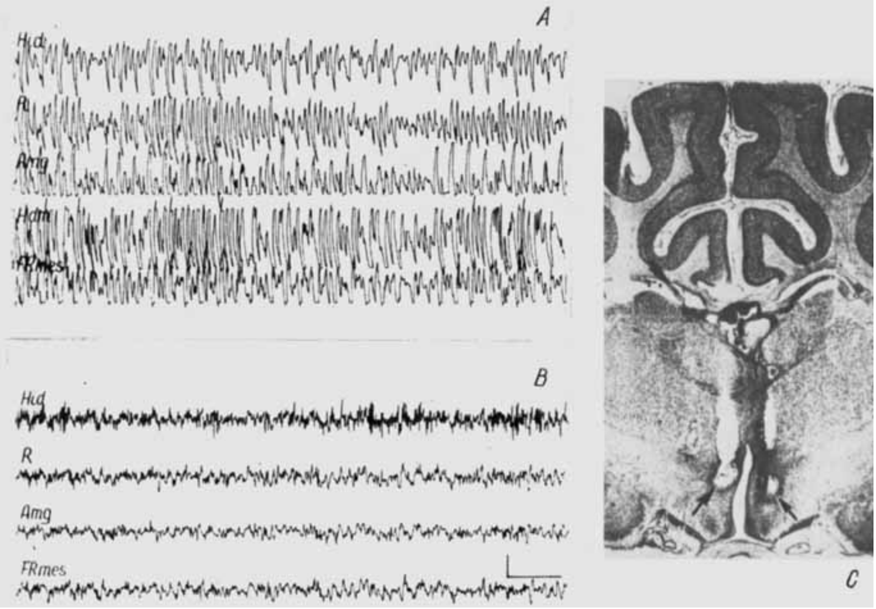


Fig. 15. (A) EEG patterns during meat consumption in intact kitten. (B) Same kitten after destruction of dorsomedial hypothalamus. (C) Microphotograph of destroyed region. Age of kitten: 45 days. Calibration: 50 μV/sec.

its function is not to activate but to inhibit the feeding behavior, became prevalent in the literature (Anand, 1971; Anand & Brobeck, 1951; Oomura, Ooyama, Yamamoto, Naka, Kobayashi, & Oho, 1967; Rozkowska & Fonberg, 1971). This point of view has now been subjected to considerable doubt and many propositions of this theory have been reconsidered (Bell, 1971; Panksepp, 1971a, b; Reynolds & Simpson, 1969; Shuleikina, 1971, 1972). The reason for the reconsideration was the incontestable proof that the functions of the ventromedial nucleus are of a more complex nature in that the inhibitory influences apply only to the act of feeding and not to alimentary behavior as a whole. Thus, by destroying the ventromedial hypothalamus and producing the phenomenon of hyperphagia, Grossman (1966), Lewinska (1967), and Miller (1961) showed that, although the operated animals ate more, they "worked" less to obtain this food. In short, the food-obtaining reactions were sharply decreased. Moreover, the operated animals proved extraordinarily discriminating in food preferences (Teitelbaum & Epstein, 1963). Another paradox was connected with the "motivational inertia" phenomenon appearing upon destruction of the ventromedial nucleus (Panksepp, 1971b): the operated rats lost their ability to increase the amount of consumed food after food deprivation. If this nucleus is regarded as the satiation center upon whose destruction the alimentary excitation must increase, these facts would be impossible to explain. Most likely, such facts can be explained only if the medial hypothalamus is assumed to be a structure of dual nature and has in its composition motivational elements of opposite signs capable of exerting either an inhibitory or an activating influence on the feeding motivation.

In our experiments on kittens we showed that the medial hypothalamus is really activated twice in the process of food-obtaining (Shuleikina, 1970 a, b; 1971).

It is activated once in hunger, during the search for food, and in other cases of feeding motivation. It is activated a 2nd time at the end of the feeding process, when the slow high-amplitude motivational waves cease to be recorded in the EEG and the character of bioelectric waves becomes relatively uniform; the animal meanwhile continues to eat (Fig. 16A) and bursts of rapid waves 30-40 per sec, of a small amplitude at first, begin to appear in the medial hypothalamus (Fig. 16B). As the animal becomes satiated, the latter activity increases, the potentials acquire a larger amplitude, and the intervals between the bursts decrease (Fig. 16C). When the animal ceases to eat the potentials disappear. The given waves may reflect still another aspect of the activity of the medial hypothalamus, namely, the connection of the inhibitory mechanisms that influence the feeding act and terminate it upon satiation.

The possibility that elements of a dual nature exist in the medial hypothalamus is now confirmed by many published reports: in the behavioral studies (Grastyan et al. 1966; Lewinska, 1967; Olds, William, & Briese, 1971), records of unit activity of

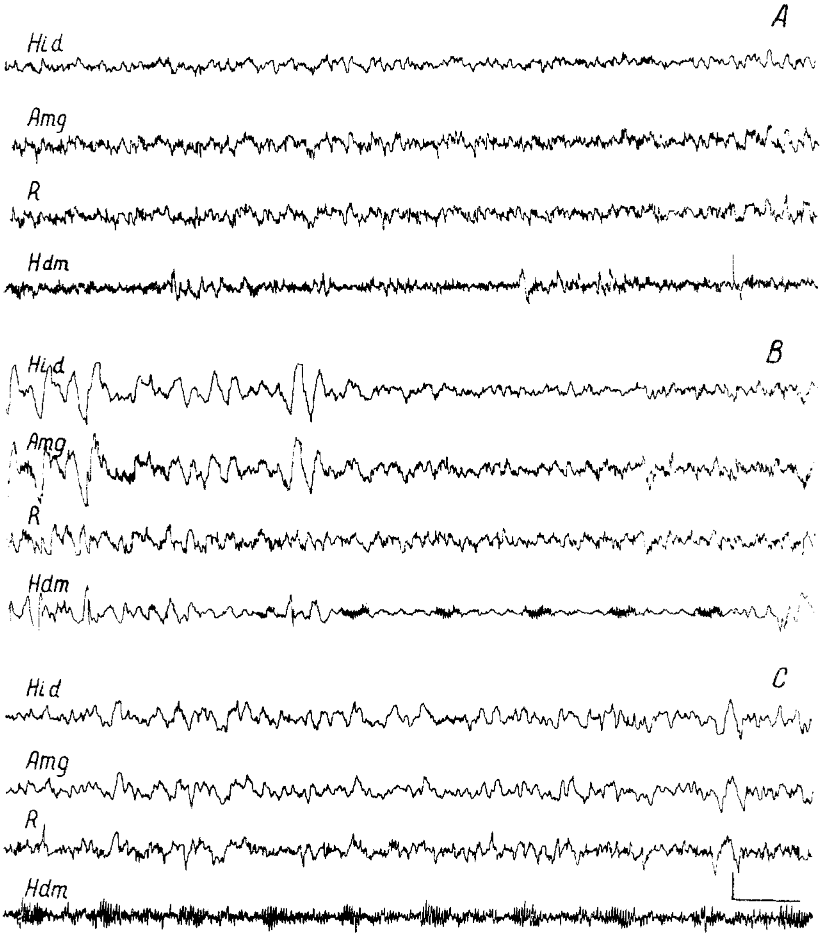


Fig. 16. EEG in successive records of food intake. (B, C) Bursts of rapid rhythms in medial hypothalamus appearing during animal's satiation. Age of kitten: 45 days. Calibration: 50 μV/sec.

ventromedial nucleus (Desiraju, Banerjie, & Anand, 1968; Murphy & Renaud, 1969), as well as by morphological studies of this structure (Leontovich, 1968; Murphy & Renaud, 1969; Szentogothai, Flerko, Mess, & Halasz, 1965).

Participation of Lateral Hypothalamus in Formation of Feeding Motivation

The question of the nature of feeding motivation is closely connected with the study of another important center of the hypothalamus: the lateral area. The direct experiments performed in our studies, as well as a number of recent reports, warrant the conclusion that the lateral hypothalamus should not be appraised as the center of hunger, but as the center that organizes the food intake and the processes of satiation that follow it. The likelihood of such an approach is supported by a series of facts that do not always agree with the theory developed in the studies conducted by Anand (1967, 1971) and Anand & Brobeck (1951).

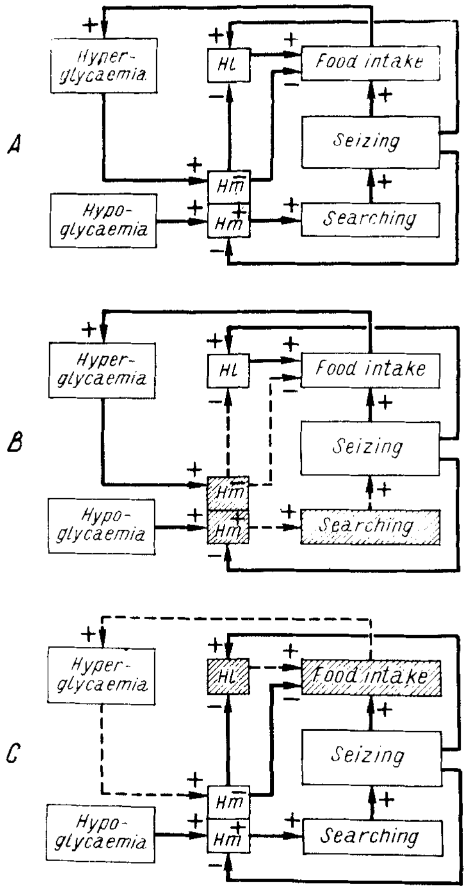
The 1st contradiction may be ascribed to the main proposition of the theory resting on the phenomena caused by destruction of this area. For example, hypophagia, which appears upon destruction of lateral hypothalamus, does not indicate a decrease in feeding excitation as a whole (Teitelbaum, 1971; Teitelbaum & Cheng, 1969). Baillie and Morrison (1963) showed that if rats (or rabbits: Anokhin & Sudakov, 1971) are taught to push a pedal in order to obtain food and the lateral hypothalamus is then destroyed, the animals refuse the food. The reaction of pushing the pedal—the motivationally most active part of feeding behavior—does not diminish. Clearly, destruction of the "hunger center" does not weaken the food-obtaining behavior in the hungry animal. Other, newer experiments lead to reexamination of the role of the lateral hypothalamus in feeding motivation (Valenstein, Cox & Kakolewski, 1970; Wise, 1974). Our own electrophysiologic findings show that the participation of the lateral hypothalamus in food-obtaining behavior is doubtful. Thus, during the search for food neither slow search motivational waves (Fig. 4B) nor any other changes in the initial background rhythms appear in the lateral hypothalamus of the kitten. In the adult cat, according to the Grastyan et al. data [1966], stimulation of the lateral hypothalamus inhibits the food-obtaining response. In addition to this are the data on the participation of the lateral hypothalamus in food-obtaining behavior [Di Cara & Wolf, 1968; Kozlovskaya & Belozertsev, 1966; Rozkowska & Fonberg, 1970].

The opinion on the participation of the lateral hypothalamus in the act of feeding is firmer. It is based on the phenomenon of hypophagia resulting from the destruction of the lateral hypothalamus, in numerous experiments of stimulating this zone, which causes or intensifies the act of feeding (Delgado & Anand, 1953), and on our findings of the existence of clear regular rhythms (10-20 cycles per sec) appearing in the lateral hypothalamus precisely during feeding as the animal becomes satiated (Fig. 3).

An analysis of morphological controls for the localization of electrodes from which we could record synchronization of 10-20 cycles per sec during feeding enabled us to demark the zone of distribution of these rhythms as covering the extreme dorsolateral portion of the lateral hypothalamus (Fig. 3B; Shuleikina, 1971). This region exactly coincides with the localization of the feeding center (Delgado & Anand, 1953), the representation of the forebrain synchronizing system in the lateral hypothalamus (Clemente & Sterman, 1963), and the zone of the maximal activity of the reward system (Olds, 1963; Olds et al., 1971). All of this indicates that these processes are interrelated in their physiological nature and probably are connected with the same population of neurons in origin.

Relationship of the Medial and Lateral Hypothalamus in Alimentary Behavior

The foregoing facts make possible the suggestion of a general scheme of interaction between the medial and lateral hypothalamus organized against the background of feeding behavior under the natural conditions of the organism's existence (Fig. 17A; Shuleikina, 1970 a,b; 1971; 1972). The state of hunger is associated with changes in many parameters of the organism's "milieu interieur" (Anand, 1971; Bell, 1971), one of which is the arteriovenous difference in glucose. For the


A
Hyper-glycaemia
HL
Food intake
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Hypo-glycaemia
Hm
Searching
B
Hyper-glycaemia
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Food intake
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Hypo-glycaemia
Hm
Searching
C
Hyper-glycaemia
HL
Food intake
Seizing
Hm
Hypo-glycaemia
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Searching

Fig. 17. Diagram of interactions between medial and lateral hypothalamus during alimentary behavior. (A) Intact animal; (B) after destruction of medial; (C) lateral hypothalamus.

sake of simplicity, we chose as the index of the internal environment only glucose for the reason that the ventromedial neurons have been shown by many researchers to be directly sensitive to glucose (Anand, 1967; Anokhin & Sudakov, 1971; Desiraju et al., 1968; Oomura et al., 1967). According to the hypothesis we are developing, a decrease in glucose activates the system of positive motivational neurons of the medial hypothalamus (Hm^+), the result of which is the search. The search is completed by a grasp of food. At this moment a burst of impulses comes from the receptors of the tongue, inhibits the positive elements of the medial hypothalamus, and simultaneously switches on the system of lateral neurons (HL). The impulses generated by the lateral hypothalamus trigger and reinforce the feeding act with the result that glucose begins to enter the blood stream from the depot. When the level of glucose reaches a certain critical value the negative neurons of the medial hypothalamus (Hm^-) are switched on to the system of feeding coordinations. They inhibit the activity of the lateral neurons and terminate the act of feeding, and final satiation ensues.

According to the above scheme, we can appreciate the behavioral changes that follow upon destruction of the medial or lateral hypothalamus. As was pointed out, contradictory information has accumulated, much of which has not been settled. The destruction of the medial hypothalamus (Fig. 17B), for example, together with its motivationally positive elements (Hm^+), manifests itself primarily in the fact that in a state of hunger the animal's feeding motivation and search for food diminish. If the animal grasps the food, the act of feeding is unaffected because the lateral hypothalamus (HL) has been preserved. Such animals, however, have no system that controls food intake, the injury having disconnected not only the positive neurons of the medial hypothalamus (Hm^+), but also the system of motivationally negative neurons (Hm^-) that normally inhibit the food intake. The injury results in a paradoxical situation in which the animal does not search for food, but having begun to eat cannot stop. This is the main and as yet unsettled contradiction in Anand and Brobeck's (1951) theory.

After coagulation of the lateral hypothalamus (Fig. 17C), the positive motivational neurons of the medial hypothalamus (Hm^+) remain intact and, thus, the food-obtaining activity is not diminished. However, although food can be grasped, the normal act of feeding is impossible because the lateral hypothalamus is destroyed and no reinforcement impulses are generated. This failure gives rise to another paradoxical situation: although the animal has high levels of hunger proper and searching activation, it rejects food and dies of emaciation.

Ontogenetic Features of Feeding Motivation

The foregoing scheme pertains to the general aspects of the motivational problem regardless of the animals' age. However, the studies of growing kittens also reveal ontogenic features of the phenomena.

The recording of motivational EEG waves during the 1st days of the kitten's postnatal life indicates that the activity of the nuclei of the medial hypothalamus at birth is fairly high. Furthermore, we have shown with destruction and stimulation of medial nuclei that the motivational waves can be deliberately reduced or reproduced even in kittens during the 1st days of life. The high level of maturation of the lateral hypothalamus is also indicated by other factors: EEG synchronization accompanying the automated rhythmic feeding movements has been recorded during this period, and synchronization can be evoked by stimulating the HL or eliminated during sucking by destroying this particular region of the brain.

Because we associate the nature of feeding motivation with the activity of these nuclei, can we regard as fortuitous the fact that the feeding motivation is fully formed at the time of birth? Of what general biological value can this be to the organism at this age? Because the mammalian offspring is born helpless but, by virtue of the biology of its feeding, is compelled to find and obtain food independently, the adequacy of the searching and sucking reactions is a *sine qua non* of its survival. The feeding reactions observed in the kitten immediately after birth and described above—the purposeful striving for the region of the teats, the active search, the struggle for "its own" teat, the almost continuous stay at the teat, and the duration of sucking during the 1st days of life—all indicate that these complex forms of behavior take place against the background of a particularly high level of motivational excitation that intensifies and supports these reactions. Figuratively speaking, the newborn kitten is a "cluster" of feeding motivations. From the point of view of survival, the additive nature of motivational excitation precisely during the 1st days of life is quite comprehensible. Only a high purposefulness of behavior and a persistence of the search can ensure the otherwise helpless organism the achievement of its reinforcement and the obtaining of food at the necessary time and in sufficient amounts. Two features may be regarded as reflections in the EEG of the elevated level of feeding motivation in the newborn kitten, namely, the independence of the motivational EEG waves from the level of appetite (in the satiated newborn kitten thay are almost as well pronounced as in the hungry kitten) and the generalization of the spread of these spindles (in the newborn they can be recorded in nearly all the structures of the brain; compare Fig. 1C and 2B,C).

The tendency of motivational excitation to spread in so generalized a manner at the early stages of ontogeny cannot be explained by the diffuseness of the process because the newborn kitten already has structures in which no motivational EEG waves are observed (Fig. 4). The generalization of motivational excitation can most likely be explained by the immaturity of its general coordinating mechanisms. Thus, bursts of rapid rhythms recorded in the medial hypothalamus at the end of feeding (Fig. 16) which reflect, in our opinion, the inclusion of inhibitory Hm^- elements of the medial hypothalamus as well as terminate the food intake are absent in kittens during the 1st days of life. In our studies these waves were not recorded before the 2nd or 3rd weeks. Therefore, we may conclude that the Hm^- elements of the medial hypothalamus do not as yet function in the younger kittens. This conclusion can be supplemented by an observation connected with destruction of the medial hypothalamus: according to literature, the destruction of the ventromedial hypothalamus in the adult leads to a dual effect, namely, a decrease in the food-obtaining function and a simultaneous appearance of hyperphagia (Anand & Brobeck, 1951; Lewinska, 1967; Miller, 1961, Rozkowska & Fonberg, 1971). By performing such operations on kittens we also produced a sharp decrease in the food-obtaining behavior. However, the phenomenon of hyperphagia was absent. If we conclude that the Hm^- neurons of the medial hypothalamus develop later, we can understand why the phenomenon of hyperphagia is not pronounced in newborn kittens. In the adult cat the destruction of the medial hypothalamus excludes the mechanisms that normally inhibit feeding, and this leads to hyperphagia. In the newborn kitten this does not happen because the inhibitory elements have not matured, and their destruction is useless. The destruction of the medial hypothalamus in such animals therefore only affects the search (already mature positive Hm^+ system) whereas the act of feeding remains unaffected: the newborn kitten has a natural hyperphagia. The immaturity of the inhibitory system (Hm^-) may also explain these peculiarities of the feeding behavior of an intact newborn animal, namely, its particular greed for food. During the 1st day of its life the kitten sucks almost incessantly (natural hyperphagia).

Conclusion

Proceeding from the principles of the functional system theory directly, we chose the structures that form the alimentary reactions for investigation in this program of studies. They comprise many formations widely known from literature, namely, Nauta's limbic brain stem circuit, the reticular formations of the thalamus and brain stem, and the synchronizing structures of the brain. We gave in this review some examples of the activity of these formations in waking animals. In all cases, we studied the EEG changes in strict correlation with behavior against the background of excitation adequate for these structures. To begin with, we managed to ascertain the role that the centers of the hypothalamus play in coordinating the alimentary reactions. With our new data we explained the contradiction in the well-known theory of hunger and satiation of Anand and Brobeck (1951). Our hypothesis is based on the notion of a dual nature of the medial hypothalamus that includes elements of both positive and negative motivational value. The analysis of morphological findings resulting from lesions and from stimulating electrodes warrants the locating of the alimentary center in the medial hypothalamus not only in the ventromedial nucleus but also the dorsomedial, periventricular, and anterior nuclei, which possesses related properties. A comparison of the facts known about the lateral hypothalamus from the literature with our findings on the distribution of synchronized rhythms appearing in this structure during food intake enabled us to distinguish in the lateral hypothalamus a locally circumscribed zone that may be regarded as the alimentary center proper. Our analysis of the observations made possible a description of the topography and properties of the activating system of the lower brain stem. After confirming Brodal's (1960) assumption and Jouvet's (1967) experimental findings that a powerful activating system exists at the level of the pons and medulla oblongata, we were in a position to show that the activating influences generated by this system can be observed not only during the paradoxical stage of sleep, but also in physiological hunger. Studies of the topography of this zone warrants the conclusion that the system activated in hunger is located below Jouvet's activating system but is directly continuous with it. According to our findings, this region covers the mediolateral part of the reticular formation at the level of the lower 1/3 of the caudal reticular nucleus of the pons and along the entire extent of the giant cell nucleus of the medulla oblongata. We assume that these structures occupy a key position in the organization of alimentary behavior by being located at the entrance of the alimentary functional system and, to a considerable extent, by determining and modulating not only the level of nonspecific hunger arousal but also the extent of feeding motivation.

Our studies enabled us to conceive the main features of the systemic organization of feeding behavior in the developing cat and to describe the succession of the processes that ensure the evolution of food-obtaining from hunger to satiation. The decrease in nutrient substances in the blood and the increasing hunger activate primarily one of the oldest mechanisms of the brain connected with regulation of homeostasis, the Nauta-Jouvet limbic brain stem structures: the dorsal hippocampus, nonspecific nuclei of the thalamus, central gray matter of the mesencephalon, and the reticular formation of the medulla oblongata and pons. The activity of these structures forms the 1st link in the development of feeding reactions in hunger, the nonspecific activation. Rapid rhythms, 30-40-60 cycles per second, are the EEG correlates of this state; general arousal is the behavioral correlate.

With the development of hunger a new system of structures which determine more specific forms of hunger–feeding motivation–joins the process. The system includes the neocortex, the amygdala, and the positive motivational neurons of the medial hypothalamus. These structures whose level of excitation is, in large measure, modulated by the activating reticular formations of the lower brain stem form the next link of the hunger behavior–the feeding motivation. The purposeful search for food is the behavioral correlate of this state and the high-amplitude, slow waves with frequencies of 3-6 and 6-8 cycles per sec are the EEG correlates.

The grasping of food and the beginning of its consumption initiate a series of processes that ensure the dynamics of satiation. The decisive role in the structural organization of these states is played by the synchronizing mechanisms of the prosencephalon and lower brain stem (lateral hypothalamus and nucleus of the solitary bundle), as well as of a group of specific relay nuclei with terminal links in the thalamus and orbital cortex that conduct the sensory information on the act of feeding and operate the processes of its self-regulation. The impulses generated by these structures ensure the mechanisms of reinforcement and the decrease in motivational excitation. Synchronization of 10-20 cycles per sec is the EEG correlate of this state; consumption of food with an increasing automation of the feeding movements and general calm of the animal are the behavioral correlates.

The terminal stage of the succession of phenomena under consideration is connected with mechanisms that regulate the amount of food intake and determine the inhibition of the feeding act when the animal is satiated. This is ensured by negative motivational neurons of the medial hypothalamus under whose influence the activity of the lateral hypothalamus is inhibited, and with their activation the food intake comes to an end and the animal passes to a state of quiet wakefulness or to sleep. At this time the EEG shows a return to the background rhythms characteristic of these states.

Notes

When the work for the manuscript was coming to its end on March 6, 1974, one of its authors, P. K. Anokhin, died. Professor Peter Kuzmich Anokhin was an outstanding Soviet physiologist, laureate of the Lenin prize, and academician of the USSR Academy of Sciences and the USSR Academy of Medical Sciences. This manuscript is his last publication. Obituaries to Prof. Anokhin were published in some of the journals (see, for example, *Brain Research, 83* (1975): 185-189).

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