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STABILITY OF THE BEHAVIORAL SPECIALIZATION OF NEURONS

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The constancy of the association of the activity of the neurons of the limbic cortex and food-procuring behavior has been analyzed in neurons specially selected on the basis of the criterion of length of recording in experiments in rabbits. Comparison of the activity in the first and second halves of the period was carried on the basis of the average frequency for the time of each half of the recording, the average frequency in each of 10 distinctive acts of cyclical behavior, as well as on the basis of the probability of the presence of activation in these acts. It was demonstrated that behavioral specialization, defined as the presence of 100% activiation of the cell in specific acts, did not change in the course of the recording, and was a stable information-containing characteristic of the association of the activity of the neuron with the animal's behavior.

Data have been obtained in investigations of the activity of neurons in the free behavior of animals regarding the link between the activity of neurons and behavior [1, 13, 14, 18, etc.]. We have also found behavioral specialization of neurons of different regions of the rabbit brain when we compare their activity with food-procuring behavior, when a rabbit is required to press on one of the pedals placed in neighboring corners of an experimental chamber in order to obtain food from a food dispenser [11]. At the same time, a relatively large number of neurons whose activity is associated with the approach of the rabbit to the pedal and with pressing it, have been found in the limbic cortex (the retrosplenial region, which is found on the dorsal surface of the hemispheres). Each neuron was recorded on the average of 3–5 min. In the process, the rabbit completed eight to ten runs from the pedals to the food dispensers and back on each side of the cage. The presence of discharges or activation of this neuron in all realizations of the "specific" act was taken as the criterion of the specialization of the neuron in relation to the behavioral act, and the degree of activation was judged on the basis of rasters, histograms, and video recordings of the activity of the neuron; the establishment of the specialization was somewhat subjective in character.

In the present study we decided to test whether the behavioral specialization of the neuron remained constant when it was recorded over a long period of time. In order to remove the element of subjectivity in establishing the specialization of the neuron, we employed a specially developed mathematical analysis; neurons with a recording time of not less than 15 min (on the average 20–30 min) were selected for analysis.

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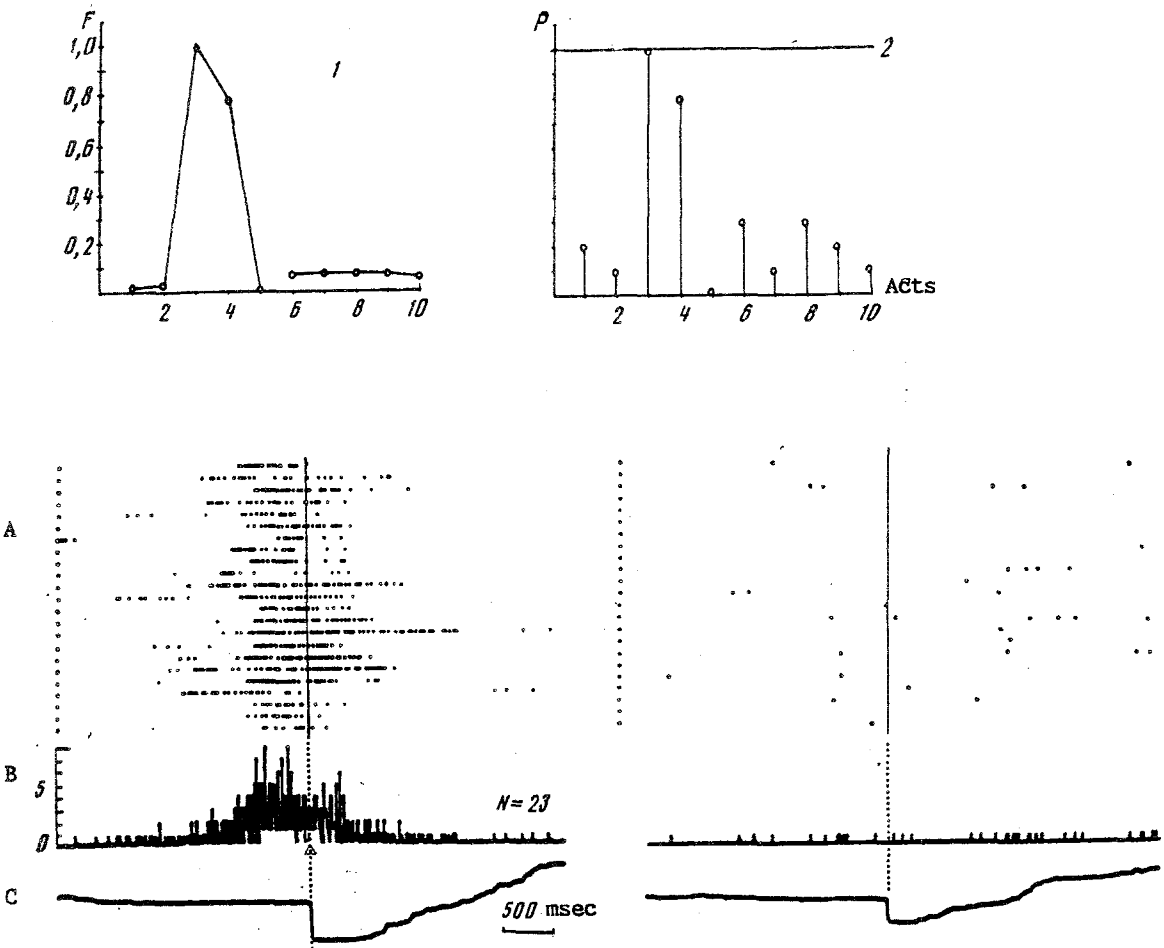

Fig. 1. Various means of representing the activity of a neuron. Above: graphic representation of the activity of a neuron. In graph 1, the pattern of the distribution of average frequencies of the activity of a neuron in acts of cyclical behavior. Along the abscissa: the numbers of the acts; along the ordinate: the normed average frequency of the activity. In graph 2, the probability of the presence of activation in the same 10 acts. Along the abscissa: the numbers of the acts; along the ordinate: the probability of the activation of a neuron in the corresponding act. Below: A) rasters of the activity of the same neuron; B) histogram; C) averaged marker of pedal pressing (on the left, the left pedal; on the right, the right pedal), relative to the beginning of which the rasters were registered and the histograms constructed.

METHODS

The experiments were carried out on rabbits during food-procuring behavior in a cage with two food dispensers and two pedals in the corners. The rabbit, in order to obtain food from the dispenser, had to press on the pedal which was located in the neighboring corner of the experimental cage. The effectiveness of the pedals was changed after 10–20 runs of the rabbit along each wall of the cage from the pedal to the food dispenser and back. The spike activity of individual neurons of the limbic region of the cortex (P = 8–10, L = 2–3) was recorded in prelin inarily trained rabbits by means of glass microelectrodes filled with a 3 M solution of KCl, with a tip diameter of 1–3 μm and a resistance of 3–7 MΩ on a frequency of 1000 Hz. The search for the neurons was accomplished by the remote-controlled embedding of a microelectrode using a pneumatically directed micromanipulator fixed to the animal's head. The neuronal activity as well as the behavioral markers were recorded on a Nihon Kohden (Japan) tape recorder with subsequent replication on paper. The behavioral markers were obtained by means of light diodes placed in the food dispenser, at the pedal, and in the middle of both side walls of the chamber, as well as by means of photoelectric narrowly-oriented plates on the head of the rabbit, in the food dispensers, and on the pedals. Therefore, in reproducing the activity of the neuron, we had markers of the placement of the rabbit's muzzle in the food dispenser, of the pedal press (the placement of the paw on the pedals), as well as of the moment of the rabbit's passing the mid-

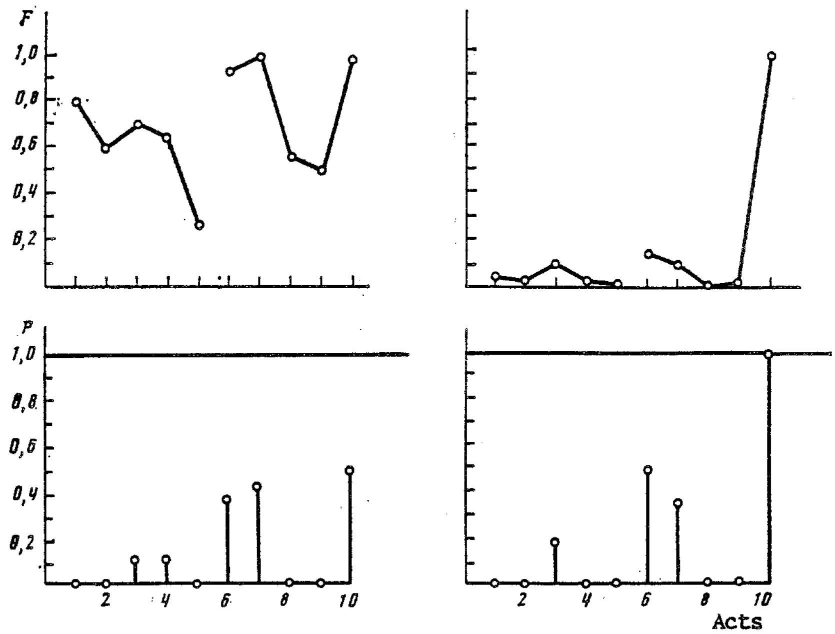

Fig. 2. Graphic representation of the activity of a nonspecialized (left) and a specialized (right) neuron in relation to act No. 10. Upper graphs) distribution of average frequencies of the activity in individual acts of cyclical behavior; lower graphs) probability of the presence of activation in the corresponding acts (designations as in Fig. 1).

dle of the side wall, i. e., of a turn toward the pedal or food dispenser. Concurrently the behavior of the rabbit was recorded on a video tape recorder, which offered the possibility of more precise comparison of neuronal activity with behavior. The data obtained were analyzed on a Sega-3000 personal computer (Japan).

INVESTIGATION RESULTS

Twenty-four neurons out of 150 neurons of the limbic cortex recorded in one rabbit were selected with a prolonged period of recording, i. e., with repeated changes of the effective pedal (50–150 behavioral cycles). These neurons were recorded during eight embeddings of the electrode in different layers of the limbic cortex of a depth of 182–1745 μm, counting from the surface of the cortex (the moment of contact).

The following were selected as the characteristics of the activity of the neuron: the average frequency of spike activity in a specific act and the probability of the presence of activation in the act. Preliminarily, each behavioral cycle on both sides of the cage was divided in accordance with the behavioral markers into five stages (as a rule, a specific behavioral act corresponded to each stage). Thus, the following acts were distinguished in the behavioral cycles on the left side of the cage: No. 1, the placement of the rabbit's muzzle in the food dispenser, the taking of food; No. 2, the chewing of food in a posture of comfort or the beginning of a turn toward the pedal (up to the marker of the turning); No. 3, the approach to the pedal (from the marker of the turning to the pressing of the pedal); No. 4, the pressing of the pedal; No. 5, the approach to the food dispenser. Analogous stages (acts Nos. 6–10) were distinguished in the behavioral cycles on the right side of the cage. The duration of each act was, in sec: No. 1, 2.2; No. 2, 1.4; No. 3, 1.5; No. 4, 0.9; No. 5, 1; No. 6, 1.9; No. 7, 1.7; No. 8, 1.5; No. 9, 0.8; and No. 10, 1.2. A program was developed for the graphic representation of the parameters of the activity of the neuron in the acts of cyclical food-procuring behavior under study in the cage (Fig. 1). The activity of the same neuron in the form of a raster and histograms, combined with the averaged markers of the behavior, is represented in the lower part of Fig. 1.

The average frequency of the activity over the entire period of its recording was calculated for each neuron. It ranged from 0.5 to 11.6 spikes in 1 sec for the neurons selected. The exceeding by the frequency of the activity in one or several acts of the average frequency of the activity of a neuron over the whole period of its recording, by not less than a factor of 1.5, was taken to indicate activation. A neuron was considered to be specialized relative to a specific behavioral act if activation in this

TABLE 1. Rank Distributions of the Coefficients of Variation of the Frequencies of Discharges of Specialized Neurons in Behavioral Acts of the Rabbit Completed on the Left and Right Sides of the Experimental Cage

Numbers of the neurons	Specialization (numbers of the acts)	Left					Right				
		№ 1	№ 2	№ 3	№ 4	№ 5	№ 6	№ 7	№ 8	№ 9	№ 10
52	Approach to the right pedal	9	5	3	8	6	10	4	1*	7	2
		8	9	2	5	4	7	6	1*	10	3
59	The same	9	5	3	4	8	7	10	1*	6	2
		10	6	5	4	2	8	7	1*	9	3
113	»	6	9	1	3	10	8	7	2*	5	4
		8	5	2	3	9	10	7	4*	1	6
57	Approach to the right food dipsenser	—	—	2	6	—	—	4	3	5	1*
		—	—	2	—	—	6	4	3	5	1*
98	The same	2	7	4	9	3	5	6	8	10	1*
		2	4	8	9	3	7	5	10	6	1*
62	Approach to the left food dispenser	6	7	8	3	1*	4	5	10	9	2
		9	4	7	3	1*	6	8	10	5	2
136	The same	1	9	5	7	2*	6	8	4	3	10
		1	10	9	7	2*	3	5	6	4	9
104	Leaning, taking from the right food dispenser	3	6	5	7	8	1*	4	9	10	2*
		3	7	5	9	6	2*	4	8	10	1*
127	The same	4	5	3	8	7	2*	9	6	—	1*
		7	6	9	4	8	2*	5	3	10	1*
66	Approach to any food dispenser	8	7	9	10	1*	3	4	5	6	2*
		10	4	9	7	2*	3	6	5	8	1*
67	Taking from any food dispenser	2*	8	6	—	5	1*	3	9	7	4
		1*	9	6	8	3	2*	4	10	7	5
132	The same	1*	7	6	10	8	2*	9	5	4	3
		2*	6	5	8	10	1*	7	4	9	3
49	Movement (head raising)	—	—	5	1*	2	3	6	7	4*	8
		6	9	1	5*	8	2	4	7	3*	10
50	Movement (turning to the right)	6	8	1*	5	10	2*	3	9	7	4
		4	8	1*	5	7	3*	2	10	9	6

Note. –) Absence of activity in an act. Opposite each neuron, the upper line of ranks represents the beginning, and the lower, the end of the recording; *) ranks of specific acts.

act was observed in all of its behavioral realization (100%). A neuron in which 100% activation was observed in act No. 3, i.e., it was specialized relative to the approach to the left pedal, is presented in Fig. 1.

In nine cells among the 24 neurons analyzed, persistent changes in activity was not found in any of the behavioral acts observed; a slowing down of the activity took place in one neuron during leaning and the taking of food by the rabbit from the right-hand food dispenser. We classified these 10 neurons as nonspecialized, i. e., not displaying persistent activations in any of the behavioral acts studied (Fig. 2, on the left). Activations which were constantly associated with any of the distinctive acts of cyclical behavior were found in the remaining 14 cells (the specialized neurons). In two of the neurons the activations were observed during certain movements of the animal; in one, during movements of the head; in the other when the rabbit turned to the right. The activity of three neurons changed during approach to any food dispenser (one neuron) or the seizing of food in it (two neurons). The activity of two neurons changed during the approach and the taking of the food in one of the food dispensers; the activity of four neurons changed only during the approach to one of the food dispensers. The activity of one of the neurons of this group is represented in Fig. 2 (on the right). Activations were observed in the neurons during the approach and the pressing of one pedal (in one of these activity changed also when the rabbit pressed the other pedal, but not in 100% of cases). The activity of one of the neurons of this group is represented in Fig. 1.

An analysis of the variation of the frequency in each of ten distinctive acts was carried out for the specialized neurons. A rank from 1 to 10 was assigned (for each neuron the rank of 1 was assigned to the act with the minimal coefficient of variation, and the rank of 10 to the act of maximal coefficient) to each of the distinctive acts in accordance with the value of the coefficient of variation. It turned out that the coefficient of variation in specific acts was significantly lower for neurons which were specialized relative to specific acts of cyclical food-procuring behavior (i. e., with the exception of two neurons specialized relative to movement) than in the remaining acts ($p < 0.001$ according to the Student t test). The average rank of the coefficient of variation in specific acts was 1.53. In ten neurons the coefficients of variation proved to be minimal in specific acts (Table 1).

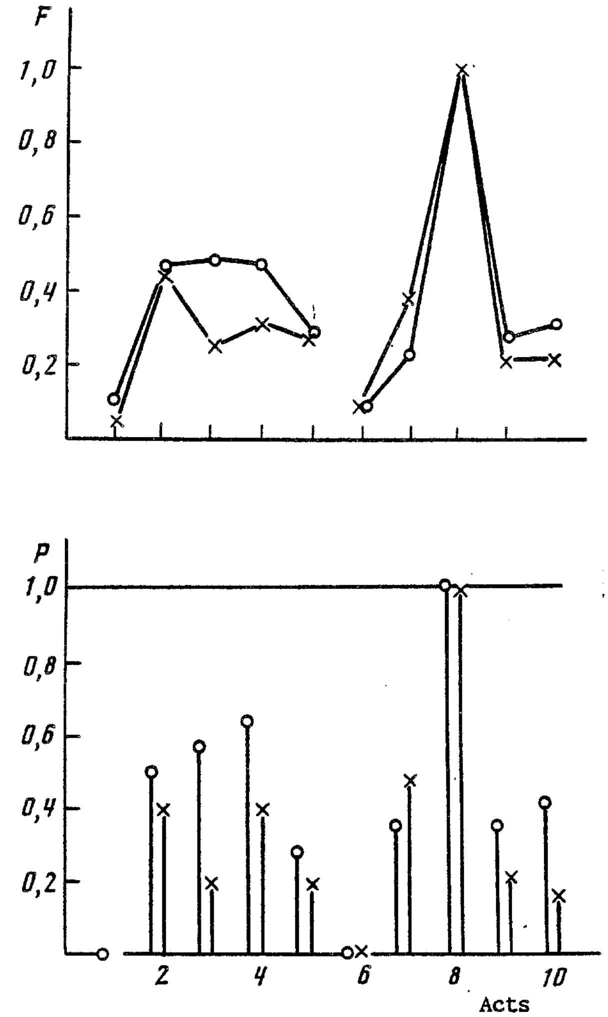

Fig. 3. Activity of a neuron specialized in relation to approach to the right pedal, at the beginning and end of recording. In the graphs, the patterns of the activity of neuron No. 59 at beginning (circles) and end (crosses) of recording. Designations as in Fig. 1.

In order to analyze the stability of the established behavioral specialization of the neurons, the recording time of each neuron was divided into two halves, the beginning and end of the recording, over the duration of which not less than 10 behavioral cycles were observed on each of the sides of the cage. The activity of the neuron was analyzed separately in each half: the average frequency of the activity in the period of the corresponding half of the recording was calculated, as well as the average frequency of activity in each act. On the basis of the calculation of the probability of activation in the individual acts of the behavioral cycle at the beginning and at the end of recording, it was determined whether the specialization of the given neuron had not changed during the time of its recording.

The analysis showed that 100% activation was observed in the same acts at the beginning and end of the recording in 12 cells out of 14 specialized neurons. Neuron 59 (specialization: approach to the right pedal) is presented as an example in Fig. 3. It can be seen from the upper graph that the maximal average frequency at both the beginning and the end of the recording is observed in act No. 8; there is a 100% activation both at the beginning and the end of the recording, as can be seen from the lower graph, in the same act.

Some changes in activity took place in the process of recording in two neurons. Thus, in neuron 113 (specialization: approach to the right pedal), 100% activation was observed in the acts of approach to the right pedal at the beginning of the recording, whereas the corresponding activation was not observed at the end of the recording in one of the behavioral cycles. It was established on the basis of the analysis of the video recording that the absence of activation during the approach of the rabbit to the right pedal in one of the cycles was associated with a non-standard performance of the act. In neuron 132 (specialization: the taking of the food in any food dispenser), 100% activation was observed at the beginning of the recording when the muzzle of the rabbit was in the right food dispenser. At the end of the recording, this activation was identified not in 100, but in 90% of cases. Additional analysis of the activity of this neuron based on the video recording and neuronogram demonstrated that activation takes place only prior to the moment that the rabbit takes the food, and not during the whole time that the rabbit's muzzle is in the food dispenser. Therefore, in one of the realizations, when rabbit's muzzle was in the food dispenser for a long time, the actual frequency of the "taking" activation, relative to the entire time the muzzle was in the food dispenser, did not reach the criterion of activation. For the same reason, the probability of activation in the movement neurons in the corresponding acts could not reach the 100% level, since the movement occupied only a part of the act with respect to the duration of the movement.

Thus, the behavioral specialization did not change in the process of the recording in all of the 14 specialized neurons. In ten neurons which were identified as nonspecialized at the beginning of the recording, specialization also was not identified at the end of the recording.

A comparison of the patterns of distribution of the average frequencies of the activity with respect to the acts of cyclical behavior at the beginning and the end of recording, as well as of the average frequencies of activity in the corresponding period of recording, was made in order to accomplish a more refined analysis of the stability of the association of the activity of a neuron with a behavior. It turned out that the average frequency of the activity in ten neurons during the time of recording increased significantly ($p < 0.05$ by the Student t test). The changes did not reach the level of significant differences in the remaining 14 neurons (a weak increase was observed in 11 cells, and in three, some decrease in frequency). We delineated on this basis highly stable (I) and relatively stable (II) recording conditions (respectively, the absence of differences, or a significant difference in the average frequencies during the time of the recording), which proved to be highly important in the subsequent analysis of the constancy of the association of the activity of a neuron with a behavior.

The extent of the changes in the pattern of activity of a neuron in the process of recording was assessed on the basis on the number of acts of cyclical behavior in which the average frequencies of the activity changed. It was found that significant changes affected from zero to eight acts (out of 10 distinguished). In recording conditions II, the changes affected a larger number of acts (on the average 4.1) than in recording conditions I, on the average 2.57 ($p < 0.05$ according to the Student test).

In addition it turned out that significantly more nonspecialized neurons were recorded in recording conditions II than in recording conditions I. Thus, there were seven nonspecialized neurons out of 10 recorded in recording conditions II, while in recording conditions I there were two nonspecialized out of 14 recorded ($p < 0.05$ by the chi-square test).

The ratio of the average frequency of activity in a specific act in the specialized neurons to the average frequency during the time of recording in recording conditions II proved to be signficantly higher than in recording conditions I ($p < 0.05$). The neuron represented in Fig. 3 may serve as an example of a small difference between the frequency in a specific act and the remaining acts; the graph presented in Fig. 2 (on the right) illustrates a high ratio of these frequencies.

Thus, the results obtained attest to a constancy of the association of the activity of specialized neurons with a specific act of cyclical food-procuring behavior both with respect to the probability of the presence of activation in a specific act and with respect to the pattern of the distribution of the average frequencies in the act. At the same time, some characteristics of the activity of the neuron in behavior depend on the conditions of its recording.

DISCUSSION OF RESULTS

The constancy of behavioral specialization was investigated in the present study in 24 neurons of the limbic cortex, selected out of 150 recorded on the principle of the duration of recording. The representativeness of this sample can be evaluated on the basis of the data obtained in our previous investigations [6, 10], in which the classification of the neurons of the limbic cortex was carried out on the basis of their belonging to functional systems of various "ages". Among 132 neurons analyzed, 57 (43%) nonspecialized in a given behavior were distinguished, 30 (22.7%) specialized in relation to the old systems, the "ur-systems" (the "movement" and "seizure in two food dispensers" neurons were assigned here), and 45 (34%) specialized in relation to the functional systems in new behavioral acts acquired by the animal directly during training in the experimental chamber (the "taking in one food dispenser" and "approach and pedal pressing" neurons, and the "neurons of place"). Of the 24 neurons selected in the present investigation, ten were nonspecialized in a given behavior (41%), five were specialized in relation to the "ur-systems" (20.8%), and nine were specialized in relation to new systems (37.5%). Differences between the number of neurons in each of these three groups were not significant; for this reason this sample can be considered sufficiently representative.

The main result obtained in this study regarding the constancy of the behavioral specialization of the neurons is in agreement with the data in the literature. Thus, in studies of B. N. Bezdenezhnykh investigating an iontophoretic effect on neurons of the visual and somatosensory region of the cortex, it was demonstrated that the structure of the activation of a neuron is preserved even after a change in the total level of its activity under the influence of a-glutamate or acetylcholine [4]. The invariability of the association of the activity of a neuron with a behavior over the course of several hours of recording has been reported in a large number of studies investigating neuronal activity in various structures of the brain during behavior [16, 17]. As the result of the analysis of numerous experimental data V. B. Shvyrkov [8] believes that all neurons are system-specific relative to the behavioral acts of different phylo- and ontogenetic ages, and that this specialization is constant over the course of the entire life of the cell.

It is evident that the identification of specialized neurons is determined to a significant degree by the criterion of specialization. In our study we used the criterion of the obligatory (100%) presence of the activation of the neuron in all realizations of the specific behavioral act. At the same time, in the studies of other authors, a significant change in the frequency of the impulse activity of the neuron at the corresponding stage of the behavior has been used as the criterion of specialization [2, 3, 15, etc.]. However, the mathematical analysis carried out by Bobrovnikov [5] has demonstrated that such a criterion at the significance levels utilized in biology for the acceptance of hypotheses (0.05–0.01) is inadequate for the corroboration of the obligatory character of the simultaneous activation of all specific neurons at the corresponding stage of a behavior. The specific activity defined on the basis of our criterion (100% presence of activation) satisfies the significance level (0.001) calculated in the study of Bobrovnikov, which makes it possible to speak of the synchronous activation of all specialized neurons during the realization of the corresponding behavioral act.

At the same time, the so-called movement neurons [12, etc.], the activity of which is associated not with one of the distinctive behavioral acts, but with a specific movement of the animal, which in terms of duration may comprise varying portions of the act, make up a substantial group among the specialized neurons. The activations of such neurons are found to be variable in relation to a specific act and do not always reach the established criterion. As can be seen from the table presented, the coefficient of variation in these neurons in acts in which specific activation is observed is not minimal as it is in the majority of the other specialized neurons. Such cells precisely, which belong to the "ur-systems" which are formed in early ontogenesis [9], constitute, in our opinion, the variable part of the integration which controls the realization of the specific behavioral act.

The coefficient of variation of the average frequency in the acts which are specific for a given neuron is significantly lower than in other acts. In our view, this implies that the activation of a specialized neuron in a concrete specific act is necessary for the realization of the functional system of this behavioral act, and, to the contrary, the variable activity in the other acts implies its nonobligatory character for the realization of the functional systems of the corresponding acts. Thus, the behavioral specialization of a neuron is an information-rich, stable characteristic of the association of the activity of a neuron with a behavior, and implies the appurtenance of the given cell to the functional system of the corresponding act [8, 9].

When the neurons whose activity was recorded in recording conditions I and II are compared, a difference with respect to the three parameters investigated is discovered. 1) A difference with respect to the classification parameter, the change in the average frequency of the activity during the recording period. We associate the significant increase in the average frequency of the activity of the neuron during the recording period in recording conditions II not with functional changes in the operation of the brain [7], but with the mechanical stimulation of the body of the neuron by the tip of the microelectrode. Favoring this are the sharp changes in the frequency of discharge and the forms of the neuronal spikes observed immediately after the recording of a number of such cells. 2) The change in the average frequency of the activity in a large number of acts in recording conditions II, which implies high variability in the activity of the neuron in each specific act in the process of recording in these conditions. 3) The large value of the ratio of the average frequency of the activity in the specialized act to the average frequency of the activity in the recording period, which was found in recording conditions II. The differences discovered attest to the unfavorable influence of recording conditions II on the identification of specialized neurons. This is confirmed by the fact that a significantly greater number of neurons with unestablished specialization are found in conditions of relatively stable recording (II). The mechanism of this influence may be the following: if a specialized cell is imagined which in the conditions of highly stable recording (I) has a small value of the ratio of the average frequency of activity in the specialized act to the average frequency of the activity in the behavior, in recording conditions II, the specific activity of this cell will not satisfy the criterion of the presence of 100% activation due to the increase in the average frequency of the activity in the behavior and the greater variability in the act.

CONCLUSIONS

1. The behavioral specialization of a neuron is a stable, information-rich characteristic of the association of the activity of a neuron with behavior.

2. The extent of changes in the pattern of the association of the activity of a neuron with a behavior in the process of recording is determined to a significant degree by the recording conditions; the extent of these changes is minimal with a constant average frequency of the activity of a neuron over the course of the entire recording period.

3. When the average frequency of a neuron changes in the course of the recording, it is possible to detect only the most distinct specializations, which leads to a decrease in the relative number of specialized neurons in the sample of the recorded neurons.

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