ROLE OF GOAL IN DETERMINATION OF NEURONAL ACTIVITY OF THE RABBIT
MOTOR AND VISUAL CORTICAL AREAS

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It was shown earlier [1] that the composition of the neurons of the rabbit motor and visual cortical areas activated when achieving one and the same result — grasping of food — is not substantially affected either by the mutual arrangement of the animal and environmental objects or by the motor characteristics of the behavioral act. Even under such an effect as preventing contact of the animal with the "visual part" of the environment (covering the eyes with lightproof hoods), the overwhelming majority of the neurons of the motor cortex and 60% of the neurons of the visual cortex continue to be activated in the behavioral act of grasping food [2]. On the basis of the data obtained it was suggested that activation of cortical neurons during a behavioral act depends on the result of the behavior and is not determined uniquely by the parameters of movements and the environment.

It follows from this assumption that the compositions of the activated neurons of the motor and visual cortical areas should differ in behavioral acts directed at achieving different results, even with the same movements in the same environment. The purpose of our investigation was to determine whether the given consequence actually occurs and thereby to check the assumption about determination of the composition of neurons activated in a behavioral act by a model of its result — goal.

METHODS

Chronic experiments were conducted on two rabbits. The animals were trained to grasp a nonfood object, a piece of plastic (P), and a food object, a piece of carrot (C), from a feeder. The P and C pieces were identical in size, shape, and visual characteristics; the differences in power at the corresponding wavelengths of the spectrum of light reflected by the P and C began in the region of 600 nm (determined on a Specord M40, East Germany), i.e., precisely in that range in which the sensitivity of the rabbit, determined by behavioral criteria, drops to zero [13]. Consequently, the "visual part" of the environment was the same for the acts being realized. In the cups of the feeder, served by the experimenter, after each P piece was placed a C piece, which the animal had the opportunity to grasp only after removing the P piece from the preceding cup. As soon as the animals were trained to grasp the P piece immediately after presentation, assuming a fixed pose before the act of grasping the P piece and act of grasping the C piece following it (the head of the rabbit was located over the feeder), the activity of the neurons of the anterolateral part of the motor and visual cortical areas were recorded (coordinates A-2-3, L-4 and P-9, L-8, respectively according to the atlas [12]). The neuronal activity was recorded by glass microelectrodes filled with a KCl solution (2.5 moles/liter). The tip diameter of the electrode was from 1 to 5 μm, the resistance was 6-12 mΩ at frequency 1.5 kHz. In addition to this, the electrical activity of the posterior part of the deep portion of the musculus masseter and head movements of the rabbit during tilting into the feeder were recorded. The activity of the m. masseter was recorded by intramuscularly implanted bipolar wire electrodes; the head movements were recorded by means of photoelectric sensors. The indicated parameters were recorded on a NO-46 tape recorder. Video recording of the behavior of the animal was carried out simultaneously on a PMV-508 video tape recorder; indicators of the time counters and the number of neuronal impulses (for more details see [4]) as well as a light indicator of serving the feeder were placed at the bottom of the frame.

Correspondence of neuronal activity to particular stages of behavior was determined by plotting histograms and scans, which made it possible to determine those instants of behavior to which, despite the variability of the latent periods of the acts and durations of individu-
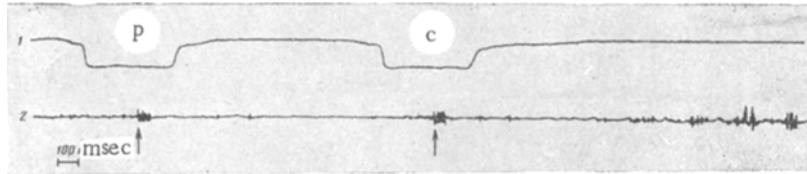
Fig. 1. Representation of motor indices of behavioral acts of grasping the plastic (P) and carrot (C): 1) record of head movements; 2) EMG of the masseter proper. Details are given in the text.

al movements, was confined activation of each individual neuron in successive realizations. An increase of the frequency of impulse activity during a certain stage of behavior by 50% and higher compared with the "background" level was considered activation. The frequency of impulse activity before realization of the next pair of acts of grasping the P and C pieces was taken as the "background" frequency. The significance of the difference of activations in the compared acts was estimated by the sign test and the significance of the differences in the number of neurons belonging to different groups by the chi-square test for $p < 0.05$.

RESULTS OF INVESTIGATIONS

The acts of grasping the P and C pieces were similar with respect to the recorded electromyo- and actographic indices (Fig. 1). In both acts the following stages were distinguished: 1) lowering the head into the feeder (downward deflection of curve 1); 2) grasping of the objects proper (opening and closing the mouth), the instant of which was determined by the phasic burst of activity on the EMG (the arrows on curve 2) following tonic activity related to maintaining the lower jaw in a resting position during movement of the head [3]; 3) lifting the head from the feeder (upward deflection of curve 1). Gnawing and chewing the C piece began after lifting the head (see curve 2; regular phasic bursts on the EMG begin after return of the head to the initial position).

The activity of 201 neurons was investigated during realization of the acts of grasping the P and C pieces: 103 of the motor and 98 of the visual cortical areas. Of them, 47 neurons of the motor and 41 of the visual cortex were activated at one or another stage of behavior.

On comparing the activity of the neurons in the acts of grasping the P and C pieces it was found that some of them are activated in both acts, and others only in one of them. The number of neurons beloinging to these groups is given in Table 1.

Figure 2 shows examples of neurons of the motor and visual areas activated both in the act of grasping the P piece (to the left of the wavy line) and in the act of grasping the C piece (to the right of the wavy line). Activation of the neurons could occur at two or all three stages of behavior (see the neuron of the motor cortex activated in both acts during tilting, grasping the object, and raising the head to the initial position) or only in one of its stages (see the neuron of the visual cortex activated only when tilting the head).

Of the 27 neurons of the motor cortex and 34 neurons of the visual cortex activated in both acts, respectively, 20 and 23 discharged in the acts of grasping the P and C pieces at the same stages (Fig. 2), and, respectively 7 and 11 at different stages (for example, during tilting of the head in the act of grasping the P piece and grasping the C piece with teeth). Even for those neurons which were activated in the same stage of the behavioral acts of grasping the P and C pieces differences were noted in impulse activity: a shift of activation in one act compared with the other; lengthening or shortening of activations; change in their expressivity. Thus, a comparison of the number of spikes in the activations of 28 neurons (13 of the motor and 15 of the visual cortex) activated in the same stage in the acts of grasping the P and C pieces revealed a significant difference in 9 cells (3 of the motor and 6 of the visual cortex). An increase of the number of spikes in the act of grasping the C piece compared with the act of grasping the P piece occurred in 8 of them, and a decrease only in 1. Thus many neurons that participated in providing both acts were activated in them differently.

It is seen from Table 1 that both in the visual and in the motor cortex there were neurons activated only in one of the acts (Fig. 3). Selective participation of neurons could be manifested not only in the presence of activation in one of the acts but also in an opposite change in the frequency of impulse activity: activation in one act and inhibition in the oth-
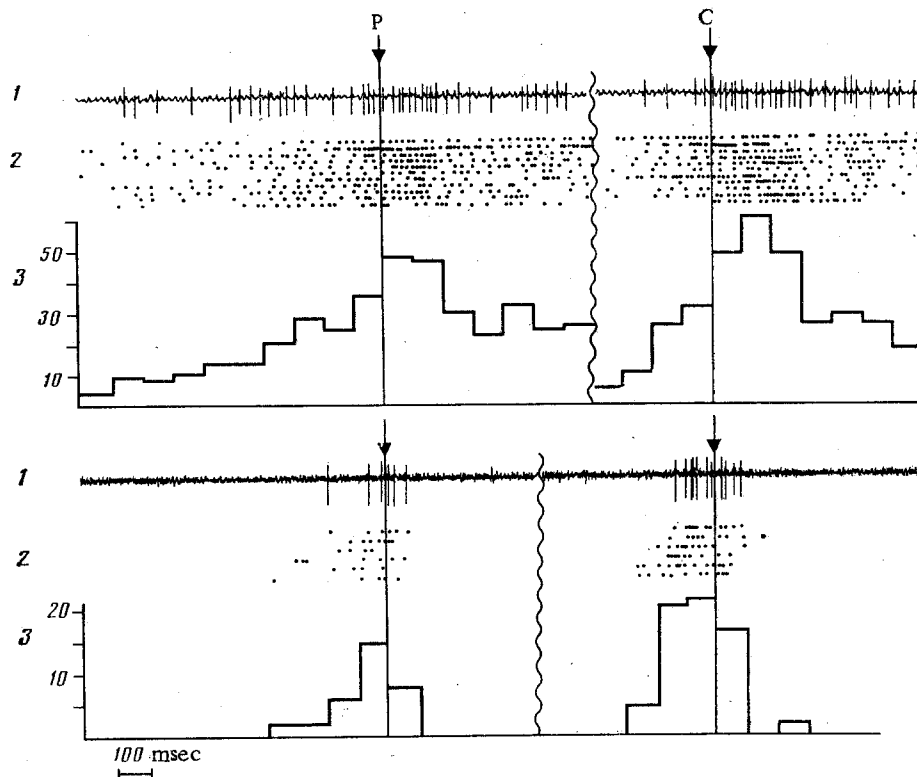
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Fig. 2. Examples of neurons of the motor (top) and visual (bottom) cortical areas activated in both acts: 1) neuronogram; 2) scans; 3) histograms of neuronal activity. The histograms and scans of the neuronal activity of the motor cortex are plotted from the instant the face intersects the plane of the opening of the feeder during tilting of the head for food, n = 11. (Tilting of the head for food began on average 346 ± 76 msec before the instant of intersecting the plane of the feeder opening.) The histograms and scans of neuronal activity of the visual cortex were plotted from the end of tilting the head into the feeder, n = 11.

TABLE 1. Number of Neurons of the Motor and Visual Cortical Areas Activated in Both Acts (grasping of the P and C pieces) and Only in One of Them

Cortical area	Total number of activated neurons	Neutrons activated in both acts	Neurons activated in the act of	
			grasping the P piece	grasping the C piece
Motor	47	27	4	16
Visual	41	34	1	6
Total	88	61	5	22

er (Fig. 3, top). There were more cells activated only during grasping of the C piece than cells activated only during grasping of the P piece (P < 0.01).

In 47 neurons (27 of the motor and 20 of the visual cortex) only weakening of impulse activity in the investigated forms of behavior was noted. This group of neurons had two characteristics relative to the acts of grasping the P and C pieces, which distinguished it from the group of activated cells. First, 30 of the 47 neurons reduced their activity irrespective of individual stages, i.e., during the entire act. Of the 88 activated neurons, only 19 intensified impulse activity during the entire act. The number of activated neurons of the "entire act" was significantly (p < 0.001) less than "inhibitory" neurons of such a
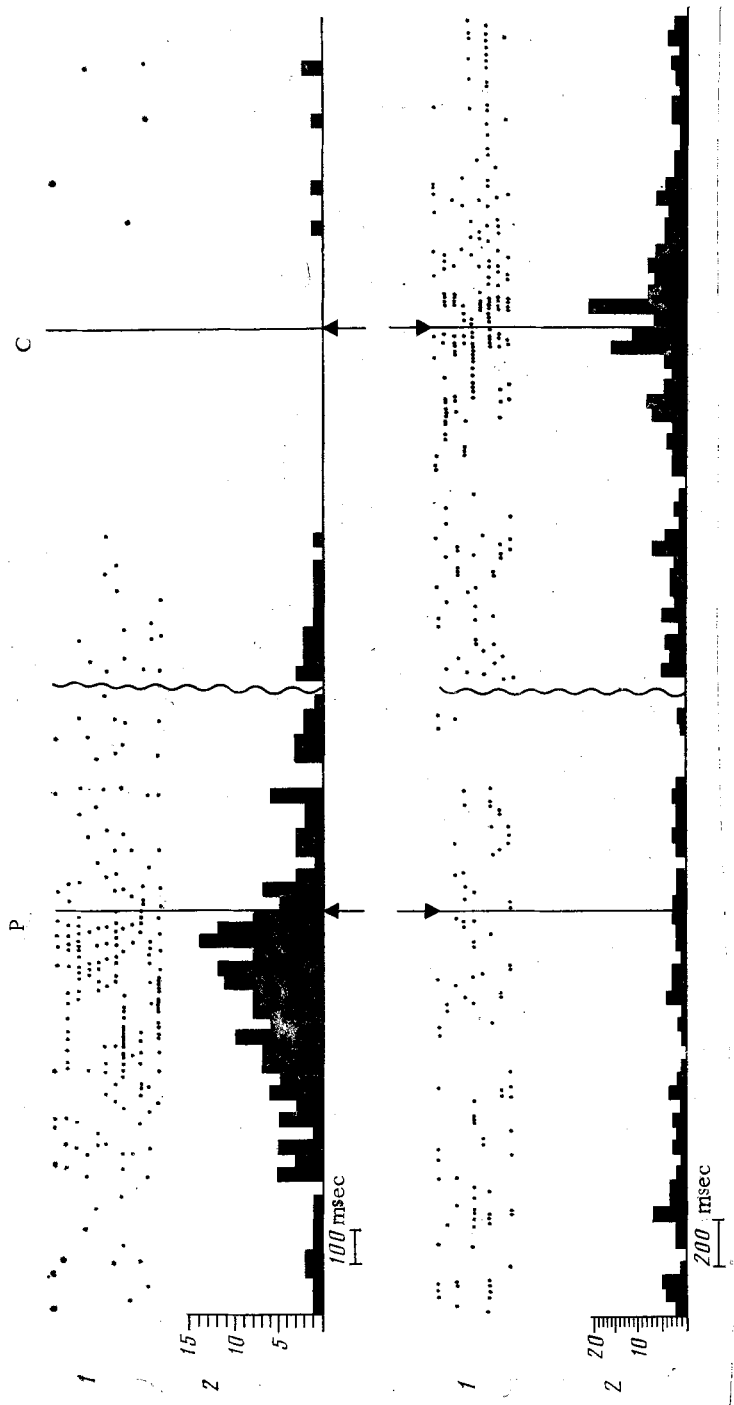
Fig. 3. Examples of neurons of the motor cortex activated only in one of the acts; 1) scans and 2) histograms of neuronal activity plotted from the start of lifting the head from the feeder (at the top; n = 12) and from the phasic burst of the EMG corresponding to grasping the object with the teeth (bottom, n = 9). The neuron represented at the top of the figure is activated when grasping food with the teeth and at the start of lifting the head from the feeder in the act of grasping the P piece (left of the wavy line); in the act of grasping the C piece (right of the wavy line) pronounced "inhibition" of activity is noted for this neuron. The second neuron is activated when grasping the C piece with teeth (right of the wavy line) but not the P piece (left of the wavy line).

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type. Second, the number of neurons that reduced activity only in one of the acts (3 of 47) was significantly (p < 0.01) less than the number of neurons activated only in one of the acts.

It is easy to note that the patterns of activity in the act of grasping the P and C pieces were different: a) the compositions of the activated neurons substantially differed; b) only a third of the neurons of those involved in both acts were activated in them at different stages.

It is necessary to note, however, that the percent of neurons activated in each of the distinguished stages of behavior (Fig. 4), although it did substantially differ for the motor and visual cortical areas, was similar for the acts of grasping the P and C pieces. That is, different sets and forms of neuronal activity stood behind the same "total pattern" of activity in various behavioral acts.

DISCUSSION OF RESULTS

The main phenomenon obtained as a result of the experiments is that different, although overlapping, compositions of neurons of the motor and visual cortical areas are activated in the acts of grasping the P and C pieces similar in motor characteristics and realized in the same environment.

It could be assumed that the difference in the compositions of the activated neurons is explained not by a change in the goal of the behavioral act but by the difference in the texture of the object being grasped. Actually, certain characteristics of the movements of the lower jaw depend on this factor [14]. However, substantial changes in the composition of the activated neurons of the motor and visual cortical areas were not found when grasping the most different sorts of food differing in texture [6].

Our data can be compared with the data in the literature, if the differences in the activity of the neurons during the acts of grasping the P and C pieces are characterized from the point of view of movements realized in these acts: the composition of neurons activated during realization of a certain movement depends in what behavior this movement is recorded. In the monkey motor cortex were found neurons whose activations were related to movements of the lower jaw only when the animal consumed food "earned" by preceding tool behavior but not "free" food [11]. It was also shown that the neurons of the motor cortex of monkeys can be activated in connection with a given movement of the wrist when performing one but not another behavioral task [10, 15]. Thus it can be assumed that our noted phenomenon is not a consequence of any characteristics inherent only to neurons of the rabbit cortex.

The data obtained in the present investigation correspond to the predicted consequence and thereby confirm the assumption formulated in the introductory part. A comparison of these data with those obtained earlier ([1, 2], see introduction) leads to the conclusion that neurons of the motor and visual cortical areas can be acrivated in one and the same behavioral act, despite a change in the parameters of the movements and environment, or only in one of the two behavioral acts (directed at achieving different results) with the same movements and in the same visual environment. Consequently, the occurrence of activations of cortical neurons in behavior is not determined uniquely by the parameters of movements and the environment and depends upon for the achievement of what result the behavior is realized: the same (grasping of food in the preceding investigations) or different (grasping of the P and C pieces in the present investigation).

It can be assumed that the difference in the properties of activations (confinement to a certain stage of behavior, expressivity, etc.) occurring in both acts is also related to the difference in the goals of these acts. However, if the composition of the activated neurons in the same behavioral act after a change in the parameters of the movements and environment does not substantially change [1], then the properties of activations of many neurons can be modified depending on many variables even when achieving the same goal [1-3, 6, etc.]. Therefore, special experiments are necessary for confirming and refining the assumption expressed.

It was shown that the receptive and motor fields of cortical neurons change upon a change in the goal of behavior realized by an animal [4, 7-9]. The change in the receptive and motor fields depending on the goal of behavior can be regarded as a factor determining the possibility of occurrence of activations of the same neurons in a different environment and during different movements or of different neurons in the same environment and with the same movements.
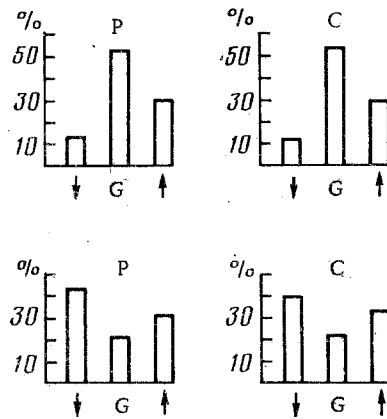
Fig. 4. "Total picture" of the activity of neurons of the motor cortex (top) and visual cortex (bottom) in acts of grasping the P piece (left) and C piece (right). On the basis of the ordinates is the number of neurons of the corresponding area (percent) activated at the corresponding stage of behavior. On the axis of the abscissas: the downward arrow is tilting the head into the feeder; G is grasping the object with teeth proper; the upward arrow is lifting the head from the feeder.

Despite the different composition of neurons activated at corresponding stages of the behavioral acts of grasping the P and C pieces, the "total pictures" of activity in the compared acts were essentially similar. This similarity can be explained by the similarity of the compared acts with respect to the criterion of motor characteristics and environment. Thus, assessing the activity of neurons of the motor and visual cortical areas in acts of grasping the P and C pieces, we can say that what is different in this activity — the composition of the activated neurons — is due to different goals of the acts; what is common — "total picture" — is related to what is common for the compared acts — motor characteritics of behavior and the environment.

On comparing the acts of grasping the P and C pieces according to the criterion of the number of neurons activated in each of them, it is shown that more neurons are activated during grasping of the C piece than during grasping of the P piece.

It is known that during phylogeny the possible length of the "chain" of successive acts preceding consummatory behavior increases [5]. If we assume that each behavioral act can be realized only in the presence of the necessary minimum of activated neurons, then, with consideration of the phenomenon obtained, an increase of the possible length of the behavioral "chains" during phylogeny can be explained by an increase of the "fund" of neurons from which are recruited cells providing realization of particular behavioral acts ever farther remote from consummatory behavior.

CONCLUSIONS

1. In different behavioral acts (grasping a carrot and plastic), which can be characterized as the same movements in the same environment, the compositions of the activated neurons of the motor and visual cortical areas differ. The occurrence of activations of cortical neurons in behavior is not determined uniquely by the parameters of the movements and environment. This ambiguity is explained by a change in the motor and receptive fields of the neurons.

2. The "total pictures" of the activity of neurons both of the motor and visual cortical areas (percent of neurons activated in each of the stages of the behavioral act) are similar in the behavioral acts of grasping plastic and carrot.

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