Polish Academy
of Sciences
Nencki
Institute
of Experimental
Biology

ACTA NEUROBIOLOGIAE EXPERIMENTALIS

Vol. 42, No. 6, 1982

Polish
Scientific
Publishers
Warszawa

PL ISSN 0065-1400

ACTA NEUROBIOL. EXP., 1982, 42: 457-468

SPECIFICITY OF VISUAL AND MOTOR CORTEX NEURONS ACTIVITY IN BEHAVIOR

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Key words: behavioral act, visual cortex, motor cortex, single-unit activity, visual function

Abstract. The involvement of the units of visual (VC) and motor cortex (MC) in the systemic behavioral mechanisms is determined by the "environment" and "executive mechanisms of behavior." The unit activity in VC and MC, head and lower jaw movements, EMG of m. masseter and latency of touching the food were recorded. In experiment I the rabbits' eyes were covered with occluders that were put on and taken off after every 4–5 repetitions of the behavioral act. It was found that the visual inflow was not necessary for the activations of both MC and VC neurons to appear. The pattern of neuronal activity changed when behavioral act was performed with the eyes closed. These changes following the "visual" influences were more pronounced in the VC. In experiment II the unit activity of both cortical areas was compared during the free head movement towards food and during the movement hampered with the rubber thread. The more pronounced susceptibility of VC neurons to activity changes was demonstrated again, this time after motor influences.

INTRODUCTION

On the basis of numerous studies of neuron activity in behavior it may be concluded that neurons in different brain areas share some common characteristics and also have many specific ones. It is known for instance that unit activity in different brain areas corresponds to all stages of behavior which is associated with the involvement of all brain structures in systemic mechanisms of behavior (19). There is also a great amount of data concerning the specificity of participation of neurons of various brain structures in behavioral mechanisms (3, 14, 15 and others). These facts are usually explained in terms of different brain structures carrying different functions in the behavior organization — such as "sensory", "motor", "activating", "motivational" etc. But it is impossible to distinguish purely sensory (related to environmental changes) and motor (related to action changes) components in the activity of neurons of sensory and motor structures, because any change of the environment is connected with reorganization of behavior executive mechanisms (20) and movement reorganization always results in changes of sensory environment (8).

The present study was carried out to reveal to what extent the participation of neurons of sensory and motor structures in systemic behavioral mechanisms is determined by one of the two interconnected variables: "environment" and "behavioral executive mechanisms" and how this participation depends on the specificity of these structures. As there is no way to change one of these variables without changing the other, an attempt was made to change one of them as much as possible leaving the other relatively constant. In experiment I neuron activity of two brain areas — motor cortex (MC) and visual cortex (VC) — was analyzed and compared in the course of the same behavioral act performed by a rabbit with eyes closed (EC) with specially designed occluders and with eyes open (EO). In experiment II the activity of neurons of these areas with the head moving freely towards the food and head movements hampered with the rubber thread was compared.

METHODS

The rabbit was gently fixed on the experimental table with limb laces and was given portions of food by means of horizontaly moving thin bar. The special photoelectric system (2) was used for registration of the head and lower jaw movements during food acquisition. Electrical activity of m. masseter and noises accompanying the taking of carrot by the rabbit were also recorded. For more details of the method see (3). The glass microelectrodes with a tip diameter of about 1 μm filled with 3 M KCl solution were used. Neuron activity was obtained from VC and MC, coordinates E 9 and A + 2 respectively according to the stereotaxic atlas (13). The data were processed by a mini-computer.

Neuron activity was analyzed by means of rasters and histograms plotting.

The occluders consisted of two frames constantly fixed around eye sockets and two nontransparent caps that were placed in the frames when required. The frames with the caps removed did not narrow the visual field of the animal. Before the experimental session rabbits were taught to acquire food with occluders on. While recording the activity of one neuron the caps were put on and removed after every 4 or 5 food presentations. For most neurons 4 and more situation changes (EO–EC) were made. In the first series the activity of 60 units was analyzed: 30 neurons of VC and 30 of MC. From each of the three rabbits used in the experiments the activity of both VC and MC neurons was obtained. In experiment II the organization of movement towards food was changed by attaching a rubber thread fixed to the cage ceiling to the animal's occipital bone, so that the force opposing head movement (max. about 250 g when the head was near the food) was directed backwards-up. The activity of 42 neurons was analyzed: 26 of MC and 16 of VC.

RESULTS

The food acquisition act (3) consisted of two phases: fast forward-down head movement and slow head movement so that the mouth is near the food, and is simultaneously opened (Fig. 2 *A*2, *B*2: downward deflection and return to baseline).

The structure of movements in food acquisition act with EO and EC appeared very much alike (Fig. 2, cf. *A*2 and *B*2); i.e., no new movements appeared and none were eliminated when the occluders were put on. The modifications of the behavior manifested themselves only in some elongation of latency and slowing down and decreasing of variability of movement.

It was shown for the neck muscles that different parts of the same muscle had different characteristics of the length-tension curves, thus providing equal efficiency of movements in spite of the wide variety of conditions and starting positions (1). Thus it was clear that hampering of the head movements in experiment II led to fundamental reorganization not only at the level of single muscles' activity but even at the level of their parts. Hence, in experiment II, in contradiction to experiment I, the behavioral act was performed in constant visual environment, but with reorganization of muscle activity in slow and fast movements.

Experiment I. The activity of 9 out of 30 VC neurons showed no relation to any stage of behavioral act both in EO and EC situations; the activity of 7 neurons was related to some stage of behavioral act in the same way in both situations; and the activity of remaining 14 VC neurons differed radically in EC and EO situations. These differences in unit activity in EO and EC situations fell into three groups.

1. The activation present with EO at a certain stage of behavioral act disappeared with EC (Fig. 1). This was observed in 10 cases — 6 neurons (one neuron could have more than one activation in one act). At the beginning of the fast movement phase an activation could be seen (1*A*), which disappeared with EC (Fig. 1*B*).

2. The activation appeared at the stages of behavioral act with EC at which no activation was seen with EO (4 cases, 4 neurons). Figure 2 shows an activation appearing in the latent period of behavioral act with EC (2*B*); with EO no activation is seen at that stage (Fig. 2*A*).

3. Three VC units showed a disappearance of phasic structure with EC. With EO separate phases of activation could be detected in the neuron's activity. In the EC situation neurons' activations were represented by uniformly increased firing during the whole act.

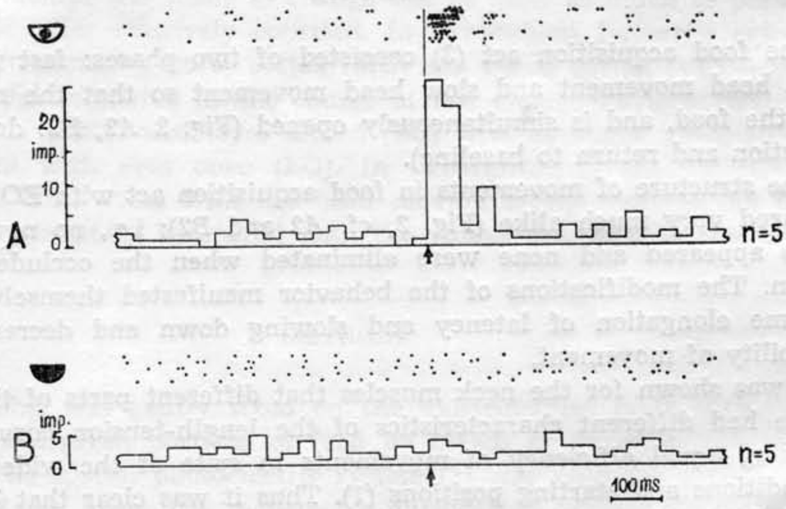

Fig. 1. The disappearance of a visual cortex neuron's activation after the occluders were put on. Above, rasters of discharges in successive acts with eyes opened (A) and with the occluders on (B); below, histograms of unit activity plotted from the moment of fast head movement phase onset (marked with an arrow). Here and below histograms marked: *abscissa*, time; *ordinate*, number of impulses in the channel (imp.). *n*, number of successive realizations of the behavioral act in which the neuron activity was analyzed. After the occluders are put on the activation at the beginning of fast head movement phase disappears.

Activity changes were seen not only in units manifesting activation but also in neurons lowering the rate of their activity in connection with some stage of behavioral act.

Few cases were noted (5 units, 6 activations) with quite similar shape of activation pattern in EO and EC situations, but showing shifts in time within one stage of behavioral act, or variations in activation (Fig. 3, I). Changes not always included all activations seen in any particular neuron. Most neurons manifesting activity changes connected

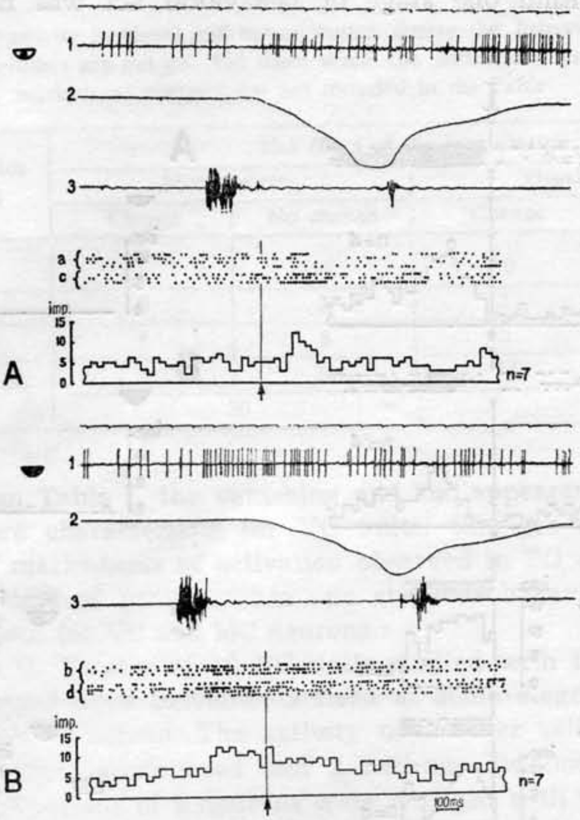

Fig. 2. The appearance of a visual cortex neuron's activation in the latent period of the behavioral act after the occluders were put on. A, the neuron activity and behavior record in the act of taking of food with the eyes opened and B, with the occluders on. A and B above: 1, unit activity; 2, head movement; 3, noises accompanying food presentation (left) and its taking by the rabbit (right) in the single realization. A and B below: histograms and rasters (see Fig. 1). The onset of fast head movement phase is marked with an arrow. Small letters indicate the succession of the occluders being put on and taken off. Time scale, 100 ms. In the latent period of the behavioral act (to the left of the arrow) after the occluders are put on an activation appears.

with some stage of behavioral act showed different "background" frequency in EO and EC situations.

Eight of 30 MC neurons showed no connection between their activity and any of behavioral act stage, both in EO and EC situations. The activity pattern of 20 MC neurons connected with some stage of behavioral act did not change with experimental situation. Two neurons had different activity in EO and EC situations. One showed no activation during EO but was activated with EC. Another neurons showed activation in EO but it disappeared in EC situation. In one case the shift of activation within one stage of behavioral act was noted after eyes

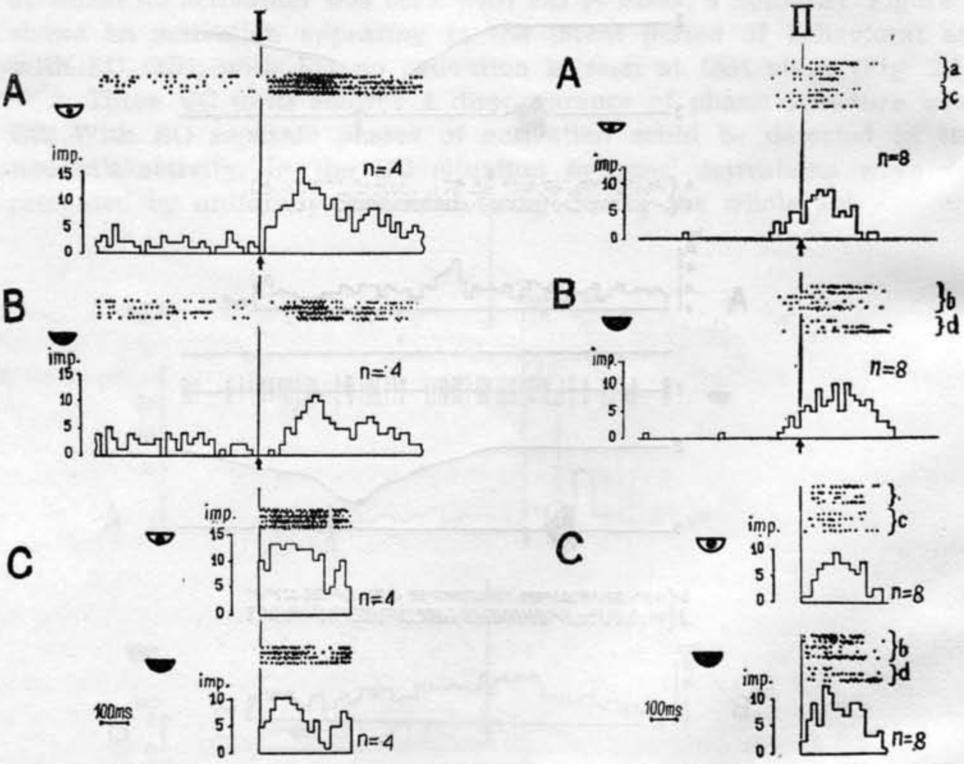

Fig. 3. Activations of visual (I) and motor (II) neurons are not extinguished by the occluders being put on. A and C (above), unit activity in the behavioral act with the eyes opened, B and C (below), with the occluders on. A and B, histograms and rasters marked as on Fig. 2. C, histograms and rasters plotted with the first spike in activation for a zero. Activations of the presented neurons appear at the same stage of the behavioral act whether eyes are opened or closed by the occluders. An averaging from the first spike in the activation for both neurons (C) clearly demonstrates that the structure of activation is not changed after the occluders are put on.

closure. Usually MC units manifested activation in connection with one and the same stage of behavioral act (Fig. 3 II *A*, *B*), the pattern of activation being rather similar in EO and EC situations (Fig. 3 II, *C*).

In most of the cases observed the discharge frequency differed in EO and EC situations. Out of 16 cells manifesting beckground activity, 6 showed the change of its frequency. Table I presents the MC and VC neurons changing their activity in the behavioral act after the eyes closure.

TABLE I

Changes of the unit activity in visual and motor cortex during the behavioral act of taking of food after the occluders are put on. The cases when the activations persisted, but their markedness changed are not included in the Table

Type of activiy with the eyes opened	The effect of the eyes closure			
	Motor cortex		Visual cortex	
	Change	No change	Change	No change
Activation	1	17	10	5
Inhibition	0	3	2	2
No reaction	1	8	2	9
Total	2	28	14	16
	30		30	

As seen from Table I, the vanishing and the appearance of activations, were more characteristic for VC units. Changes of background activity and of markedness of activation observed in EO and EC situations, shift in time of peaks within one stage of behavioral act were characteristic both for VC and MC neurons.

Experiment II. Twelve of 16 VC units studied with the free or artificially hampered head movements fired at some stage of movement without the rubber thread. The activity of 2 other cells during head movement was less pronounced and 2 neurons did not change their activity. The activations of 5 neurons were changed with the attachment of the thread: the frequency of firing of 2 neurons increased and of other 2 — decreased. In one unit the activation appeared at the stage of behavior where with the free head movement there was none (Fig. 4, I).

Fourteen of 26 MC units were fired during the behavioral act, 6 only decreased their activity and 6 didn't change it. Only 3 cells showed the change after the attachment of the rubber thread: the discharge frequency increased. Disappearance and reappearance of MC units activations were not found (Fig. 4, II). No neuron in both cortical areas that decreased or did not change it's activity during behavior showed activation in the other behavioral condition.

Thus, in spite of rather small, compared to the experiment I, amount of changes the same tendency was pronounced: the activity of VC units was more subjected to changes than that of MC units. Since the analyzed MC neurons were 50% more numerous than of VC, this tendency was even more marked.

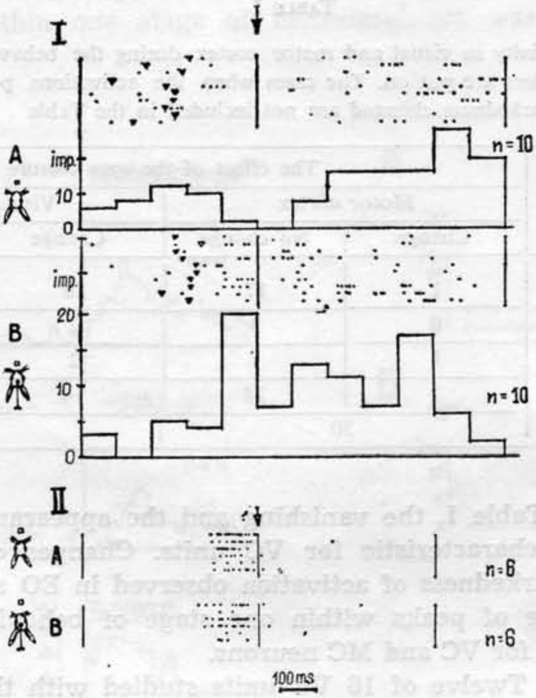

Fig. 4. Stability of motor cortex units activity (II) and appearance of activation in the visual cortex unit (I) during taking of food after the attachment of the rubber thread. I, taking of food with the head moving free (A) and head movement hampered (B). A and B above, rasters of discharges in successive acts. Triangles mark the head movement onset. Below (A and B), histograms of discharges plotted with the moment of teeth touching the food (marked with an arrow) for a zero. When the head movement is hampered the activity directly preceeding the moment of contact with food (to the left of the arrow) increases. With the head moving free, the activity at that stage decreases. II. Rasters of motor cortex unit discharges during taking of food with the rubber thread unattached (A) and attached (B). The activation preceeding the moment of teeth touching the food (marked with an arrow) appears in both experimental situations.

DISCUSSION

The EO-EC change caused the difference in composition of neuron populations in MC and VC activated during the behavioral act and the change of levels of those activations which persisted. It is known that the composition of MC neurons connected with a given behavior changes after the change of movements involved in it (flexion vs. extension, ballistic vs. exact movement, ipsi-vs. contralateral limb) but not with the change of some of the movement's characteristic, e.g., force (16). The movement composition of the behavioral act in our experiments was the same with EO and EC. Thus we think that the differences in composition of both MC and VC neurons manifesting activation in EC situation vs. EO may be due only to the changes in the environment. The change of neuron activity, of VC units in particular might be expected after the visual contact with the environment is violated.

Another aspect is of a particular interest. Even after the visual information inflow was blocked (EC situation) we observed that: (i) VC neurons manifested activations at all stages of behavior, (ii) the connection of some neurons with the same stages of behavior might be still revealed in spite of the situation change, (iii) new activations appeared, (iv) some units having no activation with EO were involved in behavior with EC. We may conclude that *no contact with the visual part of the environment is required for the activations of VC neurons to appear during behavioral act.* As it may be judged on the base of the experiments of Lashley (12) who showed behavior disorders after VC lesions in rats blinded earlier, the activity of VC neurons serves achieving a result of behavior even with EC. According to a concept of goal-directed activity of a neuron (19) its activation appears not in response to any kind of afferentation but is extracted from memory in order to reach the result of behavior. Bearing this in mind it is possible to conclude that as far as the final and intermediate results are achieved in the behavioral act in spite of the EC, the activations of MC and VC neurons connected with achieving of these results do appear.

While comparing the effects of environmental changes upon VC and MC neurons' activity, the fact connected with the difference of functions of structures under study attracts an attention: when the eyes are closed here are much more changes in the VC neurons population than in the MC. This fact, being interpreted in terms of systemic approach, can not be explained simply by attributing to VC and MC the functions of vision and motor control respectively because these functions can not be mediated just by activity of particular structures, but are carried out by the whole brain, the whole organism (4, 5). The fact that the activity of VC neurons is more changeable than that of MC is confirmed by the results of the second series of experiments. Besides, these results demonstrate that this more marked susceptibility to changes is not determined merely by elimination of the visual inflow. That is why it is impossible, as we mentioned above, to explain more pronounced susceptibility of VC neurons' activity to changes only by the specificity of the "visual" function of the VC, because the susceptibility to changes is more pronounced also after the motor influence when the behavior is performed in constant (in relation to free head movement) visual environment (the velocity parameters of head movement in relation to external objects also do not change significantly — see Fig. 4, I).

The necessary component of systemic analysis of structure-function relations is a historical approach to analyzing the formation of structure in connection with the development of its function (6, 16 and others). Thus in terms of systemic approach the understanding of function of the certain structure (being viewed at as a part of the whole brain's "work" in "achieving certain result" (11 p. 16; 18) and in the context of this discussion an understanding of differences between VC and MC, manifesting themselves after changing the conditions of achieving the result of behavior, demands an analysis of their maturation bearing in mind the necessities of behavior being formed in the ontogenesis. A great body of data concerning the pronounced parallelism between the maturation of the nervous system and of behavior is available (6, 7, 21 and many others). It is a common fact concerning the structures under present study that "motor" structures mature earlier than "visual" ones, the latter developing most intensely after eyes opening (9, 10). Such heterochrony provides explanation for the difference of the level of activity changes in MC and VC neurons if we also take into consideration that an ontogenesis, in terms of systemic approach, is the process of changing of the level of system's organization (17) and in turn — of the level of discretion of environment being used in the behavior by an organism. This makes possible the suggestion that VC maturation and eyes opening permit an organism as a whole entity to use (by involving the visual component) more discrete information about its environment as a whole in systemic mechanisms of behavior. (The growing discretization of environment we understand as the ability of an organism to describe in more details the objects previously used and to use new objects of enivronment in modification and realization of its behavior).

We think that the fact that VC matures when the environment used by organism becomes more discrete, i.e., when the number of ways to achieve the result of behavioral act increases, may serve as an explanation of the more pronounced susceptibility of VC to both "specific" and "nonspecific" influences, which alter the way of achieving the result: to environmental changes (occluders being put on) and to the behavioral executive mechanisms changes (rubber thread attached).

Authors thank L. I. Alexandrov for his participation in discussion of the data and for his help in preparation of this article for publication.

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Accepted 10 June 1982