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SPECIALIZATION OF MOTOR CORTEX NEURONS IN
RABBITS UNDER NORMAL CONDITIONS AND AFTER
ABLATION OF THE VISUAL CORTEX

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The activity of motor cortex neurons in instrumental food-acquisition behavior is compared in two control rabbits and in three rabbits after bilateral ablation of the visual cortex. Although the same types of neuron specialization were found in the experimental and control animals, their numerical ratio differed markedly in two out of the three experimental rabbits in comparison with the controls: the number of neurons activated in the act of seizing food was halved, while the number of neurons activated in connection with acts of instrumental behavior doubled. The similarity of the processes underlying behavior learning and recovery is discussed.

Experiments with local destruction of parts of the brain can teach us how the brain operates without a removed structure but they cannot give a straight answer as to how the removed part functions under normal conditions [11, 17]. It is thus of obvious importance to study the mechanisms whereby the organism restores its functioning following lesions to the brain. But an understanding of these mechanisms in turn hinges on knowledge of how the brain operates normally. The way out of this dilemma depends largely on what is meant by the term "function," which normally involves the participation of certain structures and which, consequently, is subject to recovery after injury to the brain.

In the traditional understanding of function in experiments with the ablation of sensory or motor structures, attention is generally focused on the recovery of "sensory" or "motor" functions proper and on changes taking place in the structures that are part of the same sensory or motor "systems" as the damaged region of the brain. If function is regarded as "an integral manifestation of the organism in its adaptation to the external world" [7, p. 31], its recovery signifies the restoration of the ability to achieve a specific adaptive result by organizing elements of diverse anatomical affiliation into a functional system. Such a concept of function presupposes that after local lesions to the brain there occurs a whole-brain reorganization of activity, which involves not just the structures closely bound up morphologically and functionally with the damaged structure, but also distant structures that belong to a "morphofunctional system" different from the affected region [8, 11]. Along with this, however, the literature has spawned a concept, based on the traditional interpretation of function, according to which the brain of an adult animal does not possess the capacity for functional reorganization, the recovery of behavior being a return to the utilization of nervous processes which were not affected by the injury [18, 21]. In the present study we set ourselves the following general aim: to establish whether, after a local brain lesion, there is a change in the role of distant structures in shaping the behavior geared toward attaining the same goal as prior to the lesion, and if there is a

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change, then how it is effected. The experiments were conducted on rabbits. The objects chosen for the recordings and ablation were the motor and visual cortexes, respectively, since, in the first place, unlike other regions of the rabbit cortex, these can be clearly identified [9]; second, a large amount of normative material has been accumulated on the activity of these brain regions in various forms of behavior [2-6, 14]; third, the "distance" of the motor cortex consists not only in its remoteness from the striatal cortex, but also in the fact that in mammals direct links between these regions are weakly expressed or absent, and no substantial degenerative changes in the rabbit motor cortex can be found after the removal of the visual cortex [1, 15, 25 and others].

If we base ourselves on the notion of the specialization of the central and peripheral neurons vis-a-vis the functional systems formed at successive stages of phylo- and ontogenesis [2, 13], then the role of a brain structure in determining behavior can be characterized by the pattern of behavioral specialization of its neurons, i.e., by the specific systems for which the neurons are specialized and the numerical ratio of the neurons specialized vis-a-vis systems of different age. In view of this, the overall objective of the study may be specified in the form of the following question: does the pattern of behavioral specialization of motor cortex neurons undergo a change in rabbits after removal of the visual cortex, and if so, how?

MATERIAL AND METHODS

Five adult rabbits were trained in instrumental food-acquisition behavior in a special cage (details given in [6]) equipped with two levers and two automatic feeders. The levers were situated in the right- and left-hand corners of the back wall. The feeders were placed in each corner of the front wall. Food was dispensed in the left-hand feeder when the left-hand lever was pressed, and in the right-hand feeder when the right-hand lever was pressed. After the behavior of the rabbits was standardized (right after seizing a portion of food, the animal made its way to the lever, pressed it, went to the feeder, got food, and so on), three of them were placed under nembutal narcosis (40 mg/kg), and the striatal cortex (classification according to [20]) was bilaterally removed using a surgical suction device (OKh-10).

The boundaries of the striatal cortex were determined in accordance with criteria [19] based on data of electrophysiology and morphology. After behavior recovery in the surgically manipulated rabbits (Nos. 1-3) and after the completion of conditioning in the control animals (Nos. 4 and 5), we went over to experiments recording the impulse activity of neurons (in the coordinates A - 4.0; L - 4.0; mediocaudal part of anterolateral region, the stimulation of which produced movements of the lower jaw [24]), which was led off with glass micro-electrodes filled with a 2.5 M solution of KCl (tip diameter of electrode 1-3 μ , resistance 1-5 Mohms at a frequency of 1.5 kHz). The micromanipulator attached to the animal's head was fitted with a graduated plate enabling measurement of the depth of electrode placement.

The impulse activity, the EMG of m. masseter, the behavior actogram markers, and the timer markers were taped on an NO-46 magnetograph. Simultaneous recordings were made of the behavior of the animals and of the impulse activity in numerical form using an Elektronika-509 videotape recorder (for details on the recording procedure see [4, 6]).

The difference in the time characteristics of behavior and in their variability was estimated using the t and F tests, respectively, and was considered reliable for $p < 0.05$. The analysis of impulse activity was performed using standard methods (the construction of grids and histograms), as well as with the use of a method developed by us for constructing histograms during the analysis of consecutive stop frames of the videorecording (see [4]).

During electrode implantation the localization of neurons was determined in one of the three parts of the track upper, middle, and lower. Keeping in mind the variability of the layered structure of the cortex, we considered the upper and lower parts of the track, which belong, respectively, to the surface and deep-lying layers of the cortex, as being unconditionally different vis-a-vis the cortical layers. For each neuron the frequency of the background activity and the ratio of the frequency of activation to the frequency of the background activity were determined. The differences in the distribution histograms for these values in the experimental and control rabbits were estimated using the Kolmogorov-Smirnov test. Activation was considered to be the appearance (in neurons with background activity) of impulse activity at a certain stage of behavior in 100% of cases, i.e., in all the instances of the behavior. A rise in the mean level of the background for a particular neuron by

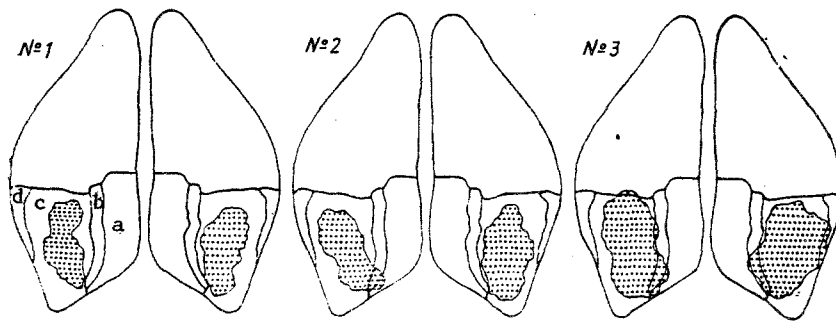


Fig. 1. Reconstruction of ablated region of cortex in rabbits Nos. 1-3. The diagrams show the boundaries of the ablated region, reconstructed from serial sections. Cytoarchitectonic regions designated after Rose and Rose [20]. a) Region retrosplenialis granularis; b) area peristriata; c) area striata; d) regio occipitalis.

a minimum of 2σ was taken to be a marked increase in frequency.

The neurons were divided into two large groups: those that were involved (i.e., activated in the behavior in question) and those that were not involved (i.e., not activated) during food acquisition.

The reliability of the variations in the number of neurons belonging to the different groups was estimated using chi-square analysis. The differences were considered reliable for $p < 0.05$.

Upon completion of the experiments, which continued for four days from the start of the recordings, the rabbits were given a lethal dose of nembutal and then perfused with a 0.9% physiological solution and 10% Formalin. Serial sections 40 μ thick were prepared on a freezing microtome, Nissl stained, and drawn with the aid of a photographic enlarger.

RESULTS

All three of the experimental rabbits suffered marked destruction of the striatal cortex (Fig. 1). The damage also affected the peristriatal cortex and, in rabbit No. 3, the occipital cortex on the right. The depth and nature of the lesions were the same for all the animals, the cortex being damaged through its entire depth, encompassing the central white matter. Prolapse of the lower cortical layers and replacement gliosis of the upper layers were observed.

The impairments of behavior and the recovery dynamics were the same for all the experimental rabbits. During the first postoperation day, instrumental food-acquisition behavior was absent, although the animals took food from the feeder provided by the experimenter. On the second day all the animals began to perform the instrumental behavior learned prior to the operation, displaying the same movements, but the mean duration and variability of the performance time of the stages of approaching and pressing the lever and of going up to the feeder were reliably higher than the control level on the second and third day. On the fourth day these indexes returned to the control level.

The activity of 575 neurons of the anterolateral region of the motor cortex was analyzed: 274 neurons in the control rabbits and 301 in the experimental animals.

The mean number of neurons which could be detected in the microelectrode tracks did not differ reliably in the two groups of animals: 27.9 ± 7.1 ($n = 15$) in the controls and 24.1 ± 8.0 ($n = 24$) in the experimental group.

The ratio between the number of neurons involved in the behavior and those not involved did not change after the operation. In the controls there were 130 (47%) neurons involved and 144 (53%) not involved. The respective figures for the experimental rabbits were 138 (46%) and 163 (54%). The distribution histograms of the background activity frequencies of the neurons and of the ratio of the activation frequency to the background frequency did not differ in the two groups of animals.

The following subgroups of involved neurons were identified in the control and experi-

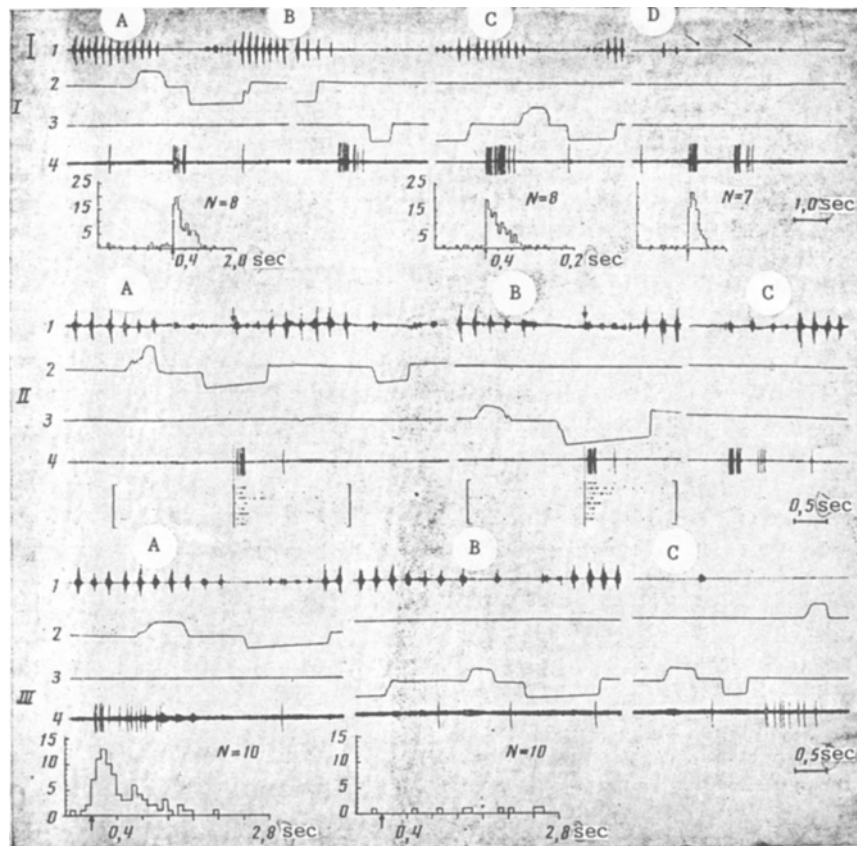


Fig. 2. Activity of neurons of various specializations in behavior: 1) EMG of m. masseter; 2) actogram of behavior at left-hand wall; 3) actogram of behavior at right-hand wall. Upward deviation of curves denotes pressing on the level; downward deviations, leaning into the feeder. 4) Impulse activity of neurons. I) Activity of M-neuron in experimental rabbit; A-D) see text. On the abscissa: time, sec; on the ordinate: number of impulses in channel (channel width 80 msec). I) Histograms constructed from the moment the animal began to move its head to the left. II) Activity of S-neuron in control rabbit; A-C) see text. Grids constructed from moment of EMG activation of m. masseter, corresponding to the first closure of the mouth during the taking of food. III) Activity of C-neuron in control rabbit; A-C) see text. Histograms constructed from the time the animal began to move toward the lever. N is the sum total of performed acts.

mental animals for the use of previously described criteria for determining the behavioral specialization of neurons [2, 13]. Subgroup I comprised neurons of the most ancient systems. The criterion was the appearance of activation in connection with a particular movement, regardless of the behavior in which this movement is used (M-neurons). M-neurons were activated during movements of the body and/or head or during movements of the lower jaw. An example of an M-neuron is shown in Fig. 2, I. The histograms here and in Fig. 2, III were constructed using the method of videorecording analysis [4]; the moment from which the histograms were constructed is indicated by an arrow. This neuron is activated during movements to the left in both food-acquisition cycles: at the left-hand wall during movement from the lever to the feeder (A), at the right-hand wall during movement from the feeder to the lever (C), as well as during exploratory behavior, when moving from one feeder to the other (B). Activations of such neurons also arose during passive-defensive behavior, when the animal's body was moved by the experimenter (in this case to the left; shown by the arrows in Fig. 2, D). The neurons normally characteristic for the anterolateral region that are activated during rhythmic movements of the lower jaw were discovered only in the control

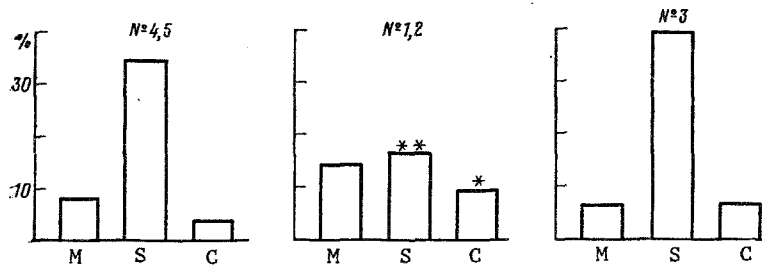


Fig. 3. Numerical ratios of neurons with different types of behavioral specialization in control (Nos. 4, 5) and experimental (Nos. 1-3) rabbits. On the abscissa: type of behavioral specialization; on the ordinate; number of neurons of particular type in relation to total number of analyzed neurons, in % (n = 274, 183, and 118, respectively). Reliability of differences in number of neurons of a certain type vis-a-vis the control; *p < 0.05; **p < 0.001.

rabbits. The second subgroup of neurons included nerve cells that are specialized vis-a-vis the systems formed at the early stages of ontogenesis. The criterion was the appearance of activation during the act of seizing food, regardless of the movements characterizing this act and the environment in which it was carried out; during chewing movements of the lower jaw and movements of the head without the seizure of food, activations did not occur (S-neurons).

The S-neurons could be activated when the food was seized in the teeth and/or when it was being nibbled. Figure 2, II gives an example of a neuron activated when food was taken in the left-hand feeder (A), in the right-hand feeder (B), and also when the animal reached for food presented by the experimenter in his raised hand, whereupon it had to make a head movement upward, opposite to the movement performed when reaching into the feeder (C) (double seizure). Activations during verifying searches into the feeder (A, right) and during movements of the lower jaw other than the act of seizing food (see EMG) were absent. In some neurons the activation began before food seizure proper, i.e., at the stages of the approach to the feeder and/or reaching into it. A tendency was noted for there to be an increased number of such neurons in the experimental rabbits as compared with the controls: 22 and 11%, respectively, of the total number of S-neurons ($\chi^2 = 3.27$; $p < 0.1$)

Belonging to subgroup III were the neurons of the new systems formed during conditioning of the animals (C-neurons) to the instrumental food-acquisition behavior. The criterion was the appearance of activations in the acts of approach to and/or pressing of the lever, and approach to the feeder during different modes of performance of these acts (for example, during their performance with opponent movements and in a different environment); another criterion was the absence of activation in connection with the movements characterizing this act in cases where the same movements were observed in a different behavior. In Fig. 2, III we see an example of a C-neuron, activated only during the approach to the left-hand lever and at the beginning of its pressing (A). In the behavior at the right-hand wall activation is absent (B). In exploratory behavior (both levers ineffective - C) activation also appears only when the left-hand lever is approached and pressed.

A quantitative analysis of the data showed that the variation of the pattern of behavioral specialization followed the same direction in rabbits Nos. 1 and 2. The most characteristic feature of the specialization of neurons in the region studied under normal conditions is a marked prevalence of neurons activated in the act of food seizure over other types of specialization [2, 6] (see also Fig. 3). The number of S-neurons in rabbits Nos. 1 and 2 was only half that in the controls; the number of C-neurons, on the other hand, was twice as high (Fig. 3). No reliable changes in the number of neurons belonging to these subgroups were found in rabbit No. 3.

Variation in the pattern of behavioral specialization led to variation in the contribution of neuron activity toward the implementation of the successive stages of recovery of the food-acquisition behavior. Figure 4 gives an overall picture of neuron activity in the behavior at the left-hand (I) and right-hand (II) walls of the cage, compiled by calculating

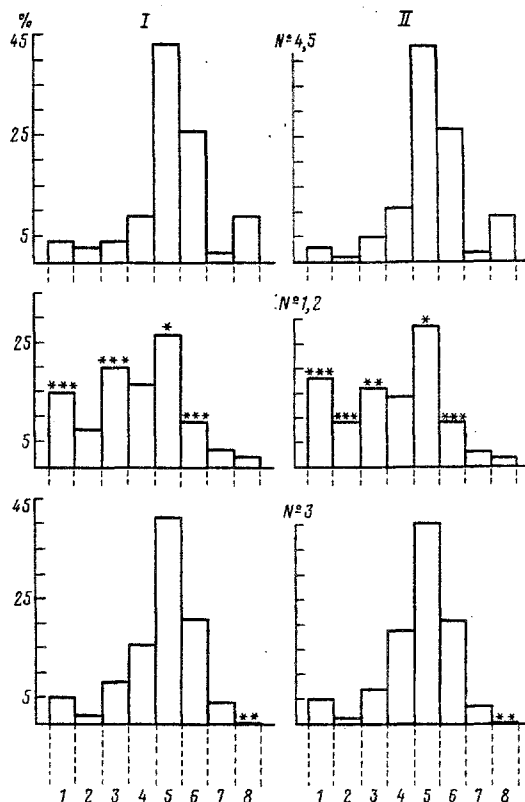


Fig. 4. Total picture of neuron activity in control (Nos. 4, 5) and experimental (Nos. 1-3) rabbits in behavior at the left-hand (I) and right-hand (II) walls of the experimental cage. On the abscissa: stages of behavior; 1) approaching the lever; 2) pressing the lever; 3) approaching the feeder; 4) reaching the head into the feeder; 5) seizing the food; 6) nibbling; 7) raising the head from the feeder; 8) chewing. On the ordinate: number of activations (in %) in relation to total number of activations in neurons involved in behavior at the corresponding wall: in rabbits Nos. 4 and 5 $n = 202$ (I) and 203 (II); in Nos. 1 and 2 $n = 101$ (I) and 97 (II); in No. 3 $n = 103$ (I) and 104 (II). Reliability of differences of number of activations at given stage vis-a-vis control: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.005$.

the percentage of activations appearing at each of the stages in the behavior in relation to the total number of activations found for rabbits Nos. 4 and 5, 1 and 2, and 3. We see that in rabbits Nos. 1 and 2 the level of activity at the stages of seizing and nibbling the food dropped reliably, whereas the activity at the stages of learned behavior reliably increased. In rabbit No. 3 activity was found to decrease during chewing, this being due to the absence of neurons activated in connection with rhythmic chewing. These were the limits of the variation in the pattern of neuron specialization in rabbit No. 3. The presence of activity at this stage in rabbits Nos. 1 and 2 can be attributed to the fact that some of the neurons of the S subgroup continue to be activated during the animals' chewing.

A comparison of the number of involved and noninvolved neurons in the upper and lower layers of the cortex (of the cells whose localization in the parts of the track was determined: in the controls $n = 80$ and $n = 106$, and in the experimental rabbits $n = 107$ and $n = 143$, respectively) did not reveal in the controls any reliable differences between the number of neurons in the compared groups in each part of the track (28 and 30%, respectively, in the upper layers and 38 and 34% in the lower layers) or differences in the number of either the involved or the noninvolved neurons between the upper and lower layers of the cortex. In the experimental rabbits a reliable difference was found between the number of involved and noninvolved neurons both in the upper (19 and 41%; $p < 0.01$) and in the lower (45

and 32%, $p < 0.05$) layers of the cortex. This difference is due mainly to the decreased number of involved neurons in the upper layers and the increased number in the lower layers; the difference between the numbers in the layers becomes reliable (19 and 45%, $p < 0.01$).

In 44 cases in the control rabbits and in 36 cases in the experimental animals the activity of two adjacent neurons was recorded simultaneously by one microelectrode. The pairs were divided into groups. Included in the first group were the pairs consisting of two non-involved or involved neurons with the same specialization, while the second group comprised involved-noninvolved neurons of involved neurons with different specializations. In the control rabbits 61% of the pairs consisted of differently specialized neurons and 39% of neurons with the same specialization. This ratio remained unchanged in the experimental animals.

DISCUSSION

The data on the absence of variation in the number of neurons discovered in the track, the frequencies of the background activity and activations in the experimental rabbits, as well as published data on the insignificance of the morphological changes taking place in the motor cortex after ablation of the visual cortex (see introduction), suggest that the variation noted in the activity of motor cortex neurons in the behavior is due not to a massive mortality of neurons and/or to their degenerative hyperexcitability, but rather to a redistribution of the behavioral specializations in the aggregate of the cells studied, resulting from changes in the array and state of the brain elements to which the neurons of the motor cortex have to adjust their metabolism and activity.

Since the proportion of involved and noninvolved neurons remains unchanged, while the number of involved neurons diminishes in the upper and increases in the lower layers of the cortex, it must be assumed that the change in the pattern of behavioral specialization (decrease in the number of neurons belonging to the older systems, i.e., the S-neurons, and increase in the number of neurons belonging to the new systems, i.e., the C-neurons) is due not simply to the selective exclusion of neurons within the involved group from taking part in the behavior, but to the recruitment in behavior recovery of new neurons, primarily from the lower layers of the cortex. The onset of specialization of different neurons is coordinated, as is evidenced by the results of the analysis of the specialization of adjacent neurons.

The neurons of the motor and visual regions of the cortex belong to different (though overlapping) functional systems; the hierarchy of these systems (as well as of the systems to which the neurons of the other central and peripheral structures belong) allows the result of the behavior to be achieved [2]. Our findings show that after ablation of the visual cortex, for the same result to be attained there has to be a restructuring of the hierarchy, manifesting itself in a change in the pattern of neuron specialization in the intact structures. This change of pattern has the result that the anterolateral region of the motor cortex to a large extent loses its specific nature - a marked prevalence, under normal conditions, of the subgroup S over the other types of specialization - and becomes similar (though not identical) to other regions of the cortex such as the visual and the limbic, which normally contain considerably more neurons belonging to the newer systems than does the motor cortex [2, 14].

Regardless of what mechanisms are invoked to account for the recovery of the preoperative array of behavioral acts, we must assume that the animal must be taught to attain the results of the behavior under the conditions of an altered "dynamic system" of the brain [8, 23].

When rabbits learn new behavioral acts, neurons specialized to perform these acts appear in the cortical regions, presumably having been recruited from the reserve of "dormant" cells; there then occurs in the motor cortex a decrease in the number of neurons specialized vis-a-vis the systems present prior to the learning, including the S-neurons [10]. The data obtained during the present study indicate that the processes lying at the basis of recovery and learning are similar; in both cases a change occurs in the pattern of original specializations, expressed in a decrease in the number of S-neurons and the recruitment of new neurons for the performance of the behavior. The source of these neurons during behavior recovery (dormant reserve neurons, noninvolved neurons, neurons of other behavioral specializations not normally activated in food-acquisition behavior) remains an open question. The only thing that is known for sure is that the source lies in the lower layers of the cortex. When behavior recovery occurs by way of the establishment of new forms

of behavior, there will apparently arise one more process observed during conditioning, namely the appearance of neurons specialized for the performance of the newly formed behavioral acts.

An analysis of the "total picture" of activity showed an enhanced activity, in comparison with the norm, at the stages of instrumental learned behavior and a decreased activity in the act of food seizure. It may be supposed that the direction of the changes is due not only to the similarity of the processes of learning and recovery, but also to the fact that normally a reliably larger number of neurons of the visual cortex is activated at the stages of instrumental behavior than during the actual seizure of food [2]. Thus, a change in the role of a distant structure - the motor cortex - in behavior performance can be regarded at least as one of the mechanisms of recovery of the original form of behavior after destruction of the striatal cortex. This change is effected by a reorganization of neuron activity, involving a change in the pattern of behavioral specialization and a change in the localization of the involved neurons.

This conclusion would seem to contradict the data of Spear and Baumann [21], who showed that in the cat the receptive fields of the lateral suprasylvian region which change immediately after the removal of areas 17-19 do not undergo any further changes corresponding to the recovery of the visual discrimination behavior. These scientists assume that a functional reorganization does not play any substantial role in behavior recovery. In connection with this it must be noted, first, that the characteristics of the activity of neurons in behavior cannot be unequivocally predicted on the basis of the properties of their receptive fields [4, 16, etc.]. Second, even if one did take the properties of receptive fields as a criterion, numerous studies have shown that a progressive change takes place in the receptive fields, correlating with the recovery of a specific behavior [12, and others].

One factor considered to determine the variability of the effects of brain lesions among different individuals is the specificity of individual development [11, 18, 23 and others], which neuron specialization depends [10, 22]. It appears that premorbid characteristics of specialization can explain the lesser degree of expression of reorganizational changes in rabbit No. 3 than in rabbits Nos. 1 and 2, although the recovery dynamics of the behavior was similar in all the experimental animals and the extent of the lesion in No. 3 was at any rate no less than in Nos. 1 and 2. Concrete reasons for this difference may be assumed to be several mutually nonexclusive factors: 1) more pronounced changes in other structures in rabbit No. 3 than in Nos. 1 and 2; 2) an initially different state of the motor cortex; 3) a change in the role of the motor cortex in the behavior in rabbit No. 3 for some reasons not taken into account by us.

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CONCLUSIONS

1. Following bilateral ablation of the visual cortex, the motor region of the cortex in two out of the three experimental rabbits as opposed to the controls showed a twofold decrease in the number of neurons activated during food seizure and a twofold increase in the number of neurons activated during instrumental food-acquisition behavior.
2. In the third rabbit the changes in neuron activity were less apparent, probably as a result of the premorbid specifics of neuron specialization.
3. After the operation, the number of neurons activated in the behavior dropped in the upper layers of the cortex and increased in the lower layers.
4. The findings show that the change in the role of the motor cortex in implementing the behavior consists in a change in the pattern of behavior specialization and the localization of the neurons involved in the behavior; they also suggest that the processes lying at the basis of behavior learning and recovery are similar.

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