SOMATOSENSORY AND VISUAL CORTICAL UNIT ACTIVITY IN RABBITS DURING RECEPTIVE FIELD TESTING AND FOOD-GETTING BEHAVIOR

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Somatosensory and visual cortical unit activity was compared in experiments on unrestrained rabbits during receptive field testing and natural "self-stimulation" of the receptive surfaces of surrounding objects in the course of food-getting behavior. Unit activity evoked by receptive field testing may correspond completely, partially, or not at all to its activity during food-getting behavior, i.e., neurons demonstrating connection during testing with particular receptive fields (parts of the body or retina) may preserve it, modify it, or lose it during food-getting behavior. Differences of activity during food-getting behavior were observed even in the case of neurons with identical receptive fields during testing. The possible nonidentity of the overall firing pattern of the neurons during food-getting behavior with the pattern which can be simulated by receptive field testing is discussed.

INTRODUCTION

In accordance with current views in sensory physiology it is assumed that, in the presence of a sufficiently complete description of the properties of the receptive field (RF) of neurons and its particular features in different animals, we can understand how information on the environment is utilized in the realization of behavioral reactions, and what differences are found in this use by animals belonging to different species [3, 5, 16]. We know, however, that the properties of RF of a neuron are not a permanent characteristic feature. Many investigations have shown that parameters of RF of central neurons — sensitivity, size, shape, orientation, location, directionality, and even submodality — can vary during modification of efferent influences, stimulation of the pyramidal tract, a change in the background illumination, or even in the absence of any controllable changes in the conditions of stimulation or in the animal's state [7, 8, 9, 20, 22]. A phenomenon of RF modification also was discovered in experiments on alert animals, but this time, in the case of variation of the behavioral situation, attraction of attention to the stimulus, or an increase or decrease in its meaningfulness [10, 12, 14, 21]. Facts of this kind suggest that RF modification is not an experimental artifact, but a mechanism used in the organization of behavior [4, 13], during the realization of which there is a constant change of relations between organism and environment, requiring prior efferent influences [11]. Nevertheless, RF has so far been studied either under special experimental conditions or on alert animals, but in a passive situation of RF testing by different stimuli. The presence of a phenomenon of RF modifiability, depending on a set of factors, including a change in the behavioral situation as a whole, suggests that patterns of activity of a neuron during testing of its RF in a passive situation and under the influence of surrounding objects on the receptive apparatus during realization of active goal-directed behavior do not necessarily coincide. In that case it is impossible, on the basis of the results of RF testing in an ordinary situation, to predict neuronal activity during a goal-directed behavioral reaction and, consequently, to understand what information about the environment is used for the realization of behavior.

Evidence in support of this hypothesis has been obtained recently. Neurons activated during testing of their RF located on the hand, but inhibited by contact of the receptive surface with a lever which is grasped during active behavior, have been found in the motor cortex of monkeys [15]. This fact, as the author cited considers, is due to the flexible connection between "input" and "output" of motor cortical neurons, and it perhaps will not be

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discovered in the course of an investigation of "sensory" structures, the main object used to study RF.

Since RF testing in a passive situation consists in establishing definite connection between unit activity and stimulation of a particular receptive surface, the investigation described below was undertaken to discover whether this connection is preserved on stimulation of the receptive surface under natural conditions, i.e., in the case of contact between it and environmental objects in a situation of food-getting behavior (FGB). For this purpose, unit activity evoked by stimulation of the receptive surface by the experimenter and by natural "self-stimulation" during realization of FGB was compared in the somatosensory and visual cortex.

METHOD

Methods of testing RF in these experiments were similar to those used previously in experiments on alert animals [15, 18, 19] and consisted in establishment of a regular connection between unit activity and stimulation of a certain part of the body or visual field. Testing was carried out on rabbits placed in a certain posture, before or immediately after the animal had performed 20 or 30 food-getting cycles [1]. RF was determined during superficial and deep palpation of skin and muscles, movement of parts of the body, skin, hair, or vibrissae in different directions and at different speeds, and during movement of objects in different parts of the visual field at different speeds and in different directions. RF discovered as a result of testing were unselective, i.e., they were activated by contact with objects of different shapes and sizes with the receptive surface. The objects could be moved about in the region of the receptive surface at different speeds and in different directions (Fig. 2A; Fig. 3b), although for some neurons directional sensitivity could be detected. Essentially, for activation of most cells to be exhibited, what mattered was the fact that the object acted on the receptive surface, and not the characteristics of stimulation, although the intensity of activation could change as a result of variation of these characteristics. Consequently, and in view of the aim of the investigation, when the situations of RF testing and FGB realization were compared, cells were classified purely on the basis of the presence or absence of activation of these units as a result of the corresponding action of the object on the receptive surface. If the cell had directional sensitivity, this property was taken into account during analysis of the effects of action of the object on the receptive surface during realization of FGB. The range of conditions, velocities, and other characteristics of stimulation used during testing included (and definitely exceeded) the range found with natural "self-stimulation" in the course of FGB. With the above considerations in mind, and also the fact that the location of the receptive surfaces inevitably predetermined their stimulation during realization of FGB (this was monitored by video recording) it is evident that during FGB contact between objects and receptive surface took placed which, in the testing situation, gave rise to a varied level of activation of the neuron population analyzed. The method used can thus be considered to be sufficiently adequate because it enables the connection between activity of neurons with a definite receptive surface to be compared during RF testing and in a situation of FGB.

The technique of the experiments in which unit activity was recorded during realization of FGB by the rabbit in a cage equipped with feeding bowls, into which food was supplied on pressing a lever, was fully described previously [1]. The rabbit's behavior in food-getting cycles (approaching the lever, pressing it, approaching the feeding bowl, and taking food) and in a situation of testing RF of the neurons was recorded by videotape recorder. Two counters were located at the bottom of the frame: a time counter with standard frequency of 50 Hz, and a pulse counter, triggered by the potential of the test neuron through a standard pulse converter. In parallel experiments, to monitor the recording, unit activity, pulses of the time counter and transformed unit activity, and markers of pressing the lever and taking food were recorded on a tape recorder. By analysis of the video recordings, by comparing readings of the pulse counter on successive stop-frames it was possible to determine the time which elapsed between one analyzed event and another, and how many spikes the neuron generated during this time interval. From this, histograms of unit activity could be constructed from any moment during the rabbit's behavior, from any stage in the changing relations between the animal's body and the environment during realization of FGB and during RF testing by the experimenter could be determined (see: Results). By using the video recording method in this way it was possible to analyze each neuron individually, depending on the properties of its RF, which is impossible or difficult by ordinary methods of recording, since the use of a certain type of marker limits the scope of analysis.

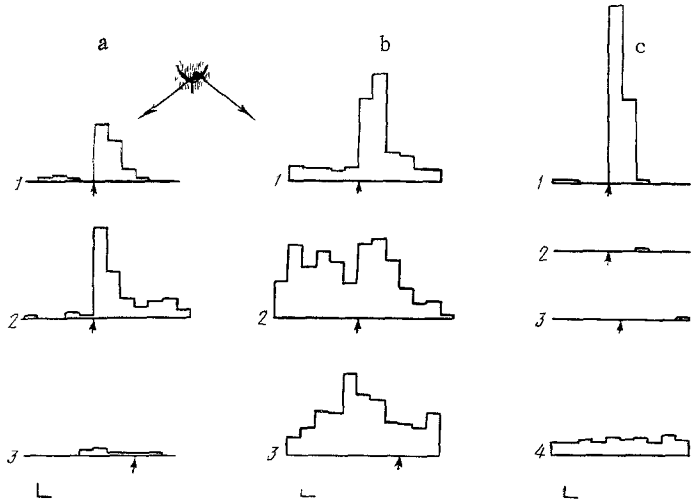

Fig. 1. Comparison of activity of three somatosensory cortical neurons (a-c) during testing of their skin receptive fields and during food-getting behavior. 1) Histograms of unit activity during testing, drawn relative to times of contact with receptive surface of skin of nose (in a, b) and corner of the mouth (in c). 2) Histograms of unit activity drawn relative to time of pressing lever; 3) time when nose crosses plane of opening into feeding bowl. 4) Histogram of unit activity while animal sits quietly. Calibration: 5 min, 200 msec. Here and in subsequent figures, times relative to which histograms were constructed are marked by arrows. n = 10. Detailed explanation in text.

TABLE 1. Comparison of Activity of Neurons with Different Types of Receptive Fields (RF) during Testing and during Food-Getting Behavior

Type of RF	Numbers of neurons with given type of RF	Number of neurons with undermentioned level of agreement of activity during RF testing and during food-getting behavior		
		complete agreement	partial agreement	no agreement
Somatosensory cortex				
Skin	11	1	4	6
Hair and vibrissae	7	2	5	0
With deep sensation and proprioceptive	5	3	0	2
Visual	4	2	1	1
Mixed				
skin-hair, visual skin	4	1	2	1
Visual cortex				
Visual	12	6	4	2
Proprioceptive	4	4	0	0
Total	47	19	16	12

Unit activity in the somatosensory and visual areas of the cortex (coordinates P1-5, L6-10, and P8-12, L6-9, respectively [17]) was derived by glass microelectrodes filled with 2.5 M KCl solution. The diameter of the electrode tip varies from 1 to 5 μm and the resistance was 6-12 MΩ at a frequency of 1.5 kHz. The microelectrode was moved by means of a modified micromanipulator [2]. For this investigation 47 neurons (31 in the somatosensory and 16 in the visual cortex) whose RF were established by testing were chosen.

RESULTS

<u>Somatosensory Cortical Neurons.</u> During testing somatosensory cortical neurons different types of their RF were distinguished (Table 1). RF of these neurons consisted mainly of activation zones, but four cells had additional inhibitory zones. In four neurons (three with skin RF and one with skin-hair RF) only an inhibitory zone was found. RFs of 12 neurons were directionally sensitive, i.e., activity of cells with different types of RF could depend on the direction of movement of the object on the skin, displacement of the hairs or vibrissae, movement of the object in the field of vision, or the direction of passive displacement of the head for proprioceptive RF. We considered that neurons activated by displacement of parts of the animal's body by the experimenter or by palpation of the muscles, and not activated by movement of objects in the animal's visual field, had proprioceptive RF. Directionality could be manifested as a change in the intensity of activation of a neuron or even its inhibition as a result of a change in the direction of movement. Twenty neurons had contralateral RFs, six bilateral, and only three had ipsilateral. It is interesting to note that all visual RFs of four somatosensory cortical neurons were directionally sensitive.

Comparison of unit activity in the RF testing situation with activity of the same cells during realization of FGB revealed three groups: cells whose activity during testing completely prevented activity in the course of FGB, cells the character of whose activity could be predicted only partially, and cells for which no correlation could be found between the two forms of activity in given situations (Table 1). Examples of each of these three varieties are given in Fig. 1. Neurons whose activity is shown in the histograms in Fig. 1a, b were located 100 μm apart and had the same receptive field on the contralateral side of the nose (marked with a circle in the scheme above), i.e., activation due to contact of the object with this zone during testing was observed in both neurons (Fig. 1a, 1; b). However, during realization of FGB they showed different patterns of activity. One neuron (a) in this state was activated in full agreement with its activity during RF testing, only as a result of contact of the nose with the feeding bowl; activation was absent at times other than during contact of the receptive zone with objects during approach to the feeding bowl (Fig. 1a, 2, on left of arrow), during approach to the lever and pressing it (a, 3), and also during taking food, either from the hand or from the cage floor. Activity of the other neuron corresponded only partially to activity during RF testing: Activation on contact of the nose with the feeding bowl was observed in this cell, just as the previous one (Fig. 1b, 2, on right of arrow). This neuron, however, also was activated during approach to the feeding bowl and lever (Fig. 1b, 2, 3, on left of arrow), when the receptive zone was not in contact with any environmental objects. This difference of activity in neurons with identical RF corresponds to the fact that motor cortical neurons with identical cutaneous "input" zones, during active contact, may generate different or even opposite forms of activity (activation and inhibition) [15]. Analysis of activity of a third neuron (Fig. 1c) showed no agreement between activities in situations of RF testing and FGB realization. On palpation and displacement of a contralateral area of skin between the nose and corner of the mouth marked activation was observed (Fig. 1c, 1). However, during realization of FGB, neither when food was taken from the feeding bowl (Fig. 1c, 2), when both contact between receptive zone and feeding bowl and food and displacement of the skin inevitably took place, nor during pressing the lever (c, 3) was activation observed. It is interesting to note that differences in the characteristics of activity of this neuron were discovered not only on comparing two behavioral situations (RF testing and realization of FGB), but also during analysis of a third situation — when the animal was sitting quietly (Fig. 1c, 4), when in the absence of any contact between receptive zone and environmental objects, increased (compared with the testing situation) activity appeared (compare Fig. 1c, 4 and 1c, 1, on left of arrow — the interval in which contact between receptive surface and object also was absent). These different versions of relations were found also for neurons with RF of different submodalities (Table 1) and also for neurons with inhibitory RF.

The three versions of relations between activity during RF testing and FGB realizations described above were observed not only for "specific" somatic RF, but also for "nonspecific" visual RF of somatosensory neurons. Histograms of activity of a neuron which was activated during testing when objects of different sizes approached the animal's mouth at different speeds and from either side (including from behind the opaque cage wall), but not when the object moved away from it (Fig. 2A, a), are illustrated in Fig. 2A. The neuron was correspondingly activated during movements of any kind during realization of food-getting (Fig. 2A, b) and orienting-investigative and searching (Fig. 2A, c) behavior. Correspondence between

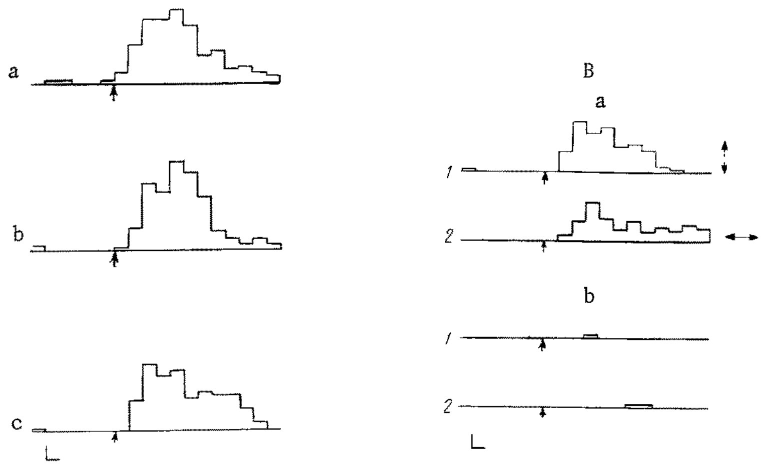

Fig. 2. Comparison of activity of two somatosensory cortical neurons (A and B) during testing of their visual receptive fields and realization of food-getting behavior: a) histograms of unit activity during testing, drawn from beginning of movement of object toward mouth from either side (in A) and from beginning of vertical (in B, a, 1) and horizontal (in B, a, 2) movements of object in contralateral visual field. b) Histograms of unit activity drawn from beginning of any (in A), vertical (in B, b, 1), and horizontal (in B, b, 2) movements in situation of standard FGB, and c) drawn from beginning of any movements during realization of searching and orienting-investigative behavior. Calibration: 5 spikes, 40 msec.

activity of the other neuron (Fig. 2B) during RF testing and in the course of FGB was absent. This neuron was activated as a result of vertical (Fig. 2B, a), and less strongly, horizontal (B, a, 2) movements of objects in the contralateral part of the visual field. In a situation of FGB activity of this neuron was absent during both vertical (Fig. 2B, b, 1) and horizontal (B, b, 2) head movements.

Visual Cortical Neurons. During analysis of visual cortical unit activity two types of RF of these cells could be distinguished: visual and proprioceptive. Of 12 visual RFs seven were directionally sensitive; 11 RFs were contralateral, and one ipsilateral. All the abovementioned types of correspondence (Table 1) were characteristic of "specific" visual RFs of visual cortical neurons and of "nonspecific" visual RFs of somatosensory cortical neurons.

An example of activity of a neuron whose activity during RF testing and during FGB corresponded completely is shown in Fig. 3a. This neuron was activated at the end of approach of an object toward the right (contralateral) eye until the distance between them was 2-5 cm (Fig. 3a, 1). Correspondingly, during realization of FGB (Fig. 3a, 2) and searching (a, 3) behavior the neuron was activated at the end of movements to the right irrespective of their duration.

Absence of correspondence of activity during RF testing and in the FGB situation is illustrated by the example given in Fig. 3b. This neuron was activated as a result of movement of different objects at different speeds and in different directions at distances of 5-15 cm from the contralateral eye (Fig. 3b, 1). During any movements in realization of FGB activity was absent. In four neurons with proprioceptive RF activity in the course of testing corresponded to that in the FGB situation.

Although indeterminacy of matching of activity in testing and FGB situations was demonstrated for both somatic and "specific" and "nonspecific" visual RFs, a difference with respect to this criterion between groups of RFs can be seen in Table 1. Statistical analysis showed that agreement between characteristics of activity of neurons with visual and proprioceptive RFs, during RF testing and during FGB realization, was found significantly ($P < 0.01$) more often than in all other cells.

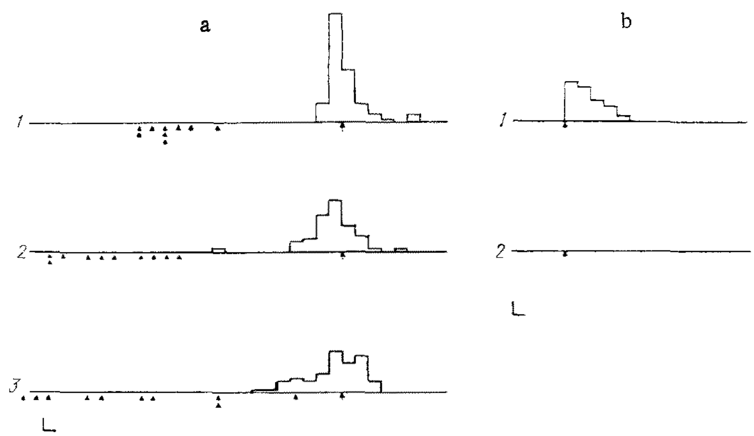

Fig. 3. Comparison of activity of two visual cortical neurons (a and b) during RF testing and during FGB. 1) Histogram of unit activity during testing, drawn from time when an object moving toward the right eye stops (in a), and from the beginning of movement of an object past the left eye (in b). 2) Histogram of unit activity drawn from cessation of movement to the right (in a) and from beginning of any movement (in b) in a situation of standard FGB. 3) Histogram of unit activity drawn from time of completion of a movement to the right during realization of searching and orienting-investigative behavior. Triangles denote times of beginning of movement of testing object (a, 1) and beginning of animal's movements to the right (a, 2, 3). Calibration: 5 spikes, 40 (for a) and 200 (for b) msec.

DISCUSSION

Testing the hypothesis expressed when the aim of this investigation was stated thus showed that unit activity of "sensory" structures, like that of the motor cortex, during stimulation of the receptive surface in an ordinary situation of RF testing differs from activity evoked by "self-stimulation" during realization of active goal-directed behavior. Neurons of the somatosensory and visual cortex, demonstrating a connection during testing with a particular receptive field — a part of the body or retina — can modify it or lose it in an FGB situation. On the basis of activity of a neuron evoked by testing it is impossible to predict reliably its activity during realization of FGB, for even neurons with identical RFs may have different activity in an FGB situation.

It has not yet been established which properties of a neuron would make it possible to predict whether the characteristics of activity of that neuron during FGB would correspond completely, partially, or not at all to those observed during RF testing. Accordingly it is clear that the overall firing pattern of neurons in a situation of active goal-directed behavior, which can be simulated by testing of their RF, is at least hypothetical. The hypothetical nature of this pattern is increased even more if it is suggested that during realization of goal-directed active behavior specific properties of RFs of neurons not characteristic of the ordinary testing situation can be found; moreover, during RF testing in experiments on an anesthetized or immobilized animal, a whole class of RFs may fail to be detected, which are activated, for example, in an FGB situation, but which are not discovered in a passive situation (by analogy with RFs that were found in a situation only of testing, but not of FGB). This hypothesis is supported by the data of Sakata and Iwamura [19], who found neurons in area SI of the monkey cortex for which no RF could be found on the hand during testing, and which are not activated during passive movements of the hand, but are activated during grasping of particular objects. In the periarcuate cortex of monkeys neurons whose RFs are demonstrable only if contact of the receptive zone with the object takes place during the animal's goal-directed movements also have been found [18].

Reference to the extensive material already accumulated in sensory physiology on RF testing with a view to development of ideas on the mechanisms of utilization of information about the environment in the course of realization of behavioral responses must evidently be undertaken with certain limitations. For example, the criterion of similarity of RF for the distinction of columns as morphological units participating in perception processes, i.e., in goal-directed behavior [3], is dubious because similarity of RF does not necessarily imply similarity of activity in behavioral situations.

RF testing in the alert animal is not simply stimulation of a certain part of the body surface or visual field, but it is alteration of the environment which evokes the realization of passive-defensive or orienting-investigative behavior. Activity of the neuron tested in a given situation can therefore be regarded not as a response to a definite afferent volley, but as activity in a situation of the corresponding behavior. Shvyrkov [6] formulated the concept of functional synaptic field (FSF), which is the total of synaptic influences to which a neuron is selectively sensitive at a given moment, irrespective of the sources from which these influences arise. From this standpoint we can regard activity in a situation of RF testing and during realization of FGB as two not necessarily coinciding forms of FSF of the neuron in two different behavioral systems. The approach to RF as a phenomenon reflecting only one possible form of FSF of a neuron, in our opinion, assumes that the above-mentioned limitations can be set only in experiments combining analysis of activity during RF testing in a passive behavioral situation and in the realization of active goal-directed behavior. Evidence in support of the view that these limitations can actually be found is given by the fact that activity corresponded more closely in the present investigation during RF testing and during realization of FGB for neurons with both visual and proprioceptive RFs than for other cells.

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