ACTIVITY OF CAT PARIETOFRONTAL NEURONS DURING THE PERFORMANCE OF A VOLUNTARY MOVEMENT

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UDC 612.822.3:612.76

The impulse activity of 227 neurons of field 5 was investigated in cats trained to complete a movement of the forepaw in response to a stimulus. The discharges of each of them were collected relative to three markers: the presentation of the conditional signal, the raising of the paw from a support, and pressing on a pedal. The reactions associated with the performance of the reflex were recorded in 224 neurons. The majority of the cells reacting to the stimulus generated a pronounced excitatory response even at the beginning of the movement, but were inhibited at the moment of the touching of the pedal. Sixty-seven percent of the neurons whose discharges were collected relative to the raising of the paw reacted prior to the appearance of the EMG response. The parietofrontal neurons were identified on the basis of the presence of an antidromic response to the stimulation of the motor cortex. The changes in the discharge frequency which were associated with the movement significantly more often anticipated the EMG response in the parietofrontal neurons as compared with non-parietofrontal cells (79.0 and 63.3%, respectively). The parietofrontal neurons reacted more actively to the conditional signal, light flashes, acoustic tone, and tactile stimulation as well. Their role in the triggering and unfolding of the program of a voluntary movement is discussed.

It has been established experimentally that the parietal associative cortex has a direct relationship to the programming and triggering of goal-directed movements of the forelimb [9, 12–14]. Movements of this type are directionally dependent and require fine control [11, 12]. Their performance is possible only with the participation of the motor cortex, where a neuronal mechanism, with a highly-developed system of backward connections, which is predestined for the differentiated control of particular parts of the body, is located. In this context the direct connections between the parietal and motoric areas of the cortex take on special significance in the processes of the programming and triggering of goal-directed movements of the forelimb. The specific carriers of these connections, the parietofrontal neurons, have been identified in experiments on anesthetized animals. Their peripheral inputs [4, 6] and the features of the connections with neurons of the motor cortex [6] have been investigated in detail. However, the natural activity of these cells during the performance of a goal-directed movement of the forelimb, and its contribution to the reaction of the entire population of parietal neurons, remain unknown. Therefore, the present study was devoted to the investigation of the impulse activity of the parietofrontal cells and other neurons of field 5 of the cortex of the cat at various phases of a conditioned reflex food-procuring movement of the forelimb.

METHODS

The experiments were carried out on seven awake cats in which an alimentary instrumental reflex was developed at the beginning of the investigation. The animals, which were loosely fixed in a sling, were trained to raise the right paw from a supporting base and to press a pedal with it in order to be reinforced with a food reward. The opening of the window through which the cat received the food reinforcement after pressing the pedal served as the triggering conditional stimulus. The raising of the paw by the animals began 213–2012 msec, and the pressing of the pedal began 802–2395 msec, after the opening of the window. The impulse activity of each neuron was collected by means of a computer relative to three markers which

Department of Physiology of Man and Animals of the M. V. Frunze State University, Simferopol'. Translated from Fiziologicheskii Zhurnal SSSR imeni I. M. Sechenova, Vol. 77, No. 2, pp. 9–16, February, 1991. Original article submitted July 10, 1989.

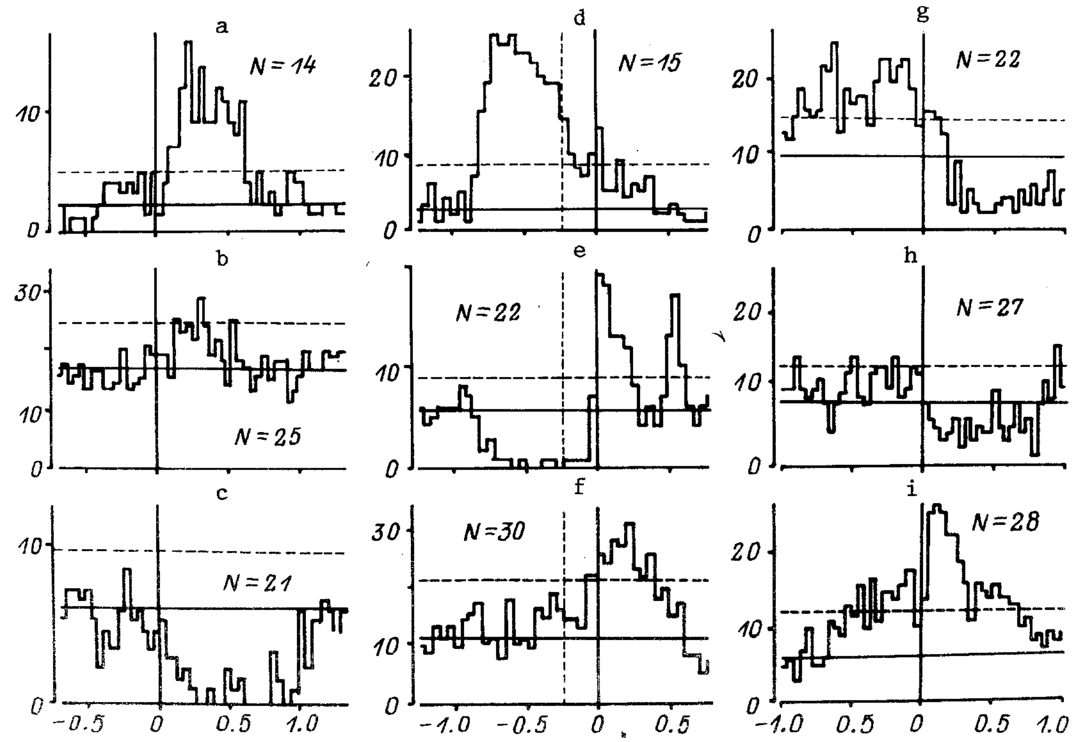

Fig. 1. Histograms of the activity of various neurons of the parietal cortex, collected from the moments of the presentation of the conditional stimulus (a–c), the raising of the paw from a support (d–f), and the pressing of the pedal with it (g–i). Along the abscissa: time, sec; along the ordinate: number of impulses in a bin. The collection markers are indicated by solid vertical lines; the beginning of the change in the myogram by broken lines. The average levels of baseline activity are indicated by solid horizontal lines; the level exceeding the average by the twice the standard deviation, by broken lines. No., the number of realizations.

TABLE 1. Characterization of the Reactions of Neurons of Field 5 at Various Stages of the Behavioral Act

Reactions, detected relative to	Beginning of the reaction: by excitation	Beginning of the reaction: by inhibition	Total reacted	Do not react	Total of neurons examined
Conditional stimulus	180 (81.5) *	20 (9.0)	200 (90.5)	21 (9.5)	221 (100)
Raising of the paw from a support	167 (74.6)	39 (17.4)	206 (92.0)	18 (8.0)	224 (100)
Pressing pedal with the paw	28 (31.5)	44 (49.4)	72 (80.9)	17 (19.1)	89 (100)

Note: Here and in Table 2, the corresponding percents are indicated in parentheses with an asterisk.

corresponded to the moments of the presentation of the conditional stimulus, the raising of the paw from the base and its contact with the pedal. Following the training the base of a micromanipulator was fixed to the skull of the animal under general anesthesia, the stimulating needle electrodes, which were insulated along their entire length (with the exception of the tip, 150–350 μm in length) were implanted into the motor cortex, and electrodes for the pickup of the EMG were placed in the muscles of the forelimb girdle (subcutaneously). The neuronal activity of the cortex of field 5 [10] was picked up by a silver microconductor in glass insulation, the resistance of which did not exceed 5 MΩ. A flash of light, an acoustic tone of 1000 Hz, 5 msec in duration, and the contact of a stimulating rod against the contralateral forepaw served as the peripheral stimulations. The significance of the results were assessed using the Student test. The level of significance was taken to be 5%. The remaining details of the methodology have been presented previously [4, 5].

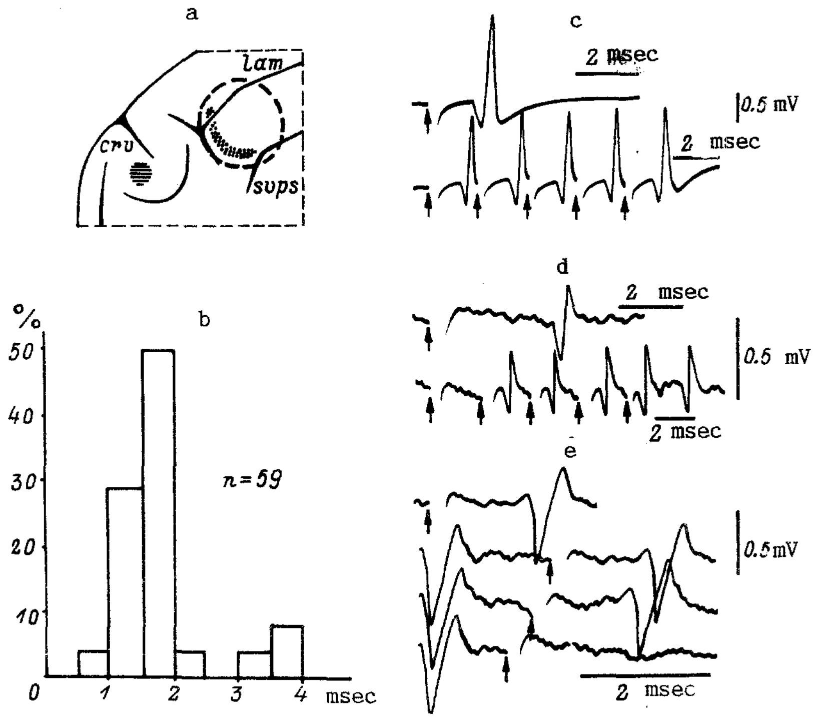

Fig. 2. Region of stimulation and pickup in the cortex of a cat (a), as well as the distribution of latent periods (b) and the general appearance of the responses (c–e) of parietofrontal neurons in response to the stimulation of the motor cortex. In a: the zone of the projection of the base of the micromanipulator to the parietal cortex is designated by a broken circle; the following are hatched: by horizontal lines, the stimulation zone; by dots, the pickup zone. cru, the cruciform; lat, the lateral; and sups, the suprasylvian sulci. In b: along the horizontal, time in sec; along the vertical, number of neurons, in % relative to the total number (n). In c–d: examples of responses of two parietofrontal neurons to solitary and trains (400–500 Hz) of stimulation. The moment of stimulation is indicated by arrow. In e: identification of a parietofrontal neuron by the method of impulse collision in the axon.

TABLE 2. Quantitative Characterization of the Association of the Activity of Various Groups of Neurons of Field 5 with the Beginning of the Movement

Group of neurons	Reacted						Did not react	Total
	bef. the beginning of the movement			during the movement				
	by excitation	by inhibition	by excitation	by inhibition	by excitation	by inhibition		
Parietofrontal	35	10	45 (79.0) *	9	2	11 (19.3)	1 (1.7)	57 (100)
Non-parieto-frontal	41	14	55 (62.5)	19	5	24 (27.3)	9 (10.2)	88 (100)
Not tested	43	7	50 (63.3)	20	1	21 (26.6)	8 (10.1)	79 (100)
All neurons	119	31	150 (67.0)	48	8	56 (25.0)	18 (8.0)	224 (100)

INVESTIGATION RESULTS

The activity of 227 neurons of field 5 was studied during the performance of the conditioned reflex by the cat. In the time interval from the moment of the presentation of the triggering signal to the end of the movement, 224 (98.7%) of the cells altered their activity. The data on the character of the reactions of the neurons at different stages of the behavioral act are pre-

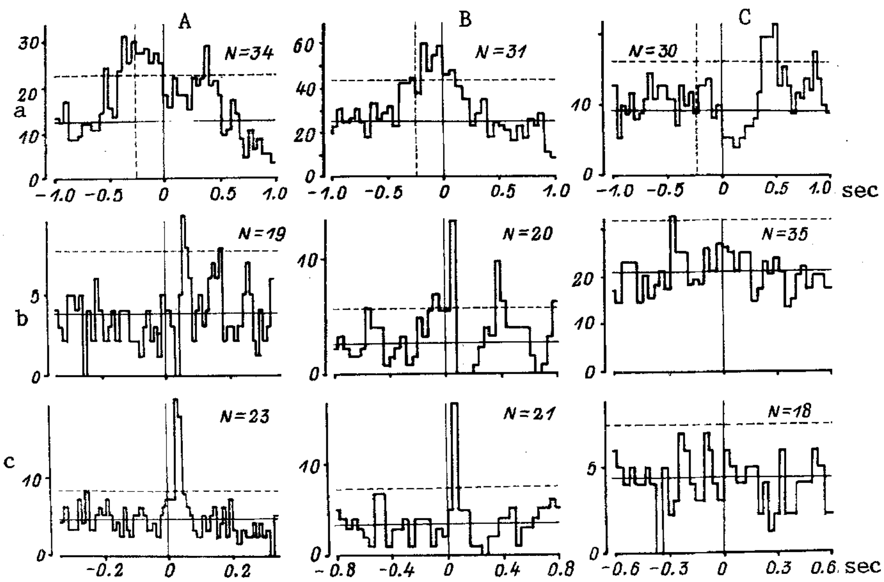

Fig. 3. Histograms of the activity of two frontoparietal (A, B) neurons and a non-frontoparietal neuron (C), collected from the moment of the raising of the paw from a support (a), and of the presentation of light (b) and acoustic (c) stimulations. Designations the same as in Fig. 1.

sented in Table 1. The collection of the neuronal discharges relative to the conditional stimulus showed that 90.5% of the investigated cells are reactive to it. The responses of the majority of these appeared 20–250 msec following the presentation of the signal, and could begin with excitation exceeding the baseline level by a factor of 2 or more (Fig. 1a), or with an insignificant exceeding of it (Fig. 1b), or more rarely, with inhibition (Fig. 1c). The averaging of the impulse activity from the moment of the raising of the paw (Fig. 1d–f) made it possible to identify its changes in 92.0% of the cells. As was the case with the responses associated with the stimulus, excitatory reactions predominated over inhibitory reactions. When the impulse discharges were collected relative to the moment of the pedal pressing (Fig. 1g–i), reliable excitatory and inhibitory responses were found in 80.9% of the cells, but, by contrast with the two preceding cases, inhibition was encountered much more often. Reactions of inhibition with excitation preceding it (Fig. 1g) and without it (Fig. 1h) were represented in equal degrees.

The characteristics of the distribution of the neuronal reactions collected relative to the raising of the paw, based on their relationship to the beginning of the movement, are presented in Table 2. It must be taken into account that the activation of a number of muscles of the shoulder girdle preceded the raising of the right limb from the base, anticipating it by 240–20 msec. The earliest changes in the EMG (240 msec), recorded in the right deltoid and biceps muscles, were taken as the reference point for the beginning of the motor act. In this connection, neurons whose activity changed 1150–270 msec prior to the raising of the paw (67.0%) were considered to be reacting prior to the beginning of the movement (Fig. 1d, e); the reactions of other cells (25.0%) began after the appearance of the first EMG changes, i.e., after the beginning of the movement (Fig. 1f). Of these neurons, 8.0% remained indifferent to the raising of the paw from the support. The appearance of a response of a cell prior to the beginning of the motor act depended to a significant degree on the intensity of its reaction to the triggering signal. Thus, a pronounced excitatory response to the stimulus exceeding the baseline level by a factor of 2 or greater, was recorded among the neurons reacting prior to the movement in 69.7% (85 out of 122; here and subsequently, the first figure in the parentheses is the number of the reacting neurons, and the second is the number of neurons investigated), while this was recorded only in 29.0% (22 out of 76) out of the number of cells which did not change the frequency of discharges prior to the movement. In other words, in the majority of the cases in which the response of the neuron to the conditional stimulus was well marked, the reaction associated with the raising of the paw also anticipated the beginning of the movement.

The cells which react prior to the beginning of the movement proved to be more sensitive not only to the conditional signal, but to peripheral stimulations of various modalities which are not conditional in the given situation: 62.5% (45 out of 72), 75.0 % (69 out of 92), and 84.2% (64 out of 76) of these responded to light, acoustic, and tactile stimulations, respectively. At the same time, the proportion among the neurons reacting following the beginning of the movement of those sensitive to light, sound and tactile stimulation was 43.5% (10 out of 23), 64.3% (18 out of 28), and 78.6% (22 out of 28), respectively.

We investigated 147 neurons of field 5 during stimulation of the motor cortex in the previously established focus of parietal projections [3, 6] (Fig. 2). Of these, 59 parietal cells reacted antidromically; 57 of these were background active, and two were "silent". The latent periods of their responses were 0.5–3.8 msec (1.65 ± 0.12 msec; Fig. 2b). These cells were identified as parietofrontal. The remaining neurons did not exhibit an antidromic response to stimulation of the motor cortex, and these were designated as non-parietofrontal. The impulse activity at the time of the performance of the conditioned reflex act was investigated in 57 parietofrontal and 88 non-parietofrontal neurons. The features of the reactions arising in the neurons of the different groups relative to the beginning of the movement are characterized in Table 2 and in Fig. 3a. There were 79.0% of the parietofrontal cells reacting prior to the beginning of the motor act, which is significantly higher than in the non-parietofrontal neurons (62.5%). We should note that intense excitatory reactions to the conditional stimulus, exceeding the level of the baseline activity by a factor of 2 and greater, were recorded in 80.0% (28 out of 35) parietofrontal neurons activated prior to the movement.

The parietofrontal neurons reacted more frequently than the others to peripheral stimulations as well. Among these, 65.5% (19 out of 29) responded to a flash of light, 86.5% (32 out of 37) to an acoustic tone, and 87.9% (29 out of 33), to tactile stimulation, whereas the proportion of cells reacting to these stimulations among the non-parietofrontal neurons was 53.7% (36 out of 67), 66.3% (55 out of 83), and 80.3% (57 out of 71). Examples of the reactions of various neurons to the peripheral stimuli applied are given in Fig. 3b, c.

DISCUSSION OF RESULTS

In our experimental situation 90.5% of the neurons reacted in response to the presentation of the triggering stimulus, while only 28.9% of the neurons of field 5 [1] respond to a more simple conditional stimulus (acoustic click, series of clicks) during the food-procuring reaction. It is possible that the degree of reactivity of the parietal neurons in relation to the signal stimulus depends on its complexity for analysis. The abundance of reactions proved to be characteristic not only for the stage of the perception of the conditional signal, but for the other stages of the realization of the behavioral act as well. It is entirely probable that field 5 serves all of the stages of the organization of the movement: from the detection of the triggering signal to the control of the sequential phases of the movement.

Of the parietal cells investigated during the movement of the forelimb, 67.0% changed their activity before its beginning. According to various data obtained in cats and monkeys, the proportion of such neurons ranges from 34.0 to 63.1% [7, 9, 13]. It is felt that the anticipatory activity of the neurons of field 5 is associated with the construction and triggering of motoric commands for the forelimb, while the lagging activity is associated with the ongoing control of the movement on the basis of peripheral feedback. We should note that in our experiments the anticipatory activity of the parietal cells was combined with greater sensitivity to peripheral stimulations of different modalities. Evidently, neurons with enhanced polysensory properties participate in the programming and triggering of the movement. When the reactions anticipating movement of the neurons of field 5 of primates were examined in detail, it turned out that some of them are closely associated in their temporal parameters with the stimulus, while some are associated with the motoric response. The former, despite the primary association with the stimulus, are necessary for the triggering of the movement, since the movement does not occur in their absence; the appearance of the latter are associated with the "copy of the efferent command" [14]. Evidently those cells in our experiments in which the response to the stimulus is collected, in which at the same time the discharges are associated with the movement and anticipated, are analogous to the stimulus-dependent neurons of field 5 of the primates. It is they in particular, in all probability, which are involved in the triggering of the motor act investigated by us.

The role of parietofrontal cells in the generation of activity, which is key for the triggering of the movement, arising between the presentation of the signal and the first changes in the EMG, proved highly significant. The modification of the discharges which was associated with the movement began in the majority of them, unlike the non-parietofrontal neurons, prior to the EMG response. There was an intense reaction to the conditional stimulus in 80.0% of the parietofrontal cells activated prior to the movement. Thus, the majority of this group of cells may be assigned to the population of those neurons of field 5 which are presumed to be triggering the movement.

According to data of acute experiments, the parietofrontal neurons form mono- and polysynaptic connections not only with interneurons, but also with cells of the pyramidal and corticorubral tracts of the motor cortex. At the same time, the connection with the parietofrontal axon is regarded as a monosynaptic axosomatic connection in some of the rapidly conducting cells of these tracts, and these may serve as a reliable relay during the transmission of signals from the parietal cortex to the targets of the pyramidal tract [6]. Given the high degree of sensitivity of parietofrontal neurons to peripheral stimulations of different modalities, this channel may be used for the rapid adjustment of the program of the movement under the influence of unexpected sensory stimuli. The region of the parietofrontal projections in the motor cortex encompasses the efferent representations of the muscles of the entire forelimb zone of the cat: axial, shoulder, forearm, and wrist [3], which evidently permits the discharges of the parietofrontal neurons to influence the state of these muscles effectively. In addition, a distinctive succession of the involvement of the various groups of neurons of the pyramidal tract in the corticofugal salvo has been established during stimulation of the parietal region [6]. This fact, in combination with the anticipatory activity of the parietofrontal cells prompts the thought of the possibility of triggering from the parietal cortex of integral local motor programs or their fragments, in which the parietofrontal cells participate in the first place.

The recording of similar anticipatory, stimulus-dependent activity in the neurons of the pyramidal tract and other cells of the motor cortex, located in the zone of the parietal projections [17] serves as evidence of the fact that the early discharges of the parietofrontal cells, which are associated with the movement and which are governed by the triggering stimulus, actually influence the neurons of the motor cortex, including the cells of the pyramidal tract.

What might be the role of the parietofrontal discharges which anticipate the movement, and of the corresponding early activation of the neurons of the motor cortex, in particular, of the cells of the pyramidal tract? After all, in this case, the discharges of the neurons of the pyramidal tract arise under the influence of the parietofrontal activity long before the first changes in the EMG, i.e., long before the synchronous discharge of the main mass of neurons of the pyramidal tract which actually triggers movement. It is possible that the "foreward" discharges, which run ahead of the main front of the impulses, create the preconditions for the triggering of the movement. The early corticofugal discharges in the motor cortex, which are governed by stimulus-dependent parietal activity, may, in keeping with the distribution of the collaterals of fibers of the pyramidal tract [15], reach not only segments of the spinal cord, but other structures as well, which are associated with the movement: the red nucleus, the substantia nigra, the ventral thalamus, the basal nuclei, the nuclei of the pons, etc. It is entirely probable that these signals, as copies of the initial "efferent commands" which anticipate the basic command, are necessary for actualization, i.e., for the regeneration in memory of the program of the movement already preliminarily developed by the animal. It is logical to hypothesize that the parietofrontal neurons (by taking into account the character of their responses to the stimulus during the movement as well) participate in the detection of the sensory triggering signal, and trigger the process of the actualization of the program of the movement during each realization of the learned act.

The specific patterns of the anticipatory activity of the parietal, including the parietofrontal, neurons are such that the activation ends in almost half the cases and shifts to a phase of inhibition upon the touching of the pedal by the paw. It is entirely probable that the parietofrontal cells with activity anticipating the movement, like other neurons of field 5, participate mainly in the triggering and direct programming only of the initial phases of the movement, the raising and the thrusting of the paw in the direction of the pedal.

Thus, it can be assumed that the anticipatory activity of the parietofrontal cells, firstly, participates in the triggering of the entire program of the behavioral motor act, thus inducing the process of its actualization, and secondly, determines the specific steps of the unfolding of the initial phase of the movement investigated by us, thus shaping its trajectory.

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