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PRE-MOVEMENT ACTIVITY OF NEURONS IN THE PARIETAL ASSOCIATIVE CORTEX OF THE CAT DURING DIFFERENT TYPES OF VOLUNTARY MOVEMENT

T. V. Khitrova-Orlova, V. G. Sidyakin, A. M. Kulichenko, and V. B. Pavlenko

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Pre-movement activation of electromyographic spike activity of 201 neurons of field 5 was studied in cats trained to carry out a stereotypical act (lifting the anterior footpad to press a pedal) in response to a conditioned stimulus (experimental series 1) and without a conditioned stimulus (self-initiated movement, experimental series 2). In series 1, 69.2% of neurons were activated and 13.5% were inhibited before the movement. Prior changes in activity were also seen in intersignal movements, with activation of 40.6% and inhibition of 21.7% of neurons. The time parameters of excitatory and inhibitory responses in both situations were similar, with pre-movement intervals of 19-1640 msec. In series 2, pre-movement inhibition was seen rather more frequently than activation (36.7% and 33.7% respectively). The earliest changes were inhibitory, occurring some 1800 msec before movements, while excitatory changes occurred only 880 msec before movement. These data indicate the involvement of the parietal associative area in the cat not only in executing, but also in preparing for different types of movement, including self-initiated movements, and that inhibition has an active role in this process.

Key words: Neuron activity, parietal associative cortex, voluntary movement.

Neurons of the parietal associative cortex are known to take part in the programming and execution of voluntary movements elicited by stimuli [3, 8, 10]. Most of the cells in this region change their activity before the start of a conditioned reflex movement. It has been suggested that these neurons are involved in detecting the sensory starting signal, and launching the movement program for execution of the learned act [1]. At the same time, their role in initiating movements remains unclear in situations of intersignal movements and self-initiated movements without a preceding conditioned signal. The aim of the present work was to assess the properties of parietal associative cortex neurons on initiation of different types of voluntary purposive movements: conditioned reflex movements, intersignal movements, and self-initiated movements.

METHODS

Experiments were carried out using four conscious cats which had initially been trained to carry out a food-related operant reflex. In series 1, two animals were trained to respond to a conditioned stimulus (opening of a window through which the cat obtained food reinforcement) by raising the right footpad from the support area and using it to press a pedal. In series 2, two cats were trained to carry out the same movement but in a self-initiated, or voluntary, rhythm. After training, a manipulator base was attached to the skull under general anesthesia, and s.c. electrodes were placed over the muscles of the right limb for electromyographic recording. Neuronal activity of field 5 [6] was recorded using silver microwires in glass insulators (wire diameter 12 μm, insulator diameter 70 μm) with tips sharpened to the level of an injection needle. Spike

Department of Human and Animal Physiology and Biophysics (Director V. G. Sidyakin), Simferopol State University.
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TABLE 1. Field 5 Neuron Activity Occurring Before Different Types of Voluntary Movement

Type of movement	Start of response		No response	Total number of neurons studied
	Excitatory	Inhibitory		
In response to a conditioned stimulus	72 (69.2)	14 (13.5)	18 (17.3)	104 (100)
Intersignal	28 (40.6)	15 (21.7)	26 (37.7)	69 (100)
Self-initiated	33 (33.7)	36 (36.7)	28 (28.6)	98 (100)

Note. Numbers in brackets are percentages.

activity from each neuron was accumulated using a computer, with reference to event markers indicating raising of the limb from the support area. Histograms of the responses of several neurons were subsequently summed. The first change in the electromyogram was taken at the moment at which movement acts began. These were recorded in the right deltoid and bicep muscles from 240 msec before the lifting of the paw from the support. Further details of the methods used here have been published previously [1].

RESULTS

The activities of 201 neurons of the parietal associative cortex field 5 were studied during the execution of different types of voluntary movement by cats. Data on the nature of pre-movement neuron activity are presented in Table 1. Activity was recorded from 104 neurons in series 1, when the cats carried out purposive movements in response to a conditioned signal. Most of the neurons (69.2%) were activated before the start of the stimulus-induced movement. Activation of different neurons took place 42 to 1640 (655.5 $\pm$ 46.3) msec before the first electromyogram change (Fig. 1*A*). A small proportion of neurons (13.5%) showed inhibition of activity before the movement (Fig. 2*A*). This type of response appeared 65-1123 (592.6 $\pm$ 95.8) msec before the initiation of the movement act.

Cats sometimes carried out intersignal movement acts, and 69 neurons were studied for changes in activity before these movements. Premovement increases in nerve cell activity occurring before intersignal movements were significantly less common, and were found in 40.6% of cases. In different neurons, these began 19-1500 (633.8 $\pm$ 67.9) msec before the movement, while inhibition (which occurred in 21.7% of cases) occurred 36-1546 (781.5 $\pm$ 114.9) msec before the onset of movement (Fig. 1*B*, Fig. 2*B*). It is of note that before intersignal movements, neurons underwent activity changes less frequently; there were no pre-movement changes in twice as many cells as before movements in response to the conditioned stimulus.

In series 2, when animals were trained to carry out self-initiated movements, measurements were made of 98 nerve cells. One third of these underwent activation prior to movements (Fig. 1*C*). Activation occurred 10-880 (330.8 $\pm$ 48.6) msec before the movement, i.e., significantly later than occurred in other types of voluntary movement. Inhibition of activity before movements occurred more frequently than activation, and was seen in 36.7% of cases; inhibition was characterized by its particularly early onset relative to the start of the movement act — 280-1800 (838.6 $\pm$ 65.9) msec. In most cases, inhibition before movement was followed by an excitatory response (Fig. 2*C*).

DISCUSSION

Among the neurons which showed alterations in activity occurring before different types of voluntary movements, some showed changes preceding the movement act by 500-1500 msec and more, while others responded 10-500 msec before movements. Similar time intervals for neuron activity occurring before voluntary movements were found in the supplementary motor region in the monkey [9]. Changes in neuron activity occurring 480 msec and 0.5-2 sec before the first electromyographic changes were described as early and late pre-movement changes. Studies of the EEG correlate of premovement neuronal reactions, i.e. the readiness potential, indicate that there are two processes corresponding to the early and late phases.

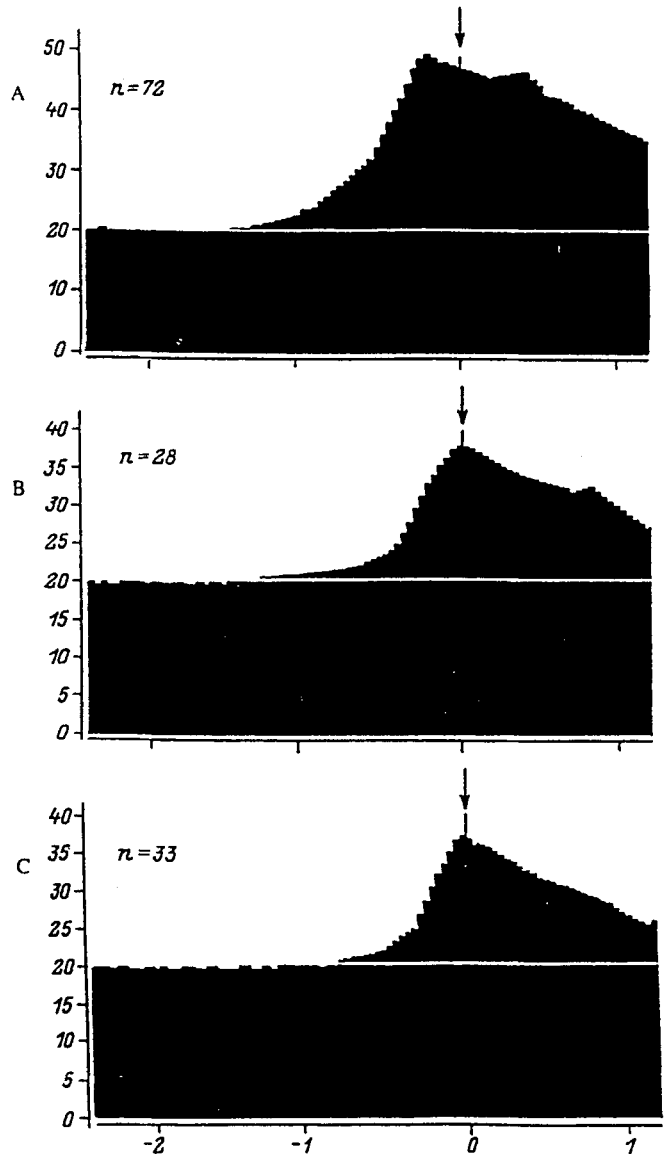

Fig. 1. Averaged normalized histograms of parietal cortex neuron activity, for neurons showing activation before the onset of voluntary movements carried out in response to a conditioned stimulus (*A*), in the intersignal period (*B*), and for self-initiated movements (*C*). The abscissa shows time in sec; the ordinate shows the numbers of spikes per bin. Arrows and vertical lines show the moments at which electromyographic activity started; the horizontal line shows the mean level of background spike activity. *n*) Number of neurons. A total of 20 movements were studied.

The first of these corresponds to planning of the programmed movement, and the second to stimulation of the movement's direct implementation [7]. It has been suggested that the early phase of readiness potential in primates carrying out any voluntary movement is generated in the supplementary motor region and reflects selection of a strategy for the movement and determination of the optimal moment for its initiation. The final part of the pre-movement process occurs in cortical regions which are more specialized for executing definite voluntary movements, for example, in the motor cortex region corresponding to the projection of the hand. Associative regions may be involved in the planning process, when the hand movement is carried out in extrapersonal space and information on the direction of movement is needed [4]. In cats, the planning function of direc-

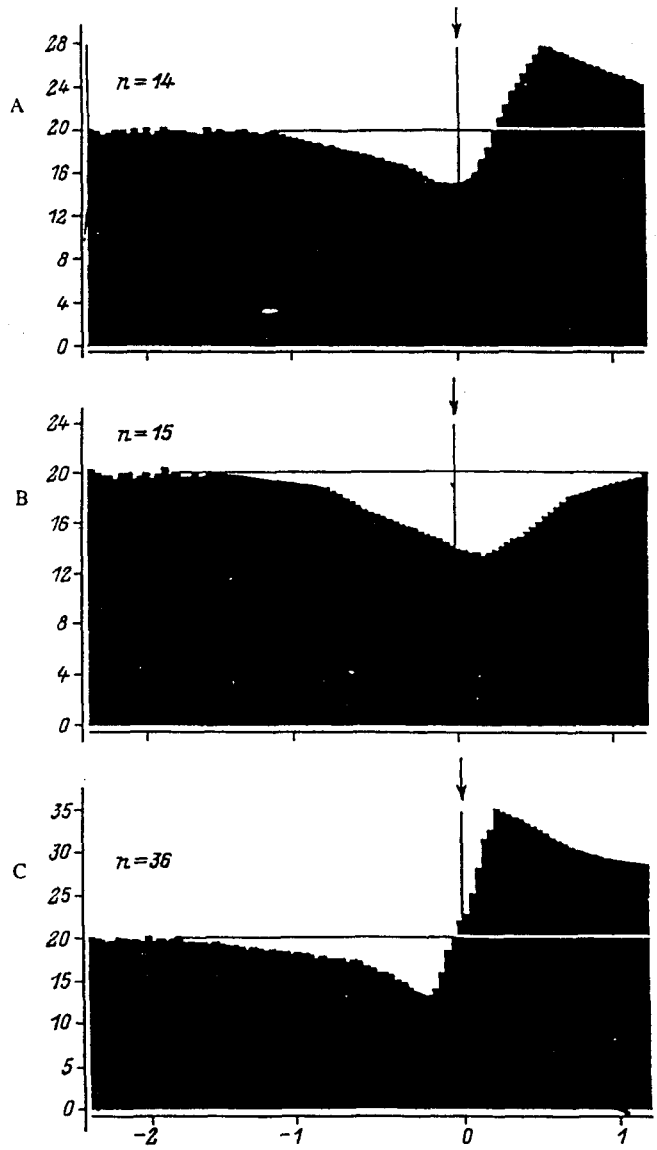

Fig. 2. Averaged normalized histograms of parietal cortex neuron activity, for neurons showing inhibition before the onset of voluntary movements carried out in response to a conditioned stimulus (*A*), in the interstimulus period (*B*), and for self-initiated movements (*C*). For other details see the caption to Fig. 1.

tion-dependent movements of the forelimb in space is thought to be less disseminated than in primates, and to be concentrated in the parietal associative cortex [2, 5].

In the experiments reported here, pre-movement changes in neuron activity occurred in two phases, corresponding to planning and initiation of the movement act. This leads to the conclusion that the parietal associative cortex in cats takes part in the planning and initiation of different types of voluntary movement, including self-initiated movements. It is of note that comparison of movements initiated by a conditioned stimulus and self-initiated movements shows that the latter involved an increase in the proportion of pre-movement inhibitory responses and an increase in the time by which changes preceded electromyogram changes. It is possible that at the early stage of preparation for movement, i.e., in the planning phase, inhibitory processes are important in the parietal cortex; these may be needed to ensure the appropriate level of release.

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