After functional blocking (cooling) or extirpation of the prefrontal cortex in primates disturbances of emotional, group, sexual, and maternal behavior have been demonstrated [9, 13, 20], short-term memory is disturbed [4, 11], the level of attention is lowered [12, 20], and the programming of voluntary behavior [3, 5] and choice of postural (spatial) responses are disturbed [17]. These observations have motivated the search for neuronal correlates of functions of the prefrontal cortex, which has been pursued vigorously in the last decade [2, 10, 14-16, 19], mainly through the introduction into research practice of the technique of recording unit activity in waking monkeys devised by Evarts [8]. Analysis of the experimental data shows that workers have tried to find "differentiated" responses of prefrontal cortical neurons belonging to one particular concrete behavioral function.

On the basis of the foregoing remarks the aim of the present investigation was to study unit activity in the prefrontal cortex of monkeys during the performance of a behavioral program including a chain of stimuli spaced out in time, association of which enabled the animal, given the right choice of motor response, to obtain food reinforcement.

METHOD

Experiments were carried out on five monkeys (Macaca rhesus) weighing 4-5 kg and aged 2-3 years. Before the beginning of the electrophysiological part of the experiments the animals were taught certain conditioned-reflex acts on an apparatus designed to present the animal with the following sequence of stimuli: 1) warning signal (the flash of a gas discharge tube from a type FS-02 photostimulator); 2) conditioned stimulus (the lighting of an incandescent lamp under one of the keys on the control panel); 3) triggering signal (the click of an electric locking device and exposing of a screen enabling the monkey to press the key). The interval between the warning signal and the conditioned stimulus was 2 or 5 sec and that between the conditioned and the triggering stimulus 5 or 10 sec. These intervals differed functionally in that in the first case the animal expected presentation of the conditioned stimulus without the need to retain in the memory the side of the conditioned stimulus (the "nonspecific" expectation period), whereas in the second case the animal awaited the triggering stimulus while storing information on the side of the conditioned stimulus (the "specific" waking period). Access to the keys during these periods was prevented by the screen, which opened automatically only after the delay period (opening time 100-200 msec) and which also closed automatically after the monkey pressed the key. The distance between the keys (right and left relative to the midline) was 35 cm. Food reinforcement, in the case of correct choice of key, was supplied automatically to a feeding bowl located above the screen in the midline between the right and left keys. The conditioned stimulus was presented in accordance with the following rule. Observations were made on the animals while in the experimental chamber by means of a television system.

This paper gives data obtained during the recording of cortical unit activity in the middle part of the sulcus principalis of the cerebral hemispheres. The method of inserting the bundles of electrodes, the operative procedures, and the electrophysiological part of the equipment were described previously [6].

So that the results of these experiments could be adequately compared with those obtained by other workers who studied the same area of the prefrontal cortex [10, 14, 15, 19], unit activity was displayed on a screen in the form of "dot displays" or as standard pulses obtained by means of a discriminator. The reliability of the unit responses during a definite period \( \Delta t \) was determined by Frolov's method [7]. The initial data were obtained by
Fig. 1. Types of unit responses to warning signal. 1-6) dot displays of responses of neurons to ten presentations of program, according to types of responses distinguished. Vertical line indicates time of stimulation. Calibration 1 sec.

averaging parameters of activity of the same neuron in at least ten realizations of the experimental program. Identification of the responses in the form of an increase (excitation) or decrease (inhibition) of discharge frequencies in this investigation is used descriptively by analogy with [10], and does not imply any particular type of synaptic processes.

EXPERIMENTAL RESULTS

Significant responses to the warning signal were given by 148 neurons (64%). Responses of single neurons are given in Fig. 1 in accordance with the six types distinguished. The first type of unit response consists of a short (from 50 to 300 msec) inhibitory pause followed by enhancement of activity (14 neurons, 6%); the second was a short inhibitory pause, corresponding to the first type, but without “postinhibitory rebound” (39 neurons, 17%); the third consisted of a tonic decrease in the spontaneous firing rate for up to 0.5-1.5 sec (62 neurons, 27%). Only in 32 neurons (14%) were responses consisting of initial excitation recorded, and seven of these neurons (3%) responded with phasic excitation followed by an inhibitory pause (the fourth type of response), 7 neurons (3%) responded by excitation without an inhibitory pause (fifth type), and 19 neurons (8%) responded with a long (from 0.4 to 1.5 sec) increase in spontaneous activity (the sixth type).

During the period of awaiting the conditioned stimulus activity of 131 neurons (57%) diminished until the time of presentation of the conditioned stimulus (Fig. 2A); the discharge frequency of 16 neurons (7%) increased (Fig. 2B); in 9 neurons (4%) responses during this period had the character of alternation of phases of an increase and decrease in spike activity (Fig. 2C, D). The duration of the phases varied from 0.5 to 2.5 sec.

Comparison of spike activity during this period after dividing the programs into those with a right- and left-sided conditioned stimulus showed that the unit responses were independent of the side of the conditioned stimulus. Only in one monkey were two neurons found whose discharge differed significantly (P < 0.01) depending on which conditioned stimulus (right or left) the animal expected.

Types of responses of neurons to the conditioned stimulus irrespective of the side of its presentation are illustrated in Fig. 3. Forty neurons (17%), which significantly (P <