Neurons of the Cat Sensorimotor Cortex: Responses Related to Differentiation of Monomodal and Heteromodal Conditioning Signals

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INTRODUCTION

In a certain sense, the sensorimotor cortex (SMC) in the cat can be regarded as one of the associative cortical regions characterized by a convergence of afferent inputs from various sensory systems [1]. The signals triggered by activation of these inputs intensively converge on the SMC neurons [2]. This fact indicates that the SMC is actively involved in the process of intersensory integration. The studies performed at a behavioral level have in fact shown [3] that bilateral lesion of this cortical region in carnivores results in an irreversible loss of the ability to differentiate a heteromodal signal from its components applied separately.

We studied earlier [4] the activity patterns generated by neurons of the SMC in awake cats under conditions of differentiation of the heteromodal complex conditioning stimulus (CS). The cells responding to the application of positive signal by excitation or inhibition were found in the SMC of the animals trained to differentiate the complex from its components. The responses of the same neurons to inhibitory signals were of the same direction and time course, but differed in their much lower amplitude. Nonetheless, such differences probably are not specific only for the heteromodal stimuli. In some cases, neuronal responses to selectively applied monomodal components were of the same amplitude as the responses evoked by the CS, and they resulted in triggering of an erroneous motor response to the inhibitory signal. The latter fact may indicate that the SMC neuronal networks participate in differentiation of sensory stimuli by preparing either triggering of the conditioned movement or its retardation, but not by specification of heteromodal or monomodal pattern of a signal. In this way, these networks can participate in the process of differential inhibition. This supposition was tested in the present study in which neuronal responses recorded under conditions of differentiation of hetero- and monomodal signals were compared in the cat SMC in more detail.
METHODS

Experiments were carried out on three adult cats. All the animals were pretrained to differentiate between two sound tones with frequencies of 1.7 and 0.8 kHz. The stimulus lasted 100 msec, with its rising and falling phases lasting 10 msec each, and the level of sound pressure being 70 dB relative to 2 µPa. The CS consisting of a 100-msec flash of the light-emmiting diode and a tone of 0.4 kHz lasting 20 msec also was applied. The latter stimulus component was perceived as a “soft” sound click. These components of the CS are referred to below as “light” and “sound.” The two cats were trained to differentiate the CS from its components; for one animal, the CS was an excitatory stimulus, and the isolated sound was an inhibitory one. The meanings of stimuli for the second animal were opposite: the sound component was an excitatory stimulus, and the CS was an inhibitory one.

It must be mentioned that the tasks with different signals were proposed for the animals in an alternative manner, within different series of the same experiment. The conditioned motor response consisted of the fast operant movement of one extremity aimed at capturing a piece of meat from the trough. The meat appeared 300-500 msec after the reinforced signal switched on. The trough was exposed for 200-300 msec; thus, the capture of the meat piece appeared successful only if the conditioned movement was triggered by the conditioning signal before the trough arrival. The applications of the inhibitory signals were not followed by the trough arrival. When the animals had succeeded in 70% of the correct differentiations of the conditioning stimuli, they were operated under hexenal anesthesia (80 mg/kg). A bundle of microelectrodes was implanted in the forepaw projection zone of the contralateral motor cortex. The methods of the microelectrode manufacturing and implanting, as well as the behavioral model used, were described in detail earlier [4].

In the course of an experiment, the neuronal activity and the actogram of the conditioned movement were recorded on magnetic tape. Then the data were processed with a computer; raster diagrams (RD) and peristimulus histograms (PSH) were plotted. As a rule, 25 test realizations of a test were stored. In the case of the response stability and low level of background activity, the latent periods (LP) of responses were measured at the RD plotted with a high temporal resolution.

If the background activity was high or the response was variable, we used another approach: PSH with a 5-msec or 10-msec bin were plotted, and the bin preceding two bins with a doubled or higher number of spikes (compared with the mean value within the 700-msec prestimulus interval) was taken as the moment of the response onset. The amplitude of the responses to the conditioning stimuli was estimated as the number of spikes above the mean +2σ level generated over the 250-300-msec interval after the stimulus. This temporal interval was selected considering the response pattern in many sensorimotor cortex neurons responding to the conditioning stimuli. The presence of two components (sometimes partially superimposed) was typical of this pattern. The first component was related to the moment of stimulus application, while the second one was related to the movement performed by an animal. The analysis of the PSH plotted from the moment of the movement initiation showed that, under our experimental conditions, the motor component of neuronal response developed 150-200 msec before the motion. The movement lasted 450-550 msec; therefore, all spikes within the 200-300-msec poststimulus interval and above the background +2σ level could be regarded as the reflection of a response to a conditioning stimulation.

At the beginning of the testing procedure, the somatic receptive field (RF) was found for each cell by palpation of various regions of the extremity. The experiment was followed by localization of the efferent output region using intracortical microstimulation (the current up to 30 µA). The bone above the recorded region was removed, and the location of this region was verified visually. All animals exhibited normal functional activity and were used later on in other experiments.

RESULTS

The responses were recorded from 125 neurons in 3 animals. In one animal, the electrodes were located within the lateral part of the anterior sygmoidal gyrus. Microstimulation of this region evoked contraction of the distal muscles of the extremity. In two other animals, the recording electrodes were inserted into more medial regions of the anterior sygmoidal gyrus, and microstimulation of the recorded sites evoked contractions of the proximal forelimb muscles.

The somatic RF were specified for 95 neurons studied. The neurons both with narrow receptive fields (including only a small part of the extremity) and with wide fields (covering whole surface of the extremity) were found in all recorded regions. The RF of 9 cells were localized on the hand surface; of 31 cells, on the forearm; and of 11 cells, on the shoulder regions. The RF of 6 neurons included most of the extremity surface; 2 cells had their RF on the head, and 36 neuronal RF were difficult to locate.

All 125 neurons studied were tested for their ability to distinguish between the two tones of different frequencies. Among these cells, 45 units responded to the positive conditioning signal (Fig. 1). In this group, 25 cells generated excitatory responses, while activity of 20