Activity of the Parietal Associative Cortex Neurons and Aminergic Brainstem Neurons at the Performance of a Voluntary Movement in Cats

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Activity of 98 neurons of the parietal associative cortex (PAC) and 189 supposedly aminergic brainstem neurons (dopaminergic in the *substantia nigra pars compacta*, noradrenergic in the *locus coeruleus* region, and serotonergic in the *raphe* nuclei) was recorded in awake cats. The animals were trained to perform a voluntary movement (pressing a pedal) not earlier than at a certain prefixed time moment. More than half of the recorded units modified their activity before the movement initiation. The PAC neurons responded mostly within the interval of planning of the movement, while reactions of aminergic neurons were observed in the course of its initiation, which probably provides facilitation of the responses of cortical neurons. The pattern of responses was rather specific for each of the studied neuronal populations.

INTRODUCTION

The entire spectrum of motor behavioral acts of animals and humans, from involuntary automatic movements, controlled mostly by the innate central behavioral programs, to voluntary motions formed in the course of storing the vital experience, forms a motor continuum [1]. Numerous experimental models based on operant behavior of awake animals were designed for studying the neuronal mechanisms controlling voluntary movements. These models allowed experimenters to elucidate some of the neuronal mechanisms providing preparation and initiation of the movements after presentation of a conditioning stimulus and the mechanisms controlling intersignal movements and movements initiated by an internal drive and based on preliminary learning. Special attention in this respect was payed to the nonspecific structures related to the processes providing attention, motivations, emotions, and the so-called approaching behavior [2, 3]. It is believed that the associative cortical regions and different aminergic brainstem systems especially closely and diversely relate to the attention-providing processes, formation of motivations, and learning [4-6]. At the same time, studies in which the neuronal activity in the associative cortex and different aminergic systems was studied under the same conditions in the course of performance of a targeted behavioral act are near absent.

This determined the aim of our study: to compare the patterns of neuronal responses in the parietal associative cortex (PAC) region and responses of supposedly (according to their localization and pattern of activity) dopaminergic, noradrenergic, and serotonergic (DE, NE, and SE, respectively) brainstem neurons at the performance of a targeted behavioral motor act, which could be considered voluntary.

METHODS

Four experimental series were carried out by studying the activity of four above-mentioned neuronal populations (eight cats, two animals in each series). The animals were trained to lift, with no preceding signal, their forelimb from a support platform and to press a pedal; this movement provided a food reward. The frequency of the movements was limited: if the pedal had been pressed earlier than 12 sec after a preceding pressing, such a movement was considered non-correct, and the animal received no reward. In the series in which we studied the activity of aminergic neurons, correctly pressing the pedal was accompanied 1 sec later

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by a positive conditioning acoustic signal (1600 Hz tone), and 1.5-2.0 sec after this signal a reward was given. The non-correct performance of a trial was accompanied by a negative conditioning signal (400 Hz tone).

After an animal had been trained, the base of a micro-manipulator was fixed to the skull under general anesthesia. When the activity of brainstem neurons was recorded, we also inserted a guidance cannula. The neurons were recorded contralaterally to the working forelimb within cortical field 5 and the regions of the *substantia nigra pars compacta, locus coeruleus,* and dorsal and anterior central *raphe* nuclei, where the somata of DE, NE, and SE neurons are localized, respectively [7-10]. As an extracellular recording electrode, we used sharpened silver microwire in glass insulation. The spike neuronal activity and EMG recorded from the right forelimb muscles were amplified, digitized, and, together with the signals from transducers on the platform and pedal, transferred to a computer controlling the experiment. Peristimulus histograms were plotted with respect to the moments of movement initiation or the moments of signals from the transducers regarded as zero points. The number of trials usually was from 15 to 30, and the bin width varied from 8 to 80 msec. Other details of techniques were described earlier [11, 12].

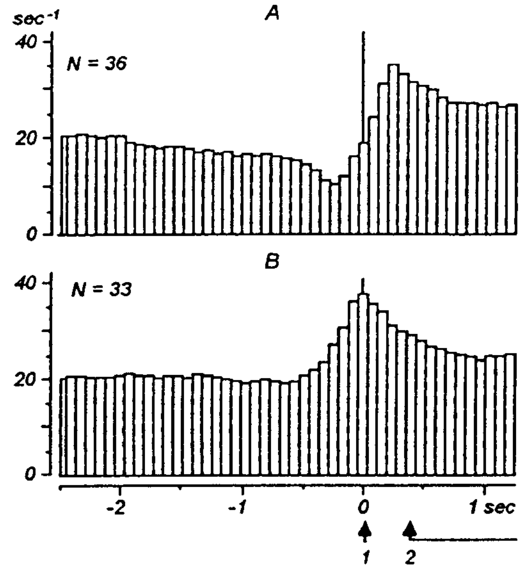

Fig. 1. Averaged normalized histograms of the activity of neurons of the parietal cortex, which were inhibited (A) and activated (B) before beginning of a self-initiated movement. The histograms are plotted from the moment of movement beginning (EMG initiation, arrow 1). Arrow 2 shows the moment of pressing the pedal. Abscissa) Time, sec; ordinate) spiking frequency, sec^{-1}; *N* is the number of neurons; bin width of 80 msec.

RESULTS AND DISCUSSION

The activity of 98 PAC neurons and of 50 supposedly DE, 78 NE, and 61 SE neurons was recorded in the course of performance of the above-described self-initiated movements. As criteria of the aminergic nature of the studied brainstem neurons, we took into account a low frequency of background spiking (below 6-8 sec^{-1}), polyphasic pattern and long duration (up to 3 sec) of the action potentials, and corresponding localization [6, 13-15].

The activity of a great majority of the studied neurons demonstrated modifications within one or another stage of the behavioral act, and more than half of the cells changed their activity before the movement initiation. The PAC neurons were activated or inhibited especially early, 1 sec or even more earlier before the EMG initiation, i.e., within the period of planning of the movement. In this group, responses including primary early inhibition and excitation were near equally frequently observed, but inhibition usually was replaced by excitation within the temporal segments close to the movement initiation or within this phase itself (Fig. 1).

Responses of DE neurons appeared somewhat later, as compared with those of PAC neurons (some of them began with a 0.5 sec forestalling of the movement, i.e., within a period of initiation of the latter); NE and SE

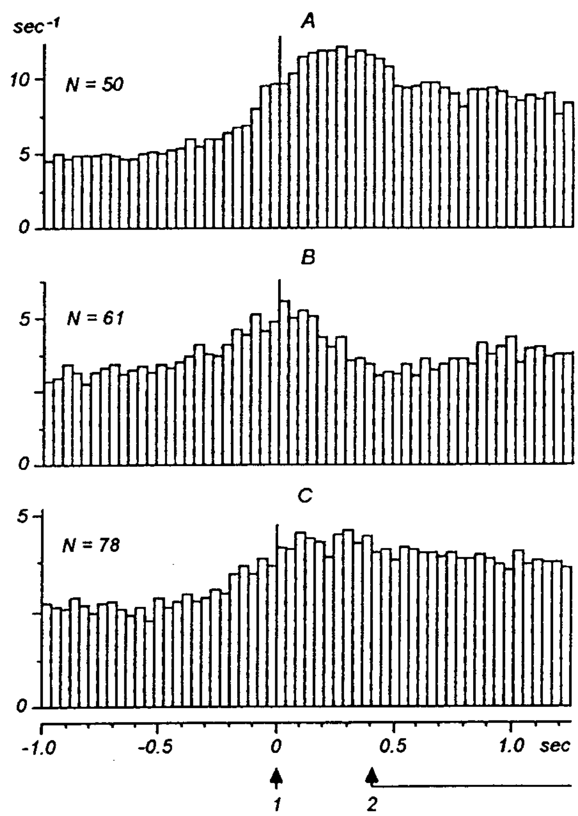

Fig. 2. Averaged normalized histograms of the responses of supposedly dopaminergic (A), noradrenergic (B), and serotonergic (C) brainstem neurons at the performance of a self-initiated movement. Bin width of 40 msec. Other designations are the same as in Fig. 1.

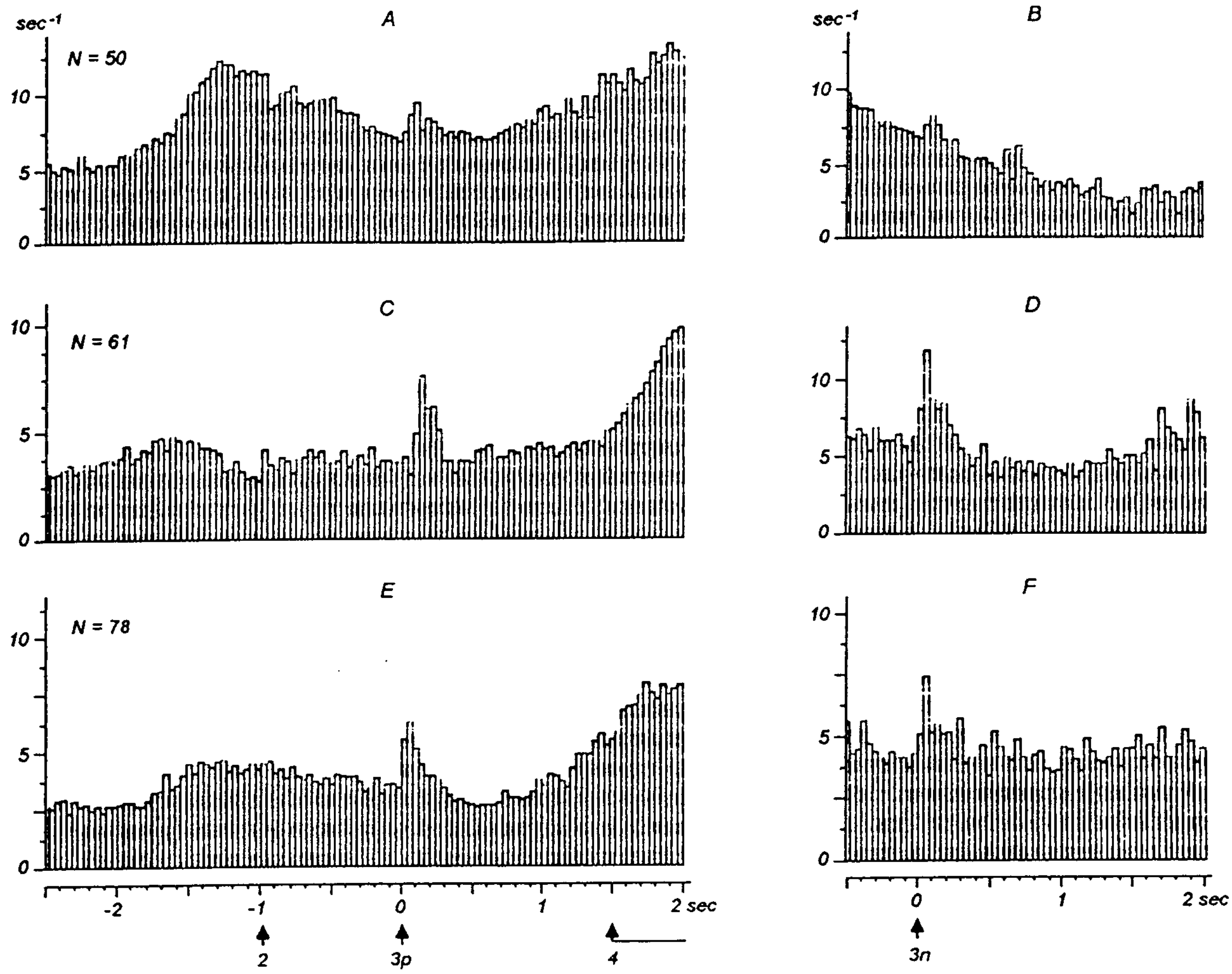

Fig. 3. Responses of supposedly dopaminergic (A, B), noradrenergic (C, D), and serotonergic (E, F) brainstem neurons related to the movement performance, capturing a reward (an arrow indicates 4), and presentation of positive (A, C, E; an arrow indicates 3p) and negative (B, D, F; an arrow indicates 3n) conditioning signals. The histograms are plotted from the moment of presentation of a conditioning signal. Arrow 4 shows the moment of presentation of a food reward. Bin width of 40 msec. Other designations are the same as in Fig. 1.

cells began to respond somewhat later. The following findings deserve attention: the neurons, whose responses forestalled the movement, were present in all studied systems of the aminergic cells. The intensity of movement-related modifications of the activity in DE neurons was not lower than that of PAC cells. The pattern of responses of DE neurons was mostly phasic, while that of SE cells was of a tonic nature (Figs. 2 and 3). It seems probable that the activity of aminergic neuronal systems, developed in the course of the movement switching on, provides amplification of reactions of the cortical neurons immediately during the movement initiation, similarly to what is supposed for the reticular formation and some other brainstem structures [2, 16].

As to perception of conditioning stimuli, which within the paradigm of our experiments informed the animal about the correctness of a trial performance, we can emphasize that in this respect NE and SE units responded more intensively than DE cells (Fig. 3). The neurons of all studied aminergic populations, as a rule, were activated simultaneously with reward presentation, but inhibition in the case of the absence of the latter was typical only of DE cells. Thus, the activity of supposedly DE, NE, and SE neurons obviously have some connection with cognitive and emotionally significant components of the experimental situation (yet, we surely cannot rule out the possibility of some connection of activation of these neuronal populations with the movements themselves, e.g., in the course of food capturing). It is also worth mentioning that the response pattern was rather specific for each of these neuronal systems. All the above data and considerations allow us to suppose that the activity of DE neurons is in a more tight relation with organization of the movement and with the presence or absence of a reward, while the activity of DE and SE cells relates to the perception of conditioning stimuli.

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