Self-Initiated Motor Behavioral Act-Related Neuronal Activity in the Cat *Locus Coeruleus*

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In experiments on awake cats, we recorded the activity of 61 putative noradrenergic neurons localized within the region of the *locus coeruleus* (*LC*) of the brainstem. The animals were trained to perform a self-initiated (voluntary) motor act aimed at obtaining a food reward by pushing a pedal by the forelimb. The intervals between pushings (stay of the limb on a platform before initiation of the movement) should not be shorter than 4 sec, and the duration of the movement itself should not exceed 1 sec. The following impulse reactions were most clearly manifested: (i) related to the pre-starting events and performance of the voluntary movement, (ii) related to the presentations of the conditioning stimuli, which predicted giving out the food reward (a positive signal) or the absence of the latter (a negative signal), and (iii) related to the reward presentation. About 50% of the *LC* units under study had changed their activities before the movement was initiated. These reactions can be related to a cognitive component (determination of the movement initiation), which is present in the experimental task. Most neurons responded by phasic activation to presentation of the conditioning signals, and this activation was more pronounced in the case of negative signals. Responses of the studied nerve cells are probably indicative of the involvement of the *LC* neuronal systems in the perception of the emotiogenic stimuli, as well as in the processes providing the maintenance of selective attention within different stages of targeted behavioral acts.

Keywords: *locus coeruleus*, noradrenergic neurons, conditioning, time counting out, voluntary movement, attention.

INTRODUCTION

Most brain structures, including the brain cortex, are known to be involved in detailed processing of specific sensory information. At the same time, besides these structures there are neuronal systems performing general regulatory functions. The noradrenergic (NA-ergic) system is one of the latter systems. A considerable proportion of the neurons of the NA-ergic system are concentrated in the *locus coeruleus* (*LC*) of the brainstem.

Neurons of the rostral part of the *LC* form ascending projections, including those to the neocortex [1-3]. Innervation of the motor cortex, parietal region, and visual cortex regions by these axons is the most abundant; the above-mentioned cortical zones are involved in processes providing attention, spatial analysis, and realization of visual/motor functions [4, 5]. The *LC* is believed to be a crucial center where signals of a different nature are processed, generalized, commutated, integrated, and exclusively extensively distributed; the *LC* output in turn influences the CNS regions realizing affective and cognitive functions [6].

NA-ergic neurons of the *LC* generate background activity whose frequency depends on the level of awakeness and usually varies within a 0.2 to 6.0 sec^{-1} range. Long-lasting (2-3 msec) action potentials are typical of

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NA-ergic cells, as well as of other aminergic neurons; under conditions of extracellular recording such potentials include a significant positive component and are distinguishable due to their complex pattern [1, 4].

Electrical or chemical (using the blockade of α2-adrenoreceptors or activation of chemoreceptors) stimulation of NA-ergic cells of the *LC* is accompanied by EEG desynchronization, an alert reaction, and behavioral excitation [6, 7]. Such a result seems to some extent surprising because direct application of NA to the target cells evokes inhibition of the latter resulting from hyperpolarization or inhibits them indirectly via GABA-ergic interneurons [8]. It is supposed that behavioral excitation and EEG desynchronization correlate with the augmentation of the responses to external stimuli due to a higher level of depression of the background spiking of the target cells, as compared with that of the evoked activity. This is why responses of the neurons to a greater extent exceed the noise, i.e., the signal/noise ratio for the given cell increases [4, 6].

The *LC* neurons are sensitive to different peripheral stimulations (light, sound, tactile stimulation, etc.), and they are more sensitive to presentation of stimuli characterized by novelty (in particular, visual perception of possible food) [1]. A novel signal determines activation of the *LC* neurons, which is a necessary condition for generation of the P300 potential, an EEG phenomenon closely related to attention processes and perception of the relevant information [9]. Conditioning signals, which switch on conditioned reflex behavioral reactions, are also effective stimuli activating the *LC* neurons [5, 10].

The responsiveness of the NA-ergic *LC* cells with respect to the above stimuli, as well as the integrative capabilities of this structure, determine its important role in the formation of emotional states. The development of an emotional state of depression and "social emotions" related to parting are considered to be dependent on certain aspects of functioning of the NA-ergic system. In addition to the control of the emotional states, the *LC* is involved in the control of such brain functions as learning, memory formation, and formation of defensive behavior in response to aversive stimulation and external danger. The *LC* is believed to transform in generalized excitation specific information on the significance of one context or another, and such a transformation increases the capabilities of the CNS for rapid processing of information [1, 11-13].

The above-mentioned considerations allow one to conclude that the NA-ergic system of the *LC* is a crucial center that regulates the levels of activity of different brain regions and provides functions of triggering and commutation of different behavioral states. Yet, the functions of the *LC* still remain inadequately studied. It is known that, in general, *LC* neurons are only to a rather limited extent involved in the organization of movements switched on by an acoustic or a visual signal [5]. At the same time, the question of how the *LC* is involved in the triggering of self-initiated motor acts (voluntary or close to voluntary movements, in particular those performed within definite time intervals) still remains open. It is also unknown how neurons of the *LC* respond to presentation of conditioning stimuli forecasting the presence of a reward or its absence and possessing, in such a way, information positively or negatively colored in the emotional aspect. This is why we examined in our experiments the patterns of reactions of putative NA-ergic neurons localized within the *LC* region of the cat brain; these reactions were related to the performance of an integral motor behavioral act including the self-initiated movement and the reaction to presentation of the conditioning signals on food reward.

METHODS

Experiments were carried out on three awake cats preliminarily trained to raise their right forelimb, after lifting it from a bearing platform, and press a pedal to obtain the food reward (Whiskas granule). Only those trials where the animal held its forelimb on the bearing platform for at least 4.0 sec and the movement (from the moment of leaving the platform to the moment of pressing the pedal) was not longer than 1.0 sec were rewarded. When the trial was correct, 1.0 sec after pressing the pedal a positive conditioning acoustic signal (tone of 1600 Hz, 0.2 sec long) was presented, and after an additional 1.0- to 1.5-sec-long interval the animal was rewarded with food (by hands, with a forceps). When the performance of the trial was incorrect, a negative conditioning signal was presented (tone of 400 Hz).

After training had been completed, the animals were operated under general anesthesia (nembutal, 40 mg/kg, i.p.). A guiding cannula with its tip localized 5 mm above the *LC* region was implanted. The cannula was inserted into the brain according to the *LC* stereotaxic coordinates, via an oblique track (20° with respect to the frontal plane and 15° with respect to the sagittal plane), to prevent contact with the tentorium. A bush with a platform for connection of a micromanipulator and a preamplifier was fixed on the skull. Electrodes for EMG recording were positioned subcutaneously in the muscles of the right (working) forelimb. Later on, we recorded the neuronal activity contralaterally with respect to the working limb, within a zone with the coordinates P = –1; L = 1 to 3, and H = 7 to 10 (Fig. 1). This is the region corresponding to the *LC* location [14], and most NA-ergic neurons projecting to the neocortex, the parietal cortex in particular, are localized within this zone [2, 3]. We used a silver microwire (diameter 12 μm) with glass insulation (total diameter 70 μm) as the recording electrode; its tip was obliquely sharpened like the tip of an injection needle. The spike activity and EMG were amplified, digitized, and, together with signals from the contacts of the support platform and pedal and synchroimpulses of the acoustic signals, were entered into the computer controlling the experiment. Peristimulus histograms of the impulse activity (PSH) were plotted using the moments of movement initiation (beginning of the EMG burst) and the moments of obtaining signals from the transducers as zero points. The number of realizations varied from 20 to 50, and the bin width was 8 to 40 msec. We estimated the number of responding and silent neurons and the power (relative intensity) of the reactions of the former. To calculate the latter index, we measured the difference between the numbers of impulses within a time window separated on the peak of reaction and a window of similar duration but separated within the background activity period (1-2 sec before initiation of the moment). The difference with the corresponding sign was normalized with respect to the level of the background activity and expressed as a percentage.

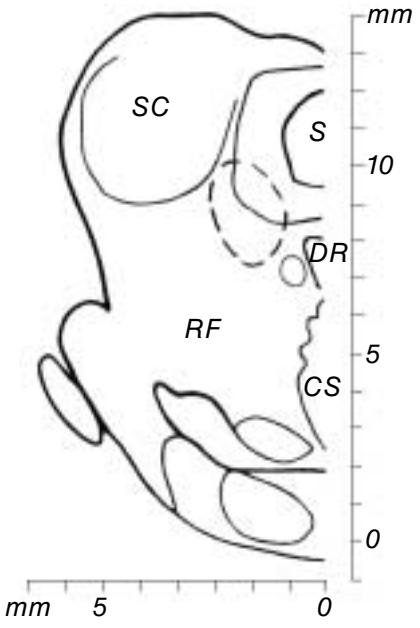

Fig. 1. Scheme of the frontal section of the cat brainstem with localization of the region where the activity of putative noradrenergic neurons of the *locus coeruleus* zone was recorded (indicated with the dashed line). The section plane corresponds to P = −1.0 (according to Reinoso-Suarez). SC are the *colliculi superior*; S is the *ductus sylvii*; RF is the reticular formation, and DR and CS are, respectively, the *nuclei raphe dorsalis et centralis*.

To verify the recording site, we electrolytically labeled this point after the experiment was over. For this purpose, the microwire electrode was replaced by a tungsten electrode insulated with lacquer except its tip. Then, the animals were euthanized with a nembutal overdose; their brain was fixed in formalin, and frontal slices were prepared using a freezing microtome.

RESULTS AND DISCUSSION

Self-initiated motor acts performed by the animals in the course of experiments were characterized by the following parameters. The mean interval between succeeding trials was 17.9 ± 0.4 sec (hereafter, we mention means ± s.e.m.) with the extremum values from 5.9 to 115.5 sec. The earliest changes in the level of the EMG activity in muscles of the right forelimb were observed 240 msec before the moment of tearing off the pad of the working limb from the support platform. The mean duration of the movement from leaving the support until pressing the

pedal was 400.5 ± 3.7 msec (extremum values 209 to 963 msec). The proportion of the correctly performed and, correspondingly, rewarded trials was 50-80%.

Altogether, we succeeded in recording the activity of 61 neurons localized within the *LC* region. One of these cells generated no background activity. The rest of the neurons were characterized by generation of single or, more rarely, grouped background spikes with a mean frequency of 2.8 ± 0.3 sec^{-1} with extremum values from 0.3 to 6.0 sec^{-1}. The recorded action potentials were polyphasic, and their duration was of the order of a 2.5 to 3.0 msec. Considering these characteristics, we classified the recorded nerve cells of the *LC* region as NA-ergic units.

The recorded neurons changed the frequency of their spiking in the course of the entire behavioral event under study. Changes in the activity related to: (i) triggering and realization of the voluntary test movement, (ii) perception of the conditioning acoustic signals forecasting the receipt or the absence of the food reward, and (iii) the reward receipt itself were the most clearly pronounced (Figs. 2 and 3). The responses demonstrated the following time characteristics with respect to the key moments of the behavioral act. Those neurons, which manifested excitation, were activated, on average, 186.1 ± 47.1 msec before EMG initiation (the earliest spike reactions forestalled the movement by about 650 msec). In the cases where the reactions were of an inhibitory

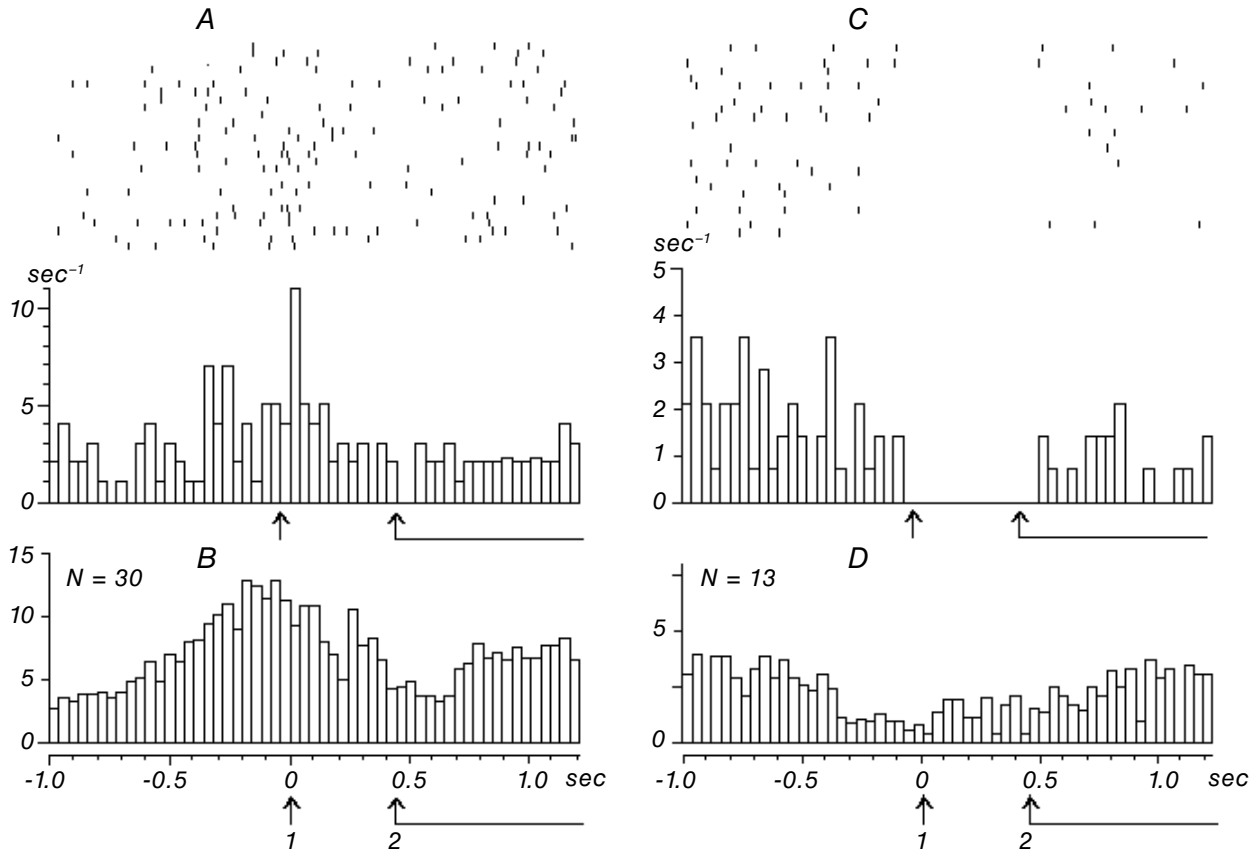

Fig. 2. Responses of putative noradrenergic neurons of the *locus coeruleus* zone activated (A, B) and inhibited (C, D) before the beginning of a self-initiated motor act. A and C) Examples of the activity of single neurons (raster diagram and corresponding histogram are shown above and below, respectively); B and D) averaged normalized histograms plotted from the moment of movement initiation (zero corresponds to the EMG initiation shown by arrow 1). Arrow 2 shows the moment of pressing the pedal. Abscissa) Time, sec; ordinate) frequency of impulses, sec^{-1}, *N* is the number of neurons. Bin width is 40 msec.

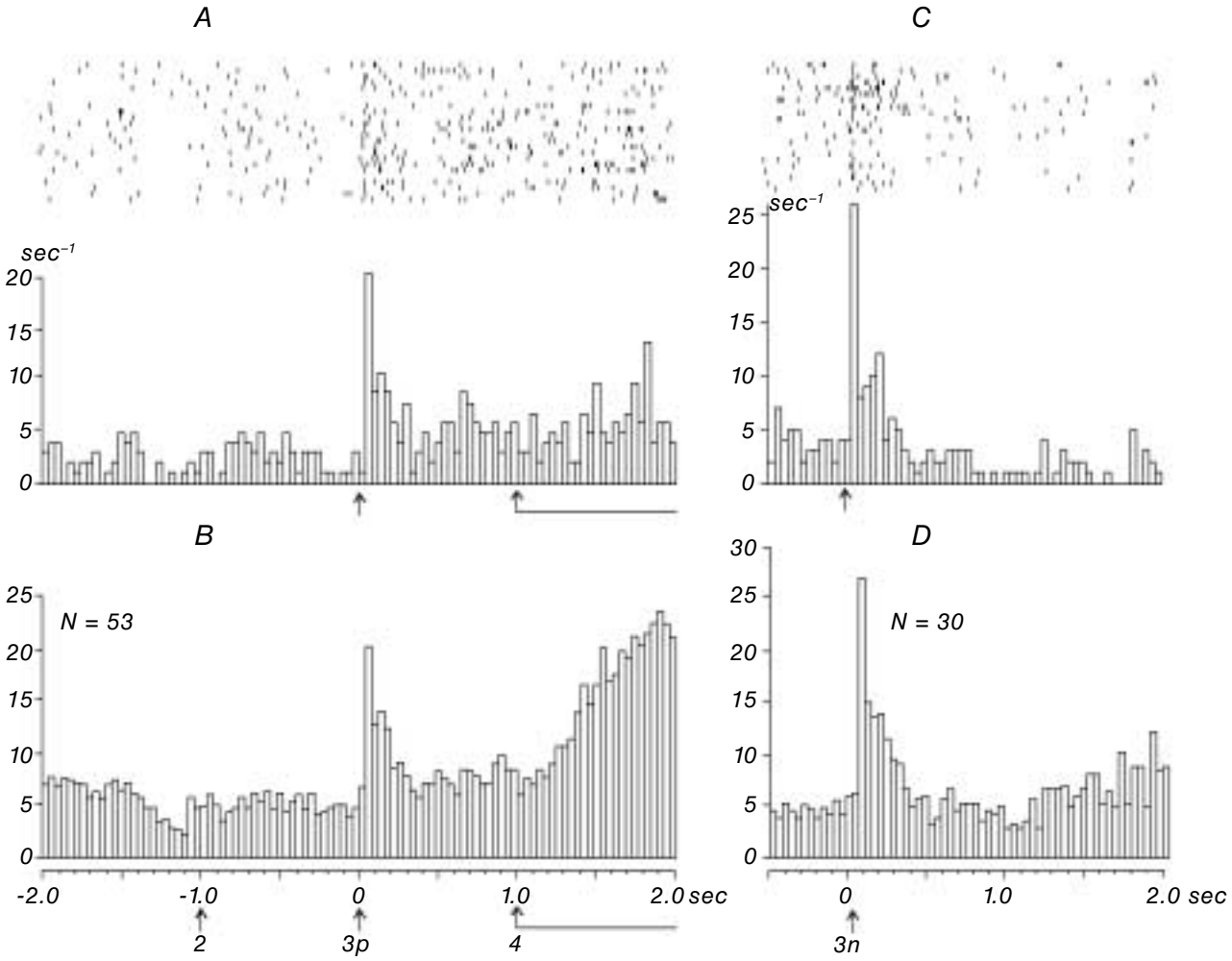

Fig. 3. Reactions of putative noradrenergic neurons of the *locus coeruleus* zone observed within the time windows corresponding to pressing the pedal (arrow 2), presentations of positive (A, B; shown with arrow 3p) and negative (C, D; shown with arrow 3n) conditioning signals, and to receipt of the reward (shown with arrow 4). Histograms are plotted from the moments of presentation of the conditioning signals (zero on the abscissa). Other designations are similar to those in Fig. 2.

nature, the decrease in the discharge frequency started, on average, 217.1 ± 52.0 msec before the movement (the earliest inhibitory reactions developed about 580 msec before the movement). Responses to presentations of the positive and negative acoustic stimuli were, as a rule, excitatory and developed with latencies of 46.2 ± 3.2 and 52.2 ± 6.3 msec from the beginning of presentation of these stimuli (extremum values 32-80 and 32-120 msec, respectively). The duration of the responses usually did not exceed 500 msec. As was mentioned, the food reward was given to the animal by the experimenter by hands; this is why we did not estimate the time parameters of the responses to its presentation.

The behavioral act under study comprised several stages. According to the pattern of the responses of most *LC* neurons, we selected the following time windows allowing us to estimate the sign and power of the responses within these intervals. These were (i) pre-starting events (300 to 0 msec before initiation

of the EMG activity in the forelimb muscles), (ii) performance of the movement (0 to 390 msec after the above moment), (iii) pressing the pedal (0 to 255 msec after the signal from the pedal contact), (iv) expectation of the conditioning feedback signal (745 to 0 msec before presentation of this signal), (v) response to the above signal (20 to 160 msec after the beginning of this signal), and, finally, (vi) response to the appearance of the food reward or its absence (1,000 to 2,000 msec after presentation of the above signal). The data on the number of *LC* neurons activated or inhibited within the above-listed stages and on the power of the neuronal responses are given in Tables 1 and 2, respectively. The stage of the movement performance in Table 2 is additionally subdivided into two subintervals. These are triggering of the movement, from the moment of EMG initiation until tearing off of the limb from the support platform, i.e., a signal from the platform contacts (0 to 240 msec from the EMG beginning) and the development of the movement itself (0 to 150 msec from the signal received from the above-mentioned contacts).

First, we should emphasize the fact that most candidates to NA-ergic neurons of the *LC* region changed their activity within the stages of preparation and performance of the voluntary test movement (Table 1). About half of the studied units were activated within this period. Studies on monkeys showed that in the course of solving a task of visual discrimination, neuronal reactions were to a greater extent related to the presentation of the target signal attracting the animal's attention than to the subsequent movement. In these experiments, movements were switched on after the conditioning stimulus, and in the course of performance of the motor reaction *per se* there were no noticeable changes in the unit activity of the *LC* cells [5, 10]. On the contrary, the experimental paradigm-determined movement in our situation was self-initiated. It was performed at a time moment determined by the animal itself, but not immediately after presentation of the conditioning stimulus. This provided attraction of the intense attention of the animal to voluntary triggering of the movement, and not to a directly determined triggering. Such a situation probably resulted in switching on of the activity of the neurons under study, which was specifically related to the motor component of the test task. In our earlier study in a similar experimental situation, we found that such an activity is generated by dopaminergic neurons of the *substantia nigra pars compacta* of the cat midbrain [15].

Analysis of the power of the movement-related reactions showed the following. The power of activating reactions reached its maximum within the stage of the movement triggering (the level of impulsation exceeded the background level about three times) (Fig. 2, Table 2). The power of these

TABLE 1. Reactions of Putative Noradrenergic Neurons of the *Locus Coeruleus* Zone of the Cat Observed within Different Stages of the Self-Initiated Behavioral Act

Stage of the behavioral act	Number of neurons		
	activated	inhibited	with no reaction
Preparation for the movement	30 (49.2)	13 (21.3)	18 (29.5)
Performance of the movement	28 (45.9)	18 (29.5)	15 (24.6)
Pressing the pedal	35 (57.4)	21 (34.4)	5 (8.2)
Expectation of a conditioning signal on receipt or absence of a food reward	23 (37.7)	9 (14.8)	29 (47.5)
Presentation of the positive signal	53 (86.9)	1 (1.6)	7 (11.5)
Receipt of the reward	50 (82.0)	1 (1.6)	10 (16.4)
Presentation of the negative signal	30 (63.8)	5 (8.2)	17 (27.9)
Absence of the reward	5 (8.2)	20 (32.8)	36 (59.0)

Footnote. Normalized numbers of the neurons, %, are shown in parentheses; total number of neurons in the group under study, $n = 61$, is taken as 100%.

TABLE 2. Powers of the Excitatory and Inhibitory Reactions of Putative Noradrenergic Neurons of the *Locus Coeruleus* Zone within Different Stages of the Self-Initiated Behavioral Act

Stage of the behavioral act	Activation	Inhibition
Preparation for the movement	104.2 ± 36.5 (14.3 to 440.6)	–59.6 ± 7.9 (–37.4 to −83.6)
Performance of the movement (the entire interval)	167.5 ± 84.7 (20.9 to 1405.2)	–48.2 ± 9.6 (–27.0 to –100.0)
Triggering of the movement	201.8 ± 117.1 (21.3 to 2037.9)	–47.9 ± 12.8 (–47.5 to –100.0)
Development of the moment	108.7 ± 28.4 (20.6 to 288.1)	–47.9 ± 7.6 (–22.0 to –100.0)
Pressing the pedal	78.2 ± 25.8 (27.4 to 290.6)	–40.1 ± 6.7 (–24.2 to –100.0)
Expectation of a conditioning signal on receipt or absence of a food reward	97.6 ± 24.8 (26.4 to 372.9)	–38.2 ± 10.4 (–23.7 to –67.0)
Presentation of the positive signal	207.8 ± 37.1 (28.5 to 606.2)	–40.7 ± 7.8 (–31.9 to –52.4)
Receipt of the reward	244.3 ± 44.1 (34.9 to 603.8)	–23.5 ± 5.9 (–18.5 to –35.1)
Presentation of the negative signal	377.8 ± 85.4 (47.2 to 959.3)	–13.7 ± 5.2 (–12.8 to +6.2)
Absence of the reward	64.7 ± 18.8 (17.9 to 140.4)	–35.6 ± 6.3 (–14.8 to +77.1)

Footnotes. Means ± s.e.m. are shown; extremum values are given in parentheses. To calculate the power (relative intensity) of the reaction, we measured the difference between the number of impulses over the time window within the period of maximum intensity of the reaction and a window of similar duration within the background activity period.

reactions dropped with change in the stages and phases of the movement, and this decrease lasted until the moment of pressing the pedal. We can suppose that such a pattern of activating spike responses of the *LC* neurons is related to the highest attention level and a pronounced arousal reaction mostly within the preparation for the test movement and its beginning stage. A slow negative EEG potential similar to the readiness potential in humans can be recorded from the cat brain within this period [16, 17]. It is possible that neurons of the *LC*, similarly to the cells of the midbrain *substantia nigra* [18], are involved in the generation of the above potential; they modulate the activity of neocortical neurons.

More than 50% of the *LC* neurons responded within the period of expectation of the conditioning signal, and most of these units were activated. The frequency of their responses was, on average, two times higher than the background level. Within this period, another slow negative potential is observed in the brain cortex; this is the contingent negative deviation [16, 17]. Generation of the latter potential is usually related to expectation of a significant signal, concentration of attention, and preparations for action [19]. The increased level of activity of *LC* neurons within this period of expectation shows that these cells are also probably involved in the generation of the above-mentioned EEG phenomenon, the contingent negative deviation.

Most studied neurons demonstrated phasic activations related to presentations of both positive and negative conditioning signals (Fig. 3, Table 1). Phasic responses to presentation of the conditioning stimuli, which trigger the movement, were earlier observed in NA-ergic neurons in monkeys [5, 10], and they are to a certain extent similar to the above-described responses. In our experimental paradigm, the signals

did not determine triggering of the movement (the latter was self-initiated); they forecasted the presence or absence of the food reward and, therefore, possessed different emotional tinges. It is interesting to note that the power of the responses evoked by negative signals was even higher than those related to positive signals. This feature may reflect a higher sensitivity of the *LC* neurons to stimuli with a negative tinge. However, we cannot rule out another possibility. Negative signals were presented somewhat more rarely than positive signals, and Swick et al. [9] showed that *LC* neurons respond more intensely to stimuli applied with a lower probability. The authors cited concluded that, if one takes into account the timing of the arrival at the cortex of action potentials generated by *LC* neurons, as well as the pattern of the effects of application of agonists and antagonists of NA-ergic transmission, it seems probable that the phasic activity of NA-ergic neurons is involved in the generation of the cortical potential P300. The latter is generated in response to meaningful (significant) stimuli with a latency of 250-500 msec after their presentation. In our experimental situation, phasic activation of *LC* nerve cells evoked by presentation of conditioning signals, which give information on the success of the task performance, could also be a significant factor in the generation of the P300 potential recorded within the framework of our experimental paradigm [16, 17].

After the animals had been supplied with the food reward, a great majority of the studied neurons were activated. When the reward was absent, inhibitory responses dominated (Table 1, Fig. 3).

The above data allow us to conclude that the activity of the *LC* neurons is modified in a rather specific manner within the different stages of preparation for and realization of the targeted behavioral act. The involvement of these neurons in processes related to organization and performance of the movement can be determined by the presence of a cognitive component in our experimental task. This is determination of the moment of initiation of the movement by the animals; the movement in this case is not directly related to an external stimulus. The neuronal reactions that develop in the course of the entire behavioral act reflect the important role of the *LC* neuronal systems in processes providing attention. Such responses generated by a considerable proportion of *LC* neurons were of an inhibitory nature. We suppose that inhibition of a part of the *LC* neurons is related to the formation of an "attention focus" in the CNS and reflects a specific pattern of involvement of this structure in the functioning of brain systems providing selective attention.

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