Neuroscience and Behavioral Physiology, Vol. 36, No. 5, 2006

Comparative Analysis of the Baseline Spike Activity of Neurons in the Fastigial Nucleus of the Cerebellum at Different Durations of Exposure to Vibration

S. G. Saakyan,[1] A. K. Kazaryan,[1] G. Yu. Grigoryan,[1] S. M. Minasyan,[1] and R. Sh. Sarkisyan[2]

Translated from Rossiiskii Fiziologicheskii Zhurnal imeni I. M. Sechenova, Vol. 91, No. 6, pp. 601–610, June, 2005. Original article submitted January 16, 2004, revised version received November 23, 2004.

Acute experiments on Nembutal-anesthetized (40 mg/kg, i.p.) white rats with extracellular recording and analysis of baseline spine activity of neurons in the fastigial nucleus of the cerebellum were performed in normal conditions and after exposure to vibration for 5, 10, and 15 days. The distribution of neurons in terms of the regularity and dynamics of spike flows and the modality of interspike interval histograms were determined, along with the mean neuron spike frequency and the coefficient of variation of interspike intervals. The results showed that the most significant changes in neuron activity in fastigial nucleus cells were formed during the first ten days of vibration. On day 15, there was a tendency for measures to return to control levels.

KEY WORDS: cerebellum, fastigial nucleus, baseline spike activity, vibration.

Current scientific approaches to studies of biological environmental factors, particularly mid-frequency vibration, involves detection of changes in the body at different levels of integration and assessment of these in the light of the concept that the body has a series of functional systems.

Vibration is perceived by specialized sensory systems: the vestibular apparatus and extero- and interoceptors which send information about stimuli to nerve centers, particularly in the cerebellum, responsible for the reflex reactions of organs and systems to the actions of vibration. According to contemporary concepts, the central nuclei of the cerebellum are subject to afferent influences, both direct and mediated via the cerebellar cortex, of different natures [7, 12, 16, 17, 20, 21, 25]. The baseline activity of neurons in the cerebellar nuclei, studied during exposure to external factors, can be used as a measure of changes in cell activity determined by the intrinsic functional mechanisms and afferent influences of various origins (intranuclear, cerebellar, extracerebellar).

Recent studies have yielded extensive data providing evidence that the baseline spike activity of brain neurons is informative; its parameters reflect the characteristics of a variety of physiological states. Additionally, baseline spike activity to a significant extent determines the types of responses to sensory signals. However, existing published reports are limited to analysis mainly of comparisons between the mean frequencies of spike flows.

The occasional studies of baseline spike activity of neurons using computer analysis and mathematical processing of biological signals are of particular value [3].

The literature available to us contains no data on the nature of baseline spike activity of neurons in the cerebellar nuclei during prolonged exposure to vibration; thus, the present study addressed the task of analyzing the baseline spike activity of neurons in the fastigial nucleus of the cerebellum in rats in normal conditions and after exposure to vibration for 5, 10, and 15 days.

[1] Department of Human and Animal Physiology, Erevan State University, 8 Charenets Street, 375025 Erevan, Armenia.

[2] Orbeli Institute of Physiology, National Academy of Sciences, 22 br. Orbeli Street, 375028 Erevan, Armenia.

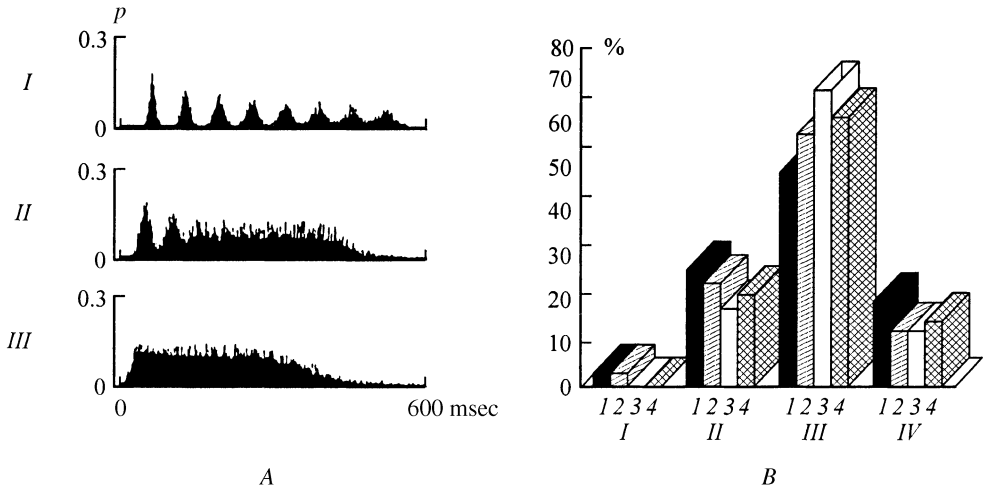

Fig. 1. Distribution of cerebellar fastigial nucleus neurons in terms of the degree of regularity of their baseline spike activity (*A*) and different durations of exposure to vibration (*B*): regular (*I*); intermediate regularity (*II*); irregular (*III*); non-stationary (*IV*). *1*) Normal conditions; *2*) day 5 of vibration; *3*) day 10 of vibration; *4*) day 15 of vibration.

METHODS

Acute experiments were performed using white rats weighing 180–240 g, anesthetized with Nembutal (40 mg/kg, i.p.). The spike activity of 305 neurons in the fastigial nucleus of the cerebellum was recorded extracellularly using glass microelectrodes (tip diameter 1 μm, resistance 3–5 MΩ) filled with 2 M NaCl. The stereotaxic orientation of the electrodes was established in terms of atlas [9] coordinates (AP = –3, L = ±1.2, V = 3.3). The baseline spike activity of cerebellar fastigial nucleus neurons was studied in rats in normal conditions (77 neurons) and at 5, 10, and 15 days of exposure to vibration (77, 80, and 71 neurons respectively).

Animals were subjected to whole-body vertical vibration (60 Hz, 0.4 mm) for 2 h daily.

Analysis of the spike activity of neurons in the cerebellar fastigial nucleus and statistical analysis of the data were performed using a computer program developed for the purpose [3, 8]. Sequential segments of interspike intervals were analyzed until 1200 action potentials had been recorded. The stationary nature of spike flows was evaluated using the non-parametric Kolmogorov–Smirnov test and from the shapes of sliding frequency plots.

Eighth-order autocorrelograms were constructed for neurons showing stationary spike flows, these reflecting the probability of spike formation at different time points. The shapes of these plots were used to identify three groups of neurons with different degrees of neuron spike flow regularity: autocorrelograms for group 1 were characterized by the presence of eight well defined peaks, interpreted as showing a predominance of a regular component in the neuron spike activity. Group 2 autocorrelograms showed only 2–3 peaks, followed by a plateau. These neurons were assigned to the group with activity of intermediate regularity. Group 3 neurons were characterized by an identical level of probability of spike appearance at different time points with no marked peaks on the autocorrelograms. Neurons with this type of activity were regarded as irregular (Fig. 1, *A*, *I*, *II*, *III*). Non-stationary neurons were combined to form group 4.

The dynamic structures of spike flows were identified by calculating the serial correlation coefficients to the 50th order, with differences from zero being regarded as significant at $p < 0.05$.

Analysis of serial correlograms of stationary and non-stationary spike flows of fastigial nuclear neurons revealed four major types of interspike interval dynamics: 1) random interspike intervals (all serial correlation coefficients = 0); 2) local changes in discharge frequency (serial correlation coefficients had only positive and zero values); 3) burst-group activity (serial correlation coefficients of both zones, along with zero values); 4) monotonic changes in discharge frequency (all serial correlation coefficients with positive values).

For stationary neurons, interspike interval histograms were constructed and their shapes were used to identify mono-, bi-, and polymodal neurons (Fig. 3, *A*, *I*, *II*, *III*); mean values for the major statistical measure of baseline spike activity were calculated, i.e., the mean neuron spike frequency and the coefficient of variation of interspike intervals.

The distributions of neurons at different spike activity frequency intervals were assessed by dividing the cells into three groups: neurons with low (1–10 spikes/sec), intermediate (from more than 10 to 30 spikes/sec), and high (more than 30 spikes/sec) discharge frequencies.

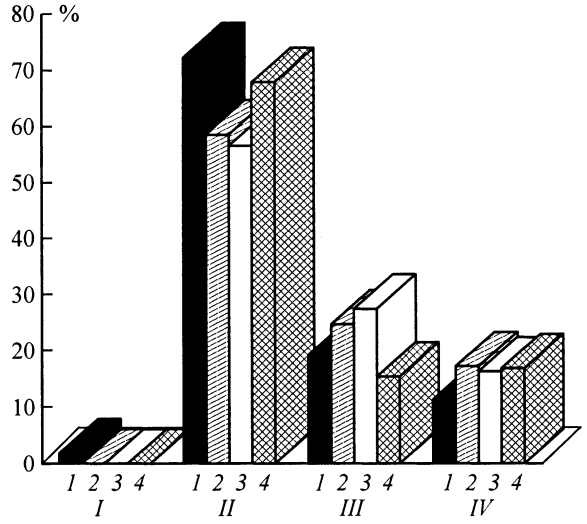

Fig. 2. Ratios of types of dynamic activity of cerebellar fastigial nucleus neurons in normal conditions and at different durations of exposure to vibration. *I*) Random sequencing of interspike intervals; *II*) local changes in discharge frequency; *III*) burst-grouped activity; *IV*) monotonic changes in discharge frequency. For further details see caption to Fig. 1.

The significance of changes in the distributions of cerebellar fastigial nucleus neurons in terms of the degree of regularity of baseline spike activity, the type of spike activity dynamics, interspike interval histogram modality, and the distribution of neurons by different frequency intervals at different durations of vibration as compared with control experiments was assessed using the χ^2 test (at $p < 0.05$). The significance of changes in the major statistical measures of baseline spike activity was assessed using Student's test (at $p < 0.05$). Statistical assessment of tendencies to changes in measures of baseline spike activity at different durations of exposure to vibration was based on calculation of a qualitative measure of correlation [1].

RESULTS AND DISCUSSION

The results obtained here showed that in normal conditions, the fastigial nucleus showed a prevalence of neurons with irregular baseline activity (50.6%) (Fig. 1, *B*, *III*). Relatively smaller proportions of neurons with intermediate-regularity activity were seen (27.3%). There were virtually no neurons with regular baseline spike activity (2.6%). The proportion of non-stationary neurons was 19.5%.

Analysis of the distribution of fastigial nucleus neurons in terms of the nature of dynamic activity showed that in normal conditions, there was a dominance of neurons showing local changes in discharge frequency (72.7%) (Fig. 2, *II*). Quantitatively, neurons whose spike flows showed periodic changes in discharge frequency in the form of grouped or burst activity and neurons showing monotonic changes in discharge frequency accounted for 19.5% and 10.4% of cells respectively (Fig. 2, *III*, *IV*). Neurons with random interspike intervals accounted for only 1.3% of cells (Fig. 2, *I*).

Analysis of histograms of interspike intervals for neurons in the fastigial nucleus in normal conditions showed a predominance of polymodal neurons (64.5%) (Fig. 3, *B*, *III*). There were significantly fewer mono- and bimodal neurons (22.6% and 12.9% respectively) (Fig. 3, *B*, *I*, *II*).

Analysis of the distribution of fastigial nucleus neurons with different spike activity frequency intervals in normal conditions demonstrated a predominance of intermediate-frequency neurons (48.4%). The proportions of high- and low-frequency neurons were 27.4% and 24.2% respectively (Fig. 4).

Calculations showed that the mean discharge frequency of fastigial nucleus neurons in normal conditions was 22.5 ± 2.0 spikes/sec, and that the coefficient of variation of interspike intervals was 51.5 ± 2.3% (Fig. 5, *A*, *B*).

Statistical analysis of the present results showed that after exposure to vibration for five days, there were insignificant changes in the distribution of fastigial nucleus neurons in terms of the degree of regularity, the dynamic types of baseline spike activity, the modality of interspike interval histograms, and the distributions of neurons in terms of spike activity frequency ranges (Figs. 1–4, see Table 1). The statistical measures of the baseline spike activity of fastigial nucleus neurons showed a significant increase only in the mean discharge frequency, to 29.5 ± 2.6 spikes/sec ($p < 0.05$) (see Table 1).

After exposure to vibration for 10 days, as compared with controls, there were statistically significant changes in the distribution of fastigial nucleus neurons in terms of the degree of regularity of baseline spike activity and interspike interval histogram modality. There was a 1.5-fold (to 17.3%) decrease in the proportion of neurons with baseline activity of intermediate regularity and a similar-factor increase (to 70.4%) in the proportion of irregular neurons (Fig. 1, *B*, Table 1). The proportion of non-stationary neurons was 12.3%. No neurons with regular baseline spike activity were recorded. The distribution of fastigial nucleus neurons into interspike interval histogram modality showed an increase in the proportion (to 83.1%) of polymodal neurons and decreases in the proportions of mono- and bimodal neurons (to 8.5%) by factors of 2.7 and 1.5 respectively (Fig. 3, *B*, Table 1).

The mean discharge frequency of fastigial nucleus neurons on day 10 of vibration returned to control levels, with a significant increase in the coefficient of variation, to 60.2 ± 2.3% ($p < 0.05$) (Fig. 5, Table 1).

After exposure to vibration for 10 days, as compared with five days, there was a statistically significant change in the distribution of fastigial nucleus neurons in terms of the interspike interval histogram modality (see Table 1). There

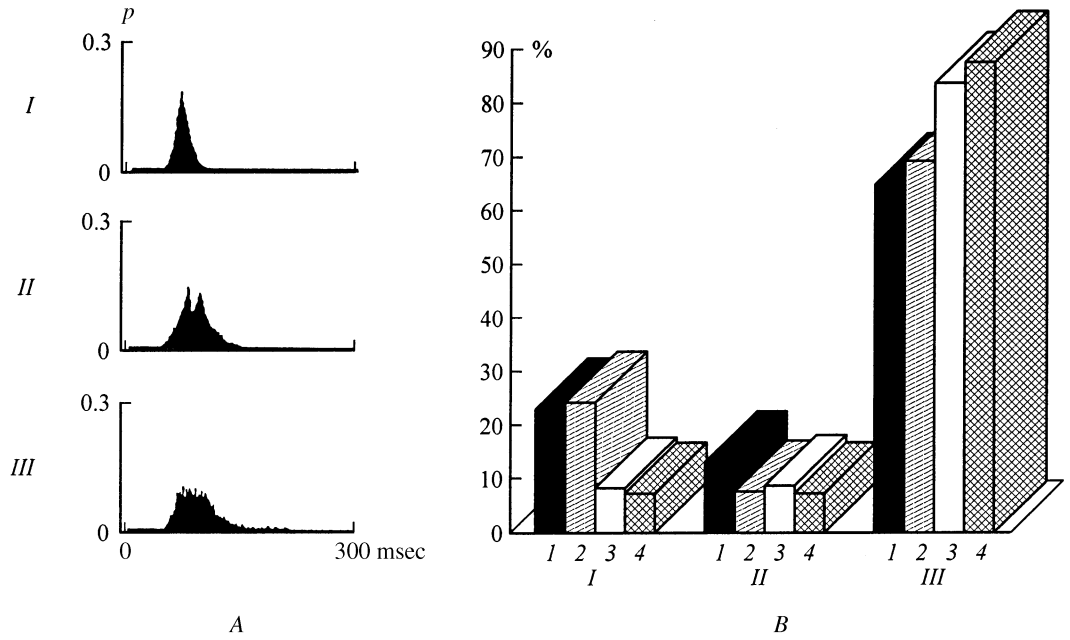

Fig. 3. Distribution of cerebellar fastigial nucleus neurons in terms of interspike interval histogram modality (*A*) in normal conditions and after 5, 10, and 15 days of exposure to vibration (*B*). *I*) Monomodal neurons; *II*) bimodal neurons; *III*) polymodal neurons. For further details see caption to Fig. 1.

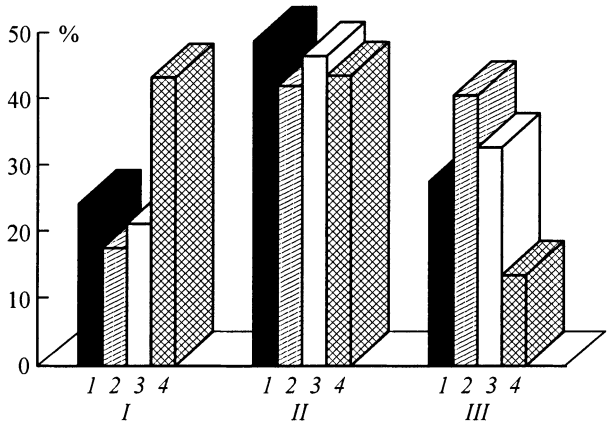

Fig. 4. Distribution of cerebellar fastigial nucleus neurons in different spike frequency intervals in normal conditions and after 5, 10, and 15 days of exposure to vibration. For further details see caption to Fig. 1.

was a 1.2-fold increase in the proportion of polymodal interspike interval histograms, while the proportion monomodal histograms decreased almost three-fold (Fig. 3, *B*). There was also a significant increase in the coefficient of variation, from 49.1 ± 2.7% to 60.2 ± 2.3% (Fig. 5, Table 1).

As compared with controls, exposure to vibration for 15 days produced statistically significant changes in the distribution of fastigial nucleus neurons in terms of interspike interval histogram modality and the distribution of neurons among the different frequency ranges (see Table 1). There was a 1.3-fold increase in the proportion of polymodal neurons (86.6%), along with 3.4- and 1.9-fold decreases in the proportions of mono- and bimodal neurons (to 6.7%) (Fig. 3, *B*, Table 1). There was a two-fold (13.4%) decrease in the proportion of high-frequency and a 1.8-fold increase (43.3%) in the proportion of low-frequency neurons; the proportion of neurons in the intermediate spike frequency range showed virtually no change (Fig. 4, Table 1). There was a significant decrease in the mean discharge frequency of fastigial nucleus neurons, to 16.6 ± 2.0 spikes/sec, along with an increase in the coefficient of variation, to 59.2 ± 2.9% (Fig. 5, Table 1).

Comparison of measures of the baseline spike activity of fastigial nucleus neurons after exposure to vibration for 5 and 15 days showed that there were significant differences for the distribution of neurons in terms of interspike interval histogram modality and the distribution among mean discharge frequency ranges (Fig. 3, *B*, Table 1). The proportion of polymodal neurons increased from 68.7% to 86.6% and the proportion of monomodal interspike interval histograms decreased more than three-fold. The proportion of high-frequency neurons decreased three-fold and there was a nearly three-fold increase in the proportion of low-frequency neurons. There were also significant differences in the mean discharge frequencies and coefficients of variation. After vibration for 15 days, as compared with five days, the mean frequency decreased to half and the coefficient of variation increased 1.2-fold (Fig. 5, Table 1).

Comparison of measures of baseline spike activity after 10 and 15 days of vibration demonstrated significant differ-

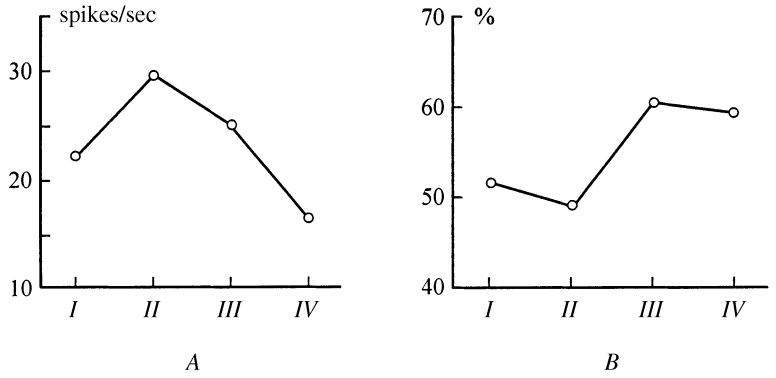

Fig. 5. Mean frequencies (*A*) and coefficients of variation (*B*) of interspike intervals of cerebellar fastigial nucleus neurons. *I*) Normal conditions; *II*) day 5; *III*) day 10; *IV*) day 15 of exposure to vibration.

TABLE 1. Significance of Differences in Measures of Baseline Activity

Experimental series		1	2	3	4	F	CV
Normal conditions	Day 5	– – – – –	– – – – –	– – – – –	– – – – –	+	0
Normal conditions	Day 10	0.05	– – – – –	0.05	– – – – –	0	+
Normal conditions	Day 15	– – – – –	– – – – –	0.02	0.05	–	+
Day 5	Day 10	– – – – –	– – – – –	0.05	– – – – –	0	+
Day 5	Day 15	– – – – –	– – – – –	0.025	0.001	–	+
Day 10	Day 15	– – – – –	– – – – –	– – – – –	0.01	–	0

Notes. Distributions: *1*) degree of regularity; *2*) type of dynamics; *3*) modality; *4*) frequency ranges (1–10, 10–30, and greater than 30 Hz). The significance of differences between distributions ($p < 0.05$) in terms of the χ^2 test is shown. Lines show non-significant changes. F is the mean spike frequency, CV is the coefficient of variation of interspike intervals. Plus signs show increased, minus signs show decreases in statistical measures at $p < 0.05$, Student's test. The number 0 identifies insignificant changes.

ences only for the distribution of discharge frequency ranges and the mean spike frequency of fastigial nucleus neurons. Thus, there was a nearly 2.5-fold drop in the proportion of high-frequency neurons, while the proportion of low-frequency neurons in this nucleus increased more than two-fold (Fig. 4, Table 1). The mean fastigial nucleus neuron frequency decreased from 25.3 ± 2.2 to 16.6 ± 2.0 spikes/sec (Fig. 5).

Calculation of the qualitative correlation coefficient showed that changes in measures of the baseline spike activity of fastigial nucleus neurons at 10 days of vibration and changes in measures of the baseline spike activity from 10 to 15 days of vibration were in the opposite directions. The qualitative correlation coefficient was –0.44 ($p < 0.05$), which is evidence for a statistically significant tendency for measures of fastigial nucleus neuron baseline spike activity to return to control values by 15 days of vibration.

Studies of the baseline spike activity of cerebellar fastigial nucleus neurons using the methods described here allowed identification of the dynamic structure of the spike flows recorded, their regularity, and their statistical characteristics in normal conditions and during exposure to vibration.

Autocorrelation analysis showed that both in normal conditions and on exposure to vibration, the spike activity of fastigial nucleus neurons was dominated by cells with irregular, stationary spike activity. Vibration led to increases in the proportion of irregular neurons, evidently due to increases in afferent spike activity from various receptors and brain structures occurring in vibration. Increases in the irregularity of neurons were accompanied by significant increases in the coefficient of variation and the number of modes in interspike interval histograms.

The data obtained here show that vibration did not lead to significant changes in the nature of the dynamic activity of fastigial nucleus neurons. Nonetheless, it should be noted that the dynamic structure of spike flows recorded in the fastigial nucleus showed a predominance of neurons with local changes in discharge frequency. Neuron activity showing irregular sequencing of interspike intervals of different duration evidently resulted from the interaction of the baseline inhibitory and excitatory synaptic flows of cere-

bellar and extracerebellar origins. These experiments also demonstrated increases in the proportion of neurons with monotonic changes in activity and cells with burst-group activity after vibration (especially on days 5 and 10), which may result from the electrical properties of the neuron membranes and the incoming afferent excitatory influences. Published data [5] indicate that burst activity reflects epileptiform activity due to prolonged stress.

Comparison of interspike interval histograms for neurons in normal conditions and after different durations of vibration (especially on day 10) showed a predominance of polymodal neurons, in all probability a result of the arrival of powerful afferent spike activity of different types after vibration.

The major inhibitory influence of the cerebellar vermis, which leads to inhibition of cerebellar nuclei in intact rats, is known to be mediated by activation of Purkinje cells via climbing and mossy fibers, the pathways by which the cerebellum receives all its sensory influences [6, 7, 11, 16, 22]. As noted above, vibration led to significant increases in the mean discharge frequency on day 5, this being followed by a significant decrease by day 15. The various components of the responses of neurons in the cerebellar nuclei are known to depend on the excitatory influences of collaterals of mossy fibers and climbing fibers acting in combination with the inhibitory actions of Purkinje cells [6, 15]. Increases in the facilitatory afferent influences on the cerebellar fastigial nucleus on day 5 of exposure to vibration can evidently be explained by the activation of the axon collaterals of afferent fibers to cerebellar nuclear neurons. This can be associated with changes in the spike frequency of cerebellar nuclear neurons, and the discharges of Purkinje cells act on the background of nuclear neuron rhythmicity already altered by the excitatory input [2, 7]. These results are supported by data which we have reported previously [4].

The physiological significance of the baseline spike activity of nuclear neurons is that it acts as a generator of a constant output; the excitation pattern of nuclear neurons of the cerebellar inputs can be modulated by the inhibitory influences of Purkinje cell axons and the excitatory efferents of mossy fiber collaterals [7]. The facilitatory effect of five days of exposure to vibration on cerebellar fastigial nucleus neurons can be interpreted in relation to published data. Thus, the Albus theory [10] indicates that the result of the combined action of mossy and climbing fibers on Purkinje cells consists not of an increase in the synaptic action of signals mediated by spines on Purkinje cell dendrites, but of a decrease in their influences, like the decrease in the inhibitory influences of basket cells. This decrease in the combined synaptic actions of signals from both inputs, according to the Albus theory, is required for maintaining stability in the functioning of cerebellar cortical mechanisms controlling motor activity in conditions of overloading of the afferent influx. Studies have demonstrated [23] that tetanic stimulation of the inputs can induce long-term depression of IPSP (inhibitory postsynaptic potentials) in nuclear neurons, which affects around 50% of the GABAergic receptor transmission. During this depression, nuclear neurons are better able to respond to excitatory signals, which leads to increases in the generation of action potentials. The overall effect is an increase in the output from the cell. Ito [19] found that long-term depression arises when spikes in the group of granule cell axons and one climbing fiber synchronously and repeatedly arrive at a single Purkinje cell, leading to a stable suppression of synaptic transmission from granule cell fibers to Purkinje cells. There are also various chemical reactions underlying this depression.

The role of disinhibition in controlling the flow of afferent spike activity arriving in the cerebellar cortex is also important. Direct inhibitory mechanisms are mediated by the synapses of basket cells on Purkinje cells and the efferent connections of these cells with the cerebellar nuclei and other cerebellar structures. Reciprocal inhibition is mediated by Golgi cells on granule cells, which facilitate the afferent input to the cerebellum. Granule cells, via their axons, in their turn excite Golgi cells. The process of disinhibition is very important, as its absence can result in powerful inhibition of neurons in the intracerebellar nuclei and the brainstem nuclei, particularly the vestibular nucleus of Deiters.

Starting from day 10 of vibration, there was a gradual transformation of the rhythm of fastigial nucleus neuron activity, which by 15 days turned into a sharp decrease in their activity. This may be evidence for adaptive processes occurring in receptor systems sending afferents to the cerebellum. This appears to be associated with ordering of the afferent flow, as a result of which the depression of Purkinje cells can be converted into activation, which in turn leads to increases in the inhibitory influences of Purkinje cells on cerebellar fastigial nucleus neurons. Similar results were obtained by Il'in et al. [2], who studied the dynamics and phasicity of changes in neuron structure and the activity of a number of oxidative-reductive enzymes in the cerebellum at different durations of exposure to vibration. The actions of different physical factors on cerebellar neurons have also been studied by other authors [13, 14, 18, 24]. Increases in the excitatory influences of factors when exposure is relatively short (five days) are also evidenced by increases in the proportions of neurons responding at frequencies of more than 30 spikes/sec and some decrease in the proportions of low-frequency cells as compared with normal conditions. However, vibration for 15 days led to an increase (almost two-fold) in the proportion of low-frequency neurons and a significant decrease in the proportion of high-frequency (more than 30 spikes/sec) neurons, which is also evidence for the development of inhibitory processes in nuclear neurons, which is in agreement with our earlier results [4].

REFERENCES

1. Yu. I. Ivanov and O. N. Pogorelyuk, *Statistical Processing of the Results of Medical-Biological Studies* [in Russian], Meditsina, Moscow (1990).
2. I. I. Il'in, B. A. Nasibulin, and V. A. Zherebitskii, "Changes in the structure of neurons and the activity of a number of oxidative-reductive enzymes in the cerebellum during continued and prolonged exposure to general low-frequency vibration," *Arkh. Anat. Gistol. Émbriol.*, **100**, No. 2, 9–15 (1991).
3. R. M. Meshcherskii, *Analysis of Neuron Activity* [in Russian], Nauka, Moscow (1972).
4. S. M. Minasyan, S. G. Saakyan, and S. G. Sarkisyan, "The role of the fastigial nucleus of the cerebellum in controlling the activity of vestibular neurons during prolonged exposure to vibration," *Sensor. Sistemy*, **16**, No. 2, 155–159 (2002).
5. K. I. Pogodaev, *Epileptology and Brain Pathology* [in Russian], Meditsina, Moscow (1986).
6. V. V. Fanardzhyan, "Inhibitory mechanisms of the cerebellum. Functional characteristics," *Usp. Fiziol. Nauk.*, **23**, No. 4, 3–29 (1992).
7. V. V. Fanardzhyan, *Selected Chapters in Neurophysiology* [in Russian], Gitutyun, Erevan (2002).
8. D. N. Khudaverdyan, A. A. Asratyan, I. V. Varterisyan, M. V. Khanbabyan, R. Sh. Sarkisyan, and G. Kh. Mushegyan, "Analysis of the baseline spike activity of locus ceruleus neurons," *Neurophysiology*, **32**, No. 4, 308–313 (2000).
9. F. Abad-Alegria, "Estereotaxis troncoencefalica," *Trav. Inst. Cajal Invest. Biol.*, **63**, No. 1, 193–224 (1971).
10. J. C. Albus, "Theory of cerebellar function," *Math. Biosci.*, **10**, No. 1, 25–61 (1971).
11. F. Benedetti, P. G. Montarolo, and S. Rabacchi, "Inferior olive lesion induced long-lasting functional modifications in Purkinje cells," *Exptl. Brain Res.*, **55**, 368–371 (1984).
12. S. J. Blakemore, C. D. Frith, and D. M. Wolpert, "The cerebellum is involved in predicting the sensory consequences of action," *NeuroReport*, **12**, 18979–1884 (2001).
13. U. Buttner and A. Fuchs, "Eyes and head movement-related activity in the fastigial nucleus of the alert monkey," in: *Vestibular and Brainstem Control of Eye, Head and Body Movements*, H. Shimazu and Y. Shinoda (eds.), Japanese Scientific Societies Press, Tokyo (1992), pp. 351–361.
14. U. Crusser-Cornehls, "Responses of flocculus and Vestibular nuclei neurons in weaver mutant mice to combined head and body rotation," *Exptl. Brain Res.*, **107**, No. 1, 26–33 (1995).
15. C. I. De Zeew and A. S. Berrebi, "Individual Purkinje cell axons terminate on both inhibitory and excitatory neurons in the cerebellar and vestibular nuclei. New directions in vestibular research," *Ann. N.Y. Acad. Sci.*, **781**, 607–610 (1996).
16. M. R. Dino, A. A. Perachio, and E. Mugnaini, "Cerebellar unipolar brush cell are targets of primary vestibular afferents: an experimental study in the gerbil," *Exptl. Brain Res.*, **140**, No. 2, 162–170 (2001).
17. A. F. Fuchs, F. R. Robinson, and A. Straube, "Participation of the caudal fastigial nucleus in smooth-pursuit eye movements. I. Neuronal activity," *J. Neurophysiol.*, **72**, 2714–2728 (1994).
18. Ch. Helmchen, A. Straube, and U. Buttner, "Saccade-related activity in the fastigial oculomotor region of macaque monkey during spontaneous eye movements in light and darkness," *Exptl. Brain Res.*, **98**, No. 3, 474–482 (1994).
19. M. Ito, "Cerebellar long-term depression. Characterization, signal transduction and functional roles," *Physiol. Rev.*, **81**, No. 3, 1143–1195 (2001).
20. Y. P. Ivanenko, R. Grasso, and F. Lacquanti, "Effect of gaze on postural responses to neck proprioceptive and vestibular stimulation in humans," *J. Physiol.*, **519**, No. 1, 301–314 (1999).
21. F. A. Middleton and P. L. Strick, "Basal ganglia and cerebellar loops: motor and cognitive circuits," *Brain Res. Rev.*, **31**, 236–250 (2000).
22. F. Rossi and P. Strata, "Reciprocal trophic interactions in the adult climbing fibre-Purkinje cell system," *Prog. Neurobiol.*, **47**, 341–369 (1995).
23. B. R. Sastry, W. Morishita, S. Yip, and T. Shew, "GABA-ergic transmission in deep cerebellar nuclei," *Prog. Neurobiol.*, **53**, 259–271 (1997).
24. C. Siebold, L. Glonti, S. Glasnauer, and U. Buttner, "Rostral fastigial nucleus activity in the alert monkey during three-dimensional passive head movements," *J. Neurophysiol.*, **77**, No. 3, 1432–1446 (1997).
25. W. R. Staines, W. E. McIlroy, and J. D. Brooke, "Cortical representation of whole-body movement is modulated by proprioceptive discharge in humans," *Exptl. Brain Res.*, **138**, No. 2, 235–242 (2001).