UNIT RESPONSES OF THE CORTEX OF THE CEREBELLAR VERMIS TO MONAURAL AND BINAURAL STIMULATION

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As a rule asymmetry of response characteristics (number of spikes per response, threshold, minimal latent period, latent period at the threshold of the response, range of fluctuation of the threshold) to acoustic stimulation on the right or left sides was found in neurons of the cerebellar cortex (lobules VI-VII of the vermis). The phenomena of ninaural summation were well marked, as also was the specific sensitivity to interaural differences in the time and intensity of acoustic stimulation.

Investigation of cerebellar unit responses to stimulation of different modalities has demonstrated their weak specificity as regards both the modality of the stimulus and the parameters of stimulation [4, 7]. In particular, cerebellar unit responses were of low specificity relative to such parameters of the acoustic stimulus as its spectrum, duration, and intensity [3, 5, 8, 10].

It has been postulated on the basis of the observed facts [3] that cerebellar neurons may be sensitive to characteristics of the acoustic stimulus determining its position in space, i.e., to interaural differences of stimulation. The investigation described below was carried out to study this problem.

EXPERIMENTAL METHOD

Cats were anesthetized with chloralose (70 mg/kg). The acoustic stimuli were tonal or noise volleys and clicks applied through telephones with identical characteristics; in only a few experiments were horn-type transmitters used in a free acoustic field. Each acoustic stimulus was applied 10-20 times at a frequency not exceeding 0.4/sec. Altogether 20 neurons were studied in the region of lobules VI-VII of the cortex of the cerebellar vermis, which is taken to be the focus of responses to acoustic and photic stimulation [6]. The details of the method were given in full in earlier publications [1, 3].

EXPERIMENTAL RESULTS

All neurons were tested with respect to comparative effectiveness of acoustic stimuli* applied on the right and left and also with respect to the comparative effectiveness of stimuli presented monaurally and binaurally. The following characteristics of the unit responses were evaluated: number of spikes per responses (N_m), response threshold (I_0), minimal latent period for a given neuron (LP_{min}), latent period at the threshold of the response (LP_{thr}), and a value characterizing the range of fluctuation of the threshold of the neuron (S; Fig. 1A; see [2]).

Of the 20 neurons only one had completely identical response characteristics to acoustic stimuli applied on the left and right sides. The rest showed some degree of asymmetry of all or some measured

* A stimulus was regarded as more effective if the threshold of the response to it was lower, the latent period was shorter, and the range of fluctuation of the threshold (S; Fig. 1A; see [2]) was smaller.

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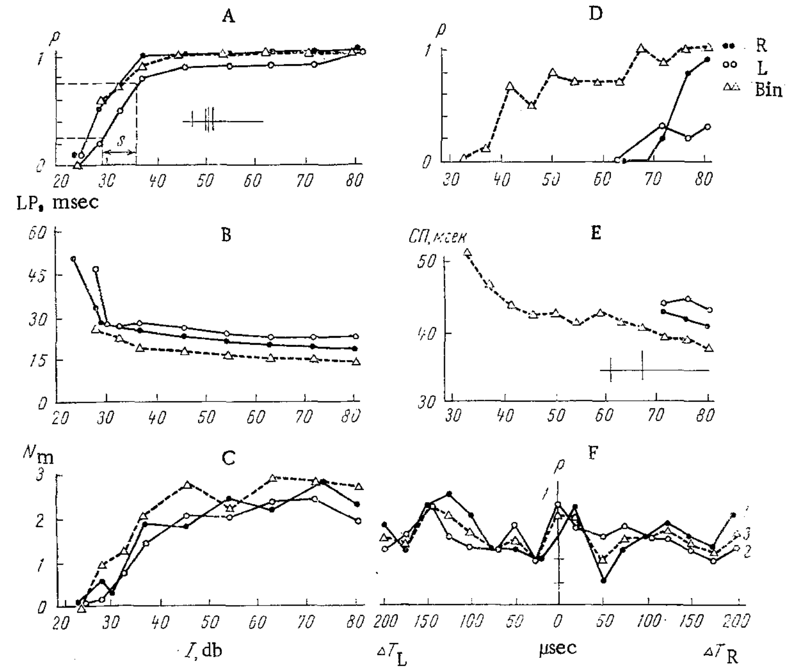

Fig. 1. Response characteristics of two neurons (A–C and D–E) located in the molecular layer to monaural and binaural stimulation by clicks: A, D) probability of discharge (p); B, E) latent period (LP, msec); C) mean number of spikes per discharge (N_m) as a function of intensity of click (I, dB); R) stimulation of right ear; L) stimulation of left ear; Bin) binarual. In A and E discharge pattern of neurons is shown schematically. F) probability of discharge (p) as a function of interval between binaurally presented clicks (ΔT_R, ΔT_L, μsec) with an intensity of 63 dB; 1) measurements at beginning of experiment, 2) at end, 3) mean of these measurements; with ΔT_L stimulation of left ear precedes, with ΔT_R right precedes.

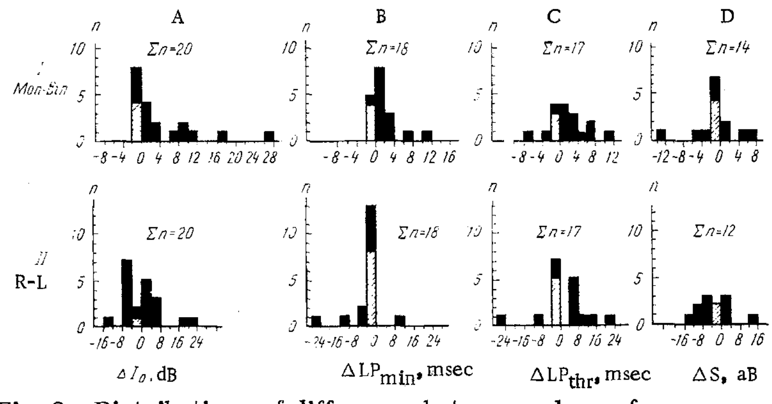

Fig. 2. Distributions of difference between values of response threshold (ΔI_0, dB), minimal latent period (ΔLP_{min}, msec), latent period at threshold of response (ΔLP_{thr}, msec), and value of S (ΔS, dB; see Fig. 1A) obtained in response to monaural and binaural stimulation (I, Mon–Bin, minimal difference) and in response to two monaural stimuli (II, R–L: right – R and left – L).

response characteristics (Figs. 1-3). The maximal difference in I_0 during acoustic stimulation on the left and right sides reached 22 dB (Fig. 2, II, A), and the maximal distance between the values of LP_{min} was 25 msec (Fig. 2, II, B), of LP_{thr} 22 msec (Fig. 2, II, C), and S 13 dB (Fig. 2, II, D). Asymmetry of the value of I_0 was observed in 95% of cases (Fig. 2, II, A), of LP_{min} in 56% of cases (Fig. 2, II, B), of LP_{thr} in 71% (Fig. 2, II, C), and of S in 83% of cases (Fig. 2, II, D). During the measurement of I_0, LP_{thr}, and S, i.e., under the conditions of threshold stimulation, marked asymmetry of the response characteristics was observed in a much higher percentage of cases than during measurement of LP_{min}, i.e., in response to stimulation of high intensity.

As a rule binaural stimulation was either more effective than either monaural stimulation or was equally effective with the more effective of the monaural stimulations (Fig. 1; Fig. 2, I). The maximum decrease in the values of I_0 with binaural stimulation (compared with the most effective monaural) reached 28 dB (Fig. 2, I, A), the shortening of LP_{min} was 12 msec (Fig. 2, I, B), the shortening of LP_{thr} 12 msec (Fig. 2, I, C), and the decrease in the value of S 6 dB (Fig. 2, I, D). Compared with the less effective monaural stimulation, the lowering of the values of all these characteristics of the response to binaural stimulation was even more marked. The phenomena of binaural summation are thus well marked in cerebellar neurons.

In some cases, however, binaural stimulation was less effective than the most effective of the monaural stimulations: with respect to I_0 this phenomenon was observed in 20% of cases (Fig. 2, I, A), LP_{min} in 6% of cases (Fig. 2, I, B), LP_{thr} in 18% (Fig. 2, I, C), and S in 46% of cases (Fig. 2, I, D).

Investigation of the specific sensitivity of the cerebellar neurons to the time delay (ΔT) between presentation of the stimulus to the right and left ears (simulating movement of a visual image from the midline – see [1]) showed that in 9 of the 13 experiments (i.e., in 69% of cases) the unit response was inhibited or intensified at certain values of ΔT (Fig. 1F). For instance, in the case shown in Fig. 1F on the curve 3, corresponding to mean values of the experiment, if the sound was applied first to the left ear a definite increase was found in the probability of a response at $\Delta T_L = 150$ μsec compared, for example, with a delay $\Delta T_L = 22$ μsec; the probability of significance of the difference between the values (p) at these points was higher than 0.99; the values of p for $\Delta T_L = 22$ μsec and $\Delta T_R = 22$ μsec differ significantly, also with a probability of 0.99; for $\Delta T_L = 150$ μsec and $\Delta T_R = 125$ μsec the probability that the difference between the values (p) was significant was 0.95. The absence of sensitivity to ΔT observed in four of the 13 cases, incidentally, was always associated with absence or a slight degree (not more than 2 dB) of lowering of the response threshold to binaural stimulation compared with monaural.

Movement of an auditory image away from the midline leads not only to changes in the value of ΔT, but also to differences in the level of intensity (ΔI) of sounds applied to the right and left ears [1]. An experiment in which the intensity of sound applied on the right (I_R) fell from 73 to 20 dB (i.e., within the range from 46 to -7 dB relative to the response threshold; see Fig. 3C), whereas the intensity of the sound applied on the left side (I_L) remained constant (69 dB or 28 dB above threshold; see Fig. 3C) during binaural stimulation in a free acoustic field is illustrated in Fig. 3. As is clear from Fig. 3A, when $I_R > 55$ dB binaural summation was virtually absent: binaural stimulation (Bin) gave almost the same effect as stronger (relative to the threshold of response) monaural stimulation on the right (R); when $I_R \leq 38$ dB, and the intensity of sound on the left (relative to the response threshold) became approximately 20 dB or more greater than on the right, the number of spikes (N_m) in the unit response to binaural stimulation corresponded exactly to N_m in response to stimulation on the left; i.e., binaural summation also was absent. Only when 38 dB < I_R < 55 dB (i.e., within the range from 11 to 28 dB above the response threshold for stimulation on the right) was an effect of binaural summation observed: binaural stimulation evoked a much greater unit response than stimulation on the right or left. The data for the latent period (Fig. 3B) gave the same qualitative results as the data for N_m (Fig. 3A), but the range of intensity was in which binaural summation was observed in this case was much wider: from 25 to 64 dB. With a sufficiently high value of ΔI the characteristics of the response to binaural stimulation thus corresponded to their characteristics in response to presentation of one (the physiologically stronger) of the sounds; with lower values of ΔI an effect of binaural summation was seen. These phenomena can be compared with the effects of perception of sounds in psychophysical experiments in which the sounds are presented in the same way.

When the experimental results are examined, the first feature to be emphasized is the marked asymmetry in the characteristics of cortical unit activity in the cerebellar vermis in response to stimulation on

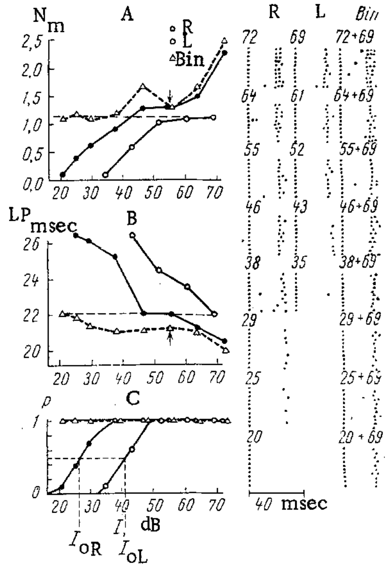

Fig. 3. Characteristics of cerebellar unit response to binaural (Bin) presentation of a noise volley (duration 60 msec) with variation in the intensity of one of them (applied to the right ear – R). Graphs show number of spikes per response (A, N_m), latent period (B, LP, msec), and probability of response (C, p) as functions of intensity (I, dB) of sound; R, L, Bin) presentation of sound on right, left, or binaurally, respectively; for Bin, I_L = 59 dB, I_R plotted along abscissa; broken line denotes values of N_m and LP for I_L = 69 dB; arrows indicate equal intensity above response threshold (I_{oL}, I_{oR}) for sounds applied on left and right. Oscillographic records show spike response of neuron to noise stimuli (R, L, bin) of different intensities (numbers above, in dB); recorded by the "dots" method [3, 11]; first vertical row of dots indicates moment of application of stimulus, remaining dots in each line show spikes generated by neuron.

the right and left ears (Fig. 1; Fig. 2, II; Fig. 3). This fact is evidence of unequal representation of afferent impulses from bilaterally symmetrical parts of the auditory system at the inputs of the cerebellar neurons. It is interesting to note that the cerebellar vermis is not only an unpaired brain structure, but that it does not possess bilateral symmetry, at least in its microstructure. Investigations of unit activity of the centers of the classical auditory pathway [1] have shown that asymmetry of the firing characteristics lies at the basis of the marked changes in unit responses during variation of interaural differences of stimulation. The results of the present investigation confirmed that this applies also to the auditory region of the cerebellar vermis. Many of the neurons tested in this structure, a percentage at least equal to the number of neurons in the centers of the classical auditory pathway [1], respond by marked changes in their activity within a certain range of interaural differences of stimulation in time (Fig. 1F) and in intensity (Fig. 3). It must be pointed out that the observed changes in cerebellar unit responses during variation of ΔT and ΔI are nonmonotonic (Fig. 1F; Fig. 3A, B), to correspond to the types of response which predominate in the higher levels of the auditory system starting from the level of the inferior colliculi. By contrast with parameters of sound such as intensity, duration, and spectrum [3], it was thus only interaural differences of stimulation which could reveal differences in the sensitivity of the cerebellar neurons to a change in the stimulus parameters. Information on the side and degree of precedence or strengthening of the stimulus could be preserved in the observed changes in cerebellar unit activity to the extent to which they were expressed in unit responses of the inferior colliculi and in the initial discharge of neurons of the medial geniculate body and auditory cortex (compare Figs. 1F, 3A, and [1]). It can be postulated on the basis of this fact that the cerebellum plays an essential role in the formation of commands sufficiently precise to organize the animal's localization movements, in which the auditory region of the cerebellum evidently plays an important part [6, 9].

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