Proc. Natl. Acad. Sci. USA
Vol. 95, pp. 15032–15036, December 1998
Neurobiology

Patches of synchronized activity in the cerebellar cortex evoked by mossy-fiber stimulation: Questioning the role of parallel fibers

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Edited by Rodolfo R. Llinás, New York University Medical Center, New York, NY, and approved October 13, 1998 (received for review July 27, 1998)

ABSTRACT **The discrepancy between the structural longitudinal organization of the parallel-fiber system in the cerebellar cortex and the functional mosaic-like organization of the cortex has provoked controversial theories about the flow of information in the cerebellum. We address this issue by characterizing the spatiotemporal organization of neuronal activity in the cerebellar cortex by using optical imaging of voltage-sensitive dyes in isolated guinea-pig cerebellum. Parallel-fiber stimulation evoked a narrow beam of activity, which propagated along the parallel fibers. Stimulation of the mossy fibers elicited a circular, nonpropagating patch of synchronized activity. These results strongly support the hypothesis that a beam of parallel fibers, activated by a focal group of granule cells, fails to activate the Purkinje cells along most of its length. It is thus the ascending axon of the granule cell, and not its parallel branches, that activates and defines the basic functional modules of the cerebellar cortex.**

The cerebellar cortex is composed of five types of neurons organized in a lattice-like structure that receives input from two sources: the mossy fibers and the climbing fibers. Briefly, the axon of each granular cell ascends through the molecular layer, forming several synaptic contacts with Purkinje cells and other cortical interneurons. The axons then bifurcate at various levels within this layer and run longitudinally along the cerebellar folium in a mediolateral direction. These bifurcating axons collectively form the parallel-fiber system, which is oriented perpendicularly to the plane of Purkinje-cell dendrites. As they cross the dendrites of the Purkinje cells, each of these fibers establishes a single, rarely a double, synaptic contact with Purkinje cells along their path (1, 2). Accordingly, the classical view of the functional organization of the cerebellar cortex asserts that the information coming from mossy fibers flows along the parallel fibers (3–5), generating an elongated band of Purkinje-cell activity underneath the parallel-fiber beam. However, peripheral tactile stimulation yielded a contradictory result; patch-like receptive fields were observed (6). Consequently, a modern view of the cerebellar organization has been proposed (7, 8). This modern view postulates a radial organization of the cerebellar cortex rather than a mediolateral organization. The radial organization emphasizes the strong input from the ascending branch of the granular-cell axon relative to its parallel branches.

To discriminate between the patterns of activity that stem from the two different functional organizations, one should use a technique that enables simultaneous recording from many sites. Optical imaging of voltage-sensitive dyes, pH-sensitive dyes, or intrinsic optical signals seems to be an appropriate method. Indeed, previous imaging studies of cerebellar activity have shown that surface stimulation generates activity that propagates along a beam of parallel fibers (9–13). By using a pH-sensitive dye, Ebner (12) has shown *in vivo* that the response to surface stimulation is a beam of activity, whereas the response to face stimulation is organized in parasagittal bands. However, because prolonged changes of pH are related only indirectly to neuronal activity and lack the necessary temporal resolution, these findings still do not identify the natural pattern of activity evoked by the mossy fibers. Furthermore, the strong correlation between the parasagittal and zebrin bands reported by Ebner suggests that the climbing fibers, not the mossy fibers, are the main activators of the bands (14). Vranesic *et al.* (13) used voltage-sensitive dye to monitor the activity in parafrontal or superficial slices after parallel-fiber stimulation. They found that throughout the activated beam of parallel fibers, a constant ratio exists between the response representing the parallel-fiber action potentials and the postsynaptic response measured at the same location. Based on this result, they erroneously argued that the ascending axon contribution to the postsynaptic response is insignificant. In fact, their experimental design, which was restricted to direct parallel-fiber stimulation, could not address this issue. As shown in this paper, direct electrical stimulation of the surface of the cerebellar cortex produces an artificially large and synchronous activation of parallel fibers that does not resemble, in space or time, the functional pattern engendered by the parallel-fiber–Purkinje-cell activation after a mossy-fiber input. Moreover, direct parallel-fiber activation masks the important role played by the ascending axons of the granule cells along the depth of the cerebellar cortex.

In this study, we use optical imaging of voltage-sensitive dyes in an isolated cerebellar preparation to characterize the pattern of activity evoked by surface stimulation and to compare it with the pattern of activity evoked by mossy-fiber stimulation.

METHODS

The isolated guinea-pig cerebellar preparation has been described in detail (15). Briefly, the intact cerebellum and the brain stem were removed from the animal, and a cannula was inserted into one of the vertebral arteries. Physiological solution was perfused via the vertebral artery at a rate of 1 ml/min with a peristaltic pump. The intravascular solution consisted of 124 mM NaCl, 5 mM KCl, 1.3 mM $MgSO_4$, 1.2 mM KH_2PO_4, 26 mM $NaHCO_3$, 10 mM glucose, 2.4 mM $CaCl_2$, and 5% dextran. A similar solution without dextran was used for the external solution. The preparation was maintained at 28°C.

Voltage-sensitive dye (16, 17) was injected into one of the cerebellar folia by using a glass micropipette filled with 2 mg/ml RH-795 (Molecular Probes). Histological examination showed that the dye spread homogeneously, deep within a wide portion of the injected folium. Optical signals were

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Abbreviation: DNQX, 6,7-dinitroquinoxaline-2,3-dione.
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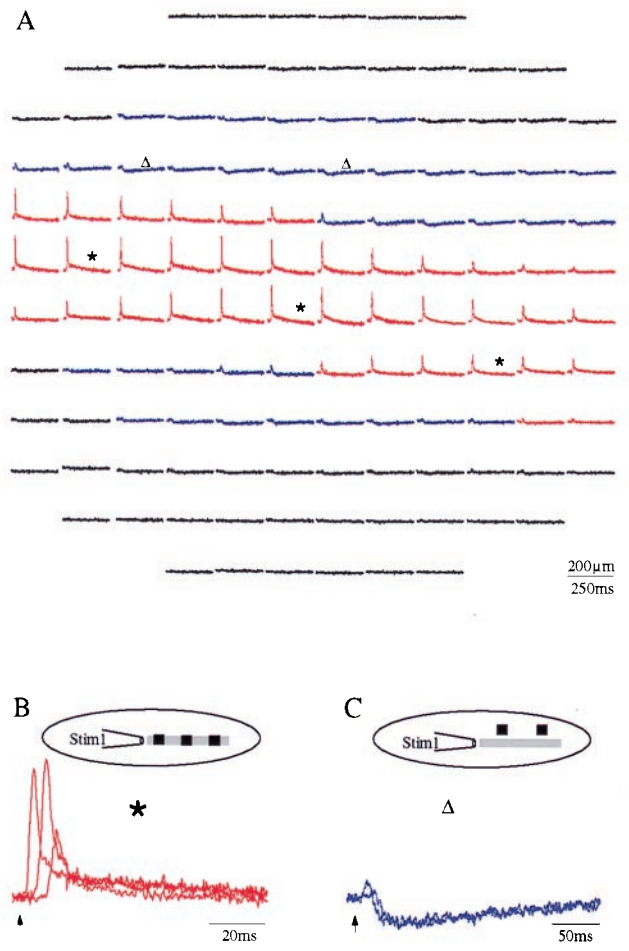

FIG. 1. A single surface stimulus elicited a beam-like response. (*A*) The data are displayed as absolute change in fluorescence as a function of time in 128 sites in the cerebellar cortex. The calibration bar gives the scales for both time and space. The stimulating electrode was placed on the surface of the cerebellar cortex to the left of the recorded area. Each of the 128 traces is an average response of three identical stimuli repeated at a frequency of 0.3 Hz. The stimulus elicited a wave of positive responses (red), which propagated in a beam along the cerebellar folium. Negative signals (blue) were observed lateral to the positive beam. This well defined, narrow positive beam was always observed, but the negative signals were not detected in all experiments. (*B*) The traces marked with asterisks in *A* were superimposed to show that the signal propagated with a conduction velocity of 0.2 m/s. (*C*) The traces marked with triangles in *A* are superimposed on one another. Arrows denote the time of stimuli. The *Insets* in *B* and *C* are schematic representations of the experimental arrangement. A thick gray line represents the activated beam. The locations of the recording sites relative to the beam are marked by black rectangles.

recorded from 128 photodiodes organized in a 12 × 12 array. While using a 10× or 40× objective, each element of the array detects light from a surface of about 200 × 200 μm or 50 × 50 μm, respectively. The signals were amplified in two AC-coupled stages with a time constant of 2 s and were sampled and digitized with 12-bit accuracy at maximal resolution of 40 μs (Microstar Laboratories, DAP 3400a, Bellevue, WA). The data were analyzed and displayed as traces of absolute change in fluorescence (not as relative change), as a function of time at each location.

Concentric metal electrodes were used to stimulate the cerebellar surface (parallel fibers) or cerebellar white matter (mossy fibers). The electrical activity was recorded simultaneously with the optical recording by using glass microelectrodes filled with physiological solution and the same digitizing system.

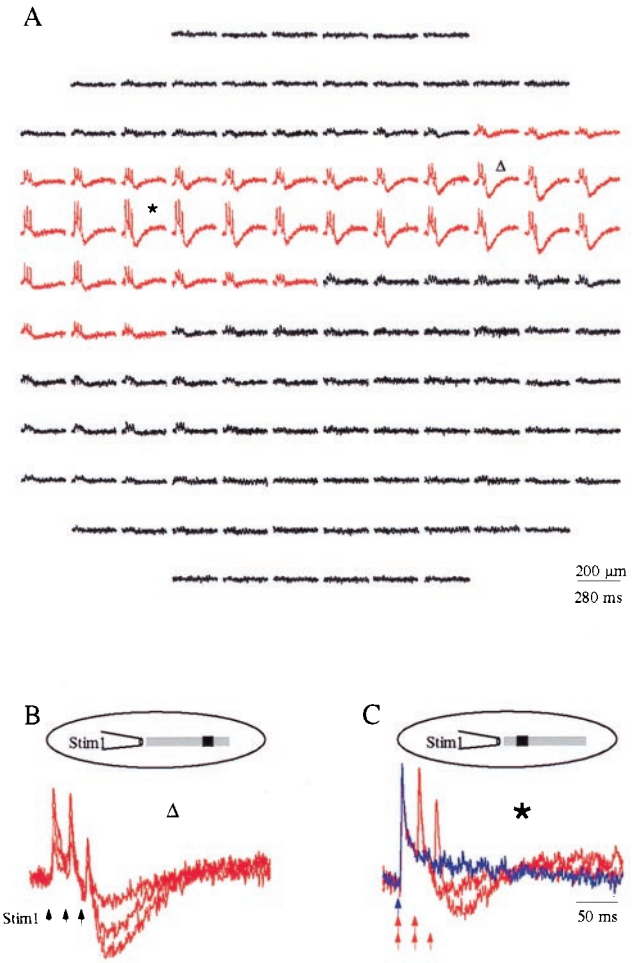

FIG. 2. A train of surface stimuli elicited on-beam inhibition. (*A*) Data presented as in Fig. 1. The stimulating electrode was placed on the surface of the cerebellar cortex to the left of the recorded area. The train of stimuli elicited a train of positive responses (red traces), followed by a prolonged negative wave. (*B*) Superimposed responses to three different stimulus intensities (recorded at the location marked by a triangle in *A*). The amplitude of the negative wave depends on stimulus intensity. (*C*) Superimposed responses to a train of one, two, and three stimuli recorded at the location marked by ∗. Note that the response to a single stimulus (blue trace) lacked the negative response. (*Insets* as in Fig. 1.)

Bicuculline (50 μM; Sigma), which is a blocker of γ-aminobutyric acid type A receptors, was added to the external solution. When Ca^{2+} was replaced by 5 mM Co^{2+} (Merck), the phosphate was removed and the osmolarity was adjusted by changing the amount of NaCl. A glutamate α-amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid (AMPA) receptor blocker, 6,7-dinitroquinoxaline-2,3-dione (DNQX; 100 μM; Sigma), was applied locally by pressure injection via a glass micropipette.

RESULTS

As shown in Fig. 1*A*, surface (parallel-fiber) stimulation generated a wave of changes of up to 0.5% in the dye fluorescence, which propagated along the cerebellar folium at a constant velocity of 0.2 m/s (Fig. 1*B*). The signal was composed of a fast, initial positive peak followed by a prolonged positive tail. The length and width of the activated beam increased with stimulus intensity. A negative signal was usually observed lateral to the positive wave of activity (Fig. 1 *A*, blue traces, and *C*). A train of stimuli to the cerebellar surface elicited a slow, on-beam, negative signal that followed the fast positive responses (Fig.

2*A*, red traces). The amplitude of this on-beam negative signal increased with the stimulus intensity (Fig. 2*B*), the number of stimuli in the train (Fig. 2*C*), and the intratrain frequency (not shown). It should be noted that the lateral inhibition characteristics differ from the on-beam inhibition characteristics.

Three different approaches were used to identify the sources of the optical signal. First, we compared the time courses of the optical signal and the field potential recorded at the same location (Fig. 3*A*, red and blue traces, respectively). The positive wave of the on-beam activity corresponded to parallel-fiber and Purkinje-cell field potential (18, 19). The negative peak of the field potential preceded the peak of the optical signal by 1 ms, indicating that the parallel-fiber action potential did not contribute to the optical signal. Note that, because each photodiode integrated responses from a larger area than that seen by the recording electrode, the temporal relationship of the two signals could be shifted by up to 1 ms.

Second, we used specific synaptic blockers to determine the source of the signal. Local application of DNQX blocked the optical signal at the injection site (Fig. 3*B Middle*, red trace) without interfering with the propagation along the parallel fibers (Fig. 3*B Upper and Lower*). This result is consistent with an insignificant contribution of the parallel-fiber action potentials to the optical signal (see also ref. 10). Bicuculline blocked both the lateral (not shown) and the on-beam negative signals (Fig. 3*C*, red trace).

Third, we examined the effect of lateral and on-beam negative signals on a positive response elicited by a second stimulating electrode, which was located either lateral to the activated beam (Fig. 3*D*) or along the same beam (Fig. 3*E*). The lateral negative signal inhibited the adjacent beam by up to 30% (Fig. 3*D Middle*, green trace), whereas the inhibitory effect induced by the on-beam negative signal could reach 60% (Fig. 3*E*, red trace). Both effects depended on the temporal relationship between the two stimuli. We conclude that the positive wave represents excitation (depolarization) and that the negative wave represents inhibition (hyperpolarization).

These results fit the classical description of the cerebellar responses to surface stimulation (3, 18, 19). Accordingly, the beam of excitatory response represents postsynaptic activity elicited by parallel fibers in Purkinje-cell dendrites and basket, stellate, and granular cells, and the lateral inhibition is the hyperpolarization of Purkinje cells evoked by the basket and stellate cells. The on-beam inhibition represents either the stellate- and basket-cell inhibition of the Purkinje cells or Golgi inhibition at the mossy-fiber–granule-cell synapse.

Stimulation of cerebellar white matter elicited a circular patch of activity 100–500 μm in diameter that was centered above the location of the stimulating electrode (Fig. 4*A*). These patches are characterized by six features: (*i*) the amplitude of the patch-like response was always smaller than the response to surface stimulus by about an order of magnitude; (*ii*) the size of the patch (marked areas in Fig. 4*A*) and the amplitude of the response (Fig. 4*B*) increased with stimulus intensity; (*iii*) activity occurred simultaneously all over the patch with a latency of 2–4 ms to stimulus onset (Fig. 4*C*); (*iv*) the patch of activity was reversibly blocked by 5 mM Co^{2+} (Fig. 4*D*); (*v*) bicuculline increased the amplitude and duration of the response evoked but did not affect the size of the activated patch (not shown); and (*vi*) the patch response was blocked by on-beam inhibition generated by a train of stimuli (Fig. 4*E*). These features suggest that the patch of activity represents the activation of Purkinje cells and interneurons via the mossy-fiber input.

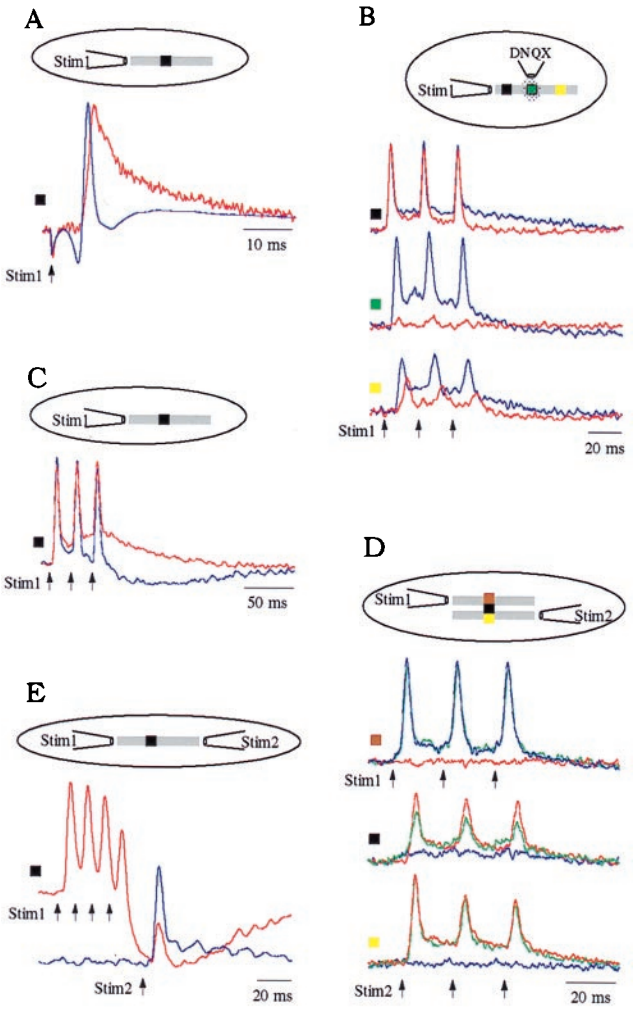

FIG. 3. Characterization of the optical signal. (*A*) The optical signal (red trace) and the field potential (blue trace) were recorded at the same location with the recording electrode close to the cerebellar surface. The negative peak of the electrical signal (inversely displayed) represents the parallel-fiber action potentials. It preceded the peak of the optical signal by 1 ms. The slow negative wave of the electrical response, which represents the postsynaptic excitation in Purkinje cells and other cortical cells, correlated with the slow positive decay of the optical response. The arrow denotes the time of stimulus. (*B*) DNQX blocked the optical response to surface stimulation. The three panels show responses recorded at three locations along the activated beam (see inset). The blue traces are the control, and the red traces are the responses after local application of DNQX at the location of the green rectangle (see inset). (*C*) Bicuculline blocked the on-beam negative signal. The blue and red traces were recorded before and after bath application of 50 μM bicuculline, respectively. (*D*) Lateral inhibition. Responses were recorded at three adjacent locations across two activated beams (see inset). The blue and the red traces are the responses to stimulation of the upper beam (stim 1) and the lower beam (stim 2), respectively. The green traces are the responses to simultaneous stimulation of both beams. The green trace (*Middle*; black rectangle) was smaller than the red trace, indicating that activity in the upper beam inhibited the lower-beam activity only in the region between the two beams. (*E*) On-beam inhibition. The response to a test stimulus (blue trace, stim 2 in the inset) was decreased by on-beam inhibition evoked by a train of stimuli (stim 1, red trace). Similar results were obtained with a shorter train of stimuli provided on-beam inhibition was generated.

DISCUSSION

Our study of the activity evoked in the cerebellar cortex clearly shows that surface stimulation generates a beam of activity that propagates along the parallel-fiber system. White-matter stimulation elicits a patch of activity that occurs simultaneously all over the activated area. The difference between these patterns of activity is significant and cannot be an artifact of the isolated cerebellar preparation. The *in vitro* preparation is bound to suffer from a certain degree of damage, but damage is unlikely

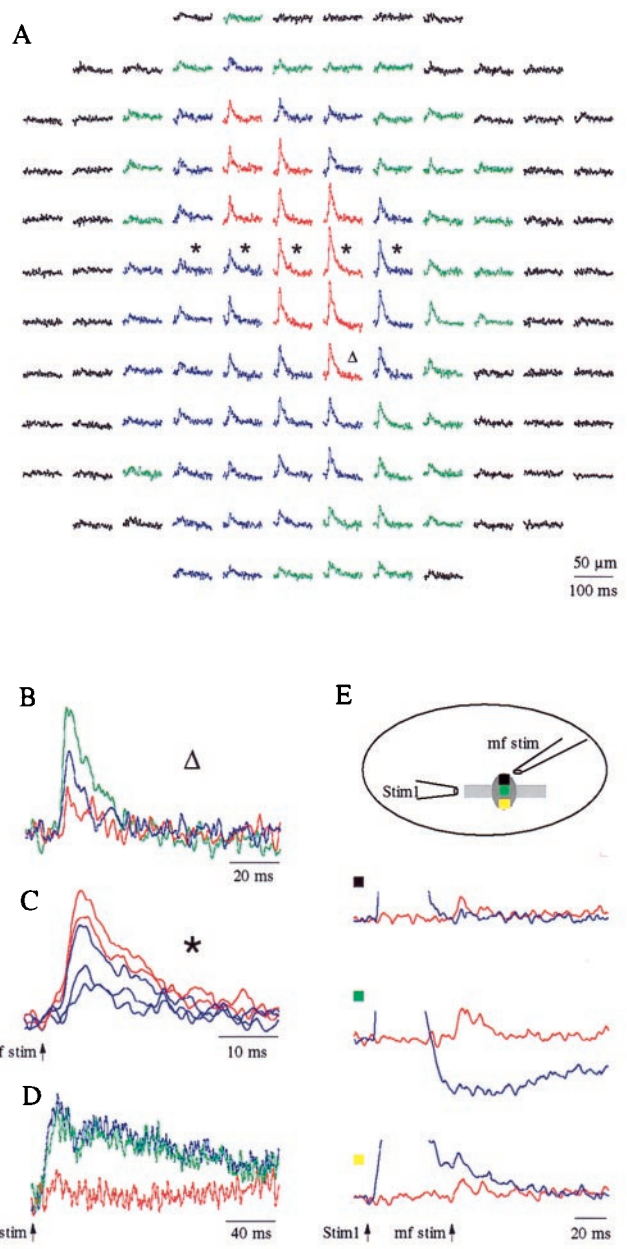

FIG 4. Patch-like response evoked by white-matter stimulation. (*A*) The traces shown (obtained at a gain of 40× and displayed as in Fig. 1*A*) were obtained at high stimulus intensity. The red, blue, and green traces denote the activated areas at increasing stimulus intensities. Only the area marked in red was activated at the lowest stimulus intensity. At intermediate stimulus intensity, the activated area increased and is marked both by red and blue. (*B*) Superimposed responses to stimulation at the three intensities, at the location marked by a triangle in *A*. (*C*) The traces marked with ∗ in *A* were superimposed to show that response onsets and peaks occurred at the same time in all locations. (*D*) The patch of activity was reversibly blocked by Co^{2+}. Each of the traces shown is the average response of seven diodes measured before (blue trace) and during (red trace) application of 5 mM Co^{2+}. After washing, the response reappeared (green trace). (*E*) The patch-like response was blocked by on-beam inhibition. Responses in three locations across the activated beam (see inset) are shown. A train of stimuli (stim 1 in the inset) generated the on-beam inhibition. The response to white-matter stimulation (mf stim, red traces) and the response to both stimuli (mf stim and stim 1, blue traces; note that the positive responses to stim 1 were truncated) were superimposed. The response to mossy-fiber stimulation was completely blocked by the on-beam inhibition in the center of the activated beam (green rectangle; the response to mf stim seen in the red trace is missing in the blue trace). The response was partially blocked near the edge of the beam (black and yellow rectangles; the response to mf stim in the red traces is larger than the response to mf stim in the blue traces).

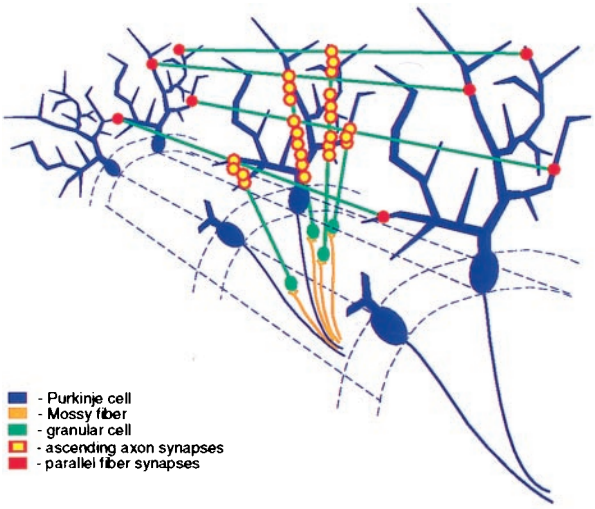

FIG. 5. A schematic diagram of the components in the cerebellar cortex studied here, with Purkinje cells in blue and granular cells in green. The red–yellow circle marks the synapses formed by the ascending axon on Purkinje-cell dendrites, and the red circle marks the synapses formed by the parallel fibers on Purkinje cells along their path. The inhibitory network is not shown.

to cause a differential effect within the same components. Before considering the functional significance of these two activity patterns, we need to identify the neuronal sources of the optical signal and the neuronal elements activated by the two stimulation paradigms and to understand how these two patterns of activity arise.

The main sources of the optical signal remained unclear. This signal is composed of both fast and slow components. The short duration of the fast component (about 5 ms) suggests an intrinsic regenerative potential, whereas the slow component likely represents postsynaptic potentials. Because the parallel-fiber action potentials do not contribute to the optical signal, only two possible sources of intrinsic regenerative potential remain. The first is action potentials in Purkinje cells and stellate cells, and the second is dendritic Ca^{2+} action potentials in Purkinje cells. Given the duration of Ca^{2+} spikes (20), the proximity of the dendritic endings to the cerebellar surface, and the large membrane area of the Purkinje-cell dendrites (the membrane area per unit of volume of Purkinje cells is five times larger than that of stellate and basket cells), it is reasonable to assume that the dendritic Ca^{2+} action potentials are the main source of the fast component. This assumption fits the previous observation that surface stimulation is capable of generating Ca^{2+} action potentials in Purkinje-cell dendrites (21).

The interpretation of the results depends critically on identifying which neuronal elements were activated during white-matter stimulation. As mentioned above, we have suggested that the patch of activity represents mossy-fiber activation, as opposed to direct stimulation of granular cells, antidromic activation of Purkinje cells, or activation of climbing fibers. This suggestion is based on several observations. First, the stimulating electrode was located deep in the white matter, excluding direct activation of granular cells. Second, the blockade of the patch of activity by Co^{2+} excluded the possibility of antidromic activation of Purkinje cells. Third, the blockade of patch-like activity by on-beam inhibition was most likely caused by the Golgi-cell inhibition that occurs at the level of the mossy-fiber–granular-cell synapses. If Golgi cells are involved in the on-beam inhibition it will not affect the responses to antidromic activation of Purkinje cells or direct stimulation of granular cells; thus, it supports activation of mossy fibers. Moreover, onset response latency was 2–4 ms,

which is longer than the monosynaptic delay that would be expected if granular cells had been stimulated directly or if climbing fibers had been activated. We therefore conclude that white-matter stimulation mainly activated the mossy fibers. It follows from this conclusion that the ascending axons, and not the parallel-fiber branches, are the main source of excitation of the cerebellar cortex when it is activated via the mossy-fiber system.

There are several reasons only a limited area is activated by the ascending axon and why there is no longitudinal response after mossy-fiber activation. The number of synapses per Purkinje cell formed by a single ascending axon of a granular cell is an order of magnitude larger than the number formed by a parallel-fiber branch. This anatomical observation is schematized in Fig. 5. The number of synapses formed by a focal group of ascending axons on Purkinje cells (red–yellow circles) is larger than the number of synapses formed by the same group on distant Purkinje cells (red circles). Furthermore, the synapses formed by the ascending axon on Purkinje cells are larger than those formed by the parallel fibers, which may increase the probability of transmitter release in ascending axon synapses (22). Cerebellar-cortex activity in the vicinity of the ascending axons may therefore be much higher than the activity along the parallel-fiber beam, and these areas of low activity may be difficult to detect. Another reason is that the conduction velocity of the parallel fibers in the lower molecular layer is higher than that of the parallel fibers in the upper molecular layer (13, 18). This difference in velocities reduces the synchronicity of the volley of action potentials propagating along the beam of parallel fibers. The resulting desynchronized volley reduces the probability of activating postsynaptic cells along the beam. The desynchronization effect is particularly significant in cases where a small number of spatially distributed fibers are activated, as is the case when functionally related mossy fibers activate a beam of parallel fibers. However, recent theoretical work (23) has shown that the accumulated desynchronicity along the distances in our system is too small to account for the failure to activate the Purkinje cells. Theoretically, conduction of action potentials may fail at the bifurcating point of the ascending axon as a result of the geometrical ratio of the diameters of the ascending axon and the parallel fibers. However, detailed morphological work does not support a substantial impedance mismatch that would explain such propagation failure (22). Finally, it has been suggested that the inhibitory system determines the shape of the patch-like response (24). However, our finding that bicuculline did not change the size of the activated patch strongly suggests that the size of the patch is determined by the number of activated granular cells and not by the cortical inhibitory network.

This study of the isolated guinea-pig cerebellum provides direct evidence that mossy-fiber activation imposes localized behavior in the cortex and that the parallel branches of the axons of granular cells alone cannot impose long-distance action. These results strongly support Llinás' hypothesis (7) that the synaptic strength of the ascending axon is responsible for this localized behavior. Our results also provide explanation for the patch-like receptive fields described by Bower and Woolstone (6). We therefore suggest that the cerebellar cortex is composed of independent modules that weakly interact via the parallel-fiber system. The importance of the parallel-fiber system thus lies in its ability to increase the responsiveness of a distant area rather than spreading the information actively along their path (5) or modulating Purkinje-cell responses to ascending axon input (24).

We thank Dr. A. Grinvald for professional advise, Dr. L. Cohen for his helpful comments, Dr. W. N. Ross for his invaluable criticism, and Dr. I. Segev for his helpful remarks. This study was supported by the U.S.–Israel Binational Science Foundation, the Israel Academy of Sciences, and the European Commission. D.C. was the recipient of a Clore Fellowship.

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