## Observations on the Cortical Mechanism of EEG Activation Accompanying Behavioral Arousal

Consideration of the special properties of dendrites has led to the hypothesis that the oscillatory potentials observed in the electroencephalogram represent variations in graded, electrotonically summated activity of cortical dendrites (*1*). This theory has been supported by the observations that the changes in electrocortical activity produced in the unanesthetized cat by the psychotogenic drug, lysergic acid diethylamide (LSD-25), is attributable predominately to an inhibition of axo-dendritic synaptic activity (*2*). This report (*3*) presents further evidence consistent with the dendritic origin of brain waves by establishing a direct correlation between the dendritic potential tested in isolation and alterations in the amplitude-frequency characteristics of electrocortical activity.

Experiments were performed on unanesthetized, paralyzed cats that had initially been prepared with ether and local skin anesthetization. Single shocks were delivered every 2 sec to the cortical surface 2 mm from bipolar transcortical electrodes that recorded the evoked surface negative potential assignable to the activity of apical dendrites (*4*). The electrocorticogram was recorded continuously in correlation with oscilloscopic registration of the testing dendritic responses. Variations in the directly evoked dendritic response were produced by high-frequency stimulation of the bulbar reticular system that caused at the same time characteristic electrocortical activation (*5*). In addition to this, the effects of cortical polarization on the dentritic response were studied during brain-stem stimulation.

Figure 1 shows the effects of brain-stem stimulation on the spontaneous electrocortical activity and on the tested, directly evoked dendritic response. Accompanying the "desynchronization" of resting activity on stimulation (first arrow), a marked inhibition in the dendritic responses occurred. Both persisted many seconds after brain-stem stimulation (second arrow). Along with the return of the resting rhythm, the dendritic potential returned to initial amplitude.

Further studies to determine the nature of the alteration in dendritic activity by brain-stem stimulation are summarized in Fig. 2. The testing dendritic response (*A*, 1) is decreased by brain-stem stimulation (*A*, 2, 4), but superposed anodal polarization of the cortex temporarily enhances the responses. The dendritic response returned to initial level (*A*, 5) 15 sec after cessation of brain-stem stimulation. The same sequence of events is shown in series *B*, 6–10, with a stronger cortical testing stimulus. In all cases, brain-stem stimulation reduced the dendritic responses. The same effect was produced by cathodal polarization of the cortex (*C*, 12). These results suggest that iterative stimulation of the brain stem activates cortical neurons which inhibit apical dendrites. The inhibitory elements are selectively activated by cathodal polarization of the cortex.

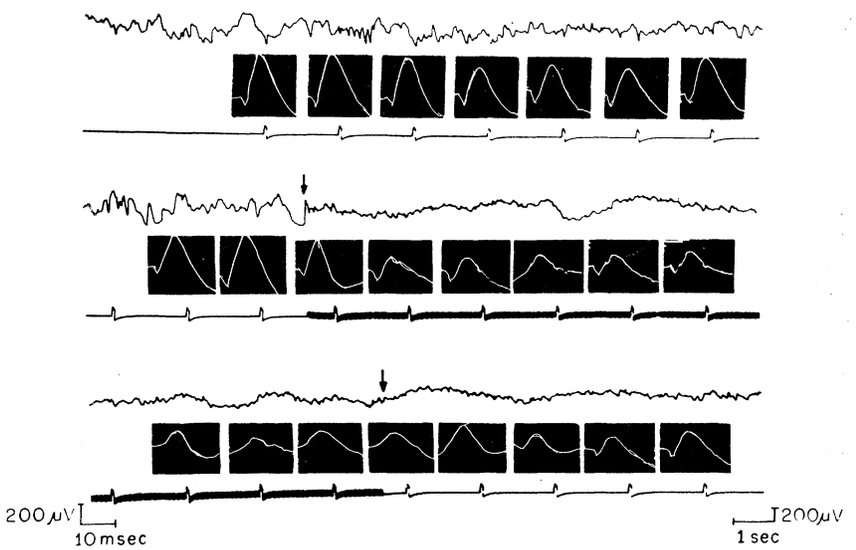


Fig. 1. Signal marker below oscillograms indicates time during recording of electrocorticogram (ECG) that testing dendritic response was evoked from anterior supra-sylvian gyrus. ECG recorded bipolarly from post-sigmoid to anterior supra-sylvian gyrus. *First arrow*: beginning of 300/sec stimulation of brain stem; *second arrow*: end of stimulation. Calibration: (left) dendritic response; (right) ECG.

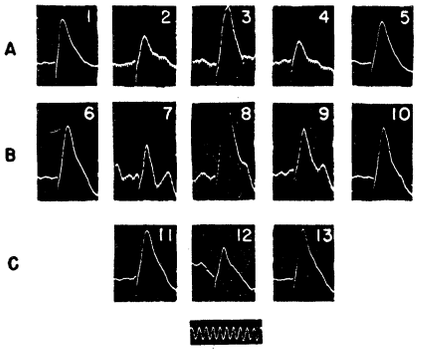


Fig. 2. *A, B,* effects of superposed anodal polarization of cortex on testing dendritic response during brain-stem stimulation. *C,* effect of cathodal polarization of cortex, 12, on dendritic response without brain-stem stimulation; (*C,* 11) before cathodal polarization; (*C,* 13) 10 sec after cessation of polarization. Calibration: 100 cy/sec; 100 μv.

The results of the present study indicate that high-frequency stimulation of the ascending bulbar reticular system alters the synaptic activity of cortical dendrites. Persisting dendritic inhibition resulting from reticulocortical synaptic excitation is believed to underlie the alteration in electrocortical activity that is associated with behavioral arousal.


DOMINICK P. PURPURA*

*Department of Neurological Surgery, College of Physicians and Surgeons, Columbia University, New York*


### References and Notes


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3. The technical assistance of Gidon F. Gestring is gratefully acknowledged.


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* Special research fellow, National Institute for Neurological Diseases and Blindness, U.S. Public Health Service.



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*Very late in life, when he was studying geometry, someone said to Lacydes, "Is it then a time for you to be learning now?" "If it is not," he replied, "when will it be?"*—DIOGENES LAERTIUS, *in The Lives and Opinions of Eminent Philosophers.*