

Postsynaptic Potentials and Spike Patterns during Augmenting Responses in Cat's Motor Cortex

Abstract. *Intracellular recordings and electroencephalograms were obtained from neurons of the motor cortex during augmenting responses elicited by repetitive stimulation of its specific thalamic nucleus. The postsynaptic potentials during fully developed augmenting responses consisted of two depolarizing waves with two separate groups of spike discharges of different latencies, the bases of the spikes, the so-called "firing-levels," sometimes shifting. This supports the concept that the postsynaptic potentials accompanying the augmenting response consist of a primary response and a response of recruiting character.*

Since the classic papers of Morison and Dempsey (1, 2), cortical responses resulting from repetitive stimulation of specific thalamic projection nuclei (5 to 12 per second) with an increase of the amplitude of the cortical evoked responses have been called "augmenting responses." In contrast to the "recruiting responses," the augmenting response (i) can be recorded only from the ipsilateral cortex (3), (ii) is more sensitive to alteration by cortical polarization (4), and (iii), has a more complex configuration of its surface positive-negative wave. Morison and Dempsey (1) postulated at least two neuronal systems for mediating these responses, and Ramon y Cajal (5) and Lorente de N6 (6) described two types of ramifications of fibers of the thalamocortical projection system, labeled "specific" and "nonspecific." In this report, the results obtained from intracellular recordings show that two components in the afferent impulses participate in the augmenting response.

Our experiments were performed on 28 cats anesthetized with Nembutal. The exposed motor cortex, from which intracellular recordings and electroencephalograms (EEG) were obtained, was kept moist with warm Ringer's solution. Bipolar stimulating electrodes, placed in the region of the nucleus ventro-oralis posterior thalami (7), delivered weak rectangular pulses of 0.5 msec duration and about 200 μ A current which were combined with stimulus frequency in such a way as to obtain optimum augmenting responses.

The augmenting response in the EEG and in the intracellular recordings developed in a characteristic manner.

The first stimulus of the thalamic pulse train caused an excitatory postsynaptic potential which was superimposed on a single discharge of short latency (Fig. 1, A_1 , B_1 , and B_2 ; the subscript indicates the number of pulse in the stimulating pulse train). In the course of the repetitive stimulation, these excitatory postsynaptic potentials increased in amplitude, often causing a double spike discharge; this was sometimes followed by a second excitatory potential (Fig. 1, B_3 and B_4). Then, the second potential also increased, and each stimulus was followed by two depolarizing waves of similar amplitude, each initiating one or two spikes. These two waves were clearly separated by the repolarization process of the first discharges (Fig. 1, A_4 , A_5 , and E). Finally, the fully developed postsynaptic potential appeared during the augmenting response, consisting of two depolarizing waves with groups of one or two and two to four spikes (Fig. 1, A_6 , B_5 , B_6 , B_7 , C_2 , D , and E). In some instances, a fusion of the two components of these potentials would occur, leading to the disappearance of the first group, while the latency of the second group decreased (Fig. 1, A_7 , C_1 , and C_3). The increase of the depolarizing waves was

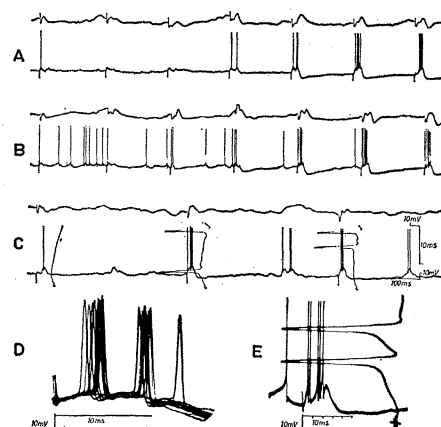


Fig. 1. Intracellular recordings of two neurons in the motor cortex showing different stages of the developing postsynaptic potentials during augmenting responses. Stimulus-frequency of the specific thalamic nucleus: 2 per second in (C), 4.5 per second in the other recordings. In (A) to (C), the upper trace shows the EEG (negativity upward), and the lower trace shows the intracellular potentials; (C) shows the first 15 msec of the stimulus responses, also vertically, in a large time scale; (D) shows the relative constancy of the discharges of the first spike group; ten single traces are superimposed. (E) Postsynaptic potentials and spike pattern of fully developed augmenting response with clear repolarization after about 10 msec. The vertical sweep in larger time scale shows only the first two discharges.

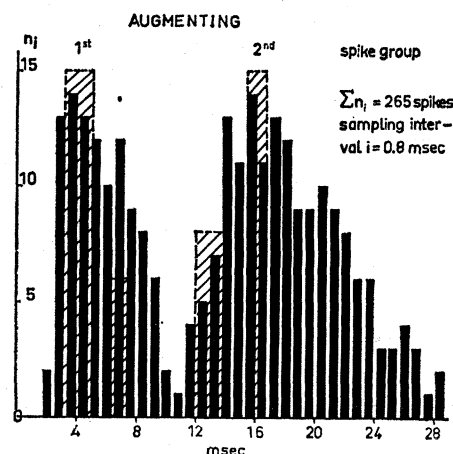


Fig. 2. Latency histogram of 265 sampled spikes of six neurons during augmenting responses. Spikes are sampled at intervals of 0.8 msec starting with the onset of the thalamic stimuli (black columns). Hatched columns show the range of the standard deviation of the latencies and the number of discharges for each latency range during 15 consecutive augmenting responses of one neuron.

accompanied by an increase of the negative wave of the augmenting response in the EEG.

Each depolarizing wave was followed by a long lasting polarizing potential of 100 to 200 msec. This may have initiated the rhythmic character of the neuronal discharges during fully developed augmenting responses in the optimum stimulus frequency (4 to 6 per second), and suggests that there is a rhythmic increase of excitation, post-anodic in character, following these polarizations. During stimulation with lower frequency (2 per second in Fig. 1 B), similar processes would sometimes occur spontaneously (see the "spontaneous" discharge between C_2 and C_3 in Fig. 1), indicating that these cellular responses are not caused by an artificial stimulation alone but may also occur in the normal state.

To evaluate the range of latencies of the two groups of spikes, we sampled the latencies of 265 spikes from different units recorded intracellularly during augmenting responses at intervals of 0.8 msec, starting with the onset of the thalamic stimuli (Fig. 2, black columns). The two groups of spikes are separated by a deep incision at 11 msec. The hatched columns show the constancy of the latencies of the discharges of one neuron during 15 consecutive augmenting responses. These four columns represent the two spikes of the first group and the first two spikes of the second group. The column width covers the range of the standard deviation of the latencies.

tion of the latencies of these spikes, the column height gives the number of discharges during these 15 augmenting responses for each latency range. The numerical values of these latencies are 4.2 ± 0.9 msec, 12.8 ± 0.9 msec, and 16.0 ± 0.7 msec.

These results—which are in keeping with those of Morillo (8), who found latencies shorter than 10 msec after stimulation of the “specific” system and a delay longer than 10 msec after stimulation of the “nonspecific” system—suggest that two systems, conventionally labeled “specific” and “nonspecific,” or different parameters of one thalamocortical system participate in the augmenting response. The different rates of rise of the prepotentials (Fig. 1, C_2 and C_3 , vertical sweeps) and the shift of the firing level of the spikes of the second group (Fig. 1, B_1 , B_7 , and C_2) are similar to the observations of Machne *et al.* (9) in frog motoneurons and of Andersen and Løynning (10) in pyramidal cells of the hippocampus, both of whom postulated the existence of locally different synaptic contacts of presynaptic fibers at the cells. The generally complete depolarization after the first group of spikes (Fig. 1E) also suggests that there are two different and clearly separate periods of afferent impulses. A second depolarizing wave of “recruiting” character was also found after a first short-latency response of “specific” character during low-frequency stimulation of the caudate nucleus (11).

However, whether these postsynaptic responses represent the effect of: (i) two sets of fibers with different conduction velocities; (ii) a direct afferent and a multisynaptic network (12); or (iii) a different location of the excitatory synapses on cell-bodies and dendrites (9, 10, 13), or a combination of these, cannot be decided from our results. But they do stress the concept that the postsynaptic potentials during augmenting waves consist also of a primary response combined with a response of a recruiting character (14).

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Atmospheric Jet Streams

In a brief report titled “Atmospheric jet streams” [*Science* **141**, 1045 (13 September 1963)], J. D. Isaacs purports to give a physical explanation for atmospheric jet streams without regard to current hypotheses.

Atmospheric physicists feel that they understand, in a general way, the formation of jet streams poleward of 30° . A mean (time-averaged) jet stream may be found in middle latitudes which can be related to the large south-to-north gradient of temperature at those latitudes produced by the distribution of solar heating on a spherical earth. Middle latitude jet streams have been obtained by integrating the fundamental equations of planetary aerodynamics without inclusion of mechanisms resembling those hinted at by Isaacs [Smagorinsky, *Monthly Weather Rev.* **91**, 3 (1963)].

Isaacs refers to a “diurnal heat pulse” from the sun’s radiation which “moves through the main body of the atmosphere at approximately Mach 1” over jet stream latitudes and at Mach 1.4 over the equator. This seems to mean that the cited Mach numbers correspond to the tangential velocities of earth points resulting from terrestrial rotation. We assume that Isaacs considers the phenomenon of sunrise on parcels of air in the free atmosphere as a “diurnal heat pulse.” Assuming that this was the sort of process Isaacs had in mind using Mach numbers, we shall try to examine the remainder of his implied hypothesis.

Isaacs implies that some special hy-

drodynamic phenomenon (jet stream) will appear near the latitude at which Mach 1 is found from the above-indicated reasoning. The very idea of expressing earth transport speeds as Mach ratios is not easy to accept, for such transport speeds are measured in a nonrotating coordinate system whose origin moves with the center of the earth, while any gas-dynamic phenomena resulting from the processes Isaacs considers will give rise to particle velocities which must be measured in a coordinate system at rest with respect to the gas. Special circumstances could not possibly be expected to arise near that latitude (about 40°) at which the transport speed of the earth happens to be the same as the speed of sound in a gas at typical atmospheric temperatures.

Other serious difficulties were overlooked by Isaacs. Direct absorption of insolation by atmospheric gases constitutes only a tiny fraction of total atmospheric energy input. The earth’s surface, not the free atmosphere, is the site of the dominant atmospheric energy input; so to suggest, without any quantitative examination, that repetitive absorption of a tiny fraction of the sunlight incident on a given parcel of the atmosphere at a series of successive sunrises is responsible for the jet stream seems quite absurd. Furthermore, the implied poleward shift of the jet stream in the case of a “more carbonic atmosphere” evidently arising from the reduced speed of sound in CO_2 would be significant only for geochemically enormous changes in the CO_2 content of the atmosphere.

Isaacs states that “at the equator, the heat pulse travels through the atmosphere at Mach 1 only at very high altitudes (about 150 km).” This remark prompted us to plot, on a meridional cross section, the locus of all points at which the local transport speeds of air parcels at rest with respect to the rotating earth are numerically equal to the local speed of sound. This locus leaves the earth’s surface, in each hemisphere, near 40° latitude, slopes upward toward the pole until it nears the tropopause at about 50° latitude, curves back toward the equator to another reversal point near the stratopause over latitude 35° approximately, recurves poleward again as it ascends to the mesopause just equatorward of 50° latitude, and then arches up into the thermosphere over the equator at about 150 km. We think Isaacs should be troubled by the fact that his argu-