DENDRITIC POTENTIALS IN THE CEREBRAL CORTEX OF MAMMALS HIBERNATING IN WINTER

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M. B. Shtark and V. P. Danilyuk

Laboratory of Electrophysiology (Head, Candidate of Medical Sciences M. B. Shtark),
Psychoneurological Institute (Director, A. G. Leshchenko), Odessa
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In previous investigations [5-8] it has been shown that at the time that mammals become torpid and enter into the period of winter sleep functional disturbances occur in the brain; there is then a loss of excitability of the pyramidal neurones, and impulses in various cortical cells cease when the temperature reaches 17-16°. A study of the evoked potential developing in the projection center in response to adequate or electrical stimuli applied to the receptors [7, 8] has shown that the pyramidal neurones of layers III and IV may become locally depolarized at a cortical temperature of 14° (in the case of the auditory projection area 9°), but that they are unable to form an excitation which travels to the uppermost cortical layers.

We have never previously investigated the role of the dendrites of the first layer in cortical function as a whole. As the basic phenomenon to be recorded we selected the dendritic potentials consisting of a negative and positive oscillation which develop in the cerebral cortex when it is indirectly stimulated electrically; these potentials reflect postsynaptic activity of dendrites in the upper cortical layers [1-3, 9-12]. The object of this investigation has been to study the changes in these potentials in hibernating animals as they become torpid at the time of winter sleep.

EXPERIMENTAL METHOD

The experiments were carried out on European hedgehogs (Erinaceus europaeus L.). In the projection area of the sciatic nerve [7] we trepanned an aperture where an area of cortex was exposed which was then electrically stimulated by means of bipolar platinum electrodes at a separation of 1-1.5 mm. The lead-off electrode was placed 6-8 mm from the stimulating electrode (unipolar lead). Stimulation was applied from an electronic stimulator with a radio-frequency output of 6-15v, and stimulus duration of 200-400 mseconds. The animal was lightly anaesthetized with chloralose, and cooled in a special trough. Simultaneous measurements were made of the temperature of the cerebral cortex by means of a low-temperature thermo couple.

The electrical changes were recorded by means of a ÉNO-1 oscilloscope and a UBP-1 amplifier. The dendritic potentials (DP) were recorded by superimposition or by triggering the oscilloscope spot so that the sweep coincided with a cortical potential. The deviation of the beam upwards represents negativity beneath the different electrode.

EXPERIMENTAL RESULTS

In the waking state at a cortical temperature of 34-29° the DP consists characteristically of a negative and positive excursion having the following characteristics: amplitude of surface negativity 250-300 μv and duration not more than 20-mseconds; surface positivity 120-230 μv, duration 40-45 mseconds (Fig. 1,A). The latent period of the negative potential did not exceed 1-1.5 mseconds (see Table). Thus the initial values of the DP do not differ from those found in homiothermic animals [3].

Increasing the output voltage from the stimulator from 6 to 15 v at a cortical temperature of 34-28° caused an increase in the amplitude of the negative component of DP by 200-400% (Fig. 1, A, B). The same voltage produced a much smaller increase in amplitude of the negative phase at a temperature of 24° (Fig. 1, C, D). Finally at 21° these effects no longer occurred (Fig. 1, E).

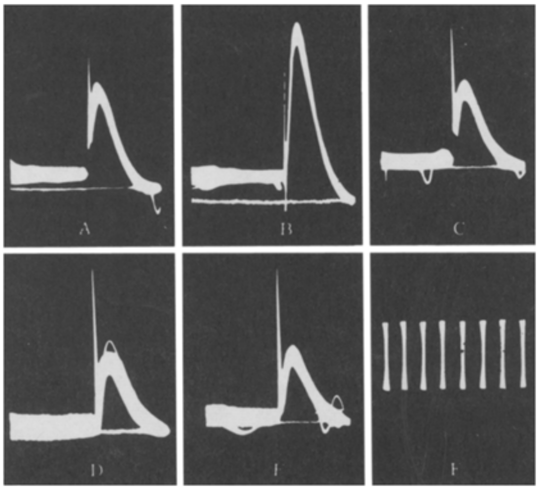

Fig. 1. Change in the dendritic potentials in relation to cortical temperature and stimulus voltage: (A) at 32° and 6 v, (B) at 32° and 15 v, (C) at 24° and 6 v, (D) 24° and 15 v, (E) 21° and 15 v. F calibration 250 μv, time marker 20 mseconds.

Parameters of the Dendritic Potentials at Various Cortical Temperatures

	Temperature of cerebral cortex (in degrees)	Latent period (mseconds)	Amplitude		Duration	
			of the negative component	of the positive component	of the negative component	of the positive component
1	32	$1^1/_2$	250	195	25	45
2	29	$1^1/_2$	195	180	25	55
3	27	$1^1/_2$	240	175	30	65
4	23	$2^1/_2$	240	165	35	65
5	20	5	105	90	40	60
6	18	7	182	82	35	65
7	14	9	90	60	43	65
8	12	9	50	15	50	90

It is known that the increase in amplitude of the superficial negative potential depends mainly on the number of synaptic endings excited at stimulation [3]. We may suppose that reduction of cortical temperature during winter sleep brings about the reduction in excitability of the postsynaptic membrane of the dendrites or else (as is less probable) a decrease in the number of excitable structures. Thus during the onset of sleep and stupor the relationship between cortical temperature and increase in amplitude of DP with increase in stimulus voltage is preserved.

Hibernation and stupor during the gradual reduction of cortical temperature and the temperature of subcortical structures is associated with regular changes in the DP (Fig. 2, A-H).

At a cortical temperature of 34-30° (Fig. 2, A) the capitals DP is comparatively stable. A tetanizing cortical stimulus does not evoke any statistically significant difference in the amplitude or duration of the components of the DP over the indicated limits of cortical temperature.

At a cortical temperature of 28-26° (while the latent period remains unchanged) there is an initial fall in the amplitude of the negative component to 180-299 μv and an increase in the duration of the positive component to 55 mseconds (Fig. 2, B; see table).

At a cortical temperature of 25-23° while the animal is becoming torpid an increase in the amplitude of the negative oscillation to 250 μv was observed, while the positive component remained unchanged (Fig. 2, C). A further temperature fall to 21-20° which occurred while stupor became complete was associated with a statistically significant increase in the negative component to 240-270 μv ($P < 0.05$), while the positive component remained unchanged (Fig. 2, D).

To us the most interesting period occurs when the cortical temperature reaches 18°. Previously we have shown that it is precisely at this time that the characteristic features of stupor become manifest and when conduction of excitation along the multi-synaptic ascending nonspecific pathways of the cerebral systems becomes blocked [5, 6]. It is at the temperature of 18-20° that the amplitude of the DP falls and that the duration increases (Fig. 1, E, F). Here we will do no more than point out the coincidence of these two phenomena which suggests a possible connection between them.

In some of the experiments the onset of stupor and final development of the hibernating condition were associated with repeated brief increases in the amplitude and duration of the negative potentials (Fig. 2, F). Nevertheless when the cortical temperature fell to 14° (Fig. 2, G) then stupor was accompanied by an inevitable fall in the amplitude of the DP, by an increase in its duration, and by a disappearance of the positive oscillation. At temperatures below 11° we were unable to record any DP in the cortex of the hibernating animal.

The latent period of the DP increased from 1 to 9 mseconds (6-9 times) in proportion to the depth of the winter sleep ($P < 0.05$).

Thus the features of the local postsynaptic potentials of the apical dendrites which arise in response to direct cortical stimulation undergo consistent changes related to reduction of cortical temperature and to functional features of the brain occurring at different phases of the hibernating condition in mammals.

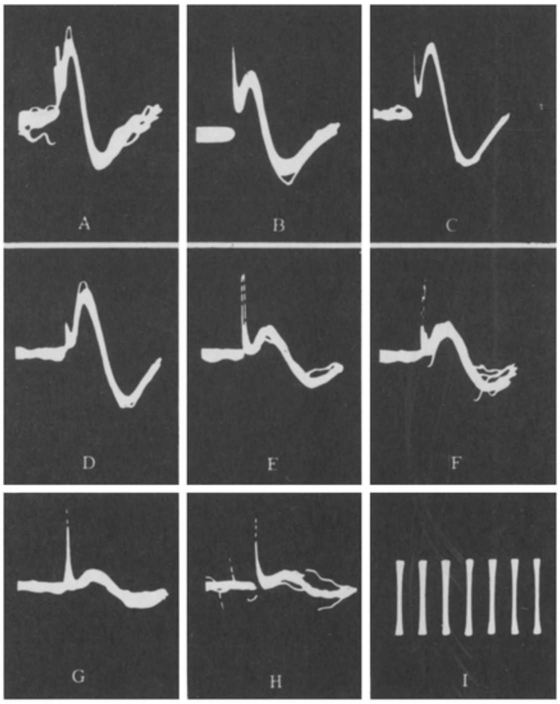

Fig. 2. Change of dendritic potentials in the cerebral cortex of a hedgehog during the development of stupor and the hibernating state. Records at a cortical temperature of: (A) 32, (B) 29, (C) 27, (D) 23, (E) 20, (F) 18, (G) 14, and (H) 12°. I) Calibration 250 μv; time marker 20 mseconds.

We must first of all note the high resistance of the apical dendrites in the cortex of the hibernating animals to low temperatures, a resistance which distinguishes them from the dendritic masses of the cortex of homiothermic animals. It is known that in the latter DP cannot be obtained at a cortical temperature below 22° [11].

Apparently this property of the apical dendrites is genetically established in hibernating animals and is subordinate to the direction of the functional properties of the cortex as a whole.

The absence of any marked positive component of the DP during profound stupor and at a low cortical temperature while the negative component is well maintained suggests that the cell bodies of the pyramids (whose local excitation is indicated by the positive oscillation of the DP which can be led off from the surface of the cortex) is unexcitable at cortical temperatures which permit local excitability of the apical dendrites.

SUMMARY

We have shown that the local postsynaptic potentials of the apical dendrites of pyramidal neurones are maintained at cortical temperatures down to 11°C during the development of the hibernating condition. In these conditions the excitability of the pyramidal cell-bodies is lost.

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