

in titrable acidity at night may be attributed to more accumulated starch during the day becoming converted into organic acids at night at the lowering of temperature^{4,5,16}.

The higher titrable acidity in young parts of both the plants showed higher concentration of organic acids in young parts than the old and confirms the findings of earlier workers^{4,6,17,18}. This could be due to the reason that the young parts were actively associated with the growth and respiration^{19,20}.

Zusammenfassung. Zwei Baumarten der ariden Zone zeigen den Crassulaceen-Säurestoffwechsel, obwohl sie keine Sukkulanten sind. Dieser Säurestoffwechsel hängt also von der Anpassung an gewisse Umweltfaktoren (Temperatur, Luftfeuchtigkeit) ab.

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Recovery Cycles of Primary Evoked Potentials in Cat Sensorimotor Cortex

Convincing evidence of recurrent collateral inhibition in sensorimotor cortex has recently been obtained by studying the inhibitory effects of antidromic pyramidal tract stimulation on pyramidal tract neurons^{1,2}. Presumably the effect would be exerted via inhibitory interneurons analogous to the Renshaw cells of the spinal cord³. However, it has not been possible to record from single cells in the cerebral cortex whose properties correspond to the Renshaw cell; that is, cells which are most active during the period of inhibition^{1,4}. This note demonstrates the presence, in the primary evoked response of sensorimotor cortex, of neural activity which may have been recorded from such interneurons.

For a study of the effects of sleep on evoked somatosensory activity, cats were prepared with chronic electrodes under pentobarbital anesthesia⁵. Stimulating electrodes in or adjacent to n. ventralis posterolateralis were placed stereotactically⁶ and their location later verified in Klüver-stained sections. The resulting evoked activity was recorded by small screws in skull overlying primary somatic cortex, displayed on an oscilloscope and photographed with a kymograph camera. The electroencephalogram, eye movements, and neck muscle activity were recorded electrographically to determine phase of sleep. Recording was begun several days postoperatively. Evoked activity relevant to the present study was large enough to measure adequately in 3 of 6 animals studied.

Figure A shows the evoked response recorded in these experiments. The various waves of the response are numbered following the convention used for the visual cortex response^{7,8}; several lines of evidence show that visual and somatic responses are equivalent^{6,9,10}. Figure C shows the recovery cycle of waves 2 and 4 when conditioning and test stimuli were given at the intervals shown. Wave 1, the afferent radiation volley, was fully recovered at an interval of 5 msec and showed no change in amplitude at longer intervals. Recovery of waves 3 and 5 was similar to that of wave 4. Wave 4 showed an early peak of recovery at 6 msec followed by a phase of inhibition lasting about 200 msec. The inhibitory phase was interrupted by a facilitory peak at 30–50 msec. The time course of inhibition was very similar to the recurrent

collateral inhibition of pyramidal tract cells^{1,2}, which also show a peak of facilitation at about 40 msec¹. Thus it is reasonable to assume that the inhibition shown in the Figure is due at least in part to recurrent collateral inhibition.

In contrast, an increased excitability of wave 2 mirrors fairly well the inhibition of wave 4 (Figure B, C). During waking (W) a maximal inhibition of wave 4 was associated with a maximal enhancement of wave 2; during 'slow wave' sleep (SS) and 'rapid' or 'rhombencephalic' sleep (RS) decreased inhibition of wave 4 was associated with decreased enhancement of wave 2. Furthermore, in test responses at a given interstimulus interval there was a good correlation between enhancement of wave 2 and depression of wave 4. Since wave 2 is maximally excitable during the period of maximal depression of waves 3–5, it is proposed that wave 2 is the summated activity of interneurons on the pathway for recurrent collateral inhibition.

The peak latency of wave 2 is about 1.0 msec, or about 0.6 msec after the arrival of the afferent volley. It is therefore probably evoked monosynaptically by the afferent volley. That the presumed interneurons on the recurrent pathway are activated monosynaptically by the radiation volley might be expected from the fact that the specific thalamic afferents end mainly among 'stellate' cells,

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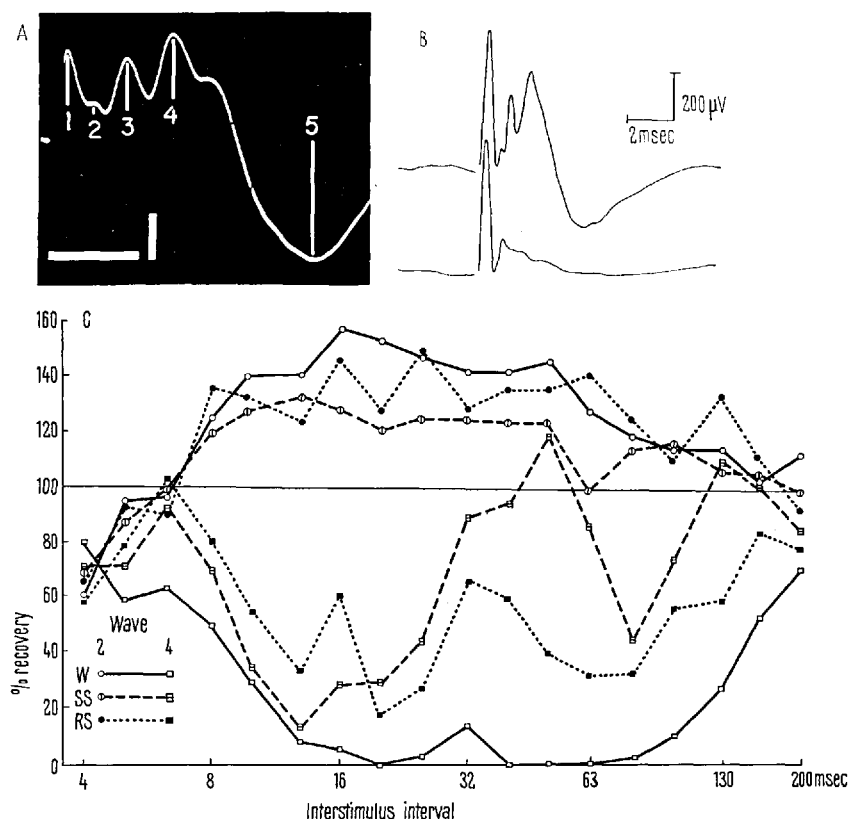
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(A) evoked potential in cat sensorimotor cortex (lateral postcruciate gyrus) to stimulation of thalamocortical afferents. Recording is monopolar, positivity upward. The various waves of the response are numbered and measured as shown. Calibrations: 2 msec, 0.2 mV. (B) conditioning (upper) and test responses at an interstimulus interval (40 msec) illustrating test response enhancement of wave 2 and almost complete suppression of waves 3-5. Conditioning and test stimuli were identical 0.1 msec pulses of submaximal intensity. (C) recovery cycle of waves 2 and 4, same experiment as in (B). Recovery is plotted as the ratio of test to conditioning response amplitude.

which are placed advantageously to receive axon collaterals of pyramidal cells^{11,12}.

The assumption that wave 2 represents postsynaptic activity of cortical elements is open to question. While some workers believe the response to be of postsynaptic origin, others regard it as an afferent volley of fibers smaller than those generating wave 1⁸. In addition to the evidence that wave 2 may be considerably modified by a conditioning stimulus (Figure), its amplitude was found to be significantly larger during SS than during W or RS¹³. These results suggest that wave 2 consists at least in part of postsynaptic activity of intracortical elements.

The results of the Figure have been observed in 2 other animals, but in most animals wave 2 is not large enough to measure adequately⁵. However, similar results have been reported for the visual cortex recovery cycle of waves 2 and 4⁷. These workers were cautious in interpreting the increase in wave 2 amplitude, concluding that it might be secondary to changes in wave 3. Wave 2 usually appears as an inflection or notch on the rising phase of wave 3 (Figure B) and might show an apparent increase secondary to increase of wave 3. But during recovery wave 2 increased concurrently with the decrease of wave 3 (Figure B, C). It may thus be concluded that the increase of wave 2 following a conditioning stimulus is a valid indicator of increased excitability in the neural elements generating the response.

On the basis of evoked response and anatomical evidence, BISHOP and CLARE¹⁴ concluded that wave 2 is due to activity of Golgi type II cells which ramify about the somas of pyramidal cells to produce excitation of the latter. The scheme proposed here is similar except that inhibition of pyramidal cells is assumed. Inhibition appears equally plausible in light of studies showing recurrent collateral inhibition by interneurons synapsing on the soma of the inhibited cell³.

The random orientation of Golgi type II cells may account for the small amplitude of wave 2¹⁴, while other data suggest that such cells are scanty¹¹. The latter finding might explain why activity from this population of cells has not been recorded with microelectrodes^{1,4,15}.

Résumé. Quoiqu'une inhibition récurrente se présente dans le cortex sensorimoteur du chat, il n'a pas été possible d'enregistrer l'activité unitaire des neurones intercalaires de la voie récurrente. Dans les expériences décrites ici, l'onde 2 du potentiel somatique primaire évoqué par la stimulation des fibres thalamo-corticales, montrait un accroissement marqué après stimulation conditionnante; simultanément il se produisait une inhibition des ondes tardives du potentiel. Donc l'onde 2 peut être due aux neurones intercalaires inhibiteurs activés durant la phase d'inhibition.

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