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Short communication

HIPPOCAMPAL THETA ACTIVITY IN THE ACUTE CERVEAU ISOLÉ CAT

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Abstract. In three cerveau isolé cats, cortical and hippocampal EEG activity were recorded. In the cortical records, spindles alternated with low-voltage activity, whereas theta activity dominated in the hippocampus. The amount and frequency of theta were similar to those described previously for the pretrigeminal cat. In confirmation of previous results on rats, although cortical EEG activity differs in cerveau isolé cat and pretrigeminal cat, both preparations show domination of theta activity in the hippocampus. It is concluded that the mesencephalic transection eliminates inhibitory effects from the lower brainstem on generators of the theta rhythm.

We found previously (3, 15) that although acute cerveau isolé rat and pretrigeminal rat have different cortical EEG activity, they both show almost permanent theta activity in the hippocampus. We also found (11) that theta activity dominates in the hippocampus of the acute pretrigeminal cat. Such domination was also shown by Olmstead and Villablanca (10) in the chronic cerveau isolé cat. They reported that hippocampal theta activity was present one day after surgery (after recovery of the animal from the pentobarbital anesthesia) but in

their figures hippocampal theta was always associated with periods of cortical EEG desynchronization, which are frequently observed in the chronic cerveau isolé cat (13). However, the figure published in Tokizane's review (14) indicated that EEG synchronization and hippocampal theta can exist simultaneously in the acute cerveau isolé cat. The problem of hippocampal theta activity in the acute cerveau isolé cat is further analyzed in the present paper.

Reliable information was obtained from three experiments. The brainstem was transected under fluothan anesthesia (cats 1 and 2), or ether anesthesia (cat 3). The anterior part of the cerebellum was removed to visualize the inferior colliculi. A thin Z-shaped spatula was inserted just behind the tentorium (see 13). During the transection, the spatula was guided by a plate attached to a holder at an angle 25° from the vertical plane. Just after the transection the narcosis was terminated. Anatomical verification showed that in all cases the transection was complete (except the lateral part of the left inferior colliculus in cat 2), and passed dorsally through the middle of inferior colliculi and ventrally through the border between the pons and midbrain. Thus, the preparations can be referred to as low cerveau isolé (9). Two pairs of silver ball electrodes were placed on the dura mater in the right frontal and occipital areas. Multipolar electrodes were placed in the left and right dorsal hippocampus. In cats 2 and 3, the electrodes were implanted just after the brainstem transection, whereas in cat 1 they were implanted a week before the transection (chronic animal). In all cats, the recording began about 1 h after the transection and lasted about 5 h. After surgery the cats received subcutaneously 10–20 ml of isotonic glucose solution. The body temperature was maintained at 38°C.

The pupils of all preparations were fissurated. In the cortical EEG records, spindles alternated with low-voltage activity (Fig. 1). The size of the spindles and duration of the interspindle lulls varied somewhat during the experiment. In the hippocampal EEG records, theta activity was abundant (Fig. 1). In cats 1 and 2 clearcut theta occuppied about 40–80% of time and in cat 3 about 70–80%. In the episodes of time when cortical EEG activity was more desynchronized, the amount and regularity of theta activity was usually increased. The theta activity had a monotonous character and its frequency was about 4 cycle/s (Table I). The frequency of theta did not vary significantly during the experiment.

In cat 1, waves frequency of the hippocampal theta recorded chronically before the transection was somewhat more fast than postoperatively. Mean values were 4.4 cycle/s during spindles in the cortex and 4.8

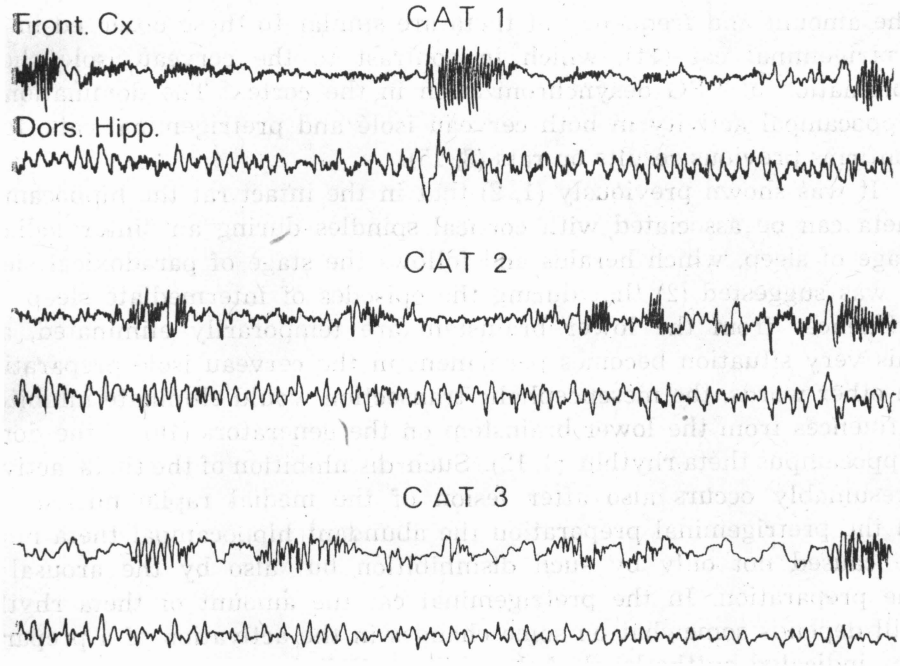

Fig. 1. EEG records showing theta activity in the hippocampus when fully developed spindles were present in the cortex. Calibration: 1s, 100 μV.

cycle/s during episodes of paradoxical sleep. In an additional cat, which was recorded chronically preoperatively but then was rejected because of an inadequate brainstem transection, mean values of theta frequency were 5.2 and 4.5 cycle/s during spindles and paradoxical sleep, respectively. The hippocampal theta activity recorded on intact cats by others authors (5, 7) also seems to be somewhat more frequent than in our transected preparations. However, Olmstead and Villablanca (10) reported a similar frequency for theta before and after high mesencephalic transection. On the other hand, we found previously (3, 15) that in the cerveau isolé and pretrigeminal rats, the frequency of theta activity was somewhat lower than in intact rat. Thus, the brainstem transection usually seems to produce a moderate lowering of the hippocampal theta frequency.

TABLE I

Frequency of hippocampal theta activity. In each cat ten scores were taken when cortical EEG records showed fully developed spindles.

Cat	Frequency (c/s): mean ± SD
1	3.5±0.36
2	3.9±0.32
3	4.6±0.46

Our results clearly show that during the acute stage of the low cerveau isolé cat the hippocampal EEG is dominated by theta rhythm.

The amount and frequency of theta are similar to those observed in the pretrigeminal cat (11), which in contrast to the cerveau isolé shows domination of EEG desynchronization in the cortex. The domination of hippocampal activity in both cerveau isolé and pretrigeminal cats, fully confirms previous results on rats (3, 15).

It was shown previously (1, 2) that in the intact rat the hippocampal theta can be associated with cortical spindles during an "intermediate" stage of sleep, which heralds and follows the stage of paradoxical sleep. It was suggested (2) that during the episodes of intermediate sleep, the influences from the lower brainstem are temporarily eliminated, and this very situation becomes permanent in the cerveau isolé preparation. In other words, the mesencephalic transection would eliminate inhibitory influences from the lower brainstem on the generators (16) of the dorsal hippocampus theta rhythm (4, 12). Such disinhibition of the theta activity presumably occurs also after lesion of the medial raphe nucleus (8). In the pretrigeminal preparation the abundant hippocampal theta might be caused not only by such disinhibition but also by the arousal of the preparation. In the pretrigeminal cat the amount of theta rhythm still depends somewhat on some changes in the activation of a preparation, indicated by the level of the cortical EEG desynchronization (see 11), and the same was true in our cerveau isolé cats. Thus, the inhibitory influence of the lower brainstem on the hippocampal theta should be destinguished from the synchronizing influence on the cortical EEG activity.

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