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# The rhythmic slow activity recorded from entorhinal cortex in freely moving cats

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**Abstract**. The relationships between the entorhinal cortex (EC) and the hippocampal formation (Hipp) field potentials were examined in the present study. The detailed analyses of the signal let us group the patterns of theta appearance into three categories: (1) Theta rhythm dominating in both recordings from the EC and from the Hipp (2) Theta rhythm dominating in the Hipp with irregular activity in the EC (3) Theta rhythm dominating in the EC with irregular activity in the Hipp. These findings provide the evidence for the intrinsic generator of theta rhythm to be localized in entorhinal cortex in cats.

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## INTRODUCTION

The best synchronized bioelectrical activity that can be recorded from the mammalian brain is theta rhythm (RSA, rhythmic slow activity). It is high voltage, very regular, almost sinusoidal waveform. The hippocampal formation (Hipp) is considered to be the main structure involved in generation of this activity (Bland 1986, Bland and Colom 1993). It has been well supported in many *in vivo* and *in vitro* experiments conducted on both rodents and cats that there are three regions in the Hipp capable of independent generating of the theta rhythm. The three hippocampal generators are CA1 and CA3c regions of the hippocampus proper, and dental gyrus (Bland 1986, Konopacki et al. 1987, Konopacki at al. 1988).

The main sources of afferents to the hippocampal formation are medial septum (MS), the ventral part of diagonal band of Broca (vDBB) and the entorhinal cortex (EC). The role of MS/vDBB as a pace-maker of the hippocampal theta rhythm was well proved (Petsche et al. 1962, 1965). The second important source of an afferent input to the Hipp comes from the EC, *via* the perforant path (Boeijinga and Lopes da Silva 1988, Witter et al. 1989, Lingenhohl and Finch 1991, Jones 1993). The EC is also strongly connected with the Hipp *via* projections from the hippocampus proper (Boeijinga and Lopes da Silva 1988, Witter et al. 1989, Lingenhohl and Finch 1991, Jones 1993). The medial EC was postulated to be involved in generating of the hippocampal theta (Montoya and Sainsbury 1985, Stewart et al. 1992). It was proved that the medial EC itself is also capable of generating theta rhythm in the rat (Mitchell and Ranck 1980). The results obtained in the *in vivo* experiments were supported by *in vitro* findings that completly deafferented EC is capable of generating RSA during cholinergic perfusion (Konopacki et al. 1992).

In contrast to the hippocampal theta, the rhythmic slow activity in the entorhinal cortex *in vivo* was not so intensively examined. In addition, most of the studies concerning the physiology and pharmacology of the EC theta rhythm were mostly conducted on rodents (rats, rabbits). There are a few experiments with use of the cat *in vivo*, revealing that it is possible to record theta activity from the EC approximately in phase with CA1 theta rhythm (Alonso and Garcia-Austt 1987).

The aim of the present study was to characterize the spontaneous theta rhythm recorded from the EC in freely moving cats and to compare it with a rhythm recorded from the Hipp simultaneously.

## METHODS

Sixteen adult cats were used in the present study. The cats, weighing 2.5 to 3.5 kg, were operated under a hexobarbital anaesthesia. Recording electrodes were placed stereotaxically in several positions in EC region, Fr = 4 - 5, L = 10 - 12, H = -6, as well as in the Hipp, Fr = 4, L = 6, H = 7 (Jasper and Ajmone-Marsan 1954). Additionally, an indifferent electrode was implanted in the frontal cortex. The electrodes were made of a stainless steel wire coated with teflon, removed on a tip to the length of 0.5 mm.

Two weeks after the operation the experiments started. The EEG activity of the two brain structures in freely moving cats was recorded. The animal was connected by a shielded cables to the amplifier. Then the EEG signal was secondary amplified, filtered and stored with use of the computer system (software for data acquisition and analysing - Spike 2, Cambridge Electronic Design Ltd., England). Spontaneous EEG activity from the Hipp and EC was always recorded simultaneously, during 30 min recording. The evaluation of amplitude and frequency and cross-correlation analyses between these two signals were performed. To estimate the dominant frequency of the recorded signal, we used Fast Fourier Transform analysis.

## RESULTS

In all the tested animals the spontaneous theta rhythm was never observed to occur continuously. Typically, the trains of theta rhythm were separated by the periods of irregular activity. Depending on

the individual differences between the animals theta rhythm was observed in 10 to 80 % of all the recording time. In the present study, the rhythm observed in the EC was found to be of similar frequency and amplitude as the hippocampal theta. It ranged from 3.3 to 6.5 Hz, and from 100 to 600 mV, respectively.

The obtained recordings let us group patterns of theta occurrence into three categories. (1) Theta rhythm dominating both in the EC and the Hipp (Fig. 1A). (2) Theta rhythm dominating in the EC with irregular activity in the Hipp (Fig. 1B) This pattern was rarely observed (in not more than 5 % of the recorded samples). (3) Theta rhythm dominating in the Hipp with irregular activity in the EC (Fig. 1C). This pattern occurred approximately in 20 % of the recorded samples.

## DISCUSSION

The main finding of the present study was a demonstration that theta field potential can be simultaneously recorded from the entorhinal cortex and hippocampal formation as a very well synchronized EEG signal. This observation would support the earlier suggestions that EC theta rhythm in the cat may be relayed from the subicular region of the hippocampal formation (Alonso and Garcia-Austt 1987, Boeijinga and Lopes da Silva 1988). How-

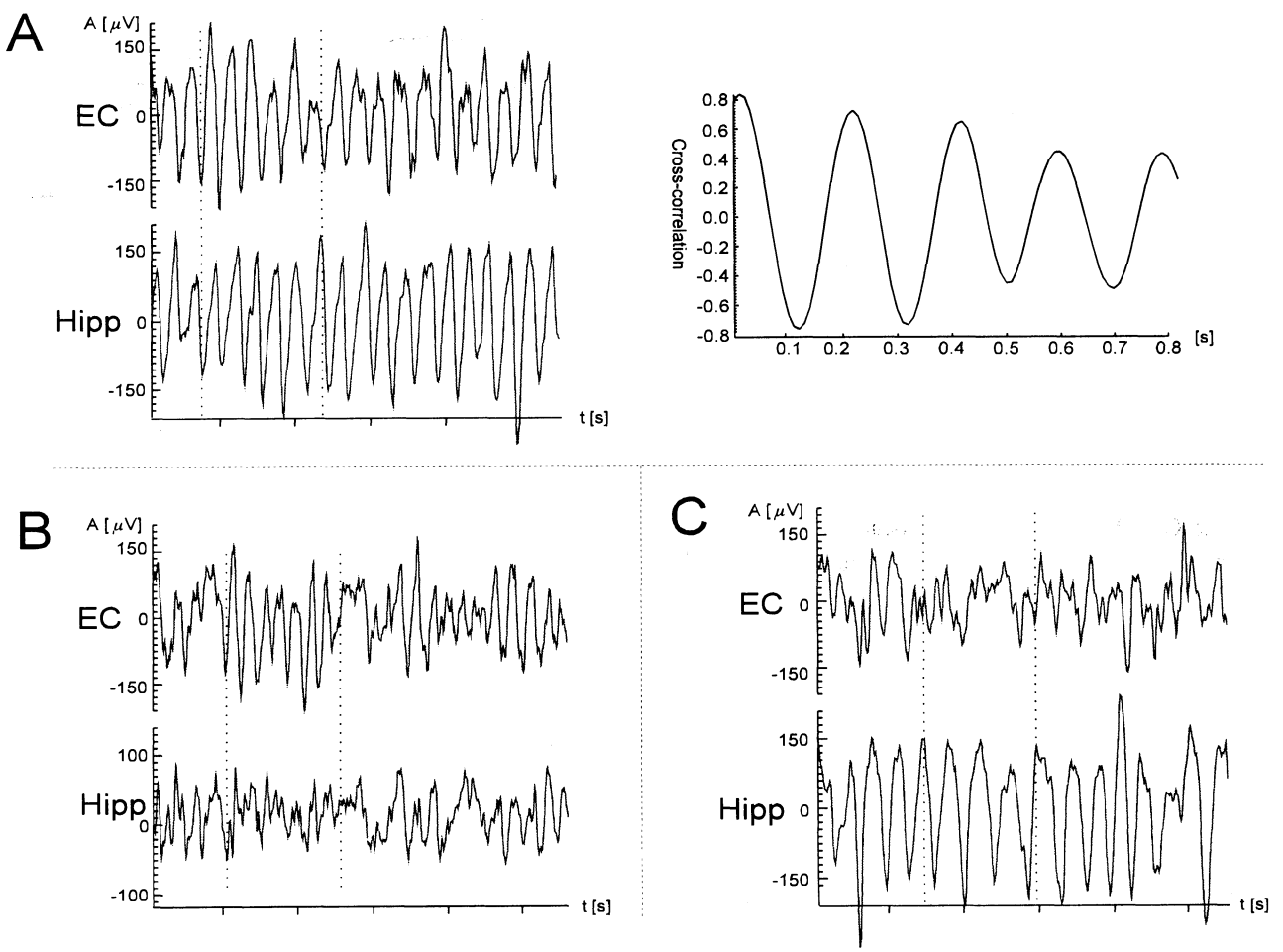


Fig. 1. The samples of EEG traces recorded simultaneously from the entorhinal cortex (EC) and hippocampal formation (Hipp) in freely behaving cats. A, when theta rhythms were observed both in the EC and Hipp (left), cross-correlation analysis revealed high synchronization of these two EEG signals (right). Please note, that the rhythms recorded from EC and Hipp were in phase. B and C, both EC and Hipp theta rhythms could be recorded independently of each other.

ever, a detailed analysis of the field potential recorded simultaneously from the EC and Hipp revealed that theta rhythm can also be present in the EC area even when Hipp field potential was completely desynchronized. This observation strongly supports our earlier *in vitro* findings (Konopacki et al. 1992, Gołębiewski et al. 1994) and provides the evidence for existence of independent intrinsic generator of theta rhythm in the entothinal cortex.

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