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# INFLUENCE OF NUCLEUS CENTRALIS MEDIALIS OF THALAMUS ON THE INFORMATION PROCESSING IN THE LATERAL GENICULATE BODY OF FREELY MOVING RAT

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The specific sensory relay nuclei of the thalamus can respond to single sensory stimuli with a rhythm of a relative constant frequency (Bartley and Bishop 1933, Bishop and O'Leary 1936, Kimura 1962, Andersen and Eccles 1962, Pickenhain and Klingberg 1965, Aitkin and Dunlop 1969). The rhythm appears both in the thalamic relay nucleus and in its cortical projection area. These rhythms can also be triggered by single electrical shocks to the relay nuclei (Dempsey and Morison 1963), and are identical in form, frequency and cortical localization with the sensory evoked afterdischarges (Kohler and Klingberg 1969). This typical response to electrical stimulation of the lateral geniculate body (LGB) remains after enucleation of both eyes (Kohler and Klingberg 1970). The main generator mechanism of the rhythmical response is lateral or recurrent inhibition and postinhibitory reexcitation (Andersen and Eccles 1962, Andersen et al. 1964, Burke and Sefton 1966*abc*, Aitkin and Dunlop 1969, Theil and Klingberg 1970).

The authors investigated a number of conditions necessary for the appearance of the so-called photically evoked afterdischarges (PhAD) in rat, especially their dependance on different stages of behavioral activation and concluded that the regulation of the degree of synchronization in the relay nucleus plays an important role in information processing (Pickenhain and Klingberg 1969, Klingberg and Pickenhain 1969, Kohler and Klingberg 1970).

Since PhAD of the LGB may be modulated by brain stem reticular

activation (Kimura 1962, Satinsky 1968, Theil et al. 1972) we wanted to ascertain if the unspecific thalamic nuclei participate in the modulation of PhAD.

## MATERIAL AND METHODS

The experiments were performed on eight freely moving rats weighing 250–300 g with chronic electrodes in the lateral geniculate body (LGB), visual cortex (VC, area 17), dorsal hippocampus (DH), a frontal medial electrode and pairs of electrodes in the nucleus centralis medialis (NCM of the thalamus: AP 2.0 to 2.5, lateral 0.5 left and right, vertical 6.0 according to the atlas of Fifková and Marśala (1967). After completion of the experiments the coordinates of electrodes were histologically checked (Nissl-staining).

Since the appearance of photically evoked afterdischarges (PhAD) is dependent on the stage of wakefulness (Pickenhain and Klingberg 1969, Klingberg 1970*a*) vigilance changes were controlled by the electrical activity of the olfactory bulb (respiration rate), DH and by movement registration (Szabó et al. 1965). The analysis of the responses was related to the stage of relaxed wakefulness which was reached by shortlasting habituation. The responses in the LGB and VC to single electrical stimuli lasting 0.1 msec applied to NCM were recorded by means of a polygraphic technics, oscilloscope monitoring and in some cases automatical average technics by the computer NTA 512 B (KFKI Budapest). Responses to light flashes were modulated by a series of stimuli applied to the NCM (250 imp/sec, 0.1 msec, 0.5-3.0 v, 1.5 sec series duration). The stimulation was repeated automatically at intervals of 10 sec in different combinations with light flashes.

## RESULTS

A single electric pulse in the NCM evoked rhythmical responses in the LGB and in the VC. These rhythms are identical with photically evoked afterdischarges (PhAD) in their form, frequency and localization. Threshold intensity was 4.3 $\pm$ 1.4 v ($\bar{x} \pm$ SD). Figure 1 demonstrates this type of response evoked by a 6 v single pulse in the NCM, accompanied by behavioral inhibition. The probability of triggering such a rhythmical response increases with habituation, relaxation or behavioral inhibition and with increasing stimulus intensities. It exceeds 30% of the responses during relaxed wakefulness, when 6 v pulses are used. Stronger stimuli evoked additionally more and more spindle groups in frontal cortical areas. Suppression of the thalamically evoked rhythmical

response occurred at a lower level of behavioral activation than the suppression of the PhAD.

Using optimal stimulus intervals lasting 4 sec the usual averaging

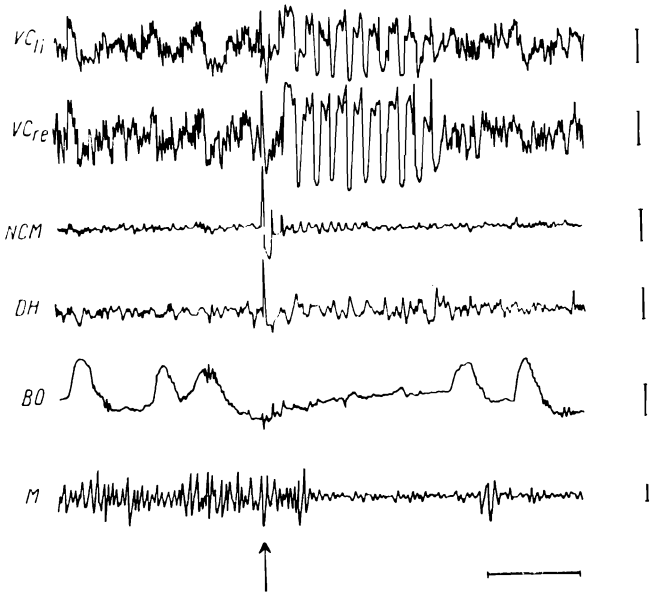


Fig. 1. Rhythmical afterdischarges in the VC triggered by a single pulse (6 v, 0.1 msec; arrow) in the nuleus centralis medialis of the thalamus, accompanied by behavioral inhibition (decrease of respiration rate and motor activity). $VC_{li}$, visual cortex left; $VC_{re}$, visual cortex right; NCM, nucleus centralis medialis of thalamus; DH, dorsal hippocampus; BO, bulbus olfactorius (respiration rate); M, motor activity (movement). Calibration: horizontal, 1 sec; vertical, 200 $\mu$v.

technics are not quite comfortable because in the freely moving rat the level of behavioral activity does not remain constant. The repetition of single thalamic stimuli favors the occurrance of sleep. Example *A* in Fig. 2 was taken from a slightly activated state, example *B* from superficial sleep, each representing 40 averaged potentials, successively evoked by 6 v NCM stimuli. The optimal conditions for triggering typical rhythmic responses are between these two states. The primary potentials have shorter latencies and peak-times in the LGB than those in the VC.

Electrical stimulation of NCM with series of 250 imp./sec, 0.1 msec impulse duration and 2 v intensity applied during 1.5 sec caused a partial or complete suppression of PhAD in the LGB and VC. Figure 3 shows this effect during NCM stimulation. This stimulation causes no signs

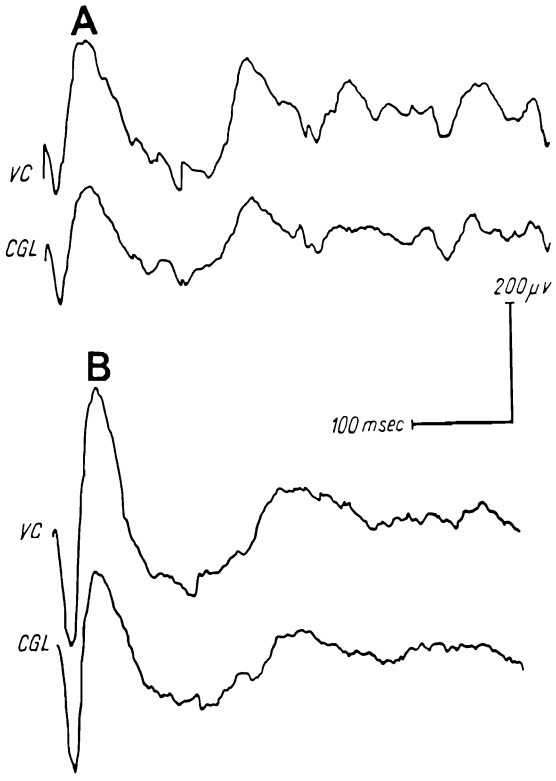


Fig. 2. Averaged responses ($n$ = 40) in the VC and lateral geniculate body (CGL) evoked by a single pulse (6 v, 0.1 msec) to the nucleus centralis medialis of the thalamus. *A*, during slightly activated behavior; *B*, during light sleep.

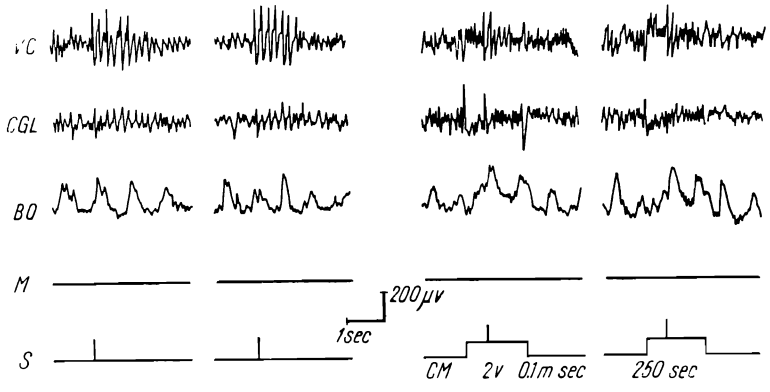


Fig. 3. Photically evoked responses in the VC and lateral geniculate body (CGL) uninfluenced (left) and during high frequency stimulation of the NCM (right). Slow speed registration. *S*, stimuli; vertical bars, light flashes; base line shift upward, stimulation of the NCM. Other abbreviations as in Fig. 1.

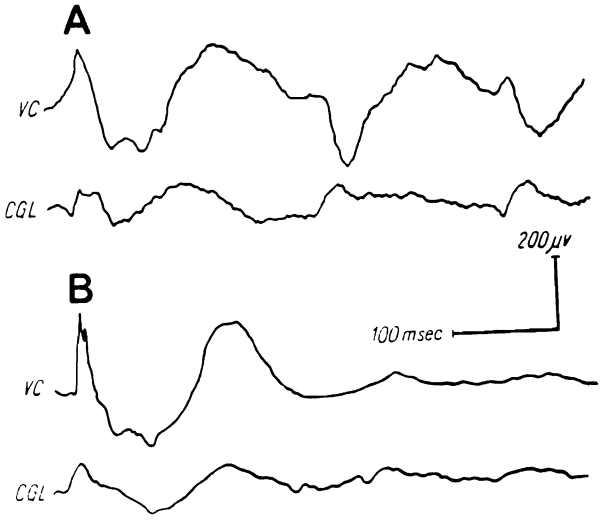


Fig. 4. Averaged responses ($n$ = 40) in the VC and lateral geniculate body (CGL) evoked by light flashes. *A*, uninfluenced; *B*, during stimulation of the NCM (250 imp/sec, 0.1 msec pulse duration, 2 v intensity, 1.5 sec series duration; light flash stimulation 0.5 sec after the onset of NCM stimulation).

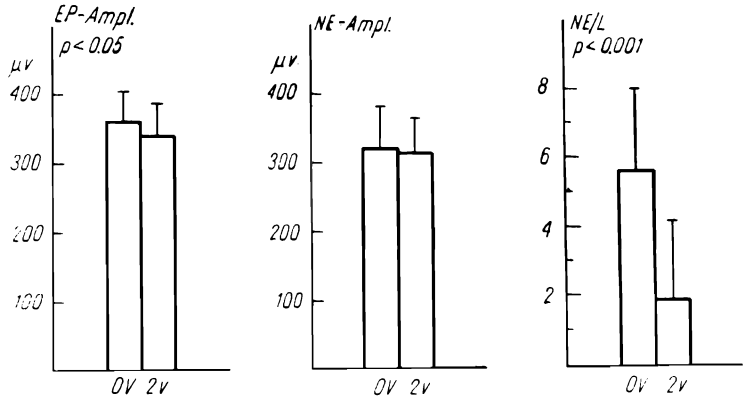


Fig. 5. Mean values and standard deviations of the amplitudes of photically evoked potentials (EP-Ampl.) and afterdischarges (NE-Ampl.) and of the number of PhADs per light flash (NE/L) uninfluenced (OV) and during high frequency NCM stimulation (2 v intensity, 250 imp/sec, 0.1 msec pulse duration, 1.5 series duration; light flash stimulation 0.5 sec after the onset of NCM stimulation). Amplitudes were measured from peak to peak ($n_1$–$p_3$); data from three rats in which 100 light flashes were applied at 10 sec intervals.

of behavioral activation in contradistinction to stimulation of the brainstem reticular formation. The suppression of PhAD occurred only during the high frequency stimulation of the NCM, but not during the

10 sec intervals. On the other hand posttetanic facilitation of the responses was not observed. Higher intensities produced also some changes during this interval, but then involvement of neighbouring structures could not be excluded. The result of averaging 40 flash-evoked potentials without and during high frequency 2 v NCM stimulation is demonstrated in Fig. 4. Latencies and peak-times of the primary components become shorter, the following positive component lasts longer and the PhADs are suppressed. The changes are evident both in the VC and the LGB.

Statistical analysis of responses in VC before and during such a stimulation shows a very little effect on the amplitude, but causes a great decrease in the number of PhADs (Fig. 5).

## DISCUSSION

The present results demonstrate a direct influence of the NCM on the specific thalamic relay nucleus (LGB). This is evidenced by short latency evoked potentials which occur earlier in the LGB than in the VC, when NCM is stimulated. As a consequence of activating directly LGB neurons by NCM stimulation rhythmical afterdischarges appear which are identical with PhAD in frequency, localization and potential form dependent on the stage of wakefulness. The evocation of primary potentials and afterdischarges in our experiment could not be explained by the current spread to the LGB, this was shown by control experiments in which the authors stimulated the nucleus reticularis of the thalamus (R), the nucleus medialis dorsalis (MD), or the zona incerta (ZI). Single stimuli in the R, MD and ZI up to 10 v did not trigger evoked potentials or afterdischarges in the VC although the electrodes were localized nearer to the LGB. The existence of intrathalamic pathways connecting the medial and lateral or ventral groups of thalamic nuclei was established by intracellular recordings (Purpura et al. 1965, Maekawa and Purpura 1967, Desiraju and Purpura 1970), and morphological studies (Nauta and Whitlock 1954, Totibadze and Moniava 1969, Miodoński 1970). Some of the fibers originating in the NCM reach the LGB (Nauta and Whitlock 1954, Totibadze and Moniava 1969), others may be connected to the LGB by a second neuron in the lateral or ventral nuclei. Crighel and Gasanov (1969) observed close relationships between lateral associative nuclei and specific nuclei (LGB, medial geniculate body and ventralis posterolateralis). Some of the reactions of the visual cortical neurons responding to single thalamic stimuli reported by Akimoto and Creutzfeldt (1958) may be mediated through the specific thalamic relay nucleus. It is possible to suppress PhAD by series of frequent stimulations from the same

points in the NCM from which EP and afterdischarges in the LGB and VC can be triggered. According to Okuda (1962) the effects of electric stimulation in some thalamic nuclei are interpreted as a simple continuation of the activating influence of the brain stem reticular formation. From our results, however, it may be concluded that a suppression of PhAD by stimulation of the NCM and of the mesencephalic reticular formation are not identical. High frequency stimulation of the NCM suppresses PhAD without a concomitant behavioral activation and has no posttetanic influence (in agreement with Hösli and Monnier 1963), whereas the same stimulation of the mesencephalic reticular formation is suppressive only when theta-activity in the DH is evoked, the respiration rate is enhanced and the motor behavior is activated (Theil et al. 1971). Moreover, the reticular activation outlasts the stimulus series for more than 5 sec. Thus we agree with the conclusion of Durinian (1968) that the unspecific thalamic nuclei have their own functional qualities and exert their influences on the information processing depending on the anatomical connections with the specific nuclei.

It is questionable, whether the duality of effects depends on the existence of two antagonizing systems like a moderating and an activating system in the medial thalamus (Monnier et al. 1963). The synchronized thalamic rhythms consist of a sequence of synchronized EPSP and IPSP and may be overcome if the excitatory drive (input) exceeds the inhibitory influence (Vastola 1959*ab*, Purpura and Shofer 1963, Purpura et al. 1966*ab*). This could be shown also in a mathematical model of the processes which are responsible for generating rhythms in the thalamic relay nuclei (Theil and Klingberg 1970, S. Theil and F. Klingberg, in preparation). The origin of the excitatory input may be different. As the intrathalamic pathways originating in the midline nuclei evoke sequences of EPSP-IPSP in specific thalamic relay neurons (Purpura et al. 1965, Purpura et al. 1966*a*) single pulses in the NCM can trigger EP and afterdischarges in the LGB and VC. The rhythm in the LGB is partially maintained by postanodal exaltation of the projective cells (Burke and Sefton 1966*c*). The excitatory drive can partially overcome the IPSP when series of high frequency stimulation (250/sec) in the NCM are used. Then PhAD may be suppressed. An alternative or additional possibility for suppression of the rhythms may be the inhibition of inhibitory interneurons which is suggested to be a function of the ascending reticular formation (Purpura et al. 1966*ab*, Fukuda and Iwama 1970). This hypothesis does not explain, however, the triggering of afterdischarges by single stimuli.

From our results and discussion it may be concluded that transmission in the LGB is modulated by nonspecific thalamic nuclei. Together with

the reticular activating system they regulate the degree of synchronization of neuron groups in specific thalamic relay nuclei, acting thus as a gating mechanism. If synchronization exceeds a certain level information processing is impaired as it can be shown in conditioning experiments (Klingberg 1970*b*). On the other hand, a certain degree of synchronization seems to be necessary to avoid information overflow and to regulate information input (channel selection).

## SUMMARY

1. Freely moving rats with chronic electrodes in the LGB, VC (area 17), DH, frontal cortex and NCM were used to investigate the influence of NCM on the information processing in the LGB.

2. Single pulses in the NCM elicited EP and afterdischarges in the LGB and VC depending on the level of wakefulness. The responses in the LGB proceded those in the VC.

3. High frequency stimulation of the NCM (250 imp/sec) suppressed PhADs in the LGB and VC without concomitant behavioral activation and had no longlasting after-effect.

4. It is concluded that nonspecific thalamic nuclei participate in the regulation of the degree of synchronization of specific thalamic nuclei, thus acting as a gating mechanism on the information processing (channel selection).

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