

Evoked potentials recorded from the somatosensory area I (SI) and II (SII) on stimulation of the contralateral deep radial nerve. The potentials were simultaneously recorded on a fast (left traces) and slow time base. The inset records (upper left traces) show, on the fast time base, the primary afferent volley triphasically recorded from the dorsal funiculus at the C3 level immediately after the cortical recording. Arrow in C indicates initial positivity signalling incoming volley. Stimulus strength in multiples of nerve threshold is indicated on each set of records. Positivity is signalled upwards. Voltage scale applies to cortical potentials (right traces). Superposed sweeps.

and thalamic relay comparable to that found at the group I relays to the cerebellar tracts in Clarke's column³ and the external cuneate nucleus⁴. The finding that the whole threshold range of group I afferents, including afferents of the lowest threshold, contributed to the evoked potential suggests that afferents from muscle stretch receptors are responsible.

Zusammenfassung. Bei Reizung der Gruppe I afferenter Fasern der Muskelnerven des Vorderbeins erhält man positive Potentiale mit kurzer Latenz in der somatischen Area I der Grosshirnrinde. Die somatische Area II bleibt

reaktionslos. Die Leitung läuft über das System, Funiculus dorsalis–Lemniscus medialis.

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³ A. K. MCINTYRE, Abstr. XIX Internat. Physiol. Congr. (1953), p. 107. – B. HOLMQVIST, A. LUNDBERG, and O. OSCARSSON, *Acta physiol. scand.* **38**, 76 (1956). – A. K. MCINTYRE and R. F. MARK, *J. Physiol. (Lond.)* **153**, 306 (1960).

⁴ B. HOLMQVIST, O. OSCARSSON, and I. ROSÉN, *Acta physiol. scand.*, in press.

Influence of the Caudate Nucleus on Hippocampal Afterdischarges in the Rabbit

The nucleus caudatus inhibits many cortical and subcortical responses^{1,2}. In a few cases, however, caudate stimulation in the cat produced motor effects such as head turning, licking, sniffing, swallowing and other autonomic reflexes^{3,4}. Stimulation of this nucleus may also facilitate a response evoked from another part of the brain, such as vestibular nystagmus⁵.

As a new, striking example of such facilitatory action, we describe here the enhancement of hippocampal after-

discharge (HA). This effect is especially clear, when compared with the influence of caudate stimulation on the resting hippocampus (Figure 1). In the latter, caudate

¹ F. A. METTLER, H. W. ADES, E. LIPMAN, and E. A. CULLER, *Arch. Neurol. Psychiat.* **41**, 984 (1939).

² F. A. METTLER and C. C. METTLER, *Brain* **65**, 242 (1942).

³ D. FORMAN and J. W. WARD, *J. Neurophysiol.* **20**, 230 (1957).

⁴ N. A. BUCHWALD and F. R. ERWIN, *Electroenceph. clin. Neurophysiol.* **9**, 477 (1957).

⁵ A. SCHEIBEL, C. MARKHAM, and R. KOEGLER, *Neurology* **11**, 1055 (1961).

stimulation produces synchronization, the potentials exhibiting a frequency of 4–7/sec (Figure 1B). This phenomenon is especially prominent in subcortical structures such as the dorsal hippocampus (lead b) and the reticular formation (lead c), but may also find an expression in cortical recordings (lead a). Cortical arousal was never observed.

If the dorsal hippocampus is stimulated first for periods of 5–10 sec and caudate stimulation applied immediately afterwards, marked prolongation and enhancement of the HA results (Figure 2, B–D). However, the HA cannot be maintained indefinitely by continued caudate stimulation. In the experiment of Figure 2, the HA dies out after about 60 sec, although excitation of the caudate nucleus was not interrupted. This observation suggests that caudate stimulation can enhance but not initiate HA, in agreement with the observations on resting hippocampus (see Figure 1). The EEG samples shown in Figure 2, B–D, are similar to the discharges, characteristic for stimulation of the hippocampus alone (Figure 2A). However, the higher frequencies of discharge, when activated by impulses from the caudate nucleus, cause closer spacing, thus producing the picture of a uniform, repetitive firing at 12–14/sec (Figure 2C). It was also observed that when the HA tended to decrease, continued caudate stimulation could sometimes reactivate it and evoke a second discharge period, during which again a frequency level could be reached, similar to the one shown in Figure 2C.

Ipsi- or contralateral caudate stimulation give qualitatively identical results on the HA. This enhancement is

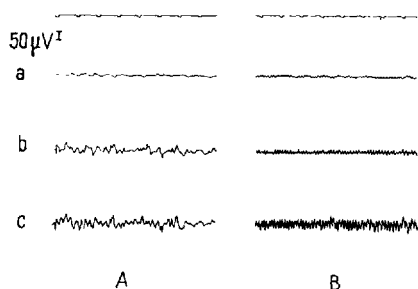


Fig. 1. Effect of nucleus caudatus on resting hippocampus; (A) recordings before, (B) during caudate stimulation. Stimulation at right caudate nucleus, 11 mm below surface of the skull, at 8 V, 200 cy/sec; stimulus duration, 1 msec. Time in sec (on top of record); (a) right sensory cortex; (b) right dorsal hippocampus; (c) right mesencephalic reticular formation. Frequency of synchronized potentials 7/sec.

Responsiveness and Discrimination during Sleep

Experiments were performed to evaluate the ability of sleeping subjects to discriminate between different pitches. For this purpose cats were trained during the wakeful period as follows: a tone of a given (e.g. 5 Kcps) pitch referred to as 'positive' was reinforced in an either classical or instrumental conditioning routine such that the former involved unavoidable unconditioned excitation to mesencephalic central gray matter¹ and the latter avoidable unconditioned excitation to skin; tones of other (e.g. 5.1–12.5 Kcps) pitches referred to as 'negative' were never reinforced. The effectiveness of each pitch was judged by its capacity to produce an EEG 'activation' of

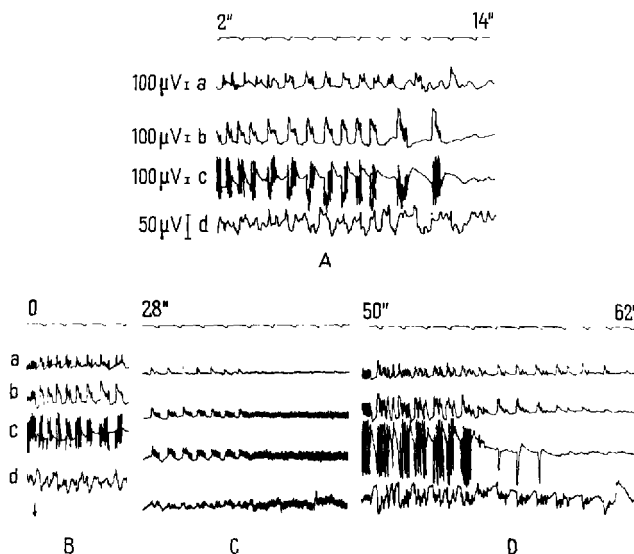


Fig. 2. Influence of nucleus caudatus on hippocampal afterdischarge (HA), produced by stimulation of dorsal hippocampus. Right nucleus caudatus stimulated 10 mm below surface of the skull, at 6 V, 200 cy/sec, 1 msec. Right dorsal hippocampus stimulated at 0.6 V, 40 cy/sec, 2 msec. Time in sec (on top); (a) right motor cortex; (b) right dorsal hippocampus; (c) left dorsal hippocampus; (d) right mesencephalic reticular formation. (A) hippocampus stimulated alone; (B)–(D) hippocampus stimulated first for 10 sec. Thereafter (at arrow ↓), caudate stimulation started. HA prolonged for about 60 sec. Note in C transformation of HA into a fast, homogeneous rhythm of 13/sec.

a specific effect: Placement of the electrodes on the borders around the caudate nucleus had no influence on HA, with the exception of the putamen and the globus pallidus. Interaction of the latter with the HA will be reported separately.

Résumé. La stimulation du noyau caudé augmente et prolonge la postdécharge hippocampale chez le lapin.

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the somatic sensory cortex and a behavioral conditioned response.

After a brief period of generalization, differentiation of 'negative' pitches was achieved in a staggered sequence in which frequency values closer to the 'positive' one were differentiated later; eventually, tone effectiveness stabilized, showing a maximum value at the 'positive' pitch and decreasing as frequency separation from the latter in-

¹ Previous experiments have shown that tones that were reinforced in this manner evoked a conditioned response and awakened the sleeping cat (D. RODGERS, N. BUENDIA, J. GELBER, and S. YRAR-RAZABAL, in preparation).