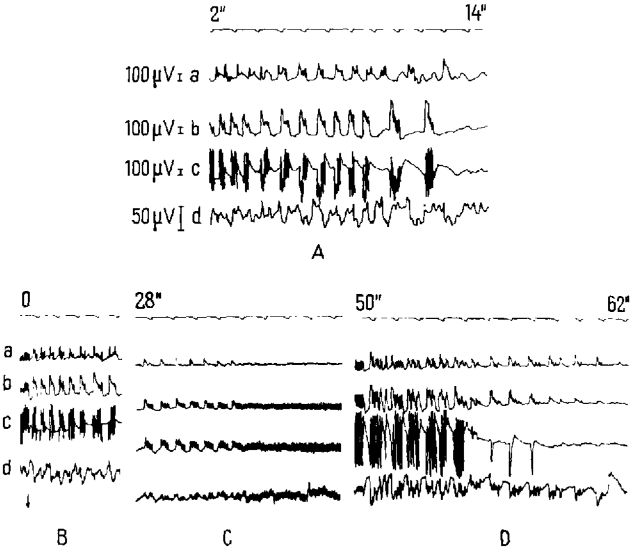

Fig. 2. Influence of nucleus caudatus on hippocampal afterdischarge (HA), produced by stimulation of dorsal hippocampus. Right nucleus caudatus stimulated 10 mm below surface of the skull, at 6 V, 200 cy/sec, 1 msec. Right dorsal hippocampus stimulated at 0.6 V, 40 cy/sec, 2 msec. Time in sec (on top); (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.

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 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.

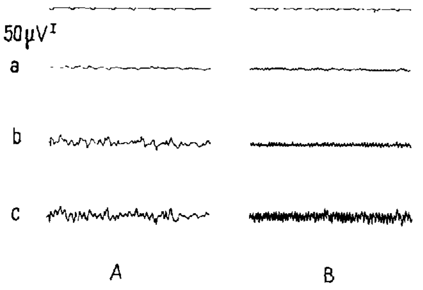

Fig. 1. Effect of nucleus caudatus on *resting* hippocampus; (A) recordings before, (B) during caudate stimulation. Stimulation at right caudate nucleus, 11 mm below surface of the skull, at 8 V, 200 cy/sec; stimulus duration, 1 msec. Time in sec (on top of record); (a) right sensory cortex; (b) right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

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

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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 matter[1] 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 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-

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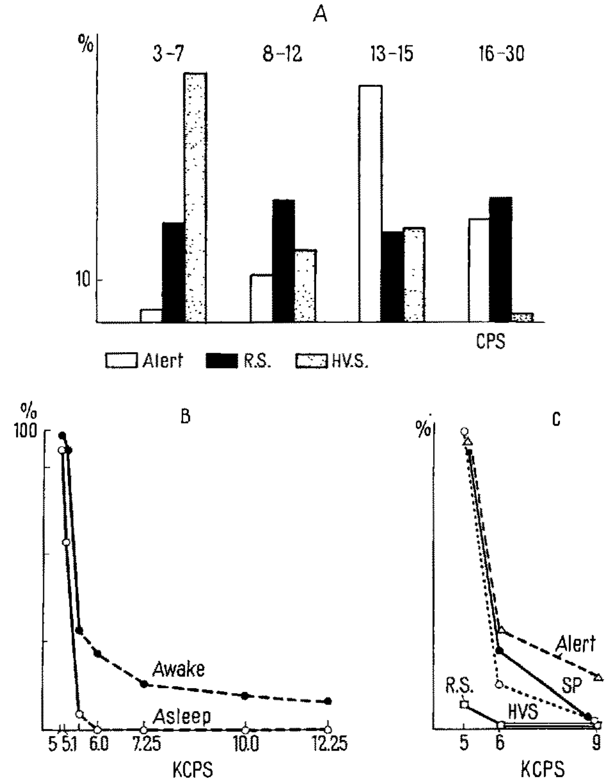
[1] Previous experiments have shown that tones that were reinforced in this manner evoked a conditioned response and awakened the sleeping cat (D. RODGERS, N. BUENDIA, J. GELBER, and S. YRARRAZABAL, in preparation).

creased (Fig. 1, B–C, curves awake)[2]. At this period, cats were tested during their natural sleep which, in agreement with other reports, showed two stages. (A) 'High voltage' sleep with animal immobile, moderate to extreme reduction of neck EMG activity and high amplitude, slow EEG. (B) The 'rhombencephalic' stage with twitches and eye movements, extreme reduction of EMG activity and low amplitude, fast EEG; as shown by the frequency analysis in Figure 1, A, the electrocorticographic pattern of the rhombencephalic stage was not identical with that of the awake and alert cat, since it had a significant percentage of slower rhythms not encountered in the wakeful preparation and lacked the abundance of 12–20 cps frequencies obvious in the latter.

Reactivity in sleeping cats (in terms of behavioral or EEG responses) was characteristic. (A) During 'high voltage' sleep effectiveness changed little for the 'positive' value but, for 'negative' tones, dropped markedly and in a degree that increased as pitch separation from the former increased (Figure 1, B–C). One may therefore infer that high voltage sleep is not an all-encompassing, uniform decrease in excitability: in this condition cats retained certain responses, including those developed as a consequence of training[2,3]. The discriminatory ability was preserved also and, as shown by the sharper contrast between the efficiency of the 'positive' pitch and the efficiency of the 'negative' frequencies, it was even enhanced: improvement came about because effectiveness of 'negative' stimuli was decreased or, in other words, because internal differential inhibition was enhanced, supporting the classical contention that both processes (sleep, inhibition) are related.



(A) Frequency analysis of the EEG, somatic sensory cortex (fore-limb avea): animal alert, during high voltage sleep (HVS) and during the rhombencephalic stage (RS). On abscissae (left to right), frequency ranges of 3–7, 8–12, 13–15, 16–30 cps. On ordinates, relative amounts of each frequency. – (B) Discrimination: awake and in high voltage sleep. (C) Discrimination: awake and alert, awake with EEG spindles (SP), in high voltage sleep (HVS), in the rhombencephalic state (RS). For B and C: On abscissae, pitch frequency (5 Kcps was reinforced); on ordinates, percentage of the presentations producing the behavioral conditioned response in all applications of each pitch.

(B) During the 'rhombencephalic' stage cats reacted little to the 'positive' pitch and not at all to 'negative' ones (Figure 1, C)[4]. The term 'deep sleep' is therefore correct, providing it implies only inoperancy of test stimuli; it appears objectionable, however, insofar as it suggests a qualitatively uniform and quantitatively progressive depression that carries the initially awake animal first to high voltage sleep and then to the rhombencephalic stage. The following considerations indicate that 'high voltage' sleep and the 'rhombencephalic' stage differ in the nature of the decreased reactivity they both exhibit[4]. Firstly, appearances favored duality, since indifference in 'high voltage' sleep (restricted to 'negative' tones) contrasted with that in the rhombencephalic stage (generalized to all pitches). Secondly, any non-responsiveness can be the outcome of one or another of the following mechanisms: (a) an increase in the threshold of the pathway (such, the abolition of a spinal reflex by reticular inhibition and that of a conditioned reflex by internal inhibition); (b) an intense activation of the pathway (such, the abolition of a spinal reflex by occlusion or of a conditioned reflex by external inhibition). A mechanism of type (b) (occlusion-like or external-inhibition-like) may cause non-responsiveness in the rhombencephalic stage: this interpretation is supported by the findings that it is associated with high rates of neuronal discharge in cats and is followed by frequent reports of dreams in humans[4,5]. In summary, the 'rhombencephalic' stage can be conceived as a physiological episode that involves an intense activation of the brain (which thus becomes relatively unavailable to intercurrent stimulation) and that, though occurring exclusively during 'high voltage' sleep, is qualitatively different from it[6].

Résumé. La discrimination tonale a été analysée chez des chats dressés pendant l'état de veille à répondre à un son d'une fréquence donnée (son «positif») et à ne pas répondre aux autres fréquences sonores (sons «négatifs»). Pendant la veille, l'efficacité des sons «negatifs» diminue au fur et à mesure que la différence de fréquence avec le son «positif» augmente. Pendant le sommeil lent et de haut voltage, l'efficacité du son «positif» ne change pas ou diminue peu, tandis que celle des sons «négatifs» est réduite: ainsi, le chat endormi possède encore la possibilité de faire des discriminations précises. Pendant la phase «rhombencéphalique» du sommeil, l'efficacité de tous les sons disparaît: on discute la nature de ce manque de réactivité.

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October 12, 1962.

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[3] M. Granda and J. T. Hammack, Science *133*, 1485 (1961).

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[6] Supported by USPHS Grant, No. M-5183.