Thalamic Reticular System and Cortical Arousal

Abstract. By electrocoagulation of the thalamic posterior commissure, the electroencephalographic arousal by high frequency stimulation of the thalamic unspecific nuclei was prevented, whereas the synchronizing influence on the cerebral cortex remained intact. On this ground, the role of the "thalamic reticular system" in the control of the cerebral rhythms is discussed.

Behavioral arousal and its ordinary electrocortical correlate (the electroencephalographic desynchronization) are known to depend upon the tonic influence of subcortical structures which form the "reticular ascending activating system" (*1*). This system is essentially composed of cell populations in the central core of the bulb, pons, and mesencephalon. Rostrally, the midline, intralaminar, and reticular nuclei of the thalamus are generally considered as the main last subcortical station. Indeed, a high-frequency electrical stimulation (more than 30 per second) carried therein would desynchronize the electroencephalogram quite as readily as if the arousing shocks were applied directly to the brain stem reticular formation lying caudally. As, in addition, a low-frequency stimulation (6 to 12 per second) of the same part of the thalamus elicits generalized recruiting waves similar to the spontaneous spindles seen at rest, it has been admitted that the cerebral rhythms are controlled from that region by common thalamocortical projections spreading toward both hemispheres. These are the main physiological arguments supporting the concept of a "thalamic reticular system" where critical frequencies of electrical stimulation are responsible for completely opposite effects: synchronization and desynchronization of the electroencephalogram.

In recent experiments performed on 35 cats unanesthetized at the time of recording, immobilized with Flaxedil, we have bilaterally destroyed by electrocoagulation a region corresponding approximately to the posterior commissure and pretectum. This lesion was posterior to the thalamus and limited to the dorsal aspect of the brain stem. Thereafter, we consistently failed to obtain a lasting electroencephalographic arousal by a previously effective 60- to 300-per-second stimulation of the thalamic nuclei: centralis lateralis, centralis medialis, paracentralis, reuniens, or rhomboidens (Fig. 1*A*). Sometimes there was a transient desynchronization, never outlasting the period of stimulation. Often spindles were seen during the excitation but most frequently they occurred at its outset (spindle tripping).

That the desynchronizing action of the thalamic stimulation was lost or strikingly reduced was further demonstrated by the following observation. Normally, the cortical synchronous potentials are swept off during the time of the electroencephalographic arousal. For instance, the recruiting responses to 10-per-second pulses applied in one of the intralaminar thalamic nuclei are depressed by a high frequency stimulation of the homologous contralateral nucleus (*1*). In our experiments this inhibiting effect disappeared after coagulation at the level of the posterior commissure (Fig. 1*B*).

It must be noted that the present results could hardly be explained on the ground of encroaching lesions of the thalamic system itself. Nor could it be argued that the cortical tonus had been lowered. Actually, the cortex was still able to desynchronize either spontaneously or by ordinary arousing procedures: upon injection of *d*-amphetamine, by electrical excitation of a peripheral nerve, or by stimulation of the mesencephalic reticular formation. So we must face the hypothesis that the desynchronizing action of the "reticular thalamic system" has to be necessarily mediated through the caudally situated reticular formation in order to reach the cortex. This is in agreement with Bremer's suggestion (*2*) that the cephalic portion of the reticular system depends on the lower portion for its functioning. Some recent data suggest that the thalamoreticular pathway passing at the site of the lesion could be a direct one (*3*).

Inasmuch as a backward action from diencephalic structures toward the lower brain stem is needed in order to elicit a generalized and lasting electroencephalographic arousal, there remains no definite evidence that these structures are more intimately implicated in the arousing mechanisms than other regions: for instance, the cerebral cortex, the cerebellum, or the various sensory afferences and central relays. Thus the physiological concept of a thalamic reticular system has to be questioned, at least in its ordinary formulation.

By special procedures, it is possible to isolate the synchronizing action of the thalamic unspecific nuclei. An anatomical transection at the level of the posterior commissure was shown to be often quite sufficient. However, a cortical desynchronization sometimes remained for the time of the stimulation. Fibers originating at a lower level in the brain stem are known to pass across the medial thalamus (*4*), and they are probably responsible for this transient cortical arousal when they are stimulated in their diencephalic course.

So, we attempted to use Nembutal, either by intravenous injection (15 mg/kg) or by topical application on the cerebral cortex (1.5 percent solution), in order to cancel the action of the excited *fibres de passage*. Under these conditions, we made the unusual observation that a 300-per-second stimulation of the thalamic midline or intralaminar

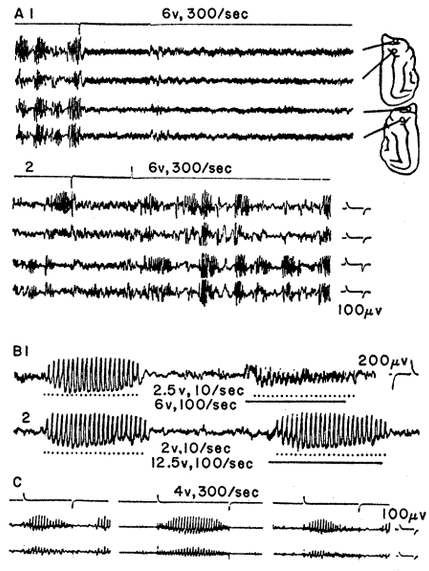

Fig. 1. Three electrocorticographic effects of a coagulation in the region of the posterior commissure. Experiments on three unanesthetized cats, immobilized with Flaxedil. (*A*) The enduring and generalized desynchronization induced by a 300-per-second stimulation of nucleus centralis medialis, as shown in the control (*A*1), no longer appeared after a coagulation of the posterior commissure (*A*2). Calibrations: 100 μv, 1 sec. (*B*) Recording from the left anterior sigmoid gyrus. The recruiting responses to a 10-per-second stimulation of the left nucleus paracentralis were prevented by a simultaneous 100-per-second stimulation of the right nucleus paracentralis (*B*1). After a coagulation of the posterior commissure, the inhibition of the recruitment was absent, even when twice as much voltage for the high-frequency shocks was used (*B*2). Calibrations: 200 μv, 0.5 sec. (*C*) Recordings from the anterior (upper trace) and posterior (lower trace) sigmoid gyri after coagulation of the posterior commissure and intravenous injection of 20 mg/kg of Nembutal. Under these conditions, a 300-per-second stimulation of the nucleus rhomboidens, which previously had an arousing effect, consistently induced spindling activities. Calibrations: 100 μv, 1 sec.

nuclei consistently elicited spindling waves on the cerebral cortex (Fig. 1*C*). The barbiturate by itself, that is, without any interruption of the postulated thalamoreticular connections, never induced this effect.

In our opinion, these latest results indicate that the unspecific thalamic system is mainly or solely concerned with the production of slow cortical activity. They also suggest that the thalamocortical mechanism of synchronization is not frequency-dependent with regard to the modalities of its activation. And finally, they give direct and further evidence that the recruiting and arousing systems of the brain are separated functional units, a fact which has already been postulated on other grounds (*5; 6*).

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Psychomotor Coordination of Auditory and Visual Space at Birth

Abstract. Before it was 10 minutes old, a human neonate was able to turn its eyes in the direction of an auditory stimulus. This demonstrates that learning is not essential for a crude form of auditory localization, directional oculomotor response, and coordination of auditory and visual functioning.

It has long been believed that space perception is dependent upon extensive learning experiences (*1*) although the results of some studies (*2*) do not appear consistent with such a belief. If it could be demonstrated that responses based upon space perception are present at birth, the nativist view of space perception would be greatly strengthened and serious doubt would be cast upon the empiricist view.

In 1952 I noticed that my child (born without anesthesia, by natural childbirth), about one-half hour after birth, turned her eyes in the direction of a soft click made near one ear or the other. This report describes a systematic attempt to replicate this observation.

The subject was born without pharmacologic anesthesia, by natural childbirth. Three minutes after birth, a series of trials were begun. On each trial a click was made (in predetermined order) with a toy "cricket" next to the right or left ear of the subject, who was lying on her back. Two observers independently recorded whether the eyes (whose movements were fully coordinated) moved to the infant's left, to the infant's right, or not at all, in response to each click.

As soon as the first click was made, the neonate, who had been crying with eyes closed, stopped crying, opened her eyes, and turned them in the direction of the click; it was clear to both observers that the movements occurred in response to the click. At about eight trials per minute, 52 successive trials were undertaken; the series was discontinued because the subject "lost interest," adapted, or satiated, in the sense that no further eye movements occurred in response to the clicks. When the experiment was over, the subject was only 10 minutes old.

The observers agreed substantially. On only one trial did they disagree on the direction of eye movement; on six trials, one observer recorded an eye movement while the other recorded none. There was perfect agreement on the remaining 45 trials; in 23 of these there was no eye movement. For 22 critical trials in which the observers both reported eye movement in the same direction, 18 were in the direction of the click and four in a direction opposite to the click. The difference between this distribution and chance (11 and 11) is significant at better than the .01 level by binomial expansion or by *t*-test based on the standard error of a proportion.

Although psychological experiments are usually performed on a fairly large number of subjects, the original informal observation, and the statistical results (as well as the unquestionable response in the first trial) in the present more systematic replication, appear sufficient to make the point. Within 10 minutes after birth, rudimentary directional auditory localization is possible; so is directional oculomotor (perhaps visual?) response. Moreover, at least on a reflex level, a rough coordination between auditory space and visual (motor) space can be observed. This finding is not compatible with the view that space perception, and particularly cross-modal spatial coordination, is based upon a long and arduous learning process (*3*).

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Stimulus Generalization of Imprinting

Abstract. Chicks were imprinted with a bluish object, then tested with different spectral values ranging to yellow-green. A systematic decrement in following was related to the stimulus series, although there was considerable generalization to all test values, which increased during testing. These data lead us to question the "irreversibility" of imprinting.

Lorenz (*1*) was the first to describe imprinting. He wrote of it as an "object-acquiring" process manifested by the behavior of an organism following the "acquired" object. The acquisition of this response occurs early in the life of the organism (typically, domesticated fowl) during a critical period, at which time the animal will follow the first moving object to which it is exposed. For Lorenz, the imprinting process is "irreversible" in that (i) the first object to elicit the following response becomes the only one capable of doing so, and (ii) this acquired behavior is never forgotten.

The first aspect of this "irreversibility" deals with response specificity, implying minimal generalization of the following response to stimuli other than the "acquired object." Moltz (*2*) points out that there is a lack of adequate re-