

## ORGANIZATION OF THE DIFFUSE THALAMIC PROJECTION SYSTEM

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IN 1942, Dempsey and Morison (1-3, 9) discovered a thalamic system, low frequency stimulation of which evoked widely distributed, high voltage, cortical waves, characterized by long latencies and initial progressive voltage increment. Attention was drawn to the close resemblance of these recruiting responses to spindle bursts, occurring spontaneously in barbiturate anesthesia, and evidence was presented that the two utilized common neural pathways. Since then, other proposals concerning the functional significance of this diffuse thalamic projection system have been made, the most dramatic being Jasper's hypothesis that it is the subcortical pacemaker in petit mal epilepsy (4, 5, 6).

Recent demonstration that EEG activation by the brain stem may be mediated, in part at least, by the diffuse thalamic projection system (8, 10), has motivated the present attempt to learn more of its organization. The centre median and intralaminar nuclei were found by Dempsey and Morison (9) to comprise the thalamic components of this system. In the absence of demonstrable connections from them to the cortex, their influence upon cortical electrical activity has since been proposed to be exerted indirectly, through the reticular thalamic nuclei (6, 11, 12) or through the rhinencephalon (12). In the present study, information concerning the origin of this diffuse system has been supplied by localization of thalamic areas which evoke recruiting responses upon stimulation, while determination of fore-brain regions from which such responses can be recorded has provided data concerning its projections.

### METHODS

Cats were employed and the recruiting response, elicited by thalamic stimulation was recorded with a Grass model-3 amplifier and inkwriter. The animals were under nembutal, Dial or chloralose anesthesia or, after preparation under ether and local procaine, were immobilized with beta-erythroidine or by transection of the cord at C1 and maintained with artificial respiration. The thalamus was stimulated with stereotaxically oriented bipolar concentric electrodes. A Goodwin stimulator was employed, the condenser discharges of which had voltages between 1 and 7, a falling phase of 1 msec. and a usual frequency of 7.5/sec. Grounding both temporal muscles effectively reduced shock artifacts.

Regional cortical pickups were between screw electrodes, 1 cm. apart, inserted into the calvarium until their tips rested on the underlying dura. More detailed pickups were obtained with silver ball tips, applied to the exposed cortex with the aid of a Grass multiple electrode holder. The most precise cortical and subcortical records were gained with bipolar concentric electrodes oriented stereotaxically. The recently prepared atlas of the cat's

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thalamus in Horsley-Clarke coordinates (7) was of the greatest aid in placement but all deep electrode positions were verified histologically.

### RESULTS

*Thalamic origins of diffuse projection system.* In appraising the sources of the recruiting response, the thalamus was explored with stimulating electrodes and electrocorticograms were obtained from rostral, middle and caudal regions of the dorsolateral cortex.

Representative recruiting responses, obtained under various anesthetics,<sup>3</sup> and from stimulating different parts of the thalamus, are shown in Figure 1 (records A-H), and the sites from which they were elicited are marked by solid circles on levels through the diencephalon. From behind forward, inciting areas included the centre median (Fig. 1, level E) and intralaminar nuclei (levels D and C), as Dempsey and Morison (9) discovered. In addition, more rostral regions—the anterior nuclei and the ventralis anterior (level B) and the anterior pole of the reticular nucleus (level A)—yielded excellent recruitment. While similar, both in form and distribution, responses from these rostral nuclei (Fig. 1, records A-E) in general had a wider distribution,

<sup>3</sup> The effect of anesthesia on the distribution of thalamic sites yielding recruiting responses was uncritical. Minor differences were noted, for in the encephalé isolé or beta-erythroidine preparation, finer localization was apparent, marked responses being obtained only when the stimulating electrode was completely within the excitable area. With barbiturate anesthesia, the possibility for evoking responses from the fringes of an effective region was enhanced. With chloralose, recruitment in successive waves was all but eliminated, the potentials being of full size from the start; in marginal regions, or with low stimulating voltage, waves were elicited only with every other shock, but again were of full size and exhibited no progressive increase in amplitude. In studies on the distribution of responses, projections were identical in the waking and anesthetized brain.

FIG. 1. Recruiting responses (records A-H, at left) and spike-wave complexes (records I-Q, at right) evoked by low frequency stimulation of thalamic sites indicated by appropriate symbols on transverse sections through diencephalon (levels A-E, center). Channels record activity from anterior (A) middle (M) and posterior (P) regions of cortex, homolateral (H) or contralateral (C) to side of stimulation, and occasionally from caudate nucleus (NC). Responses were elicited from stimulating anterior reticular nucleus (records A, B), antero-medial (C), ventralis anterior (D, E, I, J, L), centralis medialis (records F, G), centre median (H), the ventralis medialis (M), ventralis lateralis (O), medial geniculate (P), lateralis posterior (Q) and internal capsule (K, N). Anesthetics employed were: nembutal (records A, L, G, I, M, N, P, Q), chloralose (B, D, J, K), beta-erythroidine (F, O) and encephalé isolé (E, H, L). Stimulus voltages varied between 2 and 7, and were usually 5. Legends on diencephalon are: A—anterior nuclei, BP—basis pedunculi, C—centralis medialis, CA—caudate, CL—centralis lateralis, CLA—claustrum, CM—centre median, F—fornix, GP—globus pallidus, H—habenula, HP—habenulo-peduncular tract, HV—hypothalamic ventromedial nucleus, IV—internal capsule, L—lateralis posterior, LA—lateralis anterior, LG—lateral geniculate, M—medial nucleus, MB—mammillary body, MG—medial geniculate, OT—optic tract, P—pulvinar, PU—putamen, R—reticular nucleus, SU—subthalamus, VA—ventralis anterior, VL—ventralis lateralis, VM—ventralis medialis, VP—ventralis posterior. Dots indicate diencephalic sites whose stimulations did not evoke wave responses in cortex. Vertical calibration—100  $\mu$ V; horizontal calibration—1 sec.

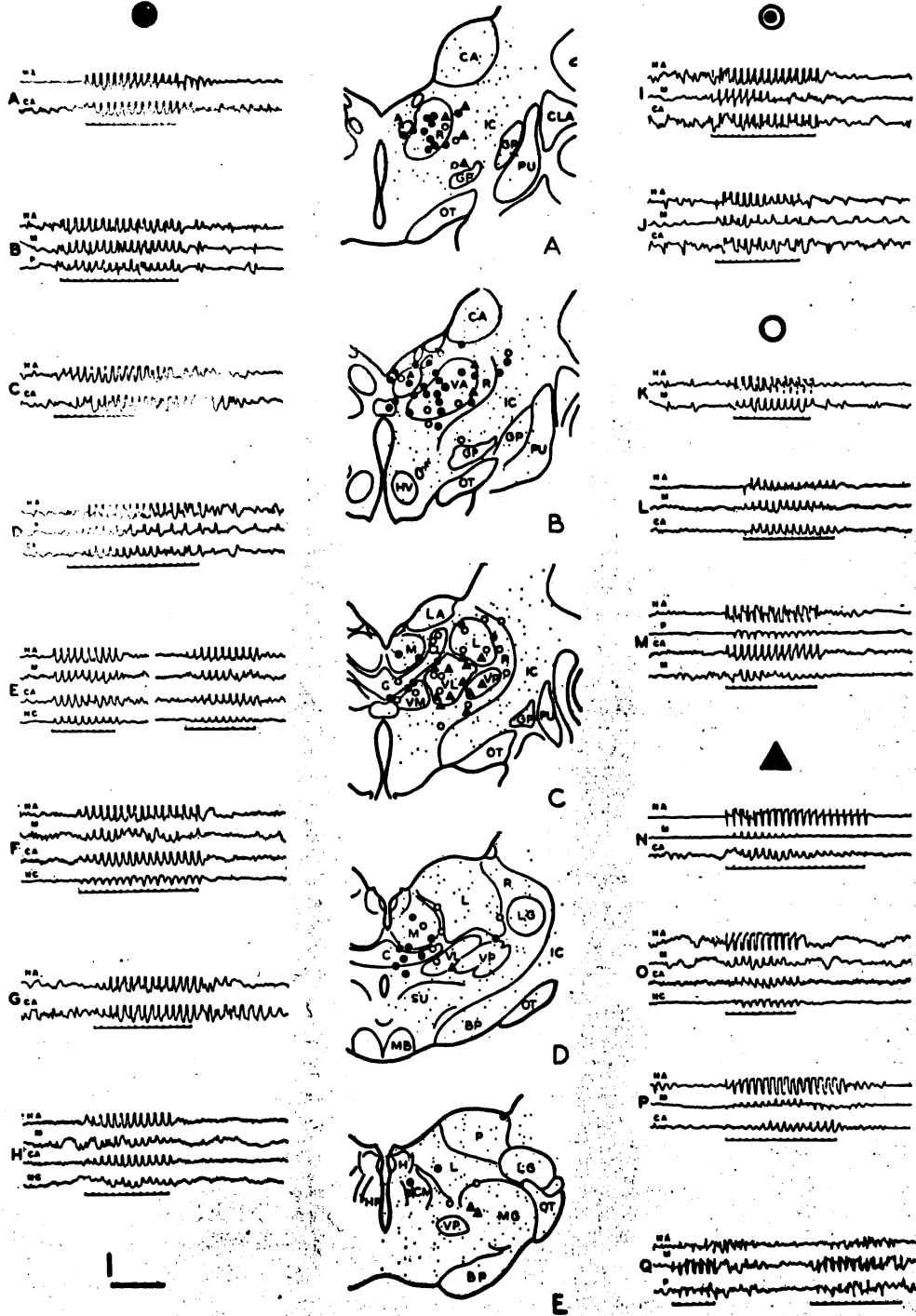


FIG. 1

a lower threshold and a briefer period of increment than those from more caudal levels (Fig. 1, records F-H). Of the entire region, the ventralis anterior was the single most powerful recruiting nucleus. Indeed, on its stimulation, no recruiting was seen on some occasions, the wave evoked by the first shock being as large as any thereafter (Fig. 1, record E).

Occasionally the more lateral thalamic nuclei, particularly the lateralis posterior and pulvinar, yielded pure recruiting responses. More frequently, spike-wave complexes were elicited from parts of the thalamus adjacent to the recruiting area. In one such type, marked by dotted circles (Fig. 1, records I and J), a spike was evoked in the anterior cortex by the first shock of a series, while the remainder yielded pure waves. In another type, shown by open circles, recruiting waves in the anterior (Fig. 1, records K-M) or middle (record Q) regions of the ipsilateral cortex were preceded by spikes, while elsewhere they were pure. In almost every instance, decreasing the stimulating voltage separated the two components, the spike usually having a lower threshold than the wave. These latter responses seem attributable to conjoint stimulation of specific and diffuse projection systems.

In still another type, indicated by solid triangles, the response commenced with a prominent spike which, with succeeding shocks, became obscured in a gradually developing wave (Fig. 1, records N-P). This alteration was recorded only from the anterior portion of the homolateral cortex, although small waves were occasionally seen elsewhere. Though best elicited from the nucleus ventralis lateralis (Fig. 1, level C), it is thought to be the augmenting response, discovered by Dempsey and Morison (3) and attributed by them to excitation of the sensory relay nuclei.

The ability of the reticular thalamic nucleus to evoke cortical potentials was explored with particular care, since its entire extent has been proposed by Rose and Woolsey (11, 12) and by Jasper (6) to constitute a distributing mechanism for the diffuse projection system. The present results are opposed to this generalization, for only the cephalic pole of the reticular nucleus (Fig. 1, level A) was found to yield recruiting responses upon direct stimulation. Nor do the present findings support the elaboration of this view that limited portions of the reticular nucleus yield such responses in restricted regions of the cortex, for recruiting responses evoked from the cephalic pole of this nucleus were distributed over the entire ipsilateral and the anterior part of the opposite hemisphere (Fig. 1, records A, B).

From these findings, then, the thalamic origins of the recruiting system are the centre median, the intralaminar nuclei, the anterior and ventralis anterior nuclei and the cephalic pole of the reticular nucleus.

*The projections of this diffuse thalamic system* were studied by evoking recruiting responses from the thalamus and recording with bipolar electrodes moved systematically through the hemisphere. All such responses, recorded from the thalamus itself, from the caudate nucleus and from portions of the cortex, possessed certain common features. As seen in Figure 2, in all regions of projection the responses appeared as waves, no matter how close the pick-

up to the stimulus. Even in Figure 2D, when the medial part of the thalamic nucleus ventralis anterior was stimulated and records taken from its lateral portion, characteristic waves were obtained. In addition, all good projection foci exhibited a reversal of potential as the electrodes were lowered through them, the turnover usually occurring abruptly within the space of 1 mm.

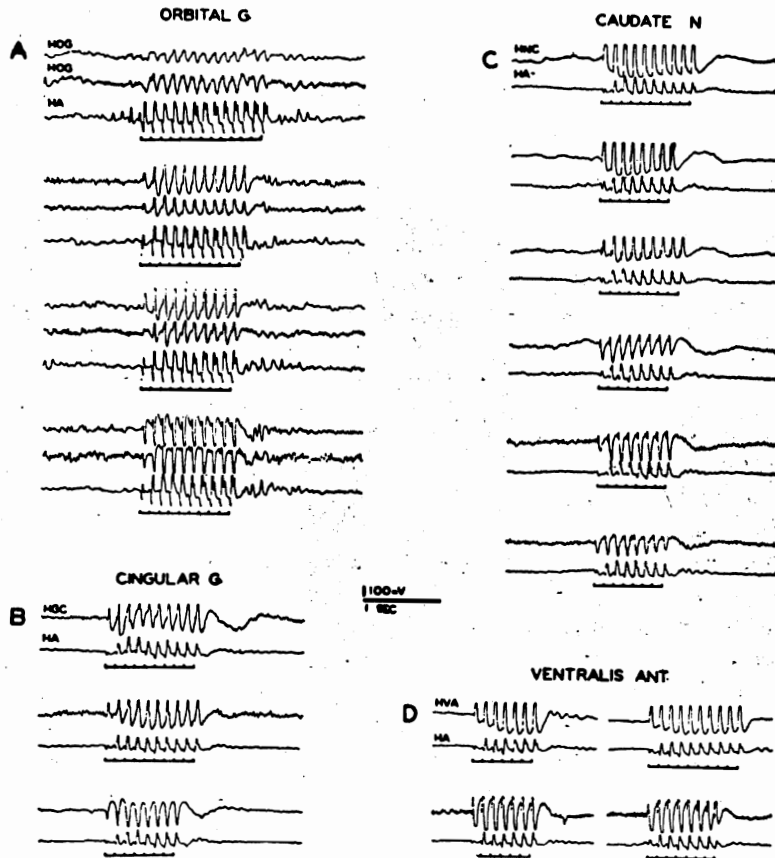


FIG. 2. Records of turnover of recruiting potentials on passing through claustrum and orbital gyrus (A), cingulate gyrus (B), caudate nucleus (C) and ventralis anterior (D). In each instance, pickups were from responding region and from anterior cortex (HA) on side of stimulation. Stimuli were applied to intralaminar nucleus (A) and ventralis anterior (B-D), under nembutal anesthesia (A) or in encephalé isolé (B-D).

(Fig. 2 A-D). Further evidence for the specific reference of the evoked potentials to the responding region was provided by their disappearance after a transection isolating this region from the thalamus (Fig. 3C, D) and by their outfall from a local area of the cortex following its thermocoagulation.

It was repeatedly noted that cortical regions from which marked recruiting responses were recorded exhibited spontaneous low voltage, fast activity for varying periods after the recording electrodes were inserted into them,

even though the EEG was highly synchronized elsewhere (Fig. 3A, B). Under barbiturate anesthesia, this activity underwent a gradual transition, with the insinuation of spindles, until ultimately only bursts or other synchronized discharges were exhibited. All responding areas, cortical or subcortical, displayed spontaneous spindle bursts under barbiturate anesthesia, and yielded repetitive after-discharge upon single shock stimuli to the thala-

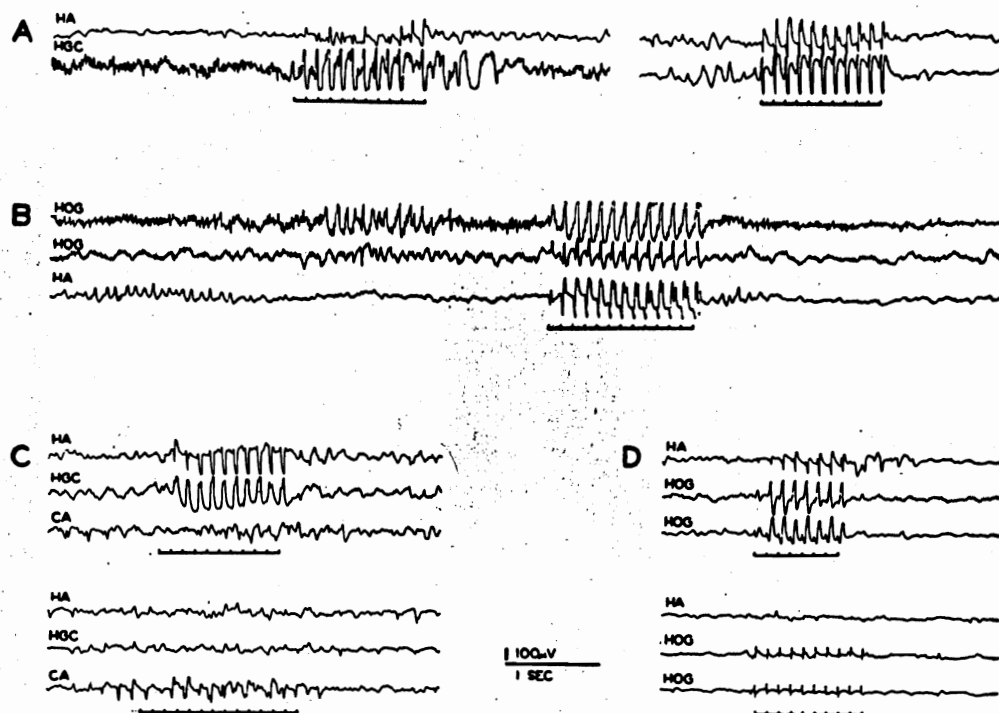


FIG. 3. A, B—Records showing spontaneous, low voltage, fast activity recorded under nembutal anesthesia from cortical areas yielding recruiting responses. A: gyrus cinguli showing initial fast activity and its later disappearance. B: orbital gyrus, with fast activity at site displaying largest recruiting response (top channel). Records from anterior cortex (HA) are included for comparison. Stimuli to intralaminar nucleus at 1.5 (A, left) and 7 volts (A, right, and B). Note spontaneous burst at B at site with best fast activity (top channel). C: recruiting responses in anterior hemisphere (HA) and cingulate gyrus (HGC) abolished (lower record) by cut between these structures and thalamus. D: recruiting responses in two regions of orbital gyrus (HOG) abolished (lower record) by cut between this gyrus and thalamus.

mus. While this after-discharge was obtained with greatest facility under barbiturate anesthesia, "spindle-tripping" was also frequently accomplished in the waking brain of the encephalé isolé against a highly desynchronized background (Fig. 4D). Illustrative records of recruiting responses, spontaneous bursts and repetitive after-discharge are shown in Figure 4 from the cruciate, cingulate and orbital areas of the cortex (A-C), from the caudate nucleus (D), and from nuclei of the thalamus itself (E-G). These

findings support the view of Dempsey and Morison (2) that these kinds of activity have at least partially a common mechanism.

With the thought that individual thalamic nuclei might have specificities of projection, the forebrain was explored in successive instances while stimulating each of the recruiting nuclei. No differences were found to exist, however, and the common projections of all parts of this system are shown by

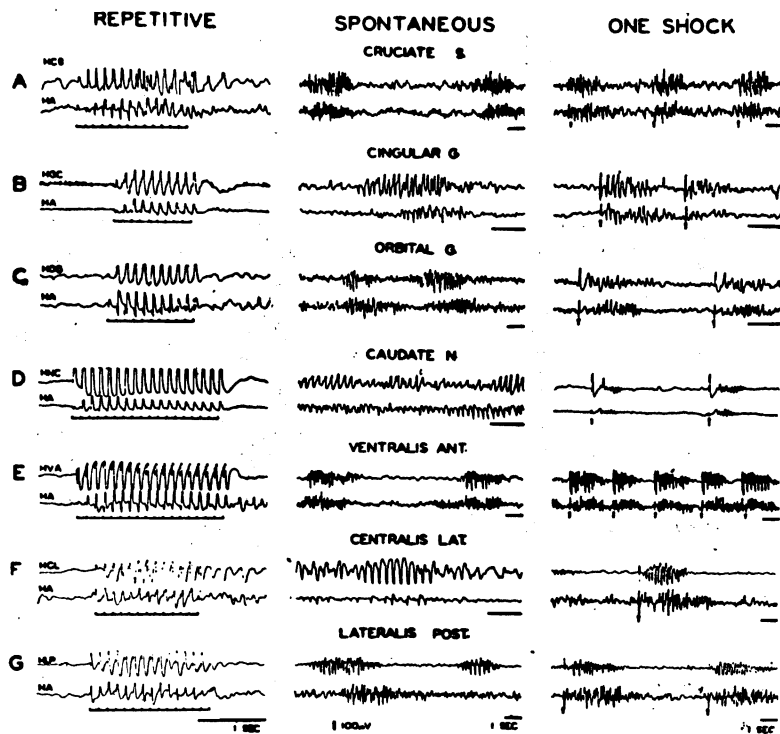


FIG. 4. Records from indicated regions and anterior cortex (HA) showing recruiting responses (left), spontaneous spindle bursts under barbiturate anesthesia (middle) and rhythmic after-discharge following single shock stimuli (right) to intralaminar nuclei (A, E), ventralis anterior (B, C, D), and anterior reticular nucleus (F, G). Stimulating voltages between 1.5 and 7.

shading in transverse sections through the hemisphere in Figure 5, and in surface views in Figure 6. At the thalamic level, excitation of any one of the nuclei of the diffuse projection system evoked a sweep of recruiting waves in all other recruiting nuclei (Fig. 5D-H), with the rostral end of the thalamus showing the greatest response potentiality. The nucleus ventralis anterior was the single most intense thalamic receiving focus (Fig. 5F), and responses to its own stimulation and to that of the centre median are shown in Figures 2D and 4E. More caudal intra-thalamic responses in the centralis lateralis and lateralis posterior, upon stimulation of the cephalic pole of the reticular nucleus, are shown in Figure 4F and G. The lateralis posterior and pulvinar



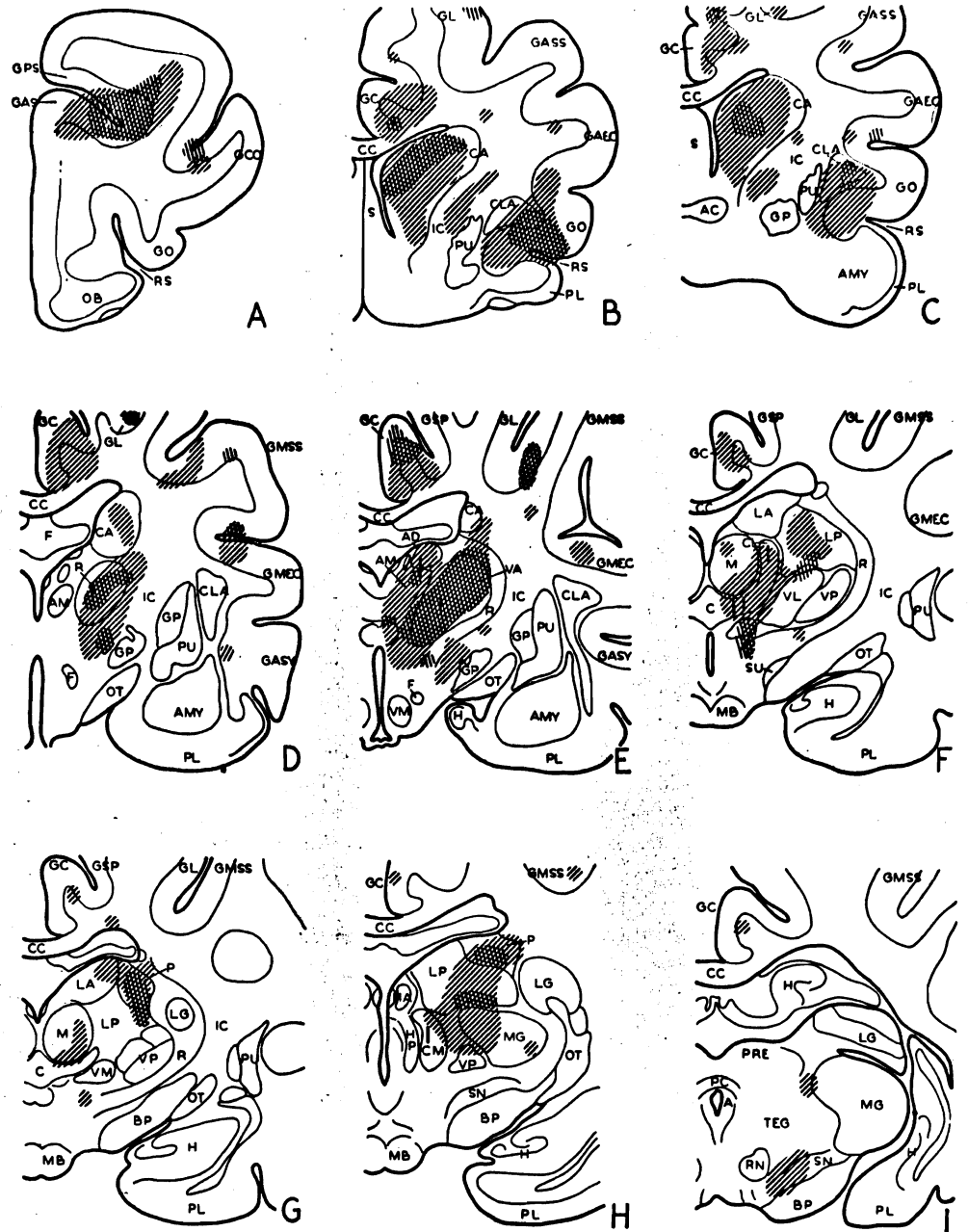


FIG. 5. Transverse sections through hemisphere with shading indicating sites from which recruiting waves may be recorded with deep pickups upon low frequency thalamic stimulation. More darkly shaded regions are those exhibiting rhythmic after-discharge upon single shock stimuli to thalamic recruiting nuclei. Structures displaying spontaneous spindle bursts under nembutal anesthesia have essentially same distribution. Abbreviations are as follows: A—aqueduct, AC—anterior commissure, AD—anterodorsal nucleus,



were the conspicuous responding regions of the lateral part of the thalamus (Fig. 5F-H), the sensory relay nuclei being for the most part silent,<sup>4</sup> as was the ventralis lateralis. Medially the lateral part of the medial nucleus and ventrally the ventromedial nucleus appeared responsive (Fig. 5F), though proximity to the intralaminar group made these distinctions difficult. Again, the cephalic pole of the reticular nucleus was the only part involved, responses being recorded also from the adjacent internal capsule (Fig. 5D).

Generalizing, the recruiting nuclei of the thalamus constitute a neural unit, excitation of any part of which sets the whole into activity. The group appears oriented caudo-rostrally, with its principal radiations departing from the front of the thalamus and, to a lesser extent, lateralward through the lateralis posterior and pulvinar. The mass discharge of this thalamic system upon stimulation of any of its parts seems of significance in accounting for its many projections.

Within the basal ganglia, the caudate nucleus throughout the extent of its head exhibited large recruiting potentials upon thalamic stimulation (Fig. 5B-D). The putamen and globus pallidus never responded. Small responses were recorded from the medial part of the substantia nigra and were the only ones obtained from the midbrain (Fig. 3I). Excellent recruiting waves were displayed by the claustrum, though only at rostral levels where it lay immediately internal to the orbital gyrus (Fig. 5B, C). The internal capsule and medullary centre of the hemisphere were remarkably silent as a rule. Immediately adjacent to good foci in grey matter, small responses could be recorded. In addition, certain capsular regions exhibited recruiting potentials (Fig. 5B-E). It is uncertain whether these represented corticopetal or corticofugal discharge.

The distribution of recruiting responses in the cortex was determined most precisely by exploration with fine electrodes thrust vertically into it so

<sup>4</sup> Recruiting potentials recorded from the medial aspect of the medial geniculate body (Fig. 5H, I) may have been picked up from the suprageniculate nucleus which occupies this position (7). Differentiation of this nucleus has been difficult in the present slide material.

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AM—anteromedial nucleus, AMY—amygdala, BP—basis pedunculi, C—nucleus centralis medialis, CA—caudate, CC—corpus callosum, CL—nucleus centralis lateralis, CLA—claustrum, CM—centre median, F—fornix, GAEC—anterior ectosylvian gyrus, GAS—anterior sigmoid gyrus, GASS—anterior suprasylvian gyrus, GASY—anterior sylvian gyrus, GC—cingulate gyrus, GCO—coronal gyrus, GO—lateral gyrus, GMEC—middle ectosylvian gyrus, GMSS—middle suprasylvian gyrus, GO—orbital gyrus, GP—globus pallidus, GPS—posterior sigmoid gyrus, GSP—suprasplenial gyrus, H—hippocampus, HA—habenula, HP—habenulo-peduncular tract, IC—internal capsule, LA—nucleus lateralis anterior, LG—lateral geniculate body, LP—lateralis posterior, M—medial nucleus, MB—mammillary body, MG—medial geniculate body, OB—olfactory bulb, OT—optic tract, P—pulvinar, PC—posterior commissure, PL—pyriform lobe, PRE—pretectal region, PU—putamen, R—reticular nucleus, RN—red nucleus, RS—rhinal sulcus, S—septum, SN—substantia nigra, SU—subthalamus, TEG—midbrain tegmentum, VA—nucleus ventralis anterior, VL—nucleus ventralis lateralis, VM—nucleus ventralis medialis, VP—nucleus ventralis posterior.

that one pole rested on the cortical surface, while the other lay 2-3 mm. deeper in the brain. It was clear that a regional topographical relation of cortical areas to thalamic recruiting sites did not exist for—just as with the subcortical projections—stimuli in any of the recruiting nuclei through a rostro-caudal extent of 7 mm. evoked recruiting waves in exactly the same foci. These findings thus fail to confirm the rostral cerebral projection of mesial thalamic regions and the posterior projection of lateral portions proposed by Jasper (6). In addition, it was clear that the receiving areas of the

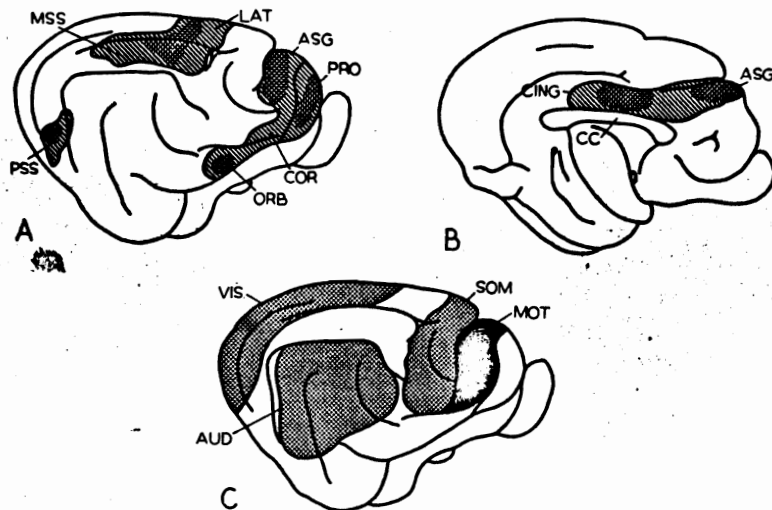


FIG. 6. Views of lateral (A) and medial (B) aspects of hemisphere of cat, with cortical regions from which recruiting responses may be recorded shown by cross-lining. More darkly shaded zones indicate most responsive areas. In C, position of sensory-receiving areas (stipple) and motor cortex (black) has been indicated on lateral aspect of hemisphere, after Rose and Woolsey (12). Abbreviations are: ASG—anterior sigmoid gyrus, AUD—auditory receiving area, CC—corpus callosum, CING—cingulate gyrus, COR—coronal gyrus, LAT—lateral gyrus, MOT—motor area, MSS—middle suprasylvian gyrus, ORB—orbital gyrus, PRO—gyrus proreus, PSS—posterior suprasylvian gyrus, SOM—somatic receiving area, VIS—visual receiving area.

diffuse thalamic projection were not truly diffuse, but were as delimited as those of the so-called specific projection systems, though more extensive. On the dorsal and lateral surface, the gyrus proreus, the anterior sigmoid gyrus and the anterior part of the coronal gyrus yielded excellent recruiting potentials (Fig. 6A). Somewhat less marked responses were obtained from two more caudal foci, one in the middle suprasylvian and lateral gyri and the other in the posterior suprasylvian gyrus (Fig. 6A). On the medial surface, the cortex bordering the cruciate sulcus and the cingulate gyrus (Fig. 6B) and, on the ventral surface, the orbital gyrus (Fig. 6A) all displayed marked recruiting potentials.

From inspection of the Figures, it appears that the somatic, auditory

and visual receiving areas (Fig. 6C) which occupy such a large extent of the cortex of the cat, are uninfluenced by the diffuse projection system, or at least fail to exhibit recruiting responses upon its stimulation. The motor cortex (Fig. 6A) was affected. The cortical areas most markedly influenced by the diffuse thalamic system were, however, located in front of, to the sides of, and between these functionally preoccupied regions, in what may be broadly called associational cortex. This finding would seem to have implications for the manner in which the influence of this thalamic system is

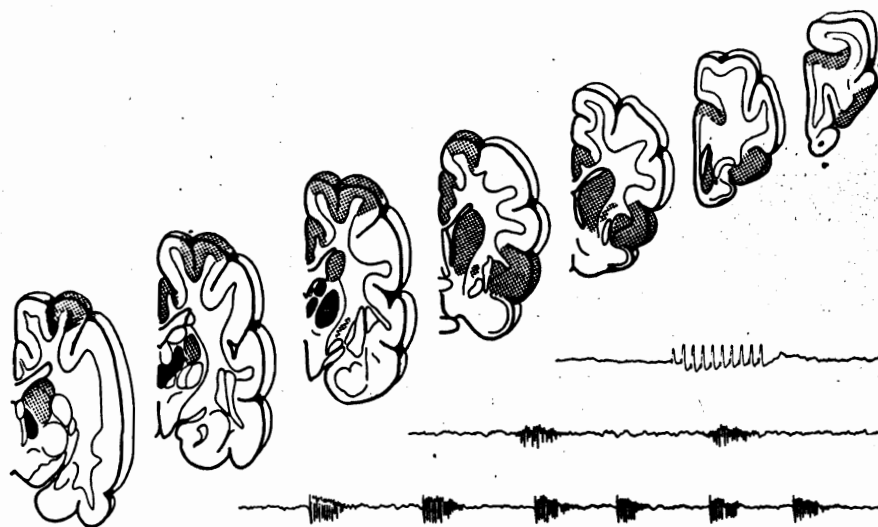


FIG. 7. Transverse sections through hemisphere of cat, upon which are indicated origins (black) and projections (stipple) of diffuse thalamic projection system. At right, records illustrate recruiting response to low frequency thalamic stimulation, spindle bursts in barbiturate anesthesia, and rhythmic after-discharge following single shock stimuli to thalamus, exhibited by all regions of projection.

conducted to the cortex and to be of importance in guiding future investigation of its significance.

All of the data bearing on the projection of the diffuse thalamic projection system just presented has been with reference to the ipsilateral hemisphere (Fig. 7). When recruiting responses were evoked by stimulating one side of the thalamus and records obtained from the opposite hemisphere, the findings were essentially the same—the thalamic nuclei of this system, the caudate nucleus, and the cortical foci mentioned, all yielding recruiting waves. The distribution of the contralateral influence of this system is, therefore, identical with its ipsilateral one, but the intensity of its contralateral influence is less pronounced. Of all contralateral responses, the largest by far were in the thalamic recruiting nuclei, particularly the ventralis anterior. These findings support earlier ideas (1, 6) that the response crossing occurs at a thalamic level.

Although Rose and Woolsey (12) have suggested, from degeneration studies, that the intralaminar nuclei project directly to rhinencephalic structures, no recruiting responses or other evoked potentials were recorded from the septum, olfactory tubercle, pyriform lobe, amygdala or hippocampus, upon thalamic stimulation. The present findings thus fail to provide any indication for a functional interrelationship between this thalamic system and the rhinencephalon.

#### DISCUSSION

Present knowledge of the system of diffusely projecting connections arising from the thalamus depends upon observations that low frequency stimulation of limited portions of this structure produce recruiting waves in a number of regions of the cortex. With respect to the thalamic origin of this system, the present study indicates that, in addition to the centre median and intralaminar nuclei, more rostral thalamic cell groups—the nucleus ventralis anterior, the anterior nuclei and probably the cephalic pole of the reticular nucleus—form integral components of this system. Their direct stimulation similarly yields widely distributed waves in the cortex, often with lower stimulating voltages and with briefer intervals before recruitment becomes maximal. These rostrally situated nuclei thus appear to constitute the most excitable portion of this system.

The greater bulk of the thalamic nuclei belonging to this system—the centre median, the intralaminar group and the ventralis anterior—possess the common feature of failing to exhibit retrograde degeneration after neocortical ablation, a finding that has been interpreted as meaning that they make no direct connections with the cortex. In some other situations in the brain, however, comparable failure of neurons to undergo retrograde degeneration has been attributed to proximal collateral branches from the axons which maintain viability of the parent cell body after the more distal axon has been interrupted. The mass excitation of this system upon local stimulation within it certainly suggests abundant interconnections between its neurons, which may be collateral in nature. The cortical influence of these thalamic nuclei has, however, been proposed to be exerted indirectly through relays, alternatively located in the reticular thalamic nucleus or in the rhinencephalon (6, 11, 12). The present findings give no indication for the participation of the rhinencephalon, nor do they indicate that the extent of the reticular nucleus is involved. The cephalic pole of this nucleus, just ahead of the ventralis anterior, yields recruiting responses upon stimulation and exhibits recruiting waves and repetitive discharge when other nuclei are excited. Though doubtless interposed amongst masses of fibers passing rostrally from more caudal levels, it probably forms a genuine component of the system. The present findings that all the recruiting thalamic nuclei are set into activity when any one of them is excited no longer makes it necessary, however, to search for a single subcortical structure that projects to the several parts of the cortex yielding the recruiting response, a feature that

appears to have made the reticular nucleus such an attractive candidate for the relay of the diffuse projection system. Instead, several thalamic nuclei and their projections may be involved, interconnections at the thalamic level enabling these parts to function as a unit. The absence of recruiting responses from the sensory receiving areas of the cortex may be associated with the failure of the sensory relay nuclei of the thalamus either to exhibit or to yield responses upon thalamic stimulation. In contrast, other of the discretely projecting nuclei of the thalamus which either exhibit or yield recruiting waves upon thalamic stimulation are known to send connections to portions of the cortex which the present findings indicate are the receiving areas of the diffuse system. Among these are the lateralis posterior and pulvinar, the ventralis medialis, a part of the medial nucleus and the anterior thalamic group. It is conceivable that the sum of these nuclei distribute influences of the diffuse system to the cortex, each to the circumscribed region of its projection, and that the centre median, intralaminar nuclei and ventralis anterior serve to interrelate their activities at the thalamic level. It is conceivable also that these latter thalamic nuclei themselves make connection with the cortex, and are protected from degeneration after cortical ablation by collateral endings of their axons within the thalamus or caudate nucleus.

By whatever means it is conducted, the influence of this thalamic recruiting system appears, both from the present findings and those of Morison and Dempsey (9), not to be exerted indiscriminately upon the cortex, as the term "diffuse" might connote. Instead, responsive cortical zones were found to be relatively specific and delimited, and were distributed in the frontal, cingulate, orbital, parietal and occipital associational regions. Overlap with the motor cortex occurred, but sensory receiving areas were avoided. Each cortical region that is not preoccupied with sensory and motor functions in the strict sense thus possesses a recruiting focus, and a thalamic system capable of exerting such a mass influence upon associational cortex would seem in a position to play a most important functional role.

#### SUMMARY

The diffuse thalamic projection system has been studied in the cat by evoking recruiting responses with thalamic stimulation and determining their distribution with recording electrodes moved systematically through the hemisphere.

The thalamic origins of this system include the centre median, intralaminar, anterior, ventralis anterior and anterior reticular nuclei. These components form a functionally interconnected unit, the excitation of any part of which sets the whole into activity. Radiations leave the thalamus principally from its rostral pole and to a lesser extent laterally, and project in a localized fashion to the caudate nucleus and to the associational cortex of the frontal, cingulate, orbital and suprasylvian portions of the hemisphere. The projection overlaps the motor region but avoids the sensory receiving areas.

The results suggest that the diffuse projection system is organized for mass thalamic influence upon associational cortex.

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