

The Distribution of Sensory Evoked Activity Within the Medial Geniculate Body of the Unanesthetized Cat

WILLIAM R. LIPPE AND NORMAN M. WEINBERGER¹

Department of Psychobiology, School of Biological Sciences, University of California, Irvine, Irvine, California 92664

Received January 2 1973

The responsiveness of the medial geniculate body to click, flash and shock stimulation was investigated in the unanesthetized, paralyzed cat. Evoked potentials and multiple unit activity were both recorded simultaneously from the same electrode by differential filtering. The ventral division of the medial geniculate body was found to be more responsive to click stimulation than the dorsal division; evoked potentials recorded within the dorsal division could be attributed to volume conduction. Flash and shock stimulation also produced evoked potentials recorded in the dorsal division which were not locally generated. Auditory and somatic stimulation often produced an increase in the amount of multiple unit activity above the background level in the dorsal division suggesting that these stimuli may engage neurons in the dorsal division in an asynchronous manner. The present findings demonstrate that the differential responsiveness of the dorsal and ventral divisions to acoustic stimulation previously observed in the anesthetized cat is not due to anesthesia. It appears that only the ventral division of the parvocellular portion of the medial geniculate body constitutes the main thalamic auditory relay nucleus. The present findings provide a functional correlate for previous anatomical data which have demonstrated a structural differentiation between the dorsal and ventral divisions of the medial geniculate body.

INTRODUCTION

We have reported that the dorsal and ventral divisions of the medial geniculate body differ markedly in their responsiveness to click stimulation in the barbiturate anesthetized cat. Whereas locally generated evoked potentials and significant amounts of evoked multiple unit activity are en-

¹ Supported by PHS research grant MH 11250 (to N. M. W.). The authors wish to thank Mrs. C. Wells for technical assistance and Miss S. Harris and Mrs. P. Lemestre for secretarial assistance. Dr. Lippe's present address is: North Carolina Department of Mental Health, Division of Research, Box 7532, Raleigh, North Carolina 27611.

countered within the ventral division, primarily volume conducted evoked potentials and only minimal amounts of evoked multiple unit activity are found within the dorsal division (4). It was suggested therefore that only the ventral division of the MGB constitutes the main auditory thalamic relay nucleus.

These data have raised two important questions. First, was the failure to evoke significant amounts of neural activity within the dorsal division a consequence of anesthesia? Second, is the dorsal division of the MGB responsive to nonauditory sensory stimulation? The present study has sought to answer these questions and constitutes a second step in the comparison of functional properties of the dorsal and ventral divisions of the MGB. In the present case, the neural activity evoked by click, flash and shock stimulation has been systematically mapped in the unanesthetized, paralyzed cat.

METHODS

Subjects and Surgical Procedure. Ten cats weighing 3.0–3.6 kg served as the subjects. Group I consisted of three cats (two males and one female) which received only click stimulation. Group II consisted of seven animals (four males and three females) which received click, flash and shock stimulation.

Each cat was initially anesthetized with an intravenous injection of sodium thiamylal (Surital); atropine methyl nitrate (1 mg ip) was administered and a venous cannula was inserted to allow for the administration of supplementary doses of the anesthetic during the operative procedure and for the subsequent infusion of gallamine triethiodide (Flaxedil). An endotracheal tube with an inflatable cuff was inserted under laryngoscopic control. Rectal temperature was continuously monitored and maintained between 36–38 C with a circulating warm water pad.

The cat was located inside a sound-attenuating chamber and mounted in a stereotaxic instrument. The operative procedure was as previously described (4). All wound edges and pressure points were heavily infiltrated with either Zyljectin, a long-lasting local anesthetic, or with lidocaine hydrochloride (Seracaine); additional doses of the latter were administered frequently throughout the course of the experiment. The animal was then allowed to return to the unanesthetized state. As soon as the cat showed evidence of spontaneous movements, the endotracheal tube was connected to a respirator located outside the acoustic chamber, and 30–40 mg of Flaxedil were administered intravenously. Supplemental doses (20 mg) given at intervals of approximately 50 min ensured maintenance of the paralyzed state.

Stimulation and Recording. Auditory stimuli consisted of clicks (84 dB

re: 0.0002 dyn/cm^2) produced by 0.1-msec square-wave pulses delivered to an earphone mounted on the earbar contralateral to the recording site. Photic stimuli were flashes produced by a Grass PS2 photic stimulator set at maximal intensity of 16. The flash tube was mounted outside the acoustic chamber to eliminate acoustic stimulation which was produced by each flash. Flashes were presented through a one-way window approximately 18 in. from the cat at its eye level, resulting in binocular stimulation. Shock stimuli consisted of 1.0-msec, 9.0-v pulses produced by a Grass S8 stimulator, led through a stimulus isolation unit and then to pairs of needle electrodes inserted subcutaneously into the forepaws and hind paws contralateral to the recording site. Evoked potentials and multiple unit activity were recorded from the same stainless steel semi-microelectrode. Details of recording have been described (4).

Experimental Procedure and Data Analysis. The experimental procedure and data analysis were similar to those described previously (4). In animals of Group I, two electrodes mounted 1.5–2 mm apart in the medial–lateral dimension were advanced in 0.3–1 mm vertical steps through the medial geniculate body, and at each level spontaneous activity was recorded (40 sec) and then clicks were presented at 2/sec for 40 sec. The same procedure was followed in Group II except that at each level click stimulation was followed by 2/sec flash and shock stimulation (40 sec each). Usually, punctures were made at three anterior–posterior planes in each animal using fresh electrodes. A total of 32 punctures were made, 13 in Group I and 19 in Group II. Marking lesions (1 mc) were made at the most ventral point of each penetration. At the termination of each experiment, the cat was killed and its brain later sectioned and stained. Electrode tracks and recording points were reconstructed without knowledge of the evoked activity, using techniques reported elsewhere (4).

Average evoked potentials, poststimulus time histograms, and levels of spontaneous activity of multiple unit activity were provided by a Lab-8 digital computer, in the same manner as reported (4).

Construction of Poststimulus Time Histograms (PSTH). We reported that neural activity having a peak latency of 5 msec in response to click stimulation appeared in almost all post stimulus time histograms from the medial geniculate body (4). This was attributable to volume conduction of activity generated at lower brain stem levels. A similar response also occurred frequently in the present study. In order to facilitate comparison of multiple unit activity data from the previous and present studies, poststimulus time histograms from animals in Group I of this study were delayed 7 msec from click onset to eliminate the short-latency activity, as done previously. As previously demonstrated, this technique does not effect the overall results (4). However, in animals from Group II (those

receiving click, flash and shock stimulation) the comparison of click-evoked activity under the anesthetized and unanesthetized conditions was not of primary interest, and the poststimulus time histograms from these animals were delayed 2 or 3 msec from stimulus onset so as to eliminate only the artifact caused by shock stimulation.

Discriminator Setting. We previously pointed out also that the specific discriminator voltage level selected for the analysis of evoked multiple unit activity can markedly effect the response patterns observed (4). Most pertinent to the present discussion is the observation that well-defined responses may be masked by high levels of spontaneous activity if a very low discriminator voltage level is selected. This did not constitute a major problem in the barbiturate anesthetized animals in which the rate of ongoing activity was rather low. However, in the unanesthetized preparations the level of spontaneous activity was significantly higher, and thus even the large evoked multiple unit activity responses encountered within the ventral division were frequently masked when using a 10 μv cut-off level. To circumvent this problem, poststimulus time histograms all were derived using a 20 μv cut-off level.

RESULTS

Responses to Click Stimulation. The ventral division of the medial geniculate body is more responsive to click stimulation than the dorsal division. Although evoked potentials are recorded from both regions, they are generally of larger amplitude in the ventral division. Furthermore, during a single penetration, conspicuous changes in evoked potential waveform occur at different loci within the ventral division, including reversals of polarity; potentials recorded from the dorsal division resemble each other in configuration and never reveal polarity reversals. The predominance in responsiveness of the ventral division to click stimulation is also evident from an analysis of poststimulus time histograms of multiple unit activity, which exhibit marked peaks from ventral division sites but not from dorsal division loci.

Examples of these findings are seen in Fig. 1, comprised of data from a Group I animal. The lateral electrode penetrated both the dorsal and ventral divisions. Evoked potentials recorded from the four most dorsal loci all consist primarily of an initial small negative component followed by a later negative-positive wave (Fig. 1B). Penetration into the ventral division is marked by a clear increase in amplitude; pronounced changes in waveform are observed more ventrally, including a reversal of polarity near the bottom of the puncture (Fig. 4).

Examination of the poststimulus time histograms (Fig. 1A) reveals associated changes in the evoked multiple unit activity. The four most

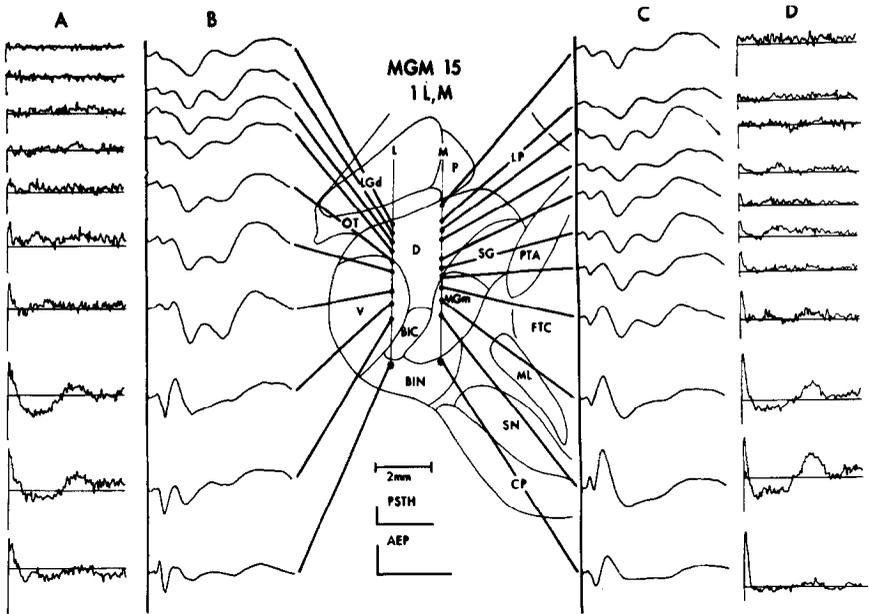


FIG. 1. Poststimulus time histograms (A,D) and corresponding averaged evoked potentials (B,C) to click stimulation from medial (M) and lateral (L) electrodes passing through the medial geniculate body. These data were obtained from a cat receiving only click stimulation. Note the similarity of AEP and minimal evoked MUA recorded dorsally vs marked AEP changes and increases in MUA encountered within the ventral division and pars magnocellularis. PSTH start 7 msec after click onset. In this and all subsequent figures horizontal lines through PSTH indicate levels of spontaneous activity. AEP shown with positive up. Asterisks at bottom of tracts indicating marking lesions. Calibration: PSTH—64 spikes, 100 msec; AEP—75 μ V, 50 msec. See Table 1 for explanation of abbreviations of brain loci.

dorsal poststimulus time histograms show no well defined peaks while penetration into and through the ventral division is associated with the appearance of an initial excitatory response which is followed by a period of inhibition (i.e., discharges below spontaneous level); a later period of excitation is seen for the more ventral recordings.

Recordings from the medial electrode show similar changes with passage from the dorsal division into pars magnocellularis. The four most dorsal averaged evoked potentials closely resemble those recorded simultaneously from the lateral electrode. As the electrode approaches within 0.5 mm of pars magnocellularis (fifth recording) there is an increase in amplitude and sharpening of the initial negative component, and entrance into pars magnocellularis is marked by conspicuous changes in slow wave configuration (eight to tenth recordings). The poststimulus time histograms also reveal correlated changes in the evoked multiple unit activity. The

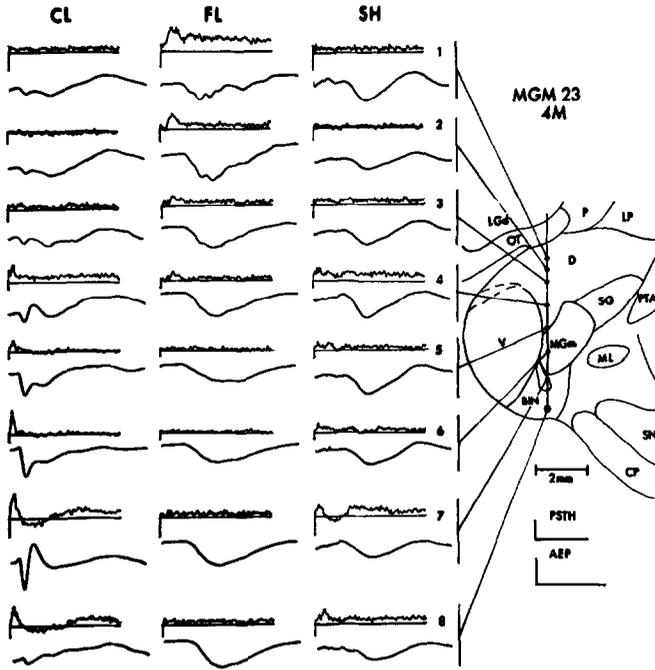


FIG. 2. AEP and PSTH recorded to click (CL), flash (FL), and shock (SH) stimulation. Responses to flash stimulation are suggestive of volume conduction from the overlying optic tract and dorsal lateral geniculate nucleus because of diminution of MUA within the dorsal division and the similarity of AEP waveform throughout the medial geniculate body. Note similarity of all AEP to shock stimulation and the absence of any well defined peaks in the PSTHs in the dorsal division. Localized responses to clicks are seen in the region of the magnocellular MGB and nucleus of the brachium. Dashed lines indicate limits of uncertainty in the dorsal border of the ventral division. PSTH start 3 msec after stimulus onset. Calibration: PSTH—128 spikes, 100 msec; AEP 75 μ V (click), 300 μ V (flash), 150 μ V (shock), 50 msec.

three most dorsal poststimulus time histograms have no obvious peaks while the next four recordings exhibit small initial and late excitatory responses which increase in size as the electrode approaches and passes through pars magnocellularis.

The greater responsiveness of the ventral division to auditory stimulation, described above for animals receiving only auditory stimulation, was also observed in those subjects which also received flash and shock stimulation (Figs. 2-5). In this regard Fig. 5 is of some interest as it shows a penetration through the caudal tip of the medial geniculate body, which is wholly part of the dorsal division. The small amplitude and similar configuration of the averaged evoked potentials as well as the paucity of evoked multiple unit activity in this region are striking, and should be

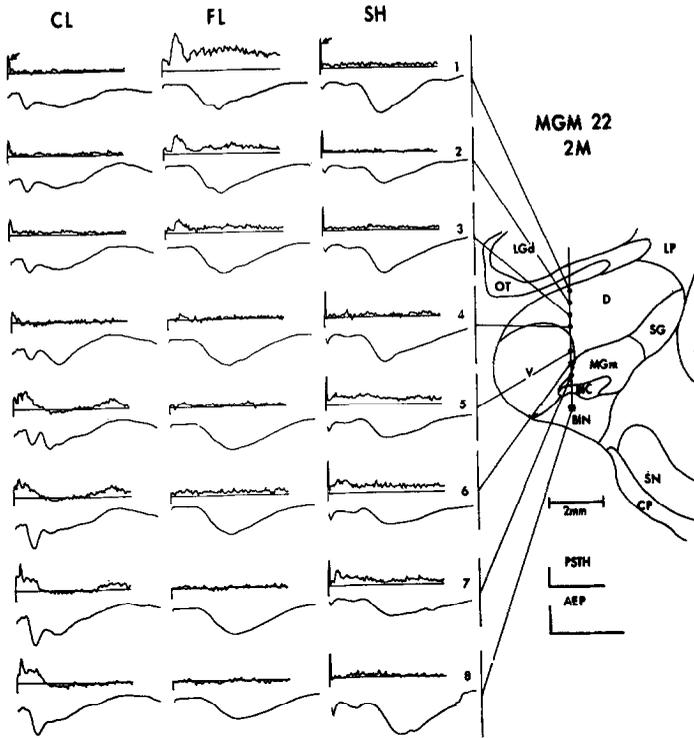


FIG. 3. AEP and PSTH recorded to click (CL), flash (FL) and shock (SH) stimulation. Similarity of AEP and gradual diminution of MUA evoked by flash stimulation suggests volume conduction of activity from the overlying optic tract and dorsal lateral geniculate nucleus. Note similarity of all AEP to shock stimulation and the absence of any well defined peaks in the PSTH in the dorsal division. These records were obtained simultaneously with those shown in Fig. 4. Arrows in the first PSTH to click and shock stimulation indicate volume conducted responses and stimulus onset but portion of shock artifact still remains. Calibration: PSTH—128 spikes, 100 msec; AEP—75 μ v (click), 300 μ v (flash), 150 μ v (shock), 50 msec.

compared with the much larger responses recorded within the ventral division (Figs. 1, 3 and 4).

The absence of pronounced peaks in the poststimulus time histograms derived from the dorsal division suggests that neurons in this area are not responsive to click stimulation. However, in several instances the amount of multiple unit activity was increased during click stimulation above the spontaneous level (Fig. 1D, 1st PSTH; Fig. 3, 3rd PSTH; Fig. 4, 2nd PSTH). Therefore it is possible that dorsal division neurons are engaged by acoustic stimulation, but not in a time-locked fashion.

Responses to Flash Stimulation. Both averaged evoked potentials and evoked multiple unit activity were recorded in response to flash stimuli in

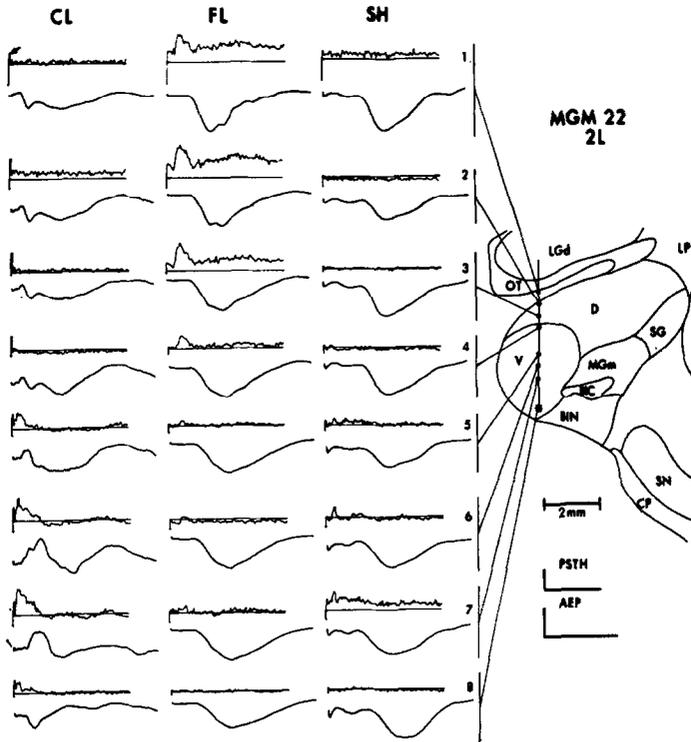


FIG. 4. AEP and PSTH recorded to click (CL), flash (FL), and shock (SH) stimulation from the lateral electrode of cat 22 whose medial electrode data are depicted in Fig. 3. Similarity of AEP and gradual diminution of MUA evoked by flash stimulation suggests volume conduction of activity from the overlying optic tract and dorsal lateral geniculate nucleus. Note similarity of all AEP to shock stimulation and the absence of any well defined peaks in the PSTH in the dorsal division to both shock and click stimulation; click evoked responses are present in the ventral division. Arrow in the first PSTH to click stimulation indicates volume conducted response obvious in all PSTH to click stimulation. PSTH start 3 msec after stimulus onset. Calibration: PSTH—128 spikes, 100 msec; AEP—75 μ v (click), 300 μ v (flash), 150 μ v (shock), 50 msec.

all punctures through the medial geniculate body, but the characteristics of these evoked responses suggest that they were not locally generated but probably volume conducted from the overlying optic tract and dorsal lateral geniculate nucleus, and possibly from the accessory optic tract as well. Thus, examination of Figs. 2-5 reveals that while averaged evoked potentials were recorded from all regions within the medial geniculate body, they were similar in amplitude and configuration at all recording points. Polarity reversals were never observed. In some cases minor changes in amplitude and configuration did occur as the electrode was advanced

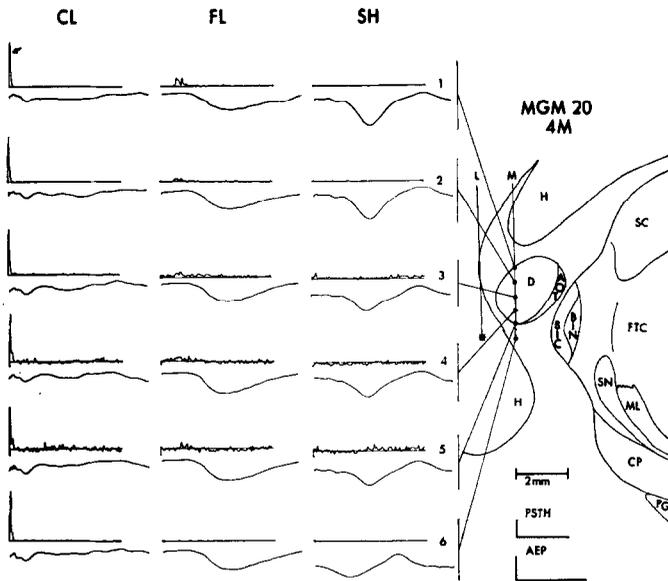


FIG. 5. AEP and PSTH recorded to click (CL), flash (FL) and shock (SH) stimulation through the caudal tip of the medial geniculate body. Exact reconstruction of recording loci was not feasible because caudal tip was not attached to the brain stem. The heights of recording on the medial electrode (M) were reconstructed on the basis of a lesion placed in the underlying hippocampus by a lateral electrode (L) which was simultaneously advanced through the brain. The appearance of MUA activity in records 4-6 indicates that the points were located within the caudal tip. Note very small short latency responses to click stimulation in the fourth and fifth PSTH immediately following volume-conducted large artifact (arrow in the first PSTH to click stimulation). PSTH start 3 msec after stimulus onset. Calibration: PSTH—64 spikes, 100 msec; AEP μV (click), 300 μV (flash), 150 μV (shock), 50 msec.

through the medial geniculate body. For example, in Fig. 4 the averaged evoked potentials to flash stimulation exhibit a slight decrease in amplitude and a gradual broadening of waveform at the successively ventral recording points. These slight changes in the evoked slow-wave activity stand in contrast to the marked changes in amplitude and configuration which occur to click stimulation at the same recording points.

Multiple unit activity evoked by flash stimulation was also recorded within the medial geniculate body (Figs. 2-4, PSTH 1-4; Fig. 5, PSTH 1, 2). However, a number of factors suggest that this activity was not locally generated but rather volume conducted from overlying visual paths. First, evoked activity was encountered only in the more dorsal portions of the medial geniculate body, i.e., within the dorsal division or within the most dorsal portion of the *ventral division* (Fig. 4, fourth PSTH).

TABLE 1
ABBREVIATIONS USED IN ILLUSTRATIONS

AOT	accessory optic tract
BIC	brachium of the inferior colliculus
BIN	nucleus of the brachium of the inferior colliculus
CP	cerebral peduncle
D	dorsal division of the medial geniculate body
FTC	central tegmental field
H	hippocampal formation
LGD	lateral geniculate body, pars dorsalis
LP	nucleus lateralis posterior
MG _m	medial geniculate body, pars magnocellularis
ML	medial lemniscus
NOT	nucleus of the optic tract
OT	optic tract
P	posterior nucleus
PG	pontine gray
PTA	anterior pretectal nucleus
PTP	posterior pretectal nucleus
PUL	pulvinar
SC	superior colliculus
SG	supragenulate nucleus
SN	substantia nigra
V	ventral division of the medial geniculate body

Second, evoked activity always appeared simultaneously on recordings from medial and lateral electrodes which were advanced through the medial geniculate body together. For example, in Figs. 3 and 4 evoked responses to flash stimulation occur in the first four poststimulus time histograms on both electrodes. Third, there was a clear gradient in the amount of evoked multiple unit activity such that large amounts were present in recordings made in the most dorsal part of the medial geniculate body while those recordings made successively more ventrally showed diminishing activity (Figs. 2-4). Finally, the pattern of evoked multiple unit activity as reflected in the shape of the poststimulus time histogram to visual stimulation was constant at different sites. The click-evoked histogram patterns within different parts of the ventral division changed as would be expected if the activity were generated locally (e.g., Fig. 4, PSTH 5-7).

Responses to Shock Stimulation. Evoked potentials to shock were recorded throughout the medial geniculate body. However, an examination of the averaged evoked potentials and multiple unit activity provide no clear evidence that shock stimulation is capable of evoking large amounts of synchronous activity within the medial geniculate body in general and

within the dorsal division in particular. Thus, in Figs. 2-4 the averaged evoked potentials to shock stimulation at all recording points are rather similar in configuration although there are frequent variations of slow-wave amplitude in recordings made from the same puncture. Although the significance of these minor differences in slow-wave amplitude are unclear, the failure to encounter major changes in either amplitude or configuration clearly suggests that no major sources of somatic slow-wave activity were encountered either within the dorsal or ventral divisions of the medial geniculate body.

Examination of the poststimulus time histograms indicates that in no instance were well-defined peaks of multiple unit activity evoked within the dorsal division. However, such peaks were found in records obtained in or near pars magnocellularis (Fig. 2, PSTH 7; Fig. 3, PSTH 6, 7) or within the nucleus of the brachium (Fig. 2, PSTH 8). Shock stimulation was correlated with an increase of multiple unit activity above the spontaneous level in numerous recordings made within the dorsal division (Fig. 2, PSTH 1, 3, 4; Fig. 3, PSTH 1, 3) or in or near pars magnocellularis (Fig. 2, PSTH 5, 6; Fig. 3, PSTH 5, 6). These observations suggest that shock stimulation is capable of evoking an asynchronous discharge of multiple unit activity within the dorsal division. Finally, in a few instances, well-defined peaks, increases of multiple unit activity above the ongoing spontaneous level, or both, were evoked within the ventral division by shock stimulation (Fig. 4, PSTH 6, 7).

DISCUSSION

The present results indicate that the ventral division of the medial geniculate body of the unanesthetized cat is more responsive to acoustic (click) stimulation than the dorsal division. Evoked potentials recorded from the latter region are attributable to volume conduction. In contrast, the marked changes in configuration and amplitude and the polarity reversals which characterize evoked potentials recorded from the ventral division suggest that this latter activity is locally generated. Furthermore, recordings of multiple unit activity indicate that whereas prominent peaks characterize poststimulus time histograms from the ventral division, such peaks are virtually absent in histograms from the dorsal division. This suggests that neurons in the ventral division are driven in a synchronous and secure manner by click stimulation. These findings replicate earlier ones in the anesthetized cat (4) and thus indicate that the previous failure to find significant amounts of click evoked activity within the dorsal division was not a consequence of barbiturate anesthesia. The present results also demonstrate that click stimulation may lead to an increase in the amount of multiple unit activity above the background level in the

dorsal division, a phenomenon not found in anesthetized preparations (4). This suggests that cells within the dorsal division may be responsive to click stimulation, but not in a time-locked fashion, an interpretation which is consistent with recent observations of single cell response characteristics (1).

Flash stimulation produced evoked potentials and multiple unit activity from the dorsal division as well as from other portions of the medial geniculate body. However, as explained in Results, this activity was probably volume-conducted from the overlying optic tract and dorsal lateral geniculate nucleus. Although it would seem that the dorsal division is not activated in a powerful manner by flash stimulation, cells within this region may be driven by visual stimulation. For example, the responses of small numbers of neurons within the dorsal division might have been masked by much greater amounts of volume conducted activity. In fact, a portion of the posterior thalamic region which is included within the dorsal division of the medial geniculate body as defined here receives projections from both the superior colliculus (3) and the lateral suprasylvian visual area (2). Furthermore, Stewart, Towns and Birt (personal communication) have observed visually responsive cells in the dorsal division of the medial geniculate body of the rabbit. Insofar as this area appears to be homologous with that of the cat (12), it is possible that similar neurons will be found in the cat as well.

Evoked potentials to shock stimulation were also recorded from the dorsal division of the medial geniculate body. However, the observations that they had the same configuration at all loci, lacked polarity reversals, and that similar potentials were recorded from other portions of the medial geniculate body suggests that these were volume conducted. The failure of shock stimulation to produce definite peaks in the poststimulus time histograms in recordings from the dorsal division further indicates that significant amounts of multiple unit activity were not engaged in a time-locked manner. However, the frequent increases of multiple unit activity above the spontaneous level during shock presentation suggests that neurons might have been driven in an asynchronous manner, an insecure manner, or both. This possibility is supported by two observations: First, midbrain structures known to project to the dorsal division appear to receive somatic input (7, 8); second, we have recorded from a single cell within the dorsal division which was activated by shock, but only during a small proportion of stimulus presentations.

Shock stimulation also produced definite peaks in the poststimulus time histograms or increased the level of multiple unit activity (or both) within the ventral division, nucleus of the brachium and pars magnocellularis. The responsiveness of pars magnocellularis can be accounted for on the basis of

its known somatic input (3, 5, 6, 11); however, the responsiveness of the ventral division is somewhat surprising since there is no evidence of somatic input to this region. The present study does not provide an explanation for this finding.

In conclusion, the present findings replicate and extend a previous study in which click evoked activity was found predominantly in the ventral division of the medial geniculate body in the anesthetized cat (4). As such, they provide evidence of a functional correlate for the previously described anatomical differentiation between the dorsal and ventral divisions of the parvocellular portion of the medial geniculate body (9, 10). The present results also show that the dorsal division is not strongly activated by flash and shock stimulation. However, the finding that shock as well as click stimulation were sometimes correlated with increases in multiple unit activity suggests that somatic and acoustic stimuli may engage dorsal division neurons in an insecure or asynchronous manner, or both. The present methods of recording cannot provide more than suggestive evidence on this point, and a final determination of the responsivity of dorsal division neurons to sensory stimulation must await an analysis of single unit discharge properties.

REFERENCES

1. AITKIN, L. M., and W. R. WEBSTER. 1972. Medial geniculate body of the cat: Organization and responses to tonal stimuli of neurons in ventral division. *J. Neurophysiol.* **35**: 365-380.
2. HEATH, C. J., and E. G. JONES. 1970. Connexions of area 19 and the lateral suprasylvian area of the visual cortex of the cat. *Brain Res.* **19**: 302-305.
3. JONES, E. G., and T. P. S. POWELL. 1971. An analysis of the posterior group of thalamic nuclei on the basis of its afferent connections. *J. Comp. Neurol.* **143**: 185-215.
4. LIPPE, W., and N. M. WEINBERGER. 1973. Distribution of click evoked activity within the medial geniculate body of the anesthetized cat. *Exp. Neurol.*, in press.
5. LOVE, J. A., and J. W. SCOTT. 1969. Some responses characteristic of cells of the magnocellular division of the medial geniculate body of the cat. *Can. J. Physiol. Pharmacol.* **47**: 881-888.
6. MEHLER, W. R. 1966. Some observations on secondary ascending afferent systems in the central nervous system, pp. 11-32. In "Pain," R. S. Knighton and P. R. Dumke, [Eds.], Little, Brown, Boston.
7. MOSTEST, D. K. 1966. The cortical structure of the inferior quadrigeminal lamina of the cat. *Anat. Rec.* **154**: 389-390.
8. MOSTEST, D. K. 1966. The non-cortical neuronal architecture of the inferior colliculus of the cat. *Anat. Rec.* **154**: 477.
9. MOSTEST, D. K. 1965. The laminar structure of the medial geniculate body of the cat. *J. Anat. Lond.* **99**: 143-160.
10. MOSTEST, D. K. 1964. The neuronal architecture of the medial geniculate body of the cat. *J. Anat. Lond.* **98**: 611-630.

11. NAUTA, W. J. H., and H. G. J. M. KUYPERS. 1968. Some ascending pathways in the brainstem reticular formation, pp. 3-30. In "Reticular Formation of the Brain," H. H. Jasper, L. D. Proctor, R. S. Knighton, W. C. Noshay and R. T. Costello, [Eds.], Churchill, London.
12. ROSE, J. E. 1942. The thalamus of the sheep: cellular and fibrous structure in comparison with pig, rabbit, and cat. *J. Comp. Neurol.* 77: 469-523.