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ORIGINAL PAPER

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Response properties of single units in areas of rat auditory thalamus that project to the amygdala

I. Acoustic discharge patterns and frequency receptive fields

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Abstract Projections from the auditory thalamus to the amygdala have been implicated in the processing of the emotional signficance of auditory stimuli. In order to further our understanding of the contribution of thalamoamygdala projections to auditory emotional processing, acoustic response properties of single neurons were examined in the auditory thalamus of chloral hydrate-anesthetized rats. The emphasis was on the medial division of the medial geniculate body (MGm), the suprageniculate nucleus (SG), and the posterior intralaminar nucleus (PIN), thalamic areas that receive inputs from the inferior colliculus and project to the lateral nucleus of the amygdala (AL). For comparison, recordings were also made from the specific thalamocortical relay nucleus, the ventral division of the medial geniculate body (MGv). Responses latencies were not statistically different in MGv, MGm ,PIN, and SG, but were longer in the posterior thalamic region (PO). Overall, frequency tuning functions were narrower in MGv than in the other areas but many cells in MGm were as narrowly tuned as cells in MGv. There was some organization of MGv, with low frequencies represented dorsally and high frequencies ventrally. A similar but considerably weaker organization was observed in MGm. While the full range of frequencies tested (1–30 kHz) was represented in MGv, cells in MGm, PIN, and SG tended to respond best to higher frequencies (16–30 kHz). Thresholds were higher in PIN than in MGv (other areas did not differ from MGv). Nevertheless, across the various areas, the breadth of tuning was inversely related to threshold, such that more narrowly tuned cells tended to have lower thresholds. Many of the response properties observed in MGm, PIN, and SG correspond with properties found in AL neurons and thus add support to the notion that auditory responses in AL reflect thalamoamygdala transmission.

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Introduction

Projections from the acoustic thalamus to the amygdala mediate the classical conditioning of emotional reactions to auditory tones paired with aversive somatosensory stimulation in rats (LeDoux et al. 1984, 1986, 1990b; Romanski and LeDoux 1992). The essential projection originates in the medial division of the medial geniculate nucleus (MGm), suprageniculate nucleus (SG), and posterior intralaminar nucleus (PIN), and terminates in the lateral nucleus of the amygdala (AL; LeDoux et al. 1985, 1990a). AL is in fact believed to be an important site, possibly the critical site, of physiological plasticity, mediated by the convergence of afferents from auditory and somatosensory pathways, during emotional conditioning (LeDoux 1987, 1992; Clugnet et al. 1990; Davis 1992).

In an effort to further understand the contribution of thalamoamygdala auditory projections to emotional learning, we recently examined the acoustic response properties of neurons in the rat AL (Bordi and LeDoux 1992; Romanski et al. 1993). This work revealed several characteristic response properties of AL cells. First, the cells have relatively short initial acoustic response latencies (12–25 ms), the earliest of which are consistent with direct transmission from the acoustic thalamus. Second, the cells respond best to high frequencies (above 16 kHz). Third, some cells have relatively sharp tuning functions, though not as sharp as the ventral division of the medial geniculate body (MGv), which is the specific or lemniscal region of the auditory thalamus. Fourth, thresholds in AL are significantly higher than in the MGv. Fifth, many of the cells habituate to repetitive stimulation. Finally, the vast majority of the acoustically responsive cells also respond to noxious somatosensory stimulation.

The purpose of the present study was to characterize the acoustic response properties of cells in the rat ex-

tralemniscal acoustic thalamus, and especially in those areas that project to AL. The areas focused on were the MGm, the PIN, and the SG. Each of these cell groups receives projections from the inferior colliculus and projects to AL (LeDoux et al. 1987, 1990a). For purposes of comparison, recordings were made in MGv. Some cells in the dorsal MG (MGd) and in the posterior thalamic region (PO) between MGm/PIN and the anterior pretectal area (APT) were also recorded. While there have been some physiological studies of the extralemniscal auditory thalamus, these have been conducted in the cat and have focused on MGm and to a lesser extent SG and subareas of PO (Phillips and Irvine 1979; Calford 1983). Although PIN provides an especially strong projection to AL (LeDoux et al. 1990a), nothing is known about the auditory response properties of cells in this region in any species and nothing is known about the auditory response properties of cells in any part of the rat thalamus. It was our hope that obtaining such information would help to explain the acoustic response properties of AL neurons and provide a foundation upon which to explore the contributions of thalamoamygdala projections to emotional learning.

Materials and methods

Animals and surgical preparation

Male Sprague-Dawley rats ($n=29$, weight 300–350 g) were anesthetized with chloral hydrate (7% in H_2O i.p., 420 mg/kg body weight) prior to surgery, and the anesthetic was supplemented as needed (every 1–2 h.) throughout the experiment. Body temperature was regulated by a heating pad. Depth of anesthesia was monitored frequently during the experiment by assessing responsivity to tail pinch.

The animals were placed in a Kopf stereotaxic frame with blunt ear bars. Stereotaxic coordinates were measured from bregma and calculated on the basis of an atlas of the rat brain (Paxinos and Watson 1986). The cranium was exposed and a small hole was drilled above the left MG. Surgery was performed as previously described by Bordi and LeDoux 1992. Briefly, three small screws were placed in the anterior part of the skull and a rod, attached to the stereotaxic frame, was cemented with dental cement to the cranial screws. The head of the animal was thereby held in the stereotaxic plane and it was possible to remove the right ear bar and replace it with a calibrated sound transmission tube for delivery of auditory stimuli (see below).

Single-unit recordings

The stereotaxic instrument and the rat were transferred to a double-walled, sound-attenuated room. A metal microelectrode (impedance 5–9 MΩ at 1000 Hz; Frederick Haer, Brunswick, Me, USA) was advanced ventrally through the skull opening towards the MG using a hydraulic micropositioner (Trent Wells, Coulterville, Calif., USA). Neural potentials were amplified ($\times$ 1 000–10 000) by an a.c. amplifier (Fintronic model WDR 420, Derby, Conn., USA), displayed on a dual-trace storage oscilloscope (Tektronix 5111A, Beaverton, Ore., USA), and sent to a BrainWave Discovery data acquisition and analysis system (BrainWave Systems, Bloomfield, Colo., USA) controlled through an AST 386 personal computer. Unit responses were segregated on-line using the Discovery algorithms. Final data analysis was based on off-line spike sorting performed with the BrainWave Common Processing Software (as described in Bordi and LeDoux 1992).

Auditory calibration and stimulation

Auditory stimuli were synthesized by the BrainWave Systems auditory stimulator (see Bordi and LeDoux 1992). The auditory stimulator is integrated with the Discovery software and hardware and consists of a digital signal processing (DSP) board (Spirit30; Sonitech International), dual 18-bit digital/analog (D/A) converters, and an external dual, 8-Ω, 250-W, passive programmable attenuator (128-dB range in 1.0 ± 0.25 dB-steps) connected to a 200 W/channel power amplifier (Denon POA 2400), all controlled by the AST computer.

Stimuli were delivered through a Sony earphone (MDR V6) mounted in a stainless steel container (Bordi and LeDoux 1992). The front wall of the container was tapered down to a centrally located hole (4 mm diameter) in which a 3-cm length of stainless steel tubing (o.d. 4 mm) was fitted and used for sound transmission. The distal end of this tube fit into the ear canal, allowing the delivery of stimuli close to the tympanic membrane. The sound transmission tube was always placed in the ear contralateral to the hemisphere from which recordings were performed. Contralateral auditory stimulation was chosen because it is known, from studies in the cat, that MG cells are more likely to be excited by stimulation of the contralateral than the ipsilateral ear (Calford 1983). The pinnae were left intact in all animals.

The sound delivery system was calibrated using the BrainWave auditory stimulator speaker calibration procedure (described in Bordi and LeDoux 1992). Briefly, determination of the power output of the sound delivery system was made with respect to a reference tone (1 kHz at 94 dB re 20 μPa) generated by a Bruel and Kjaer (B&K) model 4230 Sound Level Calibrator. A condenser microphone/preamplifier (B&K models 4133 and 2639T) was placed inside the opening of the sound level calibrator. The output of the microphone/preamplifier was further amplified by a custom-built, low-noise, high-gain operational amplifier (op-amp), the output of which was fed into an analog input of the auditory stimulator. Through the DSP board, the computer collected 8192 samples at 163.84 kHz and passed these values through a fast Fourier transform (FFT) operation to calculate the power of the reference sound. This reference power value, together with the microphone calibration curve supplied by B&K (free-field curve), allowed the conversion of additional values measured through the analog input of the auditory stimulator into absolute sound pressure level (SPL) values. The microphone/preamplifier was then inserted into a plastic holder. The holder, placed over the distal end of the sound transmission tube, positioned the microphone at approximately the same location as the tympanic membrane with respect to the end of the sound tube during the experiment. The computer delivered 400 frequencies from 200 Hz to 40 kHz (in steps of 20 Hz between 200 and 5000 Hz, and in steps of 200 Hz above 5000 Hz). For each frequency passed through the earphone, microphone, microphone preamplifier, op-amp, and auditory stimulator analog input, the computer again collected 8192 samples (at 163.84 kHz) and performed an FFT operation to determine the power output for that frequency. The values were converted into SPL values (see above). During the calibration procedure, the full output of the Denon power amplifier was attenutated by 30 dB. The output at the reference frequency (1 kHz) was 85 dB, which was thus 30 dB below the maximal output of the system for that frequency. The calibrated outputs of other frequencies were represented as deviations from the reference frequency output. A calibration curve was produced by converting $\pm$ deviations from the reference intensity (85 dB SPL) into absolute SPL values for each frequency. Over the range of frequencies calibrated, the calibration values obtained varied between 100 dB (at 4 kHz) and 40 dB (at 22–23 kHz).

Tones and intensities used for stimulus presentations were carefully selected so as to match the maximal output and attenuation limits of the sound delivery system. The maximal output for a given frequency is the calibrated intensity value of the frequency plus the amount of attenuation used in calibration (30 dB). These maximal output limits allowed us to generate intensities of at least 80 dB for all frequencies tested, except the 22- to 23-kHz range, within which we could only reach a maximum intensity of 70 dB.

To ensure the accuracy of our calibration procedure, we performed several experiments in which calibrations were performed in cadavers. After removal of the brain, the microphone was coupled to the inside of the ear canal in approximately the location of the tympanic membrane. Calibration curves obtained from these experiments had similar shapes to the calibration curves produced by our standard procedure, suggesting that there were no major resonant frequencies in our calibration system.

Cells were identified by spontaneous activity or response to search stimuli. White noise bursts (100 ms duration, including 20-ms rise and decay times, or 50 ms with 10-ms rise and decay times) or clicks (500 μs duration, with 10-μs rise and decay times) were used as auditory search stimuli (rate, one per second). Once evoked activity was detected, multiunit clusters were segregated on-line into single units or small clusters. Frequency-receptive fields were assessed by delivering several different intensities of isointensity tones (10–15 constant intensity tones varying in frequency and presented in ascending frequency order). The tones were 50 ms in duration, with 5-ms rise and 5-ms decay times. Each series of tones was repeated 10–40 times for the purpose of histogram construction. The initial tone series intensity was usually 80 dB SPL and was lowered in 10- to 20-dB steps until threshold was reached. For purposes of this on-line analysis, threshold was defined as the intensity below which the unit showed no detectable excitatory change from background, on the basis of histograms constructed on-line and on the basis of acoustically monitored spike activity. Generally, the initial sequence, presented at 80 dB SPL, included 12 tones ranging from 500 Hz to 30–35 kHz, each separated by 2–5 kHz. At intensities near threshold, a far more restricted range of tone frequencies was used. The exact tones were tailored to the response characteristics of the cell that emerged as the intensity of the isointensity tone series was lowered towards threshold, but about ten steps per octave were usually used. Tones were delivered at a repetition rate of one per second in most of the experiments, but some units were stimulated at a rate of two per second.

Data analysis

All data reported in this paper involved off-line analysis of unit recordings. Multiunit activity was sorted into multiple single units using the BrainWave Common Processing Software. In some instances (fewer than 20% of the recordings) it was not possible to isolate single units from small clusters (two or three cells) and these were therefore analyzed together. Activity that could not be segregated into single units or small clusters was not analyzed. Files were converted and transferred to a Macintosh IIci for construction of poststimulus time histograms (using the BRAHMS software provided by Dr. Weinberger and Gabriel Hui of University of California at Irvine). From these histograms, the characteristic frequency (CF), the frequency at which a unit had its lowest threshold (Møller 1983), was determined. Threshold was defined as the intensity below which the cell no longer exhibited detectable excitatory changes from background activity to the stimulus (5- to 10-dB increments of intensity were used to determine threshold). Tuning curves were made by plotting the bandwidth of excitatory response at the threshold intensity and above threshold in 10- to 20-dB step increments. The sharpness of tuning was evaluated by calculating the Q-10 value, which is the CF divided by the bandwidth of the tuning curve 10 dB above threshold (Calford 1983; Bordi and LeDoux 1992).

Histology

At the end of each experiment two small lesions (40–50 μA, 5 s) were usually made 1 mm apart in the dorsal-ventral plane of one track. Animals were perfused with 10% buffered formalin, with 5% potassium ferrocyanide, and 5% potassium ferrocyanide. The brains were frozen and cut on a sliding microtone (50-μm sections), and mounted sections were stained with thionin (0.25%) or cresyl violet (5%). Tracks were reconstructed on the basis of the lesion location using a camera lucida fitted to an Olympus BH2 microscope. Although multiple penetrations were made in each brain, it was possible to reconstruct the tracks on the basis of records of the stereotaxic coordinates of the penetrations relative to the marked track and also on the basis of visible tracks in the tissue.

Results

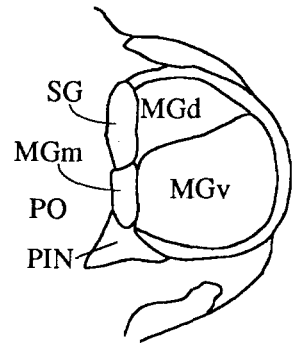
The main objective of this study was to evaluate acoustic response properties of neurons in the medial areas of the acoustic thalamus, including MGm, PIN, and SG. Response properties of neurons in MGv, the specific auditory thalamocortical relay nucleus, were used for purposes of comparison. MGv results will therefore be presented first in each section below. Some recordings were also made in MGd and in PO. Across these various regions, recordings were made from a total of 181 units responsive to auditory stimulation.

Firing characteristics

Cells were identified on the basis of spontaneous activity or in response to broadband auditory stimuli (bursts

Table 1. Activity state and response characteristics of cells in the auditory thalamus (*MGv* ventral division of medial geniculate body, *MGm* medial MG, *MGd* dorsal MG, *PIN* posterior intralaminar nucleus, *SG* suprageniculate nucleus, *PO* posterior thalamic region)

Cell state	MGv		MGm		PIN		SG		MGd		PO	
	n	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
Cell state												
Active	51	92.7	39	86.7	21	80.8	22	88.0	16	84.2	10	90.1
Silent	4	7.3	6	13.3	5	19.2	3	12.0	3	15.8	1	9.9
Total	55		45		26		25		19		11	
Responses												
Transient on	28	51.0	30	66.7	19	73.1	17	68.0	12	63.2	8	72.7
Sustained	3	5.4	13	28.9	5	19.2	7	28.0	2	10.5	3	27.3
Rhythmic	23	41.8	2	4.4	0		0		0		0	
Off	1	1.8	0		2	7.7	1	4.0	5	26.3	0	



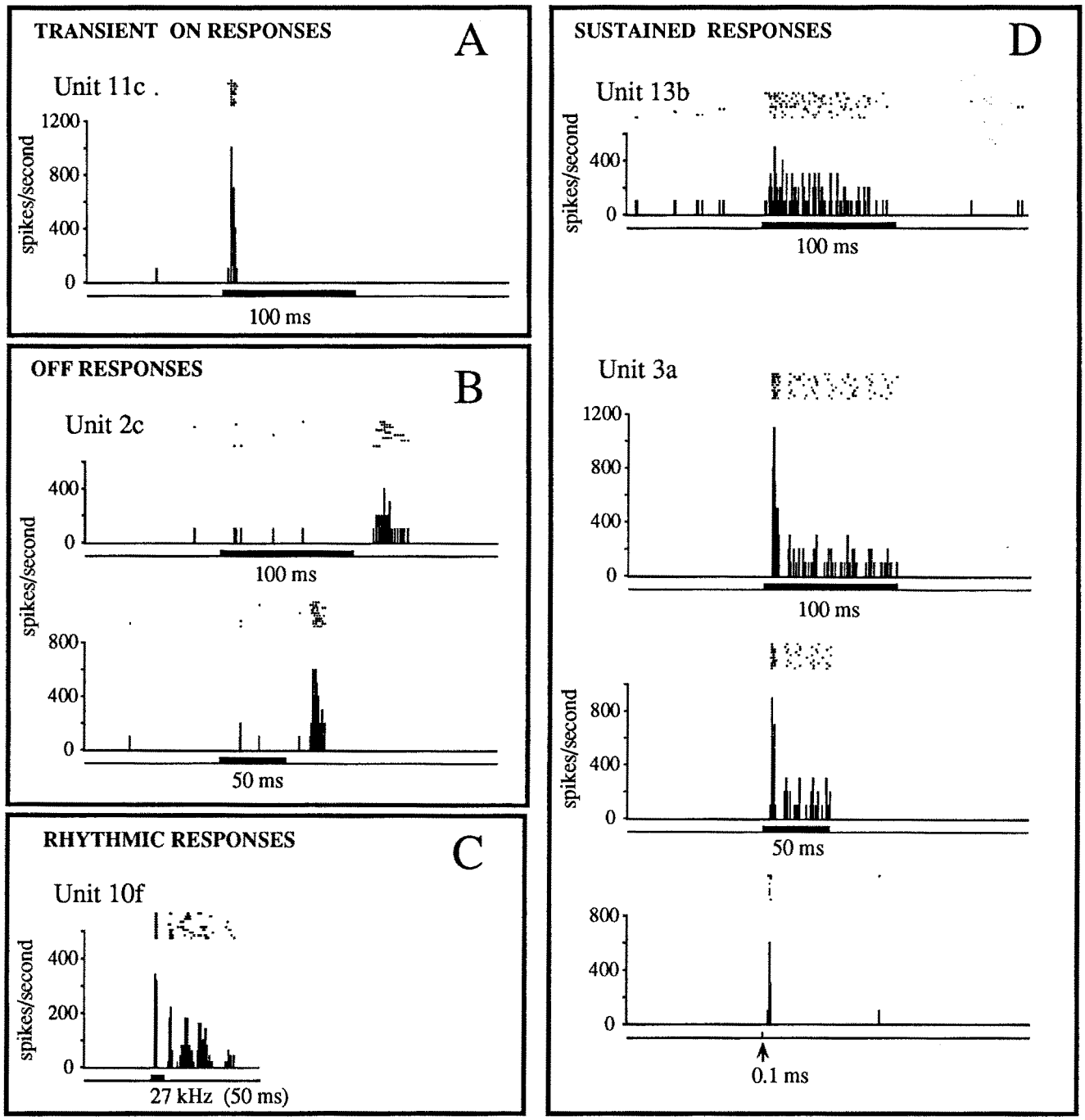


Fig. 1A–D Typical responses of units in thalamic areas to auditory stimuli (white noise 80 dB, 50–100 ms; clicks 80 dB, 0.1 ms; or tone bursts 80 dB, 50 ms). Each poststimulus time histogram represents the sum of ten trials. *Solid bar* (for white noise or tone stimuli) or *small arrow* (for click stimuli) underneath each histogram marks the stimulus period (*solid bar* indicates noise stimuli except in **C**). *Raster plots* above each histogram illustrate the temporal distribution of spikes for each trial, with the first trial plotted on the *bottom row of the raster display*. Histogram binwidth is 1 ms, except in **C** (rhythmic responses), where the binwidth is 5 ms. **A** Transient on responses were elicited by stimulus onset. **B** Off responses occured after stimulus termination. Unit 2c, tested with a 100-ms and a 50-ms stimulus, shows that the response is linked to stimulus offset and is not simply a long-latency response linked to onset. **C** Rhythmic responses occurred with a fairly consistent period after stimulus onset. Each successive period of the response tended to include fewer spikes. Unit 10f, activated rhythmically by a 27-kHz tone, gave a typical rhythmic response. **D** Sustained responses occurred throughout most of the stimulus period (though not necessarily continuously) and terminated with stimulus offset. Unit 3a shows the tight coupling of sustained responses to the stimulus period. The response terminates with the offset of either a 100-ms or a 50-ms burst of noise (top two panels) and the response is very brief to a 0.1-ms click (*bottom panel*)

of white noise 50–100 ms, 70–80 dB). Acoustically responsive cells were classified as spontaneously active or silent (less than 1 spike in 5 s). Of the 181 units identified, between 80 and 90% were spontaneously active in each area examined. As shown in Table 1, there were no obvious differences in the distribution of spontaneously active and silent cells in the different areas. For the spontaneously active cells, some differences in rates and firing patterns may be present across the various areas. For example, cells in MGv were more likely to fire in bursting patterns than cells in other areas. However, patterns of spontaneous activity were not examined in detail.

Table 1 also shows the types of responses evoked by broadband auditory stimuli in the different thalamic regions recorded from. Following Calford (1983) and Calford and Webster (1981), responses were categorized as being: *transient on* (short-latency response locked to stimulus onset), *sustained* (response throughout the duration of the stimulus or a transient response followed by a brief silent period and thereafter firing throughout the duration of the stimulus), *reverberating* or *rhythmic* (transient on and off response followed by oscillating firing with a relatively constant period), *off* (responses only triggered by stimulus termination). Examples of each response type are shown in Fig. 1.

Transient on responses were the most frequent type of evoked responses encountered across the whole acoustically responsive thalamic region, accounting for between 51 and 73% of the cells in each subregion recorded from (Table 1, Fig. 1). Some cells in the transient class responded with an on-off pattern, similar to cells in the rhythmic response class, but they did not have reverberating firing afterwards. Units from both of

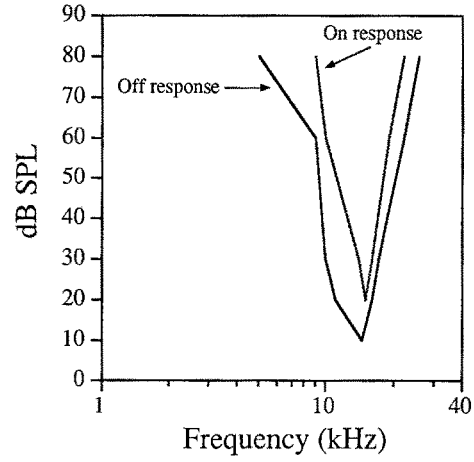


Fig. 2 Frequency threshold (tuning) curves, constructed separately for on responses and off responses, of a single neuron recorded in the ventral division of the medial geniculate body. Tuning curves were constructed by plotting the responsive frequency range for intensities at and above threshold (in 10- to 20-dB steps). These tuning curves illustrate the lower threshold and somewhat broader tuning of the off responses. (*SPL* sound pressure level)

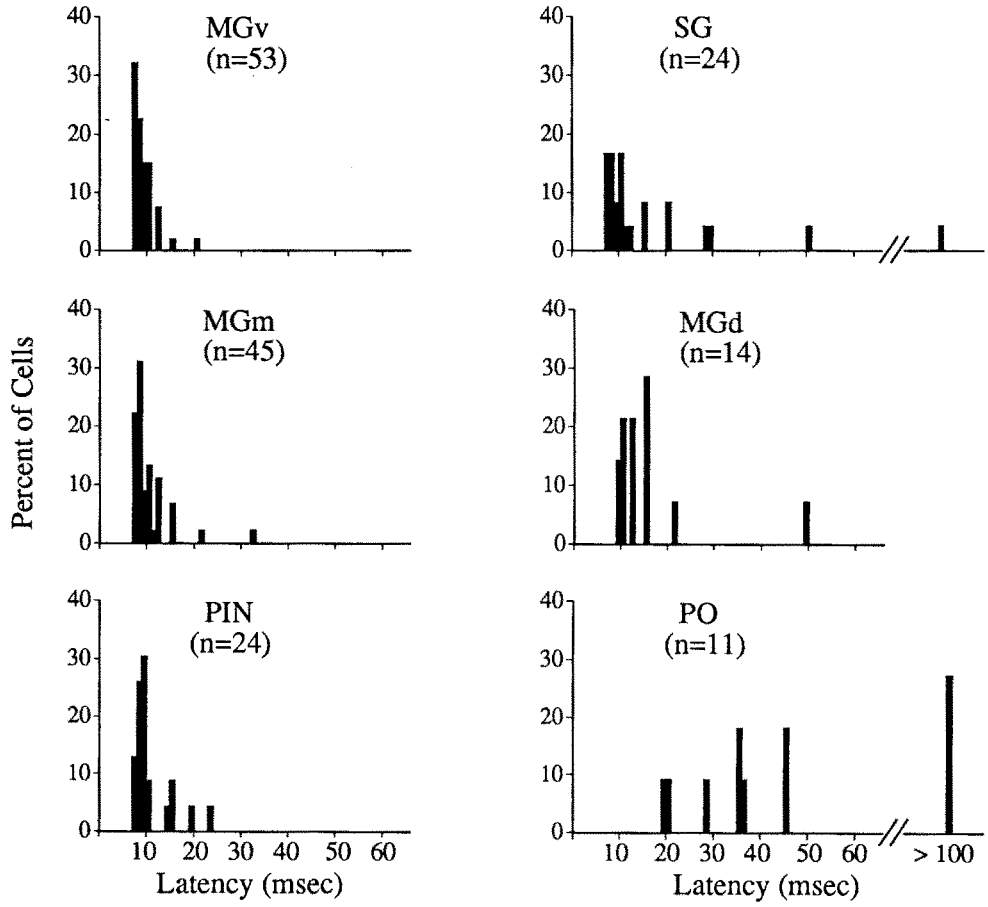


Fig. 3 Proportional histogram presentation of latencies for units recorded in all areas examined. The numbers of units forming each group are indicated in *parentheses*. Off response cells are not included (see Table 1). (*MGv* ventral division of medial geniculate body, *MGm* medial division of MG, *MGd* dorsal division of MG, *PIN* posterior intralaminar nucleus, *SG* suprageniculate nucleus, *PO* posterior thalamus)

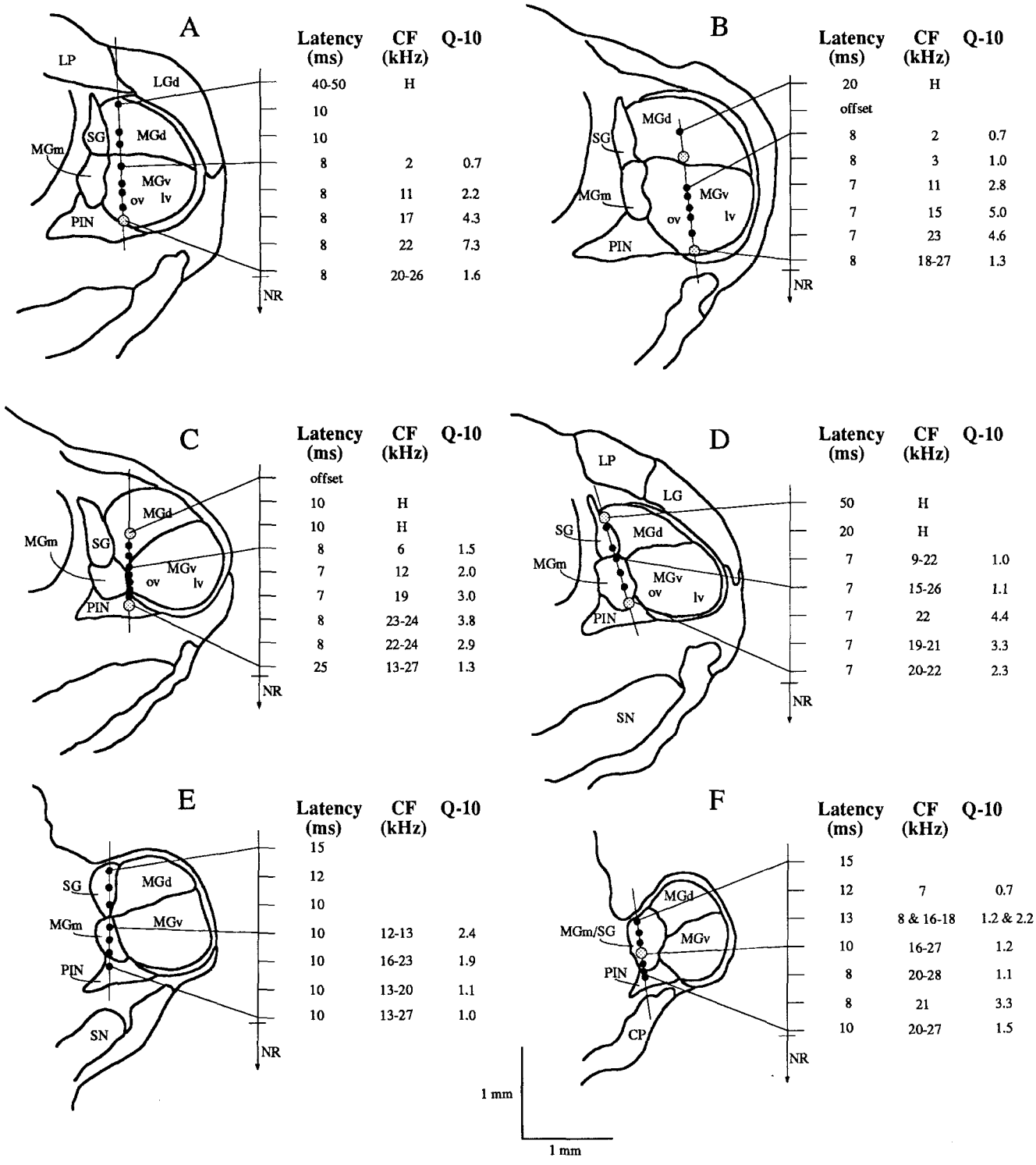
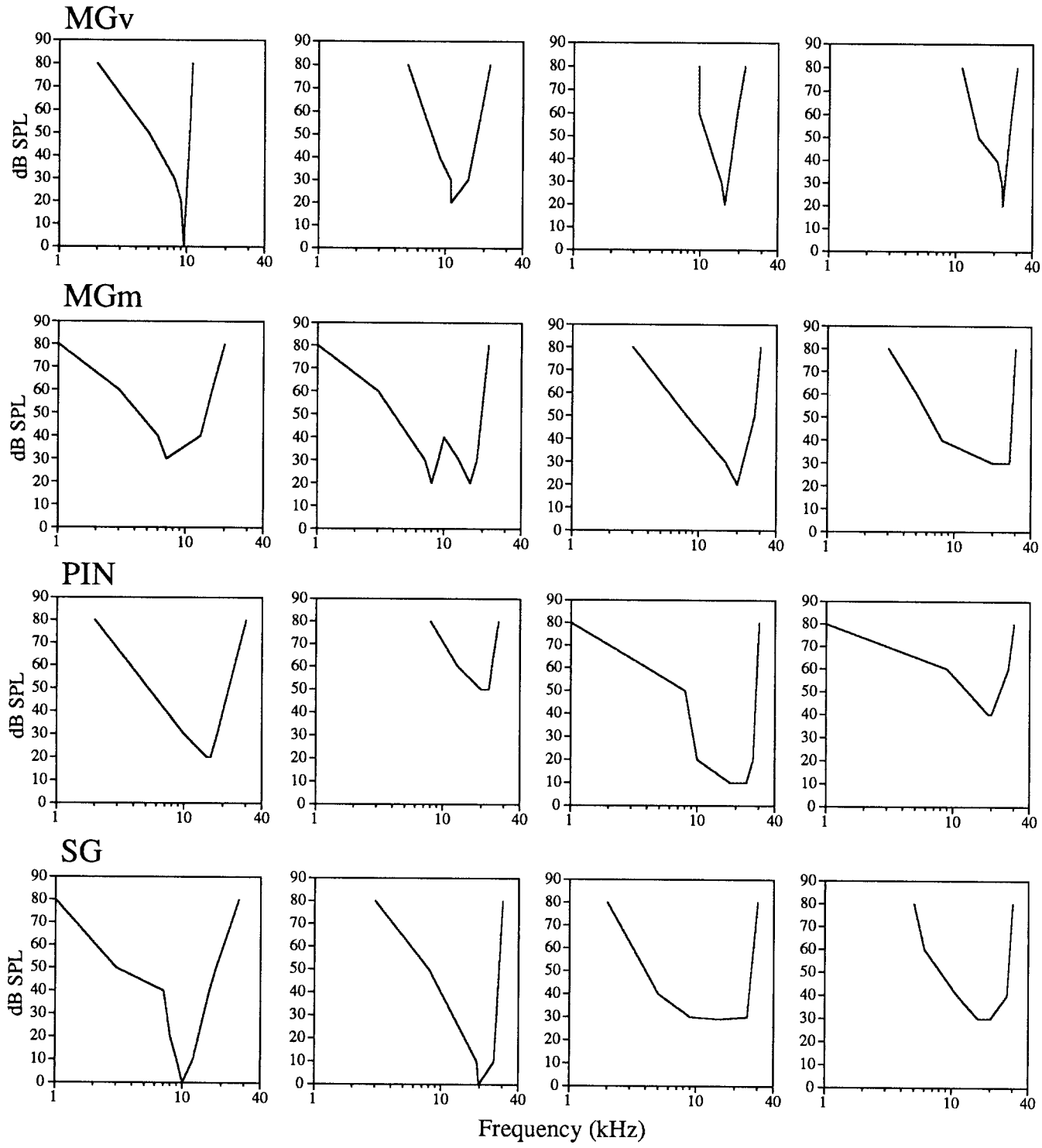


Fig. 4A–F Sections through the MG from six different experiments. For each recording track shown, the onset latency, characteristic frequency (*CF*), and *Q*-10 of the units recorded from (anatomical location indicated by *black dots*) are presented in the *table* to the *right* of each section. Lesions, used to mark tracks, are indicated by *stippled circles*. As electrodes moved through MGv in the dorsoventral direction, CFs tended to change from low to high, suggesting some degree of tonotopic organization in this region. There was a similar, but somewhat less pronounced organization within MGm. PIN, in contrast, mainly had cells with high-frequency CFs. The other regions had no obvious frequency characteristics. Acoustically responsive cells that were not characterized because of rapid habituation, inconsistent responsivity, or offset characteristics, have no entries in the CF and *Q*-10 columns. (*H* habituating cells, *NR* no acoustic response, *CP* cerebral peduncle; *LGd* dorsal lateral geniculate body, *LG* lateral geniculate body, *LP* lateral posterior nucleus, *lv* pars lateralis of MGv, *MGd* dorsal division of medial geniculate body, *MGm* medial division of medial geniculate body, *MGv* ventral division of medial geniculate body, *ov* pars ovoidea of MGv, *PIN* posterior intralaminar nucleus, *PO* posterior thalamus, *SG* suprageniculate nucleus, *SN* substantia nigra)



these classes had off responses (with or without reverberating characteristics); threshold was usually lower for the off than for the on response, as shown in Fig. 2 for a single MGv cell.

The other response types were unevenly distributed across the regions recorded from. MGv mostly had cells with transient on (51%) or rhythmic (42%) responses. MGm and SG, in addition to transient on responses (67% and 68%, respectively), had cells with sustained responses (29% and 28%, respectively), but relatively

Fig. 5 Frequency threshold (tuning) curves for cells recorded from MGv, MGm, PIN, and SG. Tuning curves were constructed by plotting the responsive frequency range for intensities at and above threshold (in 10- to 20-dB steps). The frequency (or frequency range) with the lowest threshold was identified as the CF or CF range. Cells with comparable CFs are shown for each area. Although MGv had CFs that spanned the frequency spectrum tested (1–35 kHz), for comparison with MGm, PIN, and SG (which tended to have cells with somewhat higher CFs), only higher frequency tuning curves are shown. MGv tended to have more sharply tuned cells than the other areas, as indicated by the narrower excitatory bandwidth

few with rhythmic or off responses. PIN had mostly transient on responses (73%) but also had some sustained (19%) and off (8%) responses. MGd had many cells with transient on responses (63%) and a substantial number with off responses (26%); MGd was the region where off responses were most likely to be found.

Latency

Latency (determined by visual inspection of the oscilloscope trace and by off-line analysis of the poststimulus histograms) was defined as the shortest response exhibited by the unit when presented with white noise stimuli (50–100 ms duration, 80 dB) or tone bursts (50 ms, 80 dB). The distribution of minimum response latencies for units in the six areas examined are presented in Fig. 3. Mean latencies were shortest in MGv (9 ± 2), intermediate in MGm (10 ± 4 ms) and PIN (10 ± 4 ms), and longer in SG (18 ± 20 ms) and MGd (15 ± 10 ms). Considerably longer latencies were obtained in PO (53 ± 30 ms).

Statisical evaluation of latencies, using analysis of variance, produced a significant overall F test ($P < 0.05$). Post-hoc comparisons using the Dunnett test revealed that the only significant comparison was between MGv and PO ($P < 0.05$).

Frequency tuning

Frequency-threshold (tuning) curves were constructed for all cells that consistently responded to stimulus presentations. Frequency receptive field determinations were made for 43 recordings in MGv, 45 in MGm, 22 in PIN, 25 in SG, and 15 in MGd by plotting the bandwidth of excitatory responses at the threshold intensity and at intensities above threshold in 10- to 20-dB increments. Extent of tuning was assessed quantitatively using the Q-10 statistic (see Materials and methods). In most instances, the data analysis of frequency tuning is based on isolated single units, but a small proportion of the recordings (less than 20%) involved small clusters (two or three cells). However, within these clusters, it did not appear that substantial differences existed in tuning properties, and therefore the clusters are described as well as the single units.

MGv

Frequency tuning was evaluated in 43 recordings in MGv. These cells typically had short-latency, consistent responses, and, as intensity decreased, a clear CF emerged. At intensities above threshold, the bandwidth of responsivity was relatively narrow. CFs scattered across the frequency spectrum tested (1–30 kHz) were found. However, three cells on the border between MGv and the marginal zone had distinctly broader tuning functions and longer latencies. These cells were not included in the MGv group. Representative recording tracks through MGv are depicted in Fig. 4A,B, and typical tuning curves for MGv cells are shown in Fig. 5.

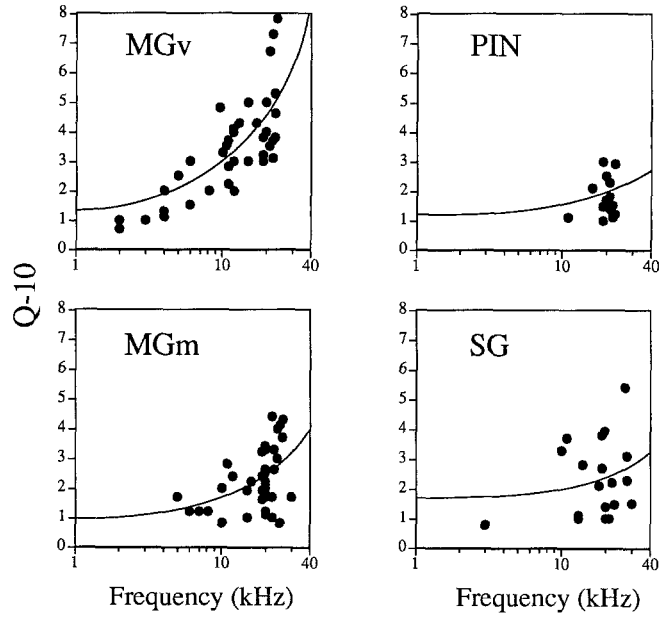
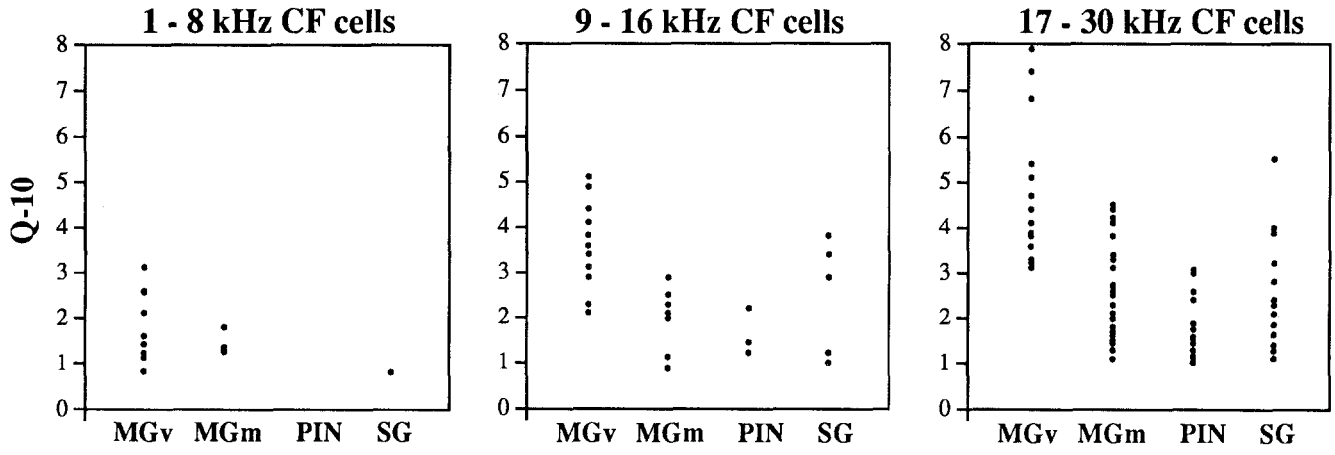


Fig. 6 Q-10 values for units in MGv, MGm, PIN, and SG. Q-10 values were calculated as CF/bandwidth at 10 dB above threshold (see Materials and methods). Curves were fit through the points using a first order polynomial equation. Examination of the fit curves shows that for a given frequency, MGv cells tended to have higher Q-10 values, and thus tended to be more sharply tuned, than cells in the other areas. The tendency of cells in MGm, PIN, and SG to prefer higher frequencies is also apparent from these plots

Q-10 for each cell recorded from in MGv is plotted in Fig. 6. A curve was fit through the points using a first-order polynomial equation. Higher Q-10 values indicate sharper tuning. Visual inspection of these curves graphically illustrates differences in tuning between the regions, especially between MGv and the other nuclei. As these curves illustrate, MGv cells tend to be more sharply tuned than cells in the other thalamic regions. The upwards slope of each of the plotted curves reflects a built-in bias in the Q-10 statistic: higher frequencies have larger Q-10s (Calford and Webster 1981). As a result, Q-10 values of different cells are most meaningfully compared if the cells have similar CFs. In order to facilitate comparisons of the sharpness of tuning between MGv, which has cells with CFs distributed throughout the frequency spectrum tested, and other thalamic subregions, some of which mainly have cells with high CFs, cells were classified on the basis of CF. Figure 7 plots Q-10 values for MGv cells in three frequency ranges (1–8, 9–16, or 17–32 kHz). For a given frequency range, MGv cells tend to have higher Q-10 values than the other regions (see below). An analysis of variance was performed for each of the Q-10 ranges. The F statistic was not significant for the lowest range (1–8 kHz) but was for the 9–16 kHz ($P < 0.001$) and 17–30 kHz



	1 - 8 kHz CF cells				9 - 16 kHz CF cells				17 - 30 kHz CF cells			
	MGv	MGm	PIN	SG	MGv	MGm	PIN	SG	MGv	MGm	PIN	SG
$\bar{X}$ =	1.58	1.33		0.75	3.52	1.95	1.57	2.36	4.59	2.46	1.85	2.48
SD =	0.78	0.22		0	0.88	0.76	0.57	1.3	1.45	1.04	0.67	1.35
n =	10	4	0	1	14	7	3	5	16	29	12	13

Fig. 7 Q-10 values for cells with comparable CFs. Cells were classified into three groups on the basis of CF: 1–8 kHz; 9–16 kHz; and 17–30 kHz. In each frequency range, MGv had the highest Q-10 values overall and thus tended to be more sharply tuned than the other areas. MGv Q-10 values were significantly different from MGm and PIN for the middle- (9–16 kHz) and high- (17–30 kHz) -frequency ranges and from SG in the middle range (see text). In spite of these differences, some cells in MGm and SG had Q-10 values that overlapped with the lower part of the MGv distributions, especially in the intermediate- and high-frequency ranges. However, PIN cells tended to be below the Q-10 distributions of MGv cells. Mean ($\bar{X}$), SD, and number of cells (n) are indicated *underneath* each CF range for each thalamic subnucleus

($P<0.001$) ranges. Post-hoc comparisons with Dunnett's test revealed that MGv differed from MGm and PIN for both significant ranges, but that SG only differed from MGv for the middle range (9–16 kHz) ($P<0.05$).

MGm, PIN, and SG were the major targets of our experiments. As a result, most of the MGv units encountered were due to misplaced electrodes within the medial part of MGv and specifically in the pars ovoidea (ov). As the electrode passed through MGd and entered ov, a clear transition in responses typically occurred. Cells with consistent, short-latency responses and sharp tuning began to predominate. Ventral movements of the electrode within ov tended to result in increases in the CF of the units encountered. No clear rostrocaudal or medial-lateral differences were apparent. Examples of the dorso-ventral organization can be seen in Fig. 4A,B.

MGm

In MGm, 37 of 45 units recorded from showed consistent response to isointensity tones. Frequency tuning was analyzed in these. The rest of the cells (8) showed habituation or responses that were not time-locked to auditory stimuli.

Frequency preferences in MGm tended to be for the intermediate and higher frequencies tested, with only 4 cells having CFs below 10 kHz. Some of the MGm cells had distinct CFs and narrow tuning functions, similar in this respect to most of MGv units; others, however, responded to a wider range of frequencies. Representative recording tracks through MGm are shown in Fig. 4 and typical tuning curves are shown in Fig. 5.

In general, cells in MGm tended to prefer higher frequencies (>10 kHz), and this was particularly characteristic of the ventral aspect of MGm as it blends with the underlying PIN (Fig. 4). When lower frequencies were encountered, they were always located dorsally within MGm. Within a track passing though MGm, CFs had some tendency to move from low to high (see Fig. 4D–F).

Three MGm units had two peaks. Multipeaked responses were distinguished from single peaked responses using criteria described by Sutter and Schreiner (1991): the thresholds of the peaks had to differ by less than 40 dB, and the separation between peaks had to be maintained at more than 15 dB above threshold. For cells that met these criteria, separate Q-10 values were calculated for each peak in the analysis described below. For the three multipeak neurons in MGm, the CFs of the two peaks approached 1 octave of each other, and were very close to the 2nd and 3rd harmonics of a fundamental frequency to which the unit was not responsive (Sutter and Schreiner 1991).

Q-10 values for MGm tended to be somewhat lower than those for MGv cells with similar CFs, as illustrated by the curve fit through the Q-10 values in Fig. 6. Segre-

gation of Q-10 values into three frequency groups illustrates the nature of MGm tuning: the fact that across the three frequency ranges roughly half (17 of 37) of the MGm cells fall within the range of MGv cells indicates that MGm cells can be relatively sharply tuned; that the overlap is restricted to the lower half of the MGv Q-10 distribution indicates that MGm cells are not as sharply tuned as the most sharply tuned MGv cells. Analysis of variance and post-hoc evaluation with Dunnett's test showed that Q-10 values differed between MGv and MGm for the 9- to 16-kHz and the 17- to 30-kHz ranges (see MGv results above).

PIN

Frequency tuning was evaluated in 16 PIN cells that responded consistently to auditory stimulation (six other cells habituated rapidly or did not show a time-locked response to the stimuli). Even more so than in MGm, cells in PIN tended to respond best to higher frequencies. Most cells in PIN had CFs between 16 and 27 kHz and no PIN cells had a CF below 11 kHz. Representative recording tracks that included PIN cells are shown in Fig. 4 and typical tuning curves are presented in Fig. 5. Q-10 calculations revealed that most of the PIN cells (13 of 16) were outside of the Q-10 range of MGv cells with similar CFs (Figs. 6, 7). Q-10 values for PIN differed statistically from those of MGv for the 9- to 16-kHz and 17- to 30-kHz ranges (see MGv results above).

SG

Frequency preferences were present in 19 of 25 cells in SG (6 cells exhibited rapid habituation). CFs below 10 kHz were rarely seen. Like MGm, some SG cells had Q-10 values that overlapped with the MGv distribution (Figs. 6, 7). In the analysis of variance of Q-10 values, SG only differed from MGv in the middle range (9–16 kHz; see MGv results above). One of the SG units was multi-peaked (see MGm results for criteria). Representative tracks through SG are shown in Fig. 4 and tuning curves in Fig. 5.

MGd

Although the aim of the present study was not primarily the investigation of MGd, 15 cells in this area were isolated and carefully investigated. However, 4 of these habituated quickly and 6 had inconsistent responses to auditory stimuli. Rapidly habituating cells were present in this nucleus more than in any other. These units tended to respond only to the first few presentations of auditory stimuli, often independent of the starting frequency, and often with varying latencies. Only 5 cells had a distinguishable CF, and 3 of these cells had CFs at relatively low frequencies (4, 7, 13.5 kHz). Q-10 values for these 3 units were within the range seen in MGv, whereas the 2 units with high frequency CFs were less sharply tuned (not shown).

Other areas

Some cells in PO were acoustically responsive; these cells responded to very broad ranges of frequencies and did not exhibit a clear CF. However, a few cells in the most ventral and lateral aspects of PO adjacent to MGm and PIN exhibited short-latency responses to white noise. These had some preferences for higher frequencies (> 16 kHz), but responded to a broad range of high frequencies. One cell located ventral to PIN and near the lateral nucleus of the substantia nigra, but within the projection field of the inferior colliculus (LeDoux et al. 1987), had a CF of 20 kHz and a Q-10 of 2.6.

Intensity thresholds

The mean intensity thresholds for cells in MGv, MGm, PIN, and SG are shown in Fig. 8. An analysis of variance produced a significant F statistic ($P<0.05$). Post-hoc comparisons with the Dunnett's test revealed that PIN cells had a significantly higher threshold than MGv cells ($P<0.05$), but none of the other areas differed. In general, threshold and tuning were inversely related, such that cells in MGm, PIN, and SG with lower Q-10 values had higher thresholds than cells with higher Q-10 values ($r=-0.562$, $P<0.01$). Thus, threshold is higher for more broadly tuned cells.

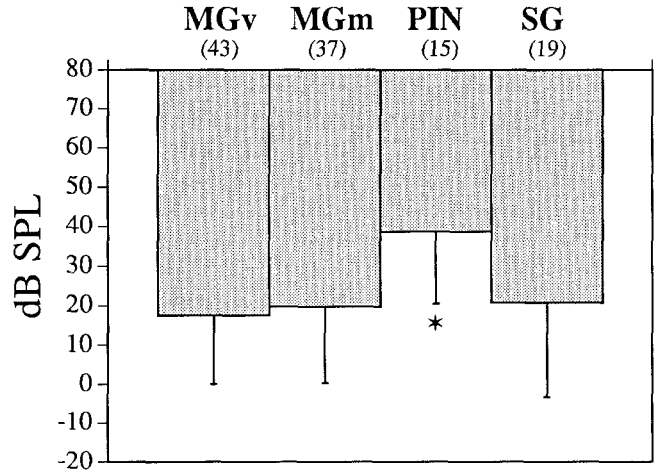


Fig. 8 Threshold intensity (the lowest stimulus intensity producing any auditory response) for units in MGv, MGm, PIN, and SG. PIN was significantly different from MGv (*$P<0.05$; see text). Mean threshold did not differ between the other areas. However, within MGm/PIN/SG, threshold was inversely related to Q-10 (see text) indicating that thresholds were higher for more broadly tuned cells. Values are shown as mean ± SD. The number of cells in each group is shown in *parentheses*

Discussion

The aim of the present study was to characterize in the rat the acoustic response properties of neurons in areas of the auditory thalamus that are known to give rise to projections to the AL. The areas focused on were MGm, PIN, and SG. Responses from these regions were compared with responses obtained from cells in the lemniscal auditory thalamic nucleus, MGv. Additionally, recordings were made in MGd and in PO.

Most work on the neurophysiological response properties of single cells in the auditory thalamus in mammals has involved studies of cats (Aitkin 1973; Rouiller et al. 1979; Calford and Webster 1981; Calford 1983; Morel et al. 1987), and, to a lesser extent, squirrel monkeys (Starr and Don 1972; Allon et al. 1981). Our findings expand the range of species studied and provide the first description of the auditory response properties and tuning characteristics of unit recordings in the MG of rats. The results demonstrate that, as in other species, the different nuclei of the auditory thalamus have different auditory coding properties. Although our main focus was on the extralemniscal regions that project to the amygdala, recordings in these regions are best understood by comparison with recordings in the specific or lemniscal thalamocortical relay nucleus, MGv.

Recording made from the *MGv* in the rat are in good agreement with previous studies in the cat (Calford 1983). Cells in rat MGv generally responded with short, initial onset latencies (7–10 ms). The responses were frequency-specific and had CFs distributed across the frequency spectrum tested (1–35 kHz). Since our recordings were almost all from the ov region of MGv (Morest 1964, 1965; Winer 1992), it seems that at least within this nucleus the full frequency range studied is represented. A large class of MGv cells (over 40% of the population recorded from) responded to auditory stimuli in rhythmic fashion. So-called reverberating responses have been commonly recorded in cat MG (Gross and Thurlow 1951; Galambos et al. 1952; Aitkin et al. 1966). In our study, reverberating responses were mainly recorded from MGv.

Frequencies appeared to be orderly represented in MGv. Cells with low CFs were often found dorsally in ov and CFs tended to increase as the electrode was moved ventrally. However, our data on this point are too limited to allow strong conclusions about a tonotopic organization of the rat MGv. Nevertheless, it is interesting that in studies of cats a similar arrangement was described by Calford and Webster (1981), but Imig and Morel (1983) found evidence for a different (more complex) organization.

Cells in *MGm* had initial onset latencies similar to those recorded in MGv. However, other response characteristics distinguished these nuclei. When cells were matched for CF, Q-10 values were on the average lower in MGm than in MGv. Roughly half of the cells in MGm were more broadly tuned than MGv cells; that is, these cells had Q-10 values outside the range of MGv cells with comparable CFs. At the same time, it is important to emphasize that almost half of the MGm cells did fall within the tuning range of MGv cells. The overlap was entirely accounted for by the lower half of MGv Q-10 values; though some MGm cells were tuned, they were not as sharply tuned as the more sharply tuned MGv cells. Multipeak or complex receptive field neurons were found in MGm, but not in MGv, as previously reported in the cat (Aitkin 1973; Calford 1983). Cells in MGm tended to respond more to higher frequencies (above 16 kHz) and did not therefore represent the full acoustic frequency range as well as MGv. Within the range of frequencies found in MGm, cells with relatively lower CFs were mainly encountered dorsally and cells with relatively higher CFs were mainly encountered ventrally, near the junction with PIN. Sustained discharge to auditory stimulation was more common than in MGv, and rhythmic responses were rare. In the cat Aitkin (1973) also described reverberatory responses in only one MGm unit. The high degree of affinity between the rat and the cat in the acoustic responsivity of MGm cells is probably accounted for by the similar architectural composition and connectivity with the inferior colliculus of MGm in these two species (Morest 1965; Calford and Aitkin 1983; LeDoux et al. 1985, 1987; Clerici and Coleman 1990; Morest and Winer 1986).

PIN in the rat is included in the auditory nuclei of the thalamus since it receives afferents from the extralemniscal areas of the inferior colliculus (LeDoux et al. 1985, 1987). However, since the extralemniscal areas of the inferior colliculus receive somatosensory inputs as well as inputs from lower auditory processing regions (Walsh and Ebner 1973; Massopust et al. 1985), anatomical evidence that PIN receives collicular inputs is insufficient for concluding that PIN is an auditory processing region. However, our physiological results clearly show that PIN cells are acoustically responsive. Their characteristics were similar in many respects to MGm cells, but differences were also apparent. Some PIN cells were broadly tuned, others had sharper frequency preferences. Cells responded best to higher frequencies (above 16 kHz); CFs in PIN seldom went below 16 kHz, whereas in MGm some cells with CFs between 8 and 16 kHz were found. PIN cells tended to be even less sharply tuned than MGm cells; only three PIN cells (out of 16 units) had Q-10 value inside the range of MGv cells with analogous CFs. Response latencies were similar to those in MGm and MGv.

Previous studies of other species have not recorded from PIN. While PIN is recognized anatomically in the rat (LeDoux et al. 1985, 1987, 1990a), opossum (Morest and Winer 1986; Winer et al. 1988), and guinea pig (Cruikshank et al. 1992), it has not been specifically identified in the cat or monkey. However, on the basis of anatomical landmarks and connectional data, it may be that the region identified as the peripeduncular nucleus (PP) in both the cat and the primate is the PIN of the rat, opossum, and guinea pig. In the cat and primate, PP is located ventral to MGm and projects to the AL (Jones

et al. 1976; Mehler 1980; Russchen 1982). The rat also has a PP, but this structure encapsulates the cerebral peduncle, as its name implies it should. Whether PP (PIN?) is acoustically responsive in cats and primates has not been reported. It is not known whether this is because acoustically responsive cells are not located there or because they have not been searched for.

SG cells responded with onset latencies similar to those of MGv, MGm, and PIN. In the cat SG, cells with very long latencies were found (Calford 1983). However, cells with very long latency responses were not seen as often in the rat SG. Of 19 cells consistently responding to auditory stimuli, 7 were within Q-10 range of MGv cells with similar CFs. Although we found some cells that habituated to repeated stimulus presentation (rate, one per second), the proportion of such cells found in the rat (about 25%) was considerably less than the 95% reported for the cat (Calford 1983). In general, SG cells of the rat responded similarly to MGm cells. Although myeloarchitecturally SG resembles MGd and was included as a subdivision of this nucleus by Morest and Winer (1986), cytoarchitectural and connection studies in the rat suggest a close resemblance of SG to MGm (Clerici and Coleman 1990; LeDoux et al. 1985, 1987, 1990a). The present physiological data suggest that SG is more like MGm than like MGd (see below).

MGd cells were the least responsive to acoustic stimulation of all MG subnuclei recorded from, as previously reported in the cat (Toros-Morel et al. 1981; Calford 1983). Onset latencies were also longer than in the other nuclei, and rapid habituation units were common. The MGd was not a focus of our investigation, and we recorded from only 15 cells in this region. Of these 15, only 5 showed auditory responses consistently. Also, 3 of these 5 cells had relatively low frequency CFs (below 13.5 kHz). Physiological characteristics studied in the cat suggest that the deep dorsal area codes mostly high frequencies (Calford 1983). The lack of agreement with our findings may be explained by the small sample examined or may reflect a species difference. MGd is morphologically and anatomically complex and the least understood of the MG subnuclei but no major morphological differences have been noted between the rat and the cat (Clerici and Coleman 1990).

Recordings were also made from the *PO*. In the rat, this region receives a strong spinothalamic projection, and a weaker inferior colliculus projection (LeDoux et al. 1985, 1987). It is thus not surprising that cells in PO respond poorly to acoustic stimulation and are highly responsive to somatosensory stimulation (Bordi and LeDoux 1994); onset latencies were typically long and thus inconsistent with direct inputs from brainstem auditory processing regions. The origin of these delayed responses is unknown. In none of these cells were we able to construct tuning curves. However, in some cases a tendency for a preference for high frequencies (above 16 kHz) was noticed, especially if FM stimuli centered around high frequencies (e.g., 20 kHz) were used. In the cat, some recordings have been made in PO areas (Phillips and Irvine 1979). Comparisons between the two species are not very easily made due to the difficulty in identifying homologous structures in the PO. The area we recorded from appears to correspond (on morphological grounds) to the caudal medial posterior Thalamus (Pom) in cat. As in the cat Pom (Phillips and Irvine 1979), we found few auditory responses in PO, except in areas adjacent to MGm and PIN.

Overall, this study suggests a high degree of functional homology between the rat and the cat. Physiological properties of units in the rat auditory thalamus seem to confirm closely the anatomical subdivisions adopted for the cat (Morest 1964, 1965) and the opossum (Morest and Winer 1983; Winer et al. 1988) and subsequently for the rat (LeDoux et al. 1985; Winer and Larue 1988; Clerici and Coleman 1990).

A major goal of the present study was to determine the extent to which acoustic responses we previously recorded in AL (Bordi and LeDoux 1992) might be accounted for by direct thalamoamygdala transmission. Several similarities, and some differences, between AL and MGm/PIN/SG were found. First, acoustically responsive cells in AL had preferences for high frequencies, mostly above 16 kHz. This was also true for MGm/PIN/SG cells. Second, many cells in AL and in MGm/PIN/SG had fairly restrictive receptive fields, but they were on the average more broadly tuned than cells in MGv. Third, most AL cells had relatively high thresholds (about 40 dB on the average, with some going as high as 80–90 dB). In MGm/PIN/SG (but especially in PIN) the more broadly tuned cells also had high thresholds. Some dissimilarities, however, were also registered between these two areas. Acoustically responsive cells in AL were more likely to be silent or to have very low rates of spontaneous activity (about 1 spike/s), while most cells recorded from in MGm/PIN/SG were spontaneosly active. Also, AL cells were more likely to habituate to repeated auditory stimulation than cells in MGm/PIN/SG.

Thus, the similarities in acoustic processing between MGm/PIN/SG and AL far outweigh the differences on the dimensions tested so far. At least some of the auditory responses in AL thus appear to be derived directly from transmission over thalamoamygdala pathways. This conclusion is further strengthened by an analysis of response latencies in these areas. The earlier response latencies in MGm/PIN/SG (7–12 ms), together with the latencies required for activation of AL by electrical stimulation of MGm/PIN/SG (4–8 ms) (Clugnet et al. 1990), are sufficient to account for the earlier auditory response latencies recorded in AL (12–20 ms). However, AL also receives the major auditory inputs from the cortex in the rat (LeDoux et al. 1991; Romanski and LeDoux 1992) and some of the auditory responses are surely transmitted over corticoamygdala pathways as well. The existence of some differences between acoustically responsive cells in AL and MGm/PIN/SG suggest that some additional integration/computation is provided by projections to the amygdala from the auditory

cortex or by the amygdala itself. Additional studies will be required to further illuminate the unique contributions of thalamoamygdala and corticoamygdala projections and of the amygdala.

The functional significance of direct thalamoamygdala transmission deserves some comment. The amygdala has long been recognized as an important region for the processing of the emotional significance of events and the control and expression of emotional reactions (see LeDoux 1987). Thalamoamygdala projections may provide a channel for rapid processing of acoustic stimuli with emotional significance. While the discriminative and analytic capacities of these systems are limited, since they bypass the neocortical auditory system, they nevertheless may be useful in responding to biologically significant events. For example, the tendency of cells in AL, as well as in MGm/PIN/SG, to prefer high frequencies (16–30 kHz) may be related to the fact that rats emit warning calls in this frequency range when threatened (Nitschke 1982; Blanchard et al. 1991). Projections from MGm/PIN/SG to AL may be used to detect and encode the warning calls and organize appropriate defensive reactions. Moreover, the relatively high thresholds of PIN cells (as well as of the more broadly tuned MGm and SG cells) and of AL suggest that the pathway connecting these areas may function as an intensity filter, allowing the amygdala to respond to relatively loud stimuli and to ignore less intense events processed by the thalamus. Loudness is of obvious importance as a cue to distance, and objects that are closer are more threatening than those that are far away. Direct thalamotransmission may then allow the amygdala to begin initiating defense responses on the basis of stimulus intensity. Also, thalamoamygdala projections have been implicated in emotional learning tasks involving auditory stimuli (see Introduction). Learning in these situations may involve an adjustment of the intensity threshold of thalamic cells, thereby allowing less intense stimuli that have been endowed with significance by their association with painful stimuli to gain access to thalamoamygdala transmission. Alternatively, learning may involve a sharpening and/or shifting of the tuning curve of thalamic cells, as Weinberger, Edeline and colleagues have shown (Edeline 1990; Edeline and Weinburger 1991a,b, 1992; Lennartz and Weinberger 1992).

In conclusion, we have shown that (1) the specific auditory thalamocortical relay nucleus, MGv, has short-latency, sharply tuned cells, very similar to those previously described in the cat; (2) regions MGm, PIN, and SG have cells with somewhat broader frequency tuning, although the tuning properties of some cells in these areas, especially in MGm, closely resemble those seen in MGv neurons; (3) cells in MGm, PIN, and SG represent a narrower range of frequencies (mostly above 16 kHz) than cells in MGv, where the entire frequency range tested was represented (1–30 kHz); and (4) cells in PIN, the major relay to amygdala, have relatively high thresholds, when compared with MGv. These findings describe for the first time acoustic properties of cells in the rat MG and provide information about the acoustic response properties of cells in areas known to project to the amygdala.

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