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Responses of Single Cells in the Medial Geniculate Body of Awake Squirrel Monkeys*

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Summary. Response properties of 142 medial geniculate (MGB) cells were investigated in the awake and undrugged squirrel monkey (*Saimiri sciureus*). Using Jordan's (1973) parcellation of this complex nucleus, cells were assigned to 3 major subdivisions *a*, *b* and *c* MGB and compared for their general characteristics and response properties. *b* MBG cells had significantly higher rates of spontaneous firing and longer latency periods than *a* and *c* MGB cells. With regard to responsiveness to various auditory stimuli, response patterns, and tuning characteristics, cells in all 3 subdivisions were statistically similar and were thus treated as one cell population. About 95% of the cells responded to broadband white noise, steady tone bursts and frequency modulated (FM) tones. Click activated only 69% of the responding cells. Various "through-stimulus" responses comprised about 80% of the responses. Among the tone-sensitive cells, 90% responded with complex patterns, out of which 50% were frequency-dependent. About 62% of the cells (for which tuning properties were determined) were quite broadly tuned ($Q_{10dB} < 2$) and had either single or multi-peaked response areas. The other 38% were quite narrowly tuned ($Q_{10dB} > 2$) and had single-peaked, symmetrical or "tailed" response areas. Different inhibitory and excitatory response components of individual cells had different characteristic frequencies and response thresholds. The *c* MGB, which is tonotopically organized in a latero-medial orientation, appears to be homologous to the cat pars lateralis of the ventral MGB. The tonotopical organization of the *b* MGB, which is probably homologous to the cat's medial or magnocellular subdivision, is less clear. Most of the cells which were activated by FM tones disclosed "direction sensitivity" with different degrees of pattern complexity. It is suggested that pitch resolution in the MGB is based on spatio-temporal mechanisms.

Key words: Medial geniculate – Awake squirrel monkey – Auditory stimuli

Most of our knowledge concerning response properties and functional organization of medial geniculate (MGB) cells comes from studies with anesthetized cats (e.g. Katsuki 1961; Aitkin et al. 1966; David et al. 1968; Dunlop et al. 1969; Altman et al. 1970; Aitkin and Webster 1971, 1972; Aitkin 1973). These studies showed that auditory evoked responses of MGB cells consist mainly of phasic onset excitation followed by a period of depression of maintained activity, that the pars lateralis of the ventral division is tonotopically organized, that the medial division, as a whole, is more broadly tuned than the ventral division, and that cells of the dorsal division are poor auditory responders. In contrast, most auditory sensitive MGB cells of unanesthetized cats respond to tonal stimuli with either a sustained excitation or a sustained suppression of activity throughout the entire tone burst (Aitkin and Prain 1974). Response areas are also more complex than those of anesthetized cats, consisting of various sequences of excitatory and inhibitory regions (Whitfield and Purser 1972).

Information concerning the response properties of MGB cells of monkeys is more limited. This includes a study on the responses of anesthetized squirrel monkey MGB units to binaural click stimuli (Starr and Don 1972), and a demonstration of

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tonotopic organization in the ventral and medial MGB subdivisions of the same species (Gross et al. 1974).

The apparent effect of anesthesia on the cell characteristics and response properties of MGB cells as observed in cats (Aitkin and Prain 1974), and the paucity of information concerning response properties of monkey MGB cells, led us to explore the auditory evoked response properties of single cells in the MGB of awake and undrugged squirrel monkeys (*Saimiri sciureus*). Herein we describe the tuning characteristics and response properties associated with clicks, broadband white noise and tonal stimuli. Response properties associated with complex intraspecific communication sounds will be reported in a subsequent paper.

A preliminary report of this work was presented at the Second European Neuroscience Meeting (Allon and Wollberg 1978a).

Methods

Experiments were performed on 2 unanesthetized, undrugged female squirrel monkeys chronically implanted with a recording chamber and a head restraining device. Surgical and implantation procedures, equipment for generating, delivering and monitoring tone bursts, recording conditions and techniques, as well as monitoring and displaying single cell activity, were similar to those described earlier (Allon and Wollberg 1978b). Here they are only briefly described.

Clicks lasting 200 μs were generated by square pulses with a repetition rate of one per 3 s. Cells were routinely tested with a sequence of 15 consecutive clicks. Broadband white noise (0.02–100 KHz) was generated by a Brüel and Kjaer (type 1405) noise generator, and shaped into a 300 ms burst with a rise and fall time of 15 ms. Tone bursts of 300 ms with an identical rise and fall time were presented 3.5 s apart in steps of 0.25 KHz over a range of 0.5 to 32.0 KHz. Frequency modulated (FM) tones were generated by a combination of a "Wavetek" (type 136) voltage controlled oscillator and a symmetrical triangular modulating waveform. A sweep of increasing frequencies from 0.5 to 32.0 KHz, at a rate of 128 KHz per s was followed by a symmetrical decrease in frequencies from 32.0 to 0.5 KHz. The complete sweep was shaped into a 500 ms burst with a 15 ms rise and fall time. All stimuli were presented under free field conditions. Sound pressure levels (expressed in dB SPL, re 20 μP) were continuously monitored and measured with a Brüel and Kjaer calibrated condenser microphone (type 4134) located close to the animal's ear, and connected to a Brüel and Kjaer sound level meter (type 2209). The frequency response of the sound generating system was nearly flat (± 5 dB) to about 12.0 KHz. It then dropped by 20 dB to 18.0 KHz, recovered by 10 dB to 20.0 KHz, and persisted around this level up to 30.0 KHz, in the range 30.0–32.0 KHz, it dropped again by about 10dB. For achieving minimum distortion, intensities within the range 12.0–32.0 KHz were compensated.

Extracellular single unit activity was recorded with glass-coated platinum iridium microelectrodes, amplified, and continuously monitored for shape and size. Discriminated spikes were displayed as rastered dot patterns on a Tektronix (type 549) storage oscilloscope, and recorded on an FM tape recorder (Ampex SP 300) for off-line analysis.

Histology and Reconstruction of Recording Sites

At the end of the last penetration several "marking lesions" were made along the track by passing 45 μA of anodal current over a period of 2–3 s. The monkey was then deeply anesthetized with Nembutal and perfused with saline via the left heart ventricle and followed by Hess fixative (Hess 1932; cited by Jasper and Ajmone-Marsan 1954). Identification of the lesions was made from 15 μm cresyl violet stained paraffin sections, cut in a coronal plane. With the aid of these lesion locations and a computer program written for this purpose (Yeshurun et al., in press), all other tracks and recording sites were reconstructed and referred to the stereotaxic coordinates according to the atlas of Emmers and Akert (1963). This computer program was also used to assign recording sites to the MGB subdivisions according to Jordan (1973), who divided the MGB of the squirrel monkey into 3 major subdivisions on the basis of cell morphology: a ventro-caudal region (*a*), a medial region (*b*) and a lateral region (*c*).

All the computational work was executed on a CDC 6600 computer and a Tektronix (type 4010-1) graphic display terminal.

Statistical Evaluation of Results

Data were obtained from a sample of 142 cells located all over the MGB. Of these, 26 were *a*MGB cells, 27 *b*MGB and 48 *c*MGB cells. The remaining 41 units were located in borderline areas and could not be assigned with any degree of confidence to one of the 3 subdivisions. These unclassifiable cells will be referred to as uMGB cells hereafter. Cell properties were evaluated for each subdivision separately and statistically compared. χ^2 tests for independent samples were used for comparing the relative incidence of discreet categories, such as response types and relative broadness of response areas. Equality of means was tested by an analysis of variance. For each analysis we used the Levene test for equality of variances (Brown and Forsythe 1974a), and whenever the group variances were not assumed to be equal ($P < 0.01$), equalities of means were tested by Welch's F statistic (Brown and Forsythe 1974b). The latter was preferred over other options because deviations from the means were relatively high, and the samples were not equal in size. Dispersions were expressed routinely by one standard deviation of the mean (± SD).

Since the relative incidence of response types, response patterns and tuning characteristics did not differ statistically in the 3 subdivisions, all cells were treated, in that regard, as a single cell population. However, for non-statistical comparisons, results from each subdivision were summarized separately in Table 1.

Results

A. Spontaneous Activity

All cells tested in the course of the present study exhibited spontaneous on-going activity in the absence of any overt auditory stimulation. The spontaneous activity was usually irregular and very few cells had bursting patterns. Ranges, means and medians of spontaneous firing rates in the 3 subdivisions are presented in Table 1. An F-test revealed inequality of means ($P < 0.01$) with relatively higher spontaneous firing rates of *b*MGB cells. The total range of spontaneous activity of MGB cells was 0.1–43.9 spikes per s.

Table 1. Response properties of MGB cells: a comparison between major subdivisions

		*a*MGB	*b*MGB	*c*MGB	uMGB
spontaneous activity (spikes/s)	N	26	32	54	40
	range	1.1–21.9	0.1–30.5	0.7–33.7	1.4–43.9
	$\bar{x} \pm$ SD	6.5± 4.5	12.0± 8.4	9.1± 7.7	10.1± 7.9
	median	5.5	8.9	7.3	8.5
latency period (ms)	N	15	18	35	11
	range	3.5–9.5	3.8–26.5	3.6–22.5	4.0–15.1
	$\bar{x} \pm$ SD	5.9±2.3	10.2± 6.3	8.9± 4.9	9.3± 4.7
	median	6.0	11.5	7.9	11.3
responses to white noise (%)	N	24	22	40	34
	on	8.3	18.2	20.0	14.7
	through	75.0	68.2	77.5	61.8
	off	16.7	13.6	2.5	23.5
responses to tone burst	N	25	26	46	41
	frequency-dependent	36.0	34.6	60.9	48.1
	not dependent	64.0	65.4	39.1	51.2
response bandwidth at 80 dB	N	24	29	47	35
	fH-fL (KHz) range	1.5–31.5	1.1–31.5	0.4–31.5	1.5–31.5
	$\bar{x} \pm$ SD	15.2±12.0	21.9±10.8	20.4±10.4	23.3±10.3
	median	8.7	26.1	23.2	30.1
	octaves range	1.1–6.0	0.2–6.0	0.3–6.0	0.9–6.0
	$\bar{x} \pm$ SD	3.8±1.7	4.1±2.0	4.0±1.8	4.9±1.5
	median	3.6	5.0	4.1	5.1
broadness of response area (%)	N	10	10	26	17
	$Q_{10dB} < 2$	60	60	73	47
	$Q_{10dB} > 2$	40	40	27	53

N – number of cells; $\bar{x}$ – mean ± one SD; *a*, *b*, *c*MGB – 3 major subdivisions according to Jordan (1973); uMGB – unclassifiable cells

A marked variation in mean firing rates was found among cells of all 3 subdivisions. Of 44 cells for which several successive measurements of spontaneous activity were made over a period of 1–2 h, 22 cells (66%) showed a remarkable increase or decrease in the mean firing rate. In most cases a two- to threefold change was encountered, but higher variations were also observed.

B. Responses to White Noise and Clicks

Out of the 131 cells tested with broadband white noise at an intensity of 80 dB, 120 cells (91.6%) responded to this stimulus. Five main types of response patterns were elicited: (1) a brief burst of spikes at the onset of the stimulus; (2) a sustained suppression of cell activity throughout the stimulus; (3) a sustained suppression of cell activity throughout the noise burst, often followed by a rebound of excitation; (4) various sequences of excitation and inhibition throughout the stimulus and sometimes beyond it; (5) a short excitation upon offset of the stimulus. Considering groups 2, 3 and 4 as "through-stimulus" responders, all patterns encountered were classified into 3 major categories: "on" (17.5%), "through" (72.5%) and "off" (10.0%) responses. The dominance of "through-stimulus" responses was highly significant (χ^2-test, $P < 0.01$).

Out of 139 cells tested with clicks, 96 (69%) responded to this stimulus, usually with a brief burst of discharges. The time lapse between presentation of a click and the onset of the elicited response (corrected for the distance between the speaker and the monkey's head) was employed for estimating latency periods. Latencies varied between 3.5 and 27.0 ms with *b*MGB cells showing significantly longer values than *a* and *c*MGB cells ($P < 0.01$). Ranges, means and median values for 79 units located in the various subdivisions are given in Table 1.

C. Responses to Tonal Stimuli

Out of 141 cells tested with steady tone burst ranging in frequencies between 0.5 and 32.0 KHz (at a

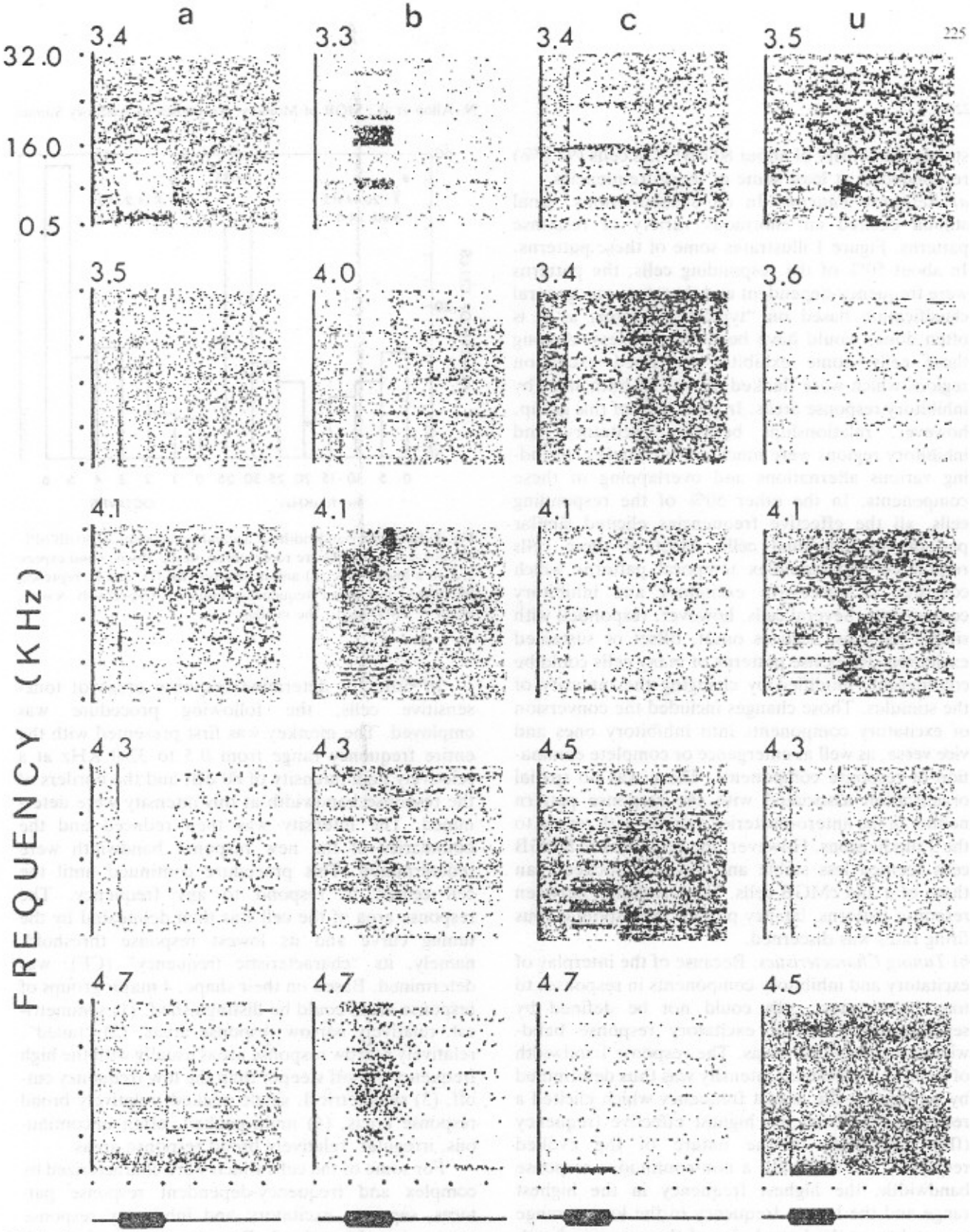

Fig. 1. Response patterns of MGB cells to pure tones. Dot displays illustrating response patterns of 20 different cells located at different sites within the MGB. *a*, *b*, *c*, and (u) designate the 3 major subdivisions and a group of unclassifiable cells, respectively. The number at top left of each display indicates the location of the cell along the AP axis according to the atlas of Emmers and Akert (1963). Each row within a dot display represents a single trial with frequencies increasing in steps of 0.25 KHz. Time scale: 200 ms between consecutive dots located below the lowest displays

standard intensity of about 80 dB), 138 cells (97.8%) responded to at least some of these frequencies.

a) Response Patterns. In all 3 subdivisions, tonal stimuli elicited an enormous variety of response patterns. Figure 1 illustrates some of these patterns. In about 50% of the responding cells, the patterns were frequency-dependent and therefore any general classification based on "typical" patterns, as it is often done, would have been meaningless. Among these cells, some exhibited sustained excitation regions which were flanked on one or both sides by inhibitory response areas. In most cells of this group, however, relationships between excitatory and inhibitory regions were much more complex, including various alternations and overlapping of these components. In the other 50% of the responding cells, all the effective frequencies elicited similar patterns in individual cells. Most of these cells responded with complex temporal patterns which consisted of successive excitatory and inhibitory components. Several cells, however, responded with simple patterns, such as onset, offset or sustained excitation. Response patterns of many cells could be considerably modified by changing the intensity of the stimulus. Those changes included the conversion of excitatory components into inhibitory ones and vice versa, as well as emergence or complete elimination of response components. There was no spatial organization associated with the response pattern neither in the antero-posterior axis nor with regard to the 3 subdivisions. However, the responses of *b*MGB cells seemed less stable and less time-locked than those of *a* and *c*MGB cells. No correlation between response patterns, latency periods, and spontaneous firing rates was discerned.

b) Tuning Characteristics. Because of the interplay of excitatory and inhibitory components in responses to tone burst, most cells could not be defined by separate inhibitory or excitatory response bandwidths and response areas. The response bandwidth of a cell at a particular intensity was thus determined by subtracting the lowest frequency which elicited a response (fL) from the highest effective frequency (fH), regardless of the nature of the evoked response. For cells with a non-continuous response bandwidth, the highest frequency in the highest range and the lowest frequency in the lowest range were taken as the boundaries of the response bandwidth. Figure 2 depicts the distribution of 135 cells according to their response bandwidths (at an intensity of 80 dB SPL), expressed in linear values (Fig. 2a) and in octaves (Fig. 2b). It can be seen that at this intensity most cells are broadly tuned, with 50% of the cells responding to almost the entire range of frequencies tested.

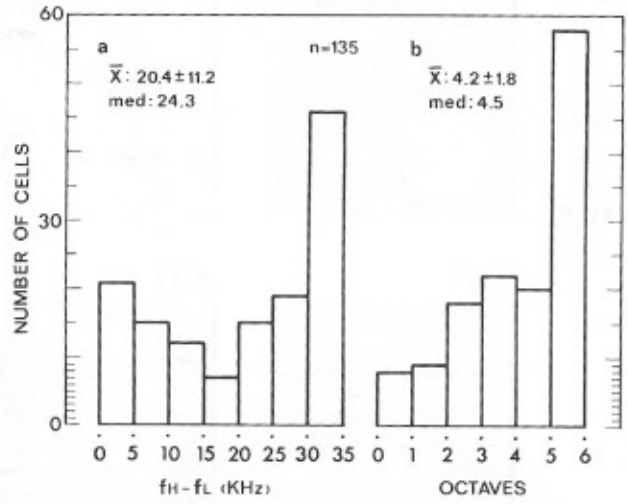

Fig. 2. Response bandwidths at a standard intensity of 80 dB SPL. Response bandwidths are represented on the abscissa and expressed on a linear scale (**a**) and in octaves (**b**). fH, and fL represent the highest and lowest frequency boundaries, respectively. $\bar{x}$ is the mean ± 1 SD, med – the median

In order to determine response areas of tone-sensitive cells, the following procedure was employed. The monkey was first presented with the entire frequency range from 0.5 to 32.0 KHz at a relatively high intensity of 80 dB, and the borders of the response bandwidth at this intensity were determined. The intensity was then reduced and the boundaries of the new response bandwidth were redetermined. This procedure continued until the cell ceased to respond to any frequency. The response area of the cell was then delineated by the tuning curve and its lowest response threshold, namely, its "characteristic frequency" (CF), was determined. Based on their shape, 4 major groups of response areas could be distinguished: (1) symmetrical, relatively narrow response areas, (2) "tailed", relatively narrow response areas usually with the high frequency cut-off steeper than the low frequency cut-off, (3) symmetrical, single peaked, relatively broad response areas, (4) multi-peaked, often uncontinuous, irregular, relatively broad response areas.

For some of the cells which were characterized by complex and frequency-dependent response patterns, separate excitatory and inhibitory response areas were determined. Response areas of 4 such cells are shown in Fig. 3. The response patterns of each cell to the entire frequency range, at an intensity of 80 dB, and their spatial localizations, are illustrated at the left of each tuning curve. More complex combinations of excitatory and inhibitory components, which we were not able to describe graphically, were also observed. It is evident that various

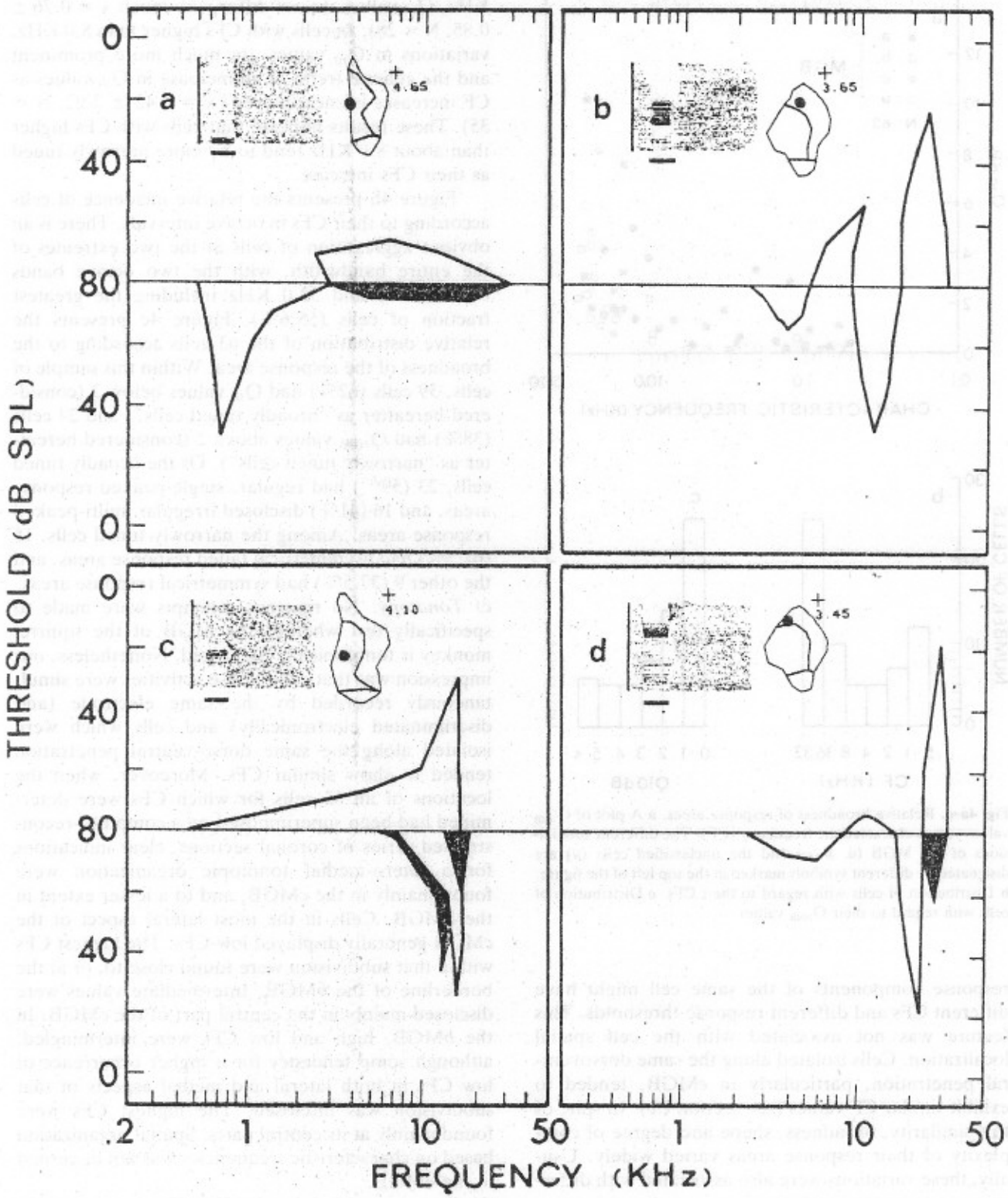

Fig. 3. Illustration of complex tuning curves. Separate excitatory and inhibitory response areas of 4 different cells (a–d). Excitatory and inhibitory responses are represented, respectively, by downward and upward deflections. Empty downward deflections represent sustained excitations. Black areas represent excitatory off-components. The inset at the left of each tuning curve describes, by a dot display, the response range and patterns at an intensity of 80 dB (see Fig. 2 for details). To the right of the dot display is a computer reconstruction of the cell's location. The cross represents a constant point for all sections at the stereotaxic location H – 3.75; L – 5; the number below it designates the AP stereotaxic location

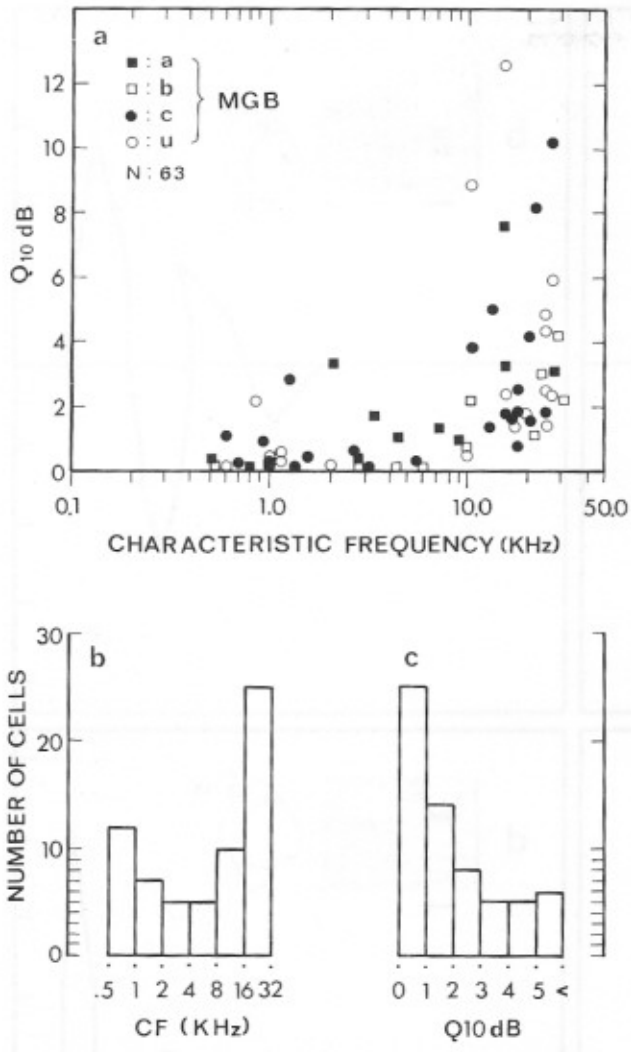

Fig. 4a–c. Relative broadness of response areas. **a** A plot of Q_{10dB} values versus characteristic frequency (CF). The different subdivisions of the MGB (*a, b, c*) and the unclassified cells (*u*) are disignated by different symbols marked at the top left of the figure. **b** Distribution of cells with regard to their CFs. **c** Distribution of cells with regard to their Q_{10dB} values

response components of the same cell might have different CFs and different response thresholds. This feature was not associated with the cell spatial localization. Cells isolated along the same dorsoventral penetration, particularly in *c*MGB, tended to exhibit similar CF values (see section Cc). In spite of this similarity, broadness, shape and degree of complexity of their response areas varied widely. Usually, these variations were also associated with differences in response patterns.

Figure 4a is a plot of Q_{10dB} values (CF divided by the bandwidth measured at 10 dB above the CF) vs. CF. It can be seen that despite the scatter of points, it is clear that for cells with CFs lower than about 8.0 KHz, Q_{10} values do not differ very much ($\bar{x} = 0.76 \pm 0.85$, N = 28). In cells with CFs higher than 8.0 KHz, variations in Q_{10} values are much more prominent and the general trend of an increase in Q_{10} values as CF increases is encountered ($\bar{x} = 3.42 \pm 2.92$, N = 35). These results indicate that cells with CFs higher than about 8.0 KHz tend to be more narrowly tuned as their CFs increase.

Figure 4b presents the relative incidence of cells according to their CFs in octave intervals. There is an obvious aggregation of cells at the two extremes of the entire bandwidth, with the two octave bands between 8.0 and 32.0 KHz including the greatest fraction of cells (55.6%). Figure 4c presents the relative distribution of the 63 cells according to the broadness of the response area. Within this sample of cells, 39 cells (62%) had Q_{10} values below 2 (considered hereafter as "broadly tuned cells") and 24 cells (38%) had Q_{10dB} values above 2 (considered hereafter as "narrowly tuned cells"). Of the broadly tuned cells, 23 (59%) had regular, single-peaked response areas, and 16 (41%) disclosed irregular multi-peaked response areas. Among the narrowly tuned cells, 15 (62.5%) had asymmetrical tailed response areas, and the other 9 (37.5%) had symmetrical response areas.

c) Tonotopy. No rigorous attempts were made to specifically test whether the MGB of the squirrel monkey is tonotopically organized. Nonetheless, our impression was that cells whose activities were simultaneously recorded by the same electrode (and discriminated electronically) and cells which were isolated along the same dorso-ventral penetration tended to show similar CFs. Moreover, when the locations of all 63 cells for which CFs were determined had been superimposed on a computer-reconstructed series of coronal sections, clear indications for a latero-medial tonotopic organization were found mainly in the *c*MGB, and to a lesser extent in the *b*MGB. Cells in the most lateral aspect of the *c*MGB generally displayed low CFs. The highest CFs within that subdivision were found close to, or at the borderline of the *b*MGB. Intermediate values were disclosed mainly in the central part of the *c*MGB. In the *b*MGB, high and low CFs were intermingled, although some tendency for a higher occurrence of low CFs in both lateral and medial aspects of that subdivision was disclosed. The highest CFs were found mainly at its central parts. Spatial organization based on characteristic frequencies was not discerned in the *a*MGB.

d) Frequency Modulated (FM) Tones. Figure 5a illustrates responses of 5 different cells to steady tone bursts ranging from 0.5 to 32.0 KHz. Figure 5b shows the responses of those cells to the same range of tones, modulated from low to high frequencies and

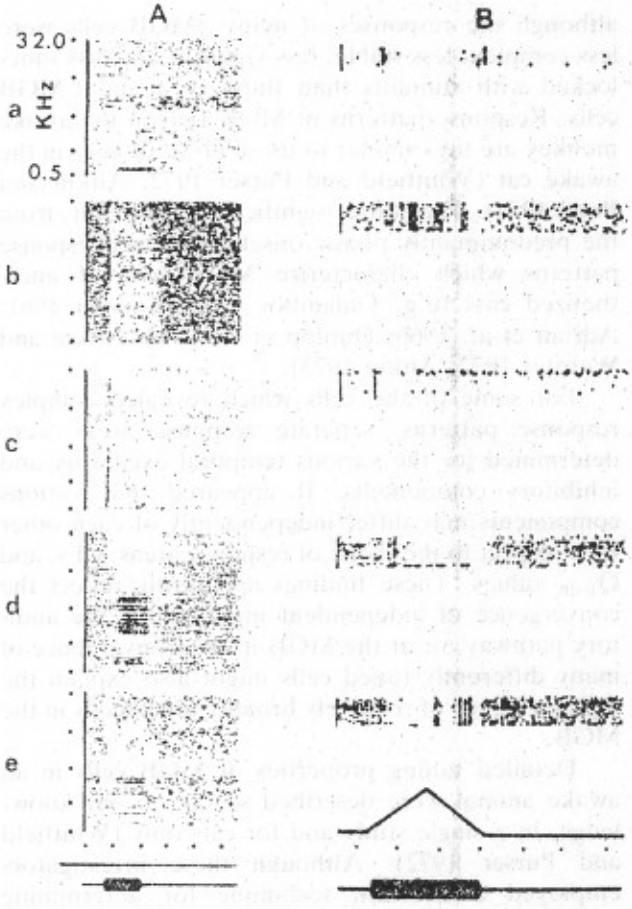

Fig. 5A, B. Response patterns to frequency modulated tones. Response patterns of 5 cells (a–e) to steady tone burst (A) and to frequency modulated tones (B). For explanation of the dot display and the generation of steady tone bursts, see Fig. 1. For each sweep of the modulated tones, frequencies increased from 0.5 to 32.0 KHz within 250 ms, and were followed symmetrically by a decrease in frequencies from 32.0 to 0.5 KHz. The shape of the modulating wave is designated by the triangle located above the burst envelope. Rate of modulation 128 KHz/s. Time scale: 200 ms between consecutive dots above the envelopes. Location of cells: a– *a*MGB; b– *c*MGB; c– *c*MGB; d– *b*MGB; e– uMGB

back at a constant rate of 128 KHz per s. Cell (a) represents a group of cells which were narrowly tuned and their responses to FM tones could be quite consistently predicted by their response to steady tones. These cells discharged whenever the FM tone crossed their response bandwidth regardless of its direction. A triangular modulating waveform thus elicited a symmetrical response. Cell (e) is an illustration of the other extreme. It represents a group of cells whose responses to FM tones were complex, asymmetrical, and could not be predicted by their responses to steady tone bursts. Most of these cells were broadly tuned and their responses to steady tones were complex and frequency-dependent. The pattern and "direction sensitivity" of these cells apparently reflect the accumulative temporal effect of the various frequencies which the modulated tone was crossing.

Between these two extremes, different degrees of complexity and asymmetry of responses were revealed (Fig. 5b–d). Out of 37 cells tested with FM tones, 36 cells responded to that stimulus, with 27 cells (75%) disclosing "direction sensitivity" with different degrees of pattern complexity.

Discussion

Parcellation of the MGB

The present report represents the first description of the response properties and tuning characteristics of single cells in the various MGB subdivisions of an awake monkey. Previous studies of the MGB have focused mainly on cats (Harrison and Howe 1974; Erulkar 1975; Webster and Aitkin 1975).

On the basis of cyto- and myeloarchitectonic organization (Jordan 1973), as well as cell morphology and cortical projections (Burton and Jones 1976), 3 major subdivisions were identified in the MGB of monkeys. Jordan (1973) denoted those subdivisions in the squirrel monkey as *a*, *b*, and *c*MGB (a denotation also used in our study), which he suggested were comparable, respectively, to the cat ventral (v), medial (m), and dorsal (d) MGB as described by Morest (1964, 1965a). The parcellation proposed by Burton and Jones (1976) for the rhesus and squirrel monkeys was similar to that of Jordan though they used similar terms to those used in describing the MGB subdivisions in the cat.

Gross et al. (1974) found that in the anesthetized squirrel monkey, the lateral aspect of the MGB, which consists of small cells (apparently identical to Jordan's $a + c$ subdivisions), is tonotopically organized in a latero-medial orientation. The nature of this tonotopical organization, which was also confirmed in our study with unanesthetized squirrel monkeys, is thus in principle identical to the one found by Aitkin and Webster (1972) in the laminated pars lateralis (PL) of the cat vMGB. Interestingly, Jordan (1973) stated that cells in the ventro-lateral portion of the *c*MGB (which he considered to be comparable with the cat *d*MGB) were often organized in semicircular layers, a feature which we have also encountered, and which recalls the cell organization in the PL of the cat vMGB.

A comparison between the properties of cells which lie dorsal to and cup the "small cell division" of Gross (1974) with those of the cat's dorsal division

(Aitkin and Webster 1972) suggests that these two regions are similar. This notion is supported by Moore et al. (1977) who think that the dorsal lobe of the medial geniculate in mammals, such as the cat or rabbit, is reduced in primates to a small nucleus which covers the rostral end of the geniculate.

Summarizing the possible homologies between the cat and monkey MGB subdivisions, it seems that Jordan's *a* and *b*MGB of the monkey (equivalent to Burton and Jones' v and mMGB), are homologous with at least part of the cat's ventral and medial subdivisions, respectively. As for the monkey's *c*MGB (equivalent to Burton and Jones' dMGB), we are left with two alternatives: (1) judging by its cortical projections it is homologous to the cat dorsal subdivision and (2) judging by its cellular organization and response properties to tonal stimuli it is homologous to the cat ventral subdivision. If the second alternative, which we favor (since projection studies are not always exclusive and the boundaries of the primary koniocortex in the monkey are also not yet clearly defined), is valid, then the monkey's *a* and *c*MGB as defined by Jordan (1973) represent its thalamic auditory nucleus, and are most probably homologous, respectively, to the cat pars ovoidea (PO) and pars lateralis (PL) of the ventral division. Under such circumstances, our study comprises a relatively small number of cells which are homologous to cells of the cat dorsal division. If, however, the first alternative reflects the real situation, then we face a remarkable difference in the response properties of dorsal MGB cells of cats and monkeys. In order to reconcile these conflicting alternatives, additional morphological analyses of cell types, dendritic patterns and inferior colliculus projections are required in the monkey.

Of all neuronal response properties we investigated, only spontaneous firing rates and latency periods of the 3 subdivisions, *a*, *b* and *c*MGB, differed statistically, with the *b*MGB cells exhibiting significantly higher rates of spontaneous activity and longer latency periods than the *a* and *c*MGB cells. We believe that these differences are associated with the polysensory nature of the medial subdivision (e.g. Morest 1965b; Wepsic 1966; Goldberg and Moore 1967; Love and Scott 1969).

Response Patterns and Tuning Properties

Auditory stimuli evoked in most of the cells various "through-stimulus" patterns which were by and large very complex, and in the case of tonal stimuli, often frequency- and intensity-dependent. Such response patterns were encountered in all 3 subdivisions, although the responses of many *b*MGB cells were less complex, less stable, less vigorous and less time-locked with stimulus than those of *a* and *c*MGB cells. Response patterns of MGB cells in the awake monkey are thus similar to those of MGB cells in the awake cat (Whitfield and Purser 1972, Aitkin and Prain 1974). They differ significantly, however, from the predominantly phasic onset and offset response patterns which characterize MGB cells of anesthetized cats (e.g. Galambos 1952; Katsuki 1961; Adrian et al. 1966; Dunlop et al. 1969; Aitkin and Webster 1972; Aitkin 1973).

For some of the cells which revealed complex response patterns, separate response areas were determined for the various temporal excitatory and inhibitory components. It appeared that various components may differ independently of each other with respect to the shape of response areas, CFs, and Q_{10dB} values. These findings apparently reflect the convergence of independent inputs along the auditory pathway, or at the MGB itself. Convergence of many differently tuned cells might also explain the high incidence of relatively broadly tuned cells in the MGB.

Detailed tuning properties of MGB cells in an awake animal were described so far, to our knowledge, in a single study and for cats only (Whitfield and Purser 1972). Although these investigators employed a different technique for determining response areas, they also considered both an increase and a decrease in spontaneous on-going activity as response components. Hence, width and shape of response areas could be compared to our results. It turned out that general features like relative broadness of response areas, their irregularity and complexity were similar to those encountered in the awake monkey. Unfortunately, no attempt was made by those authors to assign cells to the various subdivisions, and therefore comparisons in that regard could not be made. In the very detailed studies of the Australian group (Aitkin et al.) concerning tuning properties of cat MGB cells, localization of cells with regard to the subdivision was indicated. However, these results were obtained from anesthetized cats, and did not appear to include inhibitory components. From their data (Aitkin and Webster 1972; Aitkin 1973), one can see that out of 118 ventral MGB cells (PL + OP) for which tuning curves were determined, about 75% had Q_{10dB} values above 2 (according to our criterion they are considered as narrowly tuned cells) and the remaining 25% were relatively broadly tuned with Q_{10dB} values below 2. The receptive values encountered by us in the awake monkey for (*a* + *c*) MGB cells were 38% and 62%. We believe that what looks like very large

differences in the tuning properties of the two animal species, mainly reflect the effect of anesthesia on the response properties of MGB cells in the cat, as well as the different criteria used in the two studies for determining response areas. However, species variations cannot be ruled out either.

Pitch resolution along the auditory pathway is classically assumed to be associated with two mechanisms: (1) spatial analysis based on activity across tonotopically organized cell populations, and (2) time analysis based on temporal discharge patterns elicited by tonal stimuli (for detailed descriptions and discussion of these mechanisms, see Simmons 1970, Whitfield 1970 and Evans 1978). MGB cells, at least of the ventral division, are tonotopically organized, and are by and large broadly tuned even at relatively low or moderate intensities. Response patterns of many cells are frequency- and intensity-dependent. Therefore, it is reasonable to assume that coding and processing of frequencies is not exclusively executed at this nucleus by one mechanism or the other, but by a combination of spatio-temporal mechanisms.

Lesions of different regions of the MGB produced differential frequency impairments in conditioned cats (Ades et al. 1939; cited by Morest 1965a). Decorticated cats and monkeys do not lose their ability for pitch discrimination, but do lose the ability to discriminate complex auditory signals, including species-specific communication sounds (for a review see Newman 1979; Whitfield 1980). These findings suggest that resolution of pitch terminates at the level of the MGB, whereas for the resolution of more complex sounds an intact auditory cortex is required. A simple comparison between the responses of MGB and auditory cortex cells to tonal stimuli does not reveal straightforward differences which might explain this functional distinction (e.g. Goldstein and Abeles 1975; Wollberg and Newman 1972; Newman and Wollberg 1973; Miller et al. 1974). What then are the differences between these two auditory neuronal substances which are reflected by functional differences? An answer to this question was recently suggested by Creutzfeldt et al. (1980) who studied the thalamo-cortical transformation of responses to pure tones and to complex auditory stimuli, including natural calls, in the unanesthetized guinea-pig. These investigators cross-correlated discharge patterns of MGB and auditory cortex neuron pairs which disclosed some indication of being monosynaptically connected. With regard to complex natural calls, they found that MGB cells respond to more components of the call than their cortical "partners"; that cortical cells could not follow repetitive elements of a call, whereas MGB cells could; that high modulation of tonal stimuli within a call could be separated in the responses of some MGB cells but never by cortical cells. They concluded that "the internal representation of complex stimuli, such as natural noises or calls, is largely restricted to the time structure of response peaks evoked by transients, appropriately distributed across the tonotopic space of the cortex". This suggestion by Creutzfeldt et al. (1980) of a spatio-temporal mechanism for the thalamo-cortical coding of complex sounds was, however, based on a selected and relatively small sample of cells. We have some preliminary indications (in prep.) that this mechanism can indeed be related to MGB cells only when the intensity of the signal is low and close to cell threshold. At higher intensities it may apply to cells which are very narrowly tuned or whose total response area is mainly outside the range of frequencies which acquire the main energy of the call. For all other cells, like those which are broadly tuned, those which respond with complex patterns and those which are FM direction-selective, this mechanism does not fully hold. Hence, additional mechanisms, which are most probably based on other temporal cues, must be considered as accounting for the response properties of the latter group of cells.

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