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Functional Organization of the Medial Geniculate Body's Subdivisions of the Awake Squirrel Monkey

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The response properties of 138 cells in the medial geniculate body (MGB), of the awake squirrel monkey (*Saimiri sciureus*), to 7 species-specific vocalizations were studied. Cells were divided into 4 subgroups: 26 in the ventral, 24 in the medial and 46 in the lateral subdivision. Forty-two cells located on the borders between the subdivisions represent the fourth group. No significant differences were found between the subdivisions with respect to their selectivity, nor did cells in any subdivision respond preferentially to any particular vocalization. On the other hand, the response patterns of the ventral and the lateral subdivisions showed significant differences ($P < 0.001$, χ^2-test) from those of the medial subdivision. Most of the cells in the medial subdivision (87.5%) responded with similar response pattern to the 7 vocalizations (mainly 'on' or 'sustain'), while most of the cells in the ventral and the lateral subdivisions (61.5% and 69.6% respectively) responded with complex, time-locked and different patterns to the various vocalizations. Cells that exhibited a response characterized as an intermediate between the two types were accumulated mainly on or close to the borders between the medial and the other subdivisions of the MGB. The possible role of each response patterns is discussed with respect to the projection of the subdivisions to the cortex.

INTRODUCTION

The medial and the ventral subdivisions of the medial geniculate body (MGB) have been considered to play two different roles in the auditory system[30]. The medial subdivision of the MGB, which is a part of the posterior nuclear complex of the thalamus[22,30], has been suggested to play a significant role in associative classical conditioning. On the other hand, the ventral subdivision is an essential part of the auditory pathway and is involved in auditory perception[30]. Even though both subdivisions receive auditory input from the inferior colliculus (IC), they differ in their other afferent connections[13], efferents to the cortex[10,13], as well as in their cytoarchitectonic[12,17,19,20], and tonotopic organization[4,8,12]. Aitkin[1], Aitkin and Webster[3] and Symmes et al.[28] showed that the tuning curves of the cells in the medial subdivision are broader than those in the ventral subdivision. Allon et al.[8] showed that the latency is significantly longer and cells have a significantly higher rate of spontaneous activity in the medial subdivision than in other parts of the MGB. Therefore, one might expect that the discharge characteristics of cells in these subdivisions and their role in the auditory system are related. No differences were found between the subdivisions with respect to their selectivity to species-specific vocalizations, but the response pattern had not been carefully studied[6,28]. The present study investigated the differences in response patterns to biologically relevant vocalizations between the subdivisions based on the assumption that any differences in the response pattern may reflect their role.

MATERIALS AND METHODS

The experiments were conducted on two unanaesthetized, undrugged female squirrel monkeys (*Saimiri sciureus*), chronically, stereotaxically implanted with recording chamber and a head restraining device. Surgical and implantation procedures, equipment for generating, delivering and monitoring audi-

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tory stimuli, recording condition and techniques, as well as monitoring and displaying cellular activity were similar to those described earlier[5]. Here they are only briefly described. The experiments took place in a sound attenuation chamber with the monkey's head restrained in a monkey chair through a plexiglass bar previously implanted in the skull under anaesthesia[5]. Seven different species-specific vocalizations, representing 5 out of the 6 call groups of the monkey[27,32], were presented to the monkeys in the free-field situation, through an AR speaker located 1.5 m in front of the monkey's head. Each call was presented consecutively 15 times with interstimulus intervals varied randomly between 4 and 10 s. The sound pressure levels were monitored continuously through a 12 mm B and K condenser microphone (type 4134) located close to the animal's ear, connected to a B and K sound level meter (type 2209). The peak intensities of all auditory stimuli were 80 ± 5 dB SPL (re 20 μP). 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 FM tape recorder (Ampex SP 300) for off-line analyses. The spike trains were digitized using a microcomputer (Horizon) and the data transferred to a CDC 6600 for further analysis. All computational analyses were executed on a CDC 6600 computer and a Tektronix (type 4010) graphic display terminal.

Histology procedures, reconstruction of recording tracks and the location of each cell within the subdivisions of the MGB were described in earlier works[5,33]. Reconstruction of the electrode tracks with the estimated recording site was performed for every cell in the electrode plane[33]. A cell was related to one of the subdivisions if 75% of its estimated location (tip estimated location plus accumulated error) fell within this subdivision. For less than 75%, the cell was categorized as unclassified.

RESULTS

Responsiveness to vocalization

A total of 138 cells of the MGB of the awake squirrel monkey were tested for their responsiveness and response pattern to 7 species-specific vocalizations. The responses of those cells to click, noise burst, pure tones and tuning characteristics have been reported in a previous paper[8]. For each penetration, a response to an orienting stimulus (noise burst) marked the dorsal of the MGB. All the cells encountered after this point until the disappearance of all cellular activity at the ventral borders were studied. All the cells responded to at least 2 out of the 7 vocalizations tested with an average of 6.0 vocalizations per cell. The MGB cells were divided, by a computer reconstruction technique[33], into 4 subgroups using Jordan's[17] nomenclature: 26 in the aMGB (ventral MGB), 24 in bMGB (medial MGB) and 46 in cMGB (dorso-lateral MGB). Forty-two cells located on the borders between a, b and c MGB could not be reliably related to any of these subdivisions and thus represent a fourth subgroup. The distribution of cells

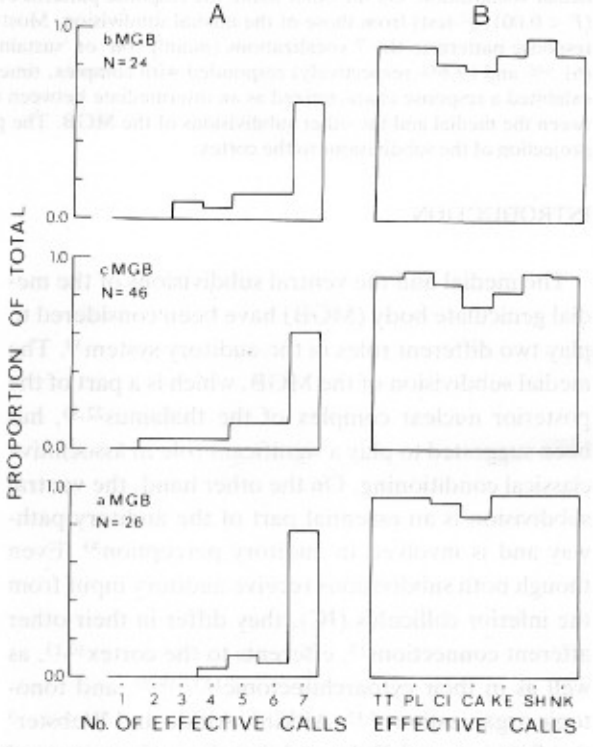

Fig. 1. Bar graphs representing the distribution of cells according to their responsiveness to vocalizations in each subdivision. A: relative selectivity profile of cells. B: relative distribution of cells according to the responsiveness to individual vocalizations. The symbols below the bars designate the 7 different vocalizations being tested: TT, twitter; PL, long peep; CI, chirp; CA, cackle; KE, kecker; SH, shriek; NK, oink. aMGB, ventral; bMGB, medial; cMGB, lateral divisions, according to Jordan[17].

Fig. 2. Response patterns of MGB cells to 7 different vocalizations. Dot displays illustrating response patterns of 15 cells (5 in each subdivision). Each block within a single set represents 15 consecutive repetitions of the same vocalization presented at 80 dB SPL in random interstimulus intervals ranging between 4 and 10 s. The envelopes of the vocalizations arranged, vertically, in the order of the presentation to the monkeys is demonstrated at the bottom of each column. The numbers are in accordance with the symbols in Fig. 1: 1, TT; 2, PL; 3, CI; 4, CA; 5, KE; 6, SH; 7, NK. The numbers at the top left of each display indicate the location of the cell along the AP axis according to the atlas of Emmers and Akert[11]: a, ventral; b, medial; and c, ventral subdivision. The numbers are increasing towards the rostral direction. Units f, g, h, i and j were classified as simple and similar, loosely time-locked to the stimuli (type 1). Units b, c, k, l, m, n and o were classified as varied and complex, time-locked to the various changes in the stimuli (type 2). Units a, d and e were classified as type 3. The column of dots at the beginning of each trace is the trigger pulse that was recorded on one channel of the tape while the call was recorded 150 ms later on the second channel. In some cases the 10–20 dB click due to the cross-talk between the channels sufficed to activate a response (see unit n) and appeared as a second line of dots closely attached to the trigger artifact. This low threshold to click was most common among cells in the lateral subdivision (c).

according to the number of vocalizations they responded to in each subdivision is shown in Fig. 1A, while the selectivity to particular vocalizations is shown in Fig. 1B. No significant differences can be seen between the 3 subdivisions with respect to their selectivity, nor their preference, for any particular vocalization (Fig. 1).

Response patterns

The response patterns of 15 cells to the 7 vocalizations are shown in Fig. 2, with respect to the cells' location within the 3 subdivisions. The cells were ranked within each subdivision (a, b and c) according to their anterior–posterior (AP) location in order to present the general tendency of response patterns among the subdivisions. Most of the cells responded to most of the vocalizations presented with different response patterns (Fig. 2b,c,k,l,m,o). The others had a tendency to respond with a similar response pattern to all the vocalizations presented (Fig. 2f–j). Cells were classified according to the following categorization of their responses: (1) simple and similar (SS) responses to all the vocalizations. These responses are mainly 'on' or 'sustained' (Figs. 2b and 3A), and are loosely time-locked to the stimulus; (2) varied and complex (VC) responses to the vocalizations. The responses are obviously dependent on the stimulus (Fig. 3B), and have time-locked inhibitory and excitatory patterns. Cells were classified as VC if at least 2 out of their 7 responses fit this criteria; and (3) responses which do not fit any of the above categories (UC) (Fig. 3C). A double-blind classification was done independently by the authors. Cells were classified as type 1 or type 2 only if classified accordingly by both authors. All other cells were classified as type 3. It must be emphasized that the responses shown in Fig. 3 are typical, in the sense that the distinction between type 1 and type 2 cells is quite clear. The distribution of the cells within the MGB subdivisions according to this classification is presented in Table I.

The distribution of response patterns (Table I) were similar for the aMGB and the cMGB: most of the cells (61.5% and 69.6% respectively) responded with complex and different patterns to the various vocalizations. In the bMGB, on the other hand, most of the cells (87.5%) responded with simple and similar response patterns to the various vocalizations.

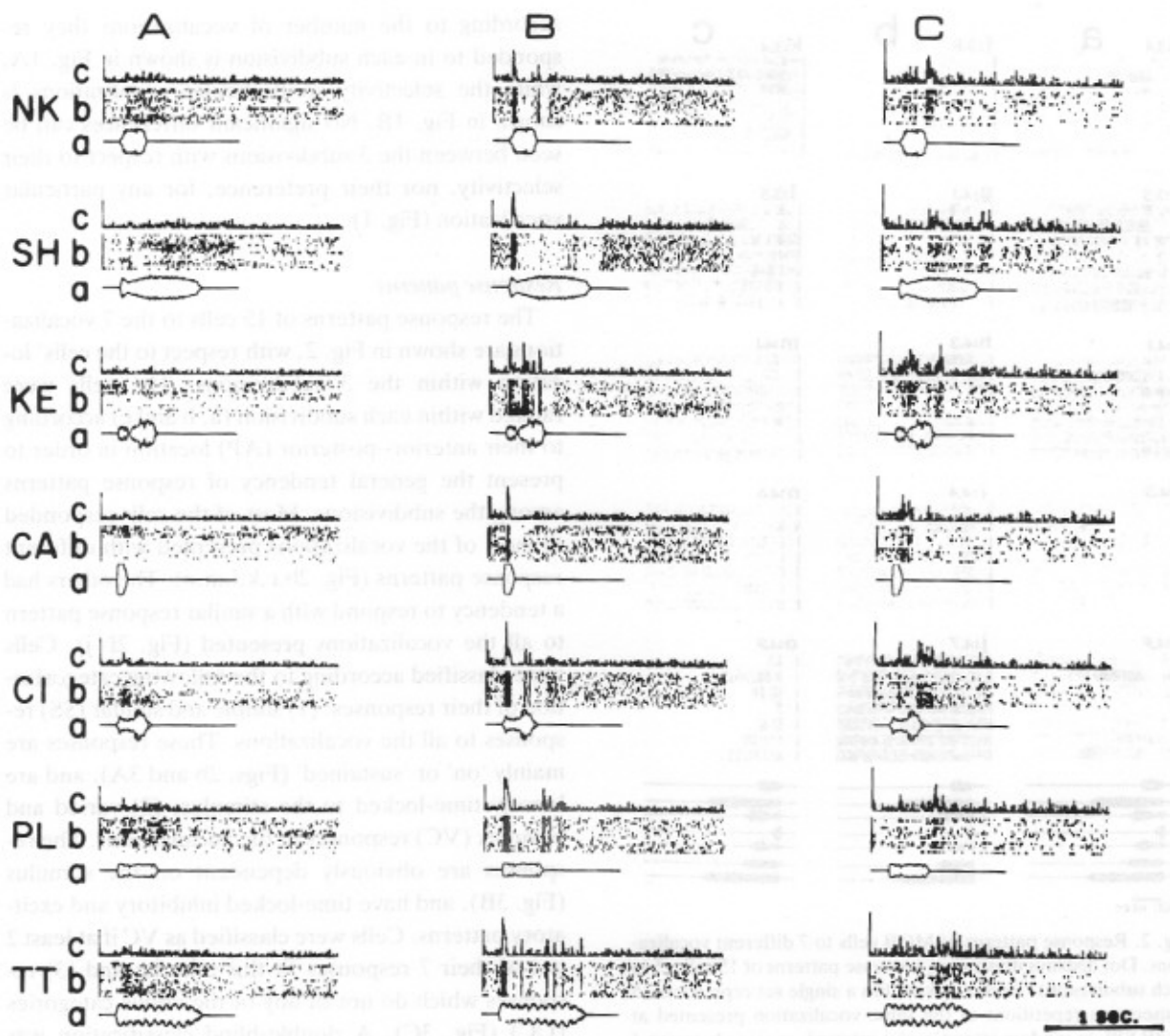

Fig. 3. Response patterns of 3 neurons to the 7 different vocalizations representing the 3 response types. A, B and C are response types 1, 2 and 3 respectively (see text). a, envelope of the vocalization; b, dot display of 15 repetitions of the same vocalization; c, peristimulus histogram of b. The symbols are as in Fig. 1 (see also legend to Fig. 2).

This difference between the bMGB and and the other subdivisions was highly significant ($P < 0.001$, χ^2 test).

The distribution of cells according to their response patterns

Since each subdivision had cells representing all 3 types, although in different proportions, we tried to determine whether cells of a particular response type were clustered or evenly distributed within a subdivision. Therefore, we reconstructed 12 successive coronal sections of the MGB (every 0.15 mm) with cell locations superimposed and classified according to their response type. Cells were superimposed on a section when their location was within ± 0.075 mm of the AP coordinate of that section (for further details see refs. 8, 33). Three of these sections are shown in Fig. 4 with a cell's response type represented by different shapes representing their location (see legend to Fig. 4). It was found that cells located in the bMGB that responded to the vocalizations with complex patterns were concentrated near the borders of the bMGB, dorsal to the cMGB. Most of the cells in the aMGB and cMGB that had a loosely time-locked re-

TABLE I

Distribution of cells responding in each response type within the subdivisions

Data show number of cells, and percentage in parentheses. SS, simple and similar response; VC, varied and complex response; UC, responses which do not fit any other category.

Type of response	*Subdivision*			
	Unidentified (n = 42)	*aMGB (ventral) (n = 26)*	*bMGB (medial) (n = 24)*	*cMGB (lateral) (n = 46)*
SS (1)	7 (16.7)	4 (15.4)	21 (87.5)	10 (21.7)
VC (2)	21 (50.0)	16 (61.5)	3 (12.5)	32 (69.6)
UC (3)	14 (33.3)	6 (23.1)	0 (0.0)	4 (8.7)

sponse to the vocalizations (37.5%) were located either in its rostral and caudal portion or at the very lateral or medial borders. Cells whose response patterns were classified as type 3 were located mainly near the borders between the bMGB and the other subdivisions of the MGB. All 3 subgroups of cells are represented at the borders between the subdivisions with a relatively high proportion of type 3 (33.3%).

Since the anatomically identified cells in the bMGB had a significantly higher spontaneous activity and a longer latency than the other subdivisions[8], we analyzed these parameters in the unidentified group, subgrouping them according to their response type to vocalizations. The average rate of spontaneous activity in the unidentified group (10.9 s/s) was non-significantly higher than that of the a+c MGB (8.2 s/s) and lower than that on the bMGB (12.0 s/s), regardless of whether the response was type 1 (11.3 s/s) or type 2 (10.9 s/s). The average latency (obtained from the cell's response to click at 75 dB SPL) of the unidentified group categorized as response type 2* (10.8 ms) was non-significantly longer than that of the a+c MGB (8.0 ms) and than that of the

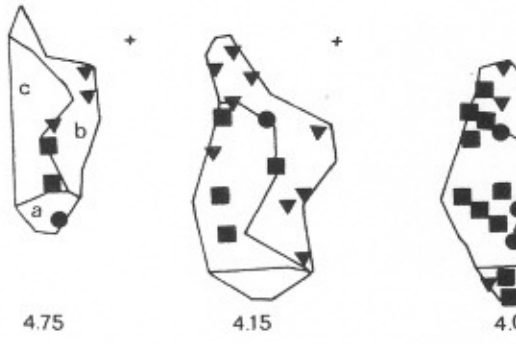

Fig. 4. Computer reconstruction of 3 frontal sections of the MGB with cell locations (shapes) superimposed: ▼, type 1; ■, type 2; and ●, type 3. a, b and c are the 3 subdivisions as in Fig. 1. Numbers below the sections designate their AP stereotaxic locations. Crosses represent the constant stereotaxic location H–3.75, L–5. Calibration: 1.5 mm.

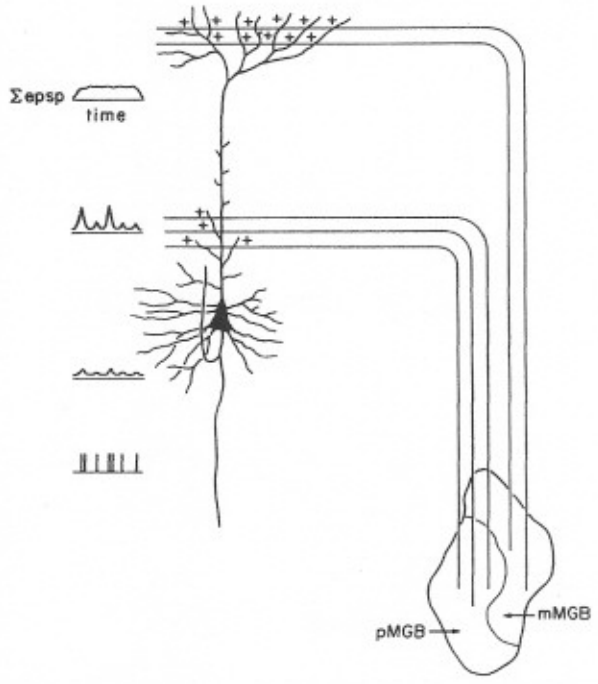

Fig. 5. A schematic model for the dual transmission line of a signal elicited by a given auditory input, and processed independently by the two subdivisions. The output of those subdivisions activate different areas of the cortical neuron, and thus have different effects on the probability of the cell to fire. Drawings of a theoretical arousal level, caused by these outputs at the target site, and the corresponding spike pattern are displayed to the left of the cell. mMGB, magnocellularis portion of the MGB; pMGB, principal portion + designate excitatory synapse. For a detailed explanation see text.

* Data about the latency of cells in the unidentified group that responded with simple and similar response patterns were not available.

bMGB (10.3 ms). Although these differences were not significant (*t*-test), due to the high variance, the cells on the borders between the subdivisions exhibited an intermediate characteristic which may have resulted from their anatomical location and the mixed type of input they received. These differences in characteristics were not correlated with the cell's response type to vocalizations.

The distribution of response patterns of the cells in the medial subdivision (bMGB)

Most of the cells in the bMGB (87.5%) responded to the vocalizations with either 'on' or 'sustain' response patterns. Since the bMGB can be further subdivided on a cytoarchitectonic basis[12,17], we studied the distribution of cells exhibiting these response patterns within the substructure. All cells whose location was within the bMGB or on its borders and were classified as type 1 (either 'on' or 'sustain' responses) were included in this sample. These cells were evenly distributed in the bMGB and no apparent clustering could be found.

DISCUSSION

The response patterns of cells in the ventral and lateral MGB subdivisions (a and c MGB respectively) to species-specific vocalization showed essential differences from those of cells in the medial MGB (bMGB). These results support earlier suggestions[8] that the a and cMGB are homologous to the pars ovoidea and pars lateralis, respectively, of the ventral subdivision of the MGB in the cat, while the bMGB is homologous to the medial subdivision of the MGB. No differences were found that may indicate the existence of any structure homologous to the dorsal subdivision in the cat[19,20]. This may be due to our small sample of cells in this area or to the relatively small size of this structure in the monkey[18].

The distribution of response patterns within the MGB showed that those 3 cells of the bMGB of the squirrel monkey that responded in complex and different response patterns (type 2) to the various vocalizations were concentrated in a distinct area dorsal to the borders of the cMGB. These findings suggest two possibilities: (a) that bMGB is not homogeneous and that the distribution of response patterns to the vocalization is an expression of its heterogeneity; (b) the response patterns near the subdivisions' borders are due to individual variability and that differences between the response patterns within this region may indicate the real borders between the subdivisions rather than those based only on cytoarchitectonic difference[17].

There is no anatomical or cytological evidence to support the first possibility. On the contrary, the cytoarchitectonic organization (magnocellular cells in the middle of the bMGB[17] may suggest an entirely different profile of cell distribution. The accumulation of cells in the bMGB that exhibit complex response patterns is a very distinct area dorsal to the borders of the cMGB, favored the second possibility, suggesting variability among animals. Furthermore, the appearance of cells whose response patterns were classified as intermediate (type 3) near the borders between the subdivisions may indicate gradual changes of response patterns between the medial and the principal subdivisions of the MGB and would support the second possibility.

These major differences between the medial and the principal subdivision may be due to modulation of firing rate by the reticular formation[29], as well as modulation of the response patterns by the auditory cortex[2,25] or interconnections in the MGB itself[2]. (Even though those studies were done in anaesthetized cats and there is no direct evidence that similar mechanisms exist in monkey MGB, the similarity of other characteristics of the MGB in these animals may suggest that it is so.) It has been shown[8,28] that, with regard to their responses to simple acoustic stimuli, only minor differences can be detected between the subdivisions. On the other hand, we showed profound differences between the response patterns of those subdivisions to species-specific vocalizations. This may suggest that similar input enters the entire MGB and that every subdivision is involved in a different transformation of that input. This transformation may involve modulation from other parts of the brain as well as the internal organization of each subnucleus.

The functional role of the different response patterns

Cells in the medial subdivision that responded with similar and simple response patterns to the vocalizations exhibited phasic (34.8%) or tonic (65.2%) responses. The responses were similar in the pattern

for a given cell to most of the vocalizations presented, but exhibited differences in the response intensity. The ascending projections from these cells are dispersed diffusely over the auditory-specific and association cortex. These afferents terminate mainly in layer I and may therefore connect the the very apical dendrites of the cells. On the other hand, projections from the principal subdivision (aMGB and cMGB) terminate in layers III and IV of the auditory cortex, closer to the cells' soma[10,16]. It has been previously calculated[15] that the input to the most distal branches decreases to only 2–3% of it original potential when it arrives at the cell body. Although this is only a fraction of the total depolarization needed to bring the membrane potential closer to the threshold, studies have shown that such small depolarizations can have marked effect on impulse frequency when the neuron is near threshold[21]. Thus, a modulating role of distal dendrites may consist of refinement in firing rate of neurons already brought close to their firing level by the afferent system that terminates closer to the cell's body[15]. The organization of the projections to the auditory cortex may represent a dual transmission line driven by the same auditory stimulus with discrete auditory relevant information transmitted close to the soma, while non-discrete, mainly tonic input is sent to the apical dendrites (for demonstration see Fig. 5).

This tonic input during vocalization may serve as an adjustment of the background excitation level[24], i.e. to increase the probability of responsiveness of cells in the auditory cortex. This organization may be important for very fine and specific adjustments of attention when needed, i.e. sorting of relevant information in noisy surroundings. The relatively high spontaneous activity of cells in the medial MGB[8], their broad tuning curves, high threshold to pure tone[1,3,28] and the fact that the associative response changes during conditioning found in the MGB is confined to this subdivision[9,26] may be significant in this respect. We have no information on whether the tonic and phasic cells send their afferents to the same area in the cortex, but we suggest that phasic cells may serve for other purposes, such as localization of the source of the signal in acousticomotor behaviors[14] or may relate to part of the MGB associated with pain mechanisms[23].

These findings of entirely different response patterns in the two subdivisions suggest a role for each in the auditory system. Although the cells in the medial subdivision respond with the same response pattern to the different vocalizations, the response intensity may be different. Since the response intensity of neurons in the medial subdivision is subject to associative changes during conditioning[9,26], this characteristic may be significant to differentiate between the vocalizations.

On the other hand, the cells in the ventral subdivision exhibited coding of the vocalizations by very discrete, highly time-locked responses to the auditory stimulus. This specificity of the responses of cells in the principal subdivision to FM direction[8] or AM of certain frequency in the vocalizations[7], suggests that this subdivision functions as a feature detector. The possible mechanisms that underlie these response patterns will be discussed elsewhere (Allon et al., in preparation).

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