Discharge Properties of Neurons in Subdivisions of the Medial Geniculate Body of the Guinea Pig

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Summary

The activity of 194 neurons was recorded in three subdivisions of the medial geniculate body (74 neurons in the ventral, 62 in the medial and 44 neurons in the dorsal subdivision, i.e. vMGB, mMGB and dMGB) of guinea pigs anesthetized with ketamine-xylazine. The discharge properties of neurons were evaluated by means of peristimulus time histograms (PSTHs), interval histograms (INTHs) and auto-correlograms (ACGs). In the whole MGB, the most frequent PSTH responses to pure tone stimuli were *onset* (43 %) or *chopper* (32 %). The onset responses were mostly present in the vMGB, whereas chopper responses dominated in the dMGB. In the whole MGB *Poisson-like* and *bimodal* INTHs were found in 46 % and 40 % of neurons, respectively. The mMGB revealed fewer bimodal and more symmetrical types of INTH. In the whole MGB, 60 % of units were found to have ACGs typical for short bursts (<100 ms), 23 % for long bursts (>100 ms) and 15 % of units fired without bursts. Neurons in the vMGB were characterized by short bursting, whereas those in the mMGB and dMGB expressed more activity in the long bursts. The results demonstrate that the type of information processing in the vMGB, which belongs to the "primary" auditory system, is different from that in two other subdivisions of the MGB.

Key words

Discharge pattern ● Single neuron activity ● Medial geniculate body ● Subdivisions ● Guinea pig

Introduction

The MGB represents a diencephalic part of the auditory pathway receiving afferents from the inferior colliculus and projecting to the cerebral cortex. The structure is morphologically non-homogeneous, being usually parceled into three subdivisions. According to Morest (1975), there is a ventral or principal division, a dorsal division and a medial division. The ventral division (vMGB) is considered to be a specific auditory relay. Its afferents run mainly ipsilaterally from the central nucleus of the inferior colliculus and project principally to the AI area of the auditory cortex (AC) and, in addition, to the AII areas. The medial (mMGB) and dorsal (dMGB) divisions receive multiple input. The mMGB receives auditory afferents from the inferior colliculus and the lateral tegmental system as well as from the somatosensory system, whereas the dMGB is supplied with afferents from the region medial to the brachium of the inferior culliculus, the superior colliculus, and also the somatosensory system. The mMGB projects to the auditory cortex in a less specific

way, and the dMGB projects to the "association" auditory cortex (Winer and Larue 1987). The vMGB contains only two cell types: principal cells, which project to the auditory cortex, and Golgi type 2 cells, which are interneurons with short axons. This subdivision is characterized by a laminar structure and tonotopic organization, basically a copy of the arrangement of the central nucleus of the IC, with high frequencies located medially and low frequencies occurring laterally (Aitkin and Webster 1972). The activity of neurons in the upper part of the auditory pathway (MGB, AC) is characterized by bursts of action potentials and oscillations of neuronal activity. The functional properties and interactions of neurons simultaneously recorded in the MGB of the cat displayed some differences, e.g. in latencies and in the occurrence of bursting/oscillations among MGB subdivisions (Heierli et al. 1987) or other thalamic nuclei (Simm et al. 1990). Neurons recorded in the cat vMGB respond vigorously to pure tones with short response latencies and have mostly a narrow frequency tuning curve, while units in the dMGB respond less vigorously to pure tones with longer latencies and have broader tuning curves (Aitkin and Webster 1972, Calford and Webster 1981, Rodrigues-Dagaeff et al. 1989). Changes in the response patterns and bursting of MGB neurons were observed after cooling of the auditory cortex in the cat (Villa et al. 1991). Functional studies mostly confirmed the characteristics of neuronal responses to tones described in the cat (Redies and Brandner 1991, Edeline et al. 1999).

The aim of the present work was to evaluate the acoustically evoked activity of neurons recorded in three MGB subnuclei of the guinea pig by statistical procedures (peristimulus time histograms, interval histograms and auto-correlograms). Whereas the studies of Redies and Brandner (1991) and Edeline et al. (1999) concentrated on the response latencies, sharpness of tuning curves, thresholds and rate/level functions, we investigated different parameters of firing patterns by the above-mentioned statistical methods. The results show that particularly the firing pattern in the vMGB is different from that found in other parts of the MGB.

Methods

Anesthesia and surgical procedures

Experiments were performed on 24 healthy, adult, pigmented guinea pigs weighing 300-500 g. Each animal was anesthetized with an intramuscular injection of 1 ml/kg b.w. of a mixture of ketamine (Narkamon 5 %, Spofa) and xylazine (Rompun 2 %, Bayer) in a ratio of 2:1, which corresponds to a dose of 33 mg/kg of ketamine and 6.6 mg/kg of xylazine. To maintain a deep level of anesthesia throughout the experiment, supplementary injections of the same dose were administered every 90 min.

Access to the right and left MGB was made by trepanation 4-7 mm anterior to the interaural line, 3-6 mm lateral from the superior sagittal sinus of the skull over the underlying cortex. Two small screws (diameter 1 mm, length 3 mm) were cemented into the frontal part of the skull with dental acrylic and used to secure the head in a stereotaxic holder. After removing the dura, an electrode was inserted into the MGB in the ventro-dorsal direction on the basis of stereotaxic co-ordinates (Luparello 1967) using a stepping motor microdrive WPI-3D controlled from the outside of the room.

Acoustic stimuli: preparation, calibration and presentation

Experiments were performed in a sound-attenuated and echo-proof room. Acoustic stimuli were presented through a low-frequency loudspeaker Tesla ARS 824 and a high-frequency loudspeaker Motorola 600 under free field conditions. The loudspeakers were placed 50 cm in front of the guinea pig's head. Animals were stimulated with pure tone pips (100 ms duration, 3 ms rise/fall times, and repetition rate of 1 Hz). Pure tones were presented with an intensity of 60 dB SPL.

On-line signal capture and spike-sorting procedure

Extracellular unit activity of MGB neurons was recorded with a glass microelectrode, tip diameter ~1 μm, filled with 3M KCl, with an impedance of about 3 MΩ. Due to the low spontaneous neuronal activity of MGB neurons, a broad-band noise burst at an intensity of 54 dB SPL was used as a search stimulus. Neuronal responses were filtered through a bandpass filter in the range of 300 Hz to 3 kHz and amplified by a differential AC amplifier WPI DAM-60. Spike capture and sorting according to spike shape (templates) were performed on-line by means of a CED-1401plus interface connected to a PC and the program Spike2. At the beginning of the recording, the characteristic frequency (CF, which is the frequency of stimulus with the lowest response threshold) was determined. Thereafter, sequences of pure tone pips at CF were presented and neural responses were stored on the PC for further off-line data processing.

Histology

At the end of each experiment, the micropipette was moved to the deepest position within the MGB, cautiously broken just above the surface of the brain and then left there. The guinea pig was sacrificed with an overdose of sodium pentobarbital and perfused with 10 % formaldehyde. After fixation, the remaining part of the electrode was removed and individual electrode tracks within the MGB were histologically reconstructed afterwards from Nissl-stained frontal brain slices. Each recording position was estimated on the basis of the microdrive co-ordinates.

Off-line analysis

Spikes originating in two adjacent neurons recorded with one electrode were chosen on the basis of well-defined spike templates. The statistical analysis of data spike trains was performed subsequently. The peristimulus time histogram (PSTH), interval histograms (INTH), and auto-correlograms (ACG) were calculated off-line using digitally stored data for each neuron. The construction of a PSTH of a single neuron's response to a pure tone burst (100 ms) at CF allows one to classify the response pattern of the unit. PSTHs, with 1-ms bin size and 200 ms duration, were differentiated into five classes similarly as in other studies (Rhode and Kettner 1987, Rodrigues-Dagaeff *et al*. 1989, Le Beau *et al*. 1996). This set of classes contains *onset*, *primary-like*, *chopper*, *sustained* and *pauser* types of neuronal responses (Fig. 1a). No inhibitory type of response was found in the MGB. The INTH represents the frequency distribution of the time intervals between two successive action potentials. The INTHs of all recorded units from the entire recording (similar to Rhode and Kettner 1987), with 1-ms bin size and 200 ms window, were classified on the basis of their shape (Bock *et al*. 1972, Bock and Webster 1974, Syka *et al*. 1975, Rhode and Kettner 1987, Kaneoke and Vitek 1996) into three groups: *Poisson-like*, *symmetrical* and *bimodal* types (Fig. 1b). A *Poisson-like* INTH characterizes a neuron discharging purely random single spikes, having an exponential or near exponential shape. A *symmetrical* INTH is typical for a regularly firing neuron with a narrower/wider Gaussian shape. A *bimodal* INTH, combining random and burst firing is characterized by two humps in the interval distribution curve; the first hump corresponds to an interspike interval within a group of spikes and the second hump to intergroup intervals. The ACG is used for estimating of the spiking behavior as single spikes/burst firing or rhythmical firing (oscillations). The ACG may also be

considered as a sum of all order interval histograms, and then the common INTH is the first order interval histogram (Eggermont *et al*. 1993). The ACG represents the probability of the appearance of subsequent spikes after each previous one in the spike train. ACGs from whole recordings, similarly to other studies (Eggermont 1992, Bowman *et al*. 1995), were computed over a 500 ms range with a 5 ms bin width. They were sorted, in agreement with others (Heierli *et al*. 1987, Simm *et al*. 1990, Gochin *et al*. 1991, Karnup 1992), on the basis of their shape into three classes (Fig. 1c). The class designated as *no burst* contains ACGs, which are flat after a short introductory dip, caused by a refractory period. It corresponds to random neuronal firing with single spikes without any burst (Poisson distribution). The *short burst* class contains a short initial peak in the ACG, which corresponds to firing in short bursts lasting up to 100 ms. In this class, two subclasses were distinguished: the first one is characterized by ACGs of neurons firing in short bursts alternating with irregular single spikes, and the second shows signs of combining short bursts and regular rhythmical activity or oscillations. Similarly, the *long burst* class represents a set of ACGs with a wide hump typical for neuronal firing in long bursts longer than 100 ms. This class was again divided into two subclasses: the first with neurons firing in long bursts mixed with non-burst periods containing single spikes, and the second subclass represented a set of neurons with spikes grouped into long bursts exhibiting oscillations (waves in the ACG with a frequency around 10 Hz). The occurrences of PSTH, INTH and ACG types in individual MGB subnuclei were evaluated by a chi-square test of equality of two multinomial distributions (2 x k contingency tables) on a 5 % significance level followed by analysis of standardized deviates.

The care and use of animals reported in this study were approved by the Ethics Committee of the Institute of Experimental Medicine and followed the guidelines of the Declaration of Helsinki.

Results

The data from 194 neurons were recorded simultaneously as 97 neuronal pairs with one microelectrode from the MGB of 29 adult guinea pigs under stimulation with a pure tone at CF. The responses of neurons were evaluated according to their firing pattern (PSTH) and discharge time characteristics, especially bursting and oscillations (INTH and ACG).

38 % of neurons were collected from the ventral subdivision, 32 % from the medial subdivision and 23 % from the dorsal subdivision of the MGB. The position of remaining neurons (7 %, i.e. 14 units) could not be assign

to any part of the MGB. Each of the following results are presented first for the whole MGB and then for particular MGB subnuclei.

a   b   c

PSTH - types   ### INTH - types   ### ACG - types
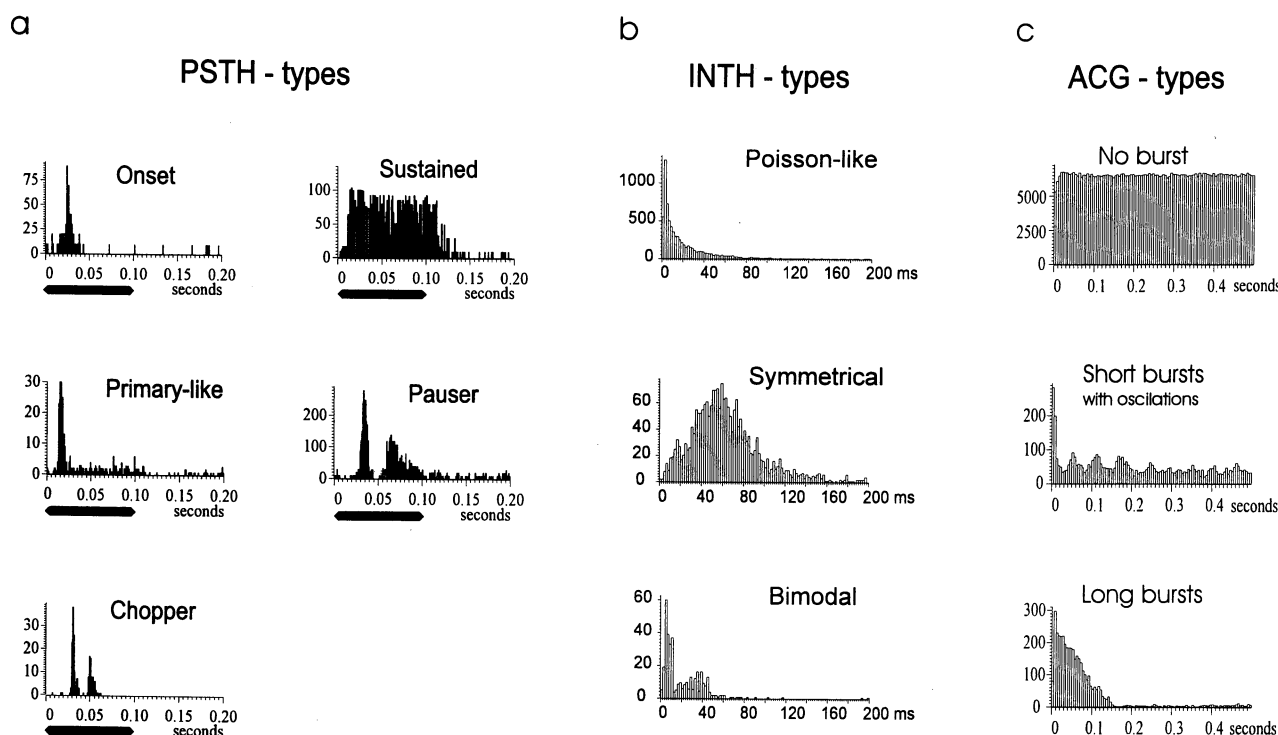
Fig. 1. *Examples of types of peristimulus time histogram (PSTHs), interval histograms (INTHs) and auto-correlograms (ACGs). The PSTHs, with 1-ms bin size and 200 ms duration, were differentiated into five classes:* **onset, primary-like, sustained, chopper** *and* **pauser** *types (Fig. 1a). The INTHs, with 1-ms bin size and 200 ms window, were differentiated into three groups:* **Poisson-like, symmetrical** *and* **bimodal** *types (Fig. 1b). The ACGs, computed over a 500 ms range with a 5-ms bin width, were sorted into three classes:* **no bursts, short bursts** *and* **long bursts** *(Fig. 1c).*

Peristimulus time histograms

The responses of neurons were classified into five PSTH types as shown in Figure 1. The distribution of 194 individual PSTH types in the whole MGB is shown in Figure 2a. The most frequent types of PSTHs were *onset* and *chopper* responses, which were observed in 43 % and 32 % of neurons, respectively. Other types of responses, i.e. *primary-like*, *sustained* and *pauser*, were found in less than 9 % of cases each. The distribution of individual PSTH types in MGB subnuclei were significantly different (p<0.05) between vMGB and mMGB, and between vMGB and dMGB, but not between mMGB and dMGB (Fig. 2b). The greatest differences were found in the *onset* and *primary-like* PSTHs. In the vMGB, 58 % of neurons responded by an *onset* type of response, while a *chopper* response in this subnucleus

was observed only in 24 % of neurons. In the mMGB, *onset* and *chopper* responses were present in approximately the same amounts (32 % and 34 %, respectively), while in the dMGB *chopper* responses (45 %) prevailed over *onset* responses (27 %). The occurrence of *primary-like* responses was found to differ between the vMGB (4 % of units) and the mMGB (13 % of units) or dMGB (14 % of units).

The types of PSTHs were also compared in the recorded pairs. In the whole MGB, 38 % of pairs contained neurons with different PSTH types. Most of these were found in the mMGB (52 %) while a smaller portion was found in the vMGB and dMGB (35 %). There was no preferred combination of particular PSTH types in the MGB subdivisions. As might be expected from the occurrences of individual PSTH types, the most

frequent combination of different response types in a neuronal pair was an *onset/chopper* pair (12 % of all pairs).

In some PSTHs, reverberation and an *off-reaction* were also found. A clear *off-reaction* appearing after the stimulus offset was not seen, but in 14 % of *onset* neurons in the MGB an *off* component of the response was found (*on-off* neurons). Reverberations, which are characterized by a higher activity occurring with some delay after the stimulus offset, were found in 10 % of all MGB neurons without any preferential localization.
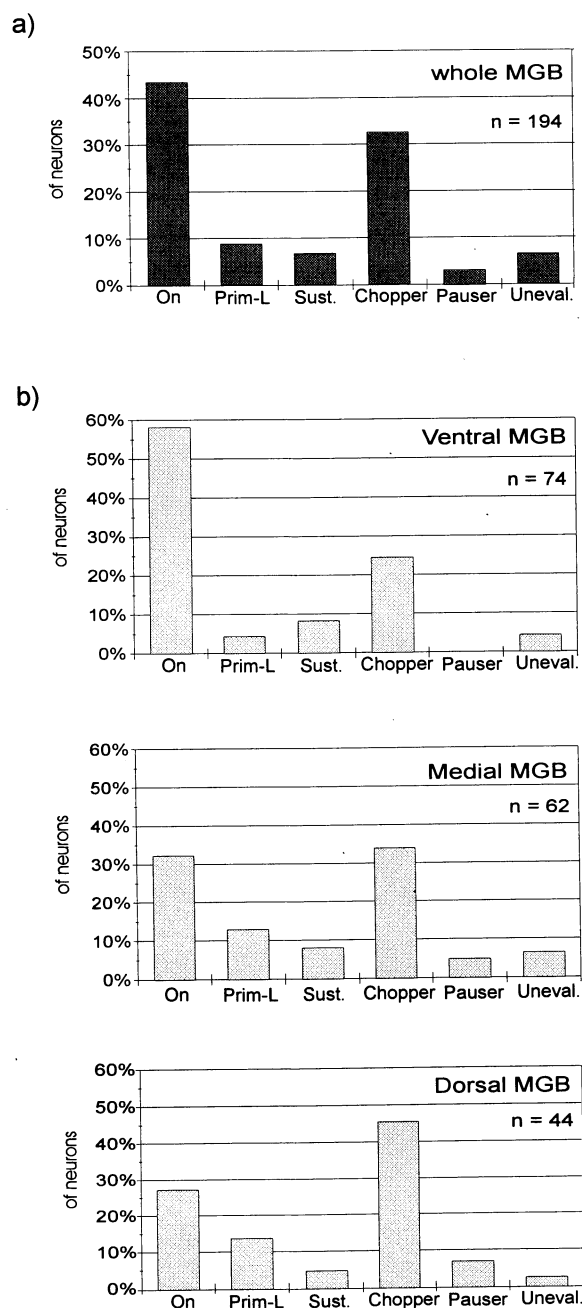
Fig. 2. *The frequency of certain PSTH types, computed from responses to pure tone at CF, for neurons in the whole MGB (a) and their percentages in three MGB subnuclei (b).*
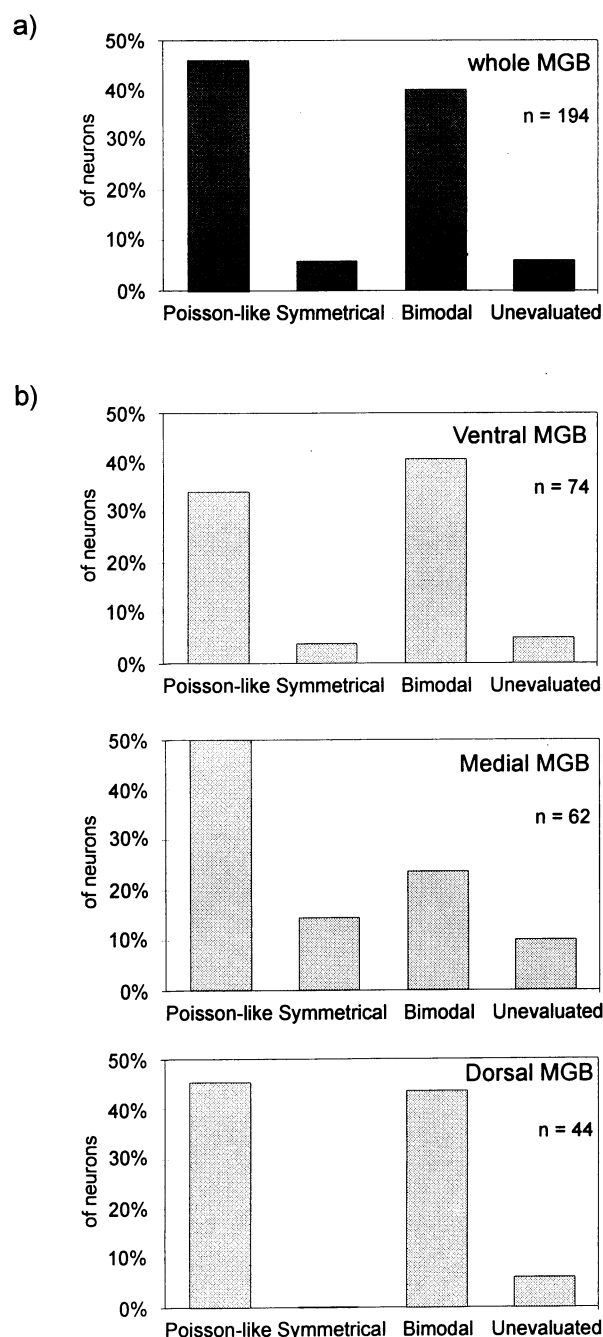
Fig. 3. *The occurrence of different types of INTHs obtained for neurons in the whole MGB (a) and their distributions in three MGB subnuclei (b).*

Interval histograms

Interval histograms computed from the whole recording including the stimulation period (in agreement with procedures previously used by Bock *et al.* 1972, Bock and Webster 1974, Syka *et al.* 1975, Rhode and Kettner 1987, Rhode 1995, Kaneoke and Vitek 1996) were differentiated into three groups: *Poisson-like*, *symmetrical* and *bimodal* type. In the whole MGB, *Poisson-like* (40 %) and *bimodal* (46 %) INTHs occurred most frequently (Fig. 3a). Only a small number of neurons (7 %) revealed a *symmetrical* INTH. Furthermore, it was not possible to clearly assign a portion of the INTHs (7 %) to one of the INTH types.

The distribution of INTHs in individual MGB subnuclei was found to be different (p<0.05, chi-square test) between the vMGB and mMGB and between the mMGB and dMGB (Fig. 3b). *Symmetrical* INTHs were found in 4 % of vMGB units and in 15 % of mMGB units but they were absent in the dMGB. *Bimodal* INTHs were expressed by 41 % of vMGB units, 43 % of dMGB units and only 24 % of mMGB units.

The INTH types of neurons recorded together from one site differed in 47 % of pairs. More than 39 % of pairs displaying different types of INTH contained a combination of one neuron with a *Poisson-like* and one neuron with a *bimodal* type of INTH. 10 % of pairs showed a combination of *Poisson-like* and *symmetrical* INTH.

Auto-correlograms

In the whole set of 194 MGB neurons, the following distribution of ACGs was observed (Fig 4a): *No burst* type, having a flat ACG, corresponding to randomly distributed single spikes in the neuronal firing, was found in 15 % of all MGB neurons. *Short bursts* or *salvos* lasting up to 100 ms, which are characterized by a narrow initial peak in the ACG, were observed in 60 % of all MGB neurons. *Long bursts*, with duration of over 100 ms, were found in 23 % of all neurons. For a small number of neurons (4 %) it was not possible to estimate the ACG type.

The occurrence of ACG types was different in individual MGB subnuclei (p<0.05, chi-square test) Figure 4b. The distribution of ACG types in the vMGB was found to be different from that in the mMGB and dMGB; however, the occurrences of ACG types in the mMGB did not differ significantly from those in the dMGB. Non-bursting neurons occurred most frequently in the mMGB (22 %), and least frequently in the dMGB (7 %); however, these percentages were not significantly
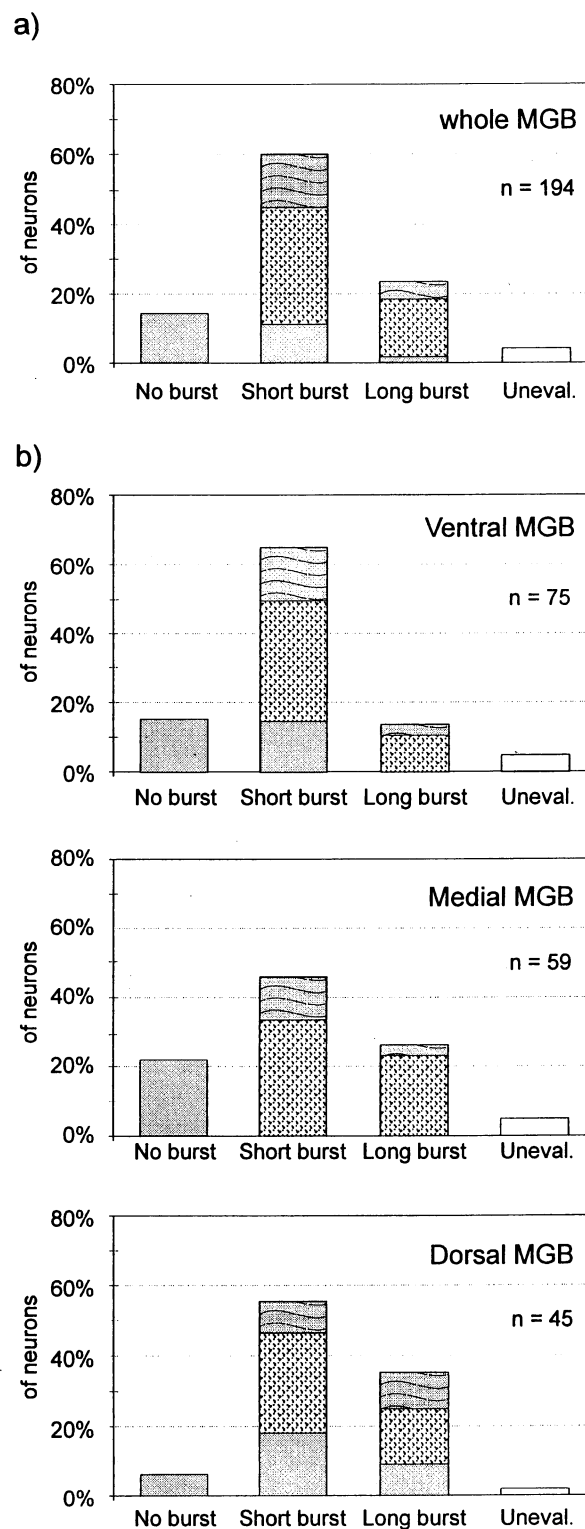
Fig. 4. *The distribution of ACG types computed for units from the whole MGB (a) and sorted according to the particular recording site in three MGB subnuclei (b). In neuronal activities with short and long bursts are signed parts containing, except sole bursts, still spikes (dots) or oscillations (waves).*

different. Most units in all MGB subdivisions expressed an ACG typical for firing in short bursts, lasting up to 100 ms. The largest number of these neurons was observed in the vMGB (65 %), whereas in the mMGB short burst neurons were found in a significantly (p<0.05, chi-square test) lower percentage of units (46 %). Neurons firing with long bursts were preferably located in the dMGB (36 %), while the smallest number of them was found in the vMGB (13 %).

In the whole MGB, 72 % of neuronal pairs recorded with one microelectrode contained units of the same type of ACG. Pairs combining a unit with a flat ACG and a unit firing in either short (6 %) or long bursts (4 %) were rarely observed. In 18 % of pairs, units showing a combination of ACGs typical for short and long bursts were found.

Neurons with ACGs displaying short bursts were differentiated into three subsets: neurons firing only by short bursts (18 % of all *short burst* neurons); neurons with short bursts mixed with irregular single spikes (57 %) and short bursts with oscillations (25 % of *short burst* neurons). A similar differentiation was seen in neurons with ACGs signalling activity in long bursts: units firing only by long bursts (9 % of neurons), units combining long bursts with irregular single spike activity (70 % of neurons) and units discharging long bursts with oscillations (21 % of neurons). In general, about half of the neurons in the whole MGB fired with irregular single spikes mixed with bursts. Oscillations of activity were found in approximately 15 % of MGB units.

Neuronal activity containing only short bursts was found most frequently in the dMGB (32 % of units displayed short bursting activity), while in the mMGB this type of activity was not observed at all. Neurons firing in short bursts mixed with single spikes were mainly located in the mMGB (74 % of all units), whereas such activity occurred less frequently in the other two MGB subnuclei (53 % of all units). Oscillations of activity in *short burst* neurons were observed in all MGB subnuclei in approximately in the same proportions (from 16 % in the dMGB to 26 % in the mMGB).

The greatest proportion of activity containing long bursts and single spikes was observed in the mMGB (84 % of *long bursting* units), whereas in the vMGB and mMGB pure long bursting activity was not found at all. Oscillations together with long bursts were recorded mainly in the dMGB (31 % of *long bursting* neurons).

The distribution of units with oscillatory activity did not differ with respect to the recording site (from 15 % in the mMGB to 20 % of units in the dMGB). The

activity in which bursts alternated with single spikes was mainly observed in the mMGB (58 % of all MGB neurons), but the occurrence of such activity was not significantly different among the MGB subnuclei.

Discussion

The present results have demonstrated that, on the basis of the firing pattern as measured by three different statistical methods, the "primary" part of the MGB – the ventral subdivision – could be distinguished from those parts that are considered as "secondary" – the dorsal and medial subdivisions.

The discharge properties of neurons in the MGB have been analyzed in several studies in the cat (Dunlop *et al.* 1969, Rouiller *et al.* 1979, Calford and Webster 1981, Heierli *et al.* 1987, Rodrigues-Dagaeff *et al.* 1989, Simm *et al.* 1990) and the guinea pig (Redies and Brandner 1991, Edeline *et al.* 1999). Unlike the authors of these studies, who described such parameters of the neuronal response and spontaneous activity as frequency tuning, latency, and thresholds, we have used three methods of discharge analysis (PSTH, INTH and ACG) to characterize the discharge properties of MGB neurons in the guinea pig. Since pairs of units were recorded with one microelectrode in our experiments, it was possible to compare the discharge properties of neighboring neurons. Only units responding to pure tones were selected, therefore our sample does not contain units that respond only to click or to more complex acoustical stimuli.

As regards the discharge pattern, evaluated with PSTHs, the most frequent type of response was the *onset* type followed by a *chopper* reaction; in a few cases we observed *primary-like*, *sustained* and *pauser* types of response. In an accompanying studies (Syka *et al.* 1998, Kvašňák *et al.* 2000), we investigated the responses of MGB units in the ketamine-anesthetized guinea pig to complex acoustical stimuli, such as species-specific vocalizations. Furthermore, in the case of complex stimuli, the MGB units preferred to respond to the beginning of the stimulus in contrast to the inferior colliculus units, which reacted mostly throughout the whole vocalization. In the MGB of the cat, *onset* responses to acoustical stimuli also dominate. For example, Rouiller *et al.* (1979) demonstrated that in cats anesthetized with nitrous oxide more than half of MGB units responded by an *onset* reaction and only a small portion of neurons reacted by a sustained excitatory response to a stimulus. Calford and Webster (1981), who performed their experiments in the MGB of cats

anesthetized with ketamine, distinguished responses by various criteria and found a higher percentage of transient responses (related mainly to *onset* and *chopper* responses in our classification) than *sustained* responses to acoustical stimuli. In contrast to our data they also recorded inhibitory and offset responses. On the other hand, Aitkin and Prain (1974) observed that only one third of units responded with an *onset* response in the MGB of cats under pentobarbital anesthesia, while two thirds of neurons responded in a sustained manner. This result is surprising in view of the fact that neurons in the inferior colliculus of the guinea pig express more *onset* responses under pentobarbital anesthesia than under ketamine anesthesia (Astl *et al.* 1996).

In individual MGB subnuclei, we observed a similar distribution of response types as in the whole MGB. Differences in the distribution of PSTH types were found between the vMGB and both the mMGB and dMGB, but differences were not evident between the mMGB and dMGB. *Onset* responses dominated in the vMGB, while *onset* and *chopper* responses were the most frequent in the mMGB, and in the dMGB *chopper* responses prevailed. Edeline *et al.* (1999), who performed experiments in awake guinea pigs, reported differences in the properties of responses to pure tones among MGB subnuclei. They distinguished somewhat different response types (PSTH) than we did, but found a substantial difference between the vMGB and other MGB subnuclei. In agreement with our results, they found a prevalence of *onset* responses in the vMGB and significantly fewer responses of this type in the other MGB subnuclei. A *sustained* type of response was observed in a somewhat higher percentage of units than in our study. Neurons in the vMGB differed from those in the mMGB and dMGB in their response latency, spontaneous firing rate and frequency tuning. On the basis of a comparison with studies performed under different depth of anesthesia, they decided that their findings were similar to those under light anesthesia but differed from those reported under deep anesthesia. In another study in the guinea pig MGB, Redies and Brandner (1991), who used the neuroleptanalgetic drugs Hypnorm (Fluanisone and Fentanyl base) and Fentanyl (Fentanyl base) (Green 1975) as anesthesia, also reported differences in tuning curves and latencies of responses to pure tones among MGB subdivisions. They observed more vigorously responding neurons in the vMGB in comparison with other parts of the MGB. Similarly, in the cat vMGB, predominantly *onset* responses were

observed (Calford and Webster, 1981, Rodrigues-Dagaeff *et al.* 1989).

In the inferior colliculus, a similar role as the ventral subdivision of the MGB is played by the central nucleus of the IC (CNIC). However, in contrast to the vMGB, the CNIC neurons responded to pure tones predominantly by a *sustained* type of discharge pattern: one third of guinea pig IC neurons responded by a *sustained* type, one quarter by an *onset* type, and one quarter of units reacted with a *primary-like* response (Syka *et al.* submitted). Only a small number of units reacted by *chopper* or *pauser* responses.

In the whole MGB, a prevalence of *Poisson-like* and *bimodal* types of INTHs was found, which refer either to discharge by random single spikes (*Poisson-like* INTH) or to firing composed by random single spikes with bursts (*bimodal* INTH). Very few neurons discharged regularly. However, there is no available study describing the occurrence of INTHs in the MGB or the percentage of INTH types in individual MGB subnuclei. The *chopper* response may be closely related to the *symmetrical* INTH, but it may also be attributed to the *bimodal* INTH. Several studies have concentrated on the interval distribution of IC neurons in the cat. Bock *et al.* (1972) used INTHs for a description of neurons in an alert cat's IC, but they did not investigate the proportions of individual INTH types. Bock and Webster (1974) reported on spontaneous firing in the IC of barbiturate-anesthetized and unanesthetized cats on the basis of INTHs. In anesthetized animals, one third of units had a *symmetrical* INTH, whereas a smaller portion of neurons revealed this type of interval distribution in awake animals. The *bimodal* type of INTH was observed three times less frequently in units of the anesthetized cat than in units of awake cats (41 %). We found the occurrence of a *Poisson-like* INTH, which corresponds with firing by random single spikes, in the guinea pig MGB as frequently as observed by Bock and Webster (1974) in the cat IC. On the other hand, they found more neurons with a *symmetrical* INTH in the cat IC and less units with a *bimodal* INTH than we found in the MGB.

Our results demonstrate that *Poisson-like* and *bimodal* INTHs are almost equally distributed in the vMGB and dMGB, whereas in the mMGB *Poisson-like* INTHs were twice as frequent as the *bimodal* type. The prevalence of *bimodal* INTHs in the vMGB is probably related to the high percentage of *chopper* responding neurons, which are necessary for time coding in acoustical information processing. Since fewer studies

were devoted to the analysis of the intervals between spikes in a train than to PSTH analysis, these results may serve as a more general description of regularities in the activity of MGB neurons.

The presence of bursts or oscillations in firing may also be investigated by constructing an auto-correlogram (ACG) of neuronal spike trains. Using this method we found that bursting activity dominated in the MGB (82 %). Most of the bursts were combined with random single spikes or oscillations. More than two thirds of bursting units fired in bursts shorter than 100 ms. A mixed activity represented one half of all units in the whole MGB. Oscillations were found in almost 20 % of all MGB units.

Our findings from the MGB of guinea pigs obtained by the method of ACGs can be compared with the results of similar studies in the cat. For example, Aitkin and Prain (1974) observed activity in the MGB of awake cat, in which spikes occurred in an irregular manner rather than in bursts. Heierli et al. (1987) divided spontaneous activity in the MGB of nitrous oxide-

anesthetized cats into roughly the same categories as we did. They found 46 % of units with purely isolated spikes, 18 % of units with short bursts, 6 % of units with long bursts and 30 % of units with mixed activity. The discrepancy between our data and their data may be explained by the different kinds of anesthesia and by differences in the animal species. The more frequent bursting behavior in the guinea pig MGB is probably due to ketamine anesthesia, which is a light anesthesia and can produce effects similar to the sleeping state, where bursting is quite common.

Acknowledgements

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