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Research Note

Processing of amplitude modulated sounds in the medial geniculate body of squirrel monkeys

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Summary. The responses of single and multi units in the medial geniculate body of the squirrel monkey (*Saimiri sciureus*) to modulation frequency, modulation depth and changes in absolute intensity of sinusoidally amplitude modulated (AM) sounds were studied. Both spike-frequency and spike rate modulation were used as a measure for neuronal response. Spike rate modulation was derived from FFT (Fast-Fourier-Transformation) analysis of the PSTHs. In all cases (N = 133) spike rate modulation was shown to be dependent on the stimulus modulation frequency: Most neurons responded best to one modulation frequency, i.e., they showed a modulation transfer function with bandpass characteristic; only a few displayed a low pass or multiple peaked transfer characteristic. The majority of the neurons responded best in a range from 4 to 64 Hz, with a peak at 32 Hz and a median at 16 Hz. Such modulation frequencies are common in parts of the species vocal repertoire.

Key words: Amplitude modulation – Temporal resolution – Best modulation frequency – Medial geniculate body – Squirrel monkey

Introduction

The modulation of sound intensity serves in many behavioral situations of various species as a carrier in the exchange of acoustic information. This has been demonstrated for various behavioral situations like orientation, detection or recognition (of a prey, or a predator) and species-specific communication. With regard to communication, the strongly modulated vocalizations found in the repertoire of many primates point to the importance of this parameter in acoustic communication in these species (Schott 1975). For example, squirrel monkeys display a variety of communications, comprising periodically amplitude modulated calls, especially err- and twitter calls (Schott 1975). Furthermore, in the same species, it has been shown that number and position of modulations of the amplitude within vocalizations have a communicative meaning (Maurus et al. 1984). In man also, periodically changing amplitudes are suggested to contain information: the perception of fluctuation strength is supposed to match the modulation of syllables in human languages (typically at 4 Hz) (Fastl 1983). Studies of neural correlates of amplitude modulated stimuli in squirrel monkeys had revealed that the majority of recorded cells in the auditory midbrain and the auditory cortex are tuned to amplitude modulation frequencies: 32–64 Hz in the inferior colliculus (Müller-Preuss et al. 1986) and 4–16 Hz in the cortex (Urbas et al. 1986). These results, indicating a centripetal decline in the best amplitude modulation frequency (BMF, have been supported by data obtained from other vertebrates (Møller 1972; Rees and Møller 1983; Rose and Capranica 1984; Schreiner and Urbas 1986). The processing of AM-stimuli in the diencephalic relay station of the auditory pathway, the medial geniculate body (MGB) in the thalamus, has been less intensively studied (Creutzfeldt et al. 1980). Therefore, we have investigated the temporal tuning characteristics of MGB-neurons in more detail and the influence of the parameters modulation frequency, modulation depth and intensity on neuronal spike-frequency. The auditory system of squirrel monkeys was considered to be well suited for investigations of the processing of amplitude modulations not only because of its AM-structured vocal repertoire but also due to its close evolutionary relationship to man.

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Material and methods

Experiments were performed on four awake squirrel monkeys (Saimiri sciureus). Preparations for, and techniques of, recording have been described in more detail elsewhere (Müller-Preuss and Ploog 1981). In a stereotaxic operation a plastic chamber (Macralon) with a removable cover was implanted epidurally, and a platform for head fixation was mounted on top of the head. The neuronal activity of single cells as well as cell groups (two or more) was recorded extracellularly with tungsten microelectrodes (1–10 MOhm at 1000 Hz). For histological verification of some of the electrode tracts electrolytic lesions (5–10 μA, 5–20 msec) were applied. Acoustic stimuli were presented in a sound isolated chamber (IAC) via a loudspeaker mounted 1.5 m in front of the animal's head. Either white noise or sine tones (1000 Hz to 19 kHz) were delivered by a noise generator (Grason Stadler 829) and a tone generator (Wavetek 146). These signals were modulated sinusoidally by an auxillary unit (Wavetek 146). The carrier frequency of an AM-tone (100% modulation depth, 4–8 Hz modulation frequency), which modulated the activity of a given neuron at the lowest sound intensity, was defined as the characteristic frequency of that cell. To obtain modulation transfer functions, AM-frequencies were selected in octave steps from 1 to 128 Hz. Stimulus length and interstimulus interval of consecutive stimuli (both ls) were controlled by an electronic switch (General Radio 1396-B). Another electronic circuit allowed variations of amplitude modulation depth in 10% steps from 0% to 100% with constant peak amplitudes. Sound pressure level was adjustable between 0 db to 94 db SPL in 10 db steps by an attenuator (HP 350D). Neuronal discharges were obtained from 15 stimulus presentations. Peristimulus-time-histograms (PSTHs) were obtained using a LSI 11/23 laboratory computer and Fourier analysis performed using a DEC 20–40 computer. Cell responses were estimated by 2 measures, the "spike-frequency" and the "discharge periodicity". The first corresponds to the average spike-frequency for the last 800 ms of the stimulus presentation. The second one corresponds to the amplitude of the fourier transform of the PSTH at the modulation frequency. The fourier analysis of each PSTH was calculated for the last 800 ms of the stimulus presentation. Both discharge rate and the amplitude of the fourier transform are thought to characterize the modulation transfer function of the cell, i.e. the neuronal transfer of the modulation of stimulus amplitude. At the end of the last experiment the animal was perfused under deep anaesthesia with 10% formalin, while an electrode was left in its brain for reference. Cresyl violet stained 10 μm-slices of the brain were used to verify the reference track, electrolytic lesions and track lesions. The position of the remaining electrode tracks without lesions was reconstructed with the aid of a stereotaxic brain atlas (Emmers and Akert 1963).

Results

Modulation transfer functions were chosen as a measure of the neuronal transfer of the modulation of stimulus amplitude. These were obtained in 115 recordings (46 multi- and 69 single units) in response to amplitude-modulated (AM) white noise and from 51 recordings (18 multi units and 33 single units) in response to an AM-tone at the characteristic frequency. Responses to both AM-tones and AM-white noise were studied in 33 cases. As multi- and single units showed no significant difference in the frequency distributions of their BMFs (χ^2-test, $p = 0.98$), and also no obvious difference in their modulation transfer functions, they were treated as a single group in this study. The modulation frequencies used in this study were 1–128 Hz. However, to reduce recording time, PSTHs were not always calculated for those modulation frequencies which produced no spike-frequency modulation; this was normally the case for modulation frequencies above 32 Hz. The modulation depth was kept at 100% and intensities at 20–30 db above response threshold to 4 Hz AM-white noise or tone.

The cells we studied were all influenced by modulation frequencies. Ninety-two per cent (106/115, AM noise; 47/51, AM-tone) displayed one clear response maximum at one particular modulation frequency (i.e. at the best modulation frequency, BMF). An example of such a neuron is shown in Fig. 1A. The modulation transfer function is shown for both the total spike-frequency and the amplitude of the fourier component at the fundamental AM frequency (hereafter refered to as "discharge periodicity"; for examples of corresponding

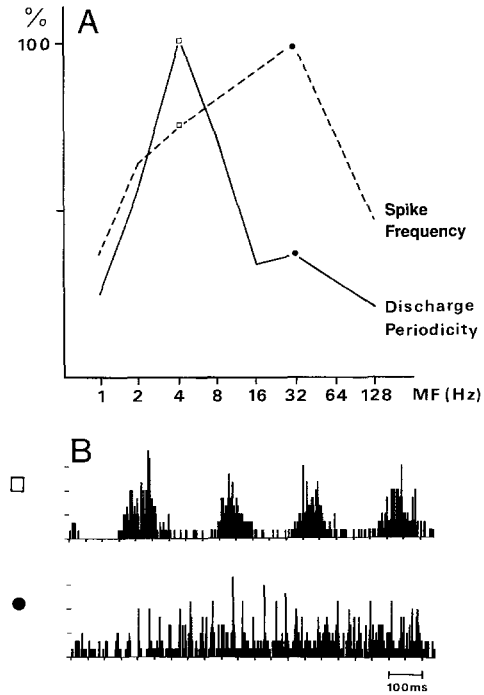

Fig. 1. A Modulation transfer fucntions of a single neuron. Stimulus was 100% AM-white noise at 64 db SPL. Cell response was measured at each modulation frequency shown. The *solid line* represents the transfer function obtained from the discharge periodicity. The *dotted line* represents the transfer function evaluated with spike-frequency. In **B**, two PSTHs corresponding to the maxima of each transfer function are shown. In the upper PSTH (modulation frequency 4 Hz) the discharge periodicity was maximum (*open square*) while in the lower PSTH (modulation frequency 32 Hz) discharge rate was maximum (*filled circle*)

PSTHs see Fig. 1B). To make these two measures more readily comparable, both are expressed as a percentage of the maximum response. The example shown exhibits two different BMFs for spike-frequency and discharge periodicity, as was the case for 33% of the recordings (38/106). However, there was no significant difference between the frequency distributions of BMFs for spike-frequency and the discharge periodicity (χ^2-test, $p=0.28$). Both distributions had their maximum at the BMF of 32 Hz and their median at 16 Hz (Fig. 2A. Dashed lines: spike-frequency, bars: discharge periodicity). Their larger part covered a range from 4 Hz to 64 Hz and represented 92% (97/106) and 77% (82/106) of the total sample for discharge periodicity and for spike-frequency, respectively, suggesting a bandpass behavior of the MGB as a whole for AM sounds. Both distributions were obtained from cells which were stimulated with AM-white noise ($n=106$). A sample of 51 neurons was investigated with AM-tones. The resulting frequency distribution of BMFs had for both discharge periodicity and spike-frequency its maximum at 32 Hz and its median at 16 Hz. In this way, the stimulus carrier was shown to have no significant effect on the frequency distribution of BMFs (χ^2-test, $p=0{,}91$ for discharge periodicity). There was no significant difference between the frequency distributions of BMFs for spike-frequency and the discharge periodicity (χ^2-test, $p=0.51$). Thirty-three neurons out of this sample were stimulated with both AM-tones and AM-noise and showed no significant influence of the carrier on their frequency distribution of BMFs (χ^2-test, $p=0.81$ for discharge periodicity). Again, the distribution had a median BMF of 16 Hz and a maximum at 32 Hz. In this situation stimulation with AM-tones produced a second maximum at 16 Hz. The behavior of the sample as a whole was in contrast to that of its individual parts. Fifteen cells changed their BMF by more than one octave with a change of the carrier from tone to noise or vice versa. No evidence was obtained of a systematic relation between BMF and characteristic frequency.

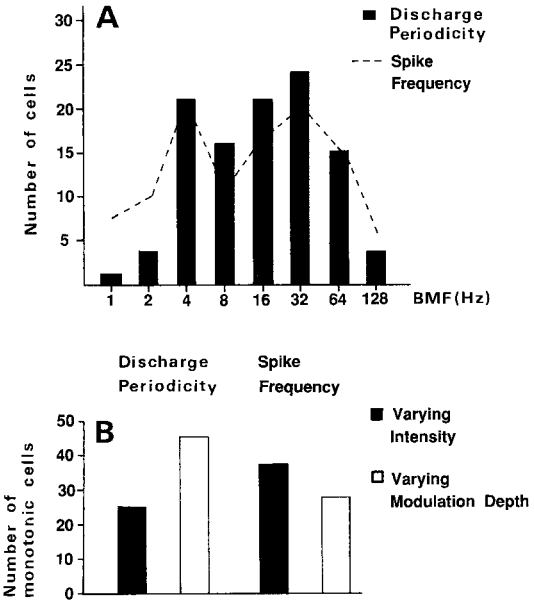

Fig. 2. **A** Distribution of BMFs of those cells which display a modulation transfer function with one clear maximum when tested with white noise is shown in the upper part of the figure (N = 106). *Filled columns* show the percentage of cells which had their discharge periodicity maxima at the particular modulation frequencies shown at the abscissa. Maxima of discharge rate are indicated by *dotted lines*. **B** Distribution of neurons with a monotonic increase in discharge periodicity (on the left) and spike-frequency (on the right), when AM-white noise intensity was increased from 24 db SPL to 94 db SPL (modulation depth was 100%, modulation frequency 4–8 Hz; *black columns*) or modulation depth was enlarged from 0% to 100% (10% steps, sound intensity 20–30 db above threshold, modulation frequency 4–8 Hz; *outlined columns*)

Stimulus intensity and modulation depth

Sixty-one cells were stimulated with 100% amplitude modulated white noise ranging from 24 db SPL to 94 db SPL, delivered in 10 steps of 10 db, with a modulation frequency of 4–8 Hz, in the most instances. The plots of total spike frequency and discharge periodicity against stimulus intensity were quite different (χ^2-test, $p<0.05$); while only 40% (25/61) of the cells displayed a monotonic increase in the discharge periodicity, 61% (37/61) of the same cells displayed a monotonic spike-rate increase (Fig. 2B). Eighty-eight per cent of the cells (22/25) which displayed a monotonic increase in discharge periodicity also showed a monotonic increase in spike-frequency.

The same number of cells was investigated using white noise stimuli with modulation depths from 0% to 100% in 10% steps and with the same modulation frequencies previously mentioned. Again, spike-rate and discharge periodicity were different (χ^2-test, $p<0.05$); while 74% (45/61) of the neurons showed a monotonic increase in the discharge periodicity, only 46% (28/61) of the cells showed a monotonic increase in spike-rate with increasing modulation depth (Fig. 2B). The remaining neurons had their spike rate maxima equally distributed over 0% to 90% modulation depth. Only 31% (14/45) of the neurons displaying a monotonic increase in discharge periodicity also showed a monotonic increase in spike-frequency. 36% (22/61) of the neurons responded with a sig-

nificant spike-frequency modulation to 40% AM stimuli and 18% (11/61) detected a modulation depth as low as 10%.

The three parts of the MGB

In his cyto- and myeloarchitectonic study Jordan (1973) divided the MGB of the squirrel monkey into three sub-nuclei, part a (ventro-caudal), b (medial) and part c (laterodorsal). We determined the position of our recording sites within these structures by means of electrode track reconstructions. Electrode tracks which penetrated more than one sub-nucleus were excluded from this histological analysis. In this way, we determined the loci of 83 neurons out of the total sample investigated with AM-noise. Moreover, nine of the loci could be verified with greater precision histologically due to their association with tracks marked by electrolytic lesions.

About half of the neurons (47/83) were found in part b, 24 neurons in part a, and 12 neurons in part c. One criterion for comparison of the neuronal populations of each subnucleus was, whether the pattern of neuronal discharge was tonic throughout, or phasic at each stimulus-modulation cycle. Phasic neurons exhibited either an On-response at the beginning, or an Off-response at the end, of each modulation cicle. In part b, a tonic response was exhibited by almost all neurons (42/47), whereas in parts a (a 12/24) and c (6/12), tonic responses were found in only half of the neurons. Another criterion was the median BMF (16 Hz in part b and 8 Hz in both part a and part c). The difference in median BMF between part b and the other sub-structures was significant (χ^2-test, $p < 0.01$) and could be due to the different proportions of tonic neurons in these sub-structures.

Discussion

A median BMF of 16 Hz was found in the MGB of the squirrel monkey, with 32 Hz being the most common BMF, lying between the corresponding BMFs in the auditory cortex (4–16 Hz) (Fastl et al. 1986; Urbas et al. 1986), and in the inferior colliculus (32–64 Hz) (Müller-Preuss et al. 1986) of this animal. This result is indicative of a stepwise decline of BMFs between the cochlear nucleus, the inferior colliculus, the MGB and the cortex of the monkey. This property has also been described in other vertebrates (Gersuni and Vartanian 1973; Møller 1972; Creutzfeldt et al. 1980; Vater 1982; Rees and Møller 1983; Schreiner and Urbas 1986) and may be general within this group. As we have demonstrated this property in a primate, it may also exist in the human auditory system. This decrease in the ability to process periodic amplitude modulations centripetally is paralleled by a decrease of BMF, which is similar to BMFs obtained with AM sounds. (Møller 1972; Schuller 1979; Vater 1982; Rees and Møller 1983). This centripetal decrease of BMF may result from a centripetal increase in the number of synapses, as supposed by Vater (1982). However, this does not affect the ability of neurons of the auditory cortex and the MGB of squirrel monkeys to process short and/or sudden amplitude changes within vocalizations (Glass and Wollberg 1983; Müller-Preuss and Maurus 1985).

The most usually occuring BMFs of 4 to 64 Hz reported here are similar to frequencies of periodic amplitude modulations described for some of the vocalizations of the squirrel monkey (Schott 1975). Especially calls of the err-type or of the twitter-type could be encoded by neurons having AM-tuning properties as shown above, because they could evoke vigorous responses in such cells. This does not necessarily suggest that these neurons are specially adapted to process such calls, as many vocalizations in other animal groups have the same modulation rates, also matching corresponding median BMFs (Gersuni and Vartanian 1973; Creutzfeld et al. 1980; Rees and Møller 1983; Rose and Capranica 1984). In general, most vertebrate vocalizations are amplitude modulated at rates lower than about 300 Hz (examples see Tembrock 1986; Poulter 1968; Schott 1975; Gersuni and Vartanian 1973). Almost all neurons were tuned to certain modulation frequencies. As we could show that the median BMF is primarily independent of the quality of the signal carrier (noise or tone), we conclude that amplitude modulation may represent a valuable temporal cue which is not distorted by the spectral content of the carrier. However, we could demonstrate that changes of the carrier from white noise to sine tone result in changes of BMFs by more than one octave in almost half of the neurons. Thus carrier changes may well be encoded by the changes in the pattern of excitation in the MGB as a whole. Differences between spike rate and discharge periodicity as a function of stimulus intensity suggest that increasing intensity could be encoded by two different mechanisms within many cells: by the monotonic increase in spike rate and, to a lesser extent, by a tuning of spike rate modulation to different intensities. This leads to the question of whether spike rate and the discharge periodicity act differently on the same stimulus parameter or whether they act on different cues

within this stimulus. A possible answer to this question emerged, when spike-frequency and the discharge periodicity were observed with respect to an increase of modulation depth: while the majority of neurons showed a monotonic increase in the discharge periodicity spike rate itself was non-monotonic in more than half of the cells. As the ratio of spike-frequency modulation to spike rate reflects the modulation depth of the PSTH, this ratio encodes more or less the modulation depth of the stimulus. In contrast to the situation with increasing intensity, increase of stimulus amplitude modulation is not paralleled by an simultaneous increase of physical energy. Thus, total spike rate may reflect more accurately the physical energy of the stimulus, while the discharge periodicity may be more suited to follow the amplitude modulation, i.e. the stimulus shape. The remarkably high sensitivity of some MGB neurons to small amplitude changes (even 10% modulation depth was detected by 18% of the neurons) may be useful in order to encode amplitude modulations within the species vocalization repertoire which have been shown to be of communicative relevance (Maurus et al. 1985). With regard to the substructure of the MGB (Jordan 1973), we found a difference of only one octave of BMF between the medial part and the other parts of MGB. Whether the medial part plays a special role is uncertain: the different structures of the MGB have been reported to vary only slightly in the processing of simple stimuli (Allon et al. 1981), but the medial part was the only part which has been reported to have at least some cells which selectively process discrete vocalizations (Symmes et al. 1980).

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