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Representation of amplitude modulation in the auditory cortex of the cat. II. Comparison between cortical fields

Christoph E. Schreiner * and John V. Urbas

Max-Planck-Institut für biophysikalische Chemie, Abteilung Neurobiologie, Göttingen, F.R.G.

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The responses of neuronal clusters to amplitude-modulated tones were studied in five auditory cortical fields of the anesthetized cat: the primary auditory field (AI), second auditory field (AII), anterior auditory field (AAF), posterior auditory field (PAF) and the ventro-posterior auditory field (VPAF). Modulation transfer functions (MTFs) for amplitude-modulated tones were obtained at 172 cortical locations. MTFs were constructed by measuring firing rate (rate-MTFs) and response synchronization (synchronization-MTFs) to sinusoidal and rectangular waveform modulation of CF-tones. The MTFs were characterized by their 'best-modulation frequency' (BMF) and a measure of their quality or 'sharpness' (Q_{2dB}). These characteristics were compared for the five fields. Rate and synchronization MTFs for sinusoidal and rectangular modulation produced similar estimates of BMF and Q_{2dB} . Comparison of averaged BMFs between the cortical fields revealed relatively high BMFs in AAF (mean: 31.1 Hz for synchronization to sinusoidal AM) and moderately high BMFs in AI (14.2 Hz) whereas BMFs encountered in AII, VPAF and PAF were generally low (7.0, 5.2, and 6.8 Hz). The MTFs were relatively broadly tuned (low Q_{2dB}) in AAF and sharper in a low modulation group containing AII, PAF and VPAF. The ventro-posterior field was the most sensitive to changes in the modulation waveform. We conclude that there are significant differences between auditory cortical fields with respect to their temporal response characteristics and that the assessment of these response characteristics reveals important aspects of the functional significance of auditory cortical fields for the coding and representation of complex sounds.

Auditory cortex; Amplitude modulation; Cat

Introduction

In the cat, at least seven different auditory cortical fields have been described (Reale and Imig, 1980). An important parameter by which these fields are physiologically distinguished is their cochleotopic organization, i.e. the spatial orientation of the frequency gradient derived from the neuronal best frequencies.

Other functional differences between fields have been described for sharpness of tuning ('spectral resolution'), latencies, minimum thresholds, and

the spatial distribution of neurons with different binaural response properties (e.g. Phillips and Irvine, 1980, 1981; Imig and Adrian, 1977; Middlebrooks et al., 1980; Phillips and Orman, 1984; Schreiner and Cynader, 1984). However, these parameters are insufficient to distinguish functionally between some auditory fields. For example, the primary auditory cortical field (AI) and the anterior auditory field (AAF) receive similar anatomical projections and have very similar response thresholds, latencies and frequency tuning (Merzenich et al., 1975; Knight, 1977; Phillips and Irvine, 1980, 1981; Imig and Reale, 1980; Reale and Imig, 1980; Andersen et al., 1980; Imig and Morel, 1983). So far, the only known functional parameter clearly distinguishing these fields is the orientation of their gradient of characteristic frequencies (CFs), i.e. by properties of the main parameter in the spectral domain.

Correspondence to: John V. Urbas, Max-Planck-Institut für biophysikalische Chemie, Abteilung Neurobiologie, 3400 Göttingen, F.R.G.

* *Current address:* Coleman Laboratory, School of Medicine, HSE 863, Department of Otolaryngology, University of California, San Francisco, CA 94143-0526, U.S.A.

Other signal characteristics that could be utilized to distinguish between functional properties of cortical fields are parameters in the temporal domain. The temporal patterning or modulation of frequency and amplitude over time is an important information-carrying feature of complex sounds such as species-specific communications sounds. Complex communication signals contain modulation frequencies over a range extending from a few events per second to up to several hundred Hertz. In this report we attempt to throw some light on the role of the auditory cortex in the coding and representation of temporally varying signals and to document differences in basic temporal response properties of neurons among five cortical fields: anterior auditory field (AAF), primary auditory field (AI) (including the 'dorsal zone' (Middlebrooks and Zook, 1983)), second auditory field (AII), posterior auditory field (PAF) and ventro-posterior field (VPAF).

Regular amplitude changes of a carrier signal (amplitude modulation (AM)) were used for this exploratory study of temporal processing within these auditory cortical fields. Temporal 'modulation transfer functions' (MTFs) of multi-unit responses have been obtained for the parametric description of the findings. Results are limited to those properties that have the potential to identify major interfield differences. General properties of cortical responses to AM signals which appeared to be common to most fields (e.g. level dependence, binaural interaction etc.) have been described for AAF in the first part of this study (Schreiner and Urbas, 1986).

Materials and Methods

The experimental procedures utilized have been described in more detail in the first part of this study (Schreiner and Urbas, 1986). Experiments were performed on 15 adult cats. Initially, ketamine hydrochloride (30 mg/kg i.m.) was administered to allow venous cannulation. An initial intravenous dose of pentobarbital (Nembutal 5 mg/kg) and subcutaneous injections of atropine (1 mg) and a corticosteroid (Solu-Decortin-H, Merck, 10 mg) were then administered to establish a surgical level of anesthesia and to control the secretion of mucus and development of brain

edema, respectively. Following tracheal cannulation and placement in a head-holder, the cat was paralyzed with gallamine triethiodide (8 mg/kg i.v.) and artificially respirated. Throughout the experiment the animal was infused with 5 mg/kg/h gallamine triethiodide and 2 mg/kg/h Nembutal in a solution of 20% glucose in Ringer's solution (infusion volume: 3 ml/h). End-tidal CO₂ and ECG were continuously recorded and maintained within stable limits with appropriate measures, e.g. supplements of the anesthetic. The temperature was maintained at 37–38°C.

After exposure of the lateral cortical surface, a well was constructed and filled with mineral oil. Recordings were made from the left hemisphere with low impedance (approximately 1 M Ω at 1 kHz) carbon fiber microelectrodes. Peristimulus-time histograms (PSTHs) were constructed for the responses from small groups of neurons (2–5 cells), and occasionally from single units. The recordings reported here were derived at an intracortical depth ranging from about 800–1200 microns, roughly corresponding to cortical layers III and IV. To allow the comparison of different cortical fields, recording of multi-unit activity was restricted to layers III and IV which produce the largest and most reliable responses. To minimize the relative contribution of thalamo-cortical axons to the response, activities with latencies shorter than 8–9 ms were not included into the data because of the strong probability that they did not originate from cortical neurons. Cortical fields were identified by their locations relative to the sulcal pattern, by the gradients of the encountered CFs, and especially for AII, by the sharpness or quality of derived tuning curves.

Auditory stimuli were presented via headphones (Sennheiser HD424) positioned directly at the pinnae and calibrated in situ with a Brüel and Kjaer sound-level meter. The characteristic frequency (CF) threshold, $Q_{10\text{dB}}$ (CF divided by bandwidth of tuning curve 10 dB above minimum threshold) and binaural response characteristic for neurons and neuronal clusters at each recording site were determined. This was accomplished by using 200 ms tone bursts and examination of the stimulus-synchronized spike record on the oscilloscope and by listening to the amplifier output fed into a loudspeaker. Amplitude modulation (AM)

signals were then presented to the contra-lateral ear. These stimuli employed carrier frequencies at the CF that were amplitude-modulated (100% modulation depth) by either sinusoidal or square wave envelopes.

Amplitude modulation stimuli were delivered as bursts of 1 s duration alternating with silent intervals of 0.8–1.5 s duration. PST histograms of the response to AM stimuli were derived at every site for a range of modulation frequencies (14 frequencies between 2.2 and 200 Hz). The signal level of each MTF was held constant at a level 10–40 dB above minimum response threshold. PSTH binwidth was 1 ms; usually, 20 response averages were collected for each stimulus setting.

Two kinds of temporal modulation transfer functions (MTFs) were constructed from the PST histograms of responses to AM tones. ‘Rate-MTFs’ were derived from the mean firing rate of a group of neurons during the presentation of a modulated tone and plotted as a function of the modulation frequency. This rate-MTF was normalized to the maximal mean firing rate for any modulation at that location. ‘Synchronization-MTFs’ were derived from the synchronization (or phase-locking) of the neuronal response to the modulation of the carrier signal. Synchronization is a measure of the accuracy of the coupling between the neural response and the temporal properties of the stimulus. The hamming-weighted PSTH was Fourier-analyzed and the contribution of the first plus the second harmonic of the modulation frequency (relative to the dc-component) were taken as a synchronization metric. The second harmonic was included into the analysis to permit an appropriate assessment of responses that showed on-responses as well as pronounced off-responses to a single period of the AM, thus resulting in a ‘frequency doubling’ of stimulus-triggered events in the histograms. Strong off-responses were seen mostly for rectangular AM. The ‘synchronization-MTFs’ were constructed relative to the maximal synchronization at a given site and plotted as a function of the modulation frequency.

Both MTFs will be described in this report by two parameters. The first is the modulation frequency that produces the maximum synchronization (or maximum mean firing rate) in the neuronal response, termed the ‘best modulation

frequency’ (BMF). The second parameter is a measure of the quality of the MTF. In this study, the bandwidth 2 dB below the maximum (approximately 20% below the tip of the MTF) will be used to quantify the quality: ‘ $Q_{2\text{dB}}$ ’ = BMF divided by bandwidth of $\text{MTF}_{2\text{dB}}$ below BMF. More details of the procedures and representative examples of individual synchronization and rate MTFs are given in the first part of this study (Schreiner and Urbas, 1986).

Results

Best modulation frequency for synchronization

For sinusoidal stimulation, synchronization MTFs have been obtained at 172 sites in five auditory cortical fields. A best modulation frequency (BMF) could be determined at 88% of these locations, covering a modulation range from 3 Hz–100 Hz. The other 12% showed a low-pass characteristic with a maximum at the lowest modulation frequency used in this study (2.2 Hz).

The distributions and mean values of the BMFs for the synchronization of the response to sinusoidally modulated CF tones encountered in AAF, AI, AII, PAF, and VPAF are shown in Fig. 1. Although the distribution of the encountered BMF values was ragged and possibly bimodal (e.g. Fig. 1A, D) mean and standard deviation have been calculated to facilitate comparison between the properties of different cortical fields. Considerable differences of mean and standard deviation between these fields were obtained. The highest average BMF was found in AAF (average 31.1 ± 27.4 Hz). The average BMFs in the other fields were 14.2 ± 8.8 Hz in AI, 7.0 ± 5.0 Hz in AII, 5.2 ± 3.2 Hz in VPAF, and 6.8 ± 11.2 Hz in PAF. Analysis of variance was significant (F-test, $P < 0.05$). Conservative statistical evaluation (post-hoc comparison, Method of Scheffe) demonstrated a significant difference ($P < 0.05$) of the average BMF of AAF from the BMFs in AI, AII, PAF and VPAF. In addition, the BMF of AI was significantly different from those of AII, PAF and VPAF, whereas the BMFs of AII, PAF and VPAF showed no significant differences. Consequently, the investigated cortical fields can be loosely grouped into three categories with regard to their ‘temporal resolution’ (or ability to follow temporal changes

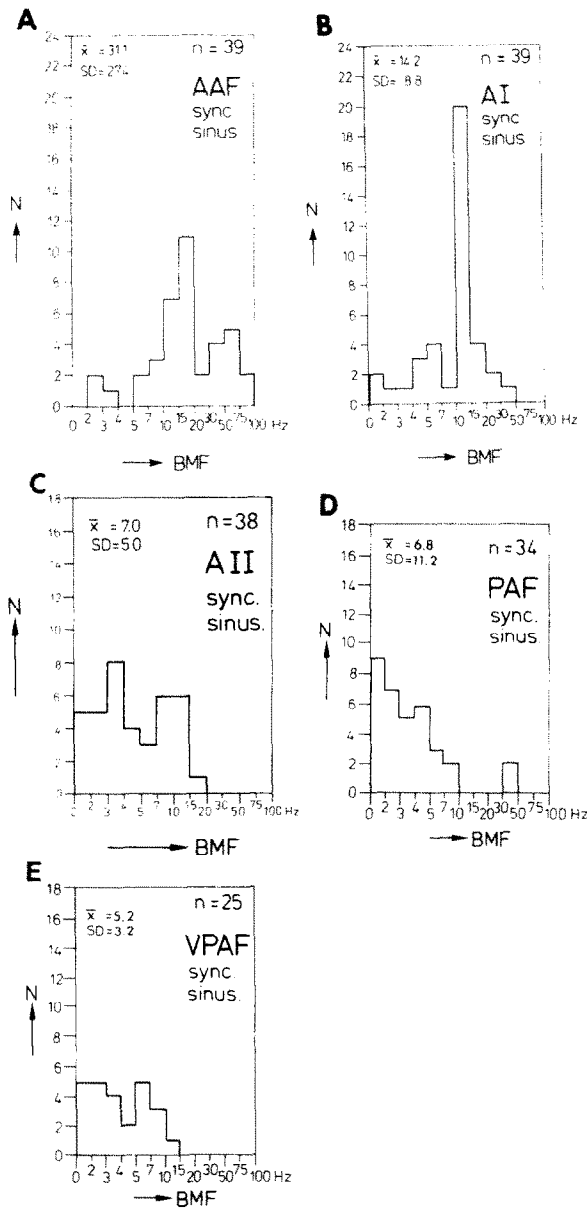


Fig. 1. Distribution of best-modulation frequencies (BMFs) of the modulation-transfer functions (MTF) for the synchronization of responses to sinusoidal amplitude modulation of a CF tone. The distributions are shown for five auditory cortical fields. Arithmetic mean and standard deviation of the distributions are indicated. Each bin contains BMFs up to but not including the next higher frequency marked on the abscissa.

as expressed by the average BMF for the synchronization to sinusoidal AM): AAF represents a 'high resolution field', AI was a 'medium resolu-

tion field', and a group of 'low resolution fields' contained AII, PAF and VPAF.

Rectangular modulation of a carrier signal produces response characteristics similar to sinusoidal modulation. However, rectangular modulation produced a higher incidence of off-responses than sinusoidal modulation. At least in AI, there was some indication that the locations with strong off-responses were spatially clustered indicating that the off-responses may be a component of the 'temporal processing mechanisms'.

In Fig. 2A the (averaged) BMFs for sinusoidal and rectangular modulation are shown for the five

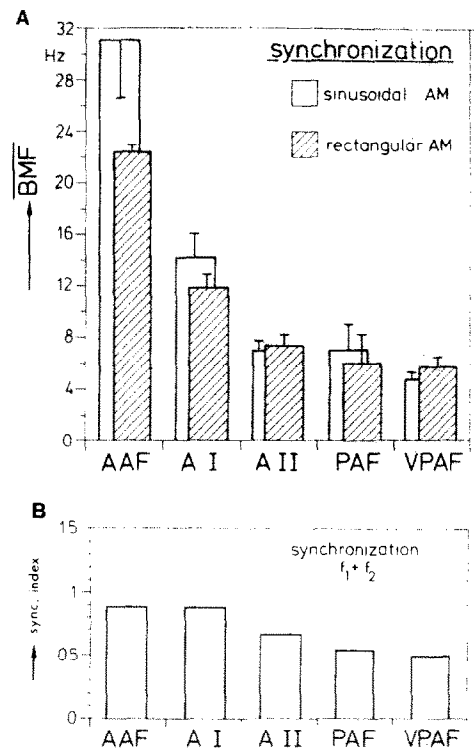


Fig. 2. (A) Averaged BMFs of the response synchronization to sinusoidal (open bars) and rectangular (shaded bars) amplitude modulation. Error bars represent the standard error of the mean. The standard deviations (SDs) for the sinusoidal modulation are given in Fig. 1. The SDs for the rectangular modulation were 13.7 (AAF), 6.5 (AI), 4.4 (AII), 4.8 (PAF), 3.9 (VPAF). (B) Synchronization index of responses to AM. The averaged maximum synchronization in each of the investigated cortical fields was determined for the first and second harmonic of the modulation frequency and added (maximal possible synchronization index: 2). The SDs for the fields were 0.39 (AAF), 0.33 (AI), 0.42 (AII), 0.23 (PAF), and 0.18 (VPAF).

cortical fields. The differences and similarities between temporal characteristics of the fields are equally expressed for rectangular and sinusoidal AM, although the BMFs in AAF and AI tended to be of slightly lower frequencies for rectangular AM. The synchronization-BMFs of AAF for rectangular modulation were significantly different ($P < 0.01$) from the other four cortical fields. With a $P < 0.1$, the average BMF of AI exhibited only a statistical trend to be different from the fields AII, PAF and VPAF. The differences between the later fields were not statistically significant.

In general, the ability of auditory cortical neurons to follow amplitude-modulated (or repetitive) signals showed only minor influences from the shape of the modulation envelope. No significant influences of modulation waveform on the average synchronization-BMF of a field were found for AI, AII, PAF and VPAF. Only AAF showed a slightly higher synchronization-BMF for sinusoidal AM as compared to rectangular AM ($P < 0.05$; see Schreiner and Urbas, 1986). A response parameter more strongly influenced by the stimulus shape was the amplitude of the synchronization and rate MTFs (see below), i.e. the degree of synchronization and responsiveness, respectively.

The low temporal resolution of fields AII, PAF and VPAF was coupled with a smaller degree of synchronization, or phase locking to the modulation, when compared to the fields with medium or high temporal resolution (AI, AAF). This is indicated in Fig. 2B in which the mean of the synchronization index obtained at BMF for a given field is plotted. AAF and AI showed, on the average, an amount of synchronization that was higher than the synchronization in AII, PAF and VPAF ($P < 0.05$). The maximal synchronization in VPAF was lower ($P < 0.05$) than that of AAF, AI and AII. The relative influence of stimulus waveform on the degree of synchronization is described below.

The relationship of synchronization-BMFs with the CF of the corresponding site is shown in the scatter diagram in Fig. 3. The sampled CF range covers approximately 1–40 kHz in AAF, AII and PAF, whereas the range of AI and VPAF was limited to sites with CFs above 2–4 kHz. For AAF a significant correlation between CF and BMF was observed, with higher BMFs recorded at

high CFs and lower BMFs seen for lower CFs ($r = 0.63$, $P < 0.01$; see Schreiner and Urbas, 1986). Besides AAF, no other field showed a significant correlation between CF and BMF.

BMFs were not highly correlated with the quality or sharpness of tuning curves. Only AAF showed a small but significant correlation ($r = 0.32$, $P < 0.05$) between BMF and $Q_{10\text{dB}}$ (see Schreiner and Urbas, 1986). The $Q_{10\text{dB}}$ of the multiunit recordings (derived at most locations in this study) appeared to be slightly lower than comparable results derived from single unit studies (Phillips and Irvine, 1980, 1981; Merzenich et al., 1975).

Best modulation frequency for firing rate

Synchronization is a measure of the accuracy of the coupling between the neural response and the temporal properties of the stimulus. Firing rate provides a different measure of the neuronal responsiveness to a stimulus. In peripheral auditory stations, firing rate and synchronization can be largely independent measures of the response activity. The influence of amplitude modulation on the firing rate in different cortical fields will be described in this section.

The shape and general feature of rate-MTFs obtained in the auditory cortex were similar to synchronization-MTFs recorded at the same site. In Fig. 4, the distribution of the BMFs of rate-MTFs of the five cortical fields is summarized. They reflect a relatively broad distribution for AAF and AI and somewhat narrower distributions for AII, PAF, and VPAF. The means of the five distributions show a tendency similar to the synchronization-MTFs with the highest average BMF (27.0 ± 26.1 Hz) obtained for AAF, a medium high BMF for AI (19.9 ± 26 Hz), and low BMFs for AII (6.6 ± 3.8 Hz), VPAF (7.1 ± 6.0 Hz), and PAF (8.2 ± 16.0 Hz). Fig. 5 shows the averaged rate-BMFs for sinusoidal and rectangular AM, both reflecting interfield differences of similar magnitude. Statistical analysis (Method of Scheffe) of the rate-BMFs for sinusoidal and rectangular modulation led to a similar categorization scheme of the temporal resolution as seen for synchronization-BMFs. Again, the five fields can be grouped into high, medium and low temporal resolution fields. The high resolution field AAF

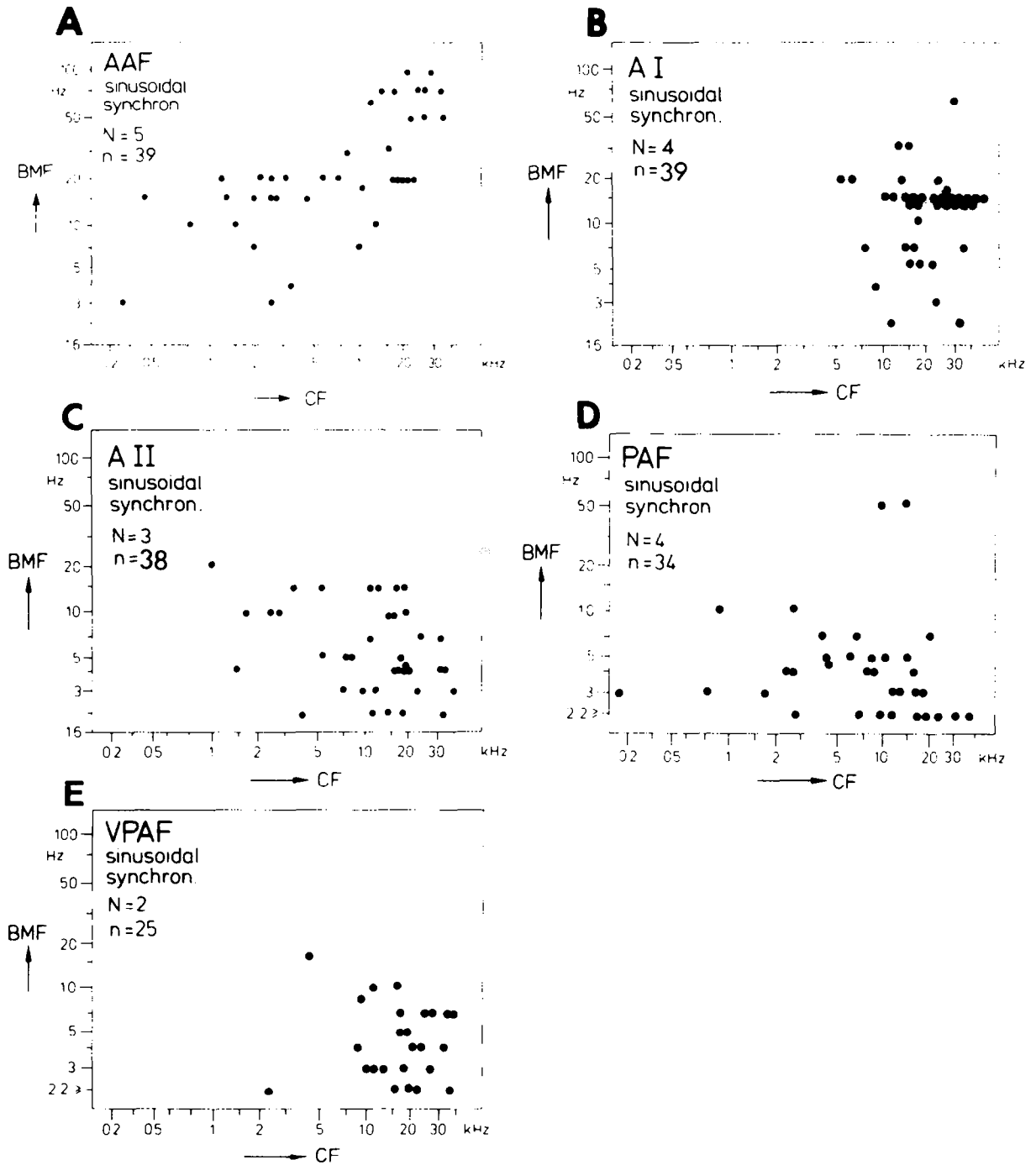


Fig. 3. Scatter diagram of BMF as function of CF for 5 auditory cortical fields. The BMFs were determined from the synchronization-MTFs for sinusoidal AM. Number of animals (N) and number of sites in each field (n) are indicated.

has significantly higher BMFs ($P < 0.05$) than all other fields. The medium resolution field AI has significantly lower BMFs than AAF ($P < 0.05$)

and exhibits a statistical trend toward higher BMFs than the fields in the low resolution group ($P < 0.1$). The low resolution group contains the fields

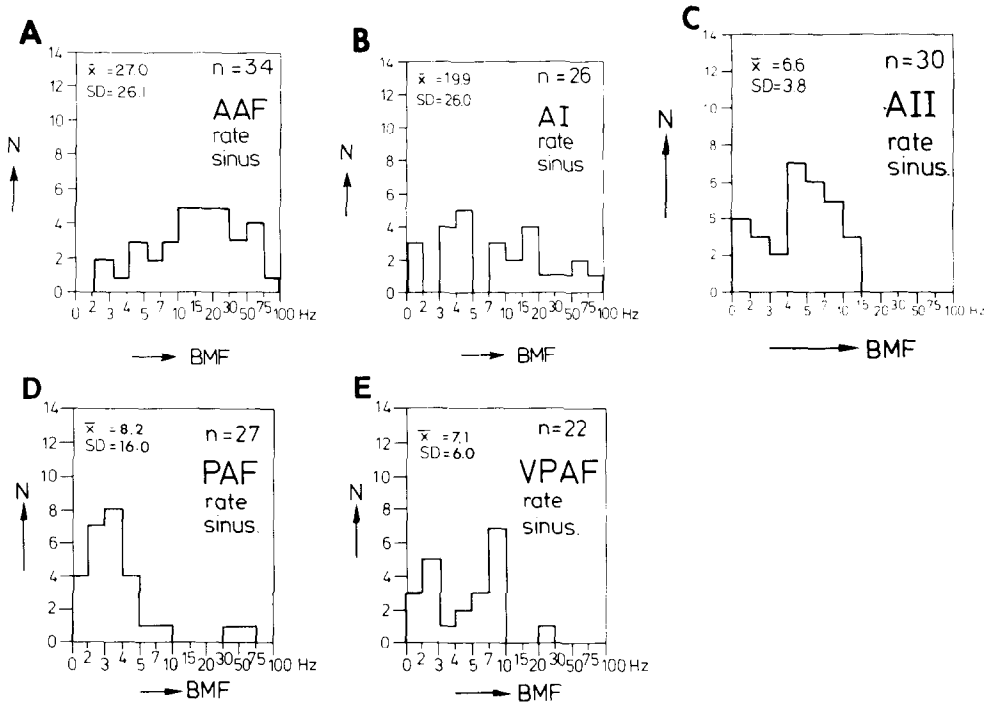


Fig. 4. Distribution of BMFs of rate-MTFs for sinusoidal AM in five auditory cortical fields. Mean and standard deviation are indicated. Each bin contains BMFs up to but not including the next higher frequency marked on the abscissa.

AII, PAF and VPAF which showed no statistically significant differences among their average rate-BMFs. Differences between rate-BMFs for

sinusoidal or rectangular modulation were statistically not significant.

A scatter diagram of the rate-BMFs for sinusoidal modulation plotted as a function of CF is shown for each field in Fig. 6. Again, only AAF showed a significant correlation between BMF and CF ($r = 0.67$, $P < 0.01$). In the other fields the BMF appears to be independent of the CF although the evidence in fields AI and VPAF is incomplete because of the somewhat limited CF range of the sample.

Bandwidth of cortical MTFs

In addition to the BMF, another parameter describing the MTFs is the sharpness or quality factor of the transfer function. The bandwidth 2 dB below (20% down from) the tip of a MTF was used to calculate the quality factor of the AM transfer characteristic (BMF divided by the bandwidth 2 dB below BMF). As illustrated in Fig. 7, the distribution of $Q_{2\text{dB}}$ in most cortical fields was between 0.5 and 4.0 for the synchronization to sinusoidal AM. The widest (least selective) syn-

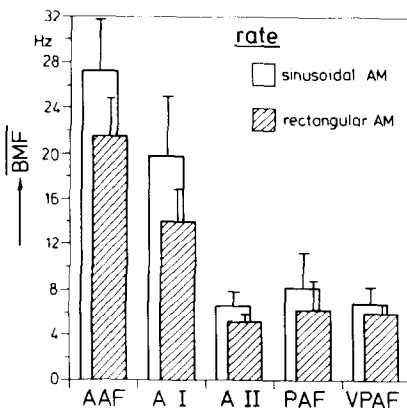


Fig. 5. Averaged BMFs of rate-MTFs for sinusoidal (open bars) and rectangular (shaded bars) amplitude modulation. The error bars represent the standard error of the mean. The SDs of the BMF distributions for sinusoidal AM are given in Fig. 4. The SDs for rectangular modulation were 22.1 (AAF), 16.9 (AI), 3.5 (AII), 1.5 (PAF), and 3.9 (VPAF).

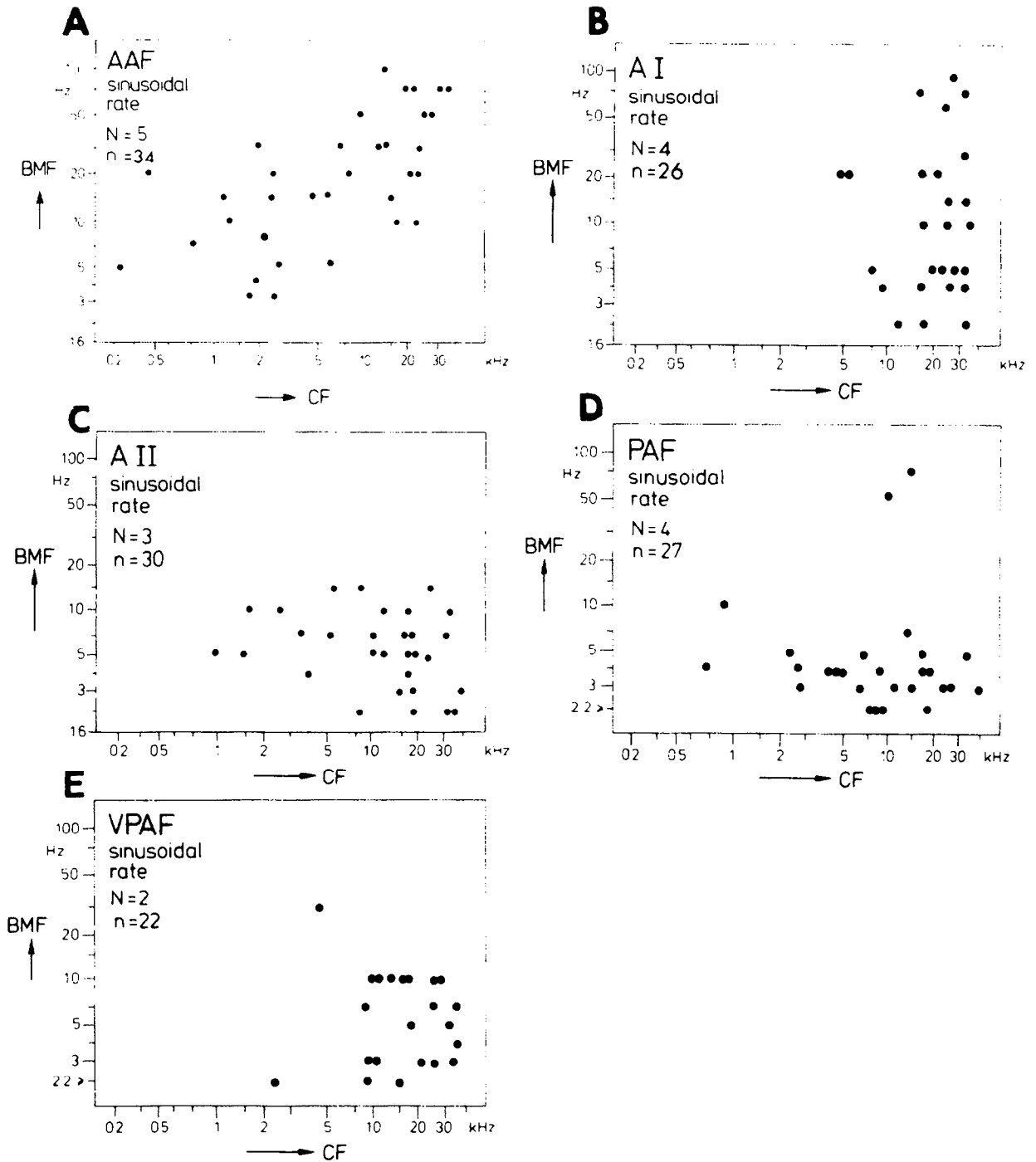


Fig. 6. Scatter diagram of BMF as function of CF of rate-MTFs for sinusoidal modulation in five auditory cortical fields.

chronization-MTFs were found in AAF. All other studied cortical fields had on the average significantly narrower synchronization-MTFs ($P < 0.05$)

of about equal Q_{2dB} (Fig. 8A) for sinusoidal modulation. The Q_{2dB} for synchronization-MTFs derived from rectangular modulation indicated a

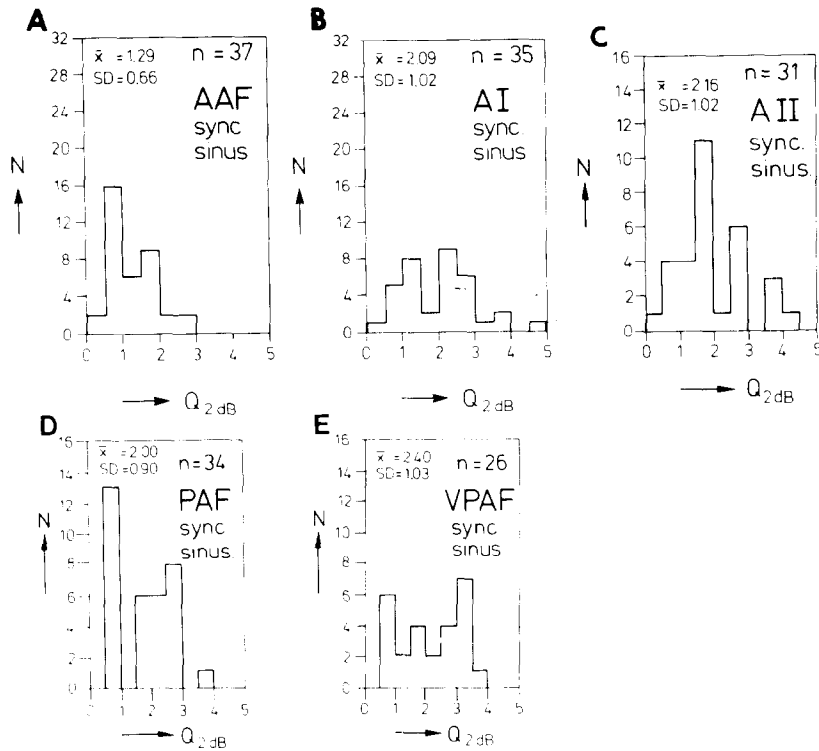


Fig. 7. Distribution of Q_{2dB} of synchronization-MTFs. Q_{2dB} is a measure of the sharpness or quality of the modulation-transfer function (BMF divided by the bandwidth of the MTF_{2dB} – approximately 20% – below the tip of the MTF). Mean and standard deviation are indicated for each cortical field.

statistical trend for AAF and AI of smaller temporal selectivity than found in AII, PAF and VPAF.

The Q_{2dB} of the rate-MTFs of different fields (Fig. 8B) showed no differences for sinusoidal waveforms. However, for rectangular modulation

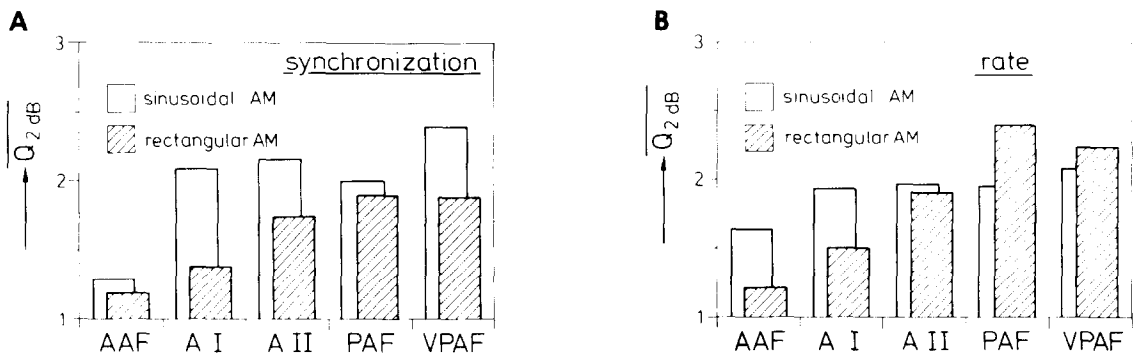


Fig. 8. (A) Averaged Q_{2dB} of synchronization-MTFs for sinusoidal (open bars) and rectangular (shaded bars) amplitude modulation. Standard deviations were (sinusoidal, rectangular): 0.66, 0.87 (AAF); 1.02, 0.70 (AI); 1.02, 0.99 (AII); 0.90, 1.11 (PAF); 1.03, 0.91 (VPAF). (B) Averaged Q_{2dB} of rate-MTFs for sinusoidal (open bars) and rectangular (shaded bars) amplitude modulation. SDs were (sinusoidal, rectangular): 1.05, 0.63 (AAF); 1.20, 0.90 (AI); 0.96, 1.03 (AII); 1.00, 1.18 (PAF); 0.82, 0.95 (VPAF).

significant differences ($P < 0.05$) were seen between AAF and the low resolution group (AII, PAF, VPAF). In addition, the $Q_{2\text{dB}}$ of AI showed a statistical trend towards being lower than the values for PAF and VPAF.

Corresponding to the categorization scheme for the temporal resolution based on the BMF, the 'temporal selectivity' of the MTFs based on the $Q_{2\text{dB}}$ measure can be used as an additional scheme in the attempt to functionally group cortical areas. A 'low selectivity field' (AAF) and a 'high selectivity group' with AII, PAF and VPAF could be distinguished. AI occupied an intermediate position between the former fields with no unequivocal statistical evidence to establish a separate 'medium selectivity field'.

Stimulus shape

As noted above, it appears that the shape of the modulation waveform, in this case sinusoidal or rectangular, had only a small influence on the BMF at a given cortical location. However, the waveform did have some influence on the shape of the MTFs, or, more specifically, on the width and height of the MTFs. By quantitatively comparing the influence of sinusoidal versus rectangular AM on responsiveness (firing rate) and degree of synchronization, it can be shown that there are field characteristic properties in the signal processing that are sensitive to the shape of a stimulus. Fig. 9 shows the ratio of the response strength of sinusoidal versus rectangular stimuli averaged for

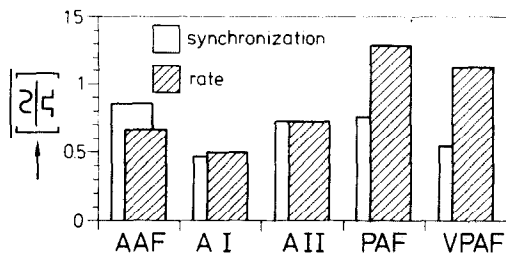


Fig. 9. Averaged 'shape ratios' of synchronization (open bars) and rate (shaded bars). 'Shape ratio' is defined as the ratio of maximal firing rate – or synchronization – of sinusoidal MTFs to rectangular MTFs. The average was determined for CFs above 5 kHz since some fields have not been sampled sufficiently below 5 kHz. Standard deviations (synchronization, rate) were: 0.31, 0.35 (AAF); 0.2, 0.35 (AI); 0.35, 0.51 (AII); 0.22, 0.55 (PAF); 0.19, 0.51 (VPAF).

each field. These 'shape ratios' were calculated by dividing the absolute response strength at the peak of a sinusoidal MTF by the strength at the peak of the rectangular MTF at the same site. Shape ratios for rate and synchronization MTFs are shown. On the average, all shape ratios for synchronization-MTFs had values below 1. This means that, on the average, rectangular AM produced a higher synchronization of the response to the stimulus envelope than sinusoidal AM. The lowest shape ratios for synchronization-MTFs were found in AI (0.42 ± 0.36) and VPAF (0.46 ± 0.23). For both fields these ratios were significantly lower than the ratios in the other fields ($P < 0.05$). This indicates a relatively strong influence of the stimulus waveform on the synchronization particularly for AI and VPAF.

Two different aspects can be noted for the influence of the modulation waveform on the firing rate. Firstly, there are two fields (PAF and VPAF) that had shape ratios with values equal or larger than 1, indicating equal or greater responsiveness of these fields to sinusoidal modulation compared to rectangular modulation. The shape ratios of these two fields were significantly higher ($P < 0.05$) than ratios obtained for other cortical fields. This finding is in sharp contrast to the usually observed tendency of neurons to respond more vigorously or more precisely to rectangular modulation than to sinusoidal modulation as indicated by the rate profiles of AAF, AI and AII and the synchronization indices for all cortical fields (see Fig. 9).

Secondly, the shape ratios for rate and synchronization-MTFs significantly differed for PAF and VPAF ($P < 0.05$). Thus, it appears that the posterior and in particular the ventro-posterior field may be able to differentiate between modulation waveforms and reflect these differences by means of their response mode. Rectangular modulation produced a relatively high synchronization whereas sinusoidal modulation produced a relatively high firing rate. The other cortical fields did not show significant influences on their response mode (e.g. rate versus synchronization) that could easily be related to changes in the waveform.

Sinusoidal and rectangular modulation waveforms were selected for these experiments because they represent two extremes with regard to their

spectral and temporal characteristics. It should be noted that using other 'shapes' than those as stimulus envelope (e.g. asymmetrical triangular modulation) may possibly lead to stronger effects on the responsiveness to AM sounds than shown here for sinusoidal and rectangular AM. However, the results described above indicate that a 'shape sensitivity' of the response does not strongly influence the best modulation frequency of the transfer function, the main parameter describing temporal response characteristic.

Discussion

Temporal response properties in the auditory cortex

Temporal resolution

In the five auditory cortical fields studied, the neuronal response properties to amplitude modulated signals were characterized by features of the obtained modulation-transfer functions, most notably the best-modulation frequency and the quality factor $Q_{2\text{dB}}$. It appears that responses within each cortical field were 'tuned' to a range of modulation frequencies. Within each of the investigated fields, these frequency ranges were similar for different aspects of the response properties as indicated by similar BMF ranges for synchronization- and rate-MTFs. This result indicates that the synchronization and rate measures are not largely independent response features at the level of the cortex. Due to the phasic response character (response confined to the onset of a stimulus) of the majority of the responses, firing rate and timing of the response to each AM cycle was closely linked. Thus, the high correlation between timing and magnitude of the response can be expected.

Differences in BMF range, due to variation of the stimulus waveform, were small in AI, AII, PAF and VPAF. Only for AAF, significant differences in the response range of the MTF characteristics could be seen between sinusoidal and rectangular modulation (Schreiner and Urbas, 1986). In AAF, the BMFs for rectangular modulation were slightly lower than for sinusoidal AM, suggesting a relatively strong influence of the rise time and/or the spectral spread of the modulation waveform on the MTF.

The relative independence of the temporal characterization of the recorded activity from response measures (i.e. synchronization vs. firing rate) and from stimulus aspects (i.e. rectangular vs. sinusoidal modulation) suggests that these temporal characteristics represent a fundamental feature of cortical processing. This consistency provides a strong argument for the validity of the modulation analysis as an additional descriptor for functional characteristics of a given cortical field.

An important finding of this study is that some cortical fields respond on the average to slightly different modulation frequency ranges. In other words, some auditory cortical fields may be statistically distinguishable by their overall ability to resolve in their response certain temporal variations of the stimulus amplitude. The distribution of best-modulation frequencies of various locations within a cortical field provides an approximation for an overall estimate of the 'temporal resolution' of a given field. Since there is considerable overlap of the BMF distribution of different cortical fields, the BMF at a given cortical location by itself does not allow an identification of the corresponding cortical field. With the exception of AAF, the width of the BMF distribution of the cortical fields is fairly narrow and appears to be largely independent of the CF location within a field. In AAF, on the other hand, a correlation between BMF and CF location was verified, explaining the relatively broad BMF distribution found for that field. In comparison, the CF range for the locations in AAF was the least biased toward high CFs. Consequently, the average BMF values for AAF were slightly lower than the results of a CF specific average. Despite this slight bias toward smaller differences between the average BMF of AAF and the other fields, the AAF values were found statistically significantly different from temporal response characteristics of the other fields, justifying the use of average AAF values instead of a CF specific analysis. Some indications for possible bimodal distributions of BMFs (e.g. in PAF) suggest a higher complexity of the relationship between BMF and other functional parameters than this exploratory study could resolve and reveal.

Based on their average BMF range, auditory

cortical fields were grouped with regard to their 'temporal resolution': 1) a 'low temporal resolution group', containing AII, PAF and VPAF, with a preferred BMF range of about 6–7 Hz; 2) a 'medium resolution field', AI, with a temporal resolution about twice as high as the former group; and 3) a 'high resolution field', AAF, with another increase of the temporal resolution by a factor of approximately two.

As discussed in the first part of this study (Schreiner and Urbas, 1986), an influence of the anesthesia on the observed temporal characteristics cannot be excluded. However, the field differences with regard to temporal response properties found under similar anesthetic conditions and the lack of evidence that the temporal resolution in unanesthetized animals largely differs from in the anesthetized animal (Whitfield and Evans, 1965; Evans, 1974; Creutzfeldt et al., 1980; Saitoh et al., 1981) suggest that the described results give a fair, although sketchy, picture of some temporal processing properties of the auditory cortex.

Other concerns with the interpretation of multi-unit data from the middle layers of the auditory cortex are a) whether the recordings represent a functionally homogeneous population and b) what is the amount of contamination of the recording with responses originating from thalamo-cortical axons. Activities with latencies shorter than 8–9 ms were not included in the data, thus eliminating a portion of the activity most likely not originating from cortical neurons (see also Schreiner and Urbas, 1986). However, neither the homogeneity of the recorded population nor the contribution of thalamo-cortical axons can be verified with the applied methods. Consequently, the given interpretations of the obtained data in terms of cortical processing have to be considered with the appropriate caution.

Temporal selectivity and 'shape sensitivity'

A second feature characterizing the temporal response properties of cortical fields is the sharpness or quality of the obtained MTFs, e.g. expressed through $Q_{2\text{dB}}$. This MTF feature can be considered a measure of the 'temporal selectivity' of a field: the narrower or sharper the MTF, the more selective is the response to a certain temporal range of signal variations. Three ranges of

temporal selectivity of cortical fields emerge. The relatively weakly defined ranges of high, medium and low temporal selectivity correspond well to the more sharply defined field characteristics found for temporal resolution with the effect that fields with a high temporal resolution tend to have a low temporal selectivity and vice versa. Fig. 10 illustrates the relation between the main temporal response characteristics for fields with high, medium and low temporal resolution. The average mean and standard deviation of BMF and $Q_{2\text{dB}}$ is shown as it appears when all four investigated aspects, i.e. synchronization, rate, sinusoidal and rectangular modulation, are combined. For the group with low temporal resolution, the data from AII, PAF and VPAF were pooled for clarity. The close correspondence of interfield differences determined by different aspects of the MTFs emphasizes again the usefulness of amplitude modulated signals for a more general functional classification of cortical fields.

Three of the five investigated cortical fields were relatively insensitive to variations of the modulation waveform, indicating that the repetition rate is the dominant factor determining the temporal resolution (de Ribaupierre et al., 1972; Creutzfeldt et al., 1980). However, a large proportion of responses in PAF and VPAF did show some sensitivity with regard to the stimulus waveform. This observation suggests the existence of some spectral/temporal processing capacities in those fields that go beyond a simple repetition rate concept. This 'shape sensitivity' is reminiscent of some aspects of the 'shape selectivity' of cortical units to noise bursts, as described by Swarbrick and Whitfield (1972) and Bock (1976).

Temporal resolution and functional specificity

The temporal resolution of the auditory cortex stands at the end of a processing sequence along the ascending auditory pathway, that progressively diminishes the ability to consistently follow fast fluctuations of the signal envelope. This phenomenon has been discussed in connection with the anterior auditory field in the first paper of this series (Schreiner and Urbas, 1986; see also Schreiner and Langner, 1988). In general, modulation rates in the input signal that are preserved

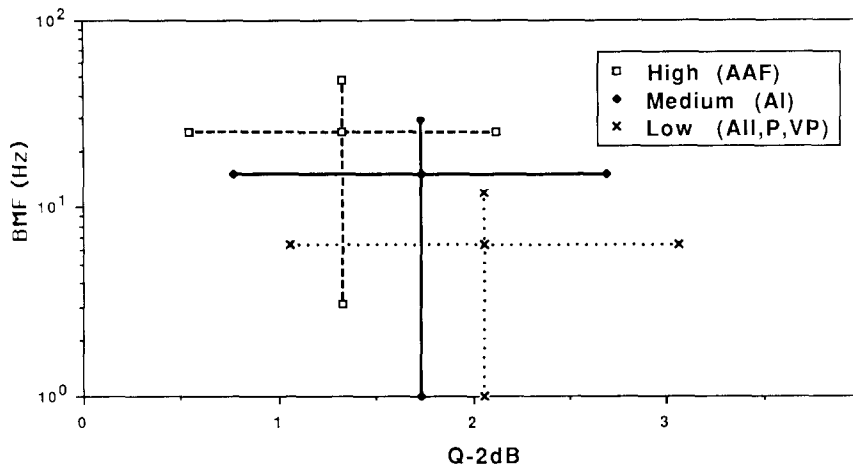


Fig. 10. Average range of temporal resolution and temporal selectivity for three categories of auditory cortical fields. The average means and standard deviations of BMFs and Q_{2dB} were derived from synchronization-MTFs to sinusoidal and rectangular AM, and from firing rate-MTFs produced by sinusoidal and rectangular AM. For the group of cortical fields with low temporal resolution (AII, PAF and VPAF) the values of all three fields were combined.

in the temporal activity pattern of neuronal elements decline from up to 1000 Hz in the auditory nerve to a few cycles per second in the auditory cortex. This progressive change in the temporal response properties may reflect consequences of processing strategies that extract, combine and distribute certain 'information-bearing parameters' (Suga, 1978, 1984). The difference in the temporal properties of the auditory cortical fields suggests that these temporal changes are not exclusively a consequence of a loss of temporal precision, e.g. due to summation of synaptic transmission jitter.

The apparent sequential processing involved in the reduction of temporal resolution along the auditory pathway up to the cortex can not be used for the explanation of the temporal disparity found between some cortical fields. Anatomical studies have clearly shown that the thalamic input to the cortical fields is organized in parallel projections (Andersen et al., 1980; Imig and Morel, 1983). Each of these projections contains a unique combination of contributions from different thalamic nuclei. Little is known about the temporal properties of these thalamic nuclei. Rouiller and colleagues (1981, 1982) studied the response properties of different parts of the medial geniculate body (MGB) using click stimulation. They found only a few units that appeared to be tuned to a

certain repetition rate of the clicks. Of these units, the 'best repetition rate' showed only minor differences between various nuclei. Most of the 'best repetition rates' in the MGB were found to be between 50 and 70 Hz, far above the BMF range of most cortical locations. Pars lateralis and pars magnocellularis of the MGB showed some differences in the sharpness of the temporal resolution defined by click trains (Rouiller et al., 1981). Creutzfeldt et al. (1980) demonstrated a dramatic reduction in the temporal resolution between synaptically connected neurons of the MGB and the auditory cortex of unanesthetized guinea pigs. This finding, in connection with the highly branched projection pattern of afferents originating in the MGB (Andersen et al., 1980; Imig and Morel, 1983) may suggest that the temporal characteristics of each cortical field are produced in each field itself, i.e. it is most likely a result of a parallel processing scheme.

Ablation studies of the auditory cortex (Diamond and Neff, 1957; Kelly, 1974; Neff et al., 1975) demonstrated the involvement of cortical processing in the identification of tonal sequences or patterns. The temporal structure of those sequences and patterns whose recognition was affected by the ablation was in a similar frequency/repetition range as the temporal resolution of the auditory cortex as demonstrated with

AM signals. This indicates that the temporal features of the auditory cortex obtained with MTFs can indeed be of behavioral significance. Limitations on the nature of the 'information-bearing parameters' represented in the cortex of the cat are imposed by the spectral and temporal filter characteristics of a given unit as expressed by frequency tuning curve and modulation transfer function. The largely independent assessment of spectral and temporal filtering characteristics of cortical neuronal elements can be used to account for a large portion of the actual response characteristics to more complex signals (Schreiner et al., 1983; Schreiner and Langner, 1987) and therefore represents a first step in defining in more detail specific properties of auditory cortical fields.

This exploratory study of the representation of amplitude modulation in different cortical fields of the cat provides only a limited view of temporal processing characteristics and capacities of the auditory cortex. Already in this first, still crude, assessment some intriguing features of cortical temporal processing principles could be discerned, although this study represents only a small step in defining the complex structure of the signal processing network of the auditory cortex. More studies, in particular with emphasis on single unit recordings, are necessary concentrating on the parametric representation of potentially important signal features in distinct cortical fields.

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