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Review Article

Periodicity coding in the auditory system

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Periodic envelope fluctuations are a common feature of acoustic communication signals, and as a result of physical constraints, many natural, nonliving sound sources also produce periodic waveforms. In human speech and music, for example, periodic sounds are abundant and reach a high degree of complexity. Under noisy conditions these amplitude fluctuations may be reliable indicators of a common sound source responsible for the activation of different frequency channels of the basilar membrane. To make use of this information, a central periodicity analysis is necessary in addition to the peripheral frequency analysis.

The present review summarizes our present knowledge about representation and processing of periodic signals, from the cochlea to the cortex in mammals, and in homologous or analogous anatomical structures as far as these exist and have been investigated in other animals. The first sections describe important physical and perceptual attributes of periodic signals, and the last sections address some theoretical issues.

Acoustic processing; Temporal analysis; Pitch; Neuronal mechanisms

Introduction

Sinusoidal signals are used as standard stimuli in auditory physiology. They are perceived as pure tones with a clear perceptual quality related to their frequency pitch. The preference of the experimentalist for such signals is based on two factors: the use of linear systems analysis and the concept of the cochlea as a frequency analyzer. The cochlea has developed for the processing of natural sounds, including those in animal communication or human speech. These are generally complex signals which, in systems analysis, are considered as a composite of frequency components. Decomposition of these signals is a major part of cochlear sound analysis. The components are mapped to certain places of maximal mechanical response along the cochlea and the neuronal response strength in the neuronal elements associated with these places code their amplitudes.

However, the restricted frequency resolution of the cochlea limits precise frequency separation, and nonlinear properties seem to be an integral part of the peripheral and central coding strategies which may not be adequately tested when using sinusoidal stimuli. Such considerations led to experiments using signals with temporal envelope variations or amplitude modulations (AM) (Møller, 1971; Moore and Cashin, 1974;

Bibikov, 1974; Watanabe and Sakai, 1975; Sachs et al., 1983; Delgutte and Kiang, 1984b; Carney and Geisler, 1986) or even natural sounds (Suga, 1972; Winter and Funkenstein, 1973; Newman and Wollberg, 1973; Aertsen and Johannesma, 1980; Symmes, 1981; Ehret and Merzenich, 1988; Møller and Angelo, 1988). It became obvious that nonlinearity and selectivity for particular signal properties increase in the hierarchy of the auditory system. One of the conclusions was that a mere place model of frequency representation in the central nervous system cannot account for many aspects of auditory signal analysis and that for complex signal processing, in particular, temporal patterns of neuronal discharges are important.

This review follows the line of processing of an important class of complex acoustic signals: of periodic signals. After a short introduction into the physics and psychophysics of periodic signals, their coding, either by periodic discharges or by spatial distribution of neuronal activation at different levels from the auditory periphery to the auditory cortex is then discussed. It will be shown that neurophysiologists have accumulated evidence for the role of temporal periodicity coding and analysis in the auditory system of various animals. Although it was not possible to cite every publication relevant to this review, the author hopes that the selection sufficiently covers the different topics under discussion.

Relation of spectral and temporal sound parameters

For a thorough understanding of the neuronal coding of complex signals, it is important to consider the

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way spectral and temporal properties of sounds are related. Periodic modulations of the amplitude (envelope) arise in sounds with just two or three frequency components. When two sinusoidal waves with different frequencies f_1 and f_2 are added, ($f_2 > f_1$) the resulting signal waveform has a sinusoidal envelope fluctuation with a frequency equal to the difference $df = f_2 - f_1$, commonly referred to as the 'beat frequency'. In spite of its envelope periodicity corresponding to df , the summed signal does not contain the frequency component df . Adding a third component with $f_3 = f_2 + df$ changes the resulting waveform, but does not affect the envelope frequency, df . With appropriate amplitudes and phases of the three components this new signal is identical with a sinusoidal amplitude modulation (AM), with f_2 as carrier, and df as modulation frequency and f_1 and f_3 as modulation sidebands (Fig. 1). Due to physical constraints, natural animated and non-animated sound sources frequently produce special types of periodic signals with components (harmonics) whose frequencies are multiples of the 'fundamental frequency'. Consequently, two or more of such frequency components combine to form a signal with a periodic envelope. The envelope frequency is equal to the smallest difference frequency of these components, which is equal to the fundamental frequency (f_0) of that sound, even if f_0 is not part of the signal itself.

Perception of periodic sounds

Quantitatively, the sensitivity of the human ear for amplitude modulations may be approximated by a

low-pass filter function (Zwicker, 1952; Viemeister, 1979) with a 3 dB point at 50 Hz (Rodenberg, 1977). This was supported even in deaf patients, by applying amplitude modulations through electrical stimulation of the cochlea or the cochlear nucleus (Shannon and Otto, 1990). Similar filter functions have been obtained in fish (Fay, 1980), in bird (Dooling and Searcy, 1981, Klump and Okanoya 1991), in mammal (Salvi et al., 1982) and also in frog auditory-nerve fibers (Dunia and Narins, 1988). Finally, the selectivity of processing channels for particular rates of frequency and amplitude modulations have been demonstrated in humans by investigating psychophysically the adaptation evoked by these signals (Kay and Matthews, 1972; Tansley and Regan, 1979; Kay, 1982).

Qualitatively, the different perceptions elicited by different rates of amplitude modulation require a distinction between at least two ranges of modulation: slow (below about 20 Hz) and fast (between about 20 and 1000 Hz). Slow modulations are associated with the perception of rhythm. Samples of running speech show distributions of modulation frequencies with peaks around 3–4 Hz, approximately corresponding to the sequence rates of words (Plomp, 1983). Another perception elicited by slow and medium fast modulations from approximately 10 to 200 Hz is called roughness and is described as an 'unpleasant, disturbing component' (Terhardt, 1974). Roughness as a function of modulation frequency has a band-pass characteristic at all intensities with a maximum between 40 and 70 Hz, depending on the carrier frequency (Fastl, 1977, 1990).

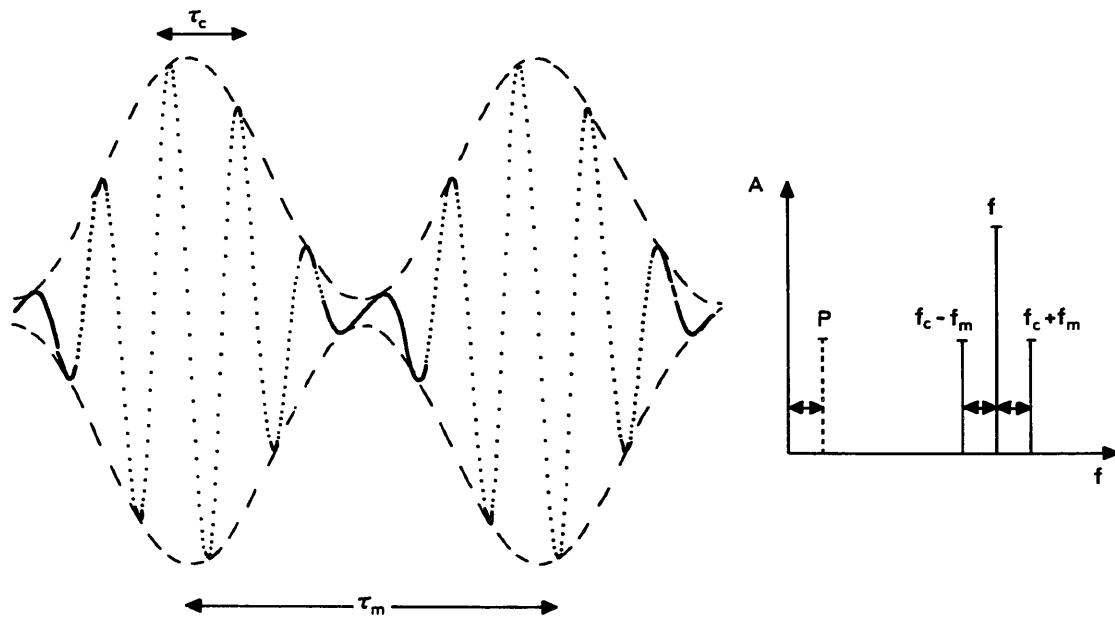


Fig. 1. Two waves of a sinusoidal amplitude modulation (AM) and the spectral representation of an AM-signal. τ_c is the period of the carrier frequency $f_{c.r.m}$, the period of the modulation frequency f_m . The broken line indicates the envelope. The frequencies of the modulation sidebands are $f_c - f_m$ and $f_c + f_m$. P indicates the periodicity pitch elicited by such signals corresponding to a frequency not present in the spectrum of the AM.

Fast modulations are typical for voiced speech sounds and elicit the perception of the so-called periodicity pitch. They are reliable indicators of a common sound source responsible for the activation of different frequency channels and for the grouping, harmonic structure seems to be even more reliable than commonality of spatial position (Buell and Hafer, 1991). Although the perceptual quality (timbre) of a fast modulated sound may be quite different from a pure tone, periodicity pitch closely corresponds to the percept elicited by a pure tone with the same frequency as the modulation (Schouten, 1940 a,b,c). A pure tone with a fixed frequency produces an amplitude maximum of the travelling wave in a certain region of the basilar membrane and evokes a certain 'tonality' or tonal pitch in humans. However, a complex signal containing several frequencies, even in completely different frequency areas, may have the same pitch as the pure tone. This may be compared to the situation when two different instruments play the same note by generating completely different, perhaps even non-overlapping, sound spectra. Similarly, every-day experience tells us that the pitch of musical sounds is not affected by drastic filtering in small transistor-radios or telephones. In summary: while mapping of frequency onto a pitch scale may be as unambiguous as the mapping of frequency information on the activity pattern of the auditory nerve (AN), a reverse mapping of pitch on frequencies is highly ambiguous.

In order to elicit the same pitch as a pure tone, a complex signal must fulfill certain conditions. For example, to a first approximation its envelope must have the same period as the pure tone and therefore this perception is called 'periodicity pitch'. Apparently, periodicity pitch may be perceived not only by human subjects (Schouten, 1940c; Schouten et al., 1962; Small, 1970), but also by cats (Chung and Colavita, 1976; Heffner and Whitfield, 1976), birds (Cynx and Shapiro, 1986), and monkeys (Schwarz and Tomlinson, 1990). New frequencies resulting from nonlinear distortion in the mechanical part of the ear may under certain conditions correspond to the fundamental frequency. However, they have been excluded as a possible origin of this perception by experiments using, for example, low intensities or masking noise (Thurlow and Small, 1955; McFadden, 1988). In consequence, it is generally accepted that the fundamental frequency does not have to be physically present in a harmonic complex in order to generate the same pitch as the fundamental presented by itself (phenomenon of the 'missing fundamental') (Schouten, 1940a,b; de Boer, 1956).

There are good reasons to assume that the neuronal mechanisms underlying the perception of periodicity pitch rely on temporal information present in the AN (Greenberg, 1988). Such an assumption may, for example, account for the fact that this percept is restricted

to certain frequency ranges of envelopes (below about 800 Hz) and of the signal components (below about 5 kHz) (Ritsma, 1962; Guttman and Flanagan, 1964). This so-called 'existence region' may be explained by certain constraints of temporal processing, such as the upper boundary for phase-locking of AN discharges at approximately 5 kHz (Ohgushi, 1983) or, as described above, the requirement that adjacent components remain unresolved by neurons in the auditory frequency channels. Under these conditions, a harmonic sound, composed of integer multiples of a fundamental frequency, elicits a periodicity pitch, even when the fundamental component is totally absent. It is noteworthy that the upper limit of musical pitch, defined by the possibility to recognize musical intervals, is also at about 5 kHz (Semal and Demany, 1990).

Measures of response to periodic stimuli

The response of a neuron to periodic signals may be judged by measuring its synchronization to the signal waveform and by computing its modulation transfer function (MTF). The maximum of a MTF with band-pass characteristic or the cutoff-frequency of a MTF with low-pass characteristic is called 'best modulation frequency' (BMF) or 'best envelope frequency' (BEF). For nonlinear or active systems, the best way to measure the MTF is with amplitude modulation (AM), presenting one modulation frequency at a time (Schroeder, 1981). In non-linear systems, the output signal contains components not present in the input. It is, therefore, necessary to consider not only the response to the actual signal components but also other aspects of the synchronized responses, such as the DC-component and the first harmonic. These are related to the response rate and the response synchronization respectively.

Alternatively, the degree of modulation or synchronization may be measured by means of circular statistics (Gumbel et al., 1955; Greenwood and Durand, 1965; Goldberg and Brown, 1969). The period of a signal is mapped onto a circle and a spike is represented by a vector of unit length pointing in a direction defined by its phase angle relative to the zero crossing of the periodic signal. By vector summation of all spikes collected, a vector is obtained, which indicates the amount of phase coupled activity and the mean phase angle. In a recent summary it was noted that the magnitude R of the vector equals half of the amplitude of the first Fourier component, R_1 , of the corresponding period histogram (Kim et al., 1990). Furthermore, the normalization of this measure with respect to the mean firing rate R_0 results in a measure called vector strength, which indicates the average degree of synchronization $VS = 0.5 \cdot (R_1/R_0)$. Its value can vary between 0 and 1. Zero is obtained for flat period

histograms, 1 for the case in which all spikes are collected in one bin. A 100% sinusoidally-modulated response results in a vector strength of 0.5. An easy way to test the statistical significance of the measured synchronization is offered by the Raleigh test of uniformity (Mardia, 1972; Buunen and Rhode, 1978). The modulation gain in dB is obtained by $g = 20 \log(2^*VS/m)$ where m is the stimulus modulation index (e.g. = 1 for 100% modulation).

Another important descriptor for amplitude modulation effects on the activity of auditory neurons is average response rate. For a linear system, the average response magnitude to a sinusoidal amplitude modulation is independent of the modulation frequency, since positive and negative deviations from the mean in response to the envelope fluctuations of the signal will be equal. In this respect, the auditory nerve (AN) may be considered to be linear, since the average discharge rate of AN fibers has been found to be largely independent of the modulation frequency of the stimulus (Rose and Capranica, 1985). This is to some extent also true for DCN and PVCN neurons (Schreiner and Snyder, 1987; Kim et al., 1990), but not at all for neurons in the auditory midbrain (Langner, 1983b; Rose and Capranica, 1985; Langner and Schreiner, 1988; Rees and Palmer, 1989).

Periodicity coding in the auditory nerve

Frequency resolution and response modulation

When a pure tone is presented to the ear, a travelling wave maximally activates a certain place on the basilar membrane, and hair cells at this place code the frequency of that signal by their position, and other information by their temporal firing patterns. When two frequencies f_1 and f_2 are presented simultaneously, the response strength of an AN fibre is modulated under certain conditions with frequencies resulting from the non-linear properties of the basilar membrane, for example, equal to the difference $df = f_2 - f_1$. This modulation is a consequence of the fact that the cochlea has a rather limited frequency resolution. Simultaneously presented frequencies differing by a sufficiently small df are processed together in one frequency channel, that is, they stimulate the same group of hair cells and hence cannot be separated by the auditory system.

However, this does not imply that these frequencies may not be discriminated when presented successively, one after the other. In humans, the frequency difference limens are in the order of only 0.2–0.3% of the stimulus frequencies, while the resolution bandwidths, which are important for the present discussion are about 10–20% of the stimulus frequencies (Pickles, 1988). The fact that df in the stimulus has to be quite

large to enable the resolution of simultaneously presented frequencies is obviously a significant limitation for the analysis of broadband signals. However, this disadvantage is compensated by an advantage of the poor spectral resolution: the components of a harmonic signal that fall into the same frequency channel produce an amplitude modulation with a frequency corresponding to their difference frequency, which, for a harmonic signal, is equal to the fundamental frequency. In that way the fundamental, in spite of its physical absence, can be encoded in the temporal discharge patterns of AN fibers (Schouten, 1970). It has been found that the bandwidths of the nerve fibers may vary significantly even for fibers tuned to the same frequency (Evans, 1972; Sachs et al., 1974). Since the bandwidths may also be fairly broad, at least some of the AN fibres should always be able to encode the envelopes relevant, for example, for speech signals.

As masking patterns in forward masking experiments in humans demonstrate, only the first three or four harmonics of a harmonic sound are clearly resolved by auditory frequency analysis, while the resolution deteriorates rapidly for higher harmonics (Moore and Glasberg, 1983). Trained human subjects may resolve even the sixth to eighth harmonic (Plomp and Mimpel, 1968). In accordance, in fibers of the AN, a decreasing frequency resolution for harmonics above order four results in considerable fluctuations of response probability with a period corresponding to the fundamental frequency of the signal (Greenberg and Rhode, 1987). A comparable resolving power was demonstrated in some units in the auditory cortex of trained monkeys (Schwarz and Tomlinson, 1990). Because harmonic communication sounds in general have many more than four harmonics, a remarkable section of the higher frequency spectrum would normally remain unresolved. Detailed information contained in that frequency range would not be decoded unless the apparently inadequate spectral analysis of such signals is complemented by a temporal analysis.

Response diversity

In comparison to neurons in the cochlear nucleus and in still higher auditory centres, AN fibers show only little response diversity. Nevertheless, fibers with the same CF may differ in the bandwidth of their tuning curve (Evans, 1972), in their dynamic properties (Yates, 1987), and in their spontaneous activity (Liberman, 1978, 1982; Kim and Molnar, 1979; Horst and Farley, 1986). In cats, raised under quiet conditions, at least two classes of AN fibers can be distinguished on the basis of their thresholds and spontaneous rate of spike discharges (Liberman, 1978). Most fibers have a low threshold of response (less than 20 dB above minimum threshold in about 80%) and high spontaneous rates (> 18 spikes/s in about 60%). Fibers,

distinguished by different spontaneous rates, differ also in their periodicity coding (Horst et al., 1985). While fibers with low spontaneous rates show enhanced responses to envelope periodicities, fibers with higher spontaneous rates code more details of the temporal fine-structure. This indicates that the auditory system tends to separate information about the envelope and the temporal fine structure of a signal as a first step of temporal analysis of sounds.

Low-pass characteristic of auditory nerve fibres

In contrast to envelope coding in the cochlear nucleus and higher auditory centres, the MTFs in the AN of mammals generally have a low-pass characteristic with modulation cut-off frequencies below about 1000 Hz (Fig. 3) (see also Table I) (Møller, 1976b; Javel, 1980; Palmer, 1982; Frisina et al., 1990a; Kim et al., 1990). Below about 10 kHz, the modulation cut-off frequency of the fibers increases with the absolute bandwidth of the tuning curves, which increases with their CF (Palmer, 1982). At modulation frequencies above the cut-off frequency, the sidebands (Fig. 1) fall outside the tuning curve and are strongly attenuated.

However, for fibers with high CFs, the temporal properties of neurons, such as refractory period and spike duration, restrict the coding of modulation frequencies to the range below about 1000 Hz. A slow rise in modulation response with increasing modulation frequency below the cut-off frequency seems to be a consequence of the very rapid adaptation of AN discharge (Yates, 1987).

In goldfish (Fay, 1980) and leopard frog (Rose and Capranica, 1985), temporal resolution of eighth-nerve responses was also found to increase with CF and bandwidth. In contrast to those measured in other animals, the MTFs of the goldfish saccular nerve already have band-pass characteristics with BMFs varying between 20 and about 300 Hz. Mechanisms of temporal contour enhancement provide a high neuronal sensitivity to AM, and it seems that the goldfish processes periodicity with even greater resolution and sensitivity than man (Fay, 1980). Moreover, comparison of psychophysical and neurophysiological results indicate that the goldfish nervous system measures inter-spike-intervals phase locked to the stimulus envelope. For example, the magnitude of change in envelope

TABLE I

Temporal resolution in various animals

Animal	Nucleus	Max. BMF [Hz]	Mean BMF [Hz]	Synchroniz Border [Hz]	References
gerbil	AN	800	370	—	Frisina et al., 1990a
cat	NC	—	—	800	Glattke, 1969
rat	NC	500	—	1000	Møller, 1972a
bat	NC	—	—	> 1000	Vater, 1982
gerbil	NC	700	—	1000	Frisina et al., 1990a
rat	IC	100	30	—	Gersuni and Vartanian, 1973
guinea fowl	MLD	680	—	1250	Langner, 1981
rat	IC	80	20–40	200	Rees and Møller, 1983
frog	Torus s.	100	20–40	—	Rose and Capranica, 1985
bat	IC	(800)	—	—	Leser et al., 1986
cat	ICC	(1000)	30–100	700	Langner and Schreiner, 1988
monkey	IC	256	32–64	—	Müller-Preuss et al., 1988
guinea fowl	MLD	750	181	950	Albert, 1988
guinea fowl	MLD	(950)	(228)	—	Albert, 1988
guinea pig	ICC	200	80–120	> 250	Rees and Palmer, 1989
rabbit	IC	450	87	925	Batra et al., 1990
rabbit	IC	[341]	—	[1300]	Batra et al., 1990
guinea pig	MGB	—	—	100	Creutzfeldt et al., 1980
cat	MGB	—	50–70	> 300	Rouiller et al., 1981
monkey	MGB	128	16–32	128	Müller-Preuss et al., 1988
cat	cortex	—	—	1000	de Ribeauville et al., 1972
guinea pig	cortex	—	—	20	Creutzfeldt et al., 1980
Mynah bird	Field L	380	4–48	500	Hose et al., 1987a
cat	cortex	100	7–28	> 100	Schreiner and Urbas, 1988
monkey	cortex	128	4–16	—	Müller-Preuss et al., 1988

Maximal BMF and highest modulation frequency eliciting synchronized responses as found in different nuclei of various animals. Values in round brackets refer to response rate as a measure, those in square brackets to binaural beat responses.

period which can be just discriminated is of the order which may be explained by the variability of the intervals representing the stimulus periodicity (Fay, 1982).

In frogs, MTFs were measured by recording intracellularly from auditory-nerve fibers and stimulating with sinusoidally amplitude-modulated noise (Dunia and Narins, 1989). The typical MTF had a low-pass-characteristic with a high-frequency attenuation rate of roughly 20 dB/oct. The highest cut-off frequency was about 940 Hz, which corresponds to a minimum integration time of 0.17 ms. AN fibers in anurans do not synchronize to frequencies above 1000 Hz (Hillery and Narins, 1987), but show strong synchronization to the envelopes of pulses and of amplitude modulations (Frishkopf and Goldstein, 1963; Rose and Capranica, 1985) as well as to the fundamentals of complex stimuli (Schwartz and Simmons, 1990).

Dynamic range of periodicity coding in the auditory nerve

Amplitude-modulated stimuli have been used for the investigation of the dynamic properties of fibre responses (Møller, 1976b; Javel, 1980; Smith and Brachman, 1980; Evans and Palmer, 1980; Yates, 1981; Yates, 1987). Due to saturation effects, the modulation depth of the response decreases with increasing intensity. This decrease in modulation represents a loss in temporal contrast and implies a significant degradation of information about the envelope (Evans and Palmer, 1980; Horst et al., 1990). A simplified scheme of the effect of intensity on period histograms from a hypothetical nerve fibre is given in Fig. 2. Because of the sharpness of tuning at threshold, the fiber in this example is able to resolve the carrier frequency. At

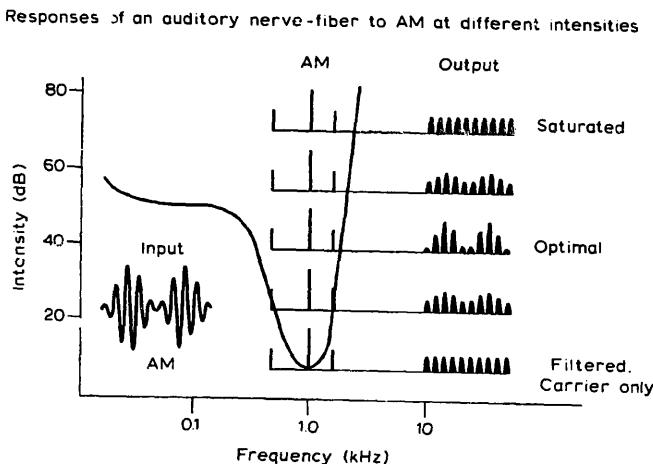


Fig. 2. The simplified scheme shows a section of an AM signal and indicates the relation of the threshold curve of a hypothetical nerve fiber and the frequency components of the AM signal at different intensities. The response of the fiber is plotted in period histograms. The scheme demonstrates that for a given AM frequency it may depend on intensity if a fiber codes the modulation envelope or resolves the carrier frequency.

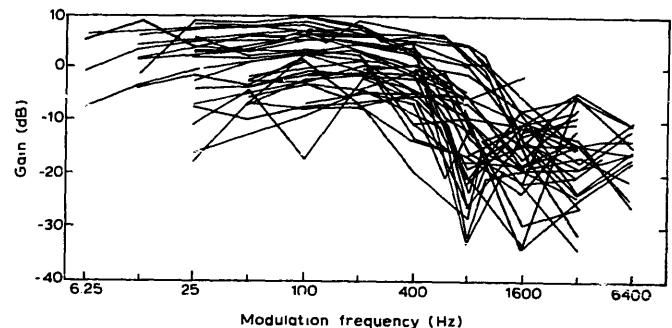


Fig. 3. Modulation-transfer functions of guinea-pig cochlear fibers. The gain is the relation of the relative depth of the discharge modulation of the fibers to the relative modulation depth of the stimulus. As a total the fibers display a low-pass characteristic with a roll-off frequency at about 800 Hz. From Palmer (1982).

medium level, the three AM-components are unresolved and the modulation is discernible in the period histogram. At highest intensity, as a result of saturation the response to AM again resembles that elicited by the carrier alone, as demonstrated for example in the AN of the chinchilla (Javel, 1980). Similarly, AM at a given intensity is coded in different ways by fibers with different thresholds, because fibers with low thresholds are saturated at a lower intensity level than fibers with high thresholds. However, the thresholds of fibers cover a range of about 40 dB and may, in combination with a dynamic range of about 40 dB, provide precise temporal information over an intensity range of at least 80 dB (Horst and Farley, 1986). Moreover, there will always be unsaturated fibers responding to a given AM with CFs deviating from the carrier frequency, as long as the signal intensity is in a physiological range (Palmer, 1982; Shivapuja et al., 1990).

Coding of modulation is supported by the dynamic response properties of nerve fibers. Rapid changes of stimulus level (as in amplitude modulations) maintain a dynamic range 15–20 dB wider than would be expected from steady-state stimuli (Yates, 1987). This effect is due to mechanisms of rapid adaptation and recovery from adaptation (Westerman and Smith, 1984). Although the effective dynamic range in auditory-nerve fibers appears to be substantially smaller than that of some cochlear nucleus units (Møller, 1976b), the response modulation in most nerve fibers is greater than the change in steady-state response produced by a corresponding change in sound intensity (Smith and Brachman, 1980). Since the rate-intensity function of the onset response to pure tones fits better to the intensity dependent variation of response modulation, it was concluded that the same dynamic response characteristics are responsible for both types of responses.

Coding of vowels in the auditory nerve

Responses of the AN may synchronize to various periodic signals like repetitive noise bursts for repeti-

tion rates as high as 3 kHz (Peake et al., 1962). In recent years, many studies focussed on the coding of vowels as a special class of periodic signal (Hashimoto et al., 1973; Sachs and Young, 1979; Young and Sachs, 1979; Reale and Geisler, 1980; Delgutte, 1980; Sinex and Geisler, 1983; Delgutte and Kiang, 1984a). Vowels are, in general, harmonic signals with several resonance maxima (formants) in their spectra. Usually, the first two formants are the most important for the identification of a vowel. Best phase-coupling to the formant frequency or to an adjacent harmonic is obtained from those nerve fibers whose CFs are close to the formant frequency. Fibers with CFs near the formant frequency show little or no envelope modulation and are dominated by a single large harmonic component. For example, when stimulated at high intensity with a harmonic complex, fibers may synchronize exclusively to a frequency component near CF, provided its intensity is at least 2 dB higher than that of the other components (Herst et al., 1990). Other fibers may show modulations corresponding to the fundamental period of a vowel due to a summation of stimulus harmonics near fiber CF (Delgutte, 1980; Miller and Sachs, 1984). In addition, a time-domain analysis of the data from Miller and Sachs suggests that for synthetic-syllable stimuli the AN behaves ef-

fectively wideband with steep high-frequency cutoffs, and that formant estimates and tracking of formant dynamics are more precise than seen in previous spectral analyses (Secker-Walker and Searle, 1990). Two simultaneously and monaurally presented vowels with different fundamental frequencies may be separated by human listeners into two voices uttering vowels with different pitches. Modelling the perception of such concurrent vowels with different types of place and time models, showed that the performance of listeners is comparable to that of a form of place-time analysis, when the model included a nonlinear compression simulating the mechanical-to-neural transduction in the cochlea (Assmann and Summerfield, 1990).

Periodicity coding in the cochlear nucleus

Faithful and enhanced responses to amplitude modulations

The AN projects exclusively to the first central processing centre, the cochlear nucleus (CN). As a pre-requisite for periodicity analysis, temporal information in the AN about the envelope of stimuli is preserved and reflected in the discharge patterns of neurons in the CN. This was demonstrated, for example, in the cat for

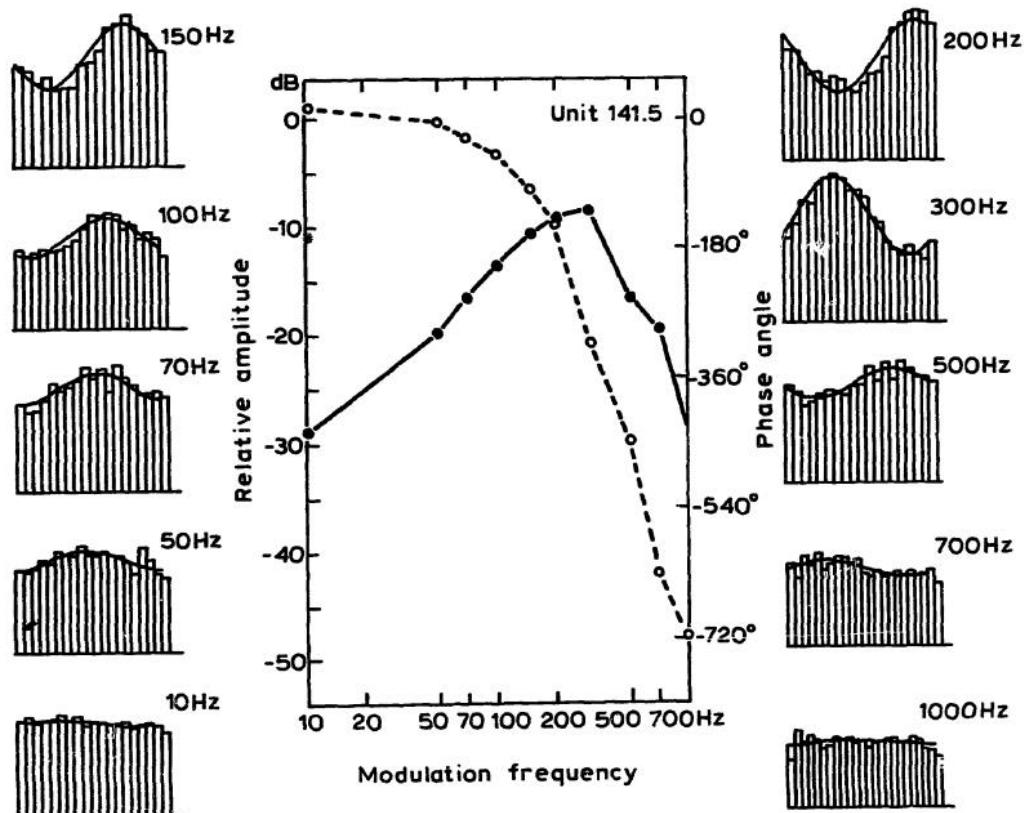


Fig. 4. Responses in the cochlear nucleus to AM. Left and right: Cycle histograms of the responses of a unit in the cochlear nucleus of the rat to AM with various modulation frequencies. Middle: Gain function (solid lines) and phase angle (dashed lines) of the sinewaves that fit the histograms. Modulation depth of the stimulus: 20%; carrier frequency at CF: 30 kHz; stimulus intensity: 60 dB SPL; unit threshold: 45 dB SPL.

In contrast to the AN, units in the cochlear nucleus may display a distinct band-pass characteristic. From Møller (1972).

periodicities up to 800 Hz (Glattke, 1968) and in the bat at least up to 1000 Hz (Vater, 1982) (see Table I).

Møller used different methods of systems analysis to investigate temporal response properties of single neurons in the CN of the rat. He was able to demonstrate that in the processing step from the nerve to neurons in the CN, periodicity information is often enhanced (Møller 1972 a,b). He modulated a tone or noise carrier with pseudorandom noise, measured the modulation depth of the neuronal response with period histograms, and computed the modulation transfer function by correlating the response to the pseudorandom signal (see Fig. 4) (Møller, 1973a,b, 1974a,b, 1983). The results showed that, in many neurons in the CN of the rat, a 20% amplitude modulation with appropriate modulation frequencies is amplified to more than 50% modulation of the discharge rate. This indicates that such neurons code rate and magnitude of the change in sound intensity, i.e. the signal envelope, but that the absolute sound intensity is coded only to a limited degree (Møller, 1974b). Amplification of the modulation depth was demonstrated up to 60 dB above threshold in contrast to only 30 dB in AN fibres, while

the dynamic range for modulation coding is often greater than expected from rate-intensity functions (Møller, 1976a).

In contrast to the AN with mainly low-pass MTFs, neurons in the CN often reveal band-pass MTFs (Figs. 4 and 6) with BMFs up to 700 Hz (Frisina et al., 1985). At low intensities, the response to low modulation frequencies increases and the MTFs become low-pass (Møller, 1972a; Frisina, 1983; Frisina et al., 1985). This effect was also found in the IC of rat and guinea pig (Rees and Møller, 1987; Rees and Palmer, 1989). Møller found that tuning properties of many neurons in the CN are quite resistant to other variations of stimulus parameters, such as modulation depth or stimulus duration. Sinusoidal amplitude modulations are reproduced with little distortion (Hirsch and Gibson, 1976; Møller, 1972a, 1974b) except at very high stimulus levels or large modulation depths, where peak clipping can be demonstrated in period histograms (Møller and Rees, 1986). The upper frequency limit for this kind of faithful temporal encoding is approximately 880–1000 Hz (see Table I) (Møller, 1972a; Frisina, 1983).

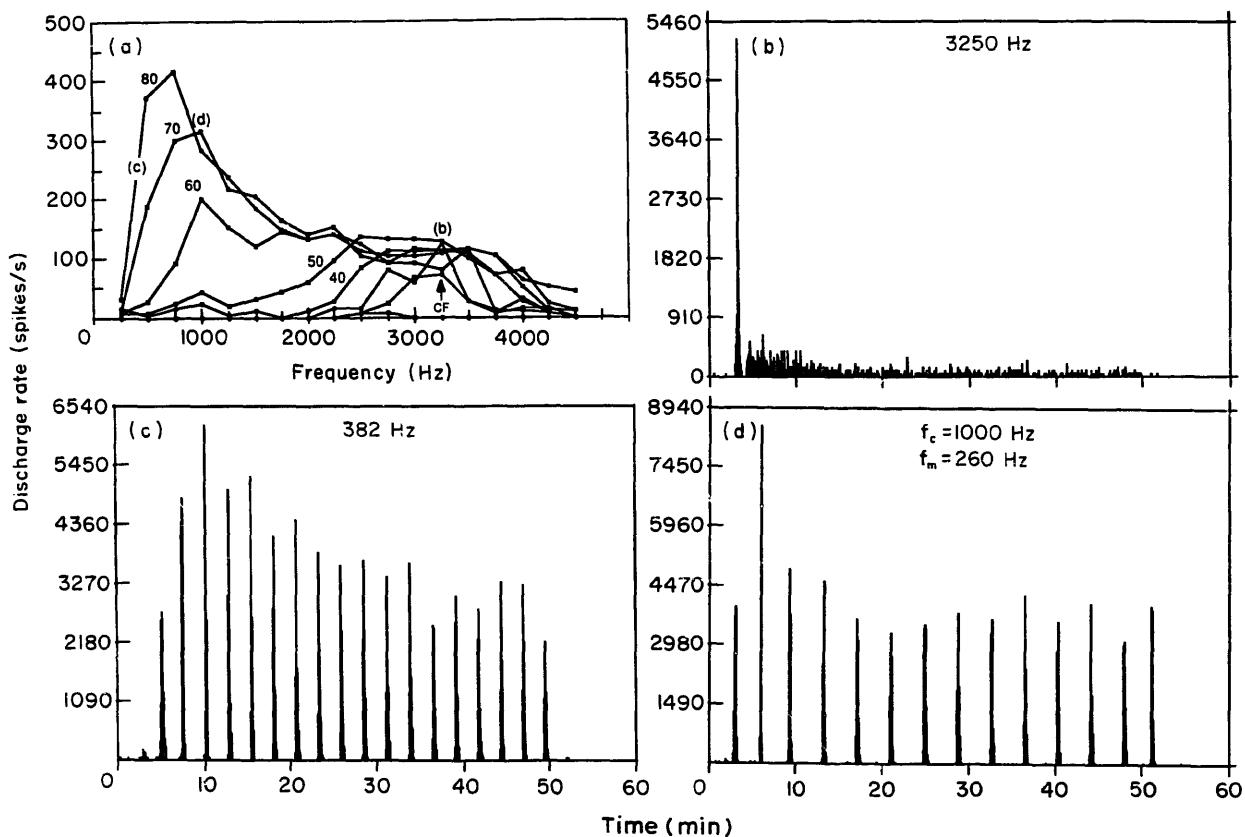


Fig. 5. Synchronized responses of an onset-unit. The response area (a) and PSTHs of an onset unit recorded from the PVCN of the cat (CF = 3.25 kHz, threshold = 20 dB SPL). The letters in a) denote the frequency and amplitude of the signals used to generate the PSTHs of (b)–(d). b) Response to a tone at CF with 45 dB SPL. c) Response to a tone at 382 Hz with 80 dB SPL. d) Response to an AM-signal ($f_c = 1$ kHz, $f_m = 260$ Hz, 80 dB SPL). The unit coded the envelope of an AM signal in a similar way as a low-frequency tone. From Greenberg (1988)

Diversity of responses to pure tones and amplitude modulations

The cochlear nucleus can be divided into a number of sections based on cell types and connections (Osen, 1969; Fekete et al., 1984; Cant and Morest, 1984a). A variety of about nine morphological cell types was described for the three main subdivisions of the CN, the anterior (AVCN) and posterior (PVCN) division of the ventral CN (VCN), and the dorsal CN (DCN) (Osen, 1969; Cant and Morest, 1984b).

Much greater diversity of responses has been found in the CN than in the AN (Kiang et al., 1965; Pfeiffer, 1966; Godfrey et al., 1975; Gisbergen et al., 1975a; Britt and Starr, 1976a; Brugge and Geisler, 1978). The responses of 'primary-like' units are very similar to

those of AN fibers, mostly characterized by an on-response followed by a tonic response. In 'onset' units a strong phasic response is shown (see Fig. 5b); in 'pauser' units a pause of few milliseconds follows an on-response; in 'buildup' units the response increases slowly, and in 'chopper' units a transient or lasting burst of action potentials with sometimes extremely regular interspike intervals is shown. All of these response types were further subdivided into subclasses.

The five major response types seem to originate mainly from neurons which project to higher auditory nuclei including the inferior colliculus (IC). Using intracellular horseradish peroxidase labelling these response types could be correlated with morphological neuron types (Rhode et al., 1983a,b; Rouiller and

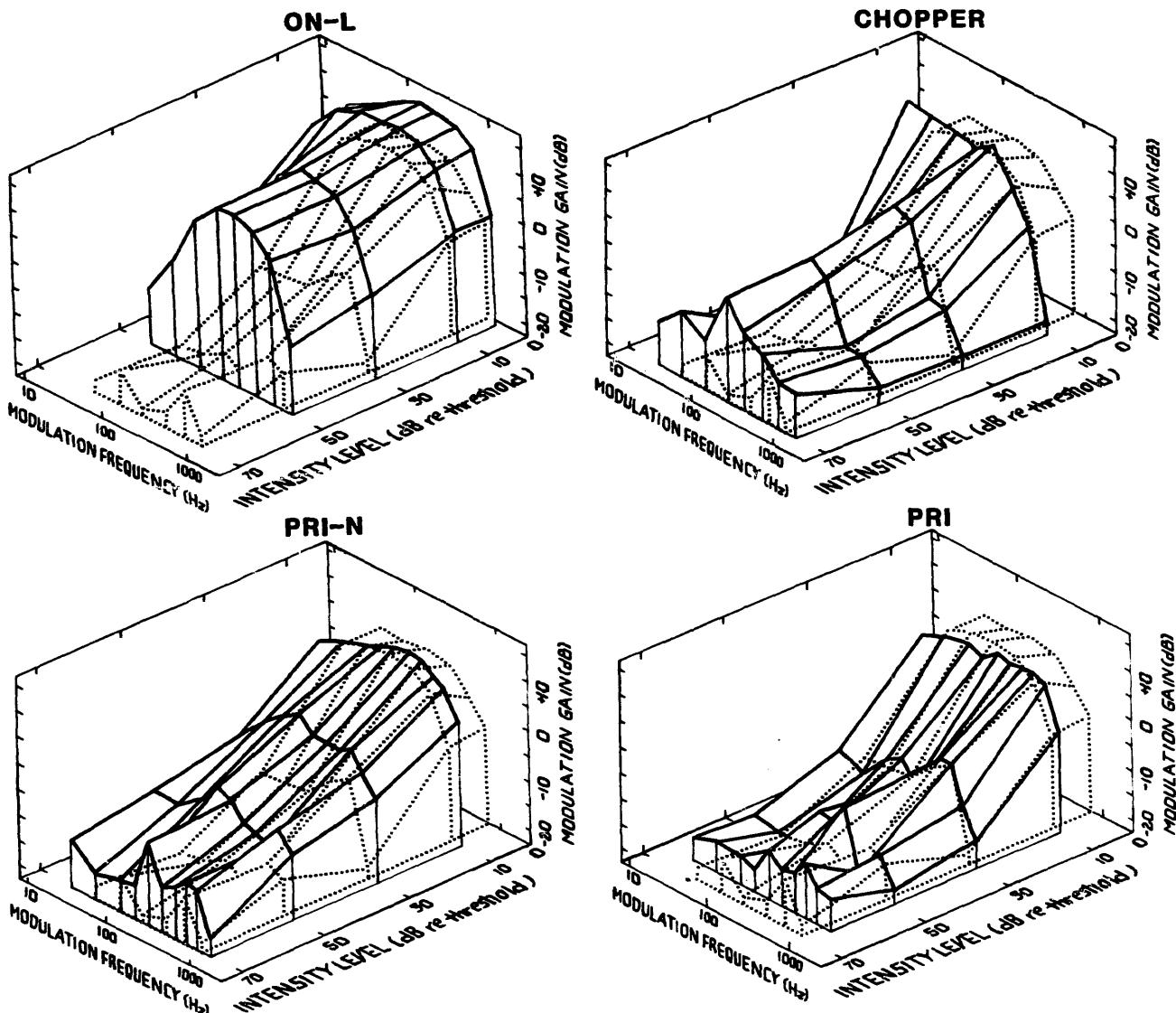


Fig. 6. 'Response surface' for the neuronal encoding of AM in the VCN of the gerbil. Onset units show the strongest AM phase-locking, followed in order by chopper, primary-like-with-notch and primary-like units. All four unit-types have a larger gain than nerve fibers. The surfaces show low phase-locking changes with modulation frequency and intensity for four VCN neurons (solid lines). ON-L: onset unit, CF = 12 kHz, threshold = 33 dB SPL, chopper: CF = 9.9 kHz, threshold = 9 dB SPL; PRI-N: primary-like-with-notch, CF = 17.1 kHz, threshold = 16 dB SPL; PRI: primary-like, CF = 15.2 kHz, threshold = 20 dB SPL; AN unit: CF = 6.5 kHz, threshold = 2 dB SPL; stimulus modulation depth = 35%. From Frisina et al. (1985)

Ryugo, 1984; Rhode and Smith, 1986b; Oertel et al., 1988). Primary-like responses were recorded from bushy cells in the AVCN, onset responses from stellate cells in the VCN and octopus-cells in the caudal pole of the PVCN (Kane, 1973; Brawer et al., 1974), chopper responses from stellate cells mostly in the VCN, but also in the DCN (Bourk, 1976; Rhode et al., 1983a; Rouiller and Ryugo, 1984). Pauser- and buildup-responses originated mostly from fusiform and giant cells in the DCN (Rhode et al., 1983b). Similar neurons were also described in birds in the nucleus angularis, a homologue to the mammalian PVCN and DCN (Sachs et al., 1978). In this context, it is certainly surprising to learn that cell responses to acoustic stimuli in insects, that is in two noctuid moths, were also classified as chopper, build up and onset. It was suggested that these neurons play a similar role to the corresponding neurons in vertebrates and are possibly involved in the coding of temporal stimulus pattern and stimulus intensity (Coro and Alonso, 1989).

Although the described response diversity has been characterized mainly by the temporal aspects of the responses to pure tones, it became apparent that different cell types also code periodicity information in different ways (Frisina et al., 1990a,b). Each particular code may be of special importance for a central periodicity analysis. For example, the ability of a neuron to produce strong synchronized responses to AM-signals is greater the more its pattern of response to pure tones deviates from that of an AN-fiber (Frisina et al., 1985). Primary-like, onset, and chopper neurons, as well as auditory-nerve fibers, show strongest phase-locking to 150 Hz AM at low intensities, but differ greatly in their abilities to encode AM at higher intensities, where phase-coupling in these neurons is even better than in the AN (Fig. 6).

Periodicity coding in primary-like neurons

The bushy cells in the AVCN, which may be further subdivided into spherical and globular cells (Osen, 1988), receive only a few, but correspondingly large, synaptic terminals from the AN. Their responses are similar to the responses obtained from the AN (primary-like), including phase-locking (Bourk, 1976). In guinea pigs, a preponderance of locking to the fundamental frequency of harmonic sounds, as well as to amplitude modulation, was found (Moore and Cashin, 1976; Caspary et al., 1977; Rupert et al., 1977). Both primary-like neurons and primary-like neurons with a short notch in their post-stimulus time histograms (PSTHs) after onset response, show enhanced responses to AM in comparison to the AN, especially at higher intensities (Frisina et al., 1985). The enhancement or gain is, however, much smaller than in the responses of onset and chopper neurons. In addition,

MTFs of primary-like neurons do not show band-pass characteristics (Fig. 6).

Since primary-like neurons were identified as bushy cells which project to the olfactory nuclei (Warr, 1982), and since these nuclei are believed to be involved primarily, or perhaps even exclusively, in binaural information processing, it may be concluded that these neurons are of minor importance for pattern and periodicity analysis (Frisina et al., 1990a). Certain binaural pitch effects, obtained for example with dichotically delayed noise (Frijns et al., 1986; Raatgever and Bilsen, 1986; Bilsen, 1976), seem to contradict the hypothesis of a strict separation of localization and pattern processing and suggest binaural processing of pitch relevant information. However, this does not necessarily mean that primary-like neurons and brain structures specialized for localization tasks are responsible for these pitch effects, since neuronal structures responsible for pattern analysis will also receive binaural information.

Periodicity coding in onset-neurons

Onset responses are characterized by sharp peaks at the beginning of a PSTH followed by little (on-L) or no response (on-I) (Fig. 5b). The on-I response pattern has been attributed to octopus cells located in the caudal pole of the PVCN (Godfrey et al., 1975). It was suggested that two types of AN endings, as described on these neurons (Kane, 1973), correspond to an excitatory and a delayed inhibitory input and could account for the on-response.

Octopus cells have already been described as onset-neurons by Pfeiffer and Kiang (Pfeiffer and Kiang, 1965). In the bat they were investigated in the VCN by Vater (1982). They may also correspond to the 'transient units' observed by Møller (1970) in the rat cochlear nucleus. 'Transient units' respond well to high repetition rates of clicks and are able to fire a single action potential to every click in a series up to a certain rate, above which the response strength sharply drops. Stimulus off-time seems to be a major limiting factor for synchronized responses of these neurons (Møller, 1969). The 'best repetition rate' of onset-neurons is typically below 800 Hz and increases with stimulus intensity (Godfrey et al., 1975).

Onset-neurons show the strongest AM phase-locking of all neurons in the CN (Frisina et al., 1985). Their gain of modulation is much greater than that in the AN and increases with increasing intensity. While AN-fibers code AM-signals over a small intensity range of 40 dB, some onset and also chopper neurons maintain their ability for synchronous AM responses over a much larger intensity range of 90 dB. In addition, MTFs of onset-neurons reveal clear band-pass characteristics (Fig. 6, top, left) (Frisina et al., 1985, 1990a).

For stimulus frequencies below 1 kHz, onset-neu-

rons also show a very good phase-locked response (Godfrey et al., 1975; Bourk, 1976; Britt and Starr, 1976b; Rhode and Smith, 1986b). Their temporal properties, in particular their ability to code accurately envelope and low frequency periodicities, suggest that they may play an important role in temporal analysis. In response to low frequencies, the neurons may fire very exactly one spike at a certain phase of each stimulus period – even for frequencies far from their CF (Fig. 5c) (Greenberg, 1988). Their synchronization and maximum discharge rates may be much higher than corresponding values of the AN (Rhode and Smith, 1986a). This could be accounted for by the large number of convergent inputs to these neurons. At higher frequencies this phase-locking behaviour is replaced by the typical short on-response (Fig. 5b).

Periodicity coding in chopper neurons

Stellate or multipolar cells, predominantly located in the VCN (Osen, 1988), receive many bouton terminals from AN fibers and are physiologically characterized by their phasic or tonic chopper responses (Cant, 1981; Smith and Rhode, 1989). Similar response patterns were also observed in other parts of the auditory system, such as the DCN (Rhode and Smith, 1986a), the olfactory nuclei (Galambos et al., 1959) or the IC (Langner, 1983a; Langner and Schreiner, 1988).

Chopper neurons were first described by Pfeiffer (1966). Since then, at least three types of chopper responses – sustained-, slowly-, and rapidly-adapting – were distinguished on the basis of temporal patterns, rate and loss of regularity due to adaptation (Bourk, 1976; Blackburn and Sachs, 1989). Similar to onset-neurons, rapidly adapting chopper neurons display a strong phasic response.

In general, the temporal pattern in the responses of chopper units in the VCN is dominated by regular discharge intervals that are not related to the period of the stimulus waveform (Pfeiffer, 1966; Rhode et al., 1983a; Rouiller and Ryugo, 1984). The regular intervals of chopper units were found to be only weakly correlated with BMFs (Frisina, 1983), and the best modulation frequencies tend to be equal or less than the natural chopping frequency (Frisina et al., 1990a). In the DCN and PVCN, intrinsic oscillations in chopper and other unit types were observed, which correlated better with the BMFs of these neurons (Kim et al., 1990). However, the underlying mechanisms of such oscillations seem to be different from those producing chopper intervals and may be understood in terms of linear band-pass filters.

Phase-locking of chopper neurons in response to pure tones is relatively weak, whereas their temporal response is strongly influenced by the fundamental frequency, when steady-state vowels are used as stimuli (Sachs et al., 1988). They have very low spontaneous

activity and rate-intensity functions that saturate 20–30 dB above threshold, without a sloping asymptote at high intensities (Frisina et al., 1990b).

With the exception of onset-neurons, choppers show the strongest AM phase-locking of all neurons in the CN, sometimes even up to 90 dB above their threshold (Frisina et al., 1990a). As with onset-neurons, their gain of modulation is much greater than seen in the AN and even increases with increasing intensity. At higher sound levels the MTFs of chopper and onset-neurons reveal clear band-pass characteristics indicating that these neurons ‘could be considered specialized for the encoding of AM at high sound levels’ (Fig. 6, top, right) (Frisina et al., 1985, 1990a).

Periodicity coding in pauser and build-up neurons

Because of striking anatomical similarities including a multilayered, cortex-like structure in subprimates, the DCN has been called the acoustic ‘cerebellum’ (Lorente de Nò, 1981, 1933; Osen, 1969). The role of the DCN in auditory signal processing is quite unclear. It contains several neuron types corresponding, for example, to the primary-like or chopper types in the VCN (Rhode and Smith, 1986a). The principal neurons are, however, fusiform and giant cells. In contrast to fusiform cells in the mouse, fusiform cells in the cat have collateral terminals in the DCN (Oertel and Wu, 1989). Principal cells of DCN provide one of the main inputs to the central nucleus of the contralateral IC (Osen, 1972; Semple and Aitkin, 1980; Ryugo and Willard, 1985).

Principal cells reveal response types restricted to the DCN: pauser and build-up. They respond to best-frequency tones with excitation from threshold only to about 20 or 30 dB above threshold, while at higher levels their response is mostly inhibited. This property is typical of so-called type-IV cells (Evans and Nelson, 1973; Young and Brownell, 1976). In addition, they display short pauses or more or less slowly increasing response rates. In contrast, their response to noise is excitatory, and discharge rate generally increases with bandwidth and intensity (Goldberg and Brownell, 1973; Young and Brownell, 1976). Inhibitory inputs are obviously essential for these response properties.

The phase-locking to pure tones in these neurons is much poorer than that of the previously described neuron types (Goldberg and Brownell, 1973; Gisbergen et al., 1975b). In spite of that, there is growing evidence that the temporal properties of a signal are of importance for these neurons. For example, they were found to follow envelope fluctuations of harmonic complexes up to at least 630 Hz and 67% of the neurons were found to have band-pass MTFs (Schreiner and Snyder, 1987). This study was performed in chloralose-anaesthetized cats in order to avoid undesired effects on inhibitory mechanisms, as

described for example by Caspary et al. (1987). Earlier studies in barbiturate-anaesthetized rats (Caspary et al., 1977) and bats (Vater, 1982) showed a lack of phase coupling to AM in the DCN.

Periodicity coding in olivary nucleus complex and lateral lemniscus

Pattern recognition and localization

The auditory system has to perform two main tasks: signal localization and pattern recognition. The olivary nucleus complex seems to be involved exclusively in the first task and contains neurons sensitive to interaural differences of the two sound parameters relevant for localization: intensity and phase. Temporal acuity necessary for localization is much higher (μ s-precision) than required for periodicity analysis (ms-precision). Neurons adequately sensitive to interaural phase differences in pure tones have been extensively studied since the concept of 'characteristic delay' neurons was proposed (Rose et al., 1966). A neural map of interaural phase differences has been demonstrated in the bird's homologue of the medial superior olive, the nucleus laminaris (Sullivan and Konishi, 1986). The responses of neurons in this nucleus show a sensitivity to changes of interaural time differences in the microsecond range.

Role of envelope modulations in localization

The classical theory whereby localization using interaural time (or phase) differences is restricted to the low frequency range and localization of high frequencies requires interaural intensity differences (Mills, 1960; Blauert, 1974) holds only for pure tones. To the surprise of many psychophysicists, it was found that high frequency signals above 1 kHz can be lateralized on the basis of interaural time differences (ITDs) provided that amplitude modulation is present (Henning, 1974, McFadden and Pasanen, 1976). Accordingly, in the lateral superior olive of the cat, high frequency cells were found to be sensitive to intensity and temporal differences in the onset of tone or noise bursts or of clicks (Caird and Klinke, 1983). Similar results have also been found in the horseshoe bat (Harnischfeger et al., 1985) and in the IC of the cat (Kuwada and Yin, 1983, Caird and Klinke, 1987).

In the superior olivary nuclei in the anuran medulla, Fuzessery and Feng (1983) found neurons that synchronized to pulse trains with repetition rates up to 280/s with low-pass characteristic. However, it was also demonstrated that neurons may have indications of MTFs with band-pass character (Schneider-Lowitz, 1983) and enhancement of small amplitude changes for modulation frequencies below 150 Hz (Gorodetskaya and Bibikov, 1985).

The dynamic properties of olivo-cochlear efferent neurones in the guinea pig cochlea were investigated with AM-signals (Gummer and Yates, 1988). The results show that the period histograms of the discharge pattern of the efferent neurons match the AM-envelope and are considerably enhanced relative to the AM-signal and to the afferent nerve fibers. Most of the MTFs had a maximum between 100 and 140 Hz. It is surprising that efferent neurons are able to follow such rapid changes in a complex signal, and it remains to be seen if this property may be useful to improve, for example, the detection of signals in background noise.

Functional role of the nuclei of the lateral lemniscus

Apart from their response properties when stimulated with pure tones studied by Brugge et al. (1970), not much is known about the functional role of neurons in the nuclei of the lateral lemniscus (LL). Suga and Schlegel (1973) found that the majority of neurons in the LL of the bat show a very short recovery period after stimulation with a tone pulse, as well as frequent facilitation of their responses to a second tone pulse. They concluded that, in the bat, these neurons are specialized for echo-detection and carry information for echolocation. Accordingly, neurons in VNLL of the horseshoe bat have been found to have a high temporal resolution (Metzner and Radtke-Schuller, 1987). They are able to synchronize to sinusoidally frequency modulated signals up to 800 Hz with an average highest synchronization frequency of 515 Hz.

Periodicity coding in the auditory midbrain

Input convergence and response types of the auditory midbrain

As the major relay to higher auditory nervous centres, the auditory midbrain has to code information relevant for pattern recognition as well as for sound source localization. In accordance, the midbrain receives its input from all auditory nuclei in the brainstem (Irvine, 1986). For example, the auditory midbrain of the chicken (MLD) receives direct input from both the subnuclei of the cochlear nucleus (Conlee and Parks, 1986). In the cat, there is anatomical evidence for at least six cell types in the central nucleus of the inferior colliculus (IC) (Paloff et al., 1989) and in a variety of species, from frog to monkey, neurons in this nucleus were found which are sensitive to several different parameters of complex acoustic stimuli (Vartanyan, 1969; Scheich et al., 1977; Plassmann, 1985; Eggermont and Epping, 1986; Müller-Preuss et al., 1988; Ehret and Merzenich, 1988), to the direction of sounds, or to both (Geisler et al., 1969; Crow et al., 1980; Aitkin et al., 1984; Fuzessery et al., 1985).

Since the IC receives direct input from the DCN and the VCN, it is not surprising that several authors were able to distinguish response patterns in this nucleus reminiscent of the CN response types: onset, sustained, and pauser (Rose et al., 1963; Semple and Kitze, 1985; Rees and Palmer, 1989). In the midbrain of guinea fowl and cat, rapid spike sequences or triggered oscillations similar to those of onset-choppers in the VCN were found and termed 'intrinsic oscillations' (see below) (Langner, 1981, 1983b; Langner and Schreiner, 1988). Chopper response patterns have been also described in the IC of the bat (Lesser et al., 1986). In the IC, different response patterns may converge on the same neuron and, under different stimulus conditions, these different patterns may appear at the output of the neuron. Therefore, classification of IC neurons is more difficult than in the cochlear nucleus. For example, in a study in the IC of the rat all neurons responded to AM and FM, and most of the neurons responding to AM were classified as onset-type neurons (Rees and Møller, 1983). It was, however, not possible to predict the response to the complex stimuli from pure tone onset- or sustained-type firing characteristics alone. Similarly, in the IC of the guinea pig it was not possible to relate pure tone response patterns to AM responses, although 97% of the neurons showed temporal modulation of their discharges when stimulated with AM signals (Rees and Palmer, 1989). In bats, in contrast, a small but significant population (13%) characterized as ON-OFF cells was judged to be unresponsive to AM signals (Lesser et al., 1990).

Synchronization and rate

It is important to study synchronization in the auditory midbrain because in order to perform temporal periodicity analysis, a nucleus needs, at least at its inputs, the representation of the envelope through synchronous modulation of spike discharges. There is general agreement among authors that synchronization deteriorates with increasing level of the auditory system (see Table I) resulting in a significant reduction of temporal resolution at the midbrain (Rees and Møller, 1983; Langner and Schreiner, 1988). This is probably due to a loss of temporal precision with each additional synapse involved in transmission or/and to the influence of inhibitory mechanisms (Rees and Palmer, 1989). However, the upper frequency limit of synchronization at the level of the IC and above also seems to be dependent on the experimental conditions and the experimental animal.

First investigations of responses to modulations in the IC of the cat, demonstrated synchronization only below 30 Hz (Nelson et al., 1966). Similarly, in the midbrain of the frog, about half of the neurons have long integration times in the range between 10 and 100 ms (Bibikov, 1977; van Stokkum, 1989). Single units

represent modulation rate by spike rate with minimal synchronized activity, independent of the depth of modulation or the stimulus intensity (Rose and Capranica, 1984). In contrast, a small number of neurons show the same synchronization capability as AN fibers (Rose and Capranica, 1985; Epping and Eggermont, 1986) and the input to the midbrain from superior olive or medullary neurons, as indicated by evoked potentials, is synchronized with an upper cut-off frequency as high as 200–300 Hz (Hillery, 1984). In anaesthetized rats, the most effective modulation rate was found in all cases to be below 120 Hz (Rees and Møller, 1983). In contrast, in awake guinea fowl, some units synchronize to modulation frequencies up to 1000 Hz and, judged by synchronization, have BMFs up to 680 Hz (Fig. 9) (Langner, 1981; Langner, 1983b). In other animals, the upper frequency limit observed for synchronized activity at the level of the midbrain has been extended in recent years. In the bat, neurons were found to be tuned to modulation frequencies up to 800 Hz (Lesser et al., 1986), while responses synchronized up to 900 Hz were found in the rabbit (Batra et al., 1986). In anaesthetized cats, synchronized responses were found occasionally up to 600 Hz modulation frequency, but synchronization above 300 Hz was usually small (Langner and Schreiner, 1988).

On the other hand, when using rate as a response measure, the highest BMF of single units in the IC of the cat went as high as 1000 Hz (Fig. 8). Approximately 75% of the single units were tuned to a BMF when measured by rate, while only 33% were tuned in their synchronization. In the midbrain of anurans, temporal selectivity was found to result in 30% of neurons tuned to particular AM rates (Rose and Capranica, 1985). Local circuits in the auditory midbrain are probably not responsible for this temporal selectivity, at least not in anurans, since correlation analysis of simultaneously recorded units in the frog showed that neuronal interactions seem to play a minor role (Epping and Eggermont, 1987; van Stokkum, 1989).

Such findings indicate that at the level of the midbrain the temporal code is to a certain degree transformed into a rate code (Langner, 1981; Rose and Capranica, 1984, Pinheiro et al., 1991). A synchronization-rate transformation is also suggested by the finding that in 43% of units recorded in a study of guinea pig midbrain, the mean discharge rates were greatest for those modulation frequencies which also elicited maximal synchronization (Rees and Palmer, 1989). In that sense, the auditory midbrain might be considered as a decoder for temporal information which transforms periodicity into rate information. Naturally, this hypothesis does not exclude the possibility that sufficiently low modulation frequencies are also represented temporally. The hypothesis is also corroborated by the fact that in contrast to the 'rate tuned' IC-units,

their main input neurons in the cochlear nucleus tend to exhibit nearly constant average discharge rate for various modulation frequencies (Kim et al., 1990).

A transformation from synchronization into rate information is also compatible with investigations of neuronal responses to binaural beats resulting from stimulation with slightly different frequencies at the two ears. Most low best frequency neurons studied in the IC of the cat have been found to be sensitive to interaural phase differences (Kuwada et al., 1979; Kuwada and Yin, 1983). In addition 7% of the units exhibited a sensitivity to the delay of the onset, indicating that fluctuations of envelope amplitudes may also provide cues for the localization of a sound source. This has also recently been demonstrated in the unanaesthetized rabbit with amplitude modulations presented binaurally (Batra et al., 1989). The phase difference of synchronization to the ipsilateral and contralateral components determined the interaural time difference which produced maximal discharge. The highest best modulation frequency found was 1000 Hz with binaural beats, while synchronization to the beat frequency extended to 1300 Hz. The highest modulation frequency of a contralateral AM tone which elicited synchronized response to the beat frequency in one unit was 925 Hz. Since most units showed synchronization only below 600 Hz, the authors concluded that high-frequency synchronization is filtered out at the level of the IC. Human listeners can most effectively lateralize such stimuli at modulation frequencies of 150–400 Hz (Henning, 1974), a frequency range which was also found to be optimal for most neurons encountered in this study.

Modulation transfer functions (MTF) affected by signal amplitude, modulation depth, and carrier frequency

Five types of MTFs have been distinguished in the midbrain of the frog: band-pass, low-pass, high-pass, band-reject, and nonselective (Bibikov and Gorodetskaya, 1981; Walkowiak, 1984; Rose and Capranica, 1985; Epping and Eggermont, 1986). Single and multiunits recorded in the midbrain of the guinea fowl, with rate as a measure, showed results that were similar to those obtained in the frog (Albert et al., 1989). At least half of the units in the auditory midbrain of frogs and birds are in one way or the other selective to modulation frequency.

Like the percept elicited by amplitude modulations, responses in the midbrain have been found to be relatively constant in the face of variations of signal amplitude and modulation depth (Fig. 7). Fluctuations in responses of neurons in the rat were found to be amplified in comparison to fluctuations in the signal envelope, with a gain factor of up to 20 dB, and independent of the signal intensity (Rees and Møller, 1983). This is a further indication that periodicity anal-

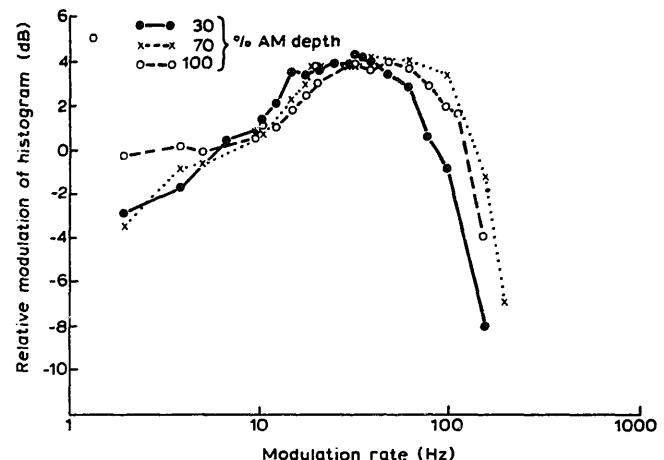


Fig. 7. Three modulation rate transfer functions for the same unit in the IC of rat obtained at three different modulation depths, ($f_c = 4.5$ kHz, mean intensity 20 dB above threshold). Shape and peak value of the transfer function are preserved at all modulation depths, indicating that the impulse distribution is determined by the modulation rate, independently of the differences in the rate of amplitude change caused by the different modulation depths. Adapted from Rees and Møller (1983).

ysis is not completed in the CN, since typical maximum gains of neurons in the CN were found to be only between 10 and 14 dB (Møller, 1972a). Comparison of evoked potentials recorded in the AN and midbrain of frog, also revealed an enhanced coding of AM signals in the midbrain for modulation frequencies below 100 Hz (Hillery, 1984), while the potentials in the midbrain indicate an overall low-pass filtering for AM with a cutoff frequency of 250 Hz.

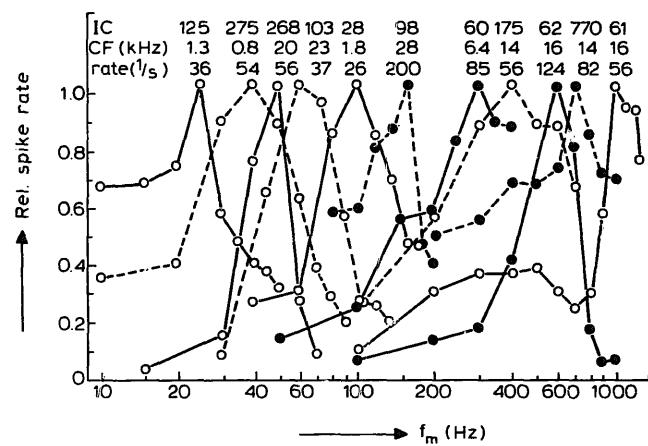


Fig. 8. Normalized average-rate responses to amplitude modulation of band-pass units of the ICC of the cat. In contrast to more peripheral auditory nuclei, many units in the ICC are tuned in terms of average rate. Numbers above the curves indicate the unit number, the CF of the unit that also served as carrier frequency of the AM stimuli, and the maximal firing rate corresponding to the tip of the MTF. Single units are indicated by circles, multiple units by dots. The range of observed BMFs (20–1000 Hz) covers approximately the range of periodicity pitch in humans. From Langner and Schreiner (1988).

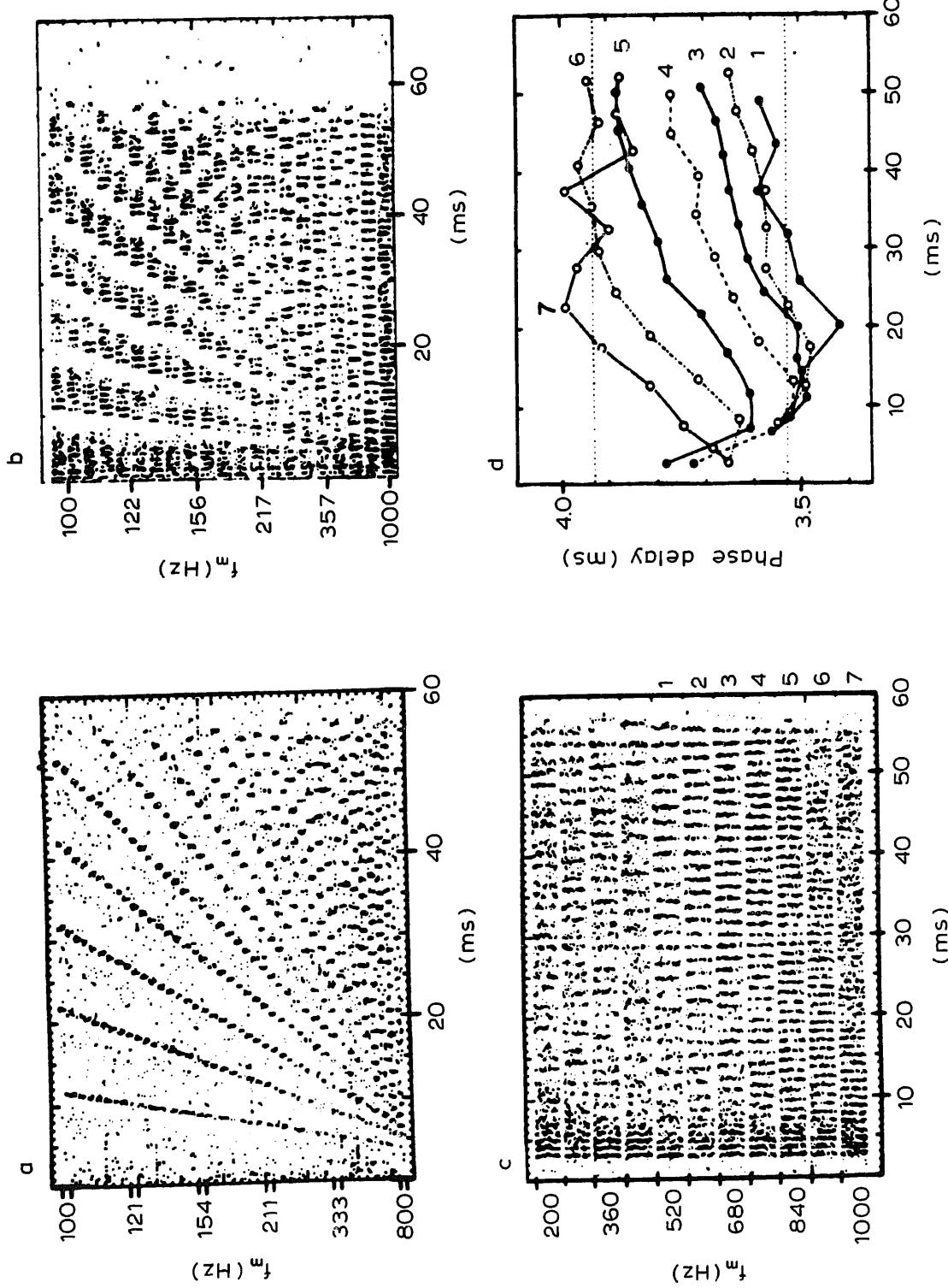


Fig. 9. Response patterns of MLD-units in the guinea fowl. Dot raster diagrams (a–c) of the responses of each of 3 units in the awake guinea fowl to AM-signals. Each dot represents one spike. Modulation frequencies f_m were varied in different number of steps in the range between 100 and 1000 Hz; for a given f_m the responses to 100 repetitions were accumulated using a restricted range on the Y-axis. Carrier frequencies of 2.5 kHz (a), and 2.8 kHz (b) were kept constant near the CFs of the 3 units; modulation depth = 80%; sound pressure level 65 dB SPL. In (a) and (b) the signals were presented from –5 to +5 ms on the time axis with 5 ms ramps and modulated from 0 to 50 ms. In (c) the ramps at the beginning were omitted. a) Onset-type unit which codes every envelope cycle with one spike. b) Chopper-type unit: every envelope cycle triggers a burst of spikes with regular intervals of about 0.8 ms. c) A coincidence-unit which, in contrast to the units in (a) and (b), shows a clear selectivity and a synchronized response to $f_m = 840$ Hz (labelled as No. 5 at the right side of (c)). Note, that synchronization to f_m increases in time for f_m increases in time for f_m s below the BMF (Nos. 6 and 7). d) The average phase delays of the spikes for the responses in the cases Nos. 1–7 in (c) were measured in relation to the zero crossing of the f_m -waveform. Note the different phase offsets for the different f_m s and the general increase of the phase delays during the first 20 or 40 ms. The assumption of a coincidence window with a certain delay after each zero crossing of the f_m -waveform (as indicated by the dotted lines) may provide an explanation for the temporal variations of synchronization in (c).

Neurons in the auditory midbrain of the bat were found to be extremely sensitive to amplitude modulations and can synchronize to modulation depths as small as 3% (Schuller, 1979). In the rat, modulation depths as small as 2%, can elicit synchronized responses, but, in spite of this sensitivity, the modulation depth of the signal did not affect the shape and peak value of the MTF (Rees and Møller, 1983).

In order to accurately relay a sinusoidal amplitude modulation, a frequency filter needs a bandwidth exceeding twice the modulation frequency, otherwise the sidebands are attenuated. As a consequence, the modulation depth of the output signal is reduced (see Fig. 2). Since the width of the peripheral tuning curves increases with CF, a general increase in the upper frequency limit of encoded modulations would be expected. This has been demonstrated in the IC of the cat (Langner and Schreiner, 1988). While for a given CF below 4 kHz various BMFs were found with values below about $CF/4$, virtually no unit was found with a BMF exceeding that value.

When AM-signals are used as stimuli, one of the effects observed in the midbrain of birds is that BMF of a tuned unit is a function of the carrier frequency: in a small range of carrier frequencies a deviation of the carrier frequency from CF has an effect not only on the width but also slightly on the position of the maximum of the MTF (Langner, 1981; Langner, 1983b). Similar effects were also observed in the ICC of the cat (Langner and Schreiner, 1988). In the midbrain of the grass frog the gross shape of MTFs was found to be independent of the carrier, while differences in the amplitude

and – to a slight extent – in the position of the maxima were also observed (Walkowiak, 1984).

Non-linearity

One aspect of periodicity coding is its increasing non-linearity along the neural axis. While envelope responses from neurons in the cochlear nucleus show little influence of non-linearities, mostly coding the envelope with high fidelity (Møller, 1974b, 1987), neuronal responses from the central nucleus of the IC are highly non-linear (Rees and Møller, 1983; Møller and Rees, 1986). For a linear system one would expect the largest changes in rate of firing when the stimulus intensity is modulated over the range corresponding to the greatest slope of a neuron's rate-intensity function. This relation was not observed in the IC of guinea pigs. Broadband noise was added to AM signals with low modulation frequencies. This increased the mean rate and also the temporal modulations of neuronal discharges. However, no relation was found to noise-induced shifts of the rate-intensity functions, which is another hint for the involvement of highly non-linear mechanisms of periodicity analysis at the level of the midbrain (Rees and Palmer, 1989).

Neuronal response patterns: temporal variations and triggered oscillations

Temporal variation of synchronization and rate during the first 30 ms to 100 ms of responses to amplitude modulations was observed in the midbrain of the guinea fowl, in the forebrain of the Mynah bird, and occasionally in the cat (Langner, 1983b; Hose and Langner,

Periodotopic Organization in the Auditory Midbrain

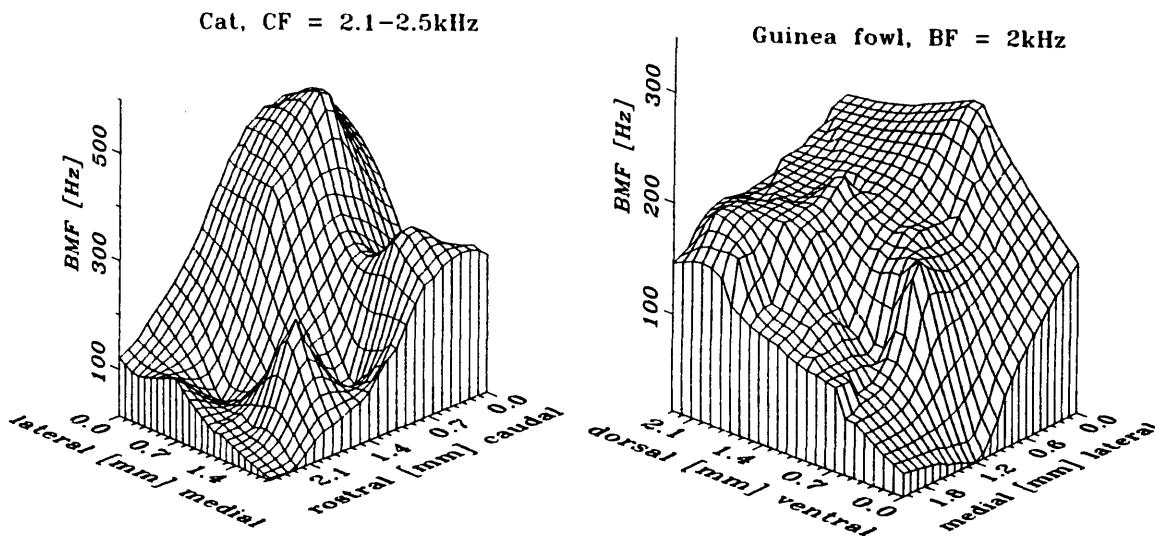


Fig. 10. Periodotopy. Representation of BMFs in the central nucleus of the auditory midbrain in the cat and in the Guinea fowl. In both species lowest BMFs were observed in a medial corner and highest BMFs in the opposite lateral corner of the mapped frequency areas. In the cat within the same frequency-band lamina CFs between 2.1 and 2.5 kHz were represented in a regular way with a medial-lateral gradient; for the BMF map in the Guinea fowl CFs between 1.5 to 2.5 kHz were lumped together.

1988; Langner and Schreiner, 1988). It was found that synchronization and rate of response to modulation frequencies *below* BMF generally increase with time after stimulus onset, while for modulation frequencies *above* BMF both response measures decrease (Fig. 9c).

At the onsets of tones or other signals many neurons in the midbrain respond with several action potentials that are separated by regular intervals. Since the intervals of these triggered oscillations are related neither to the periods of the stimuli nor to that of the CF of the neuron, they were termed 'intrinsic oscillations' (Langner, 1981). This response pattern is similar to that of an onset chopper in the VCN and it may well reflect input activity from efferent projections of chopper neurons from the brainstem. Preferred intervals in the intrinsic oscillations were found in guinea fowl as well as in cats, and in the forebrain of Mynah birds with short intervals below about 3 ms clustering around multiples of 0.4 ms (Langner, 1983b; Langner and Schreiner, 1988; Hose, 1987).

Rees and Møller (1983) distinguished onset and sustained firing patterns in the IC of the rat and found that all neurons responded to AM and frequency modulation (FM), but that onset-type neurons showed a clear preference for AM signals. They also observed multiple-peaks in the temporal response patterns with up to four peaks at low modulation rates. In a study of AM responses in the IC of a bat, most neurons were found to have on-, off-, on-off- or chopper-response patterns (Lesser et al., 1986). Whereas all chopper neurons responded to AM, some of the other neurons with different response types failed to respond. This observation is further evidence for a possible role of chopper neurons in periodicity coding.

Fig. 9 represents three different response types found in the midbrain of the guinea fowl (Langner, 1983b). While some neurons may be described as on-type and display about one spike per modulation cycle (Fig. 9a), a second type is characterized by more or less obvious intrinsic oscillations triggered by each modulation cycle (Fig. 9b), and a third type shows intrinsic oscillations triggered at stimulus onset which change into phase-coupled responses (Fig. 9c). Under different stimulus conditions neurons may reveal more than one of these response types.

Periodicity maps

The central nucleus of the IC (ICC) of the cat has a well-defined tonotopic or cochleotopic organization (Merzenich and Reid, 1974). Neuronal laminae in the ICC may be anatomically defined (Rockel and Jones, 1973; Oliver and Morest, 1984). They are oriented approximately orthogonal to the main frequency gradient and were considered by some authors to represent so-called isofrequency planes. However, the ICC has only about 40 laminae, and consequently each lamina

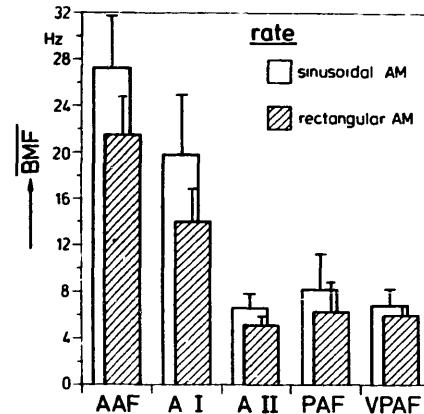


Fig. 11. Representation of periodicity in cortical fields. Averaged BMFs of the response synchronization to sinusoidal (open bars) and rectangular (shaded bars) AM in the auditory cortex of the cat. Error bars represent the standard error of the mean. From Schreiner and Urbas (1988).

has to cover a certain frequency range and thus the neurons in each lamina should have slightly different CF values. Accordingly, a three-dimensional reconstruction of CF values obtained in many parallel electrode tracks revealed a fine-structure of tonotopic organization in these 'frequency-band laminae'. In each functionally-defined lamina, CF increased over a small range of frequencies (about 1/6 of an octave) from medial to lateral and consequently orthogonal to the main frequency gradient of the ICC (Langner and Schreiner, 1987).

Tonotopic maps are examples of orderly topographic arrangements of information bearing signal parameters in the nervous system. By providing relative positions and continuous shifts of excitations, such neuronal maps may be useful for processing relations and variations in the corresponding signal space. Detailed studies in the auditory cortex of bats indicate the significance of the topographic representation of specific perceptual attributes (Suga and Manabe, 1982). Consequently, one may expect to find that the neuronal analysis or computation of periodicity within or prior to the IC results in an adequate topographic representation or computational map in this nucleus.

Therefore, in the IC of the cat, the spatial distribution of BMFs was examined not only within ranges with similar CFs (Schreiner and Langner, 1988a), but also within single 'frequency band laminae' (Langner and Schreiner, 1989). The BMFs encountered ranged from 10 Hz to 1000 Hz. Along an isofrequency-line of a given 'frequency-band lamina', BMF increased from about 20 Hz to $CF/4$ (CF below 4 kHz) with the highest BMFs located at the lateral border of the ICC. An example of an approximately orthogonal topographical representation of frequency and periodicity infor-

mation is given in Fig. 10. The frequency-band lamina of the cat represents the frequency range between 2.1 and 2.5 kHz (Fig. 10a), and the periodicity range between 20 Hz and 600 Hz. In addition, Fig. 10 gives an example of the periodotopic organization in the midbrain of guinea fowl, demonstrating again that the task of periodicity analysis may lead to similar processing strategies in different species (Albert et al., 1988; Langner et al., 1989).

Periodicity coding in the auditory thalamus

The auditory thalamus, that is the medial geniculate body in mammals (MGB) and the nucleus ovoidalis in birds, is often only considered as a 'relay station' between midbrain and forebrain (Adrian et al., 1966). This simple view and its relative inaccessibility has resulted in a paucity of studies on periodicity coding and other aspects of signal processing in this nucleus compared to other parts of the auditory system. Consequently, many questions remain open concerning the role of the MGB in the coding of complex signals and periodic modulations.

The capability of neurons in the MGB to encode temporal envelope fluctuations with synchronized discharges corresponds to its anatomical position between IC and auditory cortex (see Table I). Neurons in the MGB and in the auditory cortex of guinea pig that were synaptically linked and simultaneously recorded showed clear differences in their temporal selectivities, in spite of their direct connection (Creutzfeldt et al., 1980; Schreiner and Langner, 1988b). When using natural vocalizations as stimuli, neurons in the MGB could follow most of the amplitude fluctuations up to 150 Hz with high precision, whereas cortical neurons responded only to those modulations that were slower than about 6 Hz. This leads to the conclusion that, while cortical neurons essentially mark onsets of major segments, or transients, in acoustic signals, MGB neurons still respond to details in the signal fine structure. The fidelity of reproduction of the time course of modulation in the response pattern as often found in the peripheral auditory system seems also to degrade significantly at the MGB.

Synchronization of neurons in the MGB of the cat to repetitive clicks decreased with increasing rate, rarely exceeding rates higher than 300 Hz (Rouiller et al., 1981). Similarly, in the starling, phase-coupling of neuronal responses to amplitude modulation and frequency modulation was observed for modulation rates up to 160 Hz (Bigalke-Kunz et al., 1987). The majority of neurons in the MGB of the monkey were found to be sensitive to much lower modulation frequencies between 16 and 32 Hz (Müller-Preuss et al., 1988).

Periodicity coding in the auditory cortex

Synchronization

It has long been established that temporal properties of signals are important for neurons in the auditory cortex (AC), since their responses may depend on interstimulus interval (Abeles and Goldstein, 1972; Goldstein et al., 1959; Wollberg and Newman, 1972; Hocherman and Gilat, 1981). However, although the precision of spike timing, measured by the standard deviation of the first-spike latency, was found to be nearly as high as in the AN (Phillips and Hall, 1990), the ability of AC neurons to follow successive temporal changes in the input signal is significantly more limited than that found at more peripheral levels (see Table I) (Whitfield and Evans, 1965; Ribeau-pierre et al., 1972; Swarbrick and Whitfield, 1972; Goldstein and Abeles, 1975; Sovijärvi, 1975; Bock, 1976; Newman, 1979; Saitoh et al., 1981; Suga, 1984; Mendelson et al., 1985; Schreiner and Urbas, 1986). In a comparative study of neurons in the MGB and the AC of the guinea pig using AM and FM stimuli, cortical neurons could not be driven at modulation rates greater than 20 Hz (Creutzfeldt et al., 1980). In monkeys, neurons were found to be sensitive to modulation rates between 4 and 16 Hz and within an octave below the modulation sensitivity of neurons in the thalamus (Müller-Preuss et al., 1988). In other studies in the monkey, using human speech sounds as stimuli, 20% of cortical responses synchronized to the fundamental frequency of 100 Hz (Steinschneider et al., 1980, 1982). In the cat, a few units showed some degree of entrainment with click rates even up to 1000 Hz, although the vast majority had an upper limit of locking below 100 Hz (Ribeau-pierre et al., 1972). Finally, in the cortex analogue field L of unanaesthetized Mynah birds, the modulation frequencies that evoke a synchronized response may occasionally be much higher (see below) and the highest found was 500 Hz in a unit tuned to 380 Hz (Hose et al., 1987a). On the whole, it may be concluded that, at least in mammals, the majority of units in the cortex represent and process only relatively slow temporal modulations covering only the lower frequency range relevant for periodicity pitch (Schreiner and Urbas, 1986; Schreiner and Urbas, 1988; Schreiner and Langner, 1988b).

Fidelity and selectivity

As one moves up the neural pathways, the responses to complex signals become more and more difficult to predict on the basis of the neuronal responses to pure tones, and it appears that at the level of the cortex the 'principle of selectivity' becomes more important than the 'principle of fidelity' (Scheich et al., 1979; Langner

et al., 1981). The highest specialization for the reception and processing of species-specific sounds has been demonstrated in detailed studies of the cortex of echolocating bats (Suga, 1978; Suga et al., 1983; Suga and Tsuzuki, 1985). Whitfield (1957) described units in the AC of the awake cat which responded better to a frequency-modulated tone than to a pure tone within the frequency range of the modulation. Whitfield and Evans (1965) found that about 4% of investigated cells in the AC of the cat discharge to the ascending or to the descending portions only of a frequency-modulated signal. Also, some units were found to be selective for the direction of amplitude changes (Swarbrick and Whitfield, 1972). In addition, the ability to represent the course of rapid but infrequent changes in the spectrotemporal composition of the input signal (transients) appears to be well preserved in the spatiotemporal representation of the signal across the cortical field (Creutzfeldt et al., 1980; Schreiner and Langner, 1988b).

Phillips et al. (1989), investigated the effects of variations in repetition rate and amplitude of brief pulses at the neurons' CF on spike count, timing, and entrainment of cortex neurons in the cat. By normalizing the responses to the number of stimulus pulses they obtained low-pass sensitivity to repetition rate. Cells characterized by monotonic rate-intensity functions showed elevated response rates and extended performance to higher repetition rates with increasing stimulus level. Entrainment varied with stimulus repetition rate and the pattern of entrainment varied in a systematic way with signal amplitude.

Representation of periodicity information in different cortical fields

To gain a systematic overview of the cortical representation of temporal stimulus aspects, the response of multiunits to AM-signals has been investigated (Schreiner and Urbas, 1986, 1988; Schreiner and Langner, 1988b). For about 88% of 172 cortical locations, the MTFs had band-pass characteristics and the BMFs ranged from 3 to 100 Hz. The main finding was that different auditory cortical fields preferentially respond to significantly different frequency ranges of temporal variations (Fig. 11). This suggests field-specific functional roles of these cortical areas. The majority of BMFs in the second (AII), the posterior, and the ventroposterior auditory field were found to be equal to or below 10 Hz. The primary (AI) and the anterior field (AAF) showed higher temporal resolutions, with average BMFs of 15 and 28 Hz, respectively. In addition, within the AAF, the field with the highest temporal resolution, a gradient of BMFs across isofrequency lines was observed. In combination with results from cortical ablation studies, which showed a severe impairment of the discrimination of temporal signal prop-

erties such as duration and sequences of stimuli (Whitfield, 1971; Neff et al., 1975), these data suggest that the AC plays a major role in the coding and processing of sequences of short and relatively infrequent events in complex signals.

Since the temporal resolution for the majority of auditory cortical neurons is restricted to frequencies below 100 Hz (Goldstein et al., 1971; Ribeauville et al., 1972; Fastl et al., 1986), periodicities above 100 Hz have no temporal correlate in the cortex. At present it is not clear if periodicity-pitch information is adequately represented at this level of the auditory system. It may be encoded in the average discharge rates of the cortical neurons. However, a crucial role of the AC was suggested by behavioural experiments and bilateral ablation of the AC in two cats (Whitfield, 1980). The results indicated that cats without an AC respond only to individual frequencies of a complex tone and are unable to detect periodicity pitch.

Evidence for periodicity pitch representation at the level of the forebrain comes also from neuronal recordings in avians. In awake mynah birds, coding of AM-signals was studied within isofrequency planes of field L, the avian analogue of the mammalian AC (Hose et al., 1987a). Most of the units which synchronized their discharges to the signals were tuned to a BMF between 1 and 380 Hz. The majority of these units had BMFs in the rhythm range below 20 Hz, but a third had BMFs above 20 Hz, which lies in the perceptual range for roughness and periodicity pitch. In addition, it was found that periodicity is represented in an orderly fashion within isofrequency planes with the highest BMFs at the caudal border of the planes (Hose et al., 1987b; Scheich, 1991).

Theories of periodicity analysis

Spectral theories

A major task of theories of brain function is to explain perception on the basis of neuronal mechanisms. Although our knowledge about the neuronal processing of periodicity information at various levels of the auditory system has definitely improved, there is still no generally-accepted theory which explains why acoustic signals with particular envelope periodicities evoke the perception of periodicity pitch.

In the past, two types of models, temporal and spectral, were proposed to explain this perception and the phenomenon of the 'missing fundamental'. Walliser (1969) suggested a combination of periodicity and spectral analysis and Whitfield (1970a) was the first to suggest a purely spectral type of pattern model. All versions of these models include a neural representation of a highly resolved spectrum of periodic signals ('central spectrum') (Terhardt, 1972; Goldstein, 1973;

Wightman, 1973; Srulovicz and Goldstein, 1983; Terhardt and Grubert, 1987). A neuronal pattern analysis of this spectrum yields the best fitting fundamental frequency and the percept of periodicity pitch. This pattern-model approach was very successful in predicting the pitch of AM signals in the pitch range characterized by low resolved harmonics.

However, the model cannot explain why harmonics around the fourth give the strongest percept, although lower harmonics are even better resolved. In addition, psychophysical experiments with high-pass filtered pulse trains (clicks) showed that, in contrast to the general view, periodicity pitch can also be conveyed by high-order harmonics that the cochlea fails to resolve (Long and Cullen, 1983). In accordance, melodic interval identification remains possible even for the 20th to 30th harmonic (Houtsma and Smurzynski, 1990) and experiments with repetitive tone-bursts indicate that, at least for low repetition rate (< 250 Hz), pitch matching depends only on the repetition of the time waveform (Pierce, 1991). A major drawback of pattern-models is that the physiological mechanism underlying the pattern analysis has not been detailed or identified (Javel and Mott, 1988), while the fact that neurons in the auditory system encode envelopes in the temporal domain is ignored. Javel and Mott (1988), in a recent account of physiological and psychophysical correlates of temporal processes, presented a spectral model based on excitation patterns across the cat AN fiber population. Considering tasks like frequency discrimination, they concluded that it requires unrealistic or undemonstrated physiological mechanisms for rate-place or pattern matching schemes in order to perform as well as models assuming central auditory processing of phase-locked neural activity. For a further discussion of the subject see, for example, Moore (1982).

Temporal theories

The debate about temporal mechanisms of pitch perception dates back to the nineteenth century, when Seebeck unsuccessfully tried to convince Ohm and von Helmholtz of temporal aspects in auditory processing of sounds of sirens. Rutherford believed that the function of the ear is similar to telephone transmission with the cochlea acting as a microphone, and Wundt suggested that tones give rise to synchronous nerve impulses whose rate determines pitch (Seebeck, 1843; Ohm, 1843; von Békésy, 1928; von Helmholtz, 1863; Rutherford, 1886; Wundt, 1880).

When modern sound equipment became available, Schouten (1940c) was able to demonstrate that Seebeck's observations were not artefacts caused by nonlinear distortion products. At the same time, he discovered that envelope periodicity may not be sufficient for the prediction of periodicity pitch of AM signals and that the carrier frequency also played an important

role. Changing the carrier frequency results in definite pitch changes, the so-called 'first and second effect of pitch shift', even when the envelope period is kept constant (Ritsma, 1970). Various temporal models of pitch perception or periodicity analysis were offered subsequently (Licklider, 1951, 1954; Schief, 1963; Whitfield, 1970b; Langner, 1981; Loeb et al., 1983; Sachs et al., 1988).

In Licklider's 'duplex theory of pitch perception', the frequency analysis of the cochlea is followed by a temporal correlation analysis. In this model, neural discharges generated by an incoming waveform are fed to a processing neuron (coincidence neuron) via two pathways: the first direct, and the second through an indirect path via a chain of neurons which introduce a time delay T due to synaptic transmission times. The coincidence neuron fires when both inputs are active at the same time, that is, when incoming spikes coincide. When the input signal is periodic and has the repetition time T , coincidence may occur in each period of the signal.

Whitfield (1970b) discussed several possibilities of how the auditory system might measure periods. He argued that delay mechanisms like those proposed by Licklider are unlikely since synaptic transmission time may be too variable and axonal delays, although probably important for interaural time measurements, may hardly be great enough to accommodate periods as long as 10 ms. He put forward a clock-like mechanism where the periods of the stimulus are compared with the regular pulses from a neuronal 'clock' or oscillator.

Van Stokkum (1988, 1989, van Stokkum and Gielen, 1989) proposed a structural model which is able to reproduce monaural response properties of brainstem and midbrain neurons in the frog, including modulation transfer characteristics. In addition to the usual peripheral coding mechanisms, it includes short-term adaptation, event generation with refractory properties, coincidence detection in second order neurons and temporal integration in third order neurons. The coincidence mechanism modelled the sensitivity of a group of peripheral neurons for fast intensity changes.

Neuronal mechanisms like coincidence effects, time constants of membranes, and temporal integration appear to be essential for explaining neuronal selectivity for periodic amplitude modulations (Langner, 1988; van Stokkum, 1989). In addition, certain psychophysical phenomena such as the effect of 'pitch shift' indicate a specific role of the temporal fine-structure of the signal waveform for the detection of periodic signals. It was therefore suggested that pitch and time interval between the peaks of the acoustic waveform should be compared (de Boer, 1956; Schouten et al., 1962). This 'fine-structure' theory proved to be inadequate, however, since its predictions did not fit the observed shifts. Furthermore, pitch perception is insen-

sitive to the phase of the signal components, in contrast to the signal fine-structure (Smoorenburg, 1970; Javel and Mott, 1988). Another observation is that in some subjects pitch is not a continuous function of carrier frequency, but shows stepwise changes where the step size is often 0.4 ms (Langner, 1981).

A coincidence model

In an attempt to explain pitch perception on the basis of verifiable physiological findings, a coincidence model was proposed. This model performs a correlation between signal fine-structure and envelope (Langner, 1981, 1983c). The model was also required to provide an explanation of why the periodicity pitch of AM signals as well as the responses of neurons in the midbrain to such signals depend both on the carrier and the modulation frequency (Langner, 1983b; Langner and Schreiner, 1988).

The basic parts of the model are a trigger unit, an oscillator, a reducer circuit, and a coincidence unit. The trigger unit is activated by each cycle of the modulation and synchronizes the other components of the model. The oscillator output provides several spikes with regular interspike intervals in response to each cycle of the modulation. It was found that in the midbrain units, spike intervals may group around multiples of 0.4 ms (Langner, 1983b). A possible explanation for this preference is that synaptic delays contribute to the oscillation periods. Synaptic delays of 0.4 ms have been demonstrated in the brainstem of several species (Bishop, 1953; Clark and Dunlop, 1968; Hackett et al., 1982). In the model, oscillatory responses to the envelope are used as temporal reference or delays for a correlation analysis.

The reducer circuit receives input from the AN and performs a triggered integration. It synchronizes to the signal envelope, and, as a result of phase coupling to the carrier frequency or signal fine-structure, it generates action potentials with phase delays equal to an integer multiple of the carrier period (for carrier frequencies < 5 kHz). This function makes use of the volley principle assuming a parallel coding of several nerve fibers which results in an adequate temporal representation of frequencies even above 1 kHz (Wever, 1949). Finally, coincidence units receive inputs from the oscillator and the reducer circuit.

The model explains how the neuronal responses vary with modulation and carrier frequency and makes detailed predictions about the temporal patterns of responses and of the pitch shift effect. For example, BMFs of the coincidence units depend on the phase delay of the reducer and thereby on the carrier period. These may be computed from a linear combination of the involved signal periods (periodicity equation) (Langner, 1985). Provided the auditory system in humans performs such a temporal correlation analysis,

this may explain the effects of pitch shift and also of pitch jumps when the correlation analysis also includes oscillation intervals that are multiples of 0.4 ms. Synchronized oscillations may be important, for example, for the detection of common periodicities in different formants of vowel sounds. In visual feature detection, a similar role was suggested for oscillations observed in the visual cortex (Eckhorn et al., 1988; Gray et al., 1989).

The model was simulated on a computer and reproduced transient and steady-state responses of coincidence units faithfully (Langner et al., 1987). For example, as a result of adaptation in the simulated auditory nerve, the response of the reducer circuit shifts in phase and the coincidence neurons transform the temporal variation of phase differences at their input into temporal variations of their activity. The same effect has been frequently observed in neurons of the bird auditory midbrain (see Fig. 9c). Moreover, in order to obtain this result, all input units of the coincidence unit in the model required response properties similar to actual neuron types (on-type, chopper, and pauser) of the CN (Langner, 1988).

In summary, neuronal models incorporating temporal response properties of auditory neurons may be adequate to explain certain aspects of periodicity processing and also of pitch perception. This suggests that periodicity pitch is based on temporal processing mechanisms and should be considered as a perceptual attribute of neuronal mechanisms involved in the basic tasks of auditory signal detection.

Conclusions

- Periodic envelope fluctuations of up to 1000 Hz are coded and analyzed in the auditory system.
- Auditory-nerve fibers code signal envelopes and are characterized by low-pass filters with a maximal cutoff-frequency of about 800 Hz.
- In the cochlear nucleus, signal envelopes are faithfully reproduced by various neuron types with different signal aspect emphasis. Synchronization of several unit types is even better than in the nerve. The MTFs generally reveal band-pass characteristics and in most cases temporal selectivity is not apparent in the firing rate.
- Although some units in the auditory midbrain may synchronize very well to envelope frequencies of up to 1000 Hz, temporal selectivity, often with band-pass characteristic, is most obvious in the rate code. The auditory midbrain is distinguished by a periodotopic organization roughly orthogonal to its tonotopic organization. Temporal processing mechanisms together with the periodotopy may help to understand various effects related to periodicity pitch.

- Although at the level of the auditory cortex some neurons synchronize even to very high stimulus repetition rates, most neurons follow only slow rates below about 100 Hz. Different cortical fields show different temporal selectivities. The cortex is capable of processing rhythm-like envelope fluctuations. However, the question of how periodicities eliciting periodicity pitch are represented and processed at this level of the auditory system and also the role of some other auditory processing centres, like the olfactory nuclei or the MGB, is relatively unclear and awaits further investigation.

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