

Gap detection in the European starling (*Sturnus vulgaris*). III. Processing in the peripheral auditory system

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Summary. Gap-detection thresholds were determined for single units in the cochlear ganglion and in auditory nerve fibres of the starling from responses to two broadband noise bursts separated by a temporal gap of between 0.4 and 204.8 ms. All 35 units showed a threshold within the range of gap sizes tested. The median minimum-detectable gap was 12.8 ms with the minimum being 1.6 ms. A multiple regression analysis revealed that the size of the minimum-detectable gap was not significantly correlated with the neuron's CF, with its sharpness of tuning as given by its bandwidth 10 dB above threshold, or with its $Q_{10\text{dB}}$ value. Only the level of stimulation above the neuron's threshold showed a significant negative correlation with the size of the minimum-detectable gap. These results are discussed with respect to theoretical considerations of limits posed on temporal resolution by the characteristics of peripheral filters. These findings are also discussed in the context of the coding of gaps at different levels of the starling's auditory system and in relation to psychoacoustic results in the starling on gap detection and time resolution described by temporal modulation transfer functions.

Key words: Bird – Hearing – Auditory nerve – Temporal resolution – Gap detection

Introduction

Temporal resolution in auditory systems has been studied mainly with two experimental paradigms: the detection of sinusoidal amplitude modulations and the detection of single temporal gaps in broadband noise. Green and Forrest (1988) modified a model previously described by Viemeister (1979) to fit human psychoacous-

tic data for the detection of temporal gaps and sinusoidal amplitude modulations. This model is composed of a bandpass filter followed by a half-wave rectifier and a lowpass filter. The output of the lowpass filter is monitored by a detection mechanism comparing minimum and maximum amplitude values in a specific time window. Although their model fits the human psychoacoustic data extremely well, it is not based directly on physiological evidence on frequency and time resolution in the auditory periphery. Animal models in which both the psychoacoustics and the neuronal coding of temporal patterns in broadband noise is studied may provide us with direct evidence on the relationship between neuronal coding in the auditory periphery implicit in the models of temporal perception and the psychoacoustics of temporal resolution.

The European starling (*Sturnus vulgaris*) is one of the few experimental animals in which time resolution phenomena relevant for gap detection have been studied both psychoacoustically (Klump and Maier 1989) and neurophysiologically (Buchfellner et al. 1989) using experimental paradigms comparable to those used in the study of temporal pattern perception in humans. This study provides information concerning the peripheral coding of temporal gaps in broadband noise and discusses the results with respect to central coding of the same stimulus in the starling's auditory forebrain areas and to the psychoacoustics of gap detection.

The relation between gap thresholds measured psychoacoustically and the peripheral coding of temporal gaps in broadband noise has been studied so far in 3 other animal species: an acridid grasshopper (*Chortippus biguttulus*, von Helversen 1972; Ronacher and Römer 1985), the goldfish (*Carassius auratus*, Fay 1985), and the Chinchilla (*Chinchilla laniger*, e.g. Giraudi et al. 1980; Zhang et al. 1990). The present experiments extend these observations to birds. An interspecific comparison should reveal to what extent common mechanisms may be operating in the perception of rapid fluctuations of the signal envelope.

Psychoacoustic studies on gap detection in humans

Abbreviations: CF characteristic frequency; TW time window; $Q_{10\text{dB}}$ the unit's characteristic frequency divided by the bandwidth 10 dB above threshold

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(Shailer and Moore 1983), chinchilla (*Chinchilla laniger*, Salvi and Arehole 1985), and in budgerigars and zebra finches (*Melospittacus undulatus*, *Poephila guttata*, Okanoya and Dooling 1990) have shown that time resolution varies with the spectral range of the signal containing the gap. With the exception of the results from budgerigars (Okanoya and Dooling 1990), there is an inverse relationship between the size of the minimum detectable gap and the animal's critical bandwidth in the spectral range of the signal containing the temporal information. This suggests that the duration of the temporal response of the peripheral filters is responsible for the frequency-dependence of temporal resolution. We studied this question in the starling's peripheral neurons by comparing the neuron's tuning characteristic with the size of its minimum detectable gap.

Materials and methods

Preparation and recording procedure. Experiments described here were performed on 9 wild caught European starlings (*Sturnus vulgaris*), weighing between 70 and 90 g. The preparation for recording from primary auditory afferents in the starling has been described in detail (Manley et al. 1985) and is briefly summarized as follows. The birds were anaesthetized with an initial dose of Pentobarbital-Na (90 mg/kg body weight). Deep anaesthesia was maintained during the experiments by supplementary doses when a heart rate increase or when skeleton-muscle activity was observed in the electrocardiogram. The birds were artificially respired and the core temperature kept at 40 ± 1 °C with a regulated heating-pad.

We used two approaches to record primary auditory afferents. In a first series of experiments, neurons ($n=10$) were recorded from the cochlear ganglion which was accessed via a dorsolateral approach through an opening in the recessus scalae tympani. In a second series of experiments, recordings were obtained from the primary auditory fibres of the VIIIth nerve ($n=25$) without opening the cochlea. The course of primary auditory-nerve fibres between the foramen, where they entered the brain stem, and the Nucleus magnocellularis became accessible for electrode penetrations after removing the bone overlying the cerebellum and aspiration of the cerebellum. After surgery, glass micro-electrodes filled with 3 M KCl and having resistances of 30–80 M Ω were located close to the ganglion or the nerve, then the birds were placed in an electrically-shielded sound-proof room. To record the neuronal response electrodes were advanced into the ganglion or the nerve using a hydraulic drive.

Sound system. Acoustic stimuli were presented via a closed sound system which was fit tightly into the outer ear canal of the bird. The sound system consisted of a speaker (AKG DKK 32) and a calibrated measuring microphone (Brüel & Kjaer 4133) for monitoring the stimulus near the ear drum. The output of the sound system was flat within ± 3 dB in a frequency range between 0.05 and 4 kHz. Tones were generated by a Wavetek-Rockland model 5100 frequency synthesizer; noise stimuli were presented from a prerecorded tape (TEAC 2340SX, tape speed 19 cm/s).

Analysis of a fiber's response to tones. Upon encountering a nerve fibre, the response to a matrix of tone bursts (100 ms, 2.5 ms rise and fall time, rate 4/s) covering a range of frequencies (3 octaves in 0.2 octave steps) around the characteristic frequency (CF, frequency of highest sensitivity) and sound pressure levels (generally between 10 and 90 dB SPL varying in 4 dB steps) were measured using an automated procedure. Each combination of frequency and sound pressure was presented twice. Iso-rate contours were calculated from the responses to the tone bursts of the test matrix.

By increasing the rate criterion above spontaneous rate the first 'smooth' iso-rate curve (generally 40% above the spontaneous activity) was taken as the tuning curve (Gleich and Narins 1988). The CF, the threshold at CF, the bandwidth 10 dB above CF-threshold, and the Q_{10dB} value (CF/bandwidth) were determined from the tuning curves.

Analysis of a fiber's response to noise stimuli with gaps. Next, the neuron's response to a series of broadband noise stimuli with gaps of various sizes was recorded. The gap-stimuli were composed of two bursts of digitally-generated frozen Gaussian noise (i.e. always generated from the same time series of amplitude values), a leading burst of 800 ms (8 ms rise time at the beginning only) and a trailing burst of 100 ms (8 ms fall time at the end only) separated by a gap (for more details on stimulus generation see Klump and Maier 1989). Rise and fall times at the gap were less than 150 μ s. The gap stimuli were presented in a series starting with a gap size of 0.4 ms and doubling the gap-size with each new stimulus in the series up to 204.8 ms. A control stimulus that was composed of the two noise bursts, but without a gap between, was presented as the first stimulus of a gap series. The stimuli were repeated at a rate of one gap stimulus per 2.7 s. The whole series was repeated between 8 and 15 times. Sound-pressure levels between 30 and 87 dB SPL were used. Some neurons were tested at more than one SPL.

The statistical analysis of the response followed the procedure given in Buchfellner et al. (1989) for the same stimulus series. Briefly, spikes were counted in two types of time windows (TW), one starting at the end of the leading noise burst to measure the neuron's OFF-response (Constant TW, durations were 5, 10, 15, 30 ms), and the other starting at the beginning of the trailing noise burst to measure the neuron's ON-response (Variable TW, durations were 5, 10, 15, 30, 100 ms). The starting points of both types of TWs were adjusted for the neuron's latency of the response. The neuronal activity in the corresponding TWs for the stimulus without a gap was used as the control.

The minimum-detectable gap was determined as follows: if the activity in the corresponding TWs of the 11 different gap stimuli was not uniformly distributed (KS-test), the TWs with spike numbers that differed significantly from the number in response to the control stimulus (no gap) were determined using a binomial test. The smallest gap duration for which the activity significantly ($P_2 < 0.05$) differed between gap stimulus and control was defined as the unit's threshold for the corresponding TW. Additionally, the response to the next larger gap also had to show a significant deviation from the control. The minimum-detectable gap was finally defined as the minimum gap threshold of all TWs.

General data analysis. All P -values given are two-tailed. Gap durations were log-transformed before statistical analysis, to ensure a Gaussian distribution of minimum-detectable gaps. Correlation coefficients are Pearson's r or the multivariate correlation coefficient R . All correlations and their P -values given in the text are based on one data-point per neuron at the sound-pressure level that was within a range of SPLs where in the study of behavioural gap thresholds no effect of SPL was found (Klump and Maier 1989). Additionally, this SPL was also the nearest to the one used in the gap-detection study of forebrain neurons (Buchfellner et al. 1989).

Results

Sufficient data for analysis of both tuning and temporal coding were obtained from 35 primary auditory afferents. Ten units were recorded in the cochlear ganglion and 25 in the VIIIth nerve. Response characteristics from units recorded under these two conditions were not different; however, units with higher CFs were more easily

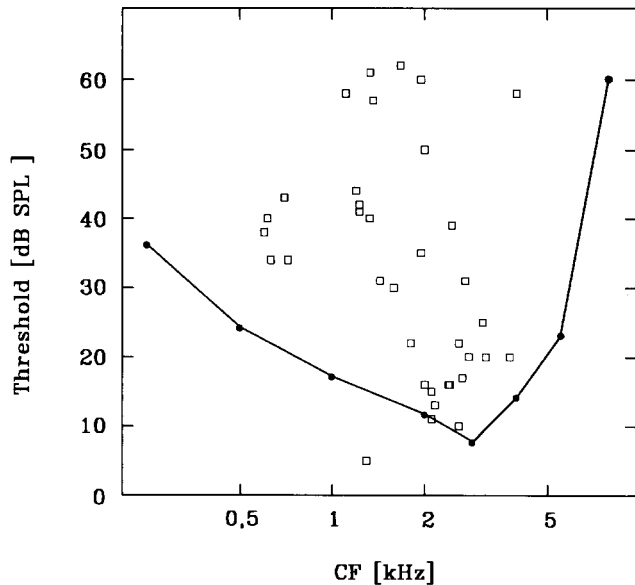


Fig. 1. Thresholds of single units at CF in the auditory periphery of the starling and their relation to the starling's behavioural threshold curve (Dooling et al. 1986)

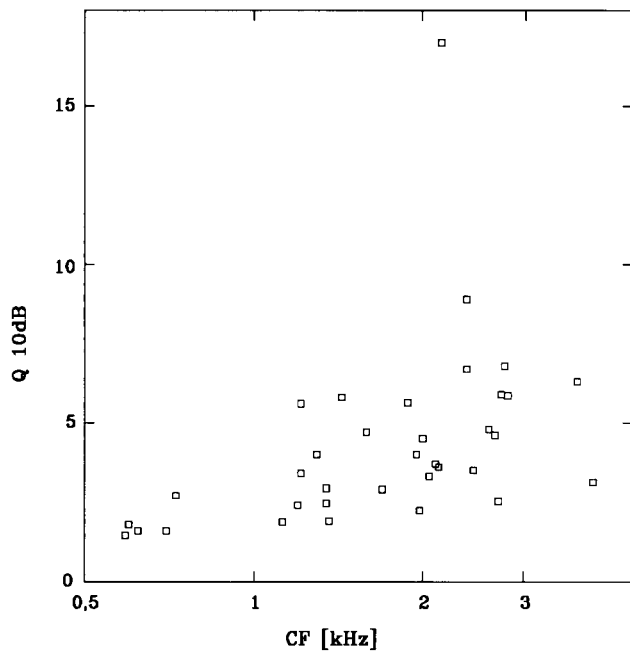


Fig. 2. Relationship between the CF and the Q_{10dB} of single units in the starling's auditory periphery

accessible with the brain-stem approach than with ganglion recordings (Manley et al. 1985).

CFs, tuning and thresholds

The neuron's CFs ranged from 0.6 to 4 kHz. The lowest threshold was 5 dB SPL at a CF of 1.3 kHz (Fig. 1), and no threshold at CF was higher than 62 dB. The lowest thresholds of neurons in this study are close to the behavioural absolute threshold curves of the starling

(Fig. 1). The units' spontaneous discharge rates ranged from 1.9 to 101.3 spikes s^{-1} (mean 28.9 spikes s^{-1}). The sharpness of tuning as measured by the Q_{10dB} showed the same average increase with CF (Fig. 2, $r=0.402$, $P<0.02$) as has been shown before in the starling by Manley et al. (1985). The range of Q_{10dB} values was 1.45 to 17.

The neurons' coding of gaps

A minimum-detectable gap could be determined in all of the neurons within the range of gap durations tested (0.4 to 204.8 ms; in one neuron a minimum-detectable

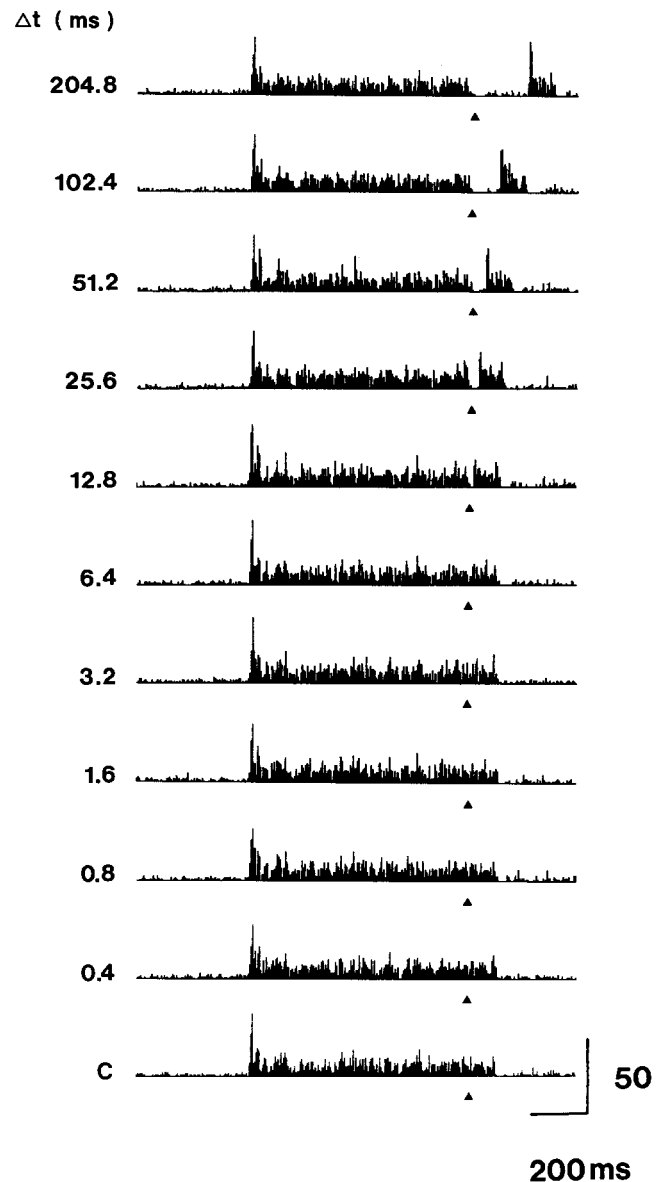


Fig. 3. An example of the coding of gaps by an 8th nerve fibre (the peri-stimulus time histograms have a bin-width of 10 ms; the arrow indicates where the gap starts). Gaps can be coded either by response decrement at the end of the leading noise burst (from 12.8 ms gap size on in this recording), or by the ON-excitation at the beginning of the noise burst trailing the gap (the phasic response component is detectable at a gap size of 25.6 ms and above)

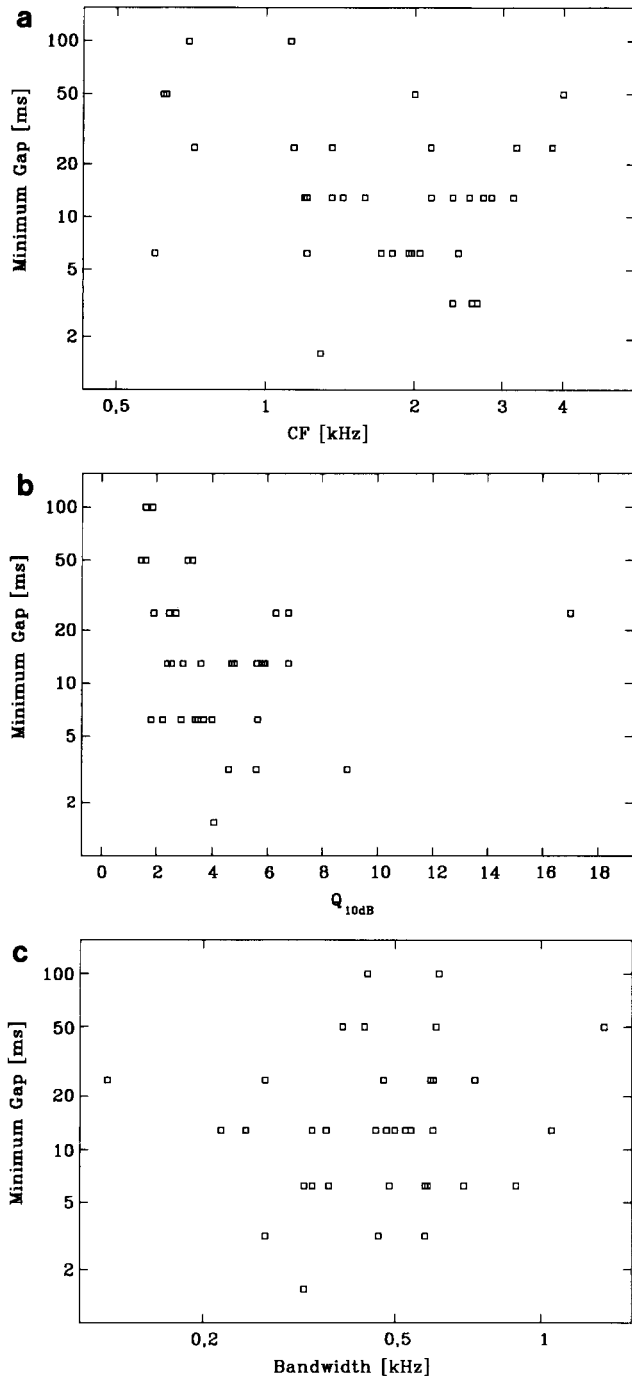


Fig. 4a-c. Size of the minimum-detectable gap in relation to neuronal tuning: **a** minimum-detectable gap vs. CF; **b** minimum-detectable gap vs. Q_{10dB} ; **c** minimum-detectable gap vs. bandwidth 10 dB above threshold at CF

gap could not be determined at a stimulus level of 60 dB SPL, but it was measured at both 75 and 87 dB SPL). If a gap threshold could be determined for a constant TW, it resulted in all cases from the reduction in spike-rate at the end of the leading noise burst. If a gap threshold could be determined for variable TW, it resulted in all cases from an ON-excitation triggered by the beginning of the trailing noise burst (for an example of a neuron that shows both decrement in spike rate and

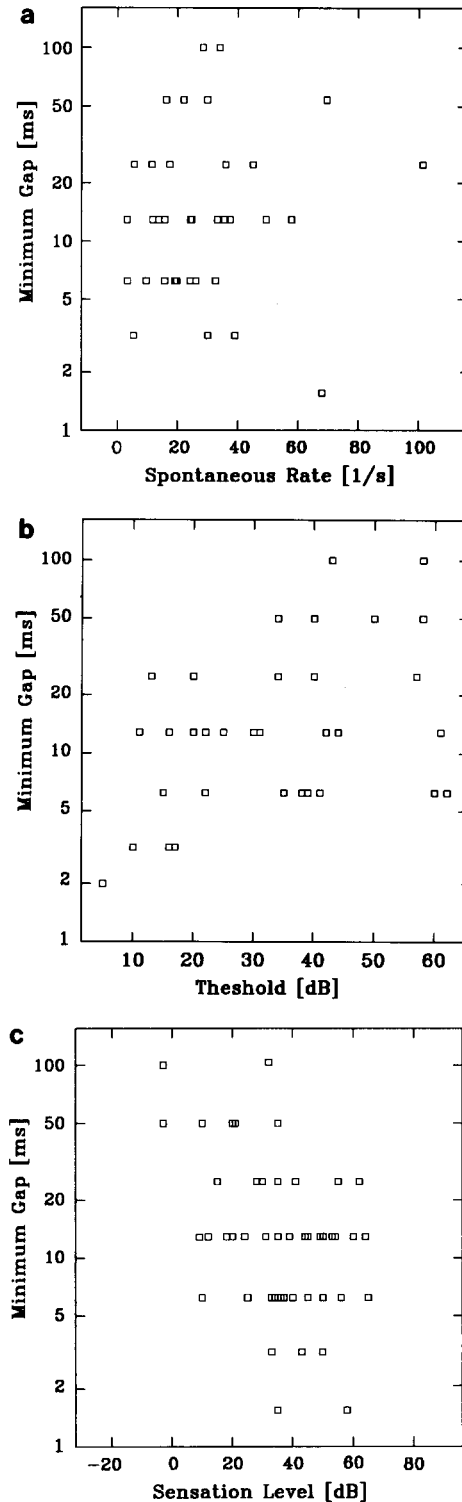


Fig. 5a-c. Size of the minimum-detectable gap in relation to the neuron's activity patterns: **a** minimum-detectable gap vs. spontaneous rate; **b** minimum-detectable gap vs. neuronal threshold at CF; **c** minimum-detectable gap vs. level of stimulation above the neuronal threshold (data points in this figure also include repeat measurements of the same fibres at different SPL of the stimulus)

ON-excitation, see Fig. 3). The minimum-detectable gap resulted significantly more often from gap thresholds defined by reduced spike-rates (66% of all measurements) than by gap thresholds defined by ON-excita-

tions (20% of all measurements). In only 14% of all measurements did ON- and OFF-responses result in the same gap threshold.

A stepwise multiple regression analysis of the influence of spontaneous rate, absolute threshold, sound pressure level of stimulation relative to threshold ('sensation level'), CF, and $Q_{10\text{dB}}$ on the minimum-detectable gap revealed that the most important factor determining the minimum-detectable gap is the sound-pressure level of stimulation relative to the neuron's threshold (partial correlation coefficient = -0.39 , $P < 0.05$, $n = 35$ neurons). None of the other variables showed a significant influence on the minimum-detectable gap in this analysis. Replacing the $Q_{10\text{dB}}$ with the bandwidth in kHz 10 dB above threshold at CF did not yield different results.

None of the bivariate relationships between the independent variables used in the multiple regression analysis describing the tuning of the neuron and the minimum-detectable gap lead to a significant correlation (Fig. 4). Both the neuron's threshold and its 'sensation level' show a significant correlation with the minimum detectable gap (Fig. 5). However, the multivariate correlation coefficient shows that the neuron's thresholds by themselves do not influence time resolution, and that the significant bivariate relationship is the result of a correlation between the neuron's thresholds and the 'sensation levels' of the presentation of the sound.

Discussion

The relationship between temporal resolution and tuning in peripheral neurons

In general, there is a trade-off in signal-analysis systems between resolution in the frequency domain and the time domain. Because filters with small bandwidths that are needed for good frequency resolution have longer time constants than filters with large bandwidths, time resolution is inversely related to frequency resolution. Therefore, we would expect a negative correlation between the bandwidth of a neuron 10 dB above threshold and its minimum-detectable gap (which can be considered as a measure of a neuron's time resolution). By similar argument, a positive correlation between the sharpness of tuning measured by a neuron's $Q_{10\text{dB}}$ and its minimum detectable gap is to be expected. We found neither correlation in our study, and furthermore the signs of the non-significant correlation coefficients that we report here are not consistent with the theoretical expectation.

Viemeister (1979) proposed a model consisting of a bandpass filter followed by a half-wave rectifier and a lowpass filter to explain human psychophysical data on temporal resolution. The output of this model was monitored by a decision mechanism analyzing the variance to detect changes in the amplitude of a broadband noise signal passed through the model. Green and Forrest (1988) used the same model, but with a different decision mechanism (i.e. a detector performing a comparison of

the maximum and the minimum amplitude within a certain time window), to explain human gap detection and temporal modulation transfer function data. Their criteria were equivalent to those used in our single cell study on gap detection. For a bandwidth of 4000 Hz for the bandpass filter and a time constant of 3 ms for the lowpass filter, their model resulted in a good fit to the measured human gap detection and modulation transfer function data. The bandwidth of 400 Hz and above and the time constants between 1.5 and 12 ms used in their simulations and model resulted in a weaker influence of bandwidth on temporal resolution than would be expected using a simple inverse relation between bandwidth and time resolution (de Boer 1985). This is in accord with our findings on the starling's peripheral neurons ability to detect gaps. As Patterson (1988) pointed out, however, the bandwidth necessary to give a good fit to the psychoacoustic data using Green's and Forrest's model does not reflect the bandwidth of the human's peripheral auditory filters (already Viemeister 1979 discussed this discrepancy for his formulation of the model). Also the starling's peripheral neurons show bandwidths which in general are an order of magnitude smaller than those assumed for the models discussed above (Manley et al. 1985; this study).

Klump and Maier (1989) estimated the starling's peripheral time constants using data from Manley et al. (1985) on peripheral tuning and de Boer's (1985) theoretical estimate of the time constant of peripheral auditory filters. They conclude that in the starling's peripheral auditory system time constants may only be limiting for time resolution at frequencies below 1 to 2 kHz. However, considering only the bandwidth as an effector of temporal resolution is probably too simplistic. The work by de Boer (1985) and de Boer and Kruidenier (1990) indicate that the temporal resolution decreases with increasing order of a filter for a given bandwidth. The high- and low-frequency slopes of tuning curves from starling auditory afferents that can exceed 200 dB/octave (Manley et al. 1985) are obviously the result of complicated higher order filter systems and thus their temporal resolution tends to be overestimated if it is only based on filter bandwidth. Furthermore, the large variability of tuning curve slopes and the increase in the tuning curve slopes with increasing CF (Manley et al. 1985) will lead to a large variation in the unit's time constants and may thus obscure a relationship between bandwidth and minimum detectable gap. Since it was suggested that the tuning mechanisms in the starling cochlea differs for low (< 1 kHz) compared to high (> 1 kHz) CF-regions (Gleich 1989; Manley 1986), a resolution of this issue requires a large amount of data from a restricted frequency region which currently is not available. In contrast to our results in the starling, Dunia and Narins (1989), report a correlation between the minimum time constant measured for phase locking to the sinusoidal amplitude modulations of a broadband carrier and $Q_{10\text{dB}}$ for frog auditory afferents. However, this correlation was quite weak and accounts for only 5% of the variance in the minimum integration time.

Apparently conflicting psychophysical results be-

tween a measure of frequency selectivity (i.e. critical bandwidth) and a measure of temporal resolution (i.e. gap-detection threshold for bandlimited signals) have been described in the budgerigar (Okanoya and Dooling 1990). In this species temporal resolution does not correlate with predictions generated from the measures of frequency resolution. At 3 kHz, where frequency selectivity is very high, the minimum detectable gap is about 3 ms, although even conservative estimates would predict values above 5 ms (Okanoya and Dooling 1990; de Boer 1985). This discrepancy might be explained, however, if the budgerigar's auditory afferents show similar variability in tuning as reported for other birds and use different subpopulations of neurons for different tasks.

The relationship between temporal resolution and the neuron's activity pattern

Peripheral neurons in the starling show no correlation between their spontaneous discharge rate and the absolute threshold at the neuron's CF (Manley et al. 1985; this study). Similarly, the precision of the coding of time patterns seems not to correlate with the neuron's spontaneous rate (see Fig. 5a). This suggests that neither the factors responsible for the variation in spontaneous activity nor the spontaneous activity itself influence the coding of stimulus intensity or its changes. In the starling's forebrain, however, Buchfellner (1987) described a correlation between the size of the minimum-detectable gap and the spontaneous activity. The mean spontaneous activity of the neurons in her study, which also in-

cluded different response types other than primary-like, was only half than that found in the auditory periphery of the starling; and the neurons coding the shortest gaps had an average spontaneous activity that was similar to the average spontaneous activity of the starling's peripheral neurons.

The factors influencing the driven activity of a starling's peripheral neuron, or the driven activity itself, seem to have an impact on the neuron's ability to code rapid changes in stimulus intensity with time (i.e. such as short gaps). The threshold at CF itself and the level of stimulation above the neuron's threshold seem to correlate with the size of the minimum-detectable gap. However, a multiple regression analysis revealed that the level of stimulation correlates better than the threshold itself (which by definition is correlated with the level of stimulation). If the effect of level of stimulation is removed from the regression equation, the threshold at the CF itself no longer correlates with the minimum detectable gap. This result is comparable to findings of Smith (1977, 1979) and by Harris and Dallos (1979) who studied neural adaptation and its effect on forward masking in the auditory nerve of the Mongolian gerbil (*Meriones unguiculatus*) and the Chinchilla (*Chinchilla laniger*). Smith (1979) suggests that the strength of a neuron's response during the stimuli is a very strong determinant of its response towards a probe stimulus presented following a silent gap after a masker in a forward-masking paradigm. Furthermore, the decrement in spike-rate after the offset of a stimulus depends on the activity elicited by it. Since both the decrement and ON-activation are the two responses by which a gap is coded, the effects of stimulus level that influence the amount of forward masking will also influence gap-detection by peripheral neurons.

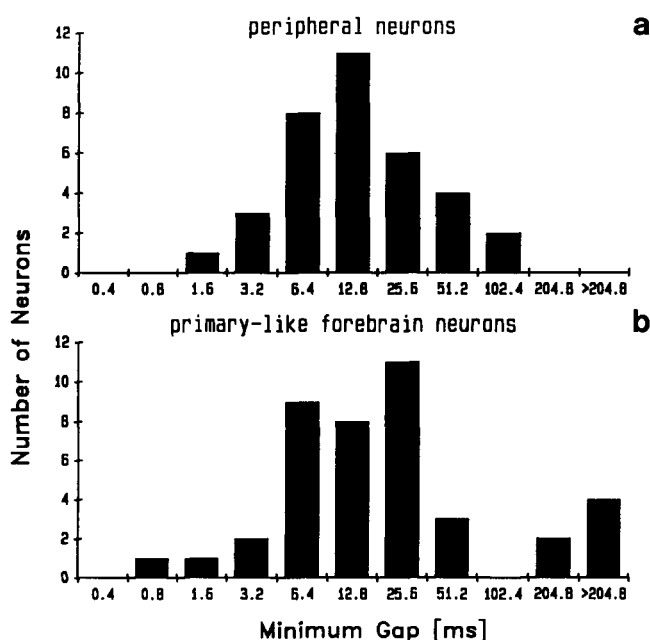


Fig. 6a, b. Distribution of minimum-detectable gaps in the periphery of the auditory system (a) and of minimum-detectable gaps in primary-like neurons in the starling's auditory forebrain (b, data from Buchfellner 1987)

Temporal resolution of neurons at different levels of the starling's auditory system and the psychophysics of gap detection

Both in the starling (forebrain neurons, Buchfellner et al. 1989) and in the acridid grasshopper (interneuron AN4, Ronacher and Stumpner 1988) the time resolution provided by the peripheral auditory system is preserved in the auditory pathway (see peripheral and central distribution of minimum detectable gaps in Fig. 6). The median minimum-detectable gap of primary-like neurons in the starling's auditory forebrain (12.8 ms for stimuli with a sound pressure level of 55 dB SPL) is equal to the median minimum-detectable gap found in primary fibres in the peripheral auditory system for sound pressure levels of 55 to 70 dB SPL. Thus, integration of temporal information across many neurons in the auditory pathway is not needed to achieve the high temporal resolution found in a recent behavioural study (the psychoacoustic measure of the minimum-detectable gap was 1.8 ms; Klump and Maier 1989). The peripheral neurons with the lowest gap detection thresholds (below 6.4 ms) would adequately transmit the information on the temporal pattern with a resolution necessary to account for

the psychoacoustic thresholds. The effect of sensation level on the size of the minimum-detectable gap in the psychoacoustic study is paralleled by our finding that the amount of stimulation relative to a peripheral neuron's threshold (i.e. the neuron's 'sensation level') is a determinant of the ability to detect short gaps.

The fact that in the starling's peripheral neurons a decrease in spike rate is a better indicator of the presence of a gap, whereas in the starling's auditory forebrain an ON-response elicited by the noise burst following the gap is the better indicator of a gap suggests that there may be a change in the neuronal encoding of temporal patterns between the peripheral and the central auditory system. It has been shown in studies on the encoding of sinusoidal amplitude modulation in toads (Rose and Capranica 1985) and mammals (see review in Rees and Palmer 1989) that in the peripheral auditory system, a synchronization pattern more precisely encodes the fluctuations in the signal envelope than an intensity-rate-code, whereas more centrally it is the reverse. The change in the way the minimum-detectable gap is encoded in the starling's auditory system suggests a similar transition in codes.

The similarity of the limits of peripheral temporal resolution in gap detection tasks in different animals

The observation that the study of the detection of short intensity decrements in broadband noise results in the same minimum-detectable gap in many different taxa suggests that it is based on very common neural mechanisms. Ronacher and Römer (1985) showed that single primary receptor cells of the hearing organ of an acridid grasshopper (*Chorthippus biguttulus*) can code minimum gap sizes of about 2 ms. The study of acoustical primary receptor cells in two species of noctuid moths (*Agrotis segetum* and *Noctua pronuba*) by Surlykke et al. (1988) showed a similar minimum-detectable gap of 2 ms. Zhang et al. (1990) found minimum-detectable gaps of below 2 ms in the chinchilla (*Chinchilla laniger*), and also in this study the shortest minimum-detectable gaps in the starling are in the range of 1.6 to 3.2 ms. In all these examples, the size of the minimum-detectable gap was either defined by the difference between the spike rate at the onset of the noise-burst following the gap and the reduced spike rate during the gap, or by the decrement of the steady-state rate during the ongoing noise stimulus to rates close to zero after the end of noise burst preceding the gap.

The only species in which an unusually low capacity for coding temporal gaps in broadband noise has been found is the goldfish (Fay 1985). Saccular nerve fibres of the goldfish have little capacity for coding very short gaps by spike-rate decrements because of their large variability in spike rate over time. Fay suggested that only the increment in spike rate at the onset of the second noise pulse ending the gap may be analyzed by the goldfish's auditory system. However, an increase in this spike rate requires a relatively large size of the gap. The low capacity of the goldfish to code noise energy decrements

is also obvious in the size of its psychoacoustically-determined minimum-detectable gap of 35 ms (Fay 1985).

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