Lehrstuhl für Zoologie der Technischen Universität München

Across-Channel Processing in Auditory Perception: A Study in Gerbils (*Meriones unguiculatus*) and Cochlear-Implant Subjects

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1 General Introduction

In the natural environment we rarely find quiet conditions for acoustic communication. Acoustic signals like speech or communication sounds of animals will always be affected by masking background noise that impairs the detection of the signal. Therefore, the auditory system of humans and animals had to develop mechanisms to separate a useful and important signal from background noise. A large number of experiments indicate that the peripheral auditory system contains a bank of band-pass filters, called auditory filters, each tuned to a different center frequency (e.g. Fletcher 1940, Zwicker and Feldtkeller 1967, Scharf 1970, Patterson and Moore 1986). The auditory filters seem to play an important role in many aspects of auditory perception. They determine the frequency selectivity of the auditory system, i.e. the ability to resolve frequency components of an acoustic signal (Moore 1997).

The frequency selectivity of the auditory system has often been measured by studying signal detection in noise. Fletcher (1940) showed that thresholds of a pure tone spectrally centered in masking noise of a constant spectral density were strongly influenced by the bandwidth of the masker. Signal-detection thresholds first increased with increasing masker bandwidth until a critical value of the bandwidth was reached. Further increases in noise bandwidth had no effect on the signal-detection threshold, meaning that thresholds remained constant. The results of this experiment imply that the auditory system behaves as a bank of overlapping band-pass filters. The optimal auditory filter for detecting a signal in a masking noise is the one with a center frequency that is identical to the signal frequency. Beside the signal, only the masker energy within the frequency range of the auditory filter passes the auditory filter and influences signal detection. The masker energy outside the frequency range of the auditory filter will be ignored. At signal-detection threshold, the masker energy falling within the frequency range of the auditory filter is the same as the sound energy of the signal presented at the center frequency of the auditory filter. For signal detection the auditory filter with the best signal-to-noise ratio is used and the detection threshold of the signal is determined by the amount of noise passing through the auditory filter centered on the signal frequency. This model has come to be known as the "power spectrum model of masking" (Patterson and Moore 1986).

The power spectrum model of masking proposes, that for signal detection in masking noise only the one auditory filter is used, which has a center frequency that is centered close to the signal frequency. This model, however, fails under special circumstances. In some cases the output of auditory filters tuned away from signal frequency can be used to improve signal detection. If the masker shows coherent amplitude fluctuations in different frequency regions a prominent release of masking can be observed. This release of masking has been called "Comodulation Masking Release" (CMR) by Hall et al. (1984). Mechanisms within one auditory filter ("within-channel cues") as well as mechanisms comparing information across different auditory filters ("across-channel cues") are involved in CMR. Depending on the stimulus parameters within- and across-channel cues can be studied separately. Thus, CMR experiments are a suitable method to investigate the contribution of within- and across-channel effects in the auditory system. Several authors mentioned that the masking release caused by within-channel cues lead to an overestimation of CMR (e.g. Moore 1992). They proposed that only the amount of masking produced by across-channel comparisons should be considered as "true" CMR (e.g. Schooneveldt and Moore 1987, Carlyon et al. 1989). In a more general way, CMR is defined as the improvement of signal detection due to coherent amplitude fluctuations in different frequency regions of a masking noise (e.g. Hall et al. 1984, Moore 1990).

CMR, representing a mechanism to improve signal detection in noise is an important feature of the auditory system. The mechanisms underlying CMR are not yet well understood. Working with animal models could help to reach a better understanding of the underlying mechanisms. In the first part of this thesis, CMR was studied in an animal model, the Mongolian gerbil (*Meriones unguiculatus*), using a psychoacoustical method. The results of two classic CMR experiments will be presented and discussed with the available literature. In the second part of this thesis, psychoacoustic experiments with cochlear-implant listeners as subjects were conducted. Cochlear implants (CI) are surgically implanted devices for profoundly and completely deaf people. By inserting a multi-channel electrode into the cochlea the defect inner ear is bypassed, and the intact auditory nerve is stimulated electrically by frequency and amplitude specific electric signals. The benefit subjects can have varies considerably. Most CI subjects perform well in quiet. In the presence of competing noise, however, the performance of most of the CI subjects deteriorates considerably. The aim of the second part of this thesis was to examine, whether the often compromised signal detection of

CI listeners in fluctuating background noise is due to a reduced ability to utilize CMR. Subjects were tested in two experimental paradigms that are well established in the study of CMR in normal-hearing humans and in animal models. In addition, the temporal resolution and the ability of processing information across frequencies of cochlear-implant subjects were investigated in a gap-detection task studying both within- and across-channel processing.

2 CMR in the Mongolian Gerbil

2.1 Introduction

The advantage of working with an animal model is that in addition to psychoacoustical data, physiological data can be collected. The comparison of both kinds of data provides for a better understanding of the basic mechanisms of the auditory system. Furthermore, conclusions can be drawn from the comparison of differences and similarities between species. For example, if the same psychoacoustic performance is observed in two species despite considerable differences in cochlear anatomy, it could be concluded that very basic mechanisms of coding of acoustic signals are involved. The Mongolian gerbil *(Meriones unguiculatus)* has become a commonly studied model animal in auditory research (e.g. Plassmann et al. 1987, Schmiedt 1989, Müller 1995, Chatterjee and Zwislocki 1998). The gerbil has a good low frequency sensitivity that is unusual for small rodents. Its audiogram is similar to that of humans over a wide frequency range (Ryan, 1976). The animals can easily be trained for psychophysical experiments (Sinnott et al. 1992, 1995). Therefore, more and more psychoacoustic data have been collected in recent years to complement the wealth of physiological and anatomical data (e.g. Sinnott et al. 1992, 1997, Kittel et al. 2002). These studies have shown that the gerbil's auditory system is comparable to that of the human in various characteristics. For example, the temporal resolution of the gerbil's auditory system measured with a gap-detection task (Wagner et al. 2002) and the frequency selectivity of the gerbil (Kittel et al. 2002) match that of humans very well. These similarities of results obtained from psychoacoustic experiments renders the gerbil an excellent animal model for studying auditory perception and provides the opportunity for a direct comparison of behavioral performance and neuronal response patterns (e.g. Ohl et al. 1999, Schulze et al. 1997, Foeller et al. 2001).

To investigate CMR, two types of experiments have been traditionally used: the band-narrowing paradigm and the flanking-band paradigm. In the band-narrowing paradigm, the detection of a pure tone in a continuous band-limited noise masker of equal spectral density is measured in relation to the bandwidth of the masker. Hall et al. (1984) conducted this experiment first. They used two types of maskers: one masker was a random noise with irregular fluctuations in amplitude across frequencies (unmodulated masker). The second masker had coherent amplitude fluctuations in different frequency regions, i.e. all frequency components showed correlated temporal variations of amplitude (comodulated masker). They measured masked thresholds for a 1-kHz signal of 400-ms duration in relation to the bandwidth of the masker. The masker was centered at the signal frequency, presented continuously and with constant spectrum level. The data for the unmodulated masker corresponded to the results obtained by Fletcher (1940). Masked thresholds first increased with increasing masker bandwidth up to about 100-200 Hz (which is about the auditory filter bandwidth for humans at 1 kHz) and then remained constant. It is assumed that only one auditory filter is involved in the detection task, i.e. only the energy within the auditory filter centered on the signal frequency influences signal detection. The results for the comodulated masker were similar to those for the random masker up to a bandwidth of 100 Hz. Thresholds first also increased with increasing masker bandwidth. As the bandwidth of the comodulated noise was increased further, i.e. the masker bandwidth exceeded the critical bandwidth of the auditory filter at the signal frequency and additional auditory filters were involved, thresholds started to decrease. The release of masking, i.e. the difference between thresholds in unmodulated and comodulated maskers, thus increases with increasing masker bandwidth. Hall et al. (1984) suggested that the release of masking is produced by across-channel comparisons. In recent years it has been pointed out that these "across-channel" effects are only one component contributing to CMR. Schooneveldt and Moore (1989), for example, showed masking release in a band-narrowing paradigm already when the masker bandwidth was less than the auditory filter bandwidth. In this case, the release from masking could not arise from comparison of information from different auditory filters, but from cues available within one auditory filter ("within-channel" effects). Therefore, within- and across-channel processes are involved in the mechanism of CMR. To separate the contribution of the two processes, the amount of masking produced by across-channel comparisons is called "true" CMR (e.g. Schooneveldt and Moore 1987, Carlyon et al. 1989).

The band-narrowing paradigm has been previously investigated behaviorally in the Mongolian gerbil by Kittel (2000). He used a 2-kHz pure tone of 410-ms duration as the test signal. In a physiological experiment, Foeller (2001) searched for neuronal correlates of CMR in the gerbil's auditory cortex using the same noise maskers as Kittel, but the test signal had a shorter duration (200 ms). Since the signal duration may affect the masking release, I extended the findings by Kittel by using shorter signal durations (200 ms, 100 ms, 50 ms). One aim of the first experiment in the gerbil was to get a set of behavioral and physiological data collected with identical stimulus parameters by repeating the band-narrowing paradigm with a 200-ms signal.

The second paradigm, the flanking-band paradigm, has not been applied so far to study CMR behaviorally in any other mammal besides humans. The classic flanking-band paradigm is an appropriate method to separate the contribution of within- and across-channel effects. The masker consists of two narrow bands of noise. One band of noise, the on-frequency band, is centered on the signal frequency. The center frequency of the other band of noise, the flanking band, is located away from the signal frequency. The envelopes of the flanking band and of the on-frequency band are either correlated or uncorrelated. Usually, the masking of the test signal is also measured in a third condition, called the reference condition, in which only the on-frequency band is present. In the uncorrelated condition, adding the flanking band to the on-frequency band has little effect on signal-detection thresholds if the flanking band is outside the auditory filter centered on the signal frequency. Presenting the uncorrelated flanking band and the on-frequency band within one auditory filter results in an increase of detection threshold of about 3 dB due to the additional sound energy falling within the frequency range of the auditory filter. In the correlated condition, however, the addition of the flanking band produces a prominent release of masking. This general pattern has been found in humans (e.g. Schooneveldt and Moore 1987) and in starlings (Hamann 1998). However, a difference between these two species can be seen in the degree to which the amount of masking release depends on the flanking-band center frequency. In humans the largest amount of masking release occurs when the flanking-band center frequency is close to the signal frequency. With increasing frequency distance between on-frequency band and flanking band, the amount of masking release in humans deteriorates strongly. Starlings in contrast show a large release of masking over a wide frequency range (Hamann 1998). This indicates that starlings are able to integrate information over more auditory filters than humans and that across-channel effects appear to be larger in starlings than in humans. Because of the differing results in starlings and humans, it is interesting to study CMR in another mammalian species using the flanking-band paradigm. The aim of the second experiment in the gerbil was to study CMR with the flanking-band paradigm and to explore the contribution of the within-and across-channel cues to CMR in this species.

2.2 Methods

2.2.1 Subjects

In the experiments applying the band-narrowing paradigm, three adult male Mongolian gerbils served as subjects. Two of them (Tom, Max) were fourth-generation offspring of wild gerbils imported from Tuva Providence in Russia (Sinnott et al. 1997). One (Romeo) was first-generation offspring of wild gerbils imported from Central Mongolia (Stürmer et al. 1997). Over the time course of testing, their ages ranged from 32-38 months.

In the experiments applying the flanking-band paradigm five adult Mongolian gerbils (3 male, 2 female) served as subjects. Three of them (Olga, Tom, Max) were fourth-generation offspring of wild gerbils imported from Tuva Providence in Russia (Sinnott et al. 1997). Two (Ida, Romeo) were first-generation offspring of wild gerbils imported from Central Mongolia (Stürmer et al. 1997). Over the time course of testing, their ages ranged from 24-32 months.

The gerbils lived in individual cages (48x 49x 52 cm) equipped with sleeping houses, running wheels, sufficient nesting materials and free access to water. A special cage was used for transporting the animals between their home cage and the experimental cage without direct handling. The gerbil's weight was checked daily and access to food was limited to keep the weight at approximately 90 % of their free-feeding weight. During experiments the gerbils were rewarded with 20 mg food pellets (Bioserve: Dustless Precision Pellets Rodent Grain-Base Formula #FO 163-J5O). Upon successful completion of a session that yielded useable data, they received two sunflower seeds. At the end of the day the diet was supplemented with 1-4 g of rodent dry food (Alma Spezialfutter, Ratten/Mäuse H) and a piece of apple or carrot. Treatment of the animals followed the NIH guide for the care and use of laboratory animals and was also in accordance with the German law for conducting animal experiments. The state veterinarian of the Landkreis München approved animal facilities and treatment.

2.2.2 Apparatus

Gerbils were tested in a custom-built double-walled sound-attenuated chamber (180*180*180 cm) lined with sound-absorbing acoustic foam (Illbruck Illsonic Pyramid 70/100 and Waffel 75/50). The test apparatus is shown in Figure 1. The experimental cage was constructed using two concentric wire mesh cylinders forming a "doughnut"-shape, which allowed the gerbils to run on a circular track (7 cm width, 20 cm height). For better handling, it was positioned on a stand (50 cm high, covered with sound absorbing foam) built from thin wooden rods (Ø 2 cm). A platform was placed in this circular track and a light-interrupting switch sensed the gerbils' jumping on and off the platform. In addition, the cage contained a feeder cup and two cue lights, one at the platform and the other one at the feeder cup. An automatic feeder delivered the 20 mg pellets via a plastic tube into the feeder cup for reinforcement. The loudspeaker (Canton Twin 700) was mounted on a microphone stand at the height of the gerbil's head while sitting on the platform and at a distance of 60 cm. A Silicon Graphics Iris Indy workstation controlled the experiment through a Tucker-Davis Technologies PI2 interface. The workstation recorded the gerbils' response, displayed a protocol of the current session, controlled the automatic feeder and the lights in the sound-attenuated chamber and generated the sound stimuli (16-bit D/A converter; 32 kHz sampling rate). Test signal and masker were delivered separately to two computer-controlled attenuators (Tucker-Davis PA4), which adjusted the level. Signal and masker were added, amplified (Harman/Kardon HK 6350) and presented through the speaker inside the sound-attenuated chamber. All test sessions could be monitored by a CCD-camera (Conrad Type 116785-15) placed on top of the loudspeaker and a video monitor (Santec VM 23).

Sound spectra for calibration were measured with a Hewlett-Packard 3651A Dynamic Signal Analyzer (1,91 Hz bandwidth) through a 1982 General Radio sound-level meter with a ½-inch condenser microphone (General Radio Type 1961-9610). For obtaining a flat sound spectrum in the sound-attenuating booth, frequency spectra of the noise maskers were equalized using an inverse FFT-filter synthesized with "Cool Edit" (Syntrillum Software Corporation). To generate the FFT-filter the frequency distribution of white noise was measured at ten possible positions of the gerbil's head when sitting on the platform. A mean frequency distribution was calculated from these 10 measurements forming the basis of the correcting filter. After filtering, the noise spectra were flat (± 1dB, compared to ± 6 dB before filtering) and the slopes of the spectrum of the band-passed noise signals were at least 256 dB/octave. At least once a day sound-pressure levels were determined with a microphone (Sennheiser ME 40 with a custom-built 40 dB-amplifier) that was placed in a fixed position in front of the loudspeaker and that was calibrated against the ½-inch condenser microphone. Sound-pressure levels in dB were displayed on a Philips Multimeter (PH 2525).

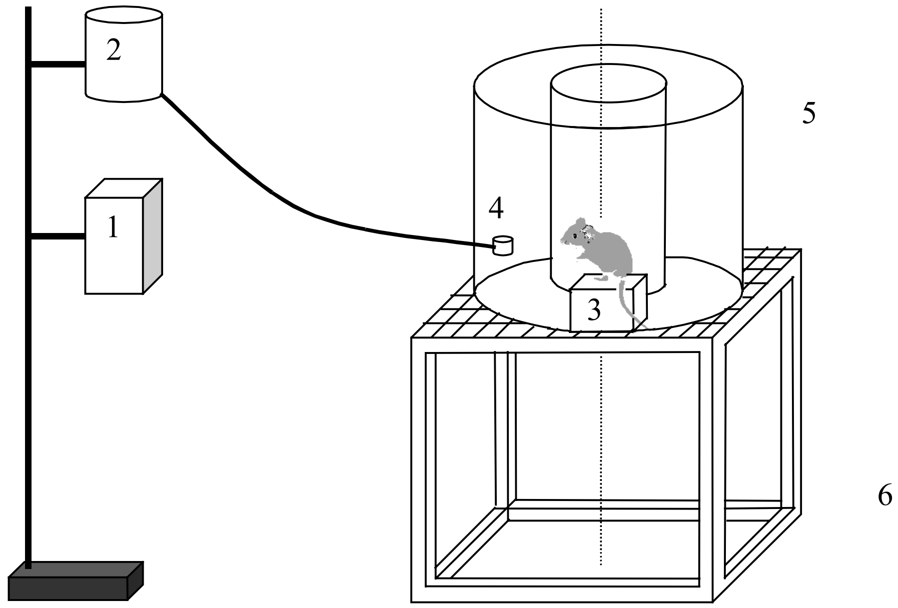

Figure 1: Schematic diagram of the gerbil test apparatus: 1 speaker, 2 automatic feeder, 3 platform, 4 feeder cup, 5 experimental cage, 6 wooden stand, the light-interrupting switch is indicated by the dotted line.

2.2.3 Stimuli

2.2.3.1 Band-narrowing Paradigm

The test signal was a pure tone of 2 kHz and had a total duration of 200, 100 or 50 ms (including 10-ms raised cosine ramps). The band-passed noise maskers had a spectrum level of 40 dB/Hz and were generated by digitally filtering of Gaussian white noise using a 1024-point FIR filter (programs: SAP, fir_noise by Georg Klump). Noise maskers with bandwidths of 50, 200, 800, 1600 and 3200 Hz centered on the test-signal frequency were used. 5-min segments of the band-passed noise were stored on disc and played repeatedly during the test sessions to produce a continuous masking background. To avoid clicks at the transition, 50-ms linear ramps were applied to the beginning and the end of the noise fragments. Comodulated noise bands were generated by multiplying a Gaussian white noise with a 50-Hz low-pass noise before subjecting it to band-pass filtering (program: cmr_noise_test by Georg Klump).

2.2.3.2 Flanking-band Paradigm

The test signal was a 2-kHz pure tone (410-ms total duration including 10-ms raised cosine ramps). The continuous masker presented at a spectrum level of 40 dB/Hz consisted of two narrow-band noise stimuli (bandwidth 25 Hz). The on-frequency band was centered on the signal frequency. The center frequency of the flanking band was 400, 1200, 1600, 1800, 1900, 2100, 2200, 2400, 2800 or 3600 Hz, respectively. In the reference condition, only the on-frequency band was presented at a spectrum level of 40 dB/Hz. To generate the noise bands a 6-min low-pass noise (cut-off frequency 12.5 Hz) was multiplied with a pure tone (used programs: "bandpassnoise.new" by Moritz Franosch, "multi" by Georg Klump). This produced a 25-Hz wide band of noise centered on the frequency of the pure tone. Since the same low-pass noise was used for the multiplication, the noise bands showed identical envelopes. To create the correlated maskers, the on-frequency and the particular flanking band were added together ("addi" by Georg Klump). To create the uncorrelated maskers, the first 2 s of the on-frequency band were removed before adding on-frequency band and flanking band (i.e. the envelope of the flanking band is time shifted in relation to the envelope of the on-frequency band by 2s). The composite masker was shortened to 5-min ("Cool Edit", Syntrillum Software Corporation) and these 5-min segments of the noise were played repeatedly to get a continuous masking background. To avoid clicks at the transition, 200-ms linear ramps were applied to the beginning and the end of the 5-min noise segments.

2.2.4 Procedure

A GO/NOGO paradigm was used. Gerbils were trained to jump and sit on the platform when the reference stimulus (masking noise alone) was presented, and to jump off the platform when the test stimulus (masking noise plus 2 kHz signal) was presented. Switching on the cue light at the platform signaled to the gerbil that a trial could be initiated by jumping onto the platform. At that time a variable waiting interval (2-6 s) began that was terminated with the presentation of a test stimulus. If the gerbil jumped off the platform within 1 s after the start of the test stimulus, the cue light at the feeder cup was turned on for 2 s and the subject was immediately reinforced by a food reward from the automatic feeder with a probability of 100 %. To obtain a measure of spontaneous responding, catch trials during which no test stimulus was presented were inserted on 30 % of the trials. Jumping off the platform in the absence of a test stimulus (false alarm) or during the waiting interval resulted in a 4 s time-out period during which all lights were extinguished and trials could not be initiated. After a miss (failure to jump off the platform after presenting a signal) a new trial followed without interruption. Thresholds were obtained by the method of constant stimuli. A block of ten trials, consisting of 3 catch trials and 7 test trials with sound pressure levels of the test tone differing in 3 dB steps, was repeated 10 times in a session with a randomized sequence of the trials in each block. At the beginning of each session, a block of 10 additional "warm-up" trials was presented. Sessions were excluded from the analysis if the false-alarm rate exceeded 20 % or if the two best-detectable test stimuli were reported with a probability of less than 80 %. A psychometric function displaying the sensitivity measure d' in relation to the sound pressure level of the test stimulus was constructed by combining the results of two successful sessions (20 trials at each sound pressure level and 60 catch trials). A detection threshold was computed by linear interpolation of the value of the sound pressure level at which the detection measure d' was 1.8.

2.3 Results

2.3.1 Band-narrowing Paradigm: Effect of Signal Duration

For signal duration of 200, 100 and 50 ms, masked thresholds were measured for maskers of 200- and 1600-Hz bandwidth. For signal duration of 200 ms, thresholds were also determined for maskers of 50-, 800- and 3200-Hz bandwidth. Figure 2 shows mean signal-to-noise ratios at detection threshold (S/N ratio) in relation to the masker bandwidth for the different signal durations (for individual data see Appendix A). For comparison, data for a 410-ms signal from the previous study by Kittel (2000) are also shown.

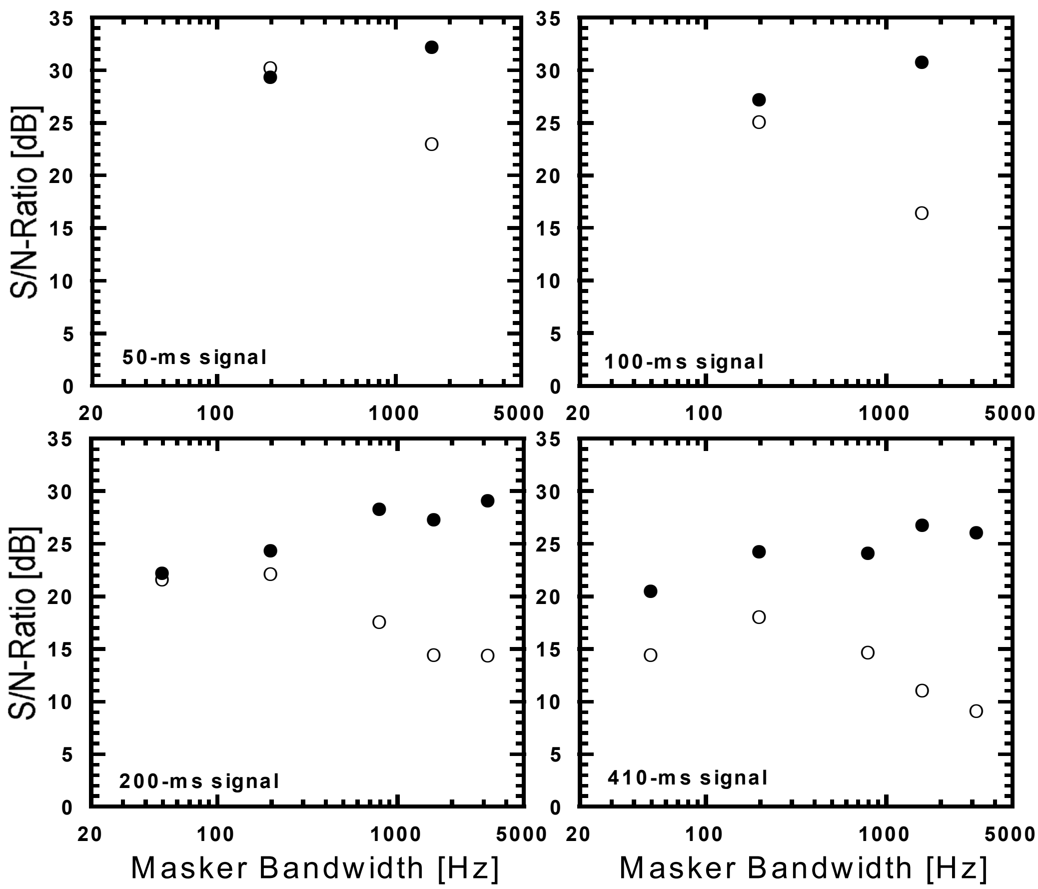

Figure 2: Mean signal-to-noise ratios (S/N ratios) at the detection threshold for three gerbils for a signal presented in unmodulated noise (filled symbols) and in comodulated noise (modulator bandwidth 50 Hz, open symbols) as a function of masker bandwidth. Signal duration was either 50 ms (upper left), 100 ms (upper right), 200 ms (lower left) or 410 ms (lower right). Signal frequency was 2 kHz. Data for the 410-ms signal from Kittel (2000).

T-tests revealed that for the 50-ms and the 100-ms signal the S/N ratios at detection threshold in unmodulated and comodulated noise were significantly different for the 1600-Hz wide maskers (t-test: $P_{50ms} \leq 0.001$, $P_{100ms} \leq 0.001$), but not for the 200-Hz wide maskers (t-test: $P_{50ms}=0.352$, $P_{100ms}=0.373$). For the 200-ms signal there was a significant difference between S/N ratios in unmodulated and modulated noise for masker bandwidths of 800, 1600 and 3200 Hz (t-test: $P_{800Hz}=0.002$, $P_{1600Hz} \leq 0.001$, $P_{3200Hz} \leq 0.001$), but not for the 50- and 200-Hz wide maskers (t-test: $P_{50Hz}=0.965$, $P_{100Hz}=0.066$). For the 410-ms signal, S/N ratios in the study by Kittel differed significantly for all masker bandwidths. A Two-Way-Repeated-Measures ANOVA with the S/N ratio as the dependent variable and duration and type of modulation (unmodulated, comodulated) as factors was conducted for the 200-Hz and the 1600-Hz wide maskers for which data for all signal durations are available. Figure 3 shows S/N ratios at detection threshold for the 200-Hz and 1600-Hz wide maskers in relation to signal duration.

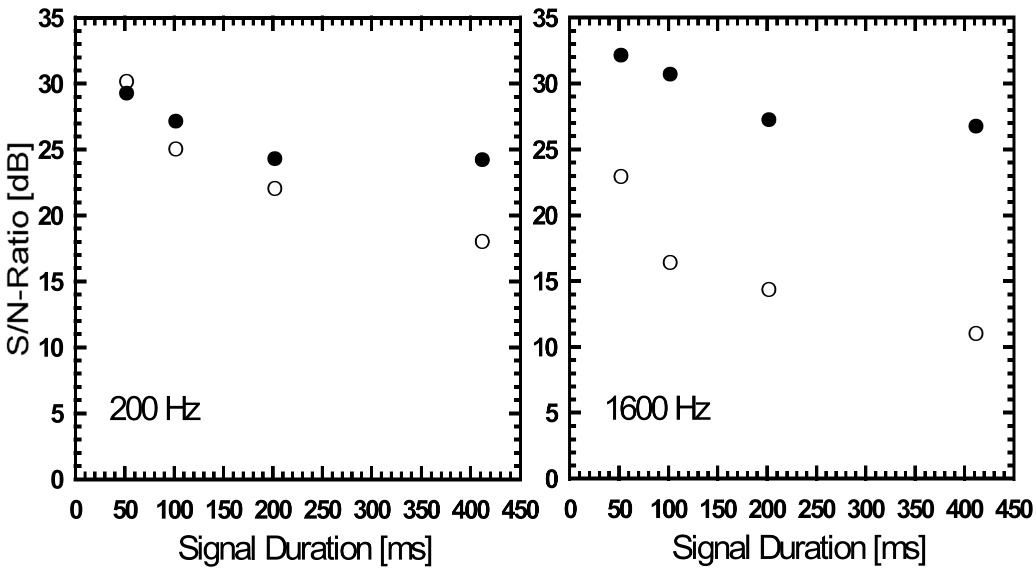

Figure 3: Mean S/N ratios (n=3) at detection threshold for the 200 Hz wide masker (left panel) and for the 1600 Hz wide masker (right panel) in relation to signal duration. Open symbols: Presentation in comodulated noise. Closed symbols: Presentation in unmodulated noise. Data for the 410-ms signal from Kittel (2000).

For the 1600-Hz masker bandwidth, there was a significant effect of duration ($P \leq 0.001$) and of type of modulation ($P=0.002$). The interaction between type of modulation and duration was significant ($P=0.003$). Pairwise comparisons between the S/N ratios for the different signal durations (Tukey test) showed significant differences for all durations. In the following, signal-to-noise ratios (S/N) necessary for the detection of tones are compared within one type of modulation. In the unmodulated condition, only S/N ratios for the detection of the two shortest signals (50 ms, 100 ms) differed significantly ($P \leq 0.002$) from the S/N ratios for the detection of the two long signals (200 ms, 410 ms). In the comodulated condition, there was a significant difference for the S/N ratios between results for all signal durations ($P \leq 0.003$). For the 200 Hz masker bandwidth, there was a significant effect of type of modulation ($P=0.017$) and of duration ($P=0.001$). The interaction between type of modulation and duration was not significant ($P=0.069$). Pairwise comparisons between the S/N ratios for the different signal durations (Tukey test) showed significant differences for the S/N ratios for the 50-ms signal versus the S/N ratio for the two longest signal durations (200 ms, 410 ms, $P \leq 0.005$) and for the S/N-ratio for the 100-ms signal versus the S/N ratios for the 410-ms signal ($P=0.018$). Concentrating on the data within one type of modulation, in the unmodulated condition only the S/N ratios for the shortest signal (50 ms) was significantly different from the S/N ratios for the 200-ms and 410-ms signal ($P \leq 0.040$). In the comodulated situation, the S/N ratios for the 50-ms signal differed from the S/N ratios for all other durations ($P \leq 0.030$) and the S/N ratios for the 100-ms signal differed from the S/N ratios for the 410-ms signal ($P=0.003$). The S/N ratios for the tones of different durations were used to estimate the time constants of the temporal-integration function. The model proposed by Feldtkeller and Oettinger (1959) was applied to fit a theoretical curve to the data. Threshold intensity for a tone of duration t is given by: $I_t = I_\infty / (1-e^{(-t/\tau)})$ where I is the threshold intensity, t is the signal duration, e is the Euler's constant in exponential function, and τ is the integration time. I_∞ and τ were adapted in a numerical fitting procedure to achieve the best least-square fit of the theoretical curve to the data. A fit of a theoretical curve to the data was only possible for the S/N ratios in the unmodulated maskers. Integration times that resulted from the fitting were 157 ms for the masker bandwidth of 200 Hz and 197 ms for the masker bandwidth of 1600 Hz, respectively. In the comodulated maskers, the model could not account for the increase in S/N ratios observed in the experiment. In the comodulated masker, the increase in the S/N ratios with decreasing stimulus duration is much higher compared to the expectation derived from the temporal-integration model of Feldtkeller and Oettinger (1959). Figure 4 shows the release of masking for the different signal durations in relation to the masker bandwidth. A One-Way-Repeated-Measures ANOVA conducted separately for each signal duration revealed that the masker bandwidth affected the amount of CMR for all signal durations (P≤0.027). Concentrating on the masker bandwidth of 200 Hz and 1600 Hz, the increase of masking release with increasing masker bandwidth is similar for all signal durations. The amount of masking release increased 9.0 dB, 10.6 dB, 12.2 dB and 10.1 dB between the masker of 200 Hz and 1600 Hz for the 410, 200, 100 and 50-ms signal, respectively. The amount of CMR was also affected by the signal duration (P=0.008). However, pairwise comparison showed that the effect of duration was only significant when comparing the amount of CMR for the 410-ms signal with the amount of CMR for the 50-ms signal (P≤0.006). Figure 5 shows the release of masking for maskers with a bandwidth of 200 and 1600 Hz in relation to the duration of the signal. For the 200-Hz masker bandwidth the masking release is reduced from 6.3 dB to -0.9 dB with shortening the signal duration from 410 ms to 50 ms. For the 1600-Hz masker bandwidth the masking release is reduced from 15.7 dB to 9.2 dB with shortening the signal duration from 410 ms to 50 ms.

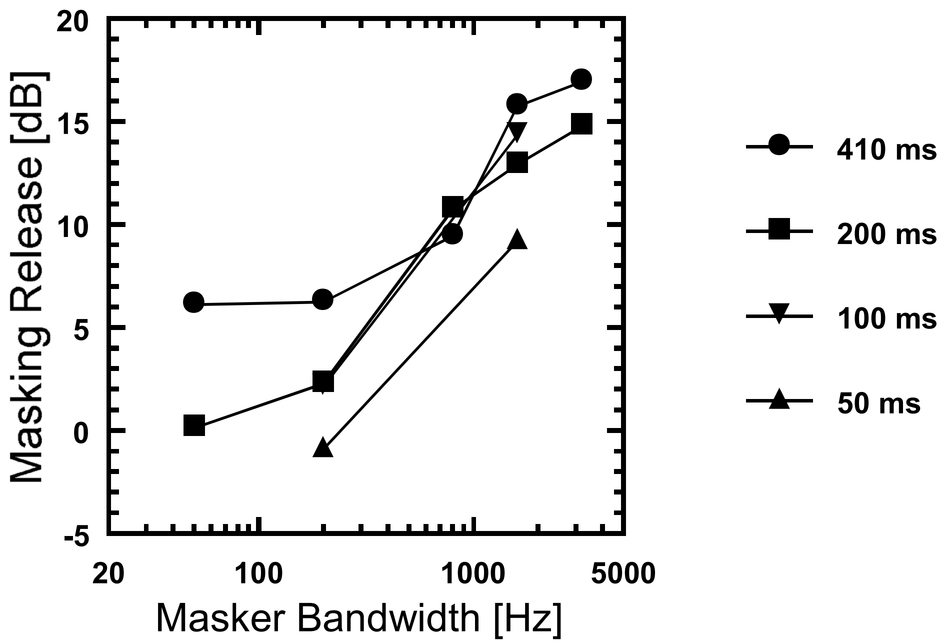

Figure 4: Mean release of masking (n=3) for four different signal durations in relation to masker bandwidth. Data for the 410-ms signal from Kittel (2000).

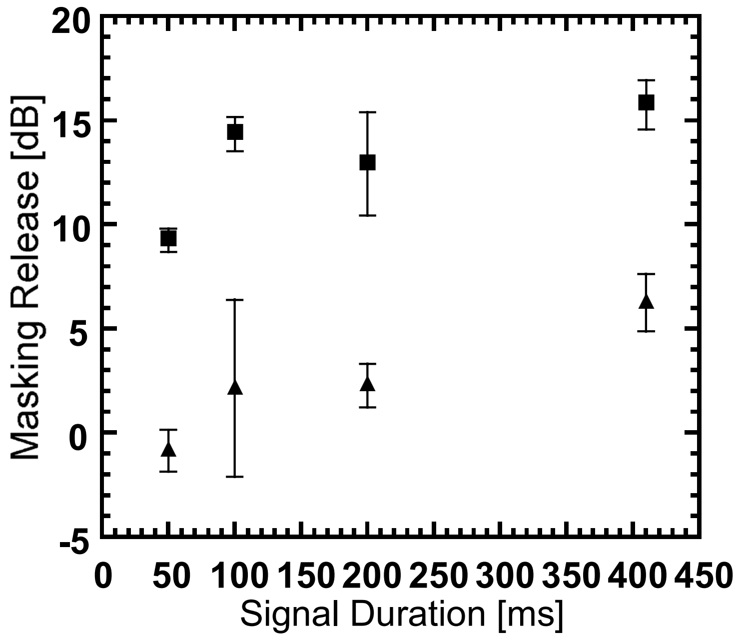

Figure 5: Mean masking release (n=3) for 200-Hz (triangles) and 1600-Hz wide maskers (rectangles) in relation to signal duration with standard deviation shown by the error bars. Data for the 410-ms signal from Kittel (2000).

2.3.2 Flanking-band Paradigm

In four of five gerbils masked thresholds for all conditions were measured. In one animal it was not possible to collect the full set of data (for individual data see Appendix B). Figure 6 shows mean signal-to-noise ratios (S/N ratio) for the detection of a 2-kHz tone presented either in an uncorrelated or a correlated masker in relation to the center frequency of the flanking band. In the reference condition a mean S/N-ratio of 16.2 dB was measured. Adding an uncorrelated 25-Hz-wide band of noise did not affect the gerbils' detection threshold notably. Pairwise comparisons between S/N ratios for the different flanking-band center frequencies (Tukey test) revealed a significant difference between S/N ratios in the uncorrelated condition only for the flanking-band center frequency of 400 Hz ($P \leq 0.018$). The mean S/N ratios for flanking-band positions from 1200 Hz to 3200 Hz ranged from 16.9 dB to 18.6 dB, the mean S/N ratio for the flanking-band position of 400 Hz was 12.9 dB. Adding a correlated 25-Hz-wide band of noise improved the detection threshold considerably at all flanking-band center frequencies.

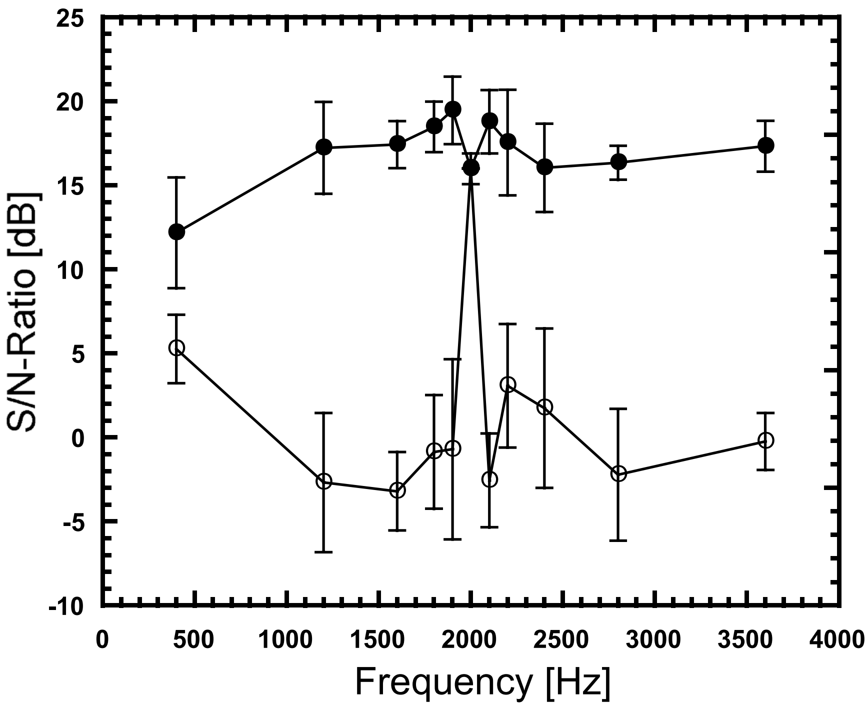

Figure 6: Mean signal to noise ratios (S/N-ratio) for gerbils (n=4-5) for the detection of a 2-kHz tone presented together with an on-frequency masker and a flanking-band masker of 25-Hz bandwidth in relation to the center frequency of the flanking band (filled symbols: uncorrelated noise bands, open symbols: correlated noise bands). At 2-kHz, only the on-frequency masker was presented. Error bars show the standard deviation across subjects.

A-Two-Way-Repeated-Measures ANOVA with the S/N ratio as the dependent variable and flanking-band center frequency and type of correlation as factors revealed a significant effect of flanking-band center frequency ($P=0.002$) and of type of correlation ($P\leq0.001$). Pairwise comparisons between the S/N ratios for the different flanking-band center frequencies (Tukey test) showed significant differences of the S/N ratios for the flanking-band center frequency of 2200 Hz with the S/N ratios for the flanking-band frequencies of 1200 Hz, 1600 Hz and 2800 Hz ($P\leq0.016$). Concentrating on the data within one type of correlation, in the uncorrelated condition only the S/N ratio for the flanking band at 400 Hz center frequency were significantly different ($P\leq0.019$) compared to the S/N ratios for all other flanking-band frequencies. In the correlated situation, the S/N ratios for the flanking band centered at 400 Hz differed significantly from the S/N ratios for all other flanking-band center frequencies besides 2200 Hz and 2400 Hz (P≤0.002). The S/N ratio for the flanking band centered at 2200 Hz was significantly different from the S/N ratios for the flanking bands centered at 1200 Hz, 1600 Hz, 2100 Hz and 2800 Hz (P≤0.003). Also S/N ratios for the flanking band centered at 2400 Hz differed significantly from the S/N ratios for the flanking bands centered at 1200 Hz, 1600 Hz and 2100 Hz (P≤0.037). The difference between the S/N-ratio in uncorrelated versus the correlated noise shows the amount of CMR (Table 1). On average, the release from masking that was observed with an additional correlated flanking band was 17.4 dB. A One-Way-Repeated-Measures ANOVA with the CMR as dependent variable revealed a significant effect of flanking-band position (P≤0.001). Pairwise comparisons (Tukey test) showed that the amount of CMR differed significantly for comparisons with the amount of CMR for the flanking band centered at 400 Hz (P≤0.001) versus the amount of CMR for all other flanking-band center frequencies. The comparison of the amount of CMR for the flanking bands centered at 2100 Hz versus 2400 Hz was barely significant (P=0.048).

Table 1: The amount of masking release in the gerbil in dB measured as a function of the center frequency (f_c) of the flanking band. Individual data and averages.

f_c flanking-band	400 Hz	1200 Hz	1600 Hz	1800 Hz	1900 Hz	2100 Hz	2200 Hz	2400 Hz	2800 Hz	3600 Hz
max	6.1	17.5	22.5	18.2	14.9	22.1	10.4	9.5	13.7	15.3
tom	9.0	22.5	18.4	13.5	13.6	18.8	11.8	13.2	20.7	18.9
olga		13.5		19.9	24.0	21.3	18.4	13.2	13.3	17.7
julia	8.4	25.1	22.4	25.5	22.7	20.9	16.6	21.1	20.7	17.5
romeo	4.1	20.9	21.1	19.6	25.6	23.6	15.1	14.5	24.4	18.4
mean	6.9	19.9	21.1	19.3	20.2	21.3	14.5	14.3	18.6	17.6
± SD	2.2	4.5	1.9	4.3	5.5	1.8	3.3	4.2	4.9	1.4
median	7.3	20.9	21.8	19.6	22.7	21.3	15.1	13.2	20.7	17.7

2.4 Discussion

2.4.1 Band-narrowing Paradigm

2.4.1.1 CMR as a Function of Masker Bandwidth

The pattern of masking release found in the gerbil is similar to that found in humans (e.g. Hall et al. 1984, Schooneveldt and Moore 1989, Haggard et al. 1990). In the unmodulated masker, the gerbils' thresholds for detecting a test signal of 200 ms increased with increasing masker bandwidth up to a bandwidth of 800 Hz and then remained constant. In the comodulated masker, detection thresholds first also increased, after exceeding the critical bandwidth of 216 Hz (Kittel et al. 2002) they decreased. For the two smallest masker bandwidths (50 Hz, 200 Hz) no significant CMR was observed. With increasing masker bandwidth the release of masking increased to a maximum of 14.8 dB (mean of three gerbils) for the masker bandwidth of 3200 Hz. Schooneveldt and Moore (1989) measured CMR in humans using a 200-ms signal. They used a 12.5-Hz low-pass noise instead of a 50-Hz low-pass noise to generate the comodulated maskers. For the smallest masker bandwidth of 50 Hz a small CMR of 3 dB was found. The release of masking increased with increasing masker bandwidth up to 11 dB for the 3200-Hz-wide masker. In contrast to the data in the gerbil, the masking release seemed to asymptote for masker bandwidths wider than 800 Hz. The authors suggested that the frequency range over which acoustical information could be integrated was 800 Hz wide corresponding to the bandwidth of about three auditory filters. The increase of masking release in the gerbil up to the bandwidth of 3200 Hz indicates that gerbils, which appear to have auditory filter bandwidth similar to that of humans, are able to integrate information over more than three auditory filters. To specify the effect of across-channel cues on CMR ("true CMR"), Carlyon et al. (1989) suggested another method to calculate CMR. Instead of calculating the CMR as the difference between the masked thresholds in unmodulated and comodulated maskers they used the difference between the masking release in maskers of subcritical bandwidths and wide-band maskers. Comparing the masking release in the 200 Hz and 3200-Hz-wide maskers, this method results in a true CMR of 12.5 dB in the gerbil and in a true CMR of 5 dB in humans. This indicates that gerbils can make better use of across-channel cues than humans.

The only other rodent providing data on CMR obtained in a behavioral experiment is the chinchilla *(Chinchilla laniger,* Niemiec et al 1999, 2000). The authors measured the detection of a 1-kHz pure tone (1 s duration) centered in a band-passed noise of 30-2000 Hz bandwidth. As modulator they used a 50, 25 and 10-Hz low-passed noise. In these conditions they did not find a release of masking. Instead, the thresholds in the comodulated masker were even higher than in the unmodulated masker. Only when they used masker bandwidths of 4000 and 8000 Hz, they were able to measure a small CMR of 4 and 6 dB, respectively. Based on these data, the authors assumed that chinchillas are not able to follow the temporal structure of the masker envelope effectively. However, Giraudi et al. (1980) studied the temporal resolution of the chinchilla using a gap-detection task. Minimum detectable gaps of 3 ms were determined in the chinchilla, which is similar to results in humans (e.g. Plomp 1964, Penner 1977, Shailer and Moore 1983) and gerbils (Wagner et al. 2002). Therefore, a reduced temporal resolution should not be a reason for the small amount of CMR in the chinchilla. More likely, the small amount of masking release in the chinchilla could be due to a reduced frequency selectivity. The reduced frequency selectivity is indicated by the much broader auditory filter bandwidths found in the chinchilla (510 Hz at 1 kHz, Niemiec et. al 1992) compared to that found in humans and gerbils. Due to the broader auditory filter bandwidth, fewer auditory filters will be involved in signal detection even for the wide-band maskers. Therefore, the independence of information in different frequency regions will be reduced, resulting in a reduction of the magnitude of across-channel cues upon which at least part of the CMR is based.

Another mammal providing data on CMR obtained in a behavioral experiment is the cat (*Felis catus*, Budelis et al. 2002). CMR effects were demonstrated by varying the bandwidth and the correlation of the masking noise. The center frequency of the masker and pure-tone signals was 4 kHz. The masking noise was pulsed in 650-ms bursts at a 1-Hz repetition rate. Signals were delayed 275 ms relative to masker onset and ended 25 ms before masker offset. Comodulation was achieved by multiplying the masking noise with a low-pass noise. Detection thresholds in 8 kHz-wide maskers were determined. "True" CMR was estimated by removing the within-channel effects observed in subcritical maskers from the wide-band masked thresholds. After correction for the within-channel cues, a mean "true" CMR of 5.2 dB at a masker bandwidth of 8 kHz was observed in the cat. The amount of "true" CMR in the cat is comparable to that found in humans (6-10 dB "true" CMR, Carlyon et al. 1989).

2.4.1.2 Effect of Signal Duration on CMR

Before discussing the effect of signal duration on CMR, it is noteworthy that the S/N ratios at detection threshold both in unmodulated and comodulated noise increase with decreasing signal duration. This observation could be explained in terms of temporal integration processes of the auditory system. A large number of studies demonstrated that the detection of short signals in quiet depends on signal duration (e.g. Watson and Gengel 1969, Viemeister and Wakefield 1991, Moore 1997). For long-duration signals, detection thresholds are relatively independent of duration. For durations of less than about 200 ms, detection thresholds increase as signal duration decreases. Up to signal durations of about 200 ms, the human auditory system appears to integrate the energy of the signal over time to improve the detection of a signal. The model proposed by Feldtkeller and Oettinger (1956) for temporal integration processes could account for the increase in S/N ratios in the unmodulated maskers in gerbils indicating an integration time slightly below 200 ms. However, the model could not fully account for the increase in S/N ratios in the comodulated maskers. According to the model, an increase in the S/N ratios of 3 dB would be expected for signals of half the duration. In the gerbil, with decreasing stimulus duration from 100 ms to 50 ms an increase in S/N ratios of 6.5 dB was observed in the 1600-Hz-wide comodulated masker and of 5.1 dB in the 200-Hz-wide comodulated masker, respectively.

Another explanation for the elevated S/N ratios for short signals could be a decreased frequency selectivity with decreasing signal duration. Several psychophysical studies in humans indicated that the bandwidth of auditory filters is duration dependent (for a review see Hant et al. 1999). Auditory filters have been shown to be broader for short-duration signals than for long-duration signals. A broader auditory filter leads to more masker energy within the one auditory filter that is used for signal detection. Therefore, a higher S/N ratio is necessary to detect a short-duration signal.

In the gerbil a significant reduction of the amount of CMR within one masker bandwidth is only found for the shortest signal duration of 50 ms. Schooneveldt and Moore (1989) studied the effect of signal duration on CMR in humans. Their data are in good agreement with our data in the gerbils. They used a 2-kHz pure tone with signal durations of 400, 200, 100, 50 and 25 ms at the 6-dB down point. The signal was gated with 10-ms raised-cosine ramps. The maskers were band-limited noise centered at 2 kHz. As modulator they used a 12.5-Hz low-passed noise. Among others they tested masker bandwidths of 200 and 1600 Hz. The amount of CMR was not substantially reduced until the signal duration was 50 ms or less. For the short-duration signals presented in maskers with bandwidths less than the critical bandwidth only little CMR was found in humans and in gerbils.

The lack of CMR for the short duration signal presented in a masker with narrow bandwidth could be explained by the lack of reliable within-channel cues (Schooneveldt and Moore 1989, Verhey et al 1999). Assuming that signal detection in modulated noise is achieved by using a single frequency channel, a sufficiently long time window for the sampling of the envelope of the noise is necessary for sensitive signal detection in a narrow-band masker. It is assumed that the applied time window is matched to the signal duration (e.g. Viemeister and Wakefield 1991). If the signal and thus the time window is too short to adequately sample the envelope, within-channel cues can not be used effectively. Therefore, a decrease of CMR with shortening of the signal can be expected. In this case, the auditory system would have to rely on across-channel cues. This may explain the restoration of CMR for short-duration signals in the wide-band masker. Verhey et al. (1999) replicated the experiment from Schooneveldt and Moore (1989) for signal durations of 25, 200 and 400-ms and a modulator bandwidth of 12.5 Hz. Their main aim was to investigate the influence of within-channel cues versus across-channel cues for explaining the CMR effect and to quantify the amount of masking release due to within-channel cues. Their data corresponded well to the data obtained by Schooneveldt and Moore (1989). In addition to the experiments they applied a model, which relied only on the information from one channel. With this single-channel model they were able to predict the effects of signal duration on CMR reasonable well. Nevertheless, for short-signal durations and large masker bandwidths the simulated CMR was slightly smaller than in the experimental data. This difference, which was smaller than 3 dB, is attributed to across-channel processes by the authors. Verhey et al. (1999)

suggested that in the band-narrowing experiment the across-channel contribution to CMR might be overestimated and that this paradigm probably is not appropriate to investigate across-channel processes. They proposed that the flanking-band paradigm is the better experiment to study masking release due to across-channel cues.

2.4.1.3 Neural Correlate of Comodulation Masking Release in a Band-narrowing Paradigm

Foeller (2001) investigated neural correlates of CMR in the primary auditory cortex of the anaesthetized gerbil. She recorded neural detection thresholds from single units. The acoustic stimuli were identical to those of this study and generated by the same software. As the test signal she used a 2-kHz pure tone of 200-ms duration (10 ms rise/fall time). Band-passed noise with a bandwidth of 50, 200, 800, 1600 and 3200 Hz centered on signal frequency was used as the masker. A modulator with a bandwidth of 50 Hz was used for generating comodulated noise. Before testing CMR an average filter bandwidth of the auditory cortex neurons in the gerbil of 1400 Hz was determined. A neural release of masking due to comodulation in the masker has been observed. The presence of a test signal in the masking noise was indicated by an increase of neuronal discharge rate. For masker bandwidths of 50, 200 and 800 Hz no significant CMR was found. For masker bandwidth of 1600 Hz and 3200 Hz, i.e. the masker bandwidth exceeding the neuronal filter bandwidth, the neurons' response thresholds were significantly lower in the comodulated condition than in the unmodulated condition ($p<0.01$, Wilcoxon test). This indicates that acoustical information could be integrated across frequency channels to improve signal detection. Similar to the results in the behavioral experiment, the amount of masking release increased with increasing bandwidth. The median neuronal release from masking was 3.7 dB and 6.0 dB for maskers with bandwidths of 1600 Hz and 3200 Hz, respectively. The largest median neuronal masking release of 6.0 dB for the 3200-Hz wide masker is much smaller than the 15.6 dB observed in the behavioral experiment. However, a small fraction of neurons showed a release of masking, that was close to the behavioral value or even larger. For example, tested with the 3200-Hz masker, 4 out of 40 neurons (10%) showed a masking release of 16 dB or more. Parker and Newsome (1998) suggested that the behavioral performance is produced not by the neuronal population average, but by the response of the most sensitive neuron.

Nelken et al. (1999) searched for neuronal correlates of CMR in the primary auditory cortex of the cat. They used noise bands of different bandwidths centered on the best frequency of the neuron. Stimulated with unmodulated maskers, the neurons responded with pure onset discharge (23/53) or with onset discharge followed by unpatterned increase in firing rate (12/35). For maskers modulated with a 10 Hz sinusoidal or trapezoidal envelope, a substantial fraction of neurons (35/56, 63%) modulated their firing rate coherently with the temporal envelope of the modulated masker. This envelope locking was decreased in a substantial fraction of neurons (25/35, 71%) by adding a test tone. The authors suggested that the loss of envelope locking indicated the presence of a test tone and resulted in an improved signal detection in comodulated maskers compared to unmodulated maskers. Envelope locking was often observed to increase with increasing bandwidth (23/35, 66%) and therefore, the population signal for the release from masking increased with increasing bandwidth. Calculating a population masking release from all tested neurons results in 10 dB for the smallest noise bandwidth and over 30 dB for the largest bandwidth.

2.4.2 Flanking-band Paradigm

Verhey et al. (1999) proposed that the flanking-band paradigm is the more suitable experiment to investigate the contribution of within-channel and across-channel effects to CMR. The gerbil showed clear evidence for CMR in the flanking-band paradigm comparable to humans, but some differences to humans are obvious. Adding a correlated flanking band resulted in a considerable improvement of detection thresholds. In general, a larger release from masking was observed in gerbils than in humans. Contrary to the results in humans, the masking release in the gerbil was less dependent on the center frequency of the flanking band.

In humans, the largest masking release was found for flanking bands positioned in the auditory filter centered at the on-frequency band. In this condition only within-channel cues are available producing a maximum CMR of about 13 dB in humans. Gerbils also show the largest amount of masking release in this condition compared to all other tested flanking-band positions (21.3 dB, mean CMR at a flanking band center frequency of 2100 Hz). Schooneveldt and Moore (1989) suggested a special cue that could improve signal detection within one auditory filter: If narrow bands of noise are presented together, periodic minima occur in the envelope of the composite masker caused by beating of the carrier frequencies. The occurrence of such minima increases for slow rates of beats. The rate of beats depends on the difference in the center frequencies and it is slowest for flanking-band center frequencies close to the signal frequency. These additional minima could enhance signal detection. In contrast to humans, in gerbils the amount of masking release for flanking bands tuned away from the signal frequency was similar to the amount of masking release observed with flanking bands positioned close to the on-frequency band, i.e. within one auditory filter. Only for the flanking band centered at 400 Hz a clear decrease of the masking release was found. An explanation for this decrease could be that the hearing sensitivity of the gerbil is deteriorated at 400 Hz. Ryan (1976) determined the auditory sensitivity of the gerbil by measuring the detection of pure tones. Between 1 and 16 kHz the gerbils' detection thresholds were stable (mean 4.6 dB SPL). Between 1 and 0.1 kHz the hearing sensitivity in the gerbil declined at a higher a rate (12 dB/octave) than observed in the human, resulting in a detection threshold of about 25 dB SPL at 400 Hz. Therefore, at 400 Hz stimuli are presented at a lower sensation level. Moore and Shailer (1991) showed that the presentation at low sensation levels reduces the amount of CMR. In contrast to the data in gerbils, the release from masking in humans decreased considerably with increasing distance between on-frequency band and flanking band. For flanking-band frequencies of 1000, 1400, 2600 and 3000 Hz there is only about half the amount of masking release in humans than for flanking band frequencies close to the signal frequency of 2000 Hz.

Thus, across-channel components of CMR seem to be larger in the gerbils than in the humans. These findings are consistent with the results from the band-narrowing experiment that also demonstrated that gerbils seem to be able to integrate acoustic information over a wider frequency range than humans.

3 Cochlear-Implant Listeners

3.1 Introduction

Cochlear implants (CI) are surgically implanted devices electrically stimulating the auditory nerve that are used as a treatment for profoundly and completely deaf people with sensorineural hearing loss. The field of cochlear implantation is developing rapidly. In the last 20 years the implementation of cochlear implants has progressed from a highly experimental procedure to a standardized clinical application with steady improvement. A large number of studies have demonstrated that the majority of CI subjects benefit considerably from the devices. However, auditory performance varies widely ranging from the simple detection of sound to the recognition of normal speech without visual support. Until now there is no satisfactory explanation for the wide variation in performance in CI subjects and it still is not possible to predict how an individual will perform after implantation. A number of factors possibly influence the performance. Uncontrollable factors are, for example, the subjects' cause of deafness, cochlear pathology, survival of cochlear ganglion cells and other structures in the auditory pathway or the surgical placement of the electrode. Biographical factors, for example, the age of onset of deafness and the duration of unaided profound deafness play an important role. It has been shown that the success of implantation for prelingually deaf adults is limited probably due to degeneration effects resulting from long-term sound deprivation (e.g. Busby et al 1993, Tong et al. 1988, Ponton et al. 1999). Former knowledge and experience with speech and other acoustic signals seems to be important to interpret the information transmitted by the implant. Nowadays cochlear implants are increasingly used in children. The tendency goes towards implanting as early as possible in life after a profound deafness has been ascertained and before the development of the auditory system is complete. Thus the auditory input can be of considerably assistance in developing both speech production and speech perception.

CI subjects usually perform well in quiet conditions. In the presence of noise, however, most of them have severe problems extracting important signals like speech from background noise (e.g. Müller-Deiler et al. 1995, Fu et al. 1998, Friesen et al. 2001). Unfortunately, most everyday listening conditions contain background noise and, therefore, the improvement of signal detection in noise is of great importance for cochlear-implant subjects. The detection of pure tones in the presence of masking noise in normal hearing has been explained by the power spectrum model of masking (Patterson and Moore 1986). According to this model, the auditory system behaves as a bank of overlapping band-pass filters. For detecting a signal in a masking noise, the auditory filter is used with a center frequency that is tuned to the signal frequency. Signal threshold is determined by the signal-to-noise ratio at the filter output that is required to detect the signal. A narrow filter bandwidth would limit the amount of masking noise and render the signal easy to hear. A broad bandwidth would allow more noise to pass through the filter and render the signal more difficult to hear. Therefore, the width of the auditory filters is decisive for signal detection in noise. Since the inner ear is not functioning in cochlear-implant listeners, the speech processor using a set of band-pass filters realizes the frequency analysis externally. The number of band-pass filters depends on the number of available electrodes, which vary in the different implant systems (8-22 electrode channels). The frequency range divided by the band-pass filters also varies across implant systems. Additionally, the frequency maps can be adjusted for each subject to allow for individual conditions, e.g. the number of functioning electrodes in a subject is reduced due to physiological or anatomical restrictions. Therefore, the width of the filters varies across implant systems and subjects (300 Hz –900 Hz for electrodes corresponding to about 2 kHz). The reduced frequency selectivity compared to normal-hearing subjects could impair signal detection in noise of cochlear-implant subjects.

Comodulation masking release (CMR) is a mechanism of the auditory system to improve signal detection in noise. The ability to use this mechanism would be helpful for cochlear-implant subjects to improve their performance in noisy situations. Good frequency selectivity is an important prerequisite for the mechanism of CMR. Since one component of CMR is based on the integration of information across channels, the presence of independent frequency channels is necessary. The amount of CMR increases the more channels are involved. A problem in electric stimulation could be that due to electric current spread, the independence of the different channels is limited. To utilize the CMR mechanism, a good temporal resolution of the auditory system is necessary. Mechanisms to explain CMR are based on the extraction and comparison of the temporal envelope either in one or in different auditory filters. Therefore, the auditory system must be able to resolve the temporal fluctuations of the masking noise. In addition, correlated amplitude fluctuations in different frequency regions must be preserved to enable across-channel effects. Besides the CI subjects' residual auditory function, the ability of the speech processors and the speech coding strategy will be crucial to code the temporal structure precisely. By assessment of the psychophysical characteristics of sensation produced by the implant, coding strategies that make the best use of these characteristics can be developed. Therefore, it is important to investigate basic features of the auditory system of CI subjects to further improve their performance. The CMR measure may be informative about the ability of cochlear-implant subjects to separate and analyze competing sounds.

3.1.1 Function of Cochlear Implants

A cochlear-implant device is composed of two main components: an internal, implanted component and an external component, which is worn on the body. There are multiple manufacturers and designs for CI devices, but all operate on similar principles. The internal part of a cochlear implant is the receiver-stimulator package with the electrode array. The electrode array with 6-22 electrode contacts is inserted by the surgeon into the scala tympani in an attempt to stimulate a localized region of the auditory nerve using frequency- and amplitude-specific electric signals and thus take advantage of the normal tonotopic organization of the cochlea. The receiver-stimulator is placed permanently into the mastoid bone under the skin. The external parts of the system are the headset and the speech processor. The headset consists of the transmitting coil, which is held by a magnet opposite to the implanted receiver, and the microphone. The speech processor either is worn in a little pocket on the body (WSP, wearable speech processor) or it is combined with the headset and worn behind the ear (BTE).

The acoustic signal is picked up by the microphone of the headset and processed by the speech processor converting the acoustic signal into an electric signal using different speech coding strategies. Today most coding strategies are based on spectral analysis of the signal that is achieved by dividing the signal into frequency bands using a set of band-pass filters. The output of each filter is allocated to one electrode on the electrode array. The electrodes can be operated sequentially or simultaneously. An advantage of sequential stimulation compared to simultaneous stimulation is a reduction of interaction between the electric fields of the electrodes. Speech coding strategies can be divided into two main categories: one using analog signals for stimulation, the other using trains of electric pulses. There are three electric parameters, which can deliver information to the auditory nerve: the amplitude, the pulse rate and the place of stimulation. The coded electric signal is sent to the transmitting coil via a cable and further through the skin to the implanted receiver/stimulator via a radio signal. The receiver/stimulator delivers the correct amount of electrical stimulation to the appropriate electrodes on the array to represent the sound signal. The electrodes along the array then stimulate the remaining auditory-nerve fibers in the cochlea.

3.1.2 Coding Strategies

The subjects in this study used implant systems of three different manufacturers that are the leading companies in cochlear implant production: Cochlear Incorporation (Nucleus), Advanced Bionics (Clarion), Med-El (Combi 40). Other available CI system will not be mentioned as they were not studied. Here I only describe coding strategies used by the participating subjects.

3.1.2.1 Cochlear Incorporation (Nucleus)

In the Nucleus cochlear implant system, 22 active electrodes are available. Only pulsatile sequential stimulation is possible. The common feature of the coding strategies is the division of the incoming acoustic signal into several frequency channels. Each of these channels stimulates one specific electrode along the electrode array. The coding strategies differ in the number and choice of channels and in pattern and rate of stimulation. The choice of electrodes can be fixed or dynamic. The SPEAK strategy divides the acoustic signal into 20 continuous frequency bands spanning a maximum frequency range of 0.15 to 18.8 kHz with intervening frequencies spaced on a logarithmic scale. The energy in each frequency band is measured and a dynamic choice of electrodes takes place according to the amplitude of each channel. Between 1 and 10 frequency bands with the highest energy are selected and the electrodes assigned to these bands receive biphasic pulses. The number of selected electrodes depends on the frequency content of the signal and represents the largest spectral peaks in the signal. The stimulation of the chosen electrodes takes place from the base to the apex of the cochlea. The rate of stimulation is not fixed but optimized according to the number of maxima detected in each processing cycle and the stimulus intensity. It varies dynamically between 180 and 300 Hz, resulting in a mean pulse rate of 250 Hz/channel. The CIS (Continuous Interleaved Sampling) strategy uses no dynamic choice of electrodes, but stimulates a fixed set of electrodes (4, 6, 8 or 12) at a high rate. The incoming signal is first passed through a bank of bandpass filters. The number of filters corresponds to the number of active electrode channels. Each electrode is stimulated for every sound. The pulse amplitude depends on the energy content of the spectrum and is derived from the envelope of the filter output. Available pulse rates are 900, 1200, 1800 or 2400 Hz/channel. The ACE strategy combines the best features of the SPEAK and CIS coding strategies. Like the SPEAK strategy the ACE strategy allows a dynamic choice of electrodes. ACE selects 1-20 frequency bands, which contain most information. Additionally, ACE offers the possibility of high rate stimulation. Stimulation rates between 250 and 2400 Hz/channel can be chosen with a total maximum stimulation rate of 14.400 pps.

3.1.2.2 Advanced Bionics Corporation (Clarion)

The Clarion system offers the possibility of two types of stimulation: A simultaneous stimulation at each electrode at the same time and sequential stimulation at one electrode after another. The Clarion system is equipped with 16 electrode contacts arranged in 8 staggered pairs. This results in 8 independent channels, which can generate analog and pulsatile waveforms. The CIS strategy converts sound into digital pulses and stimulates the electrodes sequentially. The SAS strategy (Simultaneous Analog Stimulation) converts sounds into analog waveforms and stimulates the electrodes simultaneously. In both strategies the acoustic signal is divided into several frequency bands corresponding to the number of active electrodes spanning a maximum frequency range from 250 Hz to 6800 Hz. The band-pass filters are based on a logarithmic division of the channels in accordance with the frequency arrangement of the basilar membrane. With a reduction of numbers of electrodes, the total frequency range remains the same, but the range of each electrode is broadened. The output of seven or eight filter bands is directed to seven or eight electrode pairs assigned to those frequency bands.

3.1.2.3 Med-El (Combi 40+)

The Combi 40+ implant is a 12-channel device implementing a high-rate CIS strategy. The system generates biphasic current pulses up to a maximum pulse rate of 18.180 pulses per second. Stimulation occurs always in monopolar mode with reference to the extra-cochlear ground electrode. The signal is separated into 12 logarithmically spaced frequency bands covering a total range of 300-5500 Hz. The output stages produce series of biphasic pulses, which are delivered sequentially to each electrode. The amplitude of each pulse is determined by the output of the envelope detector for its respective channel at the time of stimulation.

3.2 CMR in Cochlear-Implant Listeners

3.2.1 Methods

3.2.1.1 Subjects

Time for testing each subject was restricted. Because of the distance between the subjects' place of residence and place of testing, it was not possible to see the subjects several times. Therefore, a full set of parameter variations usually seen in CMR experiments could not be realized. In both experiments I chose parameters for which the largest amount of CMR could be expected. Additionally, CI subjects are not able to perform time-extensive sessions due to their limited resilience. Therefore, most of the masked thresholds were determined in only one session. If additional time was available, a second session was conducted and data were averaged.

3.2.1.1.1 CMR in Wide-band Noise Maskers

22 CI-listeners with different CI systems volunteered in this experiment. Subjects' electrical hardware details are shown in table 2. Subject's everyday speech processor settings,

coding strategies and their individually adjusted frequency allocation maps were used. All subjects were postlingually deaf adults to reduce the variability between subjects. Their age ranged from 20 to 68 years.

Table 2: Implant system, speech processor and speech coding strategy of the participating subjects.

Subject	Implant System	Speech Processor	Coding Strategy
1	Nucleus	Spectra 22 (WSP)	SPEAK
2	Clarion	WSP	SAS
3	Nucleus	Spectra 22 (WSP)	SPEAK
4	Med-El	Tempo+ (BTE)	CIS
5	Nucleus	Sprint (WSP)	ACE
6	Nucleus	Spectra 22 (WSP)	SPEAK
7	Clarion	WSP	CIS
8	Nucleus	Spectra 22 (WSP)	SPEAK
9	Nucleus	Esprit (BTE)	SPEAK
10	Clarion	Platinum (WSP)	SAS
11	Med-El	Tempo+ (BTE)	CIS
12	Med-El	Cis Pro+ (WSP)	CIS
13	Nucleus	Esprit (BTE)	SPEAK
14	Clarion	Platinum (WSP)	SAS
15	Nucleus	Esprit (BTE)	SPEAK
16	Nucleus	Esprit (BTE)	SPEAK
17	Clarion	WSP	CIS
18	Med-El	Tempo+ (BTE)	CIS
19	Nucleus	Spectra 22 (WSP)	SPEAK
20	Nucleus	Sprint (WSP)	CIS
21	Clarion	WSP	SAS
22	Clarion	Platinum (WSP)	CIS

3.2.1.1.2 CMR in Narrow-band Noise Maskers

20 CI-listeners with different CI systems volunteered in this experiment. Subject's electrical hardware details are shown in table 3. Subject's everyday speech processor settings, coding strategies and their individually adjusted frequency allocation maps were used. All subjects were postlingually deaf adults to reduce the variability between subjects. Their age ranged from 21 to 65 years.

Table 3: Implant system, speech processor and speech coding strategy of the participating subjects.

Subject	Implant System	Speech Processor	Coding Strategy
1	Nucleus	Sprint (WSP)	ACE
2	Med-El	Cis Pro+ (WSP)	CIS
3	Clarion	Platinum (WSP)	CIS
4	Med-El	Tempo+ (BTE)	CIS
5	Med-El	Tempo+ (BTE)	CIS
6	Med-El	Tempo+ (BTE)	CIS
7	Nucleus	Sprint (WSP)	ACE
8	Clarion	WSP	SAS
9	Nucleus	Esprit (BTE)	SPEAK
10	Med-El	Tempo+ (BTE)	CIS
11	Clarion	Platinum (WSP)	SAS
12	Clarion	WSP	CIS
13	Clarion	Platinum (WSP)	SAS
14	Nucleus	Esprit (BTE)	SPEAK
15	Med-El	Tempo+ (BTE)	CIS
16	Clarion	Platinum (WSP)	SAS
17	Clarion	Platinum (WSP)	CIS
18	Med-El	Cis Pro+ (WSP)	CIS
19	Nucleus	Spectra 22 (WSP)	SPEAK
20	Clarion	WSP	CIS

3.2.1.2 Apparatus

Stimuli were presented in the free sound field and processed by each CI system. Subjects were seated in front of the speaker (Canton Twin 700), with the microphone of the headset in 1 m distance from the speaker. A Gericom laptop generated the sound stimuli (16-bit D/A converter; 44.1 kHz sampling rate). In the first period of experiments, 30-min segments of the noise stimuli were stored on a CD and played via an external CD player (Technics SL-XP140). Test signals and noise stimuli were delivered separately to two computer-controlled attenuators (Tucker-Davis PA4), which adjusted the level. Test signal and noise stimuli were then amplified (Harman/Kardon HK 6350) and presented through the speaker. Sound levels were determined with a sound-level meter (RadioShack 330-2050) prior to each session at the subject's ear position. To report the detection of the signal the subjects pressed a button. The subjects' response was recorded by the Gericom Laptop via a Tucker-Davis PI2 interface.

3.2.1.3 Stimuli

3.2.1.3.1 CMR in Wide-band Noise Maskers

The test signal was a 2-kHz pure tone of 410-ms total duration including 10-ms raised cosine ramps. The masker was a 3200-Hz-wide band of noise spectrally centered on the signal. I chose this condition out of the set of parameters commonly used in the band-narrowing paradigm (e.g. Schooneveldt and Moore 1989, Moore and Shailer 1991) because it revealed the largest amount of CMR in normal-hearing subjects and because within-channel cues as well as across-channel cues are available to produce CMR. The band-passed noise maskers were generated by digital filtering of Gaussian white noise using a 1024-point FIR filter (programs: SAP, fir_noise by Georg Klump). 5-min segments of the band-passed noise were stored on disc and played repeatedly during the test sessions to get a continuous masking background. To avoid clicks at the transition, 200-ms linear ramps were applied to the beginning and the end of the noise fragments. Comodulated noise bands were generated by multiplying a Gaussian white noise with a 12.5-Hz low-pass noise before subjecting it to a final band-pass filtering (program: cmr_noise_test by Georg Klump). The masker was presented at a spectrum level of 30 dB/Hz. In 3 subjects, the spectrum level of the masker had to be reduced to 25 dB/Hz.

3.2.1.3.2 CMR in Narrow-band Noise Maskers

The masker consisted of two narrow-band noise stimuli (bandwidth 25 Hz). For each listener, signal frequency and on-frequency band were adjusted to match the peak frequency of an electrode representing about 2 kHz. The flanking band was positioned close to the upper cut-off frequency of this electrode's filter function, i.e. both noise bands are placed within one channel. There were two reasons for the choice of these stimulus parameters: First, since a single channel is stimulated, only within-channel cues are available to produce CMR, excluding the contribution of across-channel cues. A second reason was that normal-hearing subjects showed the largest amount of CMR in this condition of the flanking-band paradigm. To generate the noise bands, a 6-min lowpass noise (cut-off frequency 12.5 Hz) was multiplied with a pure tone (used programs: "bandpassnoise.new" by Moritz Franosch, "multi" by Georg Klump). This method produced 25-Hz-wide bands of noise centered on the frequency of the pure tone. Since the same low-pass noise was used for the multiplication, both noise bands showed identical envelopes. To create the correlated masker, on-frequency and flanking band were added ("addi" by Georg Klump). To create the uncorrelated masker, the first 2 s of the on-frequency band were removed, which means that the envelope of the flanking band was time shifted in relation to the envelope of the on-frequency band by 2s. The on-frequency and particular flanking band were added together and shortened to 5-min segments ("Cool Edit", Syntrillum Software Corporation). These 5-min segments of the noise were played repeatedly to get a continuous masking background. To avoid clicks at the transition, 200-ms linear ramps were applied to the beginning and the end of the 5-min noise segments. The spectrum level of the noise was 40 dB/Hz.

3.2.1.4 Procedure

In both experiments, the subjects' task was to detect a pure tone presented at randomly chosen times in a continuous masker. The subject did not receive any feedback during the measurements. Thresholds were measured using a Go/Nogo procedure. Test signals were presented according to the method of limits and using a three-down, one-up paradigm. The signal level was increased after each incorrect response and decreased after three successive correct responses to converge on a signal amplitude that would produce 79.4% correct responses (Levitt 1971). The step size was 8 dB down to the first reversal and then 2 dB for the remaining reversals. An experimental run continued until the signal level reversed 12 times and the last 8 reversals were averaged as the measure of masked threshold.

3.2.2 Results

3.2.2.1 CMR in Wide-band Noise Maskers

Comodulation masking release is defined as the difference between detection thresholds in the unmodulated and comodulated maskers. Signal-to-noise ratios at the detection threshold in the unmodulated or comodulated maskers for each subject are shown in Figure 7.

14 subjects show higher S/N ratios in the comodulated noise masker than in the unmodulated noise masker. For 4 subjects masked thresholds in both types of maskers are more or less equal. For only 4 subjects signal detection did improve slightly in the comodulated masker compared to the unmodulated masker, as it would be expected. There is a wide variation between individuals in S/N ratios necessary for signal detection in the unmodulated masker (17.6 dB to 47.0 dB) as well as in the comodulated masker (23.6 dB to 47.0 dB).

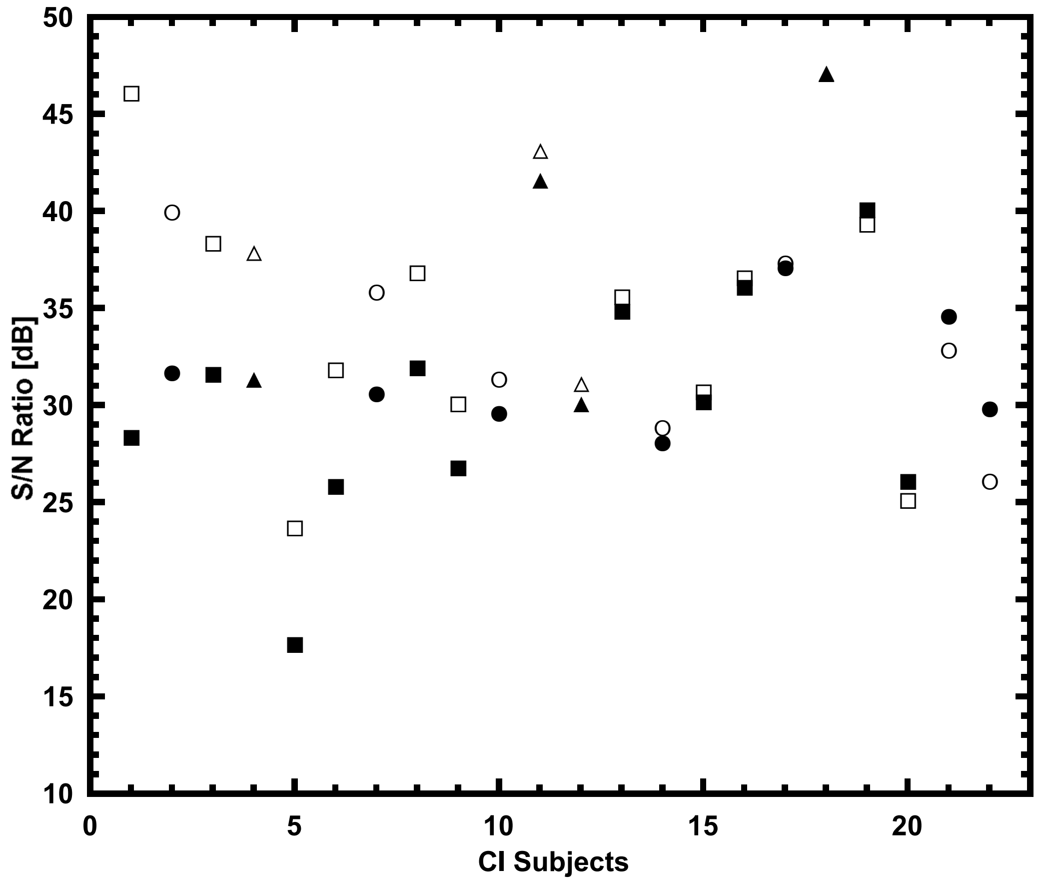

Figure 7: Signal-to-noise-ratios at the masked threshold for 22 CI listeners: closed symbols show thresholds in unmodulated 3200-Hz-wide noise maskers, open symbols show thresholds in comodulated noise maskers. Subjects are ordered according to the observed amount of CMR. Different symbols indicate the implant system (circles: Clarion, triangles: Med-El, rectangles: Nucleus).

The effects of implant type and coding strategy on the S/N ratios were tested separately for the unmodulated and comodulated condition in a set of One-Way-ANOVAs. The analysis revealed no significant difference between the S/N ratios neither for the type of implant nor for the different coding strategies in both masker conditions. Since there were no significant differences between the performance of the subjects using different types of implant and coding strategies, all data were pooled. A Wilcoxon signed ranks test was conducted with the complete set of data to test for differences between the two conditions: the S/N ratios in the unmodulated masker were significantly lower than the S/N ratios observed for the comodulated masker ($p<0.006$). Averaging the data of all subjects results in a mean S/N ratio in the unmodulated masker of 31.8 dB and of 34.7 dB in the comodulated masker, respectively. Therefore, no CMR was found, but rather a converse effect (-2.9 dB).

3.2.2.2 CMR in Narrow-band Noise Maskers

Signal-to-noise ratios in uncorrelated or correlated maskers for each subject are shown in figure 8. 16 subjects show higher thresholds in the uncorrelated noise masker than in the correlated noise masker. For 4 subjects masked thresholds in the correlated masker were higher than in to the uncorrelated masker. Again there is a wide variation in S/N ratios between individuals in the uncorrelated masker (17.5 dB to 34.8 dB) as well as in the correlated masker (15.8 dB to 31.0 dB). A mean S/N ratio of 25.0 dB for uncorrelated maskers and of 22.4 dB for correlated maskers was found, resulting in a small amount of CMR (2.6 dB). The effect of implant type and coding strategy on the S/N ratios was tested separately for the unmodulated and comodulated condition in a set of One-Way-ANOVAs. No significant difference was found between the S/N ratios neither for the type of implant nor for the different coding strategies in both masker conditions. Since there were no significant differences between the performance of the subjects using different types of implant and coding strategies all data were pooled. A Wilcoxon-signed-ranks test showed that in correlated noise maskers S/N-ratios at the detection threshold were significantly lower than in uncorrelated noise maskers ($p<0.006$).

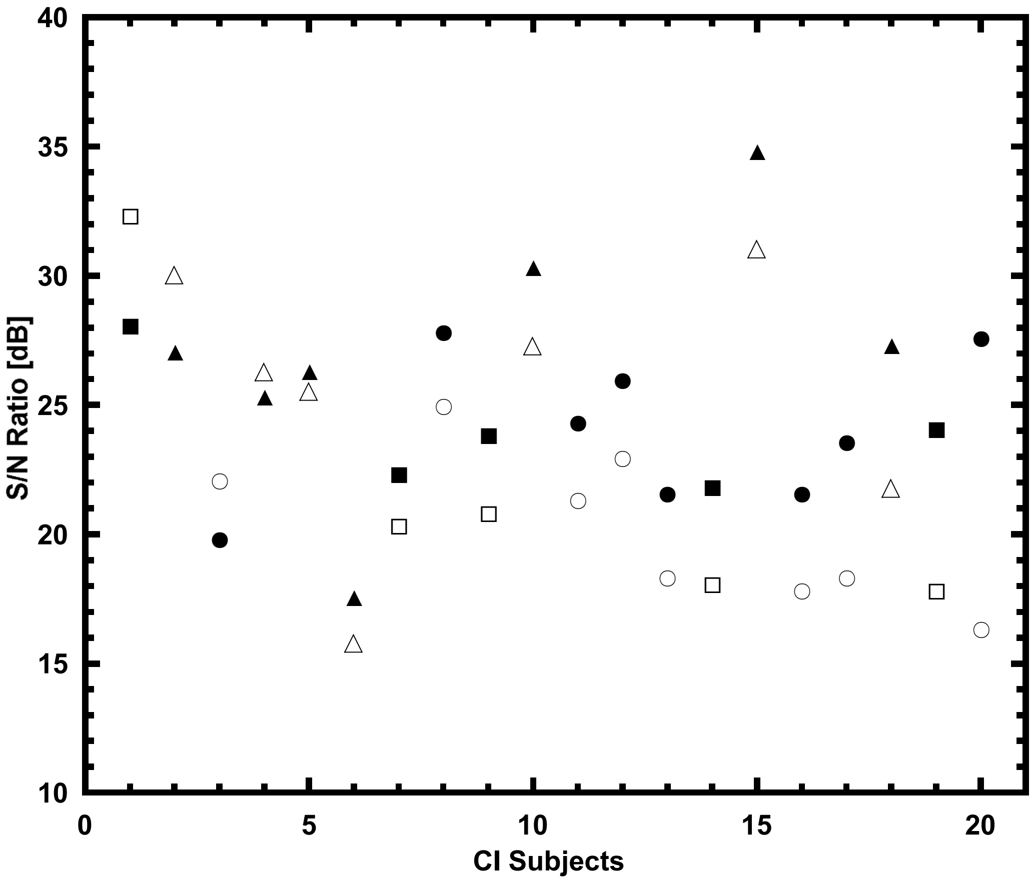

Figure 8: Signal-to-noise ratios at the masked threshold for 20 CI listeners: closed symbols show thresholds in uncorrelated noise maskers, open symbols show thresholds in correlated noise maskers. Subjects are ordered according to the observed amount of CMR. Different symbols indicate the implant system (circles: Clarion, triangles: Med-El, rectangles: Nucleus).

3.2.3 Discussion

CI listeners appear not to be able to fully exploit CMR mechanisms for improving signal detection. When presenting a single 3200-Hz wide on-frequency noise masker, we could not find CMR, but rather a converse effect. For most CI listeners, the comodulation of the noise made it even harder to detect the 2-kHz tone. For normal-hearing listeners in comparable conditions signal detection in comodulated noise is improved by 12 dB (Schooneveldt and Moore 1989). In this condition within- and across-channel cues should be available for the listeners. In the flanking-band paradigm presenting two narrow bands of noise within one channel, we could observe a small CMR in the CI listeners (2.6 dB). For normal-hearing listeners in comparable conditions a CMR of 14 dB has been found (Schooneveldt and Moore 1987). The results of both experiments indicate that CI listeners are not able to use across-channel cues and that the utilization of the within-channel cues is impaired in CI listeners.

Before discussing possible reasons for the lack of CMR in CI listeners, it is noteworthy that CI subjects in general need higher S/N ratios to detect the signal compared to normal-hearing subjects. In the experiment with the 3200-Hz-wide masker, the mean S/N ratio for the CI subjects in the unmodulated masker was 31.8 dB. In normal-hearing subjects a S/N ratio of about 16 dB has been found (Schooneveldt and Moore 1989). The S/N ratios in the comodulated masker are even more elevated compared to normal-hearing subjects. A mean S/N ratio of 34.7 dB has been found in the CI listeners. In normal-hearing subjects the S/N ratios necessary for signal detection in comodulated noise decreased to 4 dB (Schooneveldt and Moore 1989). According to the "power spectrum model of masking" the elevated thresholds in cochlear-implant listeners imply broader auditory filters than are present in normal-hearing listeners. A broader filter would allow more noise to pass through the filter and, therefore, the signal would be harder to detect. However, this is not an explanation for the elevated S/N ratios in the experiment with the narrow-band noise masker in which the stimulation occurs within one auditory filter. In this experiment the CI subjects needed a mean S/N ratio of 22.4 dB to detect the signal in the uncorrelated masker compared to a S/N ratio of about 14 dB in normal-hearing subjects (Schooneveldt and Moore 1987). One reason for the difficulties of CI subjects to detect the pure-tone signal in a narrow-band noise masker could be that a poor temporal resolution in the CI subjects prevents the analysis of the temporal fluctuations of the masker and, thus, the separation of the signal from the masker. Therefore, the temporal resolution of CI subjects was investigated in a gap-detection task in the present study and data from this experiment will be presented below. The raised S/N ratios found in both experiments confirm that CI-subjects do have additional problems detecting signals in noise. Thus, the utilization of the mechanisms of CMR would be of great importance for the CI subjects. Several factors may contribute to the diminished CMR in CI subjects. First, poor frequency selectivity may reduce the independence of information at different frequency regions, thereby reducing the magnitude of across-channel cues. A lower number of independent frequency channels might also contribute to a reduced CMR. A second factor could be that due to an impaired temporal resolution CI listeners are not able to analyze the temporal structure of the masker sufficiently. Finally, the presentation of the stimuli at low sensation levels due to the limited dynamic range of the CI subjects could influence the amount of CMR negatively.

Several studies investigated CMR in subjects with cochlear hearing loss using a band-narrowing paradigm (Hall and Grose 1989, Hall et al. 1988, Moore et al. 1993). In general, they found the same pattern as for normal hearing subjects, but a reduced amount of masking release. The stagnation of the S/N ratios in the unmodulated noise and the decrease of S/N ratios in the modulated noise with increasing masker bandwidth occurred at wider bandwidths. This higher critical bandwidth indicates that hearing-impaired subjects have broader than normal auditory filters. Due to the broader auditory filters of the hearing impaired subjects only a small number of auditory filters is involved, even for the wide masker bandwidth. Compared to normal-hearing listeners, CI subjects have only a small number of frequency channels available. The number of frequency channels depends on the number of available electrodes ranging between 8 and 22 depending on the implant type and the subject's individual conditions. Therefore, the segregation of the frequency components of the acoustic signal is less accurate than in normal-hearing subjects. Since good frequency selectivity is a prerequisite for large CMR, one possible reason for the small or even absent CMR in cochlear implant listeners may be reduced frequency selectivity. Testing the "place" pitch percept by stimulating different electrodes, it has been shown that pitch estimation in CI subjects across electrodes was consistent with the tonotopic organization of the cochlea. The perceived pitch increased as the stimulating electrode became more basal (Tong et al. 1982, Busby et al. 1994, Busby and Clark 2000, Nelson et al 1995, Donaldson and Nelson 2000). Electrode ranking performance improved linearly with spatial separation between electrodes. Some subjects were able to discriminate between electrodes separated by the minimum possible distance (0.75 mm), i.e. between two adjacent electrodes (Nelson et al. 1995). However, there was a wide variation in performance across subjects. Poor performing subjects were not able to discriminate between electrodes until the electrodes involved in the comparison were separated by 13 mm (17 electrodes). The inability to distinguish between electrodes could be a reason for the lack of CMR in the experiment with the wide-band masker. In this experiment, information from adjacent electrodes has to be analyzed to fully utilize CMR. If the CI subjects cannot distinguish between the electrodes they will not receive independent information from the different electrode channels and across-channel cues will not be available. It has been shown in normal-hearing subjects that the amount of CMR increases the larger the number of auditory filters involved in signal detection. Furthermore, the independence of the output of the filters involved is important. Multi-channel cochlear implants can only be effective if their channels are analyzed independently of each other. Under optimal conditions, each electrode should activate a separate population of neurons. If there is an overlap between the populations of neurons stimulated by different electrodes, the frequency selectivity created by the band-pass filtering of the acoustic signal in the speech processor will be diminished. Electric current spread could produce interaction between electrodes and limit spectral resolution in cochlear-implant subjects. A method to measure the current spread around the stimulating electrode and thereby the independence of the different electrodes is forward masking. In this type of experiment the detection threshold of a signal following a masker is determined. With increasing time between signal and masker signal detection thresholds decrease. Since both stimuli activate the same neural population, the threshold shift is assumed to be dependent on the time the system needs to recover from the masker. If the masker and the signal stimulate the same neural population, we expect to find a larger threshold shift due to the masker than if the masker and the signal activate different neural populations. If signal and masker on different channels in a cochlear implant stimulate the same neural population, the signal threshold will be similar to that when signal and masker are on the same channel. The amount of the increase in threshold depends on the extend of overlap between the neural populations. Thus, the pattern of threshold shift as a function of separation between signal and masker electrode is a measure of channel interaction. Several studies using direct electric stimulation in CI subjects showed masking patterns similar to normal-hearing subjects. Signal threshold was highest when signal and masker were presented at the same electrode. With increasing spatial separation of signal and masker, the amount of masking is decreasing (Shannon 1983b, Tong and Clark 1986, Lim et al. 1989, Chatterjee and Shannon 1998). The comparable forward masking patterns in normal-hearing subjects and in cochlear-implant subjects using direct electric stimulation imply that the independence of the electrode channels of cochlear implants is efficient. Therefore, information from different electrode channels should be available in CI subjects for across-channel comparisons. However, this experiment requires only a discrimination between different stimulated electrodes, but not a comparison of information across channels.

In addition to frequency selectivity, another factor that is important for signal detection in modulated noise is the temporal resolution of the auditory system (e.g. Hall and Grose 1989). To make use of the fluctuation in the masker envelope, the auditory system must be able to follow the envelope fluctuations. This feature is important for both components contributing to CMR, within- and across-channel effects. There are different methods to measure the temporal resolution of the auditory system. One of them is gap detection. Cochlear-implant subjects generally show gap-detection thresholds comparable to normal-hearing subjects when using direct electrical stimulation (e.g. Shannon 1989). However, when using acoustic stimulation in combination with their speech processor performance deteriorates (e.g. Tyler et al. 1989). A gap-detection experiment studying both within and across-channel processing was part of this thesis and the results will be discussed with the available literature in section 3.3. Another experiment often applied to describe the temporal resolution of the auditory system uses the temporal modulation transfer functions (TMTF). In this paradigm, the detection of amplitude modulation as function of the modulation frequency is determined. TMTFs for normal hearing listeners show a low-pass filtering characteristic with a cut-off frequency around 100 Hz. Hearing-impaired listeners did show functions of similar shape although sometimes with a reduced sensitivity (e.g. Bacon and Viemeister 1985). TMTFs in cochlear-implant listeners have been determined using direct electrical stimulation of one electrode pair. For example, Shannon (1992) demonstrated that the TMTF of cochlear-implant subjects had the same low-pass characteristics as the TMTF of normal-hearing subjects. However, there were large differences between subjects. Cochlear-implant listeners' TMTFs had low-pass characteristics with a cut-off frequency near 140 Hz. Subjects could detect modulations best at modulation frequencies between 80 Hz and 100 Hz. Temporal resolution in CI subjects measured by electric direct stimulation seems to be even better than in normal-hearing subjects. Since the temporal resolution in cochlear-implant subjects using acoustic stimulation is compromised, the limiting factor seems not to be the capacity of their residual auditory system but the capacities of the speech processor and the implemented speech coding strategies.

Finally a factor that may contribute to the reduced amount of masking release in CI subjects is the presentation of the signals at lower sensation levels that is due to the limited dynamic range of the speech processor and electric stimulation. Moore et al. (1993) investigated CMR in subjects with unilateral hearing impairment. Because of their elevated absolute thresholds and the differences of loudness recruitment, a much smaller dynamic range is available in hearing-impaired subjects. The magnitude of CMR was smaller for the impaired ears than for the normal ears when tested at equal sound pressure level, but not when tested at equal sensation level. In addition, Moore and Shailer (1991) demonstrated that the amount of CMR in normal-hearing subjects is reduced at low sensation levels. This indicates that a low sensation level of the stimuli reduces the amount of masking release. Since the dynamic range in electric stimulation (30-60 dB) is much smaller than in acoustic stimulation (120 dB), the acoustic signal has to be compressed prior to further processing. Measurements showed that the dynamic range in CI-subjects is reduced to a maximum of 30 dB (e.g. Shannon 1983a). Therefore, cochlear-implant subjects have a limited dynamic range available and this could be an explanation for the reduction or lack of the release from masking.

3.3 Within- and Across-channel Gap Detection

3.3.1 Introduction

The CMR experiments in CI listeners reveal that they are not able to use the CMR mechanism sufficiently. Since they do show a small CMR in the within-channel task but not in the across-channel task it seems that CI listeners have difficulties in analyzing information form different channels at the same time. In addition, an impaired temporal resolution in the CI subjects could be responsible for the reduced CMR. To investigate within- and across-channel effects of temporal resolution in more detail, a gap-detection experiment using a white-noise carrier and an across-channel gap-detection experiment were conducted (e.g. Plomp 1964, Penner 1977, Phillips et al. 1997).

The white-noise gap-detection paradigm is one of the standard methods to measure auditory temporal resolution. The subjects' task in this paradigm is to detect a brief silent period (gap) at the temporal center of a white-noise stimulus. In normal hearing subjects the minimum-detectable gap in white noise ranges between 2 and 5 ms (e.g. Plomp 1964, Penner

1977). Although white noise excites many different frequency channels in the auditory system, it is generally assumed that this task depends primarily on within-channel processes, rather than on a comparison across channels (e.g. Phillips et al. 1997). Any perceived interruption in the stimulus, onset or offset, within one auditory channel could be used as a cue to detect the gap. Therefore, a discontinuity detection is performed by the activity in one single auditory filter activated by the sound.

In a new class of gap-detection experiments, the stimulus before (leading marker) and after the gap (trailing marker) consists of different frequencies, which means different places in the cochlea are stimulated (e.g. Phillips et al. 1997, Phillips 1999). Thus, for the detection of the gap across-channel processing is necessary in this type of experiment. A silent interval between the offset of excitation in one frequency region and the onset of excitation in a distant frequency region must be detected. Therefore, a comparison of the timing between different channels is required. However, in the across-channel task additional cues could play a role. Since the two markers contain different frequencies they elicit different pitch percepts. Due to this effect, even two markers without a gap between them can give rise to a gap percept. Therefore, in the across-channel task, gap detection could not only be influenced by the ability to detect differences in time but by the ability to detect differences in relative timing of excitation between different frequency channels of the auditory system.

3.3.2 Methods

3.3.2.1 Subjects

11 CI subjects with different CI systems volunteered in this experiment. Subject's electrical hardware details are shown in table 4. Stimuli were presented in the free sound field and were processed by each subject's speech processor. All subjects were postlingually deaf adults. Their age ranged form 20 to 69 years.

Table 4: Implant system, speech processor and speech coding strategy of the participating subjects.

Subject	Implant System	Speech Processor	Coding Strategy
1	Clarion	WSP	SAS
2	Nucleus	Sprint (WSP)	ACE
3	Nucleus	Esprit (BTE)	SPEAK
4	Nucleus	Spectra 22 (WSP)	SPEAK
5	Nucleus	Esprit (BTE)	SPEAK
6	Clarion	WSP	CIS
7	Clarion	Platinum (WSP)	SAS
8	Clarion	WSP	CIS
9	Med-El	Tempo+ (BTE)	CIS
10	Med-El	Tempo+ (BTE)	CIS
11	Med-El	Tempo+ (BTE)	CIS

3.3.2.2 Stimuli

In the within-channel task, a pulse of white noise (frequency range 100 to 10000 Hz) was repeated every 1300 ms as the reference stimulus. The total duration of the noise pulses was 800 ms, including 50-ms linear ramps at the beginning and the end. For the test stimulus a gap of varying duration was inserted in the temporal center of the noise pulse. In the across-channel task the frequency spectrum of the noise before the gap (leading marker) and the noise after the gap (trailing markers) were different. The two markers were 0.25-octave band-passed noise stimuli. In each listener, the center frequency of the leading marker was adjusted to match the peak frequency of an electrode representing about 2 kHz. The trailing marker was positioned in the middle of the frequency range of one or two electrodes higher in frequency. Since the frequency allocation maps are adjusted individually for each subject, the center frequencies of the marker vary between subjects. The center frequencies of the leading marker ranged from 1892 Hz to 2008 Hz, resulting in a mean center frequency of 1920 Hz. The center frequencies of the trailing marker ranged from 3100 Hz to 4668 Hz, resulting in a mean center frequency of 3985 Hz. The mean distance between the center frequencies of the two markers was 2065 Hz. The stimuli were presented at an overall level of 70 dB SPL.

3.3.2.3 Procedure

A GO/NOGO paradigm was used. Noise pulses without a gap were presented as the reference stimulus. After exceeding a randomly varying time interval a gap was presented in the center of a noise pulse. The subject's task was to report the detection of the gap between the markers by pressing a button. The subject did not receive any feedback during the measurements. Test signals were presented according to the method of constant stimuli. To obtain a measure of spontaneous responding, catch trials during which no gap was presented were inserted on 30 % of the trials. A block of ten trials, consisting of 3 catch trials and 7 test trials with different gap durations, was repeated 10 times in a session with a randomized sequence of the trials in each block. Since the task was difficult for the subjects, they were allowed to listen to markers with an easily detectable gap between them before the beginning of each session. This training continued until they were able to detect the large gap at every presentation. Sessions were excluded from the analysis if the false alarm rate exceeded 20 % or if the two best detectable test stimuli were reported with a probability of less than 80 %. A psychometric function was constructed and a threshold estimate was computed by linear interpolation of the value of the gap duration at which the detection measure d' was 1.8. Due to subjects' time limitations, only a single measure of gap-detection threshold in each condition was collected.

3.3.3 Results

Gap-detection thresholds for both conditions are shown in figure 9. With white-noise markers, the minimum detectable gaps range between 6.8 and 37.9 ms, resulting in a mean minimum detectable gap of 25.4 ms. In the condition in which the two markers were 0.25-oct band-passed noise stimuli with different center frequencies, the gap-detection thresholds are significantly higher (between 53.5 and 131 ms, mean 80.7, Wilcoxon-signed-ranks test p=0.003). The effect of implant type and coding strategy on the gap-detection thresholds was tested for both types of markers in a set of One-Way-ANOVA's. The analysis revealed no significant difference between the gap-detection thresholds neither for the type of implant nor for the different coding strategies in both marker conditions.

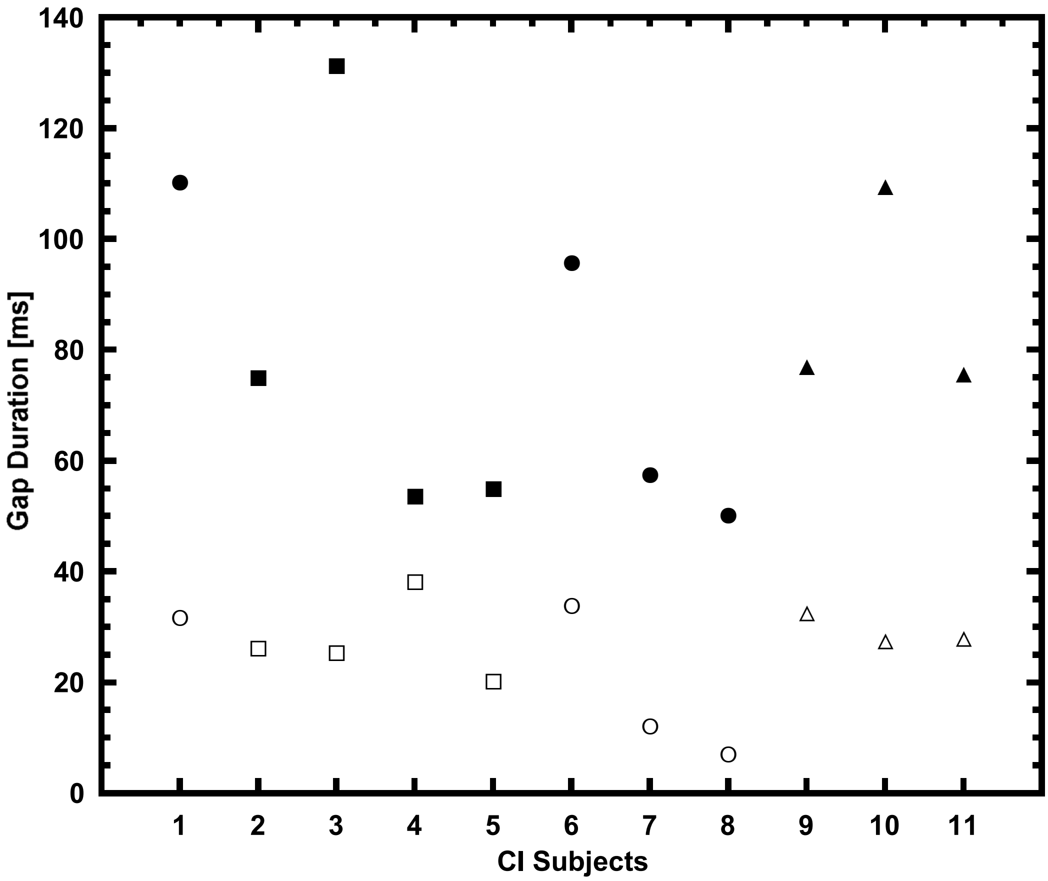

Figure 9: Gap-detection thresholds for 11 CI-subjects. Open symbols show thresholds for the within-channel task, closed symbols show thresholds for the across-channel task. Different symbols indicate the implant system (circles: Clarion, triangles: Med-El, rectangles: Nucleus).

3.3.4 Discussion

In the classical within-channel gap-detection task (identical leading and trailing marker containing white noise), the CI subjects in this study show elevated gap thresholds compared to normal hearing subjects resulting in a mean minimum detectable gap of 25.4 ms. However, there is a large variability across subjects with gap-detection thresholds ranging from 6.8 ms to 37.9 ms. With a gap-detection threshold of 6.8 ms the best performing CI subject shows a performance which is in the range of that observed in normal-hearing subjects. Only few studies on gap detection using acoustic stimulation in CI subjects are available. Tyler et al. (1989) used two octave bands of noise centered at 500 Hz (355-710 Hz) as marker. The duration of one marker was 500 ms including 10 ms raised cosine-shaped ramps at the beginning and the end of each marker. Consistent with results presented here, the gap-detection thresholds varied widely across subjects spanning an even wider range of gap-detection thresholds (7.5 to 200 ms). Muchnik et al. (1993) also used acoustic stimulation and measured gap detection between two noise bursts of 85-ms duration that had a frequency spectrum from 100 Hz to 4000 Hz. They divided the participating subjects in two subgroups using their speech-recognition performance as criterion. For the group of subjects with speech recognition ability they found a mean gap-detection threshold of 12.18 ms. For the group of subjects that could not recognize speech without the help of lip-reading, the mean minimum-detectable gap was 41.0 ms. Using acoustic stimulation in CI subjects the results are not only influenced by the residual auditory function of the subjects, but also by the speech processor's abilities. Most of the gap-detection studies in CI listeners are based on measurements with direct electrical stimulation, ruling out the influence of the speech processor. A general finding is that gap-detection thresholds in CI subjects using direct electrical stimulation are similar to those found in normal-hearing subjects (e.g. Moore and Glasberg 1988, Preece and Tyler 1989). Moore and Glasberg (1988) measured gap detection in sinusoids and band-pass filtered noise in subjects with a single-channel extracochlear implant. The electrode was not permanently implanted, but was mounted on an earmold, and inserted when required so as to make contact with the promontory. Electric stimuli were delivered by a custom-built isolated stimulator. The minimum-detectable gaps in sinusoidal markers varied across subjects, but the best performing subject showed thresholds comparable to those of normal-hearing subjects. The band-pass noise markers had center frequencies of 100, 200 and 400 Hz. For a center frequency of 100 Hz, noise bandwidth of 100 and 200 Hz were used. At 200 Hz, bandwidths were 100, 200 and 400 Hz. At 400 Hz, bandwidths were 200, 400, 800 Hz. The CI subjects showed larger gap-detection thresholds than normal-hearing subjects. For a fixed bandwidth of 200 Hz, the gap-detection thresholds increase with increasing center frequency, from about 29 ms at 100 Hz to 53 ms at 400 Hz. For a given center frequency, gap-detection thresholds decrease with increasing masker bandwidth. The gap-detection thresholds in band-pass noise were larger than those observed in sinusoidal markers. However, in normal hearing subjects thresholds in noise bands are higher than in sinusoids as well. A possible explanation for this is that inherent fluctuations in the noise limit the performance, which means that dips in the noise can be confused with the gap to be detected. One reason for the additional deterioration seen in the CI subjects could be their reduced dynamic range, which increases the probability to confuse the gap with dips in the noise. Shannon (1989) measured gap-detection thresholds in cochlear-implant subjects using electrical sinusoidal stimuli and trains of biphasic pulses. He found minimum-detectable gaps of 20-50 ms for low level stimuli and of 2-5 ms for high level stimuli, thus the magnitude and the level effect is very similar to normal-hearing subjects. These results indicate that temporal resolution, at least measured in a gap- detection task, is not impaired in subjects with cochlear implants when tested with direct electrical stimulation.

In the across-channel gap-detection task, it has been shown that in normal-hearing subjects gap-detection thresholds increase when the markers are presented to different channels (Phillips et al. 1997). Phillips et al. (1997) investigated within- and across-channel gap detection in normal-hearing listeners. In their study two noise pulses of 0.25-octave-wide bands of 300-ms duration bounded the gap. The noise stimuli were shaped with 0.5 ms linear rise-fall times, including those defining the gap. The leading marker was centered on 2-kHz, the center frequency of the trailing marker was the independent variable. For all subjects the minimum-detectable gaps for the within-channel condition, i.e. the center frequency of both markers was 2 kHz, were the smallest, ranging between 5.3 and 6.3 ms. These values are comparable to those found by others for similar stimulus conditions (e.g. Moore and Glasberg 1988, Formby and Muir 1988, Eddins et al. 1992). In the across-channel condition, i.e. if leading and trailing marker had different center frequencies, gap-detection thresholds increased with increasing spectral distance of the markers. Thresholds were between three and ten times worse than in the within-channel condition if a two-octave disparity between the markers was existent. Contrary to the within-channel task, a large variation between subjects occurs, indicating that the across-cannel task is more difficult even for normal-hearing subjects. In the sample of CI subjects studied here, the minimum-detectable gap in the across-channel task range between 53.5 and 131 ms. In the study in normal-hearing subjects by Phillips et al. (1997), gap-detection thresholds for a comparable distance between the center frequencies of the two markers varied between 10 ms and 20 ms across subjects. The results indicate that cochlear-implant subjects do have additional difficulties compared to normal-hearing listeners. Data on across-channel gap detection in CI listeners are only available using direct electrical stimulation. Hanekom and Shannon (1998) measured gap-detection thresholds as a function of electrode separation in three CI subjects. They presented the two markers either on the same electrode (standard electrode) or the trailing marker was presented on a different electrode. They measured gap-detection thresholds as a function of the separation of the two stimulated electrodes using several electrodes as standard electrodes. For markers presented at the same electrode, thresholds were lowest for all tested electrodes, ranging between 1 and 4 ms. With increasing channel distance, gap-detection thresholds increase considerably up to a factor of 10. For stimulus conditions comparable to those used in the present study (i.e. using the electrode corresponding to about 2 kHz as the standard electrode), a mean minimum-detectable gap of 2.2 ms was found presenting the leading and trailing marker at the same electrode. For markers with a frequency distance comparable to that used in the present study, the mean gap-detection threshold was 21.7 ms. The results indicate that CI subjects using direct electric stimulation show gap-detection thresholds within the range observed in normal-hearing subjects in both stimulus conditions. Wieringen and Wouters (1999) also looked at the influence of electrode distance on gap detection. Their results are in agreement with those of Hanekom and Moore (1998). Gap-detection thresholds increased with increasing channel distance. However, they did find a large improvement of performance after additional training. The deterioration of gap detection with increasing channel distance could be interpreted in terms of differences in neural interaction. If the distance between channels is small, the neural interaction will be larger resulting in smaller gap-detection thresholds. If the distance between channels is large, there will not be any neural interaction and an across-channel comparison has to be performed. However, Chatterjee et al. (1998) found deteriorated gap-detection thresholds in CI subjects also when presenting dissimilar markers at one electrode, i.e. in this condition only one neural channel will by involved and therefore neural interaction is not relevant. They used stimuli with a fixed amplitude and pulse rate of the leading marker and either different amplitude or pulse rate of the trailing marker. The lowest thresholds were found when both markers were identical. Both for pulse rate and for amplitude, gap-detection thresholds increased with increasing difference in these stimulus characteristics between leading and trailing marker. The authors conclude that in this condition a different mechanism is involved which is not reflecting the temporal acuity but rather a detection of the perceptual difference between the markers.

The impaired temporal resolution and the impaired across-channel processing observed in the CI listeners using acoustic stimulation could be an explanation for the reduced or lack of CMR in the CI subjects. The extraction of the temporal structure of the acoustic signals is necessary to utilize the mechanisms of CMR. CI listeners seem not to be able to use the mechanism of CMR to improve signal detection in noise. It is noteworthy that the experiments in the present study were performed using acoustic stimulation in the free sound field, i.e. the acoustic signals were processed by the speech processor. However, if direct electric stimulation is used, CI listeners show performances in basic psychoacoustic tasks like gap detection or forward masking that are comparable to that of normal-hearing subjects. The differences in performance of cochlear-implant subjects between acoustical and direct electric stimulation imply that their difficulties are not due to limitations of their residual auditory system. It is more likely that important features of the acoustic signal are not processed sufficiently by the speech processor and the implemented coding strategies. It would be interesting to investigate if CI listeners show a comparable amount of masking release to that observed in normal-hearing subjects if direct electric stimulation is used. Such a test, however, was not possible within the time limits given for this thesis.

4 Summary

In the natural environment we rarely find quiet conditions for acoustic communication. Acoustic signals like speech or communication sounds of animals will always be affected by masking background noise that impairs the detection of the signal. Therefore, the auditory system of humans and animals had to develop mechanisms to separate a useful and important signal from background noise. A mechanism that improves auditory signal detection in background noise is Comodulation Masking Release (CMR). The release of masking occurs if different spectral bands of the masker are coherently modulated in amplitude. Analysis within one auditory filter as well as the comparison of information across different auditory filters is necessary to fully utilize the mechanism of CMR. Therefore, CMR experiments can be used to study within- and across-channel processing of the auditory system.

Two CMR experiments were conducted in the gerbil (*Meriones unguiculatus*): the band-narrowing paradigm and the flanking-band paradigm. In both paradigms the gerbils showed clear evidence for CMR. Gerbils showed a larger amount of masking release than humans. The results of both experiments indicate that across-channel components of CMR seem to be larger in gerbils than in humans, i.e. gerbils are able to integrate acoustic information over a wider frequency range than humans. Despite the differences between humans and gerbils, the general pattern of masking release in the gerbil is similar to that observed in humans. Therefore, the Mongolian gerbil proved to be a suitable animal model for studying mechanisms underlying CMR. The comparison between behavioral and physiological performance in the same species, that is possible in the gerbil, can aid in finding its neural basis.

Cochlear-implant (CI) listeners usually perform well in quiet. The presence of noise results in a strong deterioration of their performance. The aim of the second part of this study was to examine whether the often compromised signal detection of CI listeners in fluctuating background noise could be due to a reduced ability to utilize CMR mechanisms. Subjects were tested in two experimental paradigms. CI listeners appear not to be able to fully exploit CMR mechanisms for improving signal detection. When presenting 2-kHz signals in a single

3200-Hz-wide on-frequency noise masker, no CMR was found, but rather a converse effect. For most CI listeners, comodulation of the noise made it even harder to detect the 2-kHz tone. In the experiment presenting two narrow bands of noise as the masker within one channel, a small CMR effect was observed in the CI listeners. The amount of masking release was clearly reduced compared to that found in normal-hearing listeners. The finding that a small CMR effect is present in the within-channel task, but not in the task in which additional across-channel cues are available indicates that the CI subjects are not able to use the across-channel cues. In a within- and across-channel gap-detection task CI listeners showed a performance that was worse than that of normal-hearing listeners. This indicates an impaired temporal resolution both in within- and across-channel processing.

5 Zusammenfassung

Akustische Kommunikation findet im täglichen Leben selten in einer ruhigen Umgebung statt. Akustische Signale wie z.B. die menschliche Sprache oder Kommunikationslaute von Tieren werden meistens von störenden Hintergrundgeräuschen maskiert, welche die Wahrnehmung des relevanten Signals beeinträchtigen. Das Hörsystem von Menschen und Tieren mußte daher Mechanismen entwickeln, welche die Wahrnehmung von Signalen in Störgeräuschen verbessern. "Comodulation Masking Release" (CMR) ist ein Mechanismus des Hörsystems, der die Signalentdeckung in Störgeräuschen verbessert. Ins Deutsche übertragen bedeutet dieser Begriff soviel wie "verminderte Maskierung durch kohärente Amplitudenmodulation". Die Verbesserung der Signalentdeckung tritt dann auf, wenn das Störgeräusch kohärente Amplitudenmodulationen in verschiedenen Frequenzbereichen aufweist. Für die effektive Nutzung von CMR ist sowohl eine Analyse innerhalb eines auditorischen Filters nötig, als auch der Vergleich von Informationen zwischen verschiedenen auditorischen Filtern. Aus diesem Grund sind CMR Versuche geeignet, sowohl die Verarbeitung von akustischer Information innerhalb eines Kanals als auch die Verarbeitung zwischen verschiedenen auditorischen Kanälen zu untersuchen.

In Verhaltensexperimenten wurden mit Wüstenrennmäusen zwei klassische CMR Versuche durchgeführt: Das sogenannte "band-narrowing paradigm" und das sogenannte "flanking-band paradigm". In beiden Versuchen konnte bei den Wüstenrennmäusen CMR nachgewiesen werden. Das Ausmaß des CMR ist bei Wüstenrennmäusen größer als bei Menschen. Die Ergebnisse beider Experimente deuten an, daß die Verarbeitung zwischen verschiedenen auditorischen Kanälen bei Wüstenrennmäuse eine größere Rolle spielt als bei Menschen. Wüstenrennmäuse können akustische Information über einen weiteren Frequenzbereich verarbeiten als Menschen. Trotz dieser Unterschiede ist das generelle Muster der Verminderung der Maskierung bei den Wüstenrennmäusen dem der Menschen sehr ähnlich. Die Mongolische Wüstenrennmaus eignet sich daher gut als Tiermodel, um die dem CMR zugrundeliegenden Mechanismen zu untersuchen.

In ruhiger Umgebung können Cochlea-Implantat (CI) Träger akustische Signale zum

Teil gut wahrnehmen, allerdings bereitet ihnen die Wahrnehmung von relevanten akustischen Signalen in Störgeräuschen große Schwierigkeiten. Ein Ziel der vorliegenden Arbeit war herauszufinden, ob CI Träger den CMR Mechanismus nutzen können, um die Wahrnehmung von Signalen in Störgeräuschen zu verbessern. Zwei CMR Versuche wurden mit CI Trägern durchgeführt. Die CI Träger sind anscheinend nicht in der Lage den CMR Mechanismus vollständig zu nutzen. Bei Verwendung eines 3200 Hz breiten Rauschmaskierers konnte kein CMR gefunden werden, sondern eher ein gegenteiliger Effekt. Den meisten CI Trägern fiel die Signalentdeckung in comoduliertem Rauschen schwerer als in unmoduliertem Rauschen. Bei Verwendung von zwei Schmalbandrauschen innerhalb eines auditorischen Filters als Maskierer konnte ein geringes CMR beobachtet werden. Das Ausmaß des CMR war deutlich geringer als bei Normalhörenden. Die Tatsache, daß ein geringes CMR nur innerhalb eines auditorischen Filters gefunden wurde, läßt vermuten, daß CI Träger nicht in der Lage sind, Informationen aus mehreren auditorischen Filtern in der Verarbeitung zu kombinieren. In einem zusätzlichen Experiment wurde die Fähigkeit der CI Träger untersucht, zeitliche Lücken zwischen zwei Signalen wahrzunehmen. Zwei Versuchsbedingungen wurden gewählt. Zum einen konnte die Lückenerkennung durch Verarbeitung innerhalb eines auditorischen Filters erfolgen, zum anderen mußte zwischen zwei auditorischen Filtern verglichen werden. Unter beiden Bedingungen zeigten die CI Träger schlechtere Leistungen als Normalhörende. Dies läßt auf ein schlechteres Zeitauflösungsvermögen des Hörsystems der CI Träger schließen.

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8 Appendix

A: Effects of signal duration on CMR

Signal-to-noise ratio (S/N) at detection threshold in dB for different signal durations.

200-ms signal duration:

S/N [dB] unmodulated noise

Masker Bandwidth	50 Hz	200 Hz	800 Hz	1600 Hz	3200 Hz
max	20.8	24.8	29.9	27.5	30
tom	19.3	24	26.5	28.5	30.3
romeo	26.3	24	28.2	25.6	26.8
mean	22.1	24.3	28.2	27.2	29.0
± SD	3.7	0.5	1.7	1.5	1.9
median	20.8	24	28.2	27.5	30

S/N [dB] comodulated noise

Masker Bandwidth	50 Hz	200 Hz	800 Hz	1600 Hz	3200 Hz
max	19.9	23.7	17.4	15.5	14.4
tom	20.4	21.4	19.6	12.8	14.3
romeo	25.7	20.9	15.4	14.6	14.1
mean	22.0	22.0	17.5	14.3	14.3
± SD	3.2	1.5	2.1	1.4	0.2
median	20.4	21.4	17.4	14.6	14.3

CMR [dB]

Masker Bandwidth	50 Hz	200 Hz	800 Hz	1600 Hz	3200 Hz
max	0.9	1.1	12.5	12.0	15.6
tom	-1.1	2.6	6.9	15.7	16.0
romeo	0.6	3.1	12.8	11.0	12.7
mean	0.1	2.3	10.7	12.9	14.8
± SD	1.1	1.0	3.3	2.5	1.8
median	0.6	2.6	12.5	12.0	15.6

100-ms signal duration:

S/N [dB] unmodulated noise

Masker Bandwidth	200 Hz	1600 Hz
max	28.8	31.4
tom	25.9	31.4
romeo	26.6	29.2
mean	27.1	30.7
± SD	1.5	1.3
median	26.6	31.4

S/N [dB] comodulated noise

Masker Bandwidth	200 Hz	1600 Hz
max	22.5	16.6
tom	23.6	16.6
romeo	28.8	15.8
mean	25.0	16.3
± SD	3.4	0.5
median	23.6	16.6

CMR [dB]

Masker Bandwidth	200 Hz	1600 Hz
max	6.3	14.8
tom	2.3	14.8
romeo	-2.2	13.4
mean	2.1	14.3
± SD	4.3	0.8
median	2.3	14.8

<u>50-ms signal duration:</u>

S/N [dB] unmodulated noise

Masker Bandwidth	200 Hz	1600 Hz
max	28.2	33.1
tom	29	31.9
romeo	30.5	31.3
mean	29.2	32.1
± SD	1.2	0.9
median	29	31.3

S/N [dB] comodulated noise

Masker Bandwidth	200 Hz	1600 Hz
max	29.2	23.4
tom	30.8	23.3
romeo	30.3	21.9
mean	30.1	22.9
± SD	0.8	0.8
median	30.3	23.3

CMR [dB]

Masker Bandwidth	200 Hz	1600 Hz
max	-1	9.7
tom	-1.8	8.6
romeo	0.2	9.4
mean	-0.9	9.2
± SD	1.0	0.6
median	-1	9.4

B: Flanking-band paradigm

Signal-to-noise ratio (S/N) at detection threshold in dB for several flanking-band center frequencies (f_c). At 2000 Hz, only the on-frequency band was presented.

Uncorrelated masker

f_c flanking band	400 Hz	1200 Hz	1600 Hz	1800 Hz	1900 Hz	2000 Hz	2100 Hz	2200 Hz	2400 Hz	2800 Hz	3600 Hz
max	14.3	17.8	19.1	17.4	19.6	14.8	19.7	16.8	17.3	15.5	17.3
tom	15.1	21.5	18	17.8	18.2	16.8	18.6	18.4	18.1	17	19.9
olga		14.9		19.5	22.9		21.5	21.6	15	15	16.9
julia	11.5	17.1	16.6	20.6	18.3	15.7	17.1	18	17.9	17.1	16.2
romeo	7.8	14.8	16	17.1	18.3	16.6	17	12.9	11.9	17.1	16.3
mean	12.2	17.2	17.4	18.5	19.5	16.0	18.8	17.5	16.0	16.3	17.3
± SD	3.3	2.7	1.4	1.5	2.0	0.9	1.9	3.1	2.6	1.0	1.5
median	12.9	17.1	17.3	17.8	18.3	16.2	18.6	18.0	17.3	17.0	16.9

Correlated masker

f_c flanking band	400 Hz	1200 Hz	1600 Hz	1800 Hz	1900 Hz	2000 Hz	2100 Hz	2200 Hz	2400 Hz	2800 Hz	3600 Hz
max	8.2	0.3	-3.4	-0.8	4.7	14.8	-2.4	6.4	7.8	1.8	2
tom	6.1	-1	-0.4	4.3	4.6	16.8	-0.2	6.6	4.9	-3.7	1
olga	5.2	1.4	-1.3	-0.4	-1.1	0	0.2	3.2	1.8	1.7	-0.8
julia	3.1	-8	-5.8	-4.9	-4.4	15.7	-3.8	1.4	-3.2	-3.6	-1.3
romeo	3.7	-6.1	-5.1	-2.5	-7.3	16.6	-6.6	-2.2	-2.6	-7.3	-2.1
mean	5.26	-2.68	-3.2	-0.86	-0.7	12.78	-2.56	3.08	1.74	-2.22	-0.24
± SD	2.0	4.1	2.3	3.4	5.4	7.2	2.8	3.7	4.7	3.9	1.7
median	5.2	-1.0	-3.4	-0.8	-1.1	16.2	-2.4	3.2	1.8	-3.6	-0.8

9 Lebenslauf

18.10.1971:	geboren in Landshut
1977-1981:	Besuch der Grundschule Hofberg, Landshut
1981-1990:	Besuch des Hans Carossa Gymnasium, Landshut
	Abschluß: Allgemeine Hochschulreife
1990-1992:	Besuch der Chemieschule Dr.Erwin Elhardt, München
	Abschluß: staatlich geprüfte chemisch-technische Assistentin
1992-1999:	Studium der Biologie an der Technische Universität München
März-Aug.1997:	Auslandsaufenthalt im Labor von Prof. L. Wilkens, University of Missouri St. Louis, St. Louis, USA
März-April 1998:	Diplomhauptprüfung in den Fächern Zoologie (Hauptfach), Limnologie, Ethologie, Biophysik
Mai 1998-April 1999:	Diplomarbeit im Labor von Prof. G.M. Klump
	Thema: Zeitauflösung im Gehör der Mongolischen Wüstenrennmaus (*Meriones unguiculatus*).
Mai 1999:	Beginn der Promotion
Mai 1999-April 2002:	Stipendiatin im Graduiertenkolleg "Sensorische Interaktionen in biologischen und technischen Systemen" GRK 267 der DFG