

Signal detection in amplitude-modulated maskers.

I. Behavioural auditory thresholds in a songbird

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Abstract

Vertebrates have evolved mechanisms to exploit amplitude modulations in background noise for improving signal detection. However, the mechanisms underlying this masking release are not yet well understood. Here we present evidence for masking release observed in European starlings (*Sturnus vulgaris*, Aves) that were trained in a Go/NoGo paradigm to report the detection of a short tone (20 ms) in 100% sinusoidally amplitude-modulated noise maskers (400 ms duration). Maskers centred at the tone frequency were composed of one, three, or five spectrally adjacent noise bands each of auditory filter bandwidth. Envelopes of the masking noise bands were either in-phase (i.e. coherent) or successively phase shifted by 90° (i.e. incoherent). A release from masking of up to 28 dB was observed for detection of signals presented in dips of the envelope of coherent maskers compared with those presented in peaks of coherent maskers and in incoherent maskers. For maskers limited to one auditory filter (i.e. limited to the analysis channel tuned to the test signal) this masking release was about 10 dB less than that observed for maskers allowing a comparison across three or five auditory filters. This indicates that both within-channel cues and across-channel cues are important for signal detection. These behavioural data provide the reference for the study of responses of auditory forebrain neurons in the same species reported in a companion paper [Nieder & Klump (2001) *Eur. J. Neurosci.*, **13**, 1033–1044].

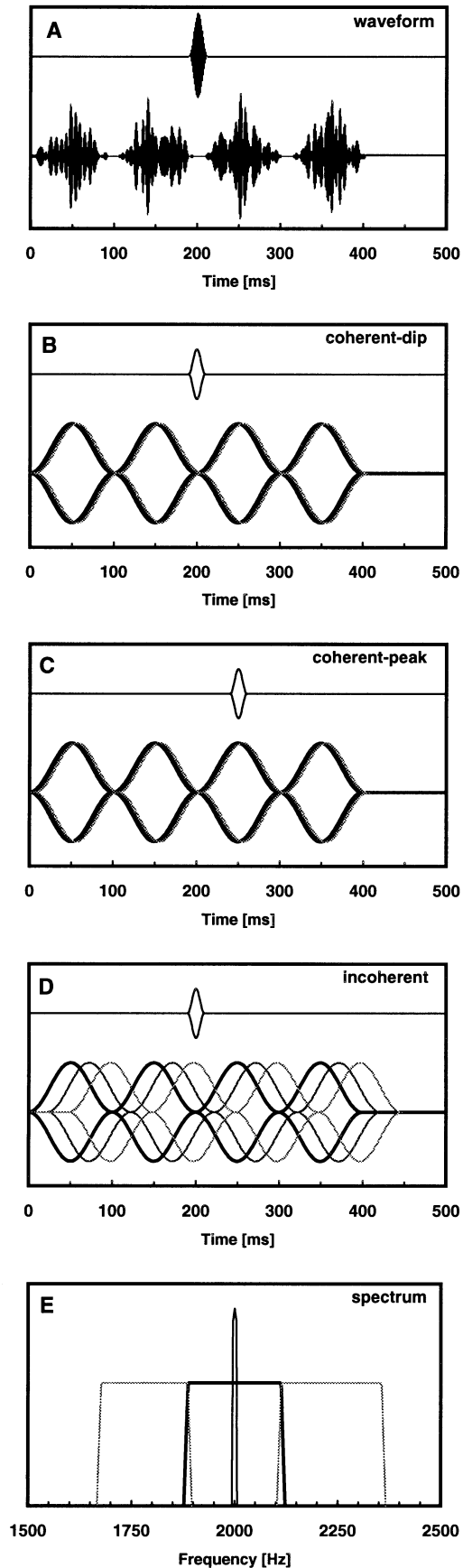
Introduction

Almost any natural environment is noisy, thus noise commonly affects the perception of auditory signals (e.g. Wiley & Richards, 1978; Richards & Wiley, 1980; Klump, 1996). As a consequence of turbulences in the atmosphere, amplitude fluctuations are often superimposed upon environmental sounds when they are transmitted. Furthermore, many natural sound sources produce temporally structured signals (e.g. a group of humans chatting or birds singing in a dawn chorus). Therefore, fluctuating background noise should be commonly experienced in the auditory world. Several studies indicated that speech perception is improved in fluctuating background noise (Festen & Plomp, 1990; Grose & Hall, 1992; Fastl, 1993; Festen, 1993). Consequently, there must be sensory mechanisms that can make use of fluctuations in background noise and other environmental sounds. These mechanisms may be used for the perceptual grouping of signal components, segregation of signals from background noise and hence in the analysis of auditory scenes (Bregman, 1990; Hall *et al.*, 1984; Hall & Grose, 1990; Moore *et al.*, 1990).

In psychophysical studies with human listeners, these mechanisms are commonly investigated with experimental paradigms that present signals in amplitude-modulated maskers. If maskers carry coherent amplitude modulations (i.e. modulations that are correlated and in-phase) in different frequency bands, signal detection may be improved considerably. This masking release has been termed 'comodulation masking release' (CMR, Hall *et al.*, 1984). Different

cues may account for the improvement of signal detectability. Some of the cues, for example the temporal pattern of envelope fluctuations, can be extracted within a single analysis channel of the auditory system (within-channel cues; Schooneveldt & Moore, 1987, 1989b). In addition, instances of low masker amplitude in single analysis channels resulting from brief temporal gaps in the background noise can facilitate signal detection (e.g. Buus, 1985). Other cues require the comparison of information derived from the output of different auditory filters (across-channel cues; Hall *et al.*, 1984; Buus, 1985; McFadden, 1986; Schooneveldt & Moore, 1987, 1989a; Gralla, 1991; Eddins & Wright, 1994). For example, Buus (1985) suggested that similar to the processes known in binaural hearing, the correlated activity elicited by the masker in separate analysis channels will be cancelled out and a signal that occurs in one of the analysis channels only will become more detectable.

CMR has also been demonstrated psychophysically in several animal species (starling, Klump & Langemann, 1995; Hamann *et al.*, 1999; Klump *et al.*, 2001; chinchilla, Niemiec *et al.*, 2000; gerbil, Kittel *et al.*, 2000). It has been suggested that neuronal correlates of CMR can be observed in the cochlear nucleus of cats (Rhode & Greenwood, 1995) and in the auditory cortex of cats (Nelken *et al.*, 1999). Henderson *et al.* (1999) reported a masking release in some neurons of the inferior colliculus of chinchillas. Winter and colleagues (2000) demonstrated CMR in ventral cochlear nucleus neurons of guinea pigs. To date, however, an animal model is lacking in which both the neuronal responses of awake animals and the behavioural performance can be compared directly using the same stimulus paradigm. The present study and the accompanying study by Nieder & Klump (2001) was designed to close this gap by investigating the response of starlings in the detection of short



signals in sinusoidally amplitude-modulated (SAM) noise bands, both in behavioural and neurophysiological experiments with similar stimuli (part of these data have been presented in abstract form; Langemann *et al.*, 2000).

Materials and methods

Subjects

The five starling (*Sturnus vulgaris*) subjects were housed in a common room with other birds in individual cages of $80 \times 40 \times 40$ cm at a natural day/night cycle. They were fed duck-food pellets ('Treff G7M', Bayerische Kraftfutter GmbH, Germany). The birds were kept at about 95% of their free-feeding weight; they had unrestricted access to water. The food rewards during the experiments consisted of pieces of mealworms (larvae of *Tenebrio molitor*) that were favourite food items for the birds. The care and treatment of the birds were in accordance with the procedures of animal experimentation approved by the Government of Upper Bavaria, Germany. All procedures were performed in compliance with the NIH Guide for the Care and Use of Laboratory Animals (1996).

Apparatus and signal generation

Masked thresholds were determined with the experimental cage ($24 \times 36 \times 32$ cm) placed in a sound-attenuating anechoic box (attenuation: 48 dB at 500 Hz; >57 dB for frequencies of 1 kHz and above). For echo reduction, the box was lined with sound-absorbing wedges (Illbruck Illsonic Pyramide 100/100 mounted on 50 mm of Illsonic Plano, cutoff frequency of 500 Hz, $\alpha > 0.99$; Illbruck GmbH, Germany). Two response keys (observation key and report key) with light-emitting diodes (key lights) were mounted on the front of the experimental cage. A rotary food dispenser operated by a stepping motor was placed in front of the cage below the keys. All behavioural protocols, including the delivery of food rewards, were controlled by a SiliconGraphics workstation (SiliconGraphics, USA).

Pure-tone signals (2 kHz, 20 ms total duration, 5 ms raised-cosine ramps) were produced using a SiliconGraphics Iris Indigo Workstation with a 16-bit digital-to-analogue converter (sampling rate 32 kHz). Signal levels were adjusted by an attenuator (TDT PA4; Tucker-Davis Technologies, USA) controlled by the workstation, then passed through a Yamaha amplifier (AX-500; Nippon Gakki, Japan) driving the speaker (Twin 700, 200–9000 Hz, ± 2.5 dB; Canton Elektronik, Germany) in the sound-proof chamber. The speaker was positioned about 30 cm above the bird's head, and slightly behind it (6 cm). The total harmonic distortion of the tones produced by the sound system was below 0.2%.

The maskers consisted of sinusoidally amplitude-modulated (SAM) noise bands. They were composed of one, three or five

FIG. 1. Masking paradigm, waveform and schematic relationship between test signal and envelope of the sinusoidally amplitude-modulated noise bands together with a schematic frequency spectrum. (A) Example of waveform of one masker noise band in the lower trace and the test signal in the upper trace. (B) Three coherent noise bands, test tone presented at envelope dip, 190 ms after masker onset. (C) Three coherent noise bands, test tone presented at envelope peak, 240 ms after masker onset. (D) Three incoherent noise bands; noise bands are successively shifted in-phase by 90° ; the first noise band (0° shift) is the on-frequency masker. (E) The frequency spectrum demonstrates the position of the test signal (2 kHz) in relation to the different bands of masking noise that are either coherently or incoherently modulated.

spectrally adjacent noise bands each of auditory-filter bandwidth, centred at the test-tone frequency (2 kHz). The bandwidth of auditory filters, also called the 'critical bandwidth' (Scharf, 1970), can be used to scale the hearing range in critical band units (CBUs). Filter bandwidth was calculated using a critical-band function developed by Buus *et al.* (1995). Based on physiological data, the function is able to predict the bandwidth of the starlings' auditory filters derived from different behavioural measures reasonably well (Buus *et al.*, 1995). The auditory filters' mid-frequencies were 1580 Hz (bandwidth 195 Hz) 1782 Hz (bandwidth 210 Hz) 2000 Hz (bandwidth 226 Hz), 2235 Hz (bandwidth 244 Hz) and 2489 Hz (bandwidth 264 Hz). Noise bands of 30 s each (sampling rate 32 kHz, 16 bit, FFT size 16384, Blackman filter, slopes at least 2200 dB/octave) were computed using the software package 'CoolEdit' (Syntrillium Software Corporation, USA). From the prepared 30 s noise files, pieces of 400 ms duration were randomly cut and shaped (modulation frequency 10 Hz, modulation depth 100%) for each sound presentation during the experiments. Envelopes of the SAM noise bands were either in-phase (i.e. coherent) or successively shifted in-phase by 90° (incoherent; see Fig. 1). When noise that was only one auditory filter wide was presented (mid-frequency 2000 Hz), three different noise files with the same mid-frequency and bandwidth were used with the envelopes in-phase or phase-shifted in the same way. All noise bands had a spectrum level of about 41 dB (reference pressure 20 μ Pa). The masker was added to the tone in the input stage of the amplifier. In the coherent stimulus paradigm, the test tone was presented either in a dip or in a peak of the envelope of the SAM masker (coherent-dip condition, 190 ms after masker onset; coherent-peak condition, 240 ms after masker onset; see Fig. 1). In the stimulus paradigm using incoherent noise bands, test tones were presented 190 ms after the onset of the masker (i.e. in the dip of the on-frequency masker). Sound levels were calibrated at least once a day (General Radio type 1982 sound-level meter; GenRad, USA) by placing the microphone (General Radio 1/2' condenser microphone type 1962-9611) at about the location where the bird's head would be in an experiment.

Behavioural testing procedures and estimate of thresholds

Details of the operant procedures and threshold determination applying signal detection theory can be found elsewhere (Langemann *et al.*, 1995). Briefly, five starlings were trained to repeatedly peck the observation key when only the background noise was presented (NoGo condition), and to peck the report key when a test signal was added to the background (Go stimulus). A trial started with a peck of the bird on the observation key. After a random waiting interval of up to 9 s, another peck on the observation key resulted in the presentation of the test signal. If the bird pecked the report key within 3 s from the start of the presentation of this signal, the food tray rotated and the bird was reinforced by a food reward with a probability of 60–80%. This reinforcement schedule ensured that the capacity of the feeder was sufficient for the whole session (a feeder light was always presented as a secondary reinforcer). The trial ended with the reinforcement or, in the case of no response, after the response time had passed. To obtain a measure of spontaneous responding, 30% of the trials were catch trials (without a test signal) in which the birds' responses were scored as in test-signal trials. A response during a catch trial or during a waiting interval before presentation of a signal resulted in a time-out period of 8 s with the lights in the experimental cage switched off.

Masked thresholds were obtained by the method of constant stimuli (e.g. Dooling & Okanoya, 1995). A block of 10 trials, consisting of three catch trials and a set of seven signal trials differing in sound

pressure level of the test tone (step-size was either 3 or 5 dB), was repeated 10 times during a session with a randomized sequence of the trials in each block. At the beginning of each session, a block of 10 'warm-up' trials was presented with test signals of an amplitude that could be easily detected by the birds. Thus, a session was made up of 110 trials that the birds would usually finish in about 35–45 min. Sessions were excluded from the analysis if the false-alarm rate exceeded 20% or if the two signals of the set with the highest sound pressure level were reported with a probability of less than 80%. If the data from two consecutive sessions differed by no more than 3 dB, the data were combined and a threshold estimate was computed by linear interpolation of the psychometric function (20 signal trials at each sound pressure level and 60 catch trials) as the sound pressure level at which the value of the signal detection measure d' was 1.8. This threshold criterion corresponds to 56% correct responses in this Go/NoGo task given the typical false-alarm rate of the starlings of about 5% (see Swets, 1964).

Data analysis

All results are based on the birds' masked detection thresholds for the short tone pip presented in the noise background. A masking release (i.e. an improvement in signal detection) was defined as the threshold difference (in dB) between two testing conditions. It was calculated in the first stimulus paradigm by subtracting thresholds for signals presented in dips of the envelope of coherent maskers from thresholds for signals presented in peaks of coherent maskers. In the second stimulus paradigm, masking release was calculated by subtracting thresholds for signals presented in dips of the envelope of coherent maskers from thresholds for signals presented in incoherent maskers.

The masking release observed for noise bands more than one auditory filter wide resulted both from information processed across different auditory filters and within the auditory channel tuned to the test tone frequency. Consequently only the masking release resulting from the comparison across different auditory filters should be considered to determine 'true' CMR. We estimated 'true' CMR following the method suggested by Carlyon *et al.* (1989). First we calculated the masking release, i.e. in this case the difference between the masked thresholds for incoherent noise bands and for coherent noise bands (dip position of the signal) of the same bandwidths. We then used the difference between the masking release obtained with wide-band maskers and the masking release obtained with a masker of one auditory filter bandwidth to estimate 'true' CMR.

The threshold data for all different testing conditions were compared statistically using an analysis of variance (ANOVA; SigmaStat 2.03, SPSS Science Software, Germany). We performed a two-way repeated measures ANOVA with the different conditions (incoherent, coherent-peak and coherent-dip) and the masker bandwidths (one, three and five auditory filters wide) as factors. To take into account the unequal distribution of thresholds induced by the different conditions, we allowed the significance level for deviation from normal distribution to be lowered to $P < 0.005$. Differences of masking release between different masker bandwidths were compared using a one-way repeated measures ANOVA. Subsequent multiple comparisons were performed using Tukey tests.

Results

To evaluate masking release in a noisy fluctuating background, we compared detection thresholds for test signals presented in three masker conditions in a two-way repeated measures ANOVA, considering masker bandwidth as an additional factor. Thresholds in the

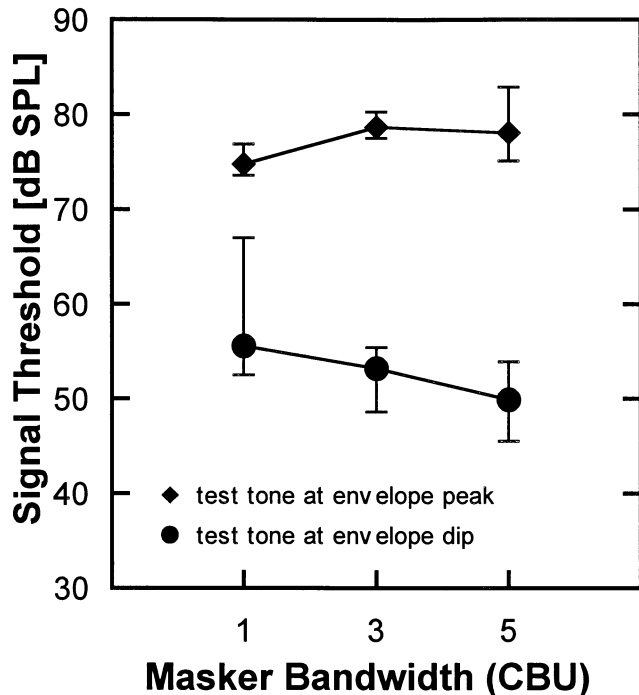


FIG. 2. Detection thresholds for different signal positions relative to the envelope of coherent maskers as a function of the masker bandwidth; median values and range of data from five starlings. Maskers consisted of adjacent noise bands of auditory-filter bandwidth (CBU, critical band units) centred at the test-tone frequency (2 kHz) and were 100% sinusoidally amplitude modulated.

three conditions (incoherent, coherent-peak, coherent-dip) differed significantly ($F_{2,42} = 237.6$, $P < 0.001$). Viewed across all conditions, no effect of masker bandwidth as an independent factor was found ($F_{2,42} = 1.4$, n.s.). As masked thresholds decrease with increasing masker bandwidth in the coherent-dip condition and masked thresholds increased with increasing masker bandwidth in the two other conditions (coherent-peak, incoherent), a significant interaction between conditions and masker bandwidth was observed ($F_{4,40} = 27.7$, $P < 0.001$). Masking effects in relation to the masker bandwidth were very similar in the coherent-peak and in the incoherent conditions. In the following, we first compare masking in the coherent-peak and coherent-dip conditions, i.e. analyse the role of the signal position for signal detection. Second, we compare masking in the incoherent and the coherent-dip conditions, i.e. analyse the role of comodulation of the masker envelope for signal detection.

Influence of signal position

The sound pressure levels of the test signal at detection threshold for different signal positions relative to the envelope of coherent noise bands are presented in Fig. 2 (median values and range of data of five starlings). For maskers of all bandwidths, thresholds in the coherent-peak and in the coherent-dip conditions differed significantly (multiple comparisons using *post hoc* Tukey tests, all $P < 0.001$). Compared with a test tone in the peak, thresholds for a test tone in the dip of coherent noise bands were improved by 27.8 dB (median value of five starling subjects) for maskers that were more than one auditory filter wide. Signal detection of individual starlings was improved between 23.3 and 31.6 dB for the dip position of the signal. For maskers limited to one auditory filter, the individual masking release was between 17.0 and 21.1 dB in four starlings and was still 8.5 dB

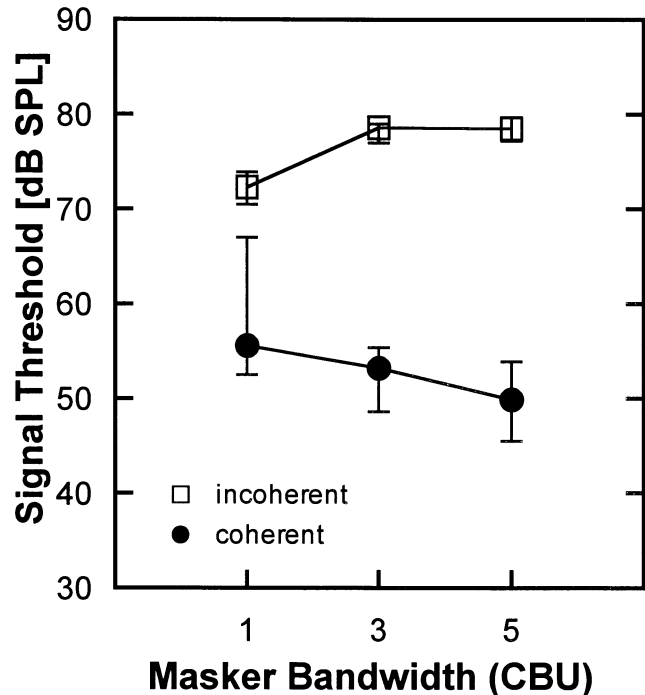


FIG. 3. Detection thresholds for coherent and incoherent testing conditions as a function of the masker bandwidth; median values and range of data from five starlings. Detection thresholds for signals in coherently modulated maskers are identical to those in Fig. 2. Maskers consisted of adjacent noise bands of auditory-filter bandwidth (CBU, critical band units) centred at the test-tone frequency (2 kHz) and were 100% sinusoidally amplitude modulated.

in the fifth individual (median 18.3 dB). The masking release for noise bands that were more than one auditory filter wide was significantly larger than the masking release within one auditory filter (one-way repeated measures ANOVA, $F_{2,12} = 23.8$, $P < 0.001$, pairwise comparisons with Tukey test, 5 vs. 1 CBU, $P < 0.001$; 3 vs. 1 CBU, $P = 0.001$); there was no significant difference between noise maskers that were three or five auditory filters wide (Tukey test, n.s.).

Influence of masker envelope

The detection thresholds for test signals in coherent and incoherent masking noise bands are presented in Fig. 3. For maskers of all bandwidths, thresholds in the coherent-dip and incoherent conditions differed significantly (multiple comparisons using *post hoc* Tukey tests, all $P < 0.001$). Compared with the incoherent condition, masked thresholds for a test tone in the dip of coherently modulated noise bands were improved by 26.3 dB (median value, range 21.2–34.2 dB) for maskers that were more than one auditory filter wide, thus demonstrating substantial masking release. Even with maskers limited to one auditory filter, a masking release of between 12.4 and 18.0 dB was observed in four subjects, with the fifth starling exhibiting only 6.9 dB of masking release (median of five starlings 15.4 dB). The masking release for noise bands more than one auditory filter wide was significantly larger than the masking release within one auditory filter (one-way repeated measures ANOVA, $F_{2,12} = 52.8$, $P < 0.001$, pairwise comparisons with Tukey test, 5 vs. 1 CBU, $P < 0.001$, 3 vs. 1 CBU, $P < 0.001$); there was no significant difference between noise maskers that were three or five auditory filters wide (Tukey test, n.s.).

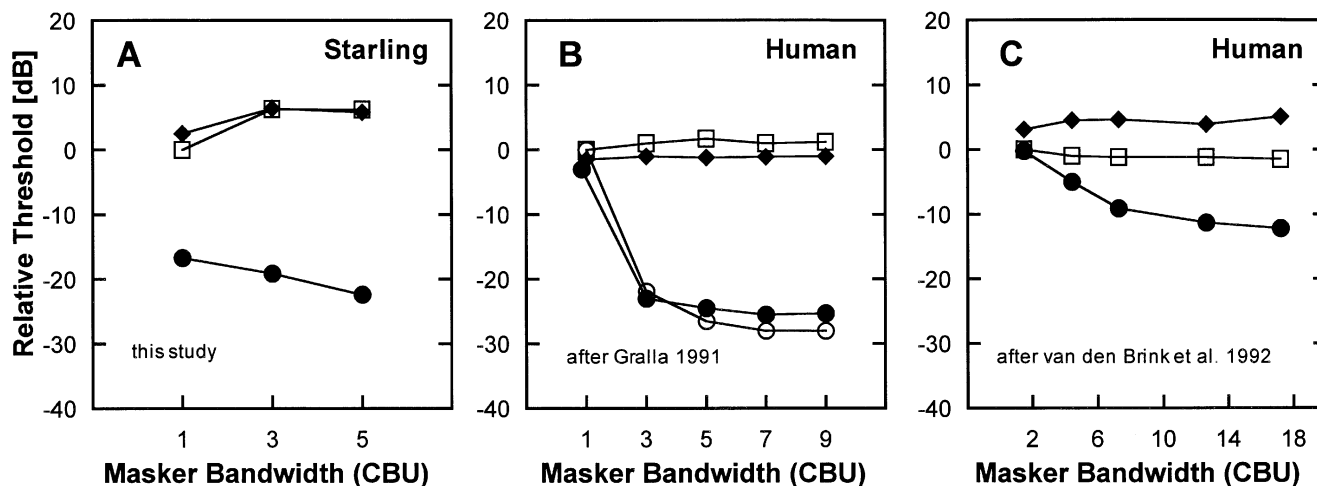


FIG. 4. Relative detection thresholds indicating the masking release for (○) coherent and (□) incoherent testing conditions and for different signal positions relative to the envelope of the coherent masker (● test tone at dip, ◆ test tone at peak; see Fig. 1) as a function of the masker bandwidth. Behavioural thresholds for the detection of a 2-kHz signal were from five starlings (median data, cf. Figs 2 and 3). Median data from human subjects by Gralla (1991; $n = 6$) with the maskers centred at the 1 kHz test signal. Mean data from van den Brink *et al.* (1992; $n = 3$); maskers were presented continuously and were centred at 1.6 kHz. All thresholds were related to the detection threshold for incoherent noise of the smallest bandwidth – 1 CBU (i.e. one auditory filter) wide in this study and in the study by Gralla (1991), and 1.5 CBU wide for the data by van den Brink *et al.* (1992).

When comparing the masking release for maskers that were five auditory filters wide and for maskers limited to one auditory filter, a ‘true’ CMR of between 10.8 and 17.7 dB (median 13.3 dB) was observed in the five starlings. This measure assesses the masking release resulting from only the comparison across different auditory filters.

Discussion

The European starling is the only animal species in which most aspects of comodulation masking release (CMR) have been demonstrated in psychophysical experiments. We found masking release with unmodulated and comodulated continuous masking noises of different bandwidth was similar to the masking release described in humans (Hall *et al.*, 1984; Klump & Langemann, 1995). CMR in the starling determined with continuous narrow-band noise maskers composed of an on-frequency band and flanking bands shared some characteristics with CMR observed in human listeners with the same stimulus paradigm. For example, flanking bands with a bandwidth of 25 Hz induced a considerable release from masking of up to 14 dB and the effect was approximately symmetrical around the test frequency (Schooneveldt & Moore, 1987, 1989b; Hamann *et al.*, 1999; Klump *et al.*, 2001). In the current study, we demonstrated masking release in a third paradigm that was previously applied in human subjects (Gralla, 1991) presenting a brief test stimulus in SAM noise bands. Similar to the study in humans, two main effects contributed to masking release in the starling. First, the instantaneous amplitude of the masker determined thresholds for short test tones; signals in envelope dips were detected more easily by the starlings than signals in envelope peaks. Second, there was a profound difference in masking between conditions with coherent or incoherent envelopes of the background noise. The following discusses these two effects in detail.

Effects of signal position on performance

It made a clear difference to the birds whether the test signal was presented in a peak or in a dip of the masker envelope. Compared

with a test tone at the envelope peak, thresholds for test tones in the envelope dip were improved by 27.8 dB (median) for maskers more than one auditory filter wide (Fig. 4A). This matches psychophysical data obtained in human subjects with similar stimuli (Gralla, 1991; 100% SAM noise maskers, 400 ms duration, $f_{\text{mod}} = 10$ Hz, 20 ms test signals at 1 kHz; Fig. 4B). Human observers revealed a masking release of about 24 dB for maskers more than one auditory filter wide. Human listeners fail to distinguish between the two different signal positions when the masker is limited to one auditory filter (bandwidth 160 Hz at 1 kHz; Gralla, 1991). This is in contrast to the starlings’ performance (Fig. 4A and B). Within the limits of one auditory filter, starlings still benefit from the signal situated in a dip of the masker envelope; the masking release compared with the signal at envelope peak was about 10 dB less than for maskers of a larger bandwidth, but it was still 18.3 dB (median). Other data presented in Gralla’s study suggest that these differences between humans and starlings are not due to the different centre frequencies used. For example (Gralla, 1991), demonstrated that the effect of masker bandwidth on forward masking does not differ much for frequencies between 0.7 and 2 kHz. Forward masking probably is the most important component in determining thresholds for the type of maskers used in this study (discussed later).

Gralla’s observations are consistent with results of another study with human observers by van den Brink *et al.* (1992). Van den Brink *et al.* (1992) used a filtered 4-ms impulse as the test signal (centre frequency 1.6 kHz, bandwidth 1/3 octave, i.e. 1.5 CBU) and a continuous noise masker centred spectrally at 1.6 kHz. Maskers consisted of bands of either random noise or 100% SAM noise modulated at a rate of 32 Hz. As in Gralla’s (1991) study, the masking release for the coherent-peak vs. the coherent-dip condition was largest for wide-band maskers (about 10–17 dB, van den Brink *et al.*, 1992; Fig. 4C). The higher modulation rate might well explain the smaller masking release. At the smallest bandwidth, that was slightly wider than one auditory filter, van den Brink *et al.* (1992) observed only a small masking release of about 3 dB (Fig. 4C). In contrast to human subjects in Gralla’s (1991) study, van den Brink

and colleagues observed a slightly compromised detection for signals presented in the coherent-peak condition.

Obviously, the starling is able to exploit the temporal pattern of the SAM noise within one auditory filter much more efficiently than humans do when they are presented with the same task (Gralla, 1991; van den Brink *et al.*, 1992). Only when noise bands allow comparison across different auditory filters do both starlings and humans show a large masking release. The starlings' behavioural data are consistent with observations on neuronal detection thresholds determined in multiunit clusters of the starlings' auditory forebrain [Nieder & Klump (2001) used stimuli similar to those in the present study]. If test tones and maskers were confined to the neurons' excitatory bandwidth (which is equivalent to presenting signal and masker within one auditory filter; Nieder & Klump, 2001), a neuronal masking release of on average 21 dB was found. This compares well with the starlings' behavioural masking release of 18 dB.

Influence of the masker envelope on performance

Experiments studying CMR with noise maskers of different bandwidths that have an irregularly fluctuating envelope usually show two main effects in both starlings and humans. Signal detection in coherently modulated noise is improved considerably in comparison with signal detection in unmodulated random noise of the same bandwidth and overall energy, and masking release increases with increasing bandwidth of the masker (e.g. Hall *et al.*, 1984; Schooneveldt & Moore, 1989b; Klump & Langemann, 1995). The second effect concerns the temporal characteristics of the coherently fluctuating noise bands with slower fluctuations resulting in a larger masking release (e.g. Hall & Haggard, 1983; Carlyon *et al.*, 1989; Schooneveldt & Moore, 1989b; Klump & Langemann, 1995). Maskers that have a more regular envelope pattern, e.g. consisting of coherent SAM noise bands modulated at a low rate, lead to an even larger amount of masking release in starlings and in human listeners than that found with maskers exhibiting irregularly fluctuating envelopes.

If noise bands spanning several auditory filters were presented, signal detection in the dip of coherent maskers compared with incoherent maskers was equally improved in starlings and humans. In this case, starlings exhibited a masking release of 26 dB (Fig. 4A). Similarly Gralla's human subjects showed a masking release of 28 dB (Gralla, 1991; Fig. 4B) for noise bands that were more than one auditory filter wide. Also, the study by van den Brink *et al.* (1992) reported a large masking release for wide-band maskers (Fig. 4C). If noise bands were limited to one auditory filter, however, signal detection in humans was not improved in the dip of coherent maskers compared with incoherent maskers (Gralla, 1991; Fig. 4B). This is in contrast to the results in starlings that still experienced a considerable masking release of 15 dB in this case (Fig. 4A). Similar to the condition described in the previous section (effect of the signal position) the starling seems to be able to benefit from the information provided by a single auditory filter while human listeners do not. For maskers of all bandwidths, both starlings and human subjects (Gralla, 1991) showed similar thresholds for detection of the test tone in the incoherent condition or in the peak of coherent 10-Hz SAM noise bands (Fig. 4A and B).

Average neuronal data in the starling obtained by Nieder & Klump (2001) with three coherent or incoherent noise bands presented within the limits of the excitatory cluster tuning curves (i.e. within one 'auditory filter') also showed a substantial masking release. The neuronal detection threshold was improved by 9 dB on average (range -5 to 37 dB), whereas the behavioural detection threshold was improved by 15 dB. The neuronal masking release was much less,

however, when the three noise maskers were arranged in a way that only one noise band was positioned within the limits of the excitatory tuning curve as before (excitatory noise band) but two noise bands were positioned in the inhibitory sidebands outside the excitatory tuning curve (inhibitory noise bands). In the latter case in which the average neuronal masking release was only 3 dB (range -4 to 17 dB; Nieder & Klump, 2001), the noise bands presumably stimulated separate 'auditory filters' affecting each other through inhibitory processes across frequencies (Nieder & Klump, 1999). Thus, in contrast to the behavioural evidence, the forebrain neurons of awake starlings on average exhibited little masking release if only information across different 'auditory filters' was available (for further discussion, see Nieder & Klump, 2001).

'True' comodulation masking release

Several authors argued that only the amount of masking release resulting from comparisons across different auditory filters should be considered 'true' CMR (e.g. Carlyon *et al.*, 1989; Moore *et al.*, 1993). This across-channel CMR was estimated differently by various authors. Moore *et al.* (1993), for example, described 'true' CMR as the decrease in threshold that occurs when the bandwidth of a coherently modulated masker is increased beyond one auditory filter. In the present study, we followed the method suggested by Carlyon *et al.* (1989) calculating the difference in masking release for wide-band maskers and for maskers limited to one critical bandwidth to estimate 'true' CMR.

In the experimental paradigm using SAM-noise bands, 'true' CMR, according to the definition of Carlyon *et al.* (1989), can be found in human listeners (Hall & Haggard, 1983; Carlyon *et al.*, 1989; Gralla, 1991; van den Brink *et al.*, 1992) and in the starling (present study). Although the masking release for wide-band maskers is almost identical in human listeners and in starlings, much more 'true' CMR is observed in humans (about 28 dB; Gralla, 1991) than in starlings (about 13 dB) in a similar behavioural task. This, of course, is a consequence of the fact that starlings benefit from coherently modulated maskers already within a single auditory filter, while humans do not. Thus, starlings appear to exploit predominantly within-channel cues, whereas the masking release in humans results mostly from exploiting across-channel cues. Both effects combined, however, yield a similar overall performance in humans and starlings. The neuronal responses in the starlings' forebrain (Nieder & Klump, 2001) suggest that much of the starlings' masking release in behaviour might already be explained by temporal effects, e.g. by the difference between simultaneous and forward masking. In this case, the envelope peak of coherent SAM noise bands would exercise forward masking on the test signal presented in the envelope dip, while phase-shifted noise bands (incoherent condition) would resemble a situation of simultaneous masking. As simultaneous masking is more effective than forward masking, a considerable masking release that is due to temporal processing should be expected already for stimuli limited to one auditory filter. The starling data are consistent with this hypothesis, whereas it is not clear why the study by Gralla (1991) found no masking release within one auditory filter.

An experimental paradigm that is expected to demonstrate across-channel CMR (i.e. 'true' CMR) unambiguously uses narrow noise bands, with one noise band being presented at the frequency of the test signal ('on-frequency band') and one or more additional 'flanking bands' positioned distant from the on-frequency band (e.g. Hall *et al.*, 1984; McFadden, 1986; Schooneveldt & Moore, 1987; Hall & Grose, 1988). In the starling, this type of experiment produced a considerable amount of CMR over a wide frequency range: a CMR of between 9 and 14 dB was found for noise bands 25 Hz wide and

positioned up to 4 CBU below and above the on-frequency band, and an even larger CMR of between 14 and 23 dB was found for noise bands of a width of 6.25 Hz (Hamann *et al.*, 1999; Klump *et al.*, 2001) demonstrating substantial 'true' CMR.

Other experiments in humans investigated the effect of within- and across-channel cues on CMR in a similar way to flanking-band experiments, i.e. with spectrally discontinuous maskers. Instead of SAM noise band maskers, Grose & Hall (1989), Moore *et al.* (1990), Hicks & Bacon (1995) and Delahaye (1999) employed maskers consisting of several SAM tones that were spread across different auditory filters. SAM tonal complexes as maskers were chosen because experimental parameters were assumed to be easier to control (Grose & Hall, 1989). These multicomponent tonal maskers yielded considerable amounts of CMR for some of the experimental conditions. Small deviations in the experimental design in these studies, however, could produce quite different results for the amount of CMR or even lead to additional masking instead of a masking release (cf. Grose & Hall, 1989; Moore *et al.*, 1990; for nine-component maskers, and Moore *et al.*, 1990; Delahaye, 1999; for seven-component maskers). Furthermore, Hicks & Bacon (1995) showed that some of the results of Delahaye (1999), Grose & Hall (1989) and Moore *et al.* (1990) probably were influenced much more by the number of test signals that were presented (i.e. single test tone vs. a train of three test tones) than by masker parameters. The deterministic character of tonal maskers may create additional problems, as the mechanism underlying CMR could be sensitive to the predictability of the modulation pattern, as suggested by Grose & Hall (1989). Choosing stimuli with a stochastic noise carrier and a regular sinusoidal envelope, as in the present study in starlings and the studies in humans by Gralla (1991) and others (Hall & Haggard, 1983; Carlyon *et al.*, 1989; van den Brink *et al.*, 1992), may be a good trade-off in the search for the mechanisms generating CMR.

Conclusions

Including the results presented here, the European starling provides us with the most detailed knowledge on comodulation masking release (CMR) in a nonhuman species. In the starling, patterns of release from masking in different stimulus paradigms are similar to those found in human subjects. The few differences between starlings and humans suggest that the temporal resolution of this songbird's auditory system provides for a better performance in signal detection (Klump & Maier, 1989; Klump & Langemann, 1995). In summary, the starling appears to be a suitable animal model for studying mechanisms of CMR that also allows testing of the underlying neurophysiological mechanisms (Nieder & Klump, 2001). The improvement of signal detection found in CMR experiments with animals suggests that many vertebrates share perceptual mechanisms that are useful for auditory grouping of sounds and the analysis of auditory scenes.

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Abbreviations

ANOVA, analysis of variance; CBU, critical band unit; CMR, comodulation masking release; SAM, sinusoidally amplitude modulated.

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