Effect of efferent activation on binaural frequency selectivity

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Abbreviations: ERB, equivalent rectangular bandwidth; MOC, medial olivocochlear.

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ABSTRACT

Binaural notched-noise experiments indicate a reduced frequency selectivity of the binaural system compared to monaural processing. The present study investigates how auditory efferent activation (via the medial olivocochlear system) affects binaural frequency selectivity in normal-hearing listeners. Thresholds were measured for a 1-kHz signal embedded in a diotic notched-noise masker for various notch widths. The signal was either presented in phase (diotic) or in antiphase (dichotic), gated with the noise. Stimulus duration was 25 ms, in order to avoid efferent activation due to the masker or the signal. A bandpass-filtered noise precursor was presented prior to the masker and signal stimuli to activate the efferent system. The silent interval between the precursor and the masker-signal complex was 50 ms. For comparison, thresholds for detectability of the masked signal were also measured in a baseline condition without the precursor and, in addition, without the masker. On average, the results of the baseline condition indicate an effectively wider binaural filter, as expected. For both signal phases, the addition of the precursor results in effectively wider filters, which is in agreement with the hypothesis that cochlear gain is reduced due to the presence of the precursor.

1. Introduction

Several psychoacoustic experiments have been designed to measure characteristics of auditory frequency selectivity. One of the earliest experiments is the bandwidening experiment where a sinusoidal signal is masked by a bandpass-noise masker spectrally centred at the signal frequency (Fletcher, 1940). Another common type of experiment is the notched-noise experiment (de Boer and Bos, 1962; Patterson, 1976; Patterson and Nimmo-Smith, 1980). For both experimental paradigms (bandwidening and the notched-noise experiment) the estimate of the bandwidth of the auditory filter centered at the signal frequency (with diotic N_0 noise) depends on binaural signal phase. For diotic stimuli (N_0S_0) the same critical bandwidth estimate is obtained as for monaural experiments, but for the dichotic binaural stimuli N_0S_π (i.e., a diotic noise and a signal with an interaural phase of π) the estimated filter bandwidth is found to be considerably larger than for the monaural or N_0S_0 case (Hall et al., 1983; Zurek and Durlach, 1987; Nitschmann et al., 2009; Nitschmann and Verhey, 2013). This increase in filter bandwidth for the N_0S_π compared to the N_0S_0 condition varies between studies. For a 500-Hz signal, it ranges from 20% (Kollmeier and Holube, 1992) to six times as large (Hall et al., 1983). In previous studies (e.g., Nitschmann et al., 2010, Nitschmann and Verhey, 2013), the filters derived from the dichotic data were referred to as (effective) binaural filters since the dichotic thresholds involve binaural processing. In contrast, the filters derived from the diotic data were referred to as monaural filters. These terms will be used interchangeably with the longer terms for the filters derived from the diotic/dichotic data whenever necessary. Different mechanisms have been proposed to account for the difference in the widths of the monaural and binaural filter (see, e.g., Hall et al., 1983, van de Par and Kohlrausch, 1999, Nitschmann and Verhey, 2013). All approaches have in common that the effective wider binaural filter results from retrocochlear processes.

Hearing-impaired individuals often show reduced frequency selectivity compared to normal-hearing individuals (Peters and Moore, 1992; Leek and Summers, 1993), so it could be assumed that a reduction in frequency selectivity may impair binaural processing. However, although hearing-impaired individuals show reduced frequency selectivity (as measured by the equivalent rectangular bandwidth; ERB), for both N_0S_0 and N_0S_π conditions, the ratio of binaural to monaural ERB is the same as for normal-hearing listeners (Nitschmann et al., 2010). This indicates that a hearing impairment has no explicit retrocochlear component which affects binaural processing, but affects a stage of the auditory pathway prior to binaural processing, i.e., leads to reduced cochlear gain (Plack et al., 2004) and nonlinearity (compression) (Oxenham and Bacon, 2003).

In normal-hearing listeners, activation of the auditory efferent system can result in a reduction of auditory gain and frequency selectivity. The mammalian auditory system includes a brainstem-mediated efferent pathway from the superior olivary complex, by way of the medial olivocochlear (MOC) reflex, which reduces the cochlear response to sound (Warr and Guinan, 1979; Liberman et al., 1996). The human medial olivocochlear response has an onset delay of between 25 and 40 ms and rise and decay constants in the region of 280 and 160 ms, respectively (Backus and Guinan, 2006). Physiological studies with nonhuman mammals indicate that onset and decay characteristics of efferent activation are dependent on the temporal and level characteristics of the auditory stimulus (Bacon and Smith, 1991; Guinan and Stankovic, 1996). In humans, this MOC feedback is suggested to be involved in improving speech perception in noisy environments (Clark et al., 2012) by reducing the effect of noise masking (Kawase et al., 1993). In addition, binaural hearing is known to greatly benefit speech intelligibility (Hawley et al., 2004). How this efferent feedback operates to influence the binaural hearing system is still largely unknown. This study will investigate the influence of efferent activation on binaural filter estimates by using a psychophysical experiment that incorporates aspects of psychophysical methodology often used to study the human efferent response (signal detectability in the presence of a forward masker with or without presentation of a prior precursor sound to activate the efferent system) and binaural frequency selectivity (signal detectability in the presence of a notched noise simultaneous masker).

In a psychophysical study using forward masking to study the effect of efferent activation on stimulus detectability, Yasin et al. (2014) showed that activation of the MOC reflex by presentation of a precursor sound (>= 40 dB sound pressure level, SPL) prior to the signal of interest, resulted in a decrease in both maximum gain and maximum compression, with linearization of the compressive function for input sound levels between 50 and 70 dB SPL. If the gain is reduced due to activation of the MOC reflex then it follows that there should also be a reduction in frequency selectivity, as shown by physiological (e.g., Guinan and Gifford, 1988) and psychophysical (Jennings and Strickland, 2012) studies.

The aim of the present study was to investigate the effect of MOC reflex activation on estimates of auditory filter bandwidths obtained in the N_0S_0 and N_0S_π condition. The notched-noise method was used to infer filter bandwidths in the N_0S_0 and N_0S_π condition for a signal frequency of 1 kHz and a series of notch widths introduced into the masker stimulus. This signal frequency (1 kHz) and a similar notched-noise masking procedure were already used by Nitschmann and Verhey (2013) to measure binaural frequency selectivity but with longer signals and maskers than in this study and no precursor was present. A probe signal frequency of 1 kHz has also been used in a study of the effect of efferent-mediated gain reduction (using a binaural elicitor) on stimulus-frequency otoacoustic emissions (Lilaonitkul and Guinan, 2009); the results showed patterns of gain reduction due to efferent activation at

1 kHz similar to that found with a higher frequency signal 4 kHz. A precursor sound (presented at a level to activate the MOC reflex) was presented prior to the N_0S_0 or N_0S_π stimulus to estimate the effect of MOC reflex activation on monaural and binaural filter bandwidth estimates. In the absence of MOC reflex activation (no precursor) it is expected that filter bandwidths in the N_0S_π case will be broader than for the N_0S_0 case. With MOC reflex activation (precursor present) it is expected that filter bandwidths would be wider for both N_0S_0 and N_0S_π conditions, but since MOC reflex activation is expected to affect mainly cochlear gain reduction and not retrocochlear processes, the relative difference in bandwidth between the N_0S_0 and N_0S_π case may remain unaffected.

2. Materials and Methods

Eleven listeners (8 male, 3 female, aged between 22 and 50 years) participated in the experiment. Four listeners were members of the research team, the seven other listeners were paid volunteers. All listeners had normal hearing within frequency range from 0.125 to 8 kHz, with hearing thresholds < 15 dB HL for the entire frequency range. Informed consent was obtained from all participants.

Thresholds of a 1-kHz sinusoidal signal were measured in the two masking conditions shown in Figure 1: a condition with precursor (right column of panels) and a baseline condition without precursor (left column of panels). The top row of panels show the temporal envelopes of signal (red), masker and precursor (both in grey) and the bottom row of panels show the spectrograms of the two conditions. In both conditions, the masker was a bandpass noise (60 to 2000 Hz) with a spectral notch that was arithmetically centered at the signal frequency. The notch width was 0 (no notch), 100, 200, 400 or 800 Hz. The spectral parameters of the notch-noise masker were similar to those used by Nitschmann and Verhey (2013). The precursor had the same spectral characteristics as the no-notch masker. The masker noise and precursor noise each had a mean spectrum level of 30 dB [see Hartmann, (1998) for a definition of spectrum level]. This results in an overall SPL for the precursor of about 63 dB SPL. They were generated by transforming a Gaussian noise of the desired duration into the frequency domain via a fast Fourier transform, setting all Fourier components outside the desired passband to zero (while Fourier components within the notch were zeroed for the masker only), and performing an inverse fast Fourier transform on the complex spectrum. The resulting noise waveforms were then gated as needed. Both the signal and masker were 25 ms in duration, gated on and off simultaneously with 12.5-ms long raised cosine ramps (0-ms steady state). A total duration of 25 ms is below the onset delay of the MOC reflex (Backus and Guinan, 2006), therefore the signal and masker stimuli will not be affected by self-activation of the efferent system, and the effect of efferent activation can be studied separately by presentation of a precursor sound (with a sufficiently long duration and level to elicit the MOC reflex). The precursor was 325 ms in duration, including 10-ms raised cosine ramps at onset and offset.

The level and duration of the precursor was chosen to be close to the precursor parameters used by Yasin et al. (2014) to elicit the maximal efferent effect. In the precursor condition, the precursor noise was switched off 50 ms before the onset of the signal and masker. This temporal interval was chosen to avoid any issues arising from perceptual “confusion” that may arise if the temporal interval is too short between offset of the precursor and onset of the masker and reduced efferent effect due to the decay of the MOC activation at longer temporal intervals [see values for MOC reflex decay constants reported by Backus and Guinan (2006)]. In addition, the temporal gap largely reduces the amount of forward masking of the signal due to the presence of the precursor. Based on our previous studies at 4 kHz of forward masking the contribution of forward masking by the precursor alone would be less than 5 dB and so would not make a significant contribution to the overall (much larger) reduction in gain due to efferent mediation (e.g., Yasin et al., 2014). Moore and Glasberg (1983) investigated forward masking by broadband noises centered at different frequencies. They showed that, for a broadband masker (8-kHz wide, 210ms long) centered at 1-kHz with a spectrum level of 30 dB SPL presented at 20 ms prior to the onset of a 10-ms signal, the amount of masking was about 11 dB. Several studies with similar stimulus parameters as used in Moore and Glasberg (1983) showed that thresholds decrease by about 5 dB per doubling of the temporal gap between signal and masker, i.e., at 50 ms, masking at 1 kHz should also be about 5 dB (Zwicker and Zwicker, 1984, Dau et al., 1996).

The experiment used different random noise samples in each interval of a trial, and different noise samples were generated for each trial. The signal was either presented in phase at the two ears (S_0), or 180° out-of-phase at the ears (S_π). The masker was always presented diotically (N_0), as was the precursor. In both masking conditions, thresholds were also measured in the absence of the simultaneous masker to assess the amount of forward masking due the presence of the precursor. The signal and masker were presented simultaneously rather than non-simultaneously, as is the case in our previous studies of precursor effects on estimated gain (e.g. Yasin et al., 2013, 2014), since only a very small binaural masking level difference (BMLD) had been reported for such short signal durations using a forward-masking paradigm (10 to 20-ms signal: Yost and Walton, 1977; Yama, 1982, 1985; Fassel and Kohlrausch, 1997), and a similar simultaneous masking paradigm has been shown to be effective for estimating monaural/binaural filter bandwidths using the notch durations in the present study (Hall et al., 1983, Nitschmann et al., 2009, Nitschmann and Verhey, 2013).

The signal level at threshold was determined with a three-alternative forced-choice procedure. Each interval was 400 ms long. They were separated by 400-ms silence intervals. Each interval contained the masker and, in the precursor condition, also the precursor. One randomly chosen interval contained the signal. The listener’s task was to indicate the number of this interval by pressing the corresponding button on a graphical user interface. An example of such a signal interval is shown (for each condition) in Figure 1. Note that the temporal gap between the maskers of a trial were the same for the two conditions, i.e., the silence interval between consecutive maskers was 775 ms in the baseline condition.

The signal level was adjusted according to a one-up two-down rule tracking the 70.7% correct response level (Levitt, 1971). The signal level in the first trial was 70 dB SPL. The initial step size of the signal level was 8 dB. The step size was halved after every second reversal of the level adjustment procedure until a step size of 1 dB was reached. At this minimum step size, the run continued for another six reversals. The mean over these last six reversals was used as a threshold estimate.

Prior to the main experiment, single threshold estimates were obtained for a reduced set of stimuli (no notch, 800-Hz notch, no masker) in a first training session. The order of the 12 runs (three masker conditions x two precursor conditions x two signal phase conditions) of this training session was randomized. In the main experiment, thresholds were measured for four runs of the experiment using the complete stimulus set. As in the first training session the order of the runs (now 96: four runs x six masker conditions x two precursor conditions x two signal phase conditions) were randomized. Per combination of masker condition, precursor condition and signal phase condition, the mean of the threshold estimates of the last three runs was taken as the final threshold estimate. The other threshold estimates were considered as practice trials. Thus all listeners received at least 1.5 hours of practice before data collection.

The listeners were seated in a double-walled sound-proof booth. The experiment was controlled using the MATLAB AFC framework described by Ewert (2013). The stimuli were generated at a sampling frequency of 44.1 kHz. They were converted from digital to analogue signals and presented monaurally via an external sound card (RME Fireface 400, Haimhausen, Germany) and headphones (Sennheiser HDA200, Wedemark, Germany). The headphones were free-field equalized according to IEC 389-5.

3. Results

3.1. Notched-noise data

Figure 2 shows the individual masked threshold results for the eleven listeners that participated in the experiment. The bottom right panel includes the figure legend. All other panels present individual thresholds for the diotic S_0 and a dichotic S_π signal embedded in a diotic notched-noise masker (N_0) as a function of notch width. In the precursor condition, diotic thresholds are indicated by squares and dichotic thresholds by diamonds. In the baseline condition (no precursor), diotic thresholds are indicated by circles and dichotic thresholds by triangles. The threshold curves predicted by an energy model with individually fitted third-order gammatone filters are shown with solid lines. Absolute thresholds for the signal are shown with the same symbols as used for the notched-noise data with a horizontal dashed line. All listeners show a trend for a decrease in thresholds with increasing notch width for both the precursor and baseline conditions. Also, for both the precursor and baseline condition, the thresholds for a dichotic stimulus are lower than for the diotic stimulus. For most listeners (except S2 and S10) the diotic and dichotic threshold curves for the precursor condition are shallower than the corresponding threshold curves stimuli for the baseline condition. Figure 3 shows the average data for all eleven subjects, which reflects the main trends seen in the individual data, i.e., i) dichotic thresholds are lower than diotic thresholds (precursor and baseline conditions) and ii) diotic and dichotic thresholds curves for the precursor condition are shallower than those for the corresponding baseline condition.

A within-subject Analysis Of Variance (ANOVA) was conducted on the values of masked threshold for the signal (data for all 11 subjects), with main factors of notch width (5 levels: 0, 100, 200, 400 and 800 Hz), precursor (2 levels: presence or absence of precursor) and signal phase [2 levels: diotic (S_0) or dichotic ($S\pi$)]. Mauchly's Test of Sphericity was shown to be significant and since the value of Epsilon was < 0.75 (Girden, 1992) the Greenhouse-Geisser correction was applied to adjust the degrees of freedom in the resultant ANOVA. There was a significant effect of notch width ($F_{(1,12)} = 163.51$, $p < 0.001$ (two-tailed), with effect size, $\eta^2 = 0.94$), signal phase ($F_{(1,10)} = 42.36$, $p < 0.001$ (two-tailed), with effect size, $\eta^2 = 0.81$), and a significant interaction between notch width and precursor ($F_{(1,15)} = 11.70$, $p < 0.01$ (two-tailed), with effect size, $\eta^2 = 0.54$).

Post hoc paired *t* tests (Bonferroni corrected) revealed that the $S\pi$ signal resulted in lower thresholds in noise than the S_0 signal, across all notch width and precursor conditions [mean difference = 3.42, SD = 1.74, $t_{(10)} = 6.51$, $p < 0.001$ (two-tailed)].

Following the hypothesis outlined in the introduction that addition of a precursor should decrease gain and therefore increase the filter bandwidth, the addition of a precursor was found to significantly increase thresholds at wider notched widths of 400 Hz [mean difference (precursor- no precursor) = 4.11, SD = 3.31, $t_{(10)} = 4.13$, $p < 0.01$, one-tailed), and 800 Hz [mean difference (precursor- no precursor) = 3.17, SD = 4.65, $t_{(10)} = 2.26$, $p < 0.05$, one-tailed).

A within-subject ANOVA only on the no-precursor data was also conducted to see if there was an interaction between notch width and signal phase (as has been reported in previous binaural no-precursor studies), with main factors of noise width (5 levels: 0, 100, 200, 400 and 800 Hz) and signal phase [2 levels: diotic (S_0) or dichotic (S_π)]. Mauchly's Test of Sphericity was shown to be significant and since the value of Epsilon was < 0.75 (Girden, 1992) the Greenhouse-Geisser correction was applied to adjust the degrees of freedom in the resultant ANOVA. There was a significant effect of notch width ($F_{(2,18)} = 240.86$, $p < 0.001$ (two-tailed), with effect size, $\eta^2 = 0.96$), signal phase ($F_{(1,10)} = 25.87$, $p < 0.001$ (two-tailed), with effect size, $\eta^2 = 0.72$), and a significant interaction between notch width and signal phase ($F_{(2,24)}$ = 3.29, $p < 0.05$ (two-tailed), with effect size, η^2 = 0.25), confirming previous findings that the shape of the threshold curve is affected by the signal phase. Post hoc paired *t* tests (Bonferroni corrected) revealed that the S_0 signal resulted in significantly higher masked thresholds than $S\pi$ signal for notch bandwidths of 0 Hz (mean difference (S_0 - $S\pi$) = 4.38, SD = 1.99, $t_{(10)}$ = 7.32, $p < 0.001$, two-tailed), 100 Hz (mean difference (S_0 - $S\pi$) = 3.76, SD = 2.34, $t_{(10)}$ = 5.33, $p < 0.001$, two-tailed), 200 Hz (mean difference (S_0 - $S\pi$) = 3.24, SD = 2.76, $t_{(10)}$ = 3.90 $p < 0.01$, two-tailed), and 400 Hz (mean difference (S_0 - $S\pi$) = 2.83, SD = 2.19, $t_{(10)}$ = 4.29 $p < 0.01$, two-tailed).

3.2 Filter shapes

Filters were characterized on the basis of a commonly used filter shape, a linear gammatone filter (e.g., Patterson et al., 2003; for the implementation used in the present study, see Hohmann, 2002). The equivalent rectangular bandwidth (ERB) of a third-order gammatone filter centered at the signal frequency was fitted to the threshold curves using a power spectrum model, where the spectrum of the gated 25-ms notched-noise masker was used as the input to the model. Prior to the gammatone filtering, an outer and middle ear band-pass filter of first order with cut-off frequencies of 0.5 and 5.3 kHz was used (as in Nitschmann and Verhey, 2013). The filter parameter bandwidth was derived independently for the N_0S_0 and N_0S_π thresholds yielding estimates of monaural and binaural filter widths. Table 1 shows ERB values of the filters fitted to individual data and also to the average data. The parameter *r(ERB)* shown in the last four columns (columns 6 to 9) of this table denote *r(ERB)*, the ratio of the corresponding ERB for N_0S_π compared with N_0S_0 thresholds (columns 6 and 7) or the ratio of the corresponding ERB for the precursor and baseline conditions (columns 8 and 9). The filter shapes are shown in Figure 4. Thin lines indicate the individual filters, thick lines the filters fitted to the average data. Each panel shows the filters for one combination of masking condition (baseline, with precursor) and interaural signal phase [monaural (diotic *S_0*), binaural (dichotic *S_π*)]. The fitted threshold curves are shown as solid lines in Figures 2 and 3.

For the baseline condition, the majority of the listeners (S1-S6 and S8-S11) measured about the same (S3, S9) or wider binaural than monaural filters. For this group of listeners (S1-S6 and S8-S11), the ratio *r(ERB)* ranged from 1.0 to 1.5. For listener S7, a slightly narrower filter was derived from the dichotic data than from the diotic data (*r(ERB)* = 0.9). For the average threshold data, an ERB ratio of 1.13 was obtained.

In contrast, for the precursor condition, the filter widths derived from the average data were about the same for the diotic (289 Hz) and dichotic (286 Hz) conditions when the precursor was present, giving a ratio r(ERB) of about 1.0. The ratio r(ERB) for the individual data ranged from 0.7 (S6) to 2.6 (S8).

For the diotic condition, the filters derived from individual data with precursor were for most listeners larger than those derived from the baseline condition. Only for listeners S2 and S10 the bandwidth was almost identical for baseline and precursor condition. For all other listeners, the ratio r(ERB) ranged from 1.2 (S3, S9) to 3 (S8). For filters fitted to the average data, when a precursor was added, the monaural filter was 45% broader than in the baseline condition. For the dichotic condition, the filters derived from individual data with precursor were generally 1.2 to 1.5 times larger than those derived from the baseline condition. Two listeners (S2, S10) had narrower filters with precursor than without precursor and one (S7) had a filter that was more than six times larger than that derived from the data of the baseline condition. This resulted from the anomalously large bandwidth derived from the dichotic data with precursor. On average the binaural filter was 27 % larger with precursor than without precursor.

Values for the estimated filter bandwidths (ERB in Hz) were also analyzed statistically for each precursor condition and signal phase.

A within-subject ANOVA was conducted on the values of relative filter widths (data for all 11 subjects) with factors of precursor (2 levels: presence or absence of precursor) and signal phase [2 levels: diotic (S_0) or dichotic (S_π)]. Mauchly's Test of Sphericity was shown to not be significant and sphericity was assumed. No significant effects were found. Since the modelled filter fit to the data for S8 were anomalous (see Table 1) all data were inspected for significant outliers. Tukey's method for eliminating outliers (Tukey, 1977) was applied. Data values greater than 1.0 interquartile range below the 25th percentile or above the 75th percentile were eliminated. Using this process the value of 12.34 of listener S8 was identified as an outlier. This one value is likely due to an anomaly of the fitting process, so S8 was not included in the subsequent ANOVA. A within-subject ANOVA (with 10 subjects; S8 data removed) showed a significant effect of precursor ($F_{(1,9)} = 6.42$, $p < 0.05$ (two-tailed), with effect size, $\eta^2 = 0.42$). A *post hoc* paired *t*-test revealed that with the addition of a precursor, filter bandwidths were significantly wider (irrespective of signal phase) compared to the no precursor condition, [mean difference (with precursor – no precursor) = 0.62, SD = 0.77, $t_{(9)} = 2.53$, $p < 0.05$ (two-tailed)].

4. Discussion

With the addition of the precursor, thresholds for detectability of the signal were decreased in both the N_0S_0 and N_0S_π condition, i.e., filter bandwidths were broadened for both conditions. A precursor has been shown to reduce cochlear gain in masker experiments where the precursor sound is presented prior to the masker-signal stimuli, similar to the stimuli used in the current study (Jennings et al., 2009; Jennings and Strickland, 2012; Yasin et al., 2014; Drga et al., 2016). Thus a broadening of the filters was expected. However, the broadening is less pronounced for the dichotic data than for the diotic data resulting in about the same monaural and binaural bandwidth in the precursor condition.

In psychophysical experiments to measure the amount of efferent gain reduction, the amount of forward masking produced by the precursor is often in the first phase of the experiment (see Yasin et al., 2013; 2014). In the second phase, the level of the signal is then raised 10 dB above the masked threshold in the subsequent measurements of efferent-mediated gain reduction where the masker is then varied adaptively. Such a two-phase approach was not used here to maintain an experimental design similar to that used typically for notched-noise measures of binaural frequency selectivity where the signal is adaptively varied and the masker level is fixed (Hall et al., 1983, Nitschmann et al., 2010, Nitschmann and Verhey, 2013). In the present study, precursor parameters were chosen to minimize the contribution of forward masking, i.e. precursor duration was set at 325 ms and precursor offset to combined masker-plus signal onset was set at 50 ms. The precursor raised average thresholds without a notched-noise masker for both signal phases by about 9 dB (Fig. 3). Average notched-noise thresholds were at least 15 dB higher than that masked threshold (with the precursor alone as the masker), i.e., the influence of forward masking in the notched-noise data should be negligible. For the individual data, notched-noise thresholds were at least 9 dB higher, i.e., all thresholds were obtained at a level above masked threshold (with the precursor alone as the masker) that was comparable to or higher than that used in our previous studies on the efferent effects. In addition, we showed in our previous studies at 4 kHz (using the two-phase approach) that the contribution of forward masking by the precursor alone would not make a significant contribution to the overall (much larger) reduction in gain due to efferent mediation (e.g., Yasin et al., 2014).

Binaural filter bandwidths have been shown to be wider than monaural filters by a number of studies by measuring detection thresholds for a sinusoidal signal as a function of the bandwidth of a noise centered at the signal frequency (Bourbon and Jeffress, 1965; Wightman et al., 1971; Hall et al., 1983; Zurek and Durlach, 1987; Cokely and Hall, 1991; van de Par and Kohlrausch, 1999), or by measuring detection thresholds for a sinusoidal signal as a function of the width of the notch in broadband noise (Hall et al., 1983; Nitschmann et al., 2009; 2010; Nitschmann and Verhey, 2013). For a similar signal frequency to the present study (1 kHz), Nitschmann and Verhey (2013) showed the ERB based on mean thresholds to be 236 Hz (N_0S_π) and 143 Hz (N_0S_0), and *r*(ERB) (dichotic ERB divided by diotic ERB) was 1.6. Comparative ERB values from the current study (for the baseline condition) are 215 Hz (N_0S_π) and 192 Hz (N_0S_0), and the ratio *r*(ERB) was 1.1. Thus the filter bandwidth for the N_0S_0 condition is larger than in Nitschmann and Verhey (2013). This could be due to the much shorter total duration of the masker and signal in the present study (25 ms) compared to 300 ms in their study. The short duration of the stimuli results in a broadening of the spectrum, partly filling the notch of the noise. This was considered when fitting the filter to the data by using the masker spectra as input of the filter. Since only the energy of one auditory filter was used for the derivation of the filter width, the broadening of the signal was not considered which may at least partly account for the difference in filter estimate of the two studies. Interestingly, the filter bandwidth for the N_0S_π condition was slightly narrower than in Nitschmann and Verhey (2013). This is presumably due to the small maximum BMLD (for the no-notch condition).

Comparing the current results with those of Nitschmann and Verhey (2013) for the same signal frequency thresholds in the no-notch condition, the shorter total signal duration used in the present study increases thresholds for detection of the stimuli, as expected from temporal integration data. N_0S_0 and N_0S_π thresholds are increased by about 5 dB and 15 dB respectively, compared to Nitschmann and Verhey (2013; Fig. 2 for the 1-kHz signal and masker without a notch). In contrast, absolute thresholds (without a masker) are increased by the same amount (10 dB).

The present results seem to be at odds with previous studies on the effect of signal duration on the BMLD. For 500 Hz, several studies reported that the BMLD for short signals was larger than for long signals (Blodgett et al., 1958, Bernstein and Trahiotis, 1998). Kohlrausch (1986) reported larger BMLD for short (25ms) than long (250 ms) signals for signal frequencies in the range from 300 to 800 Hz). That the comparison between Nitschmann and Verhey (2013) and the present study indicate the opposite effect may be partly due to the signal frequency which was higher than commonly used in studies on duration effects in BMLD. For a 4-kHz tone embedded in a 200-Hz white noise, Bernstein and Trahiotis (1998) reported a decrease in BMLD as the signal duration decreases.

A large portion of this of finding may be accounted for by differences in signal and masker gating of the two studies. The present study used synchronous gating of signal and masker whereas in Nitschmann and Verhey (2013) the signal was temporally centered in a longer masker. Robinson and Trahiotis (1972) showed that a common gating of signal and masker reduces the BMLD compared to a fringe condition as used in Nitschmann and Verhey (2013).

Precursor-mediated activation of the MOC reflex has been shown to affect psychophysical tuning curves, reducing the gain and shifting the filter's best frequency (Jennings et al., 2009) and increasing estimated bandwidths (Vinay and Moore, 2008; Jennings et al., 2009; Jennings and Strickland, 2012) consistent with a reduction in cochlear gain. The present results show that the filter bandwidths are increased for the N_0S_0 condition when a precursor is added, the results for the N_0S_π condition are somewhat more variable, but there is a general trend towards larger ERBs with the addition of a precursor also for the dichotic data.

The finding that the same filter width was derived from the diotic and dichotic data in the presence of the precursor may indicate that the binaural frequency selectivity is affected differently from the monaural system when the MOC reflex is activated. However, one should keep in mind that there are large interindividual differences when the precursor is added, much larger than without precursor. Such large interindividual differences are also found in previous psychoacoustic studies on the effect of MOC reflex on filter width (e.g., Jennings and Strickland, 2012).

Large interindividual differences for the monaural filter width were also observed in hearing-impaired listeners (Nitschmann et al., 2010). However, the individual variations in the ratio between binaural and monaural bandwidth for the hearing-impaired listeners are smaller than the variation of this ratio in the precursor condition for the normal-hearing listeners of the present study. Thus, although both MOC activation and hearing loss cause cochlear gain reduction it is difficulty to draw conclusions about the degree of similarity between underlying physiological mechanisms other than in both cases gain reduction may involve outer hair cells (Maison et al., 2013). The results of the present study compared to those of Nitschmann et al. (2010) may indicate that MOC reflex and hearing loss have different effects on auditory processing, at least on the relation between monaural and effective binaural bandwidth.

5. Summary and conclusions

The present study investigated the change in binaural frequency selectivity due to activation of the efferent effect. Frequency selectivity was assessed with a notched-noise experiment and the specific effective binaural frequency selectivity by comparing a diotic condition with a dichotic condition where the signal had an interaural phase difference of π. Efferent activation was studied by presenting a precursor prior to the signal and the notched-noise masker which is thought to activate the MOC system. In the absence of a precursor, the data indicate effectively wider binaural filters compared to monaural filters, in agreement with previous studies using the same masking paradigm. However, the difference is smaller, presumably due to the shorter signal and masker duration than used in the previous studies and a common on- and offset of signal and masker. The addition of the precursor reduces frequency selectivity and thereby broadens the filter for both diotic and dichotic stimuli, in agreement with the hypothesis that the efferent effect reduces cochlear gain. In general, addition of a precursor reduces gain (as shown by previous studies), resulting in reduced frequency selectivity in both the dichotic and diotic case.

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TABLES

Subject	ERB in Hz				r(ERB)		r(ERB)	
	Baseline		With precursor		Baseline	With precursor	diotic	dichotic
	diotic	dichotic	diotic	dichotic				
S1	272	296	378	355	1.1	0.9	1.4	1.2
S2	224	236	233	208	1.1	0.9	1.0	0.9
S3	231	232	284	285	1.0	1.0	1.2	1.2
S4	192	235	298	313	1.2	1.0	1.5	1.3
S5	145	187	243	240	1.3	1.0	1.7	1.3
S6	184	195	324	255	1.1	0.8	1.8	1.3
S7	168	145	219	220	0.9	1.0	1.3	1.5
S8	208	264	626	1637	1.3	2.6	3.0	6.2
S9	186	188	229	249	1.0	1.1	1.2	1.3
S10	162	229	163	160	1.4	1.0	1.0	0.7
S11	275	416	797	590	1.5	0.7	2.9	1.4
Average	**199**	**225**	**289**	**286**	**1.1**	**1.0**	**1.5**	**1.3**

Table 1. Auditory filter parameters a filter fitted to the notched-noise data. The equivalent rectangular band (ERB) in Hz of the third-order linear gammatone filter fitted to the diotic S_0N_0 (second and fourth columns) and the dichotic $S_\pi N_0$ (third and fifth columns) for the baseline condition (second and third columns) and the precursor condition (fourth and fifth columns) are shown. The sixth and seventh columns show the ratio of the dichotic ERB divided by the diotic ERB value. The eighth and ninth columns show the ratio of the ERB with precursor divided by the ERB in the baseline condition for the diotic and the dichotic condition, respectively. Filter parameters are shown for each listener individually. The last row shows the filter fit for the average data (which differs slightly numerically from the average ERB value per column).

FIGURES

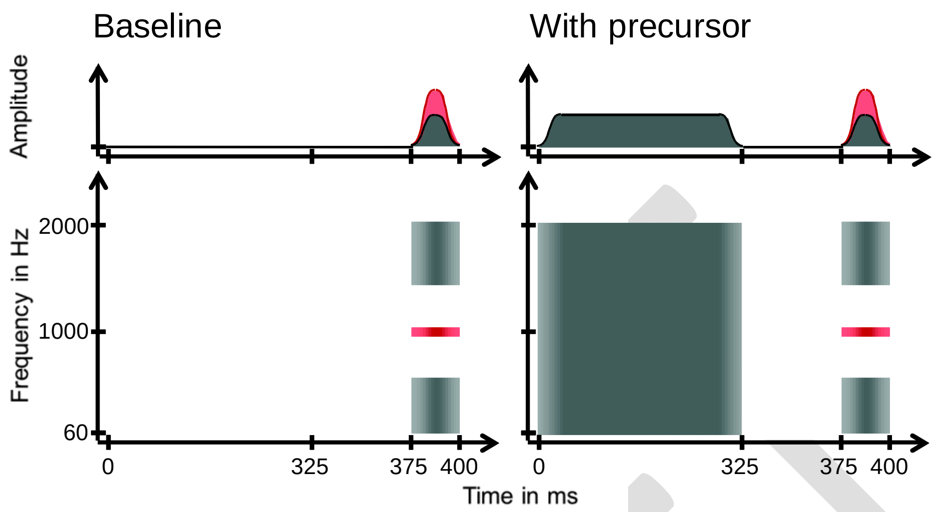

Fig. 1. Schematic plot of the stimuli for the two masking conditions: baseline condition (left column of panels) and precursor condition (right column of panels). The temporal envelopes of signal (red), masker (grey) and, for the precursor condition, the precursor (also grey) are shown in the top row of panels. The bottom row of panels shows the spectrograms of the stimuli.

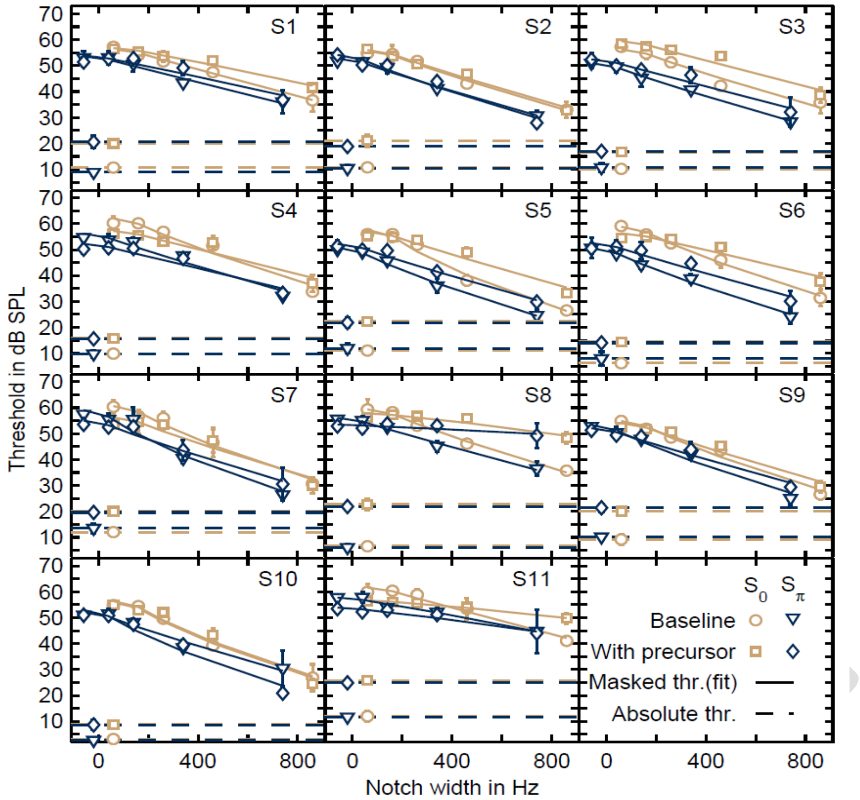

Fig. 2. Masked thresholds for diotic S_0 and a dichotic S_π signal embedded in a diotic notched-noise masker (N_0) as a function of notch width. The bottom right panel contains the figure legend. All other panels show individual data. Diotic thresholds are indicated by squares in the precursor condition and by circles in the baseline condition, dichotic thresholds by diamonds in the precursor condition and by triangles in the baseline condition. Error bars indicate plus and minus one standard deviation. For a better visibility, thresholds for the baseline condition are shifted to the left and those for the precursor condition to the right. The threshold curves predicted by an energy model with individually fitted third-order gammatone filters are shown with solid lines (see Methods for details). Thresholds without a masker are shown with the same symbols as used for the notched-noise data and a horizontal dashed line.

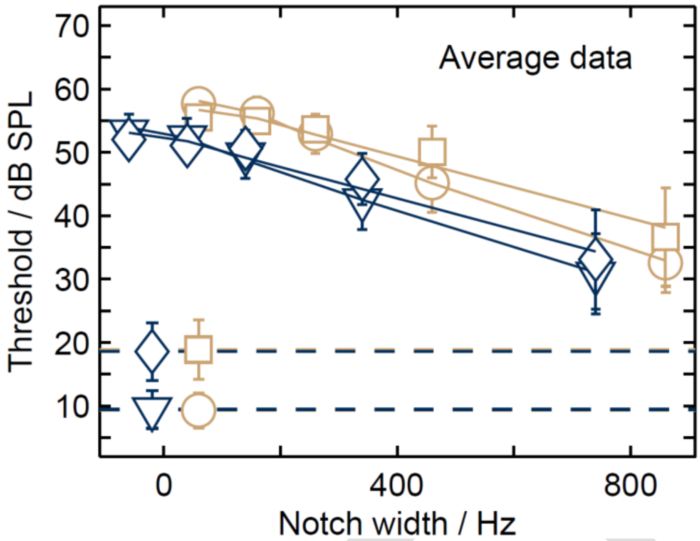

Fig. 3. Same as Fig. 2 but now showing average data across all eleven listeners.

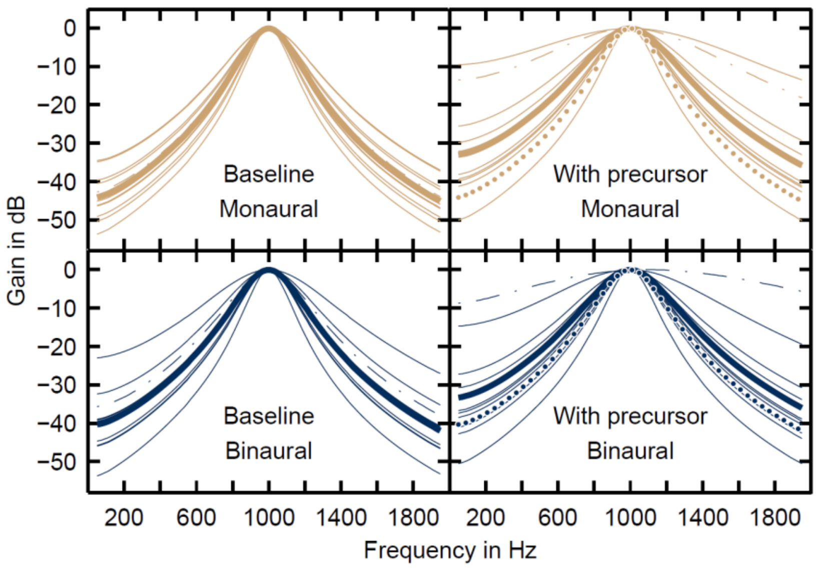

Fig. 4. Transfer functions of the linear gammatone filters of third order fitted to the diotic N_0S_0 (monaural filters, top panels) and dichotic N_0S_π (binaural filters, bottom panels) notched-noise data. Thin lines indicate filters fitted to individual data. The dashed dotted lines indicate the filters that were not used for the statistical analysis with a reduced data set. Thick solid lines indicate filters fitted to the average data. Left panels indicate the filter shapes for the baseline condition and the right panels those for the condition with the precursor. In the latter panels, the filters fitted to the average data of the corresponding baseline condition are redrawn with a thick dotted line, to facilitate a direct comparison of these two conditions.