An electrophysiological measure of tonotopic selectivity in normal-hearing humans and cats.

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ABSTRACT

We describe a non-invasive electrophysiological (EEG) measure of tonotopic selectivity and compare the results between humans and cats. Sequences of 50-ms tone-burst probes were presented at 1-second intervals against a continuous noise masker, and the averaged cortical onset response (COR) to the probe was measured using EEG electrodes placed on the scalp. The noise masker had a bandwidth of 1 or 1/8th octave, geometrically centred on 4000 Hz for humans and 8000 Hz for cats. Probe frequency was either -0.5, -0.25, 0, 0.25 or 0.5 octaves *re* 4000/8000 Hz. The COR was larger for probe frequencies more distant from the noise geometrical centre, and this effect was greater for the 1/8th-octave than for the 1-octave masker. This pattern broadly reflected the masked excitation patterns obtained psychophysically with similar stimuli in a companion paper. However, the positive signal-to-noise ratio used to obtain reliable COR measures meant that some aspects of the data differed from those obtained psychophysically, in a way that could be partly explained by the upward spread of the probe's excitation pattern. We argue that although COR measures are affected by some factors that differ from those that influence psychophysical masked detection thresholds, they can reveal differences in the width of excitation patterns produced by different stimuli. We also argue that the paradigm may be effectively applied to cochlear-implant experiments in humans and animals.

Introduction

The tonotopic representation of sound in the auditory system is essential for many auditory tasks, including the recognition of spectral shape and the perceptual segregation of competing sounds. For normal-hearing humans and animals, this representation is highly selective, thanks to the exquisite tuning of the basilar membrane (Liberman and Kiang 1978; Sachs et al. 1988). As a result, individual frequency components of a given sound excite more-or-less discrete sets of auditory nerve fibres, and competing complex sounds produce neural excitation patterns that overlap only partially. In contrast, the selectivity of neural excitation produced by cochlear implant (CI) stimulation is much broader (e.g. Shannon 1983; Kwon and van den Honert 2006; Carlyon *et al.* 2007). This may limit speech perception by CI users, especially when more than one sound is present at a time. Attempts to improve this peripheral selectivity by using focussed methods of stimulation have produced promising results in single-unit recordings from cats and guinea pigs (Raggio and Schreiner 1999; Rebscher *et al.* 2001; Bierer and Middlebrooks 2002; Middlebrooks and Bierer 2002; Snyder *et al.* 2004, 2008; Bonham and Litvak 2008; Bierer *et al.* 2010; George *et al.* 2014). Perhaps surprisingly, however, they have achieved only modest and quite variable success in psychophysical and speech-perception tests in human listeners (Boëx *et al.* 2003; Kwon and van den Honert 2006; Chatterjee *et al.* 2006; Bierer and Faulkner 2010; Srinivasan *et al.* 2010; Chua *et al.* 2011; Fielden *et al.* 2013; Marozeau *et al.* 2015; Padilla and Landsberger 2016, Carlyon *et al.* 2017). Although this discrepancy may stem from differences between species in the cochlear morphology and the neural health at implantation, it might also arise from the

89 differences in the methods and measures being used in animal and human
90 experiments.

91 As a step toward synergistic experiments, we are developing electrophysiological and
92 psychophysical procedures that can be conducted in parallel both in a feline animal
93 model and in human subjects, and with both acoustic and electric (CI) stimulation. The
94 present study evaluates a cortical electro-encephalography (EEG) method of
95 measuring tonotopic selectivity in normal-hearing (NH) cats and humans that can be
96 directly compared to psychophysical measures obtained in both species (cf.
97 companion paper, Middlebrooks *et al*, 2021). Our long-term aim is to use this method
98 as a bridge between psychophysical and speech-perception measures, most
99 appropriately performed in humans, and precise physiological recordings that can only
100 be obtained in animals. Our method may, for example, prove useful in assessing novel
101 CI stimulation configurations that intend to improve spatial selectivity in CI listeners or
102 for the evaluation of novel interventions that can initially be tested only in animals,
103 such as penetrating nerve arrays (Middlebrooks and Snyder 2007) and optogenetics
104 (Dieter *et al*. 2019).

105 Our paradigm is illustrated schematically in Figure 1. It mimics broad versus focussed
106 stimulation CI stimulation by comparing the selectivity of a narrow-band (NB, $1/8^{\text{th}}$ -
107 octave, panels A and C) and of a wide-band (WB) masker (panels B and D), using 50-
108 ms pure-tone probes (black lines). The maskers are presented continuously at a fixed
109 level and frequency, and the probes are presented at 1-second intervals either on-
110 frequency or off-frequency. We measure the Cortical Onset Response (COR) to the
111 probe in both humans and cats. The COR can be elicited either in response to the
112 onset/offset of a sound or to a change in an ongoing sound (cf. review by Näätänen
113 and Picton 1987). Typical COR waveforms for humans and cats are shown

respectively in panels E and F of Figure 1. We used simultaneous rather than forward masking to avoid responses to the masker onset and offset (Brattico et al. 2003), and to minimise confusion effects between the narrowband masker and probe that have been observed in psychophysical forward masking experiments (e.g., Moore et al. 1984; Neff 1985; McKay 2012; Cosentino et al. 2015).

In addition to the comparison between NB and WB maskers, we measure tonotopic selectivity in human listeners using the notched-noise method (Patterson 1976), which, although less transferrable to CI stimulation, minimises effects of off-frequency listening and of distortion products. Unlike previous studies we also measure the COR amplitude-growth functions. This allows us to convert differences in the COR amplitude across conditions to an equivalent change in probe level, thereby permitting a comparison of the COR measures obtained here with the psychophysical measures of selectivity reported in our companion paper, and for which probe level is the dependent variable.

Experiment 1: masked COR in NH humans

The COR recordings in humans were split into two sets of experiments (Experiment 1a and Experiment 1b). Experiment 1a measured the difference in tonotopic selectivity between a NB and WB masker using the paradigm shown in Figure 1, Experiment 1b measured tonotopic selectivity using the notch-noise method, as well as the level-growth of the COR, using the same participants as in Middlebrooks et al (2021). Experimental procedures were approved by the Cambridge Psychology Research Ethics Committee (project 2017.085), and written informed consent was collected prior to any testing. The numbers of right and left ears were balanced across participants

(stimulation was always monaural), and an audiogram revealed that all participants had thresholds of 20 dB HL or lower at all audiometric frequencies.

Methods

Stimulation and recording setup

All stimuli were generated using custom MATLAB scripts, played through a RME Fireface UCX sound card, TDT HB7 headphone drivers, and an ER2 insert phone. Stimuli were calibrated using an ear coupler (GRASS) and a Hewlett Packard HP3561A dynamic signal analyser. EEG signals were recorded with an 8-channel Biosemi system with electrodes located at P7, P8, Oz, Cz, AF3, AF4 and above/below the left eye. The first four electrodes (P7, P8, P10, Cz) covered respectively the left/right mastoids, the back of the head and the vertex, which are typical electrode positions for COR recordings. The last four electrodes were closer to the eyes (AF3/AF4 are in the frontal area), so as to detect eye artefacts. EEG signals were recorded at a sampling rate of 2048 Hz, and the cut-off of the anti-aliasing low-pass filter was 1/5th of this rate (~400 Hz). Digital triggers were routed from the sound card to the triggering input of the EEG system via a custom-built triggering interface (Mao et al. 2018, <https://github.com/d-mao/trigger-box>). The different conditions were marked by different digital trigger codes..

Participants were seated in a reclined armchair, inside a double-walled, electrically-shielded, sound-attenuating booth. They watched TV shows with subtitles while undergoing the test. They could freely choose which show they wanted to watch.

For each of the conditions described below, a sweep of 13 fixed-frequency probes with 1-second stimulus onset asynchronies (SOAs) was created. For the masked conditions, the masker started simultaneously with the first probe in each sweep and

lasted for 13 seconds; the first probe in each sweep was ignored in the analysis because its onset coincided with the start of the masker. There was a silent gap of approximately 1.2-s between each sweep (1 second plus computing time). All of the sweeps so obtained (e.g. various probe frequencies/levels and maskers) were randomly interleaved in one block, which was repeated 20 times. For each repetition, the order of the sweeps within that block was randomised afresh.

Analysis

The data were analysed using the Fieldtrip toolbox (Oostenveld et al. 2011) and custom Matlab (Mathworks Inc.) scripts. First, the difference between the contralateral mastoid electrode (P7 if stimulation was in the right ear, P8 for left-ear stimulation) and the vertex electrode (Cz) was computed. We picked this montage over other possible options (ipsilateral, back of the head, etc.) based on previously published studies and on the fact that it led to strong CORs in pilot measurements. For each condition, 240 epochs were created by windowing from 200 ms before to 600 ms after each probe onset (12 probes per block and 20 block repeats). All epochs were then filtered between 1 and 20 Hz with a Finite-Impulse-Response filter with a 1-Hz transition bandwidth and 2-seconds padding. For artefact rejection, the difference between the channel below and above the eye was computed. For each participant, a z-score was computed from the amplitude variation across the whole duration of their EEG recording. Epochs that contained extreme artefacts (z-score > 4) were rejected, corresponding to between 5 and 15 % of the total number of epochs, depending on the condition. The remaining artefact-free epochs were averaged using the 200 ms before the probe onset as baseline. The amplitudes of the N1 and P2 peaks of the COR were obtained by identifying a minimum and maximum in the [50-150ms] and

[100-200ms] windows after the probe onset. The N1P2 amplitude was computed by taking the difference between P2 and N1.

Experiment 1a: NB vs. WB masker

Thirteen right-handed NH participants participated; they were different from those who had taken part in the companion psychophysics study (Middlebrooks et al. 2021). Data from three of those participants were rejected due to very low N1P2 values in the no-mask conditions ($< 3 \mu\text{V}$ at all frequencies). The CORs were measured in response to 70-dB SPL, 50-ms probes at the frequencies shown in Figure 1, panels A/B, namely 2828, 3364, 4000, 4757 and 5657 Hz. There were three masking conditions: no masker, NB masker, and WB masker. We added a 55-dB SPL pink noise with an upper cut-off of 1862 Hz in the masked conditions, as in the companion study by Middlebrooks et al. 2021. The purpose of the noise was to mask quadratic distortion products (DPs) without directly masking the probe frequencies. Note, however, that for the NB masker, cubic distortion products ($2f_1-f_2$) between the masker and the probe may have been audible for some conditions, and we return to this point in the Discussion. For a given NB masker level, the WB masker level was increased by 7.9 dB, so that both maskers would have the same energy passing through an auditory filter centred on 4 kHz in NH listeners. These values were estimated using the formula relating the Equivalent Rectangular Bandwidth (ERB) of the auditory filter to its centre frequency described by Glasberg and Moore (1990). Masker levels included one condition identical to that of Middlebrooks *et al* (2021), namely 60 dB SPL/ERB, plus three other lower levels: 48, 52, and 56 dB SPL/ERB. This resulted in 45 conditions (5 probe frequencies and 4 masker levels for two masker types, plus the 5 unmasked

probes), equivalent to a little under 4 hours of actual EEG recording. Testing was split into two 3-hour sessions, with the first session including the audiogram.

Experiment 1b: Notch-noise masker and level growth

The eleven participants of Middlebrooks et al. (2021) plus experimenter AJH participated in Experiment 1b. The CORs to 70-dB SPL, 4 kHz, 50-ms probes were measured in the presence/absence of a notched-noise masker. There were five conditions: no-mask, and masked with four different notch widths ($\Delta f = 0, 10, 20$ and 30%), identical to the psychophysical experiment. At 0-% notch width, the masker is effectively a one-octave band masker (and is equivalent to the WB masker of experiment 1a). For non-zero notch widths of $\Delta f\%$, the masker was split into two bands at 4 kHz, and the resulting low-frequency and high-frequency bands were shifted in frequency by respectively $-\Delta f\%$ and $+\Delta f\%$ on a linear scale (e.g. by -400 and +400 Hz for a Δf of 10%). For a given $\Delta f\%$, the notch width was therefore twice Δf (as in Patterson et al. 1976). The level of the masker was the same as the one-octave masker in the previous experiments (67.9 dB SPL, i.e. 60 dB SPL in the ERB centred on 4 kHz for the 0-% condition).

Level-growth functions were also obtained with these participants. The CORs to 50-ms probes without any masker were measured at five levels (40, 47.5, 55, 62.5, and 70 dB SPL) and three frequencies (2828, 4000 and 5657 Hz). All level-growth and notch-noise conditions were collected in the same session. The 70-dB SPL level-growth condition was therefore used as the no-mask comparison for the data obtained in the notch-noise condition.

Results

234 *Experiment 1a: NB vs WB masker*

235 Figure 2 shows the grand average waveforms across the 10 participants. In the no-
236 mask condition (black lines), they show the typical N1-P2 morphology of the COR,
237 with a negative peak about 100 ms after probe onset, followed about 50 ms later by a
238 positive peak. These grand-average waveforms illustrate some of the main effects of
239 adding the NB and WB maskers, shown by the red and blue lines, respectively.
240 Increasing the masker level decreases the amplitude of the N1P2 complex. For the
241 NB masker, this happens mostly for the 4-kHz probes; for the WB maskers, at least at
242 high masker levels, there is a visible reduction at all probe frequencies tested.

243 In order to quantify these effects and to correct for individual differences in unmasked
244 responses, we normalised all the individual masked N1P2 values by their
245 corresponding no-masker value at the same frequency. These normalised values,
246 expressed in dB, are shown in Figure 3. A repeated-measures ANOVA on the
247 normalised amplitudes revealed significant main effects of masker level ($F(3,27) =$
248 54.5 , $p = 1.4e-11$) and of probe frequency ($F(4,36) = 7.7$, $p = 1.4e-4$). Every 2-way
249 interaction was significant: masker type x masker level ($F(3, 27) = 9.6$, $p = 1.8e-4$),
250 masker type x probe frequency ($F(4, 36) = 7.0$, $p = 2.9e-4$) and masker level x probe
251 frequency ($F(12, 108) = 5.5$, $p = 2.9e-7$). There was no 3-way (masker type x masker
252 level x probe frequency) interaction ($F(12, 108) = 1.16$, $p = 0.32$). The ANOVA reflects
253 several aspects of this dataset: increasing the masker levels increased masking
254 overall, there was more masking at 4 kHz than the other probe frequencies for the NB
255 masker, and, importantly, masking was more uniform across frequencies for the WB
256 masker. It can also be seen that, for the lower levels, some subjects showed no
257 masking even for the 4-kHz probe. We therefore additionally performed a two-way
258 ANOVA on the data for the masker level of 60 dB SPL/ERB, where all subjects showed

some masking at 4 kHz for both maskers, and where the masker levels were identical to those used in the psychophysical measures described by Middlebrooks *et al.* (2021). This showed significant main effects of masker type ($F(1, 9) = 49.0$, $p = 6.3e-5$) and probe frequency ($F(4, 36) = 19.3$, $p = 1.4e-8$) and a significant interaction between masker type and probe frequency ($F(4, 36) = 3.9$, $p = 0.011$). The interaction is of particular importance as it confirms our expectation that, as the probe frequency is moved further from the 4-kHz centre frequency of the noise, there is a larger increase in the COR for the NB than for the WB masker. However, the COR did vary somewhat with probe frequency even for the WB masker, as revealed by a significant effect of probe frequency when the WB data alone were analysed using a one-way ANOVA ($F(4,36)=8.2, p<0.001$). Paired comparisons revealed that the only differences that remained significant after Bonferonni correction involved the highest probe frequency (5657 Hz), for which the COR was significantly larger than for all other probe frequencies except the lowest (2828 Hz). As discussed later, we attribute this to the upward spread of excitation produced by a supra-threshold probe presented on the upper edge of the WB masker.

We also measured the effect of the highest-level masker on N1 and P2 latencies. A two-way ANOVA (masker type X probe frequency) revealed that for the P2 latency there was no significant effect of any factor nor any interaction, but there was an effect of masker type ($F(1, 9) = 6.8$, $p = 0.0028$) and a significant interaction between probe frequency and masker type ($F(4, 36) = 3.8$, $p = 0.0011$) on the N1 latency. This reflects the fact that at a unique frequency only (4757 Hz), the N1 latency was longer for the probe masked by the WB masker than the NB masker (cf. Supplementary Figure 1). We find it hard to interpret this finding, which may be related to the noisy nature of latency measurements.

Experiment 1b: Notched-noise masker

The results of experiment 1b are shown in Figure 4. The blue unconnected symbol to the left of Figure 4 shows the results from experiment 1a obtained with the WB masker at 60 dB SPL/ERB and a 4-kHz probe, for which the stimuli were identical to the 0%-notch-width condition. The average reduction in amplitude relative to the no-mask condition is similar to that in this new dataset ($t(20) = 0.16$, $p = 0.88$), and is about 10-11 dB. There was an effect of changing the notch width on the COR amplitude ($F(3, 33) = 5.0$, $p = 0.0056$). When the data from all participants were included in the analysis (thick black line, $N = 12$), the response to the tone was very similar across the 20- to 60-% notch widths ($\Delta f = 10$ to 30%); an ANOVA based on those data alone revealed no significant effect of notch width ($F(2,22) = 0.113$, $p = 0.871$) and no post-hoc comparisons between conditions were significant. This result differs from the psychophysical findings in which thresholds continue to drop up to the widest notch width (Middlebrooks et al, 2021; solid lines in our Fig. 11b). Two outlier participants showed a lot of masking at the 40- and 60-% conditions; removing them from the analysis did not change the statistical results (red line; $F(3, 27) = 10.5$, $p = 9.1e-5$, all notch widths included) but, numerically, made the COR amplitude continue to increase up to the 40% notch width.

Level-growth functions

Results of the level-growth measurements are shown in Figure 5. There were significant effects of level ($F(4, 44) = 30.2$, $p = 4.1e-12$) and frequency ($F(2, 22) = 3.9$, $p = 0.036$), and a significant interaction ($F(8, 88) = 2.3$, $p = 0.027$). When averaged across frequencies, the N1P2 growth function was well-fitted by a linear growth function with a slope of 0.158 dB μ V per dB SPL (2.5-97.5% confidence interval: 0.10-

0.22 dB μ V per dB SPL), i.e. equivalent to a compression ratio of 1:6.3. It can be seen that four participants had quite low CORs, with an average N1P2 value across all probe frequencies of less than 3 μ V. Excluding their data had only a modest effect on the slope estimate, which, averaged across frequencies, had a slope of 0.148 μ V per dB SPL, corresponding to a compression ratio of 1:6.8.

Experiment 2: masked COR in NH cats

Methods

In experiment 2, the maskers and the set of probe frequencies were centred on 8 kHz. That frequency band was an octave higher than those used in Experiment 1 in humans; this was done because of the inter-species difference in audible range.

At the beginning of each session, the COR was recorded in response to non-masked 8.0 kHz probe tones at varying levels (Figure 6). In most cases, a level of 75 dB SPL was at or near the top of the steep part of the COR-versus-level function, and that level was used as the probe level for subsequent measures; in one instance, the dynamic range was shifted to slightly higher levels, and a probe level of 80 dB SPL was used, with correspondingly increased masker levels. The probe levels were chosen to fall in a portion of the level-growth function such that there would be a large COR in the absence of the masker and so that a masker-induced reduction in the effective probe level would result in a reduction of the COR amplitude.

Similar to Experiment 1a, Experiment 2 consisted of presenting NB and WB maskers (1/8th- and 1-oct wide, respectively), but this time centred geometrically on 8 kHz. The

probe-tone frequencies varied in $\frac{1}{4}$ -oct steps from $\frac{1}{2}$ -oct below to $\frac{1}{2}$ -oct above 8000 (5.7, 6.7, 8.0, 9.5, and 11.3 kHz); these steps were the same as used in humans. Pink noise (having a spectrum with equal energy per octave) was added to the masker to mask quadratic combination tones arising from the interaction of the probes and masker. The pink noise (with a cut-off of 3.7 kHz) was normalized to the same root-mean-squared level as the $\frac{1}{8}$ th-oct masker and attenuated by 5 dB. The spectra of the various stimulus components are shown in Figures 1C and 1D. The $\frac{1}{8}$ th-oct masker level was held at 65 dB SPL, which was a +10-dB probe/masker ratio. At that $\frac{1}{8}$ th-oct masker level, the COR elicited by the 8-kHz probe typically was about 40-50% of that in the no-mask condition. In pilot experiments, the 1-oct masker level was set at 73.2 dB SPL, which was estimated to equalize the energy between $\frac{1}{8}$ th- and 1-oct maskers in a human-sized auditory filter centered at 8 kHz; the equivalent rectangular bandwidth (ERB) of the human auditory filter at 8 kHz is estimated to be 888 Hz (Glasberg and Moore 1990). That masker level, however, tended to suppress the response to an 8-kHz tone to near the noise floor. For that reason, in subsequent experiments, we held the 1-oct masker at 70 dB SPL; an even lower level, 68 dB SPL, was used for two cats. Empirically, that 1-oct masker level produced approximately the same amount of masking (reduction of COR amplitude) of an 8-kHz tone as did the $\frac{1}{8}$ th-oct masker at 65 dB SPL. Psychophysical measures demonstrate that this excess masking can be explained partially by the feline auditory filter being approximately 22% wider than that of humans (Middlebrooks et al. 2021).

Animals

Domestic short-haired cats (*Felis catus*) were obtained from a breeding colony at the University of California at Davis. No hearing deficits were evident. All procedures were in accordance with the NIH Animal Welfare Guidelines and with protocols approved by the Institutional Animal Care and Use Committee at the University of California at Irvine.

The COR recordings were made from 7 adult cats. Three of these were neutered males who had been trained in the detection of tones in noise and provided the psychophysical data described by Middlebrooks et al (2021). They were 21-24 months of age and weighed 4.4-6.0 kg at the time of COR recordings. The remaining 4 cats were untrained females ranging from 9 to 22 months of age and weighing 2.8-4.3 kg at the time of COR recordings.

Cats were sedated for the COR recording. A light level of anaesthesia was induced with an intramuscular injection of ketamine (20 mg/kg) and acepromazine (1 mg/ kg). At those doses, eye-blink or limb-withdrawal reflexes sometimes could be elicited, but there were no spontaneous movements. One or more supplemental doses of ketamine alone were given during the experiment if needed to maintain an immobile state. Recording sessions lasted 1 to 2 hr.

Setup

The recordings were conducted in a single-wall sound-attenuating chamber. Stimulus generation, waveform recording, and experimental control used System III hardware from Tucker-Davis Technologies (TDT; Alachua, FL) controlled by custom MATLAB scripts (The Mathworks, Natick, MA) on a Windows-based personal computer. Sounds were generated with 24-bit precision at a sample rate of 100 kHz. The broadband or narrowband masker and the probe tones were presented through a Radio Shack horn

tweeter, and the pink noise was presented through a 3-inch co-axial speaker (Pioneer TS-A878), both located 20 cm to the left of the cat's left ear. The speakers were calibrated each day in the sound field using a ½-inch precision microphone (ACO Pacific) and in the absence of the cat. Acoustic probes for calibration consisted of Golay codes (Zhou et al. 1992) for masker and pink-noise spectra and tones for the tonal stimuli. Correction spectra were derived for the speakers, intended to equalize sound levels at known levels re 20 µPa across the stimulus bands. Scalp-recorded waveforms were obtained with hypodermic needle electrodes placed over the right hemisphere (active), behind the ipsilateral ear (reference), and on the back (ground). Waveforms were amplified with a TDT low-impedance headstage, digitized at a rate of 24.4 kHz, displayed, and stored to disk.

Each block of measurements began with the onset of a continuous masker (or a period of no masker). After 1 s, the sequence of 50-ms tone pips was begun at a rate of 1/s. For Experiment 2a, each of the 5 frequencies was presented once in a random order, and then again in another random order, and so on for 100 repetitions of each frequency. The masker condition was held constant for each block of 500 tone presentations.

Off-line, waveforms were filtered between 3 and 20 Hz for analysis. Individual waveforms that exceeded 4 times the root-mean-squared background level within the 0-to-120 ms analysis window were excluded from further analysis; this was a small number of waveforms, averaging 0.6% of waveforms. Then, the remaining ~100 waveforms for each masker and tone condition were averaged. In our recording conditions in the cat, the response to the onset of a tone consisted of a positive peak (P1), followed by a negative peak (N1). A second positive peak (P2) often was present, but it was not as consistent in latency and morphology as were the P1 and N1.

Latencies of peaks were given by the time of reversal of the slope of the waveform within the specified criterion window. Based on inspection of waveforms in multiple cats and conditions, we set latency criteria of 15 to 55 ms for P1 and 55 to 120 ms for N1. We quantified the magnitudes of the COR by computing the amplitudes of P1 minus N1 (in μV) for each stimulus condition.

Results

Level-growth functions

The onset of a tone typically elicited a robust scalp-recorded COR. Figure 6A plots those values as a function of the level of an 8.0 kHz probe in the absence of a masker; each coloured line represents data from one cat. There was considerable variation across cats in COR magnitudes. We tested informally whether the age of the cats or training status might have contributed to that variation. Our three youngest cats, who were 9 to 11 months of age and untrained at the time of COR measurement produced the two highest-magnitude and the lowest-magnitude CORs. Magnitudes recorded in the remaining four cats, ranging from 21 to 24 months of age and including the three trained cats, fell between those extremes. Those results do not provide evidence for effects of age or training status on COR magnitude.

Despite the variation among cats in the overall COR magnitudes, the magnitudes tended to show qualitatively similar sensitivity to stimulus levels. In Figure 6B, the data from Figure 6A are expressed for each animal as the magnitude at each probe level relative to the magnitude for that animal elicited by a 75-dB-SPL probe, expressed in dB. Magnitudes grew with increases in sound level up to 75 dB SPL. Beyond that sound level, magnitudes for all but one cat levelled off or declined.

Figure 7 shows waveforms recorded from one cat elicited by each of the probe frequencies in no-mask, NB, and WB masker conditions. There was a characteristic pair of peaks, P1 and N1, followed by additional deflections. In the no-mask condition (Fig. 7A) there was a robust response at each of the 5 probe frequencies. The 1/8th-oct masker centred on 8 kHz, however, clearly suppressed the response to the 8-kHz probe (Fig. 7B) but showed less effect at off-centre frequencies. The 1-oct masker suppressed responses fairly uniformly across all the probe frequencies (Fig. 7C).

Plots of COR magnitudes versus probe frequency showed a characteristic pattern for each masker condition (Fig. 8A-D, with the results from the human cohort with the maskers at 60 dB SPL/ERB plotted in the same manner in panels E to H). In each panel, thin coloured lines represent individual animals, and the thick line represents the grand mean for each stimulus condition. As was true of the level plots, there was considerable variation in overall COR magnitudes across cats. Nevertheless, the dependence of response magnitude on probe frequency was similar across cats for each masker condition. The no-mask condition showed a moderate decline in magnitude with increasing probe frequency (Fig. 8A). The 1/8-oct masker produced a marked suppression of the response to the 8-kHz probe with a steep recovery of responses to off-centre frequencies (Fig. 8B). The 1-oct masker produced rather uniform suppression of responses across all the probe frequencies (Fig. 8C).

The grand means of COR magnitudes are plotted in Figure 8D. For each cat, the magnitude for each masker condition and probe frequency was expressed in dB relative to the no-mask condition for that cat, and then results were averaged across cats. The grand means differed by only ~0.6 dB for the 8-kHz probe in the two masker

conditions, indicating that the 1/8-oct band at 65 dB SPL produced about the same amount of masking at 8 kHz as did the 1-oct noise band at 70 dB SPL. In the 1/8-oct masker condition, responses to the off-centre-frequency probes showed a sharp release from masking, increasing by ~4 dB in magnitude for probes at ¼-oct on either side of 8 kHz. In the 1-oct masker condition, in contrast, responses were within a range of ~0.6 dB for all probe frequencies within most of the masker bandwidth; masking on the upper edge of the 1-oct masker, at 11.3 kHz probe was considerably less than for other probe frequencies, similar to the finding in the human experiments of experiment 1 (Fig. 8 panel H). As discussed below, this may be due to a large unmasked area at the upper edge of the 11.3-kHz excitation pattern. Analysis of variance (ANOVA) of the magnitudes in μV showed significant main effects of masker bandwidth ($F(1,24)=70.0$, $p<10^{-7}$) and probe frequency ($F(4,24)=9.1$, $p=.00013$) and a significant two-way interaction ($F(4,24)=5.71$, $p=.0022$). Bonferroni-corrected post-hoc comparisons showed significant differences in COR magnitudes between the two masker conditions for probe frequencies of 5.7, 6.7, and 9.5 kHz ($p<0.01$) but not for 8.0 or 11.3 kHz ($p>0.05$).

Magnitudes of responses in the 1/8- and 1-oct masker conditions are further compared in Figure 9, with each panel showing one probe frequency and symbols representing values from individual cats. In response to the 8-kHz probe (Fig. 9C), magnitudes are scattered fairly uniformly around the identity line, again indicating that the 1-oct masker at 70 dB SPL produced about the same amount of masking at 8 kHz as did the 1/8-oct masker at 65 dB SPL. For the off-centre frequencies of 5.7, 6.7, and 9.5 kHz, however, most of the symbols lie above the identity line, showing significantly greater magnitudes of responses (i.e., less masking) in the 1/8-oct compared to the 1-oct masker condition. That observation indicates that, for the most part, the magnitude of

the COR can distinguish narrow versus broad tonotopic spread of activation in individual animals.

Across all cats and probe frequencies, P1 and N1 latencies were significantly delayed in both the 1/8th- or 1-oct masker conditions compared to the no-mask condition. Across all cats and probe frequencies, P1 latencies averaged 28.4 ± 4.6 , 33.9 ± 6.1 , and 37.7 ± 7.0 ms in the no-mask, 1/8th oct, and 1 oct conditions, respectively, and the corresponding N1 latencies averaged 79.1 ± 11.2 , 91.9 ± 11.8 , and 92.3 ± 11.4 ms (mean $\pm$ SD); the vertical dashed lines in Figure 7 indicate the latencies in the no-mask condition averaged across all 7 cats. Two-way analysis of variance (ANOVA) of latencies showed significant main effects of masker condition for P1 latencies ($F(2,48) = 97.6$, $p < 10^{-7}$) and for N1 latencies ($F(2,48) = 28.9$, $p < 10^{-7}$). Bonferroni-corrected post-hoc comparisons showed significant differences in P1 latencies among all 3 masker conditions ($p < 0.001$). The N1 latencies were significantly shorter for the no-mask condition than for either of the masked conditions ($p < .001$), but there was no significant difference in N1 latencies between the 1/8th- and 1-oct maskers ($p > 0.05$). There was no significant main effect of frequency on P1 or N1 latencies ($p > 0.05$). This pattern of results differs from that obtained in humans, for whom no significant main effects of masker type on latency were observed.

Discussion

Comparison with previous EEG measures of tonotopic selectivity

We are aware of three types of method that have been used to measure selectivity with the COR in human listeners. One paradigm, illustrated in Figure 10A, measures the response to a tone of a given frequency in the presence and absence of intervening tones at different frequency separations (Butler 1968, 1972; Picton et al. 1978; Näätänen et al. 1988; de Boer and Krumbholz 2018). This has led to mixed results, with very broad tuning being often (Butler 1968, 1972; Picton et al. 1978), although not always (Näätänen et al. 1988) reported. For example, Butler (1972) found that the COR to 250-Hz tones presented every 5 seconds could be reduced by intervening 8-kHz tones. One feature of this method is that there is a (usually long) silent gap between the test and intervening tones, so that there is no masking *per se* between the intervening tones and test tones at the level of the cochlea or auditory nerve. Rather, the method relies on adaptation at multiple, more-central, stages of the auditory system, including at the cortex. Differences in stimulus parameters may cause the onset response to be dominated by different classes of neurons, which may in turn differ in their tonotopic selectivity. Indeed, the study by Näätänen et al. (1988), which reported sharp tuning, used an SOA of 500 ms, which is much shorter than the studies that showed broad tuning (Butler 1968, 1972; Picton et al. 1978). The measures used here involve masking of the neural response to the probe at the level of the cochlea and auditory nerve, and used a fairly short SOA of 1 second.

A second method (Figure 10B) is to change the frequency of a tone part-way through a stimulus, and to measure the size of the resulting COR as a function of the frequency separation between the two tones. He et al. (2012) measured this “Acoustic Change Complex (ACC)” in 12 normal-hearing adults in response to changes in the frequency of a 500-Hz tone. The mean ACC threshold was 5.8 Hz, corresponding to a frequency change of 1.4%. Although larger than the psychophysical thresholds obtained in the

same subjects, this value is much smaller than the smallest frequency separation of 19% between the probe and the centre frequency of the NB masker in our experiments. The ACC can also be elicited in CI users by changing the stimulating electrode mid-way through a stimulus (e.g. He et al. 2014; Mathew et al. 2016). An advantage of the ACC measure over our masking method is that, because only one stimulus is present at any one time, it avoids complications associated with masker-probe interactions such as beating and cochlear distortion products for acoustic stimulation (Moore et al. 1984) and charge interactions for electrical stimulation (Cosentino et al, 2015). A disadvantage is that an ACC can be generated to changes in intensity and/or loudness, making it important to loudness-balance the stimuli. Loudness levels can vary substantially from electrode to electrode in CIs, especially for focussed modes of stimulation (Bierer & Faulkner, 2010), making the procedure time-consuming in humans and hard to achieve in animal experiments. As our aim is to generalise our method to CI experiments with focussed stimuli, this was one reason for not choosing the ACC paradigm.

Although we are unaware of studies that measured the COR for tones masked by WB vs NB maskers, some authors have measured EEG or MEG responses to the onset of tones presented in noise containing different notch widths, analogous to our experiment 1b (Sams and Salmelin 1994; Kauramäki et al. 2007; Okamoto et al. 2007). Those studies were primarily interested in the effects of attention, but included one condition similar to ours in which the subjects listened passively. Kauramäki et al. (2007) used EEG and measured the global field power of the N100 response to a 1-kHz tone presented in quiet or in noise containing notches of different widths centred on 1 kHz. Their COR increased with increases in Δf up to 25% (notch width of 50 %) at which point it was similar to that in the no-mask condition. This differs from our

experiment 1b in which a substantial (6 dB) reduction in COR was observed even at the Δf of 30% (notch width of 60 %). In addition to using lower noise and probe levels than here, Kauramäki et al increased notch width by progressively removing more of the masking noise, such that its total bandwidth and overall power decreased with increasing notch width (cf. Figure 10C). The same was true of the study by Sams and Salmelin (1994), who measured the MEG N100m response to the onset of 1- and 2-kHz tones in notched-noise backgrounds. They observed quite variable and sometimes non-monotonic functions relating the N100m to notch width. Okamoto et al. (2007) found that the N1m to amplitude-modulated 1-kHz tones masked by notched noise increased up to the maximum notch width studied, but this corresponded to only an 8% distance between notch edge and probe frequency, so we do not know how the N1m would have varied over the range of wider widths tested in experiment 1b.

Cochlear distortion products

A stimulus consisting of two primary frequency components f_1 and f_2 can produce cochlear distortion products (DPs), the largest of which are typically the quadratic and cubic DPs having frequencies of $f_2 - f_1$ and $2f_1 - f_2$ respectively. These DPs propagate along the basilar membrane to their own characteristic place, and, despite having lower levels than the primaries, can sometimes be perceived by listeners (Goldstein 1967; Hall, 1972; Smoorenburg 1972a; Zwicker 1979, 1981). Although they are usually studied using pure tones, DPs can also arise from the combination of a pure tone and a narrow band of noise, such as the $1/8^{\text{th}}$ -octave maskers used here. The pink noise used in our experiments encompassed the predicted frequencies of the quadratic DP for all masker and probe combinations, but, for the $1/8^{\text{th}}$ -octave masker this was true

for the cubic DP (CDP) only when the signal frequency was 0.5 octaves below the masker centre frequency.

The amplitude of the CDP is generally largest with small f_2/f_1 ratios and (for human listeners) becomes inaudible at ratios of between about 1.4-1.6 (Smoorenburg 1972b). We therefore think it unlikely that the CDP would have contributed to the COR observed for masker-probe separations of plus or minus 0.5 octaves, corresponding to a ratio of 1.41. However the $\frac{1}{4}$ -octave separation used for two probe frequencies corresponds to a ratio of 1.18 where the CDP is relatively large. For our human participants, the centre frequencies of the DPs for 3364-Hz and 4757-Hz maskers would have been 2728 and 3243 Hz, respectively. In the former case the 2728-Hz DP is further than the 3364-Hz signal from the 4000-Hz masker, and so could have in principle contributed to the COR. This is less likely to be the case for the 4757-Hz signal, where the 3243-Hz DP was almost as close (frequency ratio = 1.23) as the signal (ratio=1.18) to the masker, and would have had a substantially lower level. We conclude that the CDP may have contributed to the COR for signals that were $\frac{1}{4}$ octave below the masker centre frequency, but was unlikely to have done so for other signal frequencies. In addition we performed a control experiment with an additional cat, and with the pink noise cut-off extended to 7190 Hz (i.e. above the expected CDPs at 5454 and 6486 Hz, because of the doubling of the frequencies in the cat). That noise reduced the response to the 8000-Hz probe in the absence of any other masker, so we reduced its level by 10 dB, added it to the NB masker, and measured the COR to each masker/frequency combination. This showed a pattern of COR with probe frequency that was typical of those observed in the main experiment.

Comparison of psychophysical and EEG measures of selectivity.

599 *Narrowband vs wideband maskers*

600 Figure 11A compares the results of experiment 1a to its psychophysical counterpart
601 (Middlebrooks et al. 2021) in human listeners, by plotting the psychophysical threshold
602 elevation together with an EEG estimate of that threshold elevation, for probes
603 presented against narrowband and wideband maskers. The EEG estimate for each
604 subject was calculated by multiplying that subject's COR masking (in dB re unmasked)
605 from experiment 1a by 6.3, which was the slope of the level-growth function (Figure
606 5). The two curves agree very well for the NB masker (red, panel A). This is somewhat
607 less the case for the WB masker (blue, panel A), where the EEG estimate generally
608 overestimates the amount of psychophysical masking, except for the highest probe
609 frequency where it underestimates it. These trends were confirmed statistically as
610 follows. We first performed an ANOVA with masker bandwidth and probe frequency
611 as repeated measures and "estimated vs obtained" thresholds as a between-subjects
612 factor. As expected there were highly significant main effects of probe frequency and
613 of masker bandwidth and a highly significant interaction between these two factors
614 (Probe frequency: $F(4,76)=55.7$, $p<0.001$. Masker bandwidth: $F(1,19)=180.7$,
615 $p<0.001$. Interaction $F(4, 76)=13.5$, $p<0.001$). More importantly there was a significant
616 three-way interaction between the factors "estimated vs obtained", probe frequency,
617 and masker bandwidth, reflecting the fact that the variation in the EEG-estimated
618 thresholds with probe frequency closely followed that observed for the psychophysical
619 thresholds for the NB masker ($F(4,76) = 5.5$, $p = 0.001$), but less so for the WB masker.
620 There was also a significant two-way interaction between "estimated vs obtained" and
621 probe frequency ($F(4,76) = 4.2$, $p = 0.04$). We subsequently performed separate
622 ANOVAs on the data for the WB and for the NB masker. The factor "estimated vs

predicted” interacted significantly with probe frequency only for the wideband masker (Narrowband: $F(4,76) = 2.44$, $p = 0.06$. Wideband: $F(4,76) = 5.83$, $p = 0.001$).

As noted above, the COR overestimated the amount of psychophysical masking at all but the 5657-Hz frequency, where it underestimated it. Some insight into this finding comes from simulations of the excitation patterns produced by adding different-frequency probes to the WB masker, as illustrated in the bottom row of Fig. 12. These simulations used the nonlinear gammachirp filterbank (Irino et al, 2006, Gaudrain et al. 2015) implemented in the AIM-MAT software package (Gaudrain et al, 2015). Because basilar-membrane nonlinearity results in a marked upward spread of excitation, there is a wider range of auditory-filter frequencies that convey a greater-than-masker probe response (black line versus blue line) to the 5657-Hz tone than with the 2828- and 4000-Hz tones. Interestingly, Fig. 12 also suggests that the COR should predict more masking of the 4-kHz probe by the WB (bottom row) than by the NB masker (top row), even though the psychophysical detection thresholds were very similar. Figure 11 shows that this was true numerically, but the difference was not statistically significant ($t(9) = 1.63$, $p = 0.135$).

Greater COR masking for the WB compared to the NB masking was also observed in the data obtained for the 8-kHz probe in the feline subjects of experiment 2. As noted in the methods section, in order to roughly equate the CORs for the 8-kHz probe for the NB and WB maskers, we had to reduce the level of the WB masker below that predicted from the human auditory filter bandwidth (ERB) centred on 8 kHz. This reduction was quite large, being 3.2 dB for five cats and 5.2 dB for two cats. Fig. 8D shows that, even with this correction, the COR amplitude for the 8-kHz probe was slightly smaller for the WB compared to the NB masker. Our companion paper (Middlebrooks et al 2021) shows that only about 0.9 dB of this difference could be

accounted for by the slightly wider ERB at 8 kHz for the cat compared to the human, as measured psychophysically using the notch-noise method. It may well be that, in both species, the positive probe-to-masker ratio used for the COR experiments results in larger differences in the excitation pattern between the masker-alone and masker+probe excitation patterns for the NB- compared to the WB-masker conditions, and that these differences can be at least qualitatively explained using a nonlinear auditory filterbank. The variability in level-growth slope estimates (1:1.4 to 1:9.1) in the cats did not permit reliable estimates such as achieved for humans in Figure 12A. Nevertheless, it is worth noting that the cat COR data did show an asymmetry for the WB masker, with less masking half an octave above 8 kHz than half an octave below it. This is consistent with the upward spread-of-masking explanation mentioned above for the humans.

An additional factor that may have contributed to the reduction in the COR produced by wideband maskers, and therefore for increase in predicted masking, comes from the phenomenon of wideband neural inhibition, which has been observed in single-unit recordings from animals (Marsh et al. 1972; Palmer 1995; Wiegrebe and Meddis 2004). Wideband neural effects have also been observed in humans, using the Frequency Following Response (FFR), which is an EEG measure of phase locking that is dominated by sources in the brainstem (Gockel et al., 2012). A reduction in wideband inhibition may also have contributed to the increase in COR observed with increasing notch width in previous studies, described above, where increases in notch width were accompanied by decreases in the overall bandwidth of the stimulus (Sams and Salmelin 1994; Kauramäki et al. 2007).

Notched-noise maskers

Figure 11B compares the notch-noise COR measurements made with humans in experiment 1b with the psychophysical thresholds obtained with the same listeners by Middlebrooks et al (2021). Psychophysical threshold shifts relative to the no-mask condition were predicted from the COR data by dividing the reduction of the COR amplitude, in dB, by the slope of the COR input-output function for unmasked probes. The considerable across-participant variability in both the masked CORs and the input-output function for unmasked tones warrants some caution in interpreting these results. Nevertheless, it can be seen that the COR data do a good job of predicting the psychophysical masking for notch widths of 0%, 10%, and – when the two outliers are removed, 20% - but that the amount of predicted masking does not decrease at the 30% notch width, unlike the psychophysical data.

Conclusions

Our results show that, using a paradigm that mimics focussed and broad CI stimulation, we can measure the difference in selectivity between two stimuli (NB and WB masker) using both psychophysics (Middlebrooks et al., 2021) and EEG (this paper) in two species (humans and cats). We believe that this is an important step for comparing electrophysiological and psychophysical measures of tonotopic selectivity across species.

The results presented here also reveal some limitations of our paradigm for comparing physiological and psychophysical measures of tonotopic selectivity. The CORs were somewhat variable for the wideband masker, and a contribution to this variability might come from phenomena such as wideband inhibition. In addition, the necessity of using a supra-threshold probe level for the COR measurements may cause them to be affected by the upward (and to some extent downward) edges of the probe excitation

pattern (Fig. 12), which is less likely to be the case for psychophysical detection which typically occurs at negative signal-to-noise ratios. Although we used a lowpass noise to mask quadratic distortion products, other cochlear distortion products such as the cubic may have contributed to the CORs, particularly for the narrowband maskers of experiments 1a and 2. Again, although we showed that these did not contribute to the psychophysical results in our companion paper (Middlebrooks et al, 2021), the higher signal-to-noise ratio used here may have increased the influence of cochlear nonlinearities on the EEG results.

Despite these limitations, both the psychophysical and COR measures revealed significant interactions between masker bandwidth and probe frequency, allowing us to distinguish between stimuli that produce broad vs narrow excitation patterns. In this regard, it is less important whether phenomena such as wideband inhibition contribute to the results obtained with the masker that produces a broader peripheral excitation pattern, as long as the difference between narrow and broadband excitation is revealed in the obtained pattern of CORs. We are therefore optimistic that the paradigm can be successfully applied to the study of tonotopic selectivity both in humans and in cats, and for both acoustic and electric stimulation. More generally, the method may prove useful for revealing between-species differences by studying selectivity using the same methods and stimuli.

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894

895 **Figure legends**

896

897 *Figure 1. A-D: Stimulus spectra. 1/8-oct (red) and 1-oct (blue) maskers for humans (A-*
898 *B) and cats (C-D). Maskers were centred on 4 kHz for the humans and 8 kHz for the*
899 *cats. Pink noise (magenta) was used to mask quadratic distortion products. Vertical*

900 black lines indicate probe frequencies. Panel E shows an example human Cortical
901 Onset Response (COR) to a short probe. Panel F shows an example of a cat COR..

902 *Figure 2.* Grand average waveforms across all human participants. Each column is for
903 a different probe frequency, with the probe always being presented at 70 dB SPL.
904 Black lines show the COR to the probe alone, red lines when masked by the narrow-
905 band masker and blue lines when masked by the wide-band masker. On frequency
906 (4000 Hz), increasing the masker level reduces the COR for both masker types. Off
907 frequency, this is also the case but is more pronounced for the wide-band masker than
908 the narrow-band masker.

909 *Figure 3.* Masked human COR results, re-referenced to the no-masker condition. Thin
910 lines represent individual participants, and the thick line the average ($N = 10$). The
911 error bar indicates ± 1 standard deviation. Left column: wide-band masker. Middle-
912 column: narrow-band masker. Right column: combined plots. From bottom to top:
913 increasing masker level. The probe was always at 70 dB SPL.

914 *Figure 4.* Results of experiment 1b (notch-noise masker). Thick black line shows the
915 average masked COR (± 1 S.D.), with individual results shown in thin grey lines.
916 Probe was always presented at 4 kHz and 70 dB SPL, and the notch of the notch noise
917 centred on 4 kHz. At 0 %, it is equivalent to the WB condition at 60 dB SPL/ERB of
918 experiment 1a (blue bar). Two listeners showed large amount of masking for the
919 largest notch widths; the average amount of masking without these two listeners is
920 shown in red.

921 *Figure 5.* Growth of the unmasked COR with probe level in humans. Left three panels:
922 frequency-specific level growth. Right-most panel: average across frequencies.

Figure 6. Growth with probe level of the unmasked COR in individual cats. Probe frequency is 8 kHz. A. Values in μV . B. Values in dB re the value for each cat at 75 dB SPL.

Figure 7. COR waveforms from an example cat. Left column is the probe-alone response, middle column the response masked by the NB masker, and right column shows the response when masked with the WB masker. Vertical dashed lines show the average unmasked P1 and N1 latencies across all cats. Extracted N1 and P2 values for this example cat are shown respectively with the orange circles and squares.

Figure 8. Comparison of the masked COR patterns across humans and cats. A-C. Individual (thin lines) and group (thick line) cat COR masked patterns, in μV . Panel D shows the mean masked COR when re-referenced to the no-masker condition. Blue line is for the WB masker, red line is for the NB masker. Error bars indicate ± 1 S.D. Panels E-H show the same as panels A-D but in humans, with the masker at 60 dB SPL/ERB.

Figure 9. COR magnitude with the NB masker versus with the WB masker. Each symbol is one cat (same symbols as in Figure 8).

Figure 10. Time-frequency schematic of published selectivity paradigms with the COR in response to tones. Left column: intervening tones, where the COR to the tone in black is attenuated by the presence of the blue/red tones. Middle column: Acoustic Change Complex (ACC), where the COR is elicited to a change in frequency between the probe tone and another tone. Right column: notch-noise method, where the COR is masked by a notch noise which notch is centred around the probe frequency.

Figure 11. Comparison of psychophysics and EEG. Panel A. Noise-band experiment. Thick lines show psychophysical results, and dotted lines the EEG estimate obtained by multiplying the group mean COR masking (in dB re unmasked) by 6.3, the slope of the level growth measured in experiment 2. Panel B. Notch-noise experiment. Solid line shows the psychophysical results, dashed line shows the EEG estimate. Black lines show the results with the two outlier participants removed, red line with the two participants included.

Figure 12. Simulated excitation patterns for masker-alone (blue/red lines) and masker plus probe (black lines). Top and bottom rows are for the narrow-band and wideband-masker conditions respectively. Probe frequency was 2828, 4000, and 5657 Hz in the left, middle, and right plots respectively. All simulations were generated using the nonlinear gammachirp auditory filter bank implemented in the AIM-MAT software package (Gaudrain et al. 2015)

Figure 1

Figure 2

Figure 3

Figure 4

N1P2 (dB re no-masker)

- NB vs. WB dataset
- NN dataset (N = 12)
- NN dataset (N = 10)
- NN dataset (indiv.)

0
-6
-120 10 20 30 Δf (%)

0 20 40 60

Notch Width (%)

Figure 6

Figure 7

Figure 8

INTERVENING TONES

ACOUSTIC CHANGE COMPLEX

NOTCH NOISE