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Behavioural estimates of auditory filter widths in ferrets using notched-noise maskers

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Abstract

Frequency selectivity is a fundamental property of hearing which affects almost all aspects of auditory processing. Here auditory filter widths at 1, 3, 7, and 10 kHz were estimated from behavioural thresholds using the notched-noise method [Patterson, Nimmo-Smith, Weber, and Milroy, *J. Acoust. Soc. Am.* 72, 1788–1803 (1982)] in ferrets. The mean bandwidth was 21% of the signal frequency, excluding wider bandwidths at 1 kHz (65%). They were comparable although on average broader than equivalent measurements in other mammals (~11%–20%), and wider than bandwidths measured from the auditory nerve in ferrets (~18%). In non-human mammals there is considerable variation between individuals, species, and in the correspondence with auditory nerve tuning.

1 Introduction

One of the most striking properties of the auditory system is its ability to segregate sounds based on frequency. This determines many aspects of auditory perception.² Recordings from the basilar membrane and its output pathway [auditory nerve (AN) fibers] show that a significant amount of filtering takes place in the auditory periphery.³ A crucial, unanswered, question is how the resolution of this frequency analysis arises perceptually.

A perceptual correlate of this filtering is that only sounds within a restricted frequency range (an auditory filter) will mask one another (the power spectrum model). The auditory system has been described as behaving like an array of auditory filters with different centre frequencies. Different methods have been employed to assess the shape and bandwidth of these filters [e.g., critical bandwidth (CB),² critical ratio bandwidths⁴]. One of the most widely applied in humans is the notched-noise method,¹ which overcomes various limitations of other methods (see Ref. 2 for a review). Numerous studies have characterised perceptual auditory filters in non-humans (see Ref. 5). However, only three sets of published data exist successfully applying the notched-noise method in non-human mammals.^{6–8}

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The notched-noise method relies on the power-spectrum model of masking. Subjects detect a tone of fixed frequency centred within two-bands of masking noise. Detection is most difficult when the masker has no “notch” between the bands; as the notch width increases, less masking energy passes through the filter and the tone detection threshold decreases (due to space limitations we refer the reader to Ref. 2 for a comprehensive review and citations). The shape of the filter determines the change of threshold with notch width. This is often well fitted with a rounded-exponential (roex) function, and summarised by the Equivalent Rectangular Bandwidth (ERB). The latter corresponds to the width of a perfectly rectangular-shaped filter with the same transmission and peak as the studied filter.

The ferret is an increasingly popular animal model for hearing research.⁹ The lack of any psychophysical filter estimates in ferrets, and the small number of species characterised using notched-noise motivated this study. Estimates of frequency selectivity were obtained using the notched-noise method at 1, 3, 7, and 10 kHz.

2 Methods

2.1 Behavioural experiments

Four adult pigmented ferrets (*Mustela putorius*; 2 females) were trained and tested in a 2AFC “yes/no” detection task (described elsewhere⁹), using water for positive reinforcement. All procedures were carried out under license from the UK Home Office. Ferrets were required to indicate on each trial whether or not they heard a 500 ms tone (20 ms rise/fall ramps) in a continuous noise masker. The noise had two spectral bands of equal bandwidth, logarithmically centred on the signal frequency and separated by varying notch widths. The signal was at one of the following frequencies: 1, 3, 7, or 10 kHz. Noise-bands were 0.64, 1, 1.5, and 3 kHz wide, respectively. The spectrum level was constant for each filter estimate but two to three levels [20 to 40 dB sound pressure level (SPL) ± 3 dB] were tested at each signal frequency (f_c). The level of the signal was varied¹⁰ according to the Method of Constant Stimuli. A set of ~ 5 signal levels was defined by piloting, such that at least one level was easily detectable ($\sim 90\%$ correct) and one was below threshold. This was tested for 3–5 sessions, interleaved with other notch-widths, until >30 trials, including both signal- and no-signal trials, were recorded per level. The d' and the corresponding percentage correct values for an unbiased observer, $P(c)_{\max}$ (Ref. 11), were calculated at each level. The resulting psychometric functions of tone level were fitted with logistic functions, defined such that minimum was at 50% (chance performance), and constrained so that for a single filter estimate only the midpoints varied between them.

2.2 Estimation of the auditory filter width

Auditory filter shapes were derived by fitting roex(p,r) functions.¹ The signal threshold depends on the masker energy passing through an auditory filter with shape

$$w(p,r)=(1-r)*(1+pg)e^{-pg}+r, \quad (1)$$

where g is the normalised distance to the centre of the filter ($g = (f - f_c)/f_c$), p and r determine the slope of the filter skirts at frequencies near and away from the notch centre frequency.

For a given notch-width, the signal and masker spectra were convolved with the room transfer function, scaled to equal their levels at threshold, and integrated over roex(p,r) filters with a range of centre frequencies around the signal frequency. The threshold was taken from the filter with the best signal-to-noise ratio (SNR).² This was repeated across notch-widths in a given filter measurement, and the values of p and r were found which minimised the summed squared differences between the output SNRs, in dB. The mean of these SNRs, known as the efficiency of the filter, is denoted by K . The following notch widths were used for the fitting process: up to $g = 0.5$ for $f_c = 1$ kHz, and $g = 0.3$ for $f = 3, 7,$ and 10 kHz (the widest notches should not impact on the ERB, but can compromise the fit). ERBs were derived as per Ref. 2.

To estimate the reliability of measurements, we bootstrap resampled (500 times) individual trials, with replacement, applying all the processing steps to each dataset. The 95% confidence intervals (CIs) of thresholds were calculated directly from bootstrapped distributions of thresholds. Bootstrapped distributions of the filter functions and ERBs were generally normally distributed, but some also showed extreme outliers. Therefore we used a non-parametric measurement to reject outliers: $0.953 \times$ the interquartile range of the first and third quartiles. For distributions which are perfectly normal, the resulting range equates to a 95% CI.

All comparisons between ERBs were made using linear models with log transformed ERBs, $\log(f_c)$ as a covariate, and the tested experimental variable as a factor. Significance was tested using analysis of variance with type three sums of squares.

3 Results

Figure 1 illustrates several examples of the effect of notch width on tone detection thresholds (centred at 1 and 10 kHz). Two masker spectrum levels were used (20–40 dB SPL). As expected, thresholds decreased with increasing notch width; this was also evident for signal frequencies at 3 and 7 kHz (not shown). Also represented are the thresholds estimated from the roex-fitting (thick lines). These are not completely smooth, indicating that masker spectrum and off-frequency listening can account for some of the threshold variation. The shape of the associated auditory filter is illustrated in the lower panels, together with median ERBs and confidence regions.

Figure 2(a) shows the dependence of filter width on signal frequency. Table 1 also indicates the bandwidths as a percent of signal frequency. Generally, auditory filters increased in bandwidth with increasing frequency, according to the relationship $ERB_{\text{Hz}} = 4.6 \times f_{\text{cHz}}^{0.66}$ ($p < 0.001$). Most were less than or equal to 25% of the signal frequency (median 23%), except at 1 kHz. At this frequency, however, discrepancy was large between the two ferrets (a factor of 2.6), although there was no significant difference overall between ferrets ($p =$

0.82). These trends follow observations in other species, including humans, and qualitatively resemble AN fiber tuning from the same species¹² [Fig. 2(a); dotted line].

It is clear from Fig. 2(a) (also Fig. 1) that bandwidth estimates varied somewhat at a single signal frequency. The bootstrapped range (see Sec. 2) of ERBs in Fig. 2 reveal that the variability is probably attributable to genuine differences between measurements (e.g., at 10 kHz), but some values (e.g., the smallest bandwidth at 7 kHz) should probably be discounted. Figure 2(a) (solid line) and Table 1 show the mean bandwidths weighted according to the bootstrapped ERB range. When the data are combined in this way bandwidths vary from ~19%–65% of signal frequency (mean 31%; 21% excluding 1 kHz).

In humans as the masker level increases auditory filters become wider, although this effect is relatively modest for simultaneous masking.² In our data, for any given frequency, threshold vs notch-width functions at different masker levels are approximately parallel (see Fig. 1). With the notable exception of $F2$ at 1 kHz (Fig. 1), there is little evidence that masker level influences bandwidths systematically ($p = 0.40$).

Higher masker levels also elicited higher signal detection thresholds. In most cases at narrow notch widths the elevation in threshold was similar to the elevation in masker level as expected, i.e., ~1 dB/dB.⁴ In some cases (Fig. 1; $F6$ at 10 kHz) increases in threshold were less than linear. This is also evident in the “efficiency” (K) of signal detection in the fitted filter functions (Table 1). These values suggest that there was general variation in the efficiency across different masker levels and across signal frequency (which has been observed before in animals, e.g., Ref. 5). At wider notches threshold differences at increasing masker levels became smaller. This is expected if little masker energy falls within the passband of the auditory filter. In practice, some masking often remains at wide notch widths¹ and our data reflects this (e.g., Fig. 1, $F2$ at 1 kHz; $F2$ at 10 kHz; $F6$ at 10 kHz).

4 Discussion

Auditory filter bandwidths measured behaviourally in the ferret varied across individual measurements but overall were significantly wider than similar measurements [Fig. 2(b)] in guinea pigs (~20% of signal frequency⁷), chinchilla [~14% (Ref. 6)], and humans ERB [11%–17% (Ref. 2)]. We did not observe any significant effects of masker level on bandwidth in the range of levels tested, or any significant effect of individual ferret.

Estimates of perceptual frequency selectivity have been more commonly made in other species using different methods.⁵ The most closely related measurement of tuning is the CB which is the point at which an increase in the bandwidth of a constant spectrum level noise ceases to increase the threshold of a tone in the centre of the noise band. If an auditory filter has a perfect rectangular frequency response, then the CB is equal to the ERB. In reality, the tails of the filter extend beyond the ERB, so CB estimates tend to be wider than the ERBs. This is reflected in differences between notched-noise derived ERBs and band-widening derived CBs in humans and chinchilla [Refs. 2, 5, and 6; Fig. 2(b)], and despite considerable variation, across species generally [Fig. 2(b)]. In fact, ferret perceptual ERBs are not significantly different from CBs measured in previous studies across multiple species⁵ ($p =$

0.64). However, ERBs measured using notched-noise masking in ferrets, guinea pigs⁷ (2/3 of ferret ERBs) and chinchilla⁶ (1/3 of ferret ERBs) are all significantly different from each other ($p < 0.03$ in all comparisons across species). Overall, this suggests that ferret perceptual auditory filters are broader than in other species, though this could possibly reflect other differences between studies.

It is widely believed that perceptual frequency selectivity primarily reflects cochlear frequency selectivity. ERB values estimated here (mean 31% of signal frequency; 21% excluding 1 kHz) were ~70% larger (17% excluding 1 kHz) than AN tuning in the ferret¹² (mean ~18% of signal frequency over the same range). Analysis with a linear model revealed that this difference is significant ($p < 0.001$). In humans, bandwidths derived from simultaneous notched-noise masking are broader than those from forward masking (~20% broader;² ~40% broader¹³) which is held to be a more appropriate method to compare to AN tuning. This might account to some degree for our broader behavioural measurements.

However, simultaneous notched-noise derived bandwidths in guinea pigs agreed closely with AN tuning,⁷ while in chinchilla psychophysical tuning is ~35% *narrower* than cochlea tuning.^{6,14}

The inconsistency in the relationship between central and peripheral tuning poses a problem for our understanding of the relationship between the physiology and behaviour. It is possible behavioural tuning estimates are influenced by cognitive factors.⁹ The power spectrum model used to fit filter shapes, assumes that the subject always listens to the single auditory filter with the highest SNR. Presumably any departure from this optimal strategy, such as attending to different or possibly many filters,¹⁵ might influence estimated bandwidths. Here, ferrets received initial training at 10 kHz, which might have influenced their listening strategy. A related factor to this is the “efficiency” of the signal detection (K ; Table 1), which varied in our data. Efficiency is conceptualised as the threshold SNR at the *output* from an auditory filter, but it would also be affected by listening strategy. The wide filters obtained for ferret *F1* at 1 kHz, are accompanied by unusually large negative K values (–33, –37 dB, cf. overall mean –3.9, standard deviation 12.2), implying excellent signal detection efficiency even relative to humans.² Therefore, the fits at this frequency for this animal should be considered with caution.

Perceptual filter bandwidth estimates from ferrets are qualitatively similar to other mammals, but ferret auditory filters may be broader than other non-human mammals. However, the paucity of other data using notched-noise masking, the variability in our data and across species, the lack of a consistent relationship with AN tuning across species, and the potential for interfering non-sensory factors, mean that this conclusion must be tentative.

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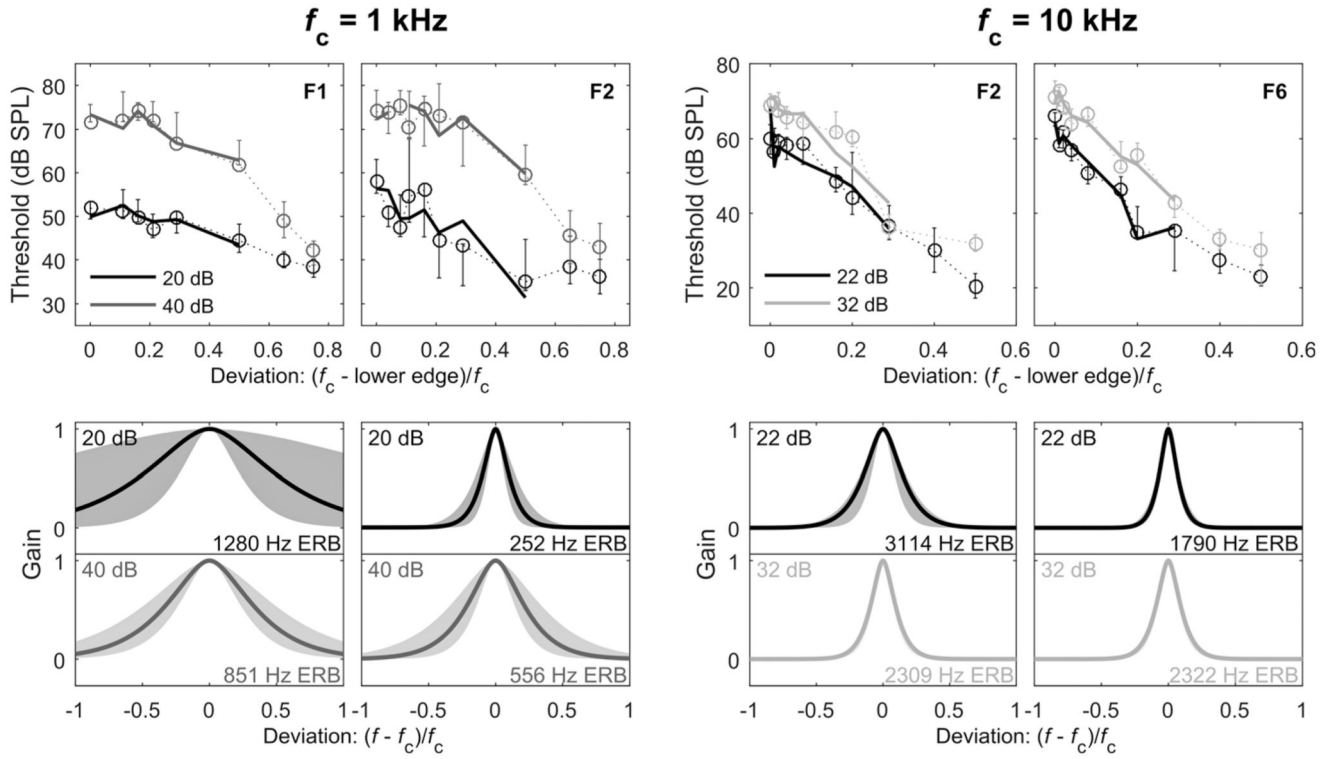


Fig. 1. Example of notched-noise data. Thresholds (circles and dotted lines) as a function of masker notch bandwidth (upper panels) and shape of the estimated auditory filter (thick lines, in upper and lower panels; shading differentiates masker levels). Shaded regions in lower panels indicate the bootstrapped range of roex functions, excluding outliers.

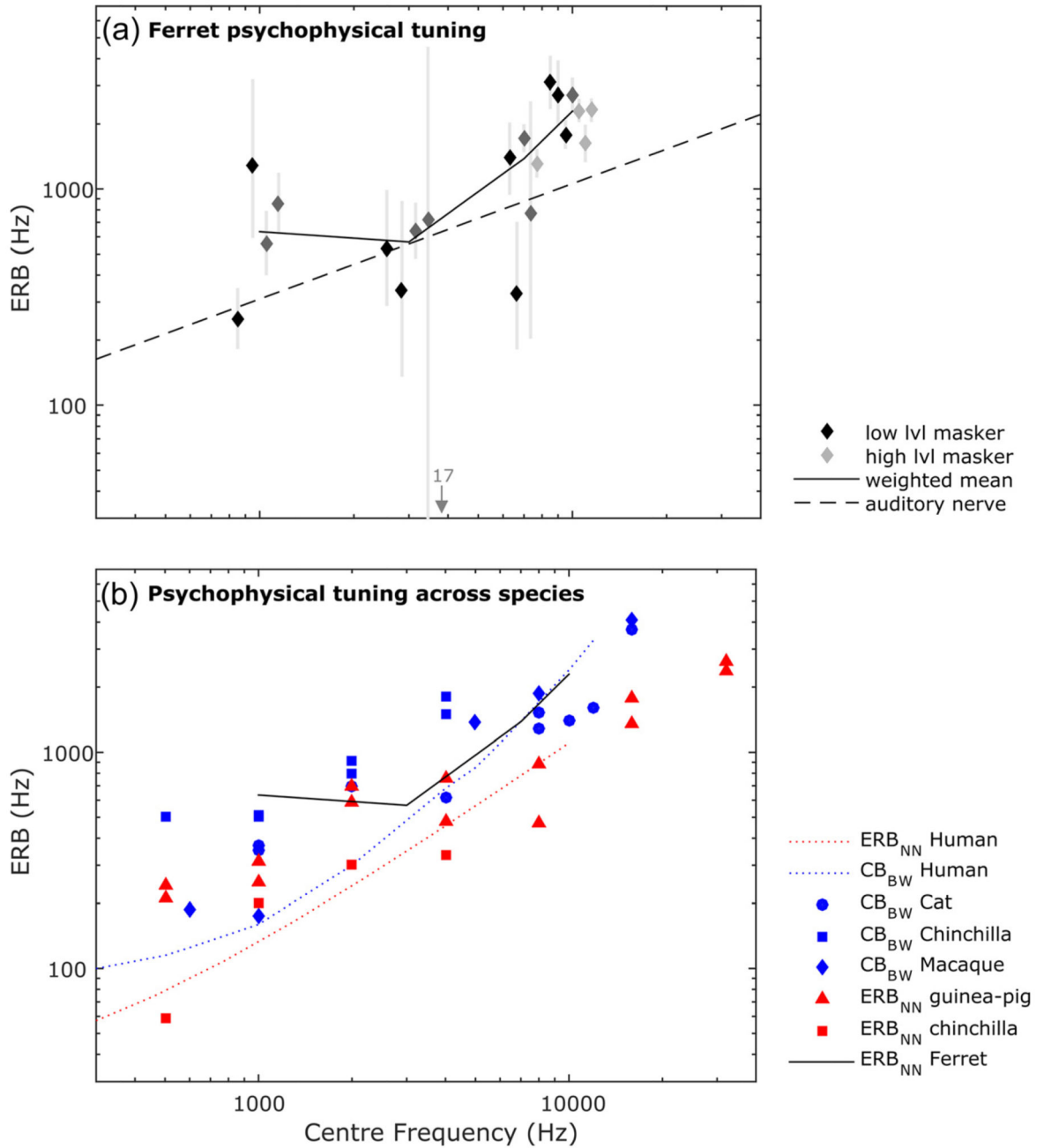


Fig. 2. (Color online) (a) Auditory filter widths (ERBs) in ferrets. Points show median bootstrapped bandwidths for high (light) and low (dark) level maskers. Error bars show the bootstrapped range of ERBs, excluding outliers. Solid line shows confidence weighted mean bandwidths. (b) Auditory filter widths in different mammals (see inset), either notched-noise ERBs (triangles and squares) or CB (circles, squares, and diamonds). Data come from: chinchilla (Ref. 6), Seaton and Trahiotis (1975), adapted from Ref. 5; cat—Pickles (1975, 1979), adapted from Ref. 5; Nienhuys and Clark (1979), adapted from Ref. 5; guinea pig (Ref. 7);

macaque—Gourevitch (1970), adapted from Ref. 5; human (Ref. 5), Glasberg and Moore (1990), adapted from Ref. 2.

Table 1

Details of the auditory filters in individual ferrets.

f_c		SL dB SPL	K dB	ERB Hz	ERB/ f_c %	f_c		SL dB SPL	K dB	ERB Hz	ERB/ f_c %
1 kHz	<i>F1</i>	20	-37.4	1282	128.2	3 kHz	<i>F1</i>	20	7.5	342	11.4
	<i>F2</i>	20	-1.4	252	25.2		<i>F2</i>	20	12.7	526	17.5
	<i>F1</i>	40	-33.4	851	85.1		<i>F1</i>	35	5.5	717	23.9
	<i>F2</i>	40	-5.5	556	55.6		<i>F2</i>	35	8.0	642	21.4
	Average ERB			650	65		Average ERB			571	19
7 kHz	<i>F3</i>	20	-6.2	1393	19.9	10 kHz	<i>F2</i>	22	-4.0	3115	31.2
	<i>F6</i>	20	5.4	329	4.7		<i>F3</i>	22	-8.8	2714	27.1
	<i>F3</i>	35	2.8	775	11.1		<i>F6</i>	22	-1.7	1790	17.9
	<i>F6</i>	35	-4.5	1714	24.5		<i>F2</i>	29	-4.3	2728	27.3
	<i>F6</i>	40	-3.7	1317	18.8		<i>F2</i>	32	-2.4	2309	23.1
						<i>F3</i>	32	-3.8	1621	16.2	
						<i>F6</i>	32	-2.8	2323	23.2	
	Average ERB			1388	20		Average ERB			2296	23