



Research paper

Auditory filter width affects response magnitude but not frequency specificity in auditory cortex



Björn Herrmann*, Molly J. Henry, Mathias Scharinger, Jonas Obleser

Max Planck Research Group "Auditory Cognition", Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstraße 1A, 04103 Leipzig, Germany

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ABSTRACT

Spectral analysis of acoustic stimuli occurs in the auditory periphery (termed frequency selectivity) as well as at the level of auditory cortex (termed frequency specificity). Frequency selectivity is commonly investigated using an auditory filter model, while frequency specificity is often investigated as neural adaptation of the N1 response in electroencephalography (EEG). However, the effects of aging on frequency-specific adaptation, and the link between peripheral frequency selectivity and neural frequency specificity have not received much attention. Here, normal hearing younger (20–31 years) and older participants (49–63 years) underwent a psychophysical notched noise experiment to estimate individual auditory filters, and an EEG experiment to investigate frequency-specific adaptation in auditory cortex. The shape of auditory filters was comparable between age groups, and thus shows intact frequency selectivity in normal aging. In auditory cortex, both groups showed N1 frequency-specific neural adaptation effects that similarly varied with the spectral variance in the stimulation, while N1 responses were overall larger for older than younger participants. Importantly, the overall N1 amplitude, but not frequency-specific neural adaptation was correlated with the pass-band of the auditory filter. Thus, the current findings show a dissociation of peripheral frequency selectivity and neural frequency specificity, but suggest that widened auditory filters are compensated for by a response gain in frequency-specific areas of auditory cortex.

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1. Introduction

Spectral processing of sounds occurs at every level of the ascending auditory pathway. Processes at the auditory periphery have been linked to frequency selectivity at the level of the cochlea in the inner ear (Moore, 1986, 2003). Frequency selectivity here refers to frequency resolution, that is, to the ability to resolve sinusoidal components of complex sounds, which supports, for example, speech perception in noise (Moore, 1986, 2003). Frequency selectivity at the auditory periphery is often operationalized in terms of the width, or pass-band, of a filter-shaped function, referred to as auditory filter (Patterson et al., 1982; Moore, 1986, 2005; Glasberg and Moore, 1990). The pass-band of auditory filters has been linked to the performance on a number of psychophysical tasks requiring spectral stimulus processing, including frequency discrimination (Moore and Peters, 1992), tone detection (Schlauch and Hafer, 1991; but see Moore et al., 1996) and perception of speech in noise (Moore, 1986).

At the cortical level, processing the spectral properties of sounds has been investigated using electroencephalography (EEG) and event-related potentials (ERPs). In particular, the N1 component of the ERP, a negative deflection that peaks at around 100 ms after stimulus onset and is generated in auditory cortex (e.g., Hari et al., 1982; Näätänen and Picton, 1987; Pantev et al., 1988; Maess et al., 2007), has been shown to be modulated as a function of sound frequency (Butler, 1968; Picton et al., 1978; Näätänen et al., 1988; May et al., 1999; Herrmann et al., 2013). That is, the presentation of a tone reduces the responsiveness of neural populations in tonotopically organized auditory cortex responding to a succeeding tone, and this decline is strongest for small frequency separations between the two tones. This phenomenon has been labeled stimulus- or frequency-specific adaptation (Jääskeläinen et al., 2007, 2011; Herrmann et al., 2013).

In addition, frequency-specific adaptation of the underlying neural population is not fixed, but has recently been shown to depend on the spectral variance in the acoustic stimulation. That is, spread of neural adaptation across tonotopically-organized regions of auditory cortex broadens for acoustic sequences with large spectral variance (Herrmann et al., 2013), and this finding resembles observations from single-neuron recordings in auditory

* Corresponding author. Tel.: +49 341 9940 2606.

E-mail address: bherrmann@cbs.mpg.de (B. Herrmann).

cortex (Bitterman et al., 2008). It has furthermore been proposed that tuning of neural populations to sound frequency varies with stimulation intensity (Phillips et al., 1994), and intensity might thus be an additional factor affecting the spread of frequency-specific adaptation observed for N1 responses.

In an attempt to relate frequency selectivity at the auditory periphery and frequency specificity at the level of auditory cortex, Sams and Salmelin (1994) modeled frequency-specific N1m amplitudes (magnetic N1, i.e., measured using magnetoencephalography; MEG) with an auditory filter function, and observed filter shapes resembling those from previous psychophysical experiments (e.g., Patterson, 1976). Furthermore, in a series of studies, Soeta and colleagues observed increasing N1m amplitudes with increasing frequency separation between two simultaneously presented tones, but only for frequency separations greater than 100 Hz (e.g., Soeta and Nakagawa, 2007; Soeta et al., 2008). Based on this, they concluded that frequency specificity of the N1m amplitude resembles properties reported for auditory filter bandwidth (e.g., Fletcher, 1940). Thus, there are indications for a link between peripheral and cortical indices of frequency resolution.

Importantly, most of these previous studies were conducted in younger, normal-hearing participants. However, aging and hearing loss are associated with changes in the signatures of spectral processing at the peripheral level. In patients with cochlear hearing loss, frequency selectivity is impaired as reflected in wider pass-bands of the auditory filters, and thus in reduced frequency resolution at the auditory periphery (Glasberg and Moore, 1986; Peters and Moore, 1992). Furthermore, widening of the auditory filter pass-band has been ascribed to aging (Patterson et al., 1982), although it seems hearing loss has a much stronger impact on frequency selectivity than aging per se (Sommers and Humes, 1993; Sommers and Gehr, 1998).

Frequency specificity of neural responses in older participants has not been thoroughly investigated. This is unfortunate, given the indications for a likely link between peripheral and cortical spectral processing, and the cited deterioration of peripheral spectral processing with age. Further complicating the picture, previous research has produced diverging findings regarding the development of overall N1 amplitude with age. Some studies report larger amplitudes in older participants (Anderer et al., 1996; Amenedo and Díaz, 1999), others observe smaller N1 amplitudes (Harris et al., 2008; Schiff et al., 2008), and still others found no difference between younger and older participants (Ford et al., 1979; Czigler et al., 1992; McArthur and Bishop, 2002; Bennett et al., 2004).

To sum up, while evidence from frequency selectivity in the auditory periphery shows clear results related to aging and/or hearing loss (i.e., widened pass-band of the auditory filter), evidence from N1 cortical responses is less clear on frequency-specific adaptation and the effects of age. Furthermore, evidence that frequency selectivity at the auditory periphery is related to the frequency specificity of auditory cortical responses only exists indirectly thus far. Hence, the current EEG study aimed to investigate (i) frequency selectivity at the auditory periphery in younger and older adults, (ii) frequency specificity of N1 responses and their dependence on spectral variance and overall sound level, (iii) whether aging affects frequency specificity in tonotopically organized regions of auditory cortex, and (iv) how frequency selectivity at the auditory periphery is linked to frequency specificity of auditory cortical responses.

2. Materials and methods

2.1. Participants and experimental sessions

Fifteen younger adults aged 20–31 (median: 24 years; 7 female) and fourteen older adults aged 49–63 (median: 56.5 years; 7 female)

took part in this study. All participants were right-handed (Oldfield, 1971), did not report any history of neurological diseases, gave written informed consent prior to the experiment, and were paid 7 €/hour for their participation. Audiometry was acquired for each participant, to ensure that all participants had normal hearing (i.e., <20 dB HL) up to 3 kHz (Jerger and Jerger, 1980). The study was in accordance with the Declaration of Helsinki and approved by the local ethics committee of the University of Leipzig.

Participants underwent two experimental sessions, one consisting of a psychophysical experiment measuring frequency selectivity at the auditory periphery (Patterson et al., 1982; Moore, 2005), and the other consisting of an EEG recording of frequency-specific neural responses in auditory cortex related to neural adaptation (Näätänen et al., 1988; Herrmann et al., 2013). The two sessions were carried out in an electrically-shielded and sound-attenuated booth on separate days and within 3 months of each other.

2.2. Frequency selectivity at auditory periphery: psychophysical experiment

2.2.1. Acoustic stimulation and procedure

In order to estimate individual auditory filter functions, we acquired detection thresholds for a 1400-Hz sine tone (500 ms duration) in noise using a notched-noise technique (Patterson et al., 1982; Moore, 2005). Specifically, filtered noise stimuli were created in which a spectral notch was centered at 1400 Hz between two white noise bands each with a width equal to 560 Hz. The notch width was varied parametrically, and took on eight different values (0, 100, 200, 300, 400, 500, 600, and 700 Hz). Listeners had to detect a 1400-Hz sine tone embedded in the noise. Critically, narrower notch widths correspond to greater masking of the 1400-Hz tone, and thus higher detection thresholds. Estimating detection thresholds as a function of notch width provides a function from which individual auditory filter widths can be estimated.

Following Jurado and Moore (2010), noise stimuli were created by applying stop-band and band-pass filters to white noise (200th-order infinite impulse response; Chebychev type II). Filters had very sharp slopes and an attenuation of 80 dB per 1.7 Hz. The level of the notched noise was fixed at 45 dB above the individual hearing threshold.

At the beginning of the experiment, the individual hearing threshold for a white noise stimulus (no notch) was determined using the methods of limits (Leek, 2001). Subsequently, participants underwent an adaptive tracking procedure for each of the eight notch widths (in separate blocks) in order to establish individual detection thresholds for the 1400-Hz tone at the center of the notch. A simple three-interval forced choice one-down one-up staircase method was implemented in order to estimate the intensity of the tone yielding 50% detection (Leek, 2001). In particular, three notched noise stimuli were presented, separated by an inter-stimulus interval of 850 ms. The notched noise stimulus in one (randomly selected) interval contained the 1400-Hz tone, and participants were asked to indicate the interval in which the tone occurred.

Stimuli with different notch widths were presented in separate blocks. Thus, participants experienced only one notch width per block (pseudorandomized across participants), and completed a total of 8 blocks. In each block, two independent tracks were simultaneously presented. The block ended when both tracks reached 12 reversals. The detection threshold for each notch width was then calculated as the average tone intensity across the last 8 reversals from each track. The psychophysical experiment lasted approximately 1 h.

2.2.2. Estimation of auditory filter shape

For each participant, a rounded exponential (roex) function was fitted to the eight measured tone thresholds as a function of

normalized frequency of the notch edge using a least squares routine (Patterson et al., 1982; Glasberg and Moore, 1990; Moore, 2005). Normalized frequency (g) was calculated using Equation (1):

$$g = \frac{|f - f_c|}{f_c} \quad (1)$$

where f reflects the frequency at one edge of the noise band and f_c the center frequency (1400 Hz) of the filter. The predicted threshold (P) was calculated as follows:

$$P(g) = 2Kf_c N_0 \int_g^{0.8} W(g) \quad (2)$$

Here K reflects a proportionality constant, N_0 the noise spectral density, and W the weighting function of the filter (i.e., the roex function). The weighting function (W) has the form

$$W(g) = (1 - r)(1 + pg)e^{-pg} + r \quad (3)$$

where r is a parameter placing a dynamic range limitation on the filter and p the pass-band (i.e., slope) of the auditory filter. Since the observed threshold data were measured in decibels, predicted values from Equation (2) were transformed by taking 20 times the base-10 logarithm before fitting to the data.

Statistical analyses were conducted on the predicted thresholds (averaged across notch widths) and the estimated pass-band of the auditory filter (p parameter, i.e., the slope of the function). On this account, two independent sample t -tests were carried out to compare age groups.

2.3. Frequency-specific adaptation in auditory cortex: EEG experiment

2.3.1. Acoustic stimulation and procedure

Stimuli consisted of two sets of 8 logarithmically-spaced sinusoidal tones centered at 1400 Hz (as described in detail also in Herrmann et al. (2013)). The two sets varied in frequency spacing (i.e., spectral variance): narrow (1046, 1137, 1236, 1343, 1459, 1586, 1724, and 1873 Hz; spanning approximately one octave), wide (782, 924, 1091, 1288, 1521, 1797, 2122, and 2506 Hz; spanning approximately two octaves). Tone duration was 170 ms, including 10 ms rise and fall times (using a Tukey window).

Prior to the EEG recording, the participant's hearing threshold was determined for the center frequency (1400 Hz) using the method of limits (Leek, 2001). Based on the hearing threshold, two sensation level (SL) versions of the tones were created (soft = 35 dB SL; loud = 60 dB SL), thereby constituting a 2×2 stimulus design with the factors Spectral Variance (narrow; wide) \times Sensation level (soft; loud).

Participants were seated in a comfortable chair, watched a silent movie (no subtitles) of their choice throughout testing, and were instructed to ignore the auditory stimulation. Auditory stimuli were presented via headphones (Sennheiser HD 25-SP II, Germany).

In the main experiment, eight blocks were presented (two per spectral variance and sensation level condition) while EEG was recorded. The presentation order of conditions was randomized separately for each participant.

Each block started with a silent period of >10 s prior to the beginning of the acoustic stimulation to ensure full responsiveness of neural populations at block onset. Within each block, a train of 8 unique tones was presented 105 times without pauses between trains. Tone frequencies within each train were randomized. No two consecutive tones ever had the same frequency, even during transitions between trains. Tones were presented with an onset-to-

onset interval of 0.55 s.¹ Overall, participants heard a total of 840 tones per block (105 for each of the 8 frequencies). The EEG session lasted approximately 2.5 h.

2.3.2. EEG recording and data pre-processing

The electroencephalogram was recorded at a 500-Hz sampling rate and low-pass filtered online at 135 Hz (TMS international, Enschede, The Netherlands). Electrodes (Ag/Ag–Cl-electrodes) were placed at the following positions according to the international extended 10–20 system (Easycap, Herrsching, Germany): Fp1, Fp2, Fz, F3, F4, F7, F8, FC3, FC4, FT7, FT8, Cz, C3, C4, T7, T8, CP5, CP6, Pz, P3, P4, P7, P8, O1, O2, nose, and at the left (A1) and right (A2) mastoids. The nose served as online reference. Electrooculogram was recorded from vertical and horizontal bipolar montages to measure blinks and eye movements. The ground electrode was placed at the sternum and impedances were kept below 5 k Ω for all electrodes.

Data analysis was carried out using Fieldtrip software (<http://fieldtrip.fcdonders.nl/>; v20110527; Oostenveld et al., 2011) in combination with custom Matlab scripts (The MathWorks Inc., Massachusetts, USA). EEG recordings were re-referenced offline to the linked mastoids, high-pass filtered at 0.5 Hz (1747 points, Hamming window, zero-phase-shift), low-pass filtered at 100 Hz (131 points, Blackman window, zero-phase-shift), and down-sampled to 250 Hz. Epochs of -1.6 – 1.9 s time-locked to the tone onset were extracted from EEG recordings. Independent components analysis was carried out to correct for artifacts such as eye movements, electrical heart activity and noisy channels. Subsequently, data were projected back to the original EEG electrodes, and epochs were excluded if they contained a signal range larger than 120 μ V in any of the EEG electrodes. Epochs were then filtered with a 20.1-Hz (129 points, Blackman window, zero-phase-shift) low-pass and re-defined for data analysis ranging from -0.1 – 0.4 s time-locked to the tone onset. Baseline correction was applied by subtracting the mean amplitude of the -0.1 to 0 s time window from the epoch.

2.3.3. Frequency specificity: analysis of quadratic fits

The current study focused on variations in N1 responses. On this account, participant-specific N1 amplitudes were extracted from a fronto-central-parietal electrode cluster (Fz, F3, F4, FC3, FC4, Cz, C3, C4, Pz, P3, P4) showing the strongest responses in the ERP (see Fig. 2; Herrmann et al., 2013). First, trials were averaged across conditions and electrodes. Second, the largest negative peak within the 0.05–0.15 s time window was identified as the participant-specific N1 latency. Third, the mean N1 amplitude for a given condition was then extracted as the mean across the trials and the 20-ms time window centered at the N1 peak latency.

Based on the tonotopic organization of auditory cortex, N1 amplitudes were expected to be smallest for tone frequencies close to the center of a spectral variance condition and largest for tone frequencies at the edge (Ulanovsky et al., 2004; Herrmann et al., 2013), because the neural population underlying the latter are less repetitively co-adapted in a random tone sequence presentation. Thus, in order to analyze overall N1 amplitudes and frequency specificity of N1 responses, a quadratic fit analysis was conducted (Herrmann et al., 2013), such that N1 amplitudes were related to their respective tone frequencies in log₂-space. Using a least-

¹ The current EEG design was chosen based on a previous study by Herrmann et al. (2013), where it has proven particularly suitable to investigate changes in cortical frequency specificity as a function of the spectral variance in the acoustic stimulation. We note, however, that previous research made also use of notched-noise stimuli to investigate N1(m) amplitude variations and cortical frequency specificity (e.g., Sams and Salmelin, 1994; Kauramäki et al., 2007; Okamoto et al., 2010).

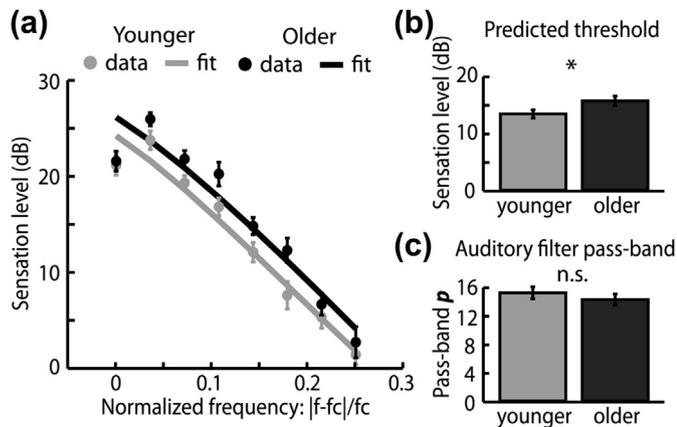


Fig. 1. Frequency selectivity at auditory periphery for younger and older participant groups. (a) Mean thresholds and fits of auditory filter shape for a 1400-Hz tone in different notched noise stimuli. Note that the x-axis depicts normalized frequency. (b) Mean predicted thresholds (averaged across individual frequencies) from fitting the auditory filter shape function. (c) Mean auditory filter pass-bands (p) from fitting the auditory filter function. * $P = 0.05$, n.s. – not significant. Error bars are provided as standard error of the mean (\pm SEM).

squares routine, the quadratic function was fitted to the N1 amplitudes as a function of frequency:

$$y = b_2x^2 + b_1x + b_0$$

where y corresponds to the predicted N1 amplitudes, x to the unique tone frequencies of one spectral variance condition (log2-transformed and zero-centered), and b to the estimated coefficients. Coefficients from quadratic function fits were estimated for each participant and condition individually, and the coefficients were subsequently subjected to group-level analyses.

Specifically, the second-order b_2 coefficient directly reflects the tightness of the best-fit quadratic function, that is, the degree of frequency specificity. A value of $b_2 = 0$ would indicate the absence of frequency specificity, while a significant difference from zero would indicate frequency-specific N1 responses. The first-order b_1 coefficient reflects the linear decrease/increase of N1 amplitudes as a function of tone frequency. A value of $b_1 \neq 0$ would indicate a linear decrease ($b_1 < 0$) or increase ($b_1 > 0$) in N1 amplitude as a function of frequency. Finally, the b_0 coefficient reflects the intercept of the function, and thus is a measure of the overall N1 amplitude (at the center of a spectral variance condition), or frequency-independent response magnitude.

For the statistical analysis, b_2 and b_1 coefficients in each condition and participant group were first tested against zero in order to determine whether N1 responses are frequency-specific (b_2) and change linearly with the tone frequency (b_1). The b_0 coefficients could not be meaningfully tested against zero because b_0 reflects the overall amplitude of the N1, the absolute value of which has no specific relation to zero (e.g., N1 amplitude could be positive, while still being a negative going deflection). In order to test for differences between conditions and groups, an analysis of variance (ANOVA) was then carried out for each coefficient independently (b_2 , b_1 , b_0), using the within-subject factors Spectral Variance (narrow; wide) and Sensation Level (soft; loud) and the between-subject factor Group (younger; older).

2.4. Linking peripheral frequency selectivity and cortical frequency specificity: correlation analysis

A major goal of this study was to link frequency selectivity at the auditory periphery to frequency specificity in auditory cortex.

Therefore, auditory filter width (as reflected in the p parameter of the auditory filter model fits; see above) was correlated with the three coefficients estimated by quadratic fits to the N1 amplitudes. To reiterate, the b_2 reflects cortical frequency specificity, b_1 reflects the strength of the linear relation between frequency and cortical responses, and b_0 provides an index of overall N1 amplitude. All coefficients were averaged across conditions before being correlated with auditory filter width, p .

3. Results

3.1. Auditory filter shape and predicted thresholds

Fig. 1 depicts the observed and predicted tone thresholds as a function of normalized frequency from the psychophysical experiment. Predicted thresholds reflect the average across normalized frequency levels of the fitted value at each point estimated from the auditory filter (roex) function.

Younger participants had a significantly smaller predicted threshold than older participants ($t_{27} = 2.06$, $P = 0.050$), reflecting overall better detection sensitivity. Auditory filter pass-band as reflected in the p parameter, on the other hand, was not significantly different between age groups ($t_{27} = 0.82$, $P = 0.418$).

Perhaps noteworthy, Fig. 1 shows a slight drop in observed thresholds at the zero-notch level that could potentially affect the fit of the roex function. In order to test the influence of this data point on the results, it was excluded prior to fitting and analyses were recalculated. Importantly, excluding this data point from the analyses had no qualitative impact on the observed results (predicted thresholds: $t_{27} = 2.24$, $P = 0.034$; p parameter: $t_{27} = 1.77$, $P = 0.089$).

3.2. Analysis of quadratic fits to N1 response magnitude

Fig. 2 depicts ERP time courses for each tone in each spectral variance and sensation level condition. The bar graphs in the lower panel of Fig. 2 depict mean participant-specific N1 amplitudes. Fig. 3 shows the predicted N1 amplitudes from the quadratic fits for each condition.

In order to test for frequency specificity of N1 responses, the b_2 coefficient was tested against zero using a F -test. For each of the four conditions and in both participant groups, the b_2 coefficient was significantly smaller than zero (for all, $F > 20$, $P < 0.001$, $\eta_p^2 > 0.6$), indicating that N1 amplitudes were modulated as a function of tone frequency (i.e., N1 amplitudes showed frequency specificity). A Spectral Variance \times Sensation Level \times Group ANOVA revealed a main effect of Spectral Variance ($F_{1,27} = 45.16$, $P < 0.001$, $\eta_p^2 = 0.626$), whereas the other effects and interactions were non-significant (for all, $P > 0.05$). Irrespective of age, the b_2 coefficients in the narrow spectral variance conditions had larger magnitude than in the wide spectral variance conditions, indicating that wide spectral variance led to broadened N1 frequency specificity (as in Herrmann et al., 2013).

To investigate whether N1 responses decreased or increased as a function of tone frequency, b_1 coefficients of the quadratic fits were tested against zero. Essentially, a non-zero b_1 coefficient would indicate an asymmetric N1 frequency specificity around the center at 1400 Hz. For both the younger and older participant groups, b_1 coefficients were significantly greater than zero for the two soft sensation level conditions, thus showing a decrease in N1 amplitude with increasing tone frequency (younger narrow: $F_{1,14} = 6.76$, $P = 0.021$, $\eta_p^2 = 0.326$; younger wide: $F_{1,14} = 5.49$, $P = 0.034$, $\eta_p^2 = 0.282$; older narrow: $F_{1,13} = 14.55$, $P = 0.002$, $\eta_p^2 = 0.528$; older wide: $F_{1,13} = 10.07$, $P = 0.007$, $\eta_p^2 = 0.437$). For the younger group, the b_1 coefficients for the loud sensation level conditions were not significantly different from zero for either spectral variance

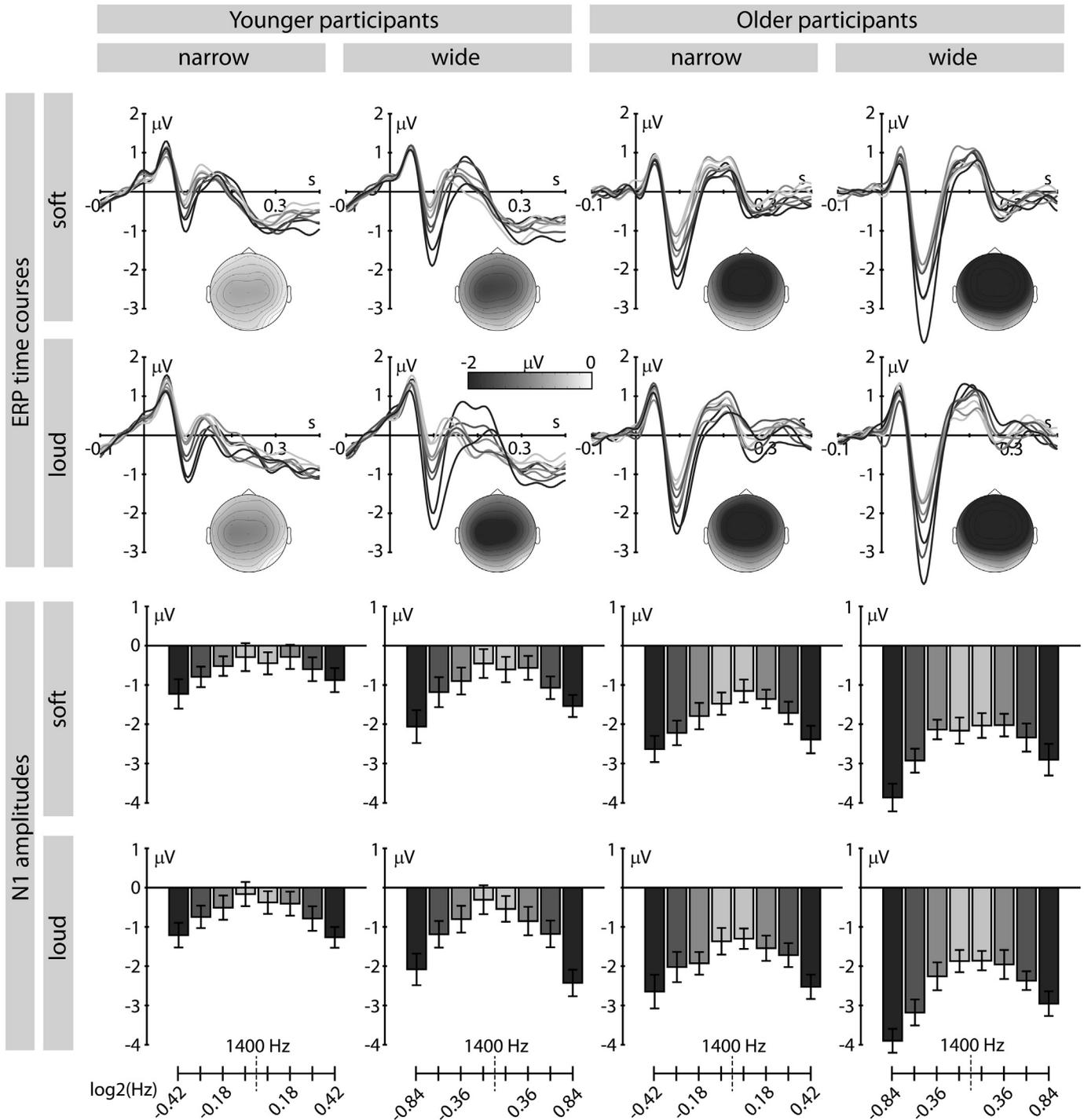


Fig. 2. ERPs to tones in each group and condition. Top panel: Response time courses for each tone frequency, with time on the x-axis and amplitude on the y-axis. Topographies are shown for the N1 averaged across the two edge frequencies of each spectral variance condition. Bottom panel: Mean participant-specific N1 amplitudes (\pm SEM) as a function of tone frequency. The frequency axis describes the log₂-distance of each tone to the 1400-Hz frequency reflecting the condition center. Note that for the N1 time window, larger brain responses correspond to more negative amplitudes.

condition (for both, $P > 0.25$). On the other hand, in the older participant group, b_1 coefficients were significantly larger than zero at loud sensation level in the wide spectral variance condition ($F_{1,13} = 9.25$, $P = 0.009$, $\eta_p^2 = 0.416$), but not in the narrow variance condition ($F_{1,13} = 1.03$, $P = 0.329$). A Spectral Variance \times Sensation Level \times Group ANOVA revealed a main effect of Sensation Level ($F_{1,27} = 6.35$, $P = 0.018$, $\eta_p^2 = 0.190$), whereas the other effects and interactions were not significant (for all, $P > 0.05$). The main effect

resulted from larger b_1 coefficients for the soft relative to the loud sensation levels, indicating a stronger decrease in N1 amplitude as a function of tone frequency.

In order to test for differences in overall N1 amplitude at the center of a spectral variance condition, a Spectral Variance \times Sensation Level \times Group ANOVA was conducted using the b_0 coefficient as dependent measure. The ANOVA revealed a main effect of Spectral Variance ($F_{1,27} = 30.53$, $P < 0.001$, $\eta_p^2 = 0.531$) and a main

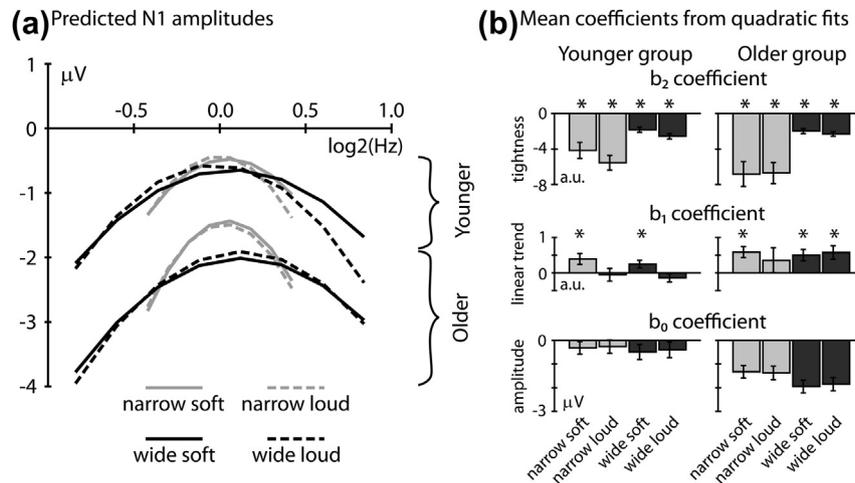


Fig. 3. Results from quadratic fits to N1 amplitudes. (a) Predicted N1 amplitudes from quadratic fits. Note that N1 amplitudes are depicted with respect to their corresponding tone frequencies (in \log_2 -transformed and zero-centered units on the x-axis). (b) Mean coefficients from quadratic fits (\pm SEM). The asterisk marks coefficients significantly different from zero. Note that testing against zero was only conducted for b_2 and b_1 coefficients.

effect of Age ($F_{1,27} = 10.25$, $P = 0.003$, $\eta_p^2 = 0.275$), which were further qualified by a Spectral Variance \times Age interaction ($F_{1,27} = 9.50$, $P = 0.005$, $\eta_p^2 = 0.260$). The b_0 coefficients were in general more negative (i.e. larger N1 amplitudes) in the older than younger participant group. However, b_0 coefficients were more negative in the wide than narrow spectral variance condition in the older ($F_{1,13} = 45.45$, $P < 0.001$, $\eta_p^2 = 0.778$), but not in the younger participant group ($F_{1,14} = 2.58$, $P = 0.130$). None of the other main effects or interactions was significant (for all, $P > 0.15$).

3.3. Relation of frequency-specific adaptation and auditory filter pass-band

Auditory frequency selectivity at the periphery, as measured by the pass-band of the auditory filter (p parameter), was correlated with the parameters from quadratic fits to neural N1 responses.

Neither the correlation between auditory filter pass-band (p) and the b_2 coefficient ($r = 0.042$, $t_{28} = 0.22$, $P = 0.830$) nor the correlation between p and the b_1 coefficient reached significance ($r = -0.229$, $t_{28} = -1.22$, $P = 0.232$).

However, the correlation between p and b_0 , reflecting the overall magnitude of the fitted brain responses (see Fig. 4), was significant ($r = 0.397$, $t_{28} = 2.25$, $P = 0.033$). That is, when p decreased (i.e., wider pass-band at the auditory periphery), the b_0 coefficient from the quadratic fit decreased (i.e., overall more negative N1 amplitude and thus larger response magnitude). In other words, while the pass-band of the auditory filter was unrelated to N1 neural adaptation spread, the overall N1 response magnitude varied as a function of the pass-band. Furthermore, partial correlations of auditory filter pass-band (p) and the b_0 coefficient controlling for pure tone audiometry (mean across hearing levels from 250 Hz to 3000 Hz; $r = 0.397$, $t_{26} = 2.20$, $P = 0.037$) or controlling for age ($r = 0.337$, $t_{26} = 1.83$, $P = 0.080$) confirmed the relationship between frequency selectivity at the auditory periphery and overall N1 response magnitude.²

² We also recalculated the fits of the auditory filter function (and the corresponding p parameter) without the data point at zero-notch level. Importantly, correlations of the re-estimated p with the coefficients from the quadratic fits to the N1 data did not change the current results. In fact, while the correlation between p and b_1 and p and b_2 remained not significant (for both, $P > 0.1$), the correlation between p and b_0 increased ($r = 0.501$, $t_{28} = 3.01$, $P = 0.006$; controlled for hearing level: $r = 0.499$, $t_{26} = 2.94$, $P = 0.007$; controlled for age: $r = 0.410$, $t_{26} = 2.29$, $P = 0.030$).

4. Discussion

The current study investigated auditory frequency selectivity at the auditory periphery and auditory frequency specificity at the level of the auditory cortex in younger and older normal-hearing adults. Frequency-specific neural responses were examined under different spectral variance and intensity conditions. The main findings of the current study are as follows: (i) Frequency selectivity as measured by auditory filter shape was comparable between age groups, (ii) N1 auditory cortex responses were larger for older than younger participants, but (iii) both groups showed frequency-specific adaptation effects that also varied comparably with the spectral variance in the stimulation. However, (iv) the width of the pass-band of the auditory filter was correlated with the overall N1 response magnitude. In the next sections we discuss these results in more detail.

4.1. Frequency selectivity at the auditory periphery

We conducted a psychophysical notched noise experiment to estimate auditory filter shapes in younger and older participants, and observed comparable filter pass-bands in both age groups. While earlier work suggested that the pass-band widens with increasing age (Patterson et al., 1982), subsequent studies controlling for hearing loss showed that widening of auditory filters is linked to hearing loss rather than to aging per se (Sommers and Humes, 1993; Sommers and Gehr, 1998). Our results are thus consistent with these previous findings and confirm unimpaired frequency selectivity in older participants who show normal hearing up to 3 kHz.

In addition, the current observation of larger tone thresholds (i.e., predicted thresholds from auditory filter fits) in older participants with normal hearing is line with previous findings (Sommers and Humes, 1993). In principle, larger thresholds could also be caused by a third variable, for example a general difference in response bias between groups (Henry and McAuley, 2013).

4.2. Frequency specificity in auditory cortex

Frequency specificity of neural responses was investigated by randomly presenting tones with different frequencies. Neural activity was modulated at around 100 ms post-stimulus onset, such that largest responses were elicited by tone frequencies at the edge of a spectral variance condition and smallest for tone frequencies at the center. This finding is expected given the tonotopic organization of

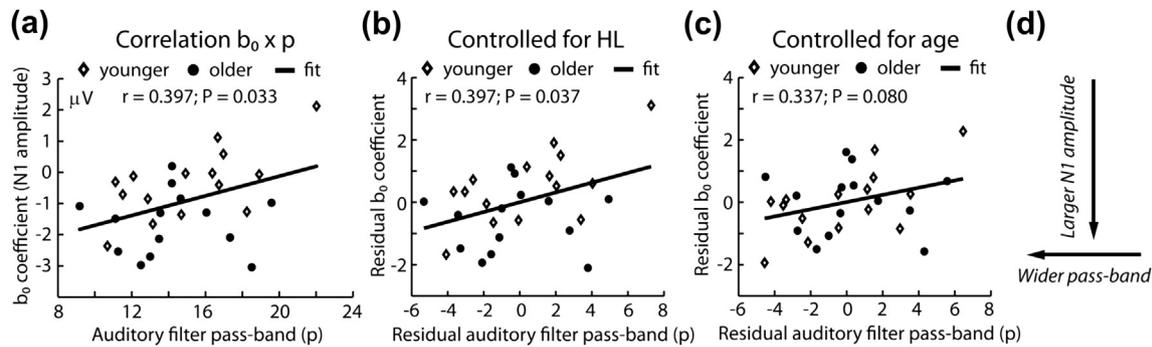


Fig. 4. Correlation of the b_0 coefficient (overall N1 amplitude) and the p parameter (auditory filter pass-band). (a) Correlation of b_0 coefficient and p parameter, (b) Partial correlation controlling for hearing level (from pure tone audiometry), (c) and controlling for age. Note that in (b) and (c) the x- and y-axis reflect the residuals of the b_0 coefficient and p parameter when hearing level or age are regressed out, respectively. (d) Provides a legend describing the x- and y-axis.

auditory cortex, where neural populations responding best to the edge frequencies become less repetitively co-adapted in random tone sequences (Ulanovsky et al., 2004; Herrmann et al., 2013), and this finding is in line with previous reports on N1 frequency specificity (Butler, 1968; Picton et al., 1978; Näätänen et al., 1988; May et al., 1999; Brattico et al., 2003).

Importantly, the extent of frequency-specific spread of adaptation in the current study depended on the spectral variance in the stimulation. Neural adaptation was broadened for sequences with wide spectral variance, and this effect was independent of sound level and age. In this regard, the current results are in line with previous studies showing that auditory cortex responses adapt to the acoustic properties in the stimulation (Kvale and Schreiner, 2004; Dean et al., 2005, 2008; Bitterman et al., 2008; Dahmen et al., 2010; Herrmann et al., 2013). However, the present results extend those findings by showing that neural populations in older listeners track variations in the acoustic stimulation properties similarly well as in younger participants. These short-term plastic changes of the underlying neural population have been proposed to serve as a mechanism of sensory memory function involved in cognitive processes (Ulanovsky et al., 2003; Jääskeläinen et al., 2007, 2011), and the current data give no indication that such sensory memory function would be principally altered or deprecated in healthy older listeners.

Furthermore, the similarity of neural frequency specificity between age groups is especially remarkable considering that older participants had overall larger N1 amplitudes. Previous studies investigating N1 amplitudes in younger and older adults led to diverging findings, with some studies reporting larger N1 amplitudes in older adults (Anderer et al., 1996; Amenedo and Díaz, 1999), while others observed smaller amplitudes (Harris et al., 2008; Schiff et al., 2008) or no age-related differences (Ford et al., 1979; Czigler et al., 1992; McArthur and Bishop, 2002; Bennett et al., 2004). This divergence might be related to an insensitivity of the N1 in older participants to variations in stimulus onset-to-onset interval, such that, compared to younger participants, the N1 amplitude is larger at fast rates but smaller at slow rates (Kisley et al., 2005). Such insensitivity would, however, indicate diminished frequency-specific adaptation in older participants, which is incompatible with the current findings.

Nevertheless, it has been proposed that the time to recover from adaptation is prolonged in older participants (Papanicolaou et al., 1984). In this regard, prolonged recovery in combination with tightened co-adaptation in older participants could in principle account for comparable frequency specificity (operationalized as b_2 coefficients) between younger and older adults (see Herrmann et al., 2013). It would, however, fail to explain the overall larger

N1 amplitude in older participants, and would furthermore fail to explain the larger N1 amplitudes in the wide compared to narrow spectral variance conditions at strong adaptation (i.e., at the center frequencies; see Fig. 3) in older participants. Alternatively, as we discuss below, the overall N1 amplitude appears to be related to the pass-band of the filter at the auditory periphery.

4.3. Sound level-tolerance of frequency-specific neural responses

In addition to varying the spectral variance of the acoustic sequences, in the current study we also presented tone sequences at two intensity levels (soft: 35 dB SL; loud: 60 dB SL). We observed decreased N1 amplitudes with increasing tone frequency (as reflected by b_1 coefficients that differed significantly from zero) at soft but not at loud sound levels; an effect that has also been observed in some previous studies (e.g., Rothman, 1970; Harris et al., 2007).

Frequency specificity of N1 responses, on the other hand, was invariant to sound level manipulations. This tolerance of frequency-specific adaptation to stimulation intensity is surprising given previous results, where widening of neural tuning was observed at higher sound intensities (Phillips et al., 1994). However, level-dependence in general decreases along the ascending auditory pathway (Sutter, 2000) and more recently, Sadagopan and Wang (2008) reported that neural populations in auditory cortex also show level-invariant frequency tuning. Sound-level tolerance of neural frequency tuning appears particularly pronounced for spectro-temporally dense acoustic stimulation sequences (Pienkowski and Eggermont, 2011). In line with these animal recording studies, intensity effects on the N1 amplitude seem to be smallest at fast stimulus presentation rates (Polich et al., 1988), which were employed here also (1.8-Hz presentation rate).

Thus, despite the large literature on N1 reduction with decreasing sound level (e.g., Rothman, 1970; Bruneau et al., 1985; Laffont et al., 1989; Kim et al., 2012), it appears that frequency-specific adaptation in a temporally fast and spectrally varying stimulation protocol is relatively sound level-tolerant, at least for the two levels tested here (35 dB SL; 60 dB SL). This suggests that neurons with level-invariant frequency tuning underlie generation of the current N1 effects.

4.4. Auditory filter pass-band and its connection to auditory cortical responses

The current study aimed to link frequency selectivity at the auditory periphery with frequency-specific N1 responses at the level of auditory cortex. Interestingly, while N1 responses showed clear frequency-specific modulations in younger and older participants,

variations in the pass-band of the auditory filter (p) were unrelated to variations in the extent of neural adaptation spread (b_2 coefficient). Thus, the current data suggest a dissociation between frequency selectivity at the periphery and frequency specificity at the cortical level.

Previous studies investigating the link between processes at the auditory periphery and processes at auditory cortex either fitted an exponential function (roex function) to N1m amplitudes (Sams and Salmelin, 1994) or descriptively related critical bandwidth to N1m amplitudes variations (e.g., Soeta and Nakagawa, 2007; Soeta et al., 2008). The current results are in line with these and other previous studies (Butler, 1968; Näätänen et al., 1988; May et al., 1999; Herrmann et al., 2013), showing that frequency-specific co-adaptation in tonotopically-organized areas of auditory cortex resembles an exponential function. Yet, a direct link between frequency selectivity and frequency specificity has not been observed, such that widening of the auditory pass-band would be connected to wider (or tighter) frequency specificity in auditory cortex. The absence of such a relationship in the current data is fully compatible with investigations of critical bandwidth behavior of single-neuron recordings in auditory cortex, where such relationship was not observed either (Ehret and Schreiner, 1997). Future research, however, might investigate whether frequency selectivity in the auditory periphery is linked to frequency-specific activity in other subparts of auditory cortex, to which for example MEG is more sensitive than EEG. Furthermore, multiple time scales of adaptation have been observed in auditory cortex (Ulanovsky et al., 2004; Costa-Faidella et al., 2011). Thus, future research might also focus on whether frequency specificity of cortical neurons responding at longer time scales is linked to changes in auditory filter pass-band.

The current data show instead that the overall N1 amplitude (here operationalized as b_0 coefficient) is linked to auditory peripheral processes, such that N1 response magnitude is larger in participants with wider auditory filter pass-bands. In other words, decreased frequency selectivity at the auditory periphery is related to an overall increase in response magnitude in auditory cortex. Thus, it appears that a wider auditory pass-band is compensated for by a frequency-unspecific sensory gain mechanism in auditory cortex, rather than by changes in the extent of neural adaptation spread.

The auditory filter pass-band is operationalized as the amount of spectral noise power that passes through the filter, which in turn defines the degree of spectral overlap with the frequency of a target tone. Thus, in participants with reduced frequency selectivity at the auditory periphery, the neural system might accomplish a boost in signal-to-noise ratio by amplifying the neural response magnitude in auditory cortex.

Previous research on the relation between behavioral measures of spectral processing and N1 auditory cortex responses, however, suggests that N1 amplitudes increase with increasing perceptual performance (frequency modulation: Harris et al., 2008; frequency discrimination: McArthur and Bishop, 2002). On the other hand, in a fast and spectrally varying experimental design that is more closely related to the current setup, reduced frequency discrimination ability was associated with larger N1 amplitudes (Brattico et al., 2003). This finding is consistent with the current link between increased N1 amplitudes in participants with widened filter pass-bands at the auditory periphery, and also suggests that this sensory gain is especially pronounced in a temporally fast and spectrally varying stimulation context.

It should be noted that the current study investigated normal-hearing adults as indicated by hearing levels below 20 dB in audiometric diagnostics for both younger and older participant groups. While it would not be surprising when this gain in N1 response magnitude would level off or be obliterated altogether in participants with widened auditory filter pass-bands due to

cochlear hearing loss (Glasberg and Moore, 1986; Peters and Moore, 1992), it appears that also hearing impaired listeners show an increase in N1 amplitude compared to normal-hearing adults (Tremblay et al., 2003). Furthermore, studies in animals observed an increase in neural activity at different levels of the ascending auditory pathway following exposure to acoustic trauma (Brozoski et al., 2002; Norëna and Eggermont, 2003; Kaltenbach et al., 2004). Thus, for a normal hearing and healthy aging population, the current data suggest that subclinical auditory degradation (related to the broadened peripheral tuning) leads to neural hyperactivity throughout the auditory system that ultimately gives rise to larger N1 responses in auditory cortex.

5. Conclusions

The current study investigated frequency selectivity at the auditory periphery and frequency specificity in auditory cortex in younger and older participants. Critically, auditory filter pass-bands associated with frequency selectivity at the level of the cochlea were similar between age groups, as was frequency-specific adaptation of auditory cortex responses. Yet, overall neural responses were larger in older compared to younger adults. Importantly, auditory filter pass-band and spread of neural adaptation in auditory cortex dissociate, whereas the overall magnitude of auditory cortex responses increases with wider auditory filter pass-bands. The current results link cortical response magnitude to frequency selectivity at the auditory periphery and open new avenues towards neural, non-invasive protocols of “objective audiometry”.

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