Cortical Responses to the Amplitude Envelopes of Sounds Change with Age

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Abstract

Many older listeners have difficulty understanding speech in noise, when cues to speech-sound identity are less redundant. The amplitude envelope of speech fluctuates dramatically over time, and features such as the rate of amplitude change at onsets (attack) and offsets (decay) signal critical information about the identity of speech sounds. Aging is also thought to be accompanied by increases in cortical excitability, which may differentially alter sensitivity to envelope dynamics. Here, we recorded electroencephalography in younger and older human adults (of both sexes) to investigate how aging affects neural synchronization to 4-Hz amplitude-modulated noises with different envelope shapes (*ramped*: slow attack & sharp decay; *damped*: sharp attack & slow decay). We observed that subcortical responses did not differ between age groups, whereas older compared to younger adults exhibited larger cortical responses to sound onsets, consistent with an increase in auditory cortical excitability. Older adults showed increased neural synchronization when the envelope shape was damped compared to ramped, whereas younger participants showed the opposite pattern. Furthermore, the response shape of synchronized neural activity was more sinusoidal in younger individuals, whereas synchronized activity in older adults was less sinusoidal and more peaked. The current results suggest that age-related changes in the excitability of auditory cortex alter responses to envelope dynamics, and this may be part of the reason why older adults experience difficulty understanding speech in noise.

Keywords: aging; hearing; neural synchronization; envelope tracking; non-sinusoidal signal shape

Significance Statement

Many adults above age 50 report difficulty understanding speech when there is background noise, which can trigger social withdrawal and negative psychosocial health outcomes. The difficulty may be related to age-related changes in how the brain processes temporal sound features. We tested younger and older people on their sensitivity to different envelope shapes, using EEG. Our results demonstrate that aging is associated with heightened sensitivity to sounds with a sharp attack and gradual decay, and sharper neural responses that deviate from the sinusoidal features of the stimulus, perhaps reflecting increased excitability in the aged auditory cortex. Altered responses to temporal sound features may be part of the reason why older adults often experience difficulty understanding speech in social situations.

Introduction

Sensitivity to temporal features of sound, such as dynamic fluctuations in the amplitude envelope, is considered critical for speech intelligibility (Drullman et al., 1994; Shannon et al., 1995). Aging is associated with a decline in processing auditory temporal features (Gordon-Salant and Fitzgibbons, 1999) and speech intelligibility, particularly in the presence of background sounds (Gordon-Salant, 2006). In addition to peripheral hearing loss (presbycusis) (Frisina and Frisina, 1997) and cognitive decline (Wayne and Johnsrude, 2015; Griffiths et al., 2020), evidence increasingly suggests that poorer speech intelligibility in older individuals may be related to changes in how cerebral cortex responds to amplitude envelopes (Millman et al., 2017; Goossens et al., 2018).

Neural activity readily synchronizes with lower-frequency (<20-Hz) sinusoidal amplitude envelopes (Aiken and Picton, 2008) in all adults, but older adults often exhibit greater synchronization than younger to such amplitude modulation (AM) rates (Goossens et al., 2016; Presacco et al., 2016a, 2016b; Herrmann et al., 2019). Enhanced AM synchronization may be disadvantageous for speech-in-noise perception (Millman et al., 2017; Goossens et al., 2018, 2019), because it may distort envelope pattern and depth cues (Moore and Glasberg, 1993; Schlittenlacher and Moore, 2016). Exaggerated AM synchronization may be related to heightened excitability of the auditory cortex in older people (Snyder and Alain, 2005; Bidelman et al., 2014; Herrmann et al., 2016; Salvi et al., 2017), perhaps resulting from reduced neural inhibition (Caspary et al., 2008).

The shape of amplitude envelopes in speech is not typically sinusoidal but varies in attack (rise) and decay (fall) (Rosen, 1992). Such envelope-shape cues are important for identifying and discriminating between consonants (e.g., /pa/ versus /ta/) (van der Horst et al., 1999). Envelope shape can also alter cochlear excitation (Carlyon, 1996) and neural synchronization patterns (Pressnitzer et al., 2000; Lu et al., 2001; Neuert et al., 2001). Inferior colliculus neurons synchronize more strongly with damped (sharp attack, gradual decay) compared to ramped (gradual attack, sharp decay) envelope shapes in aged rats, whereas the opposite occurs for young rats (Herrmann et al., 2017). Synchronization to ramped and damped envelopes may also differ between older and younger human listeners: increased synchronization to sharp attacks in sounds may explain why older individuals report difficulty suppressing distracting sounds (Parmentier and Andrés, 2009; Mishra et al., 2014), and with speech-in-noise perception when modulated background sound (containing sharp attacks) is present (Moore and Glasberg, 1993; Millman et al., 2017).

Studies in humans and animals almost exclusively focus on synchronization at the stimulation frequency (Purcell et al., 2004; Dimitrijevic et al., 2016; Henry et al., 2017; Herrmann et al., 2017, 2018). Yet, energy is also commonly observed at the harmonics (Lins et al., 1995; Zhu et al., 2013), indicating responses are not fully sinusoidal (Dallos, 1973; Mayoral et al., 2017). Analysis of non-sinusoidal response features, like the harmonics, improves classification of neural synchronization in clinical settings (Cebulla et al., 2006) and predictions about AM coding using computational modeling (Vasilkov and Verhulst, 2019; Keshishzadeh et al., 2020). Further, non-sinusoidal signal-shape features – such as sharpness – can provide important information about neural dysfunction (Cole et al., 2017). Considering neural response features other than synchronization at the stimulation frequency may provide a better understanding of age-related neural synchronization changes.

In the present study, we examine neural synchronization to stimuli with ramped and damped envelope shapes in younger and older human adults. In Part 1, we examine synchronization to either weakly or strongly ramped and damped amplitude-modulated narrowband noise stimuli in younger adults to aid stimulus selection for Part 2, which investigates changes with age. In Part 2, we examine sychronization to strongly ramped and damped narrowband noise stimuli in younger and older listeners. We use stimuli in two carrier-frequency bands (0.9-1.8 kHz, 1.8-3.6 kHz) which are within the frequency range human hearing is most sensitive, and many of the articulatory resonances that indicate speech sound identity (i.e., formants), reside. We also expand on traditional Fourier-based analyses to characterize non-sinusoidal response features.

General Methods and Materials

The current study consists of two parts. General information about methods and material are provided here. Part-specific methods and results are provided below.

Participants

Seventy-seven individuals (age-range: 18-83 years; 23 males 54 females) were recruited from the Western University Psychology subject pool and from the surrounding community of London, Ontario (Canada) via Western's neuroscience research registry (OurBrainsCAN; ourbrainscan.uwo.ca). Participants were assigned to one of three groups: one younger group listened to noises with weakly ramped/damped envelopes, while another younger and an older group listened to noises with strongly ramped/damped envelopes. All participants provided informed consent according to a protocol approved by Western's Research Ethics Board (REB #112015), and either received course credit or financial compensation of $10 CAD per hour. Data from three individuals were not analyzed due to a technical error during data recording (N=1), a neurological disorder (N=1), or hearing aid usage (N=1). The seventy-four participants included in this study (age-range: 18-83 years; 22 males 52 females) reported having no hearing loss, hearing aid usage, neurological issues, or psychiatric disorders.

Acoustic stimulation and procedure

The experiment was conducted in a single-walled sound-attenuating booth (Eckel Industries). Sounds were delivered through Sennheiser (HD 25 Light) headphones, using an RME Fireface 400 external soundcard controlled by a PC (Windows 10) and Psychtoolbox (Version 3) in MATLAB (R2017b).

Stimuli were narrowband noises generated by adding 150 randomly sampled carrier-frequency components with different onset phases from one of two possible carrier frequency bands (low: 0.9–1.8 kHz; high 1.8–3.6 kHz). Frequency bands were chosen to span the range of highest human sensitivity, and of much of the energy that contributes to discrimination of speech sounds. Narrowband noises were amplitude modulated at a rate of 4 Hz with either a ramped (gradual attack and sharp decay) or damped (sharp attack and gradual decay) envelope shape (Figure 1; Herrmann et al., 2017). Amplitude envelopes were created by varying parameters of the following equation:

$$b = t^{z-1}(1 - t) \qquad \text{Eq. 1}$$

where *t* is a time vector representing one cycle (0.250 s), *z* determines the envelope shape, and *b* is the resulting function used to modulate the narrowband noise. A *z* parameter of 2 generates a symmetrical envelope shape, while a value closer to 1 generates an envelope with a damped shape (sharp attack and gradual decay). We used a *z* parameter of 1.4491 and 1.15 (based on Herrmann et al., 2017) to generate weakly and strongly modulated envelope shapes, respectively. Weak and strong envelope shapes differ in terms of sharpness and the half-life of each damped oscillation. Strongly modulated damped envelopes have sharp onsets and a 168.4 ms half-life, while weakly modulated envelopes have more sloped onsets and a 195 ms half-life. Weakly and strongly modulated ramped envelope shapes were created by mirroring the vector *b*. Stimuli were normalized relative to peak amplitude and presented at approximately 75 dB SPL (identical for all listeners).

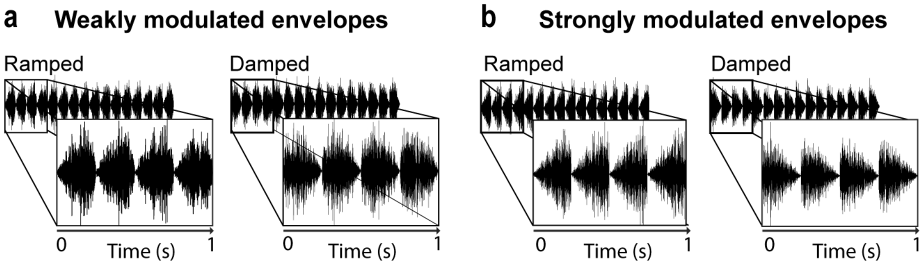

Figure 1. Samples of acoustic stimulation with different envelope shapes. Ramped shape: gradual attack and sharp decay; and damped shape: sharp attack and gradual decay. Narrowband noises were amplitude modulated at a rate of 4 Hz with either (a) weakly ramped/damped or (b) strongly ramped/damped envelopes.

During the experiment, EEG was recorded while participants passively listened to a series of the ramped and damped sounds while watching a muted captioned movie of their choice. Each stimulus had a duration of 4 s and stimuli were presented at an onset-to-onset interval of 5.021 s. Participants heard 28 ramped and 28 damped stimuli in each of the two carrier-frequency bands (low: 0.9–1.8 kHz; high: 1.8–3.6

kHz) during each of the 6 blocks, for a total of 168 trials per condition per person. In Part 1, we presented stimuli with either weak or strong envelope shapes (Figure 1a); in part 2, we only presented stimuli with strong envelope shapes (Figure 1b).

EEG recording and preprocessing

EEG was recorded from 16 active electrodes (Ag/AgCl) placed on the scalp using an electrode cap with spacing according to the 10/20 system (Biosemi ActiveTwo system). We also recorded and averaged signals from both mastoids to re-reference the data during offline analysis. During data recording, all electrodes were referenced to a feedback loop formed of two electrodes, a common mode sense (CMS) active electrode and a driven passive electrode (see www.biosemi.com/faq/cms&drl.htm). EEG was recorded at 1024 Hz to isolate primarily cortical sources during envelope tracking (online low-pass filter of 208 Hz).

All pre-processing was carried out offline using MATLAB software and the Fieldtrip toolbox (Oostenveld et al., 2011). EEG data were high-pass (0.7 Hz, 2449 points, Hann window) and low-pass filtered (30 Hz, 101 points, Hann window). The continuous EEG data were segmented into epochs ranging from -0.5 to 4 s, time-locked to the onset of each stimulus. Ocular artifacts were removed using independent components analysis (Makeig et al., 1996). Epochs in which the signal changed by more than 150 µV in any channel were rejected (average rejection rate: 5%).

EEG analysis: Cortical responses to sound onset

Single-trial time courses for each envelope shape (ramped, damped) and carrier-frequency band (low, high) were averaged separately. In order to examine the N1 onset response, a sensory-evoked response with primary sources originating in auditory cortex (Hari et al., 1982; Näätänen and Picton, 1987; Pantev et al., 1988), we averaged responses across a fronto-parietal electrode set that characterizes N1 topography (Fz, F3, F4, Cz, C3, C4) (Näätänen & Picton, 1987). N1 amplitude was calculated by finding the time point corresponding to minimum amplitude (N1 peak) with the time window (0.085 - 0.115 s), and averaging the amplitude values within a 0.03-s window centered on the N1 peak.

EEG analysis: Neural synchronization strength

In order to characterize neural synchronization to amplitude modulation in the narrowband stimuli, we calculated inter-trial phase coherence (ITPC) (Lachaux et al., 1999). For each condition, a fast Fourier transform was calculated for the 0.5 to 4 s time window of single-trial time courses (Hann window; zero-padding). The first 0.5 s were excluded from the analysis to prevent onset responses from affecting the neural-synchronization analysis. Each complex number resulting from the fast Fourier transform was divided by its absolute value and averaged across trials. ITPC values were derived by calculating the absolute value of the resulting average. ITPC can take on values between 0 and 1, with larger values indicating greater coherence. For each condition, ITPC was averaged across electrodes (Fz, F3, F4, Cz, C3, C4). Average ITPC was extracted at the amplitude modulation frequency (4 Hz; averaging window: ±0.05 Hz).

Using the fast Fourier transform on complex signals with non-sinusoidal components in the time-domain neural response yields peaks in the spectrum at the fundamental frequency as well as at harmonics (Mayoral et al., 2017). Ignoring the response to the harmonics may leave out important information, since neural synchronization to amplitude-modulated sounds is often non-sinusoidal (Dallos, 1973; Lins et al., 1995; Cebulla et al., 2006; Zhu et al., 2013). Given that responses are clearly visible in the spectrum at the harmonics of the stimulation frequency (see Figure 2) we also averaged ITPC values at the stimulation frequency (4 Hz) and harmonics up to 20 Hz (averaging window: ±0.05 Hz). By doing so, we can explore whether including non-sinusoidal response features, such as responses to the harmonics, offers additional information above and beyond what is observed at ITPC to the stimulation frequency (4 Hz).

Experimental design and statistical analysis

Statistics were conducted using a combination of IBM SPSS Statistics for Windows (v24) and MATLAB. Details of the specific variables and statistical tests for each analysis can be found in analysis subsections in Part 1 and Part 2. In general, group differences were examined either using an analysis of variance

(ANOVA) or independent-samples *t*-tests. Significant main effects and interactions were followed up using *t*-tests, with multiple comparisons corrected using the false discovery rate (FDR; Benjamini and Hochberg, 2016) correction. FDR corrected p-values are reported as p_{FDR}. Effect sizes are reported as partial eta squared (η^2_p) for ANOVAs and $r_{equivalent}$ (r_e; Rosenthal and Rubin, 2003), for *t*-tests. This experiment was not preregistered. Data are available at the project website on the Open Science Framework (OSF; https://osf.io/eq45x/).

Part 1: Contrasting responses to weakly vs. strongly modulated envelope shapes

In Part 1, we contrast neural-synchronization responses to weakly versus strongly ramped/damped amplitude envelopes in two groups of younger participants in order to inform stimulus selection for Part 2, in which we examine differences between younger and older adults in the degree of neural synchronization to sounds with different envelope shapes.

Part 1: Methods and Materials

Participants

Data from fifty younger participants are reported in Part 1. Half of the participants listened to narrowband noises with weakly ramped/damped envelope shapes (7 males and 18 females aged 18-25 years, M = 20.2 years, ± s.d. = 2.3 years), while the other half listened to noises with strongly ramped/damped envelope shapes (25 younger: 9 males and 16 females aged 18-32 years, M = 21.8 years, ± s.d. = 3.2 years). Both groups listened to narrowband noises with low (0.9-1.8kHz) and high (1.8-3.6 kHz) carrier-frequency bands.

Experimental design and statistical analysis

The dependent variables N1 amplitude and ITPC were examined using an ANOVA with envelope shape (ramped, damped) and carrier-frequency band (low, high) as within-subject factors and shape strength (weakly shaped, strongly shaped) as a between-subjects factor. Separate ANOVAs were used for ITPC at the amplitude modulation frequency (4 Hz) and for ITPC at the fundamental and harmonic series (i.e., 4, 8, 12, 16 and 20 Hz; abbreviated hereafter using 4:4:20 Hz).

Part 1: Results and Discussion

N1 amplitudes did not differ between groups presented with strong vs weak envelope shapes (effect of shape strength: $p = .431$). N1 amplitudes were larger for damped than for ramped noises (effect of envelope shape: $F_{1,48} = 11.42$, $p = .001$, $\eta^2_p = .19$, Figure 2b). For high carrier-frequency noises, N1 amplitude was larger for damped compared to ramped shapes ($t_{49} = -3.89$, $p_{FDR} = 6 \times 10^{-4}$, $r_e = 0.49$), whereas N1 amplitude for low carrier-frequency noises did not differ between damped and ramped shapes ($t_{49} = -0.54$, $p_{FDR} = .594$, $r_e = 0.08$; envelope shape x carrier frequency interaction: $F_{1,48} = 7.04$, $p = .011$, $\eta^2_p = .13$). None of the other effects or interactions were significant ($F < 3.22$, $p > .08$, $\eta^2_p < .06$).

At the 4-Hz frequency, ITPC did not differ between weak and strong envelope shapes (effect of shape strength: $p = .574$), but ITPC was larger for ramped compared to damped stimuli (effect of envelope shape: $F_{1,48} = 15.93$, $p = .001$, $\eta^2_p = .25$; Figure 2d). ITPC was also larger for high compared to low carrier-frequency stimuli ($F_{1,48} = 16.65$, $p = 1.69 \times 10^{-4}$, $\eta^2_p = .26$), and the envelope shape × carrier frequency interaction was significant ($F_{1,48} = 10.28$, $p = .002$, $\eta^2_p = .18$): the ITPC difference between ramped and damped envelopes was larger for high compared to low carrier-frequency stimuli. Other interactions were not significant ($F < 2.7$, $p > .10$, $\eta^2_p < .06$).

For ITPC at the fundamental/harmonic series (see Figure 2d), we observed larger ITPC for strong compared to weak envelope shapes (effect of shape strength: $F_{1,48} = 4.44$, $p = .04$, $\eta^2_p = .09$). None of the other effects or interactions were significant ($F < 3.7$, $p > .05$, $\eta^2_p < .1$).

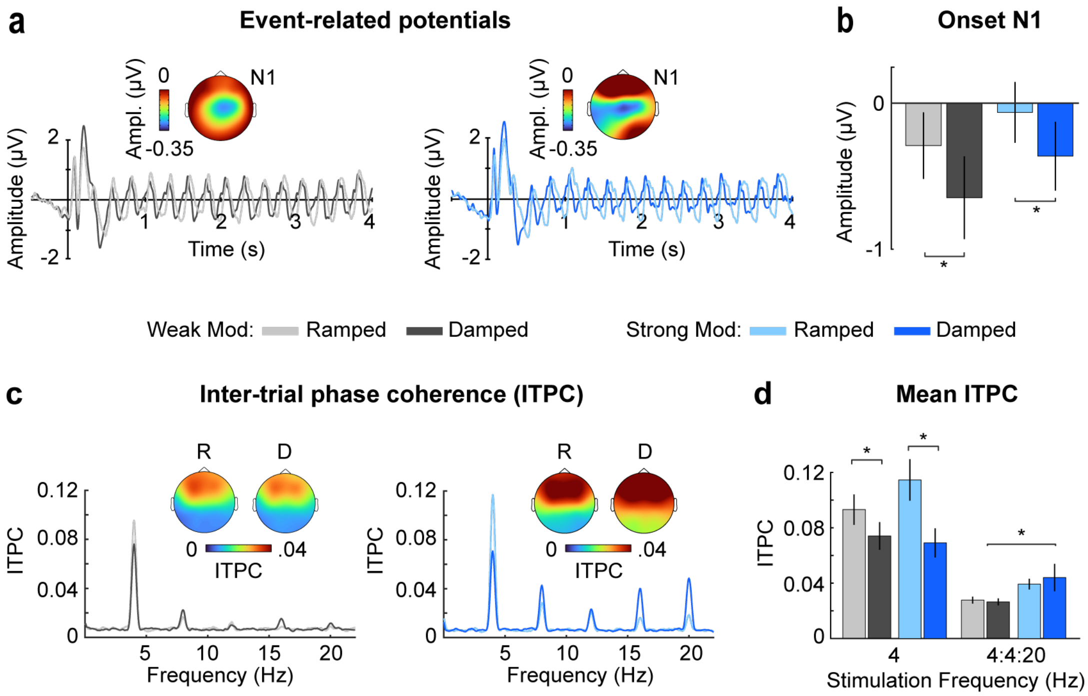

Figure 2. Results for neural responses to weakly versus strongly modulated envelope shapes. (a) Neural time courses (b) average N1 amplitudes (c) inter-trial phase coherence (ITPC), and (d) mean ITPC at the stimulation frequency (4 Hz) and at the fundamental/harmonic series (4:4:20 Hz) are each plotted as a function of shape strength (weakly shaped, strongly shaped) and envelope shape (ramped, ramped). Error bars reflect standard error. *p < 0.05.

The analyses from Part 1 indicate that synchronized neural activity was larger for strong compared to weak envelope shapes, but this effect was only observed when considering responses to the harmonic series. In Part 2, we focus on strongly shaped envelopes to investigate whether neural synchronization with ramped and damped amplitude modulations differs between age groups.

Part 2: Comparing neural responses between younger and older adults

In Part 2, we investigate whether neural synchronization to sounds with different envelope shapes differs between younger and older adults. We use traditional Fourier-based analyses for the analysis of neural synchronization and additionally develop and utilize analyses that quantify non-sinusoidal features of synchronized neural activity in younger and older adults.

Part 2: Materials and Methods

Participants

Data from forty-nine younger (25 younger: 9 males and 16 females aged 18-32 years, M = 21.8 years, ± s.d. = 3.2 years) and older individuals (24 older: 6 males and 18 females aged 50-83 years, M = 66.1 years, ± s.d. = 8.0) are reported in Part 2. Data from the younger participant group were also analyzed in Part 1.

Behavioral hearing assessment

Pure-tone thresholds were measured for all participants at octave frequencies between 0.25 and 8 kHz in the left and right ear (see Figure 3a). Pure-tone thresholds were used to calculated pure-tone averages (PTA) across octave frequencies from 0.5 to 4 kHz (averaged across ears), to characterize the presence of hearing loss in a range of frequencies relevant to the stimuli from the main portion of the experiment (see General Methods and Materials). Average PTA thresholds were submitted to an independent-samples *t*-test with age group (younger, older) as the grouping variable.

Participants also answered questions taken from the Speech, Spatial, and Qualities of Hearing Scale (Gatehouse & Noble, 2004), asking them to use using a Likert scale (0: 'not at all' to 10: 'perfectly') to rate their ability in listening situations requiring spatial hearing (N=2), speech perception in noise (N=2), and suppression of distracting background sounds (N=1). Average scores were generated for listening situation categories with multiple questions (i.e., spatial hearing, speech perception in noise). Given that SSQ scores are ordinal, not continuous, we used separate Mann-Whitney U tests (non-parametric) examine age group (younger, older) differences on each listening situation category (spatial hearing, speech perception in noise, distractor suppression).

Assessment of speech in noise perception

Participants completed the Quick Speech in Noise test (QuickSIN) (Killion et al., 2004), a clinical measure used to assess speech understanding in noise. We use this measure to assess the presence of another symptom of hearing loss: difficulty understanding speech when there is background noise. All target sentences and babble noise were taken from the QuickSIN database. During the test, a target sentence, spoken by a female talker, was presented with four-talker babble as background noise (overall 70 dB SPL). Participants were instructed to listen to each sentence and type the words that they heard. Sentences were presented in sets of 6, which began with a 25-dB signal to noise ratio (SNR) and reduced in 5 dB steps until the final sentence was completed. Participants were each asked to complete 4 sentence sets (24 total sentences) that were randomly selected from 12 possible sets. We calculated performance for each SNR separately (25, 20, 15, 10, 5, 0 dB), and report the total proportion of correct words for each SNR. Performance was at ceiling for all SNRs except 0 dB. We therefore examined age group (younger, older) differences on performance at the 0 dB SNR using an independent-samples *t*-test.

Assessment of peripheral and subcortical neural responses to sound

We recorded click-evoked auditory brainstem responses (ABR) to derive an objective physiological measure of auditory peripheral and subcortical function. Participants were asked to passively listen to a series of isochronous clicks presented monaurally to the right ear, while watching a muted captioned movie of their choice and electroencephalography (EEG) was recorded. Each click had a 0.1 ms duration (rectangular window) and was presented monaurally to the right ear with an 11.3-ms onset-to-onset interval and an approximate sound level of 88 dB SPL. A total of 4000 clicks were presented with click polarity inverted on half of the trials, resulting in an equal proportion of condensation and rarefaction clicks.

For click-evoked responses, EEG was recorded at 16.384 kHz using an identical recording montage as during cortical recordings. During offline analysis, a notch filter was first used to attenuate signal at line-noise frequencies (60 Hz and 120 Hz), and then the EEG data were high-pass (80 Hz, 2743 points, Hann window) and low-pass filtered (2000 Hz, 101 points, Hann window). Continuous data were segmented into 12-ms epochs ranging from -2 ms to 10 ms time-locked to click onset. Epochs in which signal changed by more than 25 µV during the 0–10 ms time window in any channel were rejected (average rejection rate: 16 %).

A small subset of electrodes were used for the analysis to approximate a vertical electrode montage (Cz referenced to mastoid ipsilateral to sound presentation); this subset was chosen because it is known to maximize appearance of both Wave 1 and Wave V (Picton, 2010). Peak latency was identified as the time point corresponding to maximum amplitude within a time window specific to Wave 1 (1–3 ms) and Wave V (5–7 ms). Peak amplitude was calculated by averaging the amplitude within a 0.5 ms window centered on Wave 1 or Wave V latency.

No discernible Wave I or V peak could be identified for two individuals in the younger age group, both of whom required that more than 75% trials be rejected due to excessive artifact. These individuals were excluded from ABR analysis. Wave I and V amplitudes and latencies were calculated and then analyzed for the remaining participants (24 older and 23 younger) using 4 separate independent-samples t-tests, each which had age group (younger, older) as the grouping variable.

EEG analysis: Cortical responses to sound onset

We used onset N1 amplitude as a metric of neural responsiveness to sound (see General Methods and Materials). N1 amplitudes were submitted to an ANOVA with envelope shape (ramped, damped) and carrier frequency (low, high) as within-subject factors and age group (younger, older) as a between-subjects factor.

EEG analysis: Neural synchronization strength

To examine whether neural synchronization strength differed between age groups, ITPC at the amplitude-modulation frequency (4 Hz) and for the 4-Hz fundamental/harmonic series (4:4:20 Hz) (see General Methods and Materials) were submitted to separate ANOVAs, each with envelope shape (ramped, damped) and carrier frequency (low, high) as within-subject factors and age group (younger, older) as a between-subjects factor.

EEG analysis: Time-course correlation similarity

In order to better understand whether, and to what extent, cortical time courses differ between age groups, we quantified the degree of similarity between the neural time courses. After excluding the first 0.5 s (onset response range), we averaged responses across electrodes (Fz, F3, F4, Cz, C3, C4) and the two carrier-frequency band conditions (because no relevant differences were observed), resulting in one averaged time course for each envelope shape (ramped, damped) condition and participant. Correlations between the averaged time courses were calculated, separately for ramped and damped stimuli, such that each participant's time course was correlated with the time course of each participant within their 'own' age group and with the time course of each participant from the 'other' age group. For each participant, the set of r values resulting from the correlations with time courses from other participants were averaged to obtain one mean correlation for each condition, group (own vs. other), and age group (younger vs. older). Larger own-group *r* values would indicate an individual's response time course was highly synchronous with others in their own age group, while larger other-group *r* values would indicate an individual's response time course was more synchronous with individuals in the other age group.

To quantify the degree of similarity between the neural time courses for younger and older adults, we compared average *r* values using an ANOVA with envelope shape (ramped, damped) and correlation type (own-group *r*, other-group *r*) as within-subjects factors and age group (younger, older) as the between-subjects factor.

EEG analysis: Quantification of non-sinusoidal response patterns and signal shape

The EEG analysis of time-course correlation similarity can reveal whether time courses differ between age groups, but the analysis cannot reveal the underlying source of any difference. A growing body of evidence suggests that the non-sinusoidal activity features can provide important information about neural dysfunction (Sherman et al., 2016; Cole and Voytek, 2017; Cole et al., 2017). We therefore investigated the degree to which synchronized neural responses diverge from a sinusoidal shape in three unique ways.

First, we investigated the harmonic structure of the ITPC frequency spectrum. High amplitude at the harmonics of the fundamental frequency would indicate that responses are less sinusoidal (Dallos, 1973; Mayoral et al., 2017). To approximate this, we extracted ITPC at the 4 Hz fundamental frequency (4 Hz, averaging window: ±0.05 Hz), and at the frequency of the first harmonic (8 Hz, averaging window: ±0.05 Hz) for each condition, and calculated the ratio between the two according to the following equation:

$$Q = \log_{10}(\mathrm{F}_0/\mathrm{F}_1) \qquad \text{Eq. 2}$$

where F_0 and F_1 refer to mean ITPC for 4 and 8 Hz, respectively. We limited our calculation to F_0 and F_1 for simplicity. Larger Q values indicate a more sinusoidal synchronization response, whereas smaller Q values indicate a more non-sinusoidal synchronization response. Q was submitted to an ANOVA with envelope shape (ramped, damped) and carrier frequency (0.9–1.8 kHz, 1.8–3.6 kHz) as within-subjects factors and age group (younger, older) as the between-subjects factor.

Another way to quantify non-sinusoidal response patterns is to examine the degree to which the response diverges from a cosine function. For this analysis, amplitude values of trial-averaged time courses (averaged across electrodes: Fz, F3, F4, Cz, C3, C4) were related to the 4-Hz stimulus phase. That is, the time-course amplitude data were binned according to phase values assuming a 4-Hz sinusoid (number of bins: 100; window width: 0.063 radians), such that signal amplitude was represented as a function of phase (Figure 6b). A cosine function was fit to the binned amplitude data according to the following equation:

$$y = a * \left(\frac{\cos(\mathrm{x+p})}{2} + 0.5\right) + b \qquad \text{Eq. 3}$$

where y is the vector of binned amplitudes as a function of phase, a is the parameter for amplitude, x is the starting phase value, p is a vector of the 100 linearly spaced phase values relating to amplitude values in y, and b is the intercept. The goodness of fit was calculated as the root-mean-square error (RSME) between the binned amplitude data and the predicted values from the cosine fit, separately for each condition and participant. A larger goodness-of-fit value indicates synchronized activity was less sinusoidal. RSME values were analyzed in an ANOVA with identical factors to the analysis of *Q* (i.e., envelope shape, carrier frequency, and age group).

In order to quantify non-sinusoidal signal shape features, we fit an *exponential* cosine function to the amplitude data:

$$y = a * \left(\frac{\cos(x+p)}{2} + 0.5\right)^{e} + b \qquad \text{Eq. 4}$$

Equation 4 only differs from Equation 3 only in the exponent parameter *e*, which determines the sharpness of the function (see Figure 7 top left panel). An exponent of 1 reflects a sinusoid, identical to Equation 3. An exponent larger than 1 means the signal is non-sinusoidal, and the function increases in sharpness with increasing exponent. Here, we analyzed two parameters from each fit, amplitude and exponent (sharpness), to directly quantify whether neural responses are hyper-responsive (amplitude) or contain non-sinusoidal response features (exponent) (note that *b* – the intercept – is not meaningful here as it is close to zero due to the high-pass filter). The estimated amplitude *a* and the estimated exponent *e* were submitted to an ANOVA with envelope shape (ramped, damped) and carrier frequency (low, high) as within-subjects factors and age group (younger, older) as the between-subjects factor. The absolute value of the fitted amplitude *a* was calculated prior to the ANOVA, because the inclusion of *e* in the formula sometimes led to a sign inversion of *a*.

Part 2: Results and Discussion

Younger and older listeners differ in behavioral hearing assessment, but not in subcortical responses

Pure-tone thresholds for octave frequencies between 0.25 and 8 kHz (averaged across ears) are plotted in Figure 3a. All participants had pure-tone average (PTA) thresholds (0.5 to 4 kHz averaged across ears) less than or equal to 31 dB HL. Older adults had elevated PTA thresholds relative to younger participants (+10.93 dB HL; $t_{47} = -6.96$, $p = 9.56 \times 10^{-9}$, $r_e = 0.71$), had lower self-reported ratings for spatial hearing

(U = 183.5, $p = .018$), sound distractor suppression (U = 154, $p = .003$), and understanding speech in the presence of background noise (U = 154.5, $p = .003$) (Gatehouse and Noble, 2004).

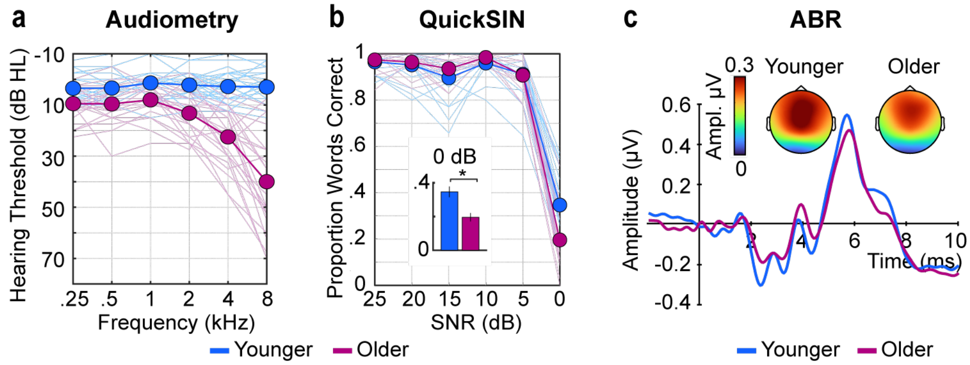

Figure 3. **Hearing assessment measures.** (a) Audiometric thresholds (b) QuickSIN performance, and (c) auditory brainstem responses (ABR) are plotted for each age group (younger, older). Topographies reflect the mean Wave V response. Thin lines in (a) and (b) reflect individual participants. Thick lines reflect the average across participants. Error bars reflect standard error. *p < 0.05

Older and younger adults performed at ceiling on the QuickSIN except for the most difficult SNR level (0 dB). At 0 dB, both groups exhibited proportions of correctly reported words that were significantly lower than 1 (younger: M = 0.34, s.e. = 0.03, 95% CI [0.28 0.40]; older: M = 0.20, s.e. = 0.02, 95% CI [0.15 0.24], and proportions were lower for older compared to younger adults (0 dB, $t_{47} = 3.66$, $p = .001$, $r_e = 0.47$; Figure 3b). Despite these age-group differences in behavioral assessment metrics, at the neural level, there was no group difference in wave I or wave V amplitude (Wave I: $p = .823$; Wave V: $p = .295$) or latency (Wave I: $p = .105$; Wave V: $p = .574$) in response to click stimulation (11.3 Hz, 88 dB SPL) (Figure 3c). To examine whether hearing loss, instead of age, was associated with a reduction in subcortical function, we calculated the partial correlation (controlling for age) between average PTA thresholds and the ratio between Wave V and I amplitude (Wave V/I ratio), but did not find a significant relationship ($r_{44} = -.1$, $p = .51$). These findings suggest comparable auditory nerve and subcortical function across age groups.

Aged auditory cortex is hyper-responsive to sound

Aging and hearing loss are associated with maladaptive cortical plasticity that leads to greater responsivity to stimulation by neural populations in auditory cortex (Snyder and Alain, 2005; Alain et al., 2014; Auerbach et al., 2014; Herrmann et al., 2016, 2017, 2018; Henry et al., 2017; Salvi et al., 2017; Herrmann and Butler, 2020). Hyper-responsiveness may be an index of reduced inhibition in cortical circuits (Caspary et al., 2008; Knipper et al., 2013; Ng and Recanzone, 2018). In order to test whether the cortex in the sample of older adults tested here is hyper-responsive, we compared neural responses elicited by sound onset between age groups (Figure 4a).

N1 amplitudes were larger for older compared to younger adults (effect of age group: $F_{1,47} = 20.68$, $p = 3.8 \times 10^{-5}$, $\eta^2_p = .31$; see Figure 4b), indicating hyper-responsiveness to sound. Stimuli with damped envelope shapes also elicited larger N1 amplitudes compared to noises with ramped envelope shapes (effect of envelope shape: $F_{1,47} = 5.36$, $p = .025$, $\eta^2_p = .10$). This is consistent with previous research showing that N1 amplitude is larger when the stimulus rise time is fast (Picton, 2008), probably because sharp onsets drive more synchronous activity than slower onsets. None of the other effects or interactions were significant ($F < 3.8$, $p > .05$, $\eta^2_p < .1$).

Neural synchronization for different envelope shapes differs between younger and older adults

We quantified how envelope shape affects neural synchronization (ITPC) in older and younger adults (Figure 4c). For ITPC at the 4-Hz stimulation frequency, there was no effect of age group ($F_{1,47} = 3.45$, $p = .07$, $\eta^2_p = .07$) nor envelope shape ($p = .611$), but the age group × envelope shape interaction was significant ($F_{1,47} = 17.82$, $p = 1.10 \times 10^{-4}$, $\eta^2_p = .28$). Younger adults showed increased ITPC for sounds with ramped compared to damped envelope shapes ($t_{24} = -3.27$, $p_{FDR} = .006$, $r_e = 0.56$), whereas older adults showed the reverse pattern ($t_{23} = 2.69$, $p_{FDR} = .013$, $r_e = 0.49$; see Figure 4d). ITPC was also larger for sounds with high compared to low carrier-frequency bands for younger adults ($t_{24} = -2.60$, $p_{FDR} = .032$, $r_e = 0.47$), but there was no difference for older adults ($p_{FDR} = .498$; age group × carrier frequency interaction:

$F_{1,47} = 6.08$, $p = .017$, $\eta^2_p = .12$). There was a significant interaction between envelope shape and carrier frequency ($F_{1,47} = 8.19$, $p = .006$, $\eta^2_p = .15$), but follow-up comparisons did not reveal any significant differences between ramped and damped low-carrier-frequency sounds ($p_{FDR} = .446$) or ramped and damped high-carrier-frequency sounds ($p_{FDR} = .225$). None of the other effects were significant ($F < 2.67$, $p > .11$, $\eta^2_p < .05$).

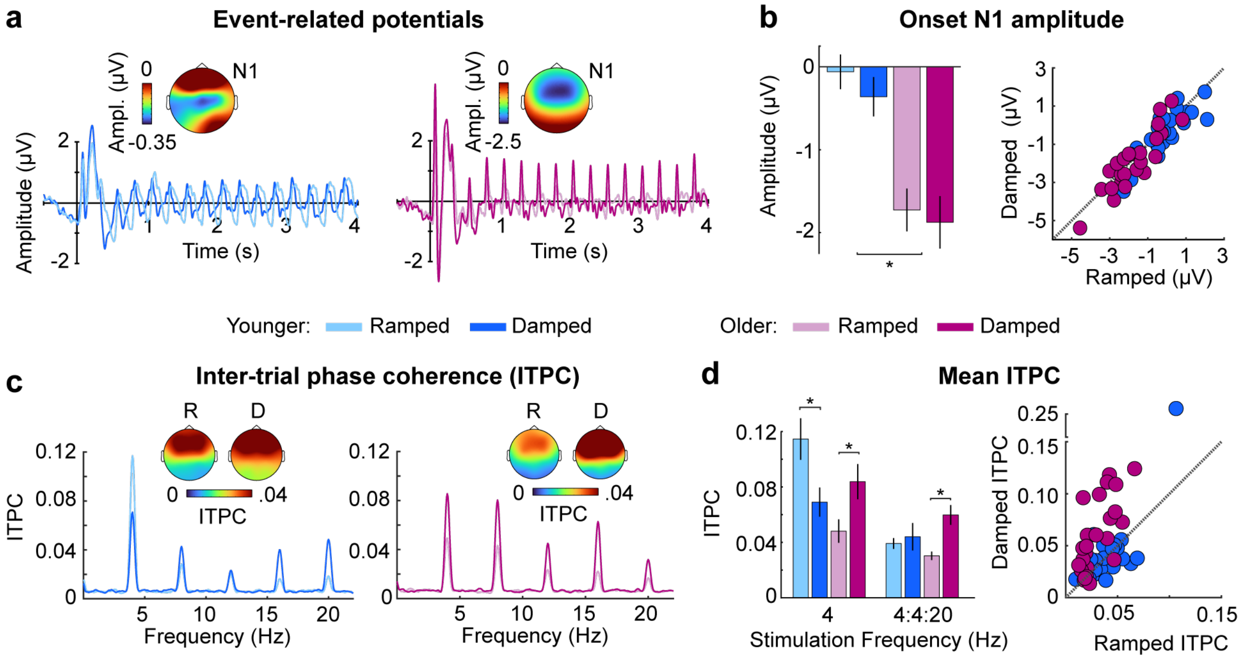

Figure 4. Neural responses to amplitude-modulated noises with different envelope shapes for younger and older adults. (a) Neural time courses (b) N1 amplitude (c) inter-trial phase coherence (ITPC), and (d) mean ITPC at the stimulation frequency (4 Hz) and at the 4-Hz fundamental/harmonic series (4:4:20 Hz) are plotted for each age group (younger, older) and envelope shape (ramped, ramped). Topographies in (a) reflect mean N1 amplitude (averaged across envelope shapes) for each age group (younger, older). Topographies in (c) reflect mean ITPC at the stimulation frequency and are shown for each envelope shape (ramped, damped) and age group (younger, older). Error bars reflect standard error. *$p < 0.05$.

ITPC for the fundamental/harmonic series (Figure 4c) did not differ between age groups ($p = .678$), but ITPC was larger for damped compared to ramped envelope shapes (effect of envelope shape: $F_{1,47} = 13.55$, $p = .001$, $\eta^2_p = .22$). Critically, the envelope shape × age group interaction was significant ($F_{1,47} = 7.01$, $p = .011$, $\eta^2_p = .13$; Figure 4d): neural synchronization was larger for damped compared to ramped envelope shapes for older adults ($t_{23} = 5.35$, $p_{FDR} = 3.9 \times 10^{-5}$, $r_e = 0.74$), but did not differ between envelope shapes for younger participants (p_{FDR} = .524). There was also an interaction between age group and carrier frequency ($F_{1,47} = 6.02$, $p = .018$, $\eta^2_p = .11$). This was driven by reduced synchronization for sounds with a high compared to a low carrier frequency band in older participants ($t_{23} = 3.17$, $p_{FDR} = .046$, $r_e = 0.55$), and a non-significant trend towards the opposite pattern in younger participants (p_{FDR} = .269). None of the other effects were significant ($F < 1.06$, $p > .31$, $\eta^2_p < .02$).

Neural time courses differ between younger and older adults

Analyses in the previous section focused on synchronization strength. Quantification of the degree of similarity between neural-response time courses for adults of different ages may also reveal differences between older and younger adults. To this end, we calculated correlations between individual participants' response time courses within and across age groups, separately for stimuli with ramped (Figure 5a top panel) and damped envelope shapes (Figure 5a bottom panel).

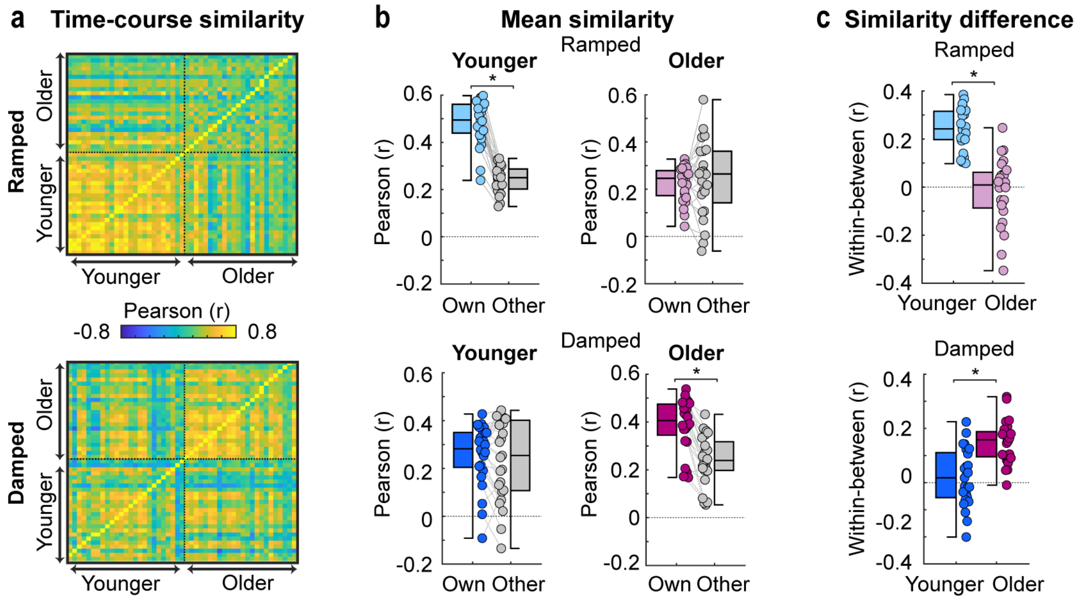

Figure 5. Results from the time-course correlation analysis. (a) Time-course similarity values (r) are plotted for ramped (top panel) and damped sounds (bottom panel). Each row contains *r* values representing an individual's correlation between their own time course and the time course of every other individual in their own age group and other age group. (b) Mean similarity scores for ramped (top panels) and damped (bottom panels) are plotted for younger (left panels) and older subjects (right panels). Similarity scores are *r* values averaged based on group identity (own-group *r*, other-group *r*). (c) The difference in mean correlation (own-group *r* minus other group *r*) for each individual are plotted for

ramped (top panels) and damped (bottom panels) and for younger and older subjects. Colored dots represent individual data points. Error bars reflect standard error. *p < 0.05.

Participants had larger own-group *r* compared to other-group *r* scores (effect of correlation type: $F_{1,47} = 80.88$, $p = 8.8 \times 10^{-12}$, $\eta^2_p = .63$), suggesting participants' time courses were more similar to others in their own age group. However, a significant correlation type x age group interaction ($F_{1,47} = 9.05$, $p =$ 004, $\eta^2_p = .16$), showed the difference between own-group and other group *r* was larger for younger compared to older subjects. Similarity scores (*r*) did not differ as a function of envelope shape ($p = .336$), but a significant envelope shape x age group interaction ($F_{1,47} = 30.59$, $p = 1.4 \times 10^{-6}$, $\eta^2_p = .39$), showed that younger subjects had larger similarity scores for ramped compared to damped ($t_{24} = 4.24$, $p_{FDR} = 6 \times 10^{-4}$, $r_e = .65$), while older subjects showed the reverse pattern ($t_{24} = -3.59$, $p_{FDR} = .002$, $r_e = .65$). Finally, there was a significant envelope shape x correlation type x age group interaction ($F_{1,47} = 90.1$, $p = 1.7 \times 10^{-12}$, $\eta^2_p = .66$).

Follow up *t*-tests indicated the 3-way interaction was driven by the following effects: for ramped-envelope stimuli, younger participants had larger own-group *r* compared to other-group *r* suggesting neural-response time courses of younger participants to ramped envelopes were correlated more strongly among their peers than with time courses from older adults ($t_{24} = 14.34$, $p = 2.9 \times 10^{-13}$, $r_e = 0.95$; Figure 5b, top left panel). Older participants showed no difference between own-group and other-group *r* for ramped envelope stimuli ($p = .527$; Figure 5b, top right panel). For damped-envelope stimuli, older adults had larger own-group *r* compared to other-group *r*, ($t_{23} = 9.20$, $p = 3.6 \times 10^{-9}$, $r_e = 0.89$; Figure 5b, bottom right panel). Younger participants showed no difference between own- and other-group *r* for damped envelope shapes ($p = .369$; Figure 5b, bottom left panel). Together, these analyses show that younger participants exhibit more synchronous neural responses when listening to *ramped envelopes* (slow onset and rapid offset) while older participants produce more synchronous neural responses when listening to *damped envelopes* (rapid onset and slow offset).

Neural synchronization is less sinusoidal in older compared to younger adults

Non-sinusoidal features, including waveform shape, cannot be well-characterized by traditional Fourier analysis. To fully characterize distinct signal features between groups, we developed a measure (*Q*) that indexes how sinusoidal (spectral peak mainly at F_0) or non-sinusoidal (spectral peaks at F_0 and F_1) the response is. *Q* was smaller, indicating a less sinusoidal response, in older compared to younger participants (effect of age group: $F_{1,47} = 8.16$, $p = .006$, $\eta^2_p = .15$) and was smaller (less sinusoidal response) for damped compared to ramped envelope shapes (effect of envelope shape: $F_{1,47} = 10.27$, $p = .002$, $\eta^2_p = .18$). An interaction between age group and envelope shape ($F_{1,47} = 5.39$, $p = .025$, $\eta^2_p = .10$) was due to younger participants having smaller *Q* for damped compared to ramped stimuli ($t_{24} = -4.24$, $p = 6 \times 10^{-4}$, $r^e = 0.65$), whereas Q was small for both damped and ramped stimuli in older individuals, with no reliable difference ($t_{23} = -0.58$, $p = .568$, $r_e = 0.12$). The synchronized response was therefore less sinusoidal for sounds with damped compared to ramped envelopes in younger adults, and non-sinusoidal for both envelope shapes in older adults (Figure 6a). Finally, there was an effect of carrier-frequency band: *Q* was smaller (less sinusoidal response) for sounds with a low compared to a high carrier-frequency band ($F_{1,47} = 11.31$, $p = .002$, $\eta^2_p = .19$). None of the other interactions were significant ($F < 2.5$, $p > .12$, $\eta^2_p < .05$).

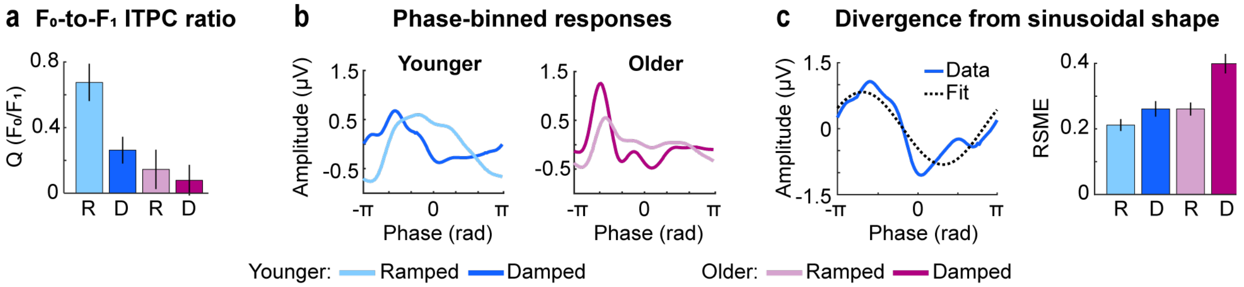

Figure 6. Results of testing the degree of sinusoidal shape of neural responses. (a) The average ratio for synchronization to the stimulation frequency (F_0) and first harmonic (F_1) (*Q*) is plotted for each group (younger, older) and envelope shape (ramped, damped). **(b)** Mean phase-binned amplitude values are plotted as a function of phase angle (radians) for younger (left panel) and older participants (right panel) and ramped and damped envelopes shapes. **(c)** A phase-binned amplitude exemplar (labelled: Data) is shown along with an example of a cosine fit to these data (labelled: Fit) in the left panel, and average root mean square error (RSME; indicates the goodness of fit) are plotted for each age group (younger, older) and envelope shape (ramped, damped). Error bars reflect standard error. $*p < 0.05$.

Using a second approach, we quantified the degree to which neural responses diverge from a sinusoidal pattern by binning the amplitude data according to phase values of a 4-Hz sinusoid (Figure 6b), and then fit a cosine function to the binned amplitude data (Figure 6c; left panel). The root-mean-square error (RSME), quantifying the goodness of fit, was larger (and the response thus less sinusoidal) for older compared to younger participants ($F_{1,47}$ = 10.19, p = .003, η^2_p = .18). The RSME was also larger (less sinusoidal response) for damped compared to ramped envelope shapes (effect of envelope shape: $F_{1,47}$ = 43.33, p = 3.5 × 10-8, η^2_p = .48) and larger (less sinusoidal response) for sounds with a low compared to a high carrier-frequency band (effect of carrier-frequency band: $F_{1,47}$ = 6.64, p = .013, η^2_p = .12). Thus, the results to this point are consistent with the analysis of Q. The age group × envelope shape interaction was significant ($F_{1,47}$ = 9.71, p = .003, η^2_p = .17): although RSME was higher for damped compared to ramped envelope shapes in both age groups (younger: t_{24} = 2.91, p_{FDR} = .008, r_e = 0.51; older: t_{23} = 5.98, p_{FDR} = 1.3 × 10^{-5}, r_e = 0.78), this difference was larger in older compared to younger adults (Figure 6c right panel). None of the other interactions were significant (F < 2.8, p > .09, η^2_p < .06). This analysis provides converging evidence that the response to a 4-Hz modulated sound is less sinusoidal in older compared to younger listeners, particularly when those sounds have a rapid onset and slow offset (damped envelope), similar to many speech sounds, such as consonants.

Neural synchronization reflects sharper responses in older compared to younger adults

Analyses in the previous section focused on characterizing whether neural signals diverged from a sinusoidal pattern. Analyzing specific aspects of the neural *signal shape* – such as sharpness – can provide important information about neural dysfunction (Cole et al., 2017). In order to capture differences in neural signal shape between age-groups, we fit an exponential cosine function to the binned amplitude data for each condition and participant (Figure 7 top left panel). We analyzed the estimated amplitude (a), and sharpness (exponent e) coefficients, with three-factor ANOVAs (envelope shape; carrier-frequency band; age group). The analysis of amplitude (indicating hyper-responsiveness) paralleled our ITPC findings

(Figure 4d): there was no age group difference (p = .508) but amplitude was larger for damped compared to ramped envelope shapes (effect of envelope shape: $F_{1,47}$ = 4.41, p = .041, η^2_p = .09; Figure 7 middle panel). The interaction between age group and envelope shape was significant ($F_{1,47}$ = 20.90, $p = 3.5 \times 10^{-5}$, η^2_p = .31), revealing larger amplitudes for damped compared to ramped envelope shapes for older individuals (t_{23} = 4.48, $p_{FDR} = 3 \times 10^{-4}$, r_e = 0.68), whereas a non-significant pattern in the opposite direction was observed for younger adults (t_{24} = -1.84, p_{FDR} = .077, r_e = 0.35). There was also an interaction between age group and carrier-frequency band ($F_{1,47}$ = 12.86, p = .001, η^2_p = .22), which indicated that responses in younger participants were larger for high compared to low carrier-frequency sounds (t_{24} = 2.11, p_{FDR} = .046, r_e = 0.40), whereas the reverse pattern was observed for older individuals (t_{23} = -3.11, p_{FDR} = .01, r_e = 0.54). None of the other interactions were significant (F < 2.8, p > .1, η^2_p < .06).

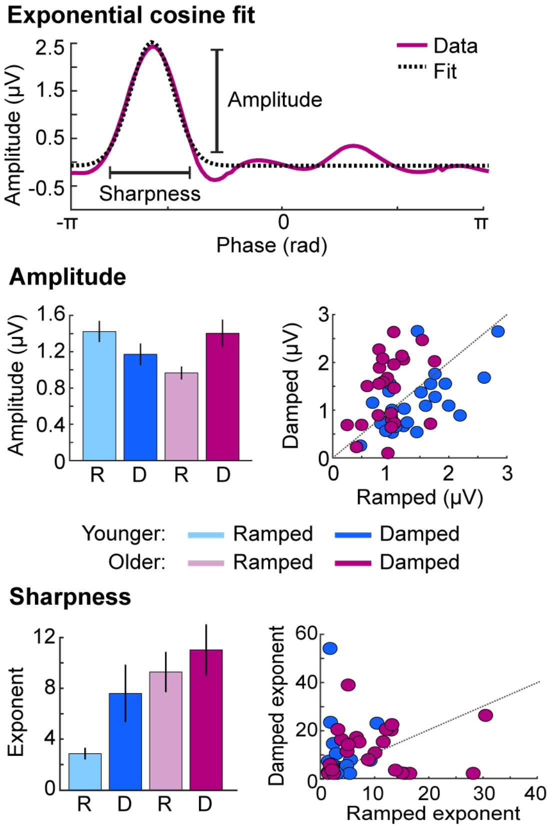

Figure 7. Exponential cosine fit: A phase binned amplitude exemplar (Data) is shown along with an example of a cosine fit to these data (Fit). **Amplitude**: mean amplitude values are plotted as a function of age group (younger, older) and envelope shape (ramped, damped) in the left panel. Individual data points are shown on the right panel with a 45-degree reference line. **Exponent**: mean exponent values are plotted as a function of age group (younger, older) and envelope shape (ramped, damped) in the left panel. Individual data points are shown on the right panel with a 45-degree reference line. Error bars reflect standard error. *p < 0.05.

The exponent (indicating the response sharpness) was larger for older compared to younger adults (effect of age group: $F_{1,47} = 25.95$, $p = 6 \times 10^{-6}$, $\eta^2_p = .36$), and larger for damped compared to ramped envelopes (effect of envelope shape: $F_{1,47} = 12.71$, $p = .001$, $\eta^2_p = .21$; Figure 7 bottom panel). No remaining effects or interactions were significant ($F < 2.8$, $p > .15$, $\eta^2_p < .04$). These results indicate that responses were sharper in older compared to younger adults, and for damped compared to ramped envelope shapes.

In sum, signal-shape analyses indicate that in older adults, responses were larger for envelopes with rapid onsets (and slow offsets) than for those with slow onsets (and rapid offsets), whereas younger adults showed the reverse pattern. Synchronized neural activity was less sinusoidal, as well as sharper, in older participants compared to younger participants.

Relating neural sensitivity to different envelope shapes with measures of hearing loss

In an effort to quantify how neural sensitivity to different envelope shapes may be related to our measures of hearing loss, we calculated partial correlations (controlling for age) between PTA and the following neural measures: the difference in synchronization to damped versus ramped envelopes (4:4:20 Hz ITPC; averaged across carrier frequencies; $r_{46} = -.09$, $p_{FDR} = .556$), the difference between damped and ramped Q scores (averaged across carrier frequencies; $r_{46} = -.06$, $p_{FDR} = .679$), the difference between damped and ramped RSME values (averaged across carrier frequencies; $r_{46} = -.12$, $p_{FDR} = .849$), overall signal sharpness (averaged across envelope shapes and carrier frequencies; $r_{46} = -0.02$, $p_{FDR} = .918$), and overall signal amplitude a (averaged across envelope shapes and carrier frequencies; $r_{44} = -.23$, $p_{FDR} = .117$), but did not find any significant relationships. We also made a similar comparison between QuickSIN performance (0 SNR) and the same neural measures: the difference in synchronization to damped versus ramped envelopes (4:4:20 Hz synchronization: $r_{46} = -.09$, $p_{FDR} = .67$), the difference between damped and ramped Q scores (averaged across carrier frequencies; $r_{46} = -.13$, $p_{FDR} = .607$), the difference between damped and ramped RSME values (averaged across carrier frequencies; $r_{46} = .14$, $p_{FDR} = .607$),overall signal sharpness ($r_{46} =$

.02, p_{FDR} = .916), and overall signal amplitude *a* (r_{46} = -.19, p_{FDR} = .607, and, but no effects reached significance.

General Discussion

In the present study, we examined neural sensitivity to sound envelopes with a ramped (gradual attack and sharp decay) or damped (sharp attack and gradual decay) envelope shape in younger and older adults. The results of Part 1 indicated a more marked effect of asymmetry for strong, compared to weak, envelope shapes in N1 and ITPC measures. Strong ramped/damped envelope shapes were therefore chosen to investigate age differences in the second part of the study.

The three main findings of Part 2 are: (1) Auditory cortex of older adults is hyper-responsive to sound compared to younger adults despite similar subcortical responses in both groups; (2) Neural activity in older adults synchronizes more strongly with rapid-onset, slow-offset (damped) envelopes, whereas in younger adults it synchronizes more strongly with slow-onset, rapid-offset (ramped) envelopes; (3) Synchronized neural activity is less sinusoidal and sharper – appearing more burst-like – in older compared to younger people, particularly for rapid-onset, slow offset sounds. Our results demonstrate that older adults' sensitivity to the amplitude envelope of sounds differs fundamentally from that of younger adults.

Auditory cortex of older adults is hyper-responsive to sound

Cortical responses to sound onset were larger in older compare to younger adults (Figure 4b). We observed this hyper-responsiveness despite higher pure-tone thresholds (lower sensitivity) in older individuals (Figure 3a) and no difference in subcortical responses between age groups (Figure 3c). Our results are consistent with a growing literature showing hyper-responsiveness to sound in the cortex of older compared to younger rats (Hughes et al., 2010) and humans (Amenedo and Díaz, 1999; Harkrider et al., 2005; Snyder and Alain, 2005; Sörös et al., 2009; Ross and Tremblay, 2009; Lister et al., 2011; Alain et al., 2012; Herrmann et al., 2016, 2018; Henry et al., 2017; Herrmann and Butler, 2020), as well as in rats following noise exposure (Popelář et al., 1987; Syka et al., 1994; Manzoor et al., 2012) and adult humans with hearing loss compared to those without (Tremblay et al., 2003; Alain et al., 2014; Millman et al., 2017).

Hyper-responsiveness is thought to arise from damage to the auditory periphery, such that deprivation of inputs from peripheral structures to brain regions downstream leads to reduced neural inhibition and increased excitation throughout the auditory pathway (Caspary et al., 2008; Auerbach et al., 2014; Salvi et al., 2017). Consistent with the current results, studies comparing noise-exposed to control animals have repeatedly shown that hyper-responsiveness manifests most strongly in auditory cortical structures of the auditory pathway (Auerbach et al., 2014; Chambers et al., 2016; Asokan et al., 2018). In fact, hyper-responsiveness in auditory cortex has been taken as an index of a loss of inhibition (Ng and Recanzone, 2018). The enhanced responses in older compared to younger adults could also be a result of reduced response variability (Garrett et al., 2010, 2011), since more consistent single-trial responses would result in a larger response magnitude in the average. Critically, decreased response variability would likely be secondary to a loss of neural inhibition.

Neural synchronization patterns differ between younger and older adults

Previous work has demonstrated larger synchronization strength at the stimulation frequency for older compared to younger adults (Goossens et al., 2016, 2018, 2019; Presacco et al., 2016b, 2016a). We did not observe overall increased synchronization at the stimulation frequency, or when we additionally considered the energy at harmonic frequencies (4:4:20 Hz), in older compared to younger subjects. Sound intensity has been shown to affect the magnitude of synchronized response to AM (Picton et al., 2003). Many studies control for audibility between normal-hearing and hearing-impaired participants by increasing the sound level for those with hearing impairment (Millman et al., 2017; Goossens et al., 2018, 2019). In some cases, a larger synchronization response in older compared to younger individuals is not observed if sounds are presented at the same level in both groups (Goossens et al., 2019), possibly due to reduced sensitivity in the older group trading off against increased responsivity. Here we used a sound level of ~75 dB SPL throughout for both age groups, and observed that older adults were hyper-responsive to sound onset, but did not show increased synchronization with the AM stimulus, compared to younger listeners.

Compatible with previous findings in spiking activity of the inferior colliculus of rats (Herrmann et al., 2017), older adults showed increased synchronization strength for damped compared to ramped envelopes, while younger adults showed the opposite pattern (Figure 4c-d). Taking these synchronization patterns as an index of an individual's sensitivity to the envelope shape, the sizable response to damped compared to ramped envelopes across all harmonics suggests the older participants have hyper-sensitivity to sounds with sharp onsets. Further, we generally observed all effects across both carrier frequency ranges, without consistent interactions between age group and carrier-frequency band. The age-linked changes in envelope sensitivity that we observe appear to generalize across the range of frequencies tested here, which covers much of the range to which humans are most sensitive, and in which many of the spectrotemporal features used to discriminate speech sounds are found.

By correlating each individual's neural time course with that of other participants, we were able to derive a metric of neural response similarity for ramped and damped sounds across participants. This analysis is conceptually similar to calculating inter-subject correlation (Hasson et al., 2008; Cohen and Parra, 2016), as it represents a measure of global synchrony with other participants. Time courses were more similar between individuals from the same age group than for individuals from different age groups, but this was only observed when participants listened to the envelope shape for which each age group showed heightened ITPC sensitivity. In younger individuals, neural-activity time courses were more synchronous with other younger participants than with older ones when listening to stimuli with a ramped envelope shape (Figure 5c). In contrast, older individuals exhibited neural-activity time courses for damped envelopes that were more synchronous with other older participants than with those of younger ones. Thus, older and younger subjects preferentially synchronize to specific envelopes shapes, and this effect is highly consistent across subjects.

The shape of synchronized neural activity differs fundamentally between age groups

Typically, neural synchronization with amplitude modulation focuses on the response at the stimulation frequency only (sinusoidal component) (Purcell et al., 2004; Zhu et al., 2013; Bharadwaj et al., 2015; Dimitrijevic et al., 2016; Henry et al., 2017; Herrmann et al., 2017, 2019), although synchronization patterns commonly include non-sinusoidal response features, such as responses to the harmonics (Dallos, 1973; Lins et al., 1995; Cebulla et al., 2006; Zhu et al., 2013). Further, there is evidence that analyzing non-sinusoidal signal shape features – such as sharpness – can provide important physiological information about neural signaling and system dysfunction (Cole et al., 2017). We first analyzed the extent to which neural responses consisted of primarily sinusoidal or non-sinusoidal response patterns by studying the ratio of responses at the fundamental to first harmonic (Q), and the magnitude of the residuals from a cosine function fit (RSME). This showed that neural responses were overall less sinusoidal for damped envelopes compared to ramped, and for older compared to younger adults.

We also analyzed specific features of the neural signal shape and showed both ramped and damped envelopes elicited sharper neural responses in older compared to younger adults (Figure 7). Sharp response features of neural activity indicates the response is likely driven by short synchronous bursts of activity: the same neural responses spread out in time would create a smoother more sinusoidal signal shape (Sherman et al., 2016; Cole and Voytek, 2017). These findings build on previous literature (Herrmann et al., 2017) and suggest that how the auditory system responds to amplitude envelopes in sounds is fundamentally changed in older individuals, such that responses are more synchronous, appearing burst-like. Given the importance of preserved envelope-shape cues for speech intelligibility (Drullman et al., 1994; Shannon et al., 1995), these changes may be related to the hearing difficulties older adults experience, such as comprehending speech in noise (Gordon-Salant and Fitzgibbons, 1999; Gordon-Salant, 2006) and finding sounds overly distracting (Parmentier and Andrés, 2009; Mishra et al., 2014).

Conclusions

We examined how different envelope shapes (damped, ramped) affect neural synchronization in younger and older human adults. Older participants demonstrated neural hyper-responsiveness to sound onsets, despite showing no major differences in subcortical and peripheral assessments. Older participants also showed increased sensitivity to noises with damped compared to ramped envelope shapes, whereas the opposite pattern was observed in younger adults. Furthermore, synchronized neural activity appeared less sinusoidal and more burst-like, in older compared to younger people. Our findings underscore the importance of characterizing sinusoidal and non-sinusoidal features of synchronized neural responses to stimuli, and suggest that aging is accompanied by major changes in the way that brain activity synchronizes with amplitude modulations in sounds.

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