

# Neural signatures of temporal regularity processing in sounds differ between younger and older adults



Björn Herrmann<sup>a,\*</sup>, Chad Buckland<sup>a</sup>, Ingrid S. Johnsrude<sup>a,b</sup>

<sup>a</sup> Department of Psychology & Brain and Mind Institute, The University of Western Ontario, London, Ontario, Canada

<sup>b</sup> School of Communication Sciences & Disorders, The University of Western Ontario, London, Ontario, Canada

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## ABSTRACT

Sensitivity to temporal regularity (e.g., recurring modulation in amplitude) is crucial for speech perception. Degradation of the auditory periphery due to aging and hearing loss may lead to increased responsiveness to sound in the auditory cortex, with potential consequences for the processing of temporal regularities. We used electroencephalography recorded from younger (19–33 years) and older adults (55–76 years) to investigate whether younger and older listeners differ in responsiveness to sound and sensitivity to amplitude modulation in sounds. Aging was associated with reduced adaptation in the auditory cortex, suggesting an age-related increase in responsiveness. Furthermore, neural synchronization in the auditory cortex to 4-Hz amplitude-modulated narrow-band noises was enhanced in ~30% of older individuals. Despite enhanced responsiveness and synchronization in the auditory cortex, sustained neural activity (likely involving auditory and higher-order regions) in response to amplitude modulation was absent in older people. Aging appears to be associated with over-responsiveness to amplitude modulation in the auditory cortex, but with diminished regularity sensitivity in higher-order areas.

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## 1. Introduction

When more than one sound source is present at a time in a listener's environment, the auditory system faces the challenge of decomposing this sound mixture into meaningful sources (e.g., a person's voice or an approaching car), so that one particular sound source can be identified and tracked over time. Each individual sound has a characteristic profile of changes in signal amplitude over time (i.e., amplitude modulation). In speech, for example, low-frequency (<10 Hz) amplitude modulations reflect the unique evolution of the word/syllable envelope of an utterance (Rosen, 1992). Tracking such modulations is thought to support speech comprehension in the presence of other sounds (Giraud and Poeppel, 2012; Kerlin et al., 2010; Peelle and Davis, 2013). Understanding how amplitude modulations in sounds are processed is thus essential for understanding success and failure during listening to real-world auditory signals including speech.

Changes in hearing are common in older adults (Cruikshanks et al., 1998; Feder et al., 2015; Goman and Lin, 2016). Sensitivity to pure tones, particularly at higher frequencies (over 8 kHz),

decreases with age, resulting in elevated hearing thresholds as measured using audiometry (Moore, 2007; Plack, 2014). Elevated hearing thresholds are considered clinically relevant if they exceed a certain threshold, for example 20–30 dB relative to normal hearing, but even older adults with thresholds below the diagnostic cutoff commonly exhibit elevated hearing thresholds relative to young adults (Herrmann and Johnsrude, 2018a; Presacco et al., 2016a; b), suggesting some degree of peripheral damage. Moreover, other peripheral impairments such as the degradation of synapses connecting inner hair cells with auditory nerve fibers (Bharadwaj et al., 2014; Liberman and Kujawa, 2017) are also likely present in older individuals but are difficult to detect with current assessment tools. Hence, it is very likely that most older individuals experience some changes in hearing, even if hearing is “normal” as assessed using audiometry.

Older people with and without clinical hearing loss do not just have difficulty hearing very quiet sounds (due to elevated hearing thresholds), but they also experience difficulty with suprathreshold sounds such as comprehension difficulties when speech is heard in the presence of background sound (Helfer and Wilber, 1990; Pichora-Fuller and Souza, 2003), perception of sounds at moderate intensities to be unpleasantly loud (Epstein and Marozeau, 2006; Tyler et al., 2014), and increased distraction by irrelevant sounds (Mishra et al., 2014; Parmentier and Andrés, 2010). These issues may be due, at least in part, to altered salience of amplitude

\* Corresponding author at: The Brain & Mind Institute, The University of Western Ontario, London, Ontario, N6A 5B7, Canada. Tel.: +1 519 661 2111 x86057; fax: +1 519 661 3613.

E-mail address: [herrmann.b@gmail.com](mailto:herrmann.b@gmail.com) (B. Herrmann).

modulation in sound. In fact, older people with hearing impairment have better detection thresholds for faint low-frequency (<10 Hz) amplitude modulations in suprathreshold sounds (Ernst and Moore, 2012; Schlittenlacher and Moore, 2016) and may perceive suprathreshold amplitude modulations to fluctuate more strongly compared with normal-hearing individuals (Moore et al., 1996).

Research in animals suggests that hearing loss and aging is accompanied by changes throughout the auditory system. Accumulated noise exposure is thought to damage the synapses that connect inner hair cells with auditory nerve fibers (Bharadwaj et al., 2014; Kujawa and Liberman, 2009; Liberman and Kujawa, 2017; Viana et al., 2015), which in turn reduces the input from the auditory periphery to neural circuits in the brainstem, thalamus, and cortex. A consequence of peripheral damage is a loss of neural inhibition throughout the auditory system (including cortex) (Auerbach et al., 2014; Caspary et al., 2008; Llano et al., 2012; Takesian et al., 2012). Consistent with a loss of inhibition after peripheral damage, neural responses to sounds are enhanced in the aged and noise-exposed auditory system of animals (Chambers et al., 2016; Hughes et al., 2010; Salvi et al., 2017) and humans (Bidelman et al., 2014; Henry et al., 2017; Herrmann et al., 2013a, 2016b; Laffont et al., 1989; Tremblay et al., 2003). A loss of inhibition is hypothesized to compensate for reduced inputs from the periphery by upregulating the responsiveness to sound in subcortical and cortical circuits (Auerbach et al., 2014; Caspary et al., 2008; Takesian et al., 2012). However, reduced inhibition and associated hyper-responsiveness in the aged auditory system are thought to contribute to maladaptive loudness perception, such as finding sounds at moderate intensities too loud and annoying (Heinz et al., 2005; Knipper et al., 2013; Zeng, 2013).

In human listeners, changes in inhibition and hyper-responsiveness may be assessed by measuring sound-evoked neural adaptation (Herrmann et al., 2016b, 2018). Neural adaptation refers to the reduction of a neural response caused by repetitive sound stimulation (Malmierca et al., 2014; Nelken, 2014). How neurons recover from adaptation can be measured by varying the time interval between 2 successive stimulus presentations, where a longer interstimulus interval enables the refractory neurons to recover for longer and thus to generate a larger response to a subsequent stimulus (Hari et al., 1982; Herrmann et al., 2016b; Sams et al., 1993; Zacharias et al., 2012). Critically, neural responses increase more strongly with longer interstimulus intervals in older compared with younger human adults, suggesting that neurons in the aging auditory cortex recover faster from adaptation (Herrmann et al., 2016b). This reduction in neural adaptation recovery time is thought to be a consequence of reduced cortical inhibition (Herrmann et al., 2016b, 2018).

How increased responsiveness affects the processing of low-frequency temporal regularities such as amplitude modulations in sounds is less well understood. Sensitivity to temporal regularity in sounds can be assessed by the strength of neural synchronization (Goossens et al., 2016; Henry et al., 2017; Herrmann et al., 2013b; Purcell et al., 2004). Neural synchronization reflects the alignment of neural activity with periodicity in sound (Henry and Herrmann, 2014; Lakatos et al., 2008, 2013; Stefanics et al., 2010; ten Oever et al., 2017) and is strongest in auditory cortex for low-frequency (<10 Hz) periodicities (Herrmann et al., 2013b; Keitel et al., 2017; Millman et al., 2017). Some studies report increased synchronization of neural activity with low-frequency amplitude modulations in sounds for older compared with younger humans (Goossens et al., 2016; Presacco et al., 2016a; Purcell et al., 2004) and nonhuman mammals (Herrmann et al., 2017; Lai et al., 2017; Overton and Recanzone, 2016; Parthasarathy et al., 2019).

Sensitivity to temporal regularity may also be assessed by the magnitude of sustained neural activity (Barascud et al., 2016;

Herrmann and Johnsrude, 2018b; Keceli et al., 2012; Sohoglu and Chait, 2016; Southwell et al., 2017; Teki et al., 2016). Sustained neural activity in electroencephalography (EEG)/magnetoencephalography is a low-frequency DC power offset that occurs when a listener hears a regular pattern in a sound, such as repeating sequences of tones with random frequencies or trains of isochronous clicks (Barascud et al., 2016; Gutschalk et al., 2002; Herrmann and Johnsrude, 2018b; Sohoglu and Chait, 2016; Southwell et al., 2017; Teki et al., 2016). Sustained activity and neural synchronization are dissociable because they are differently susceptible to the attentional state of listeners (Herrmann and Johnsrude, 2018b). Neural synchronization decreases, whereas sustained neural activity increases, when listeners attend to sounds. Moreover, neural synchronization and sustained neural activity may also involve distinct neural generators. Neural synchronization originates from the auditory cortex (Herrmann et al., 2013b; Keitel et al., 2017), whereas sustained activity is thought to originate from higher-level brain regions including frontal cortex, parietal cortex, and hippocampus (Barascud et al., 2016; Teki et al., 2016; Tiitinen et al., 2012) in addition to auditory cortex (Gutschalk et al., 2002; Keceli et al., 2012; Pantev et al., 1994, 1996). It is unclear how aging and its concomitant hearing changes affect regularity-related sustained neural activity and the relative magnitudes of synchronized and sustained activity.

The present study investigates whether the neural signatures of temporal regularities in sounds differ between younger and older people. By utilizing a sound that contains a temporally regular amplitude modulation, age group differences in sensory representation (indexed by neural synchronization) and in regularity sensitivity that may involve higher-level cortices (indexed by sustained activity) can be examined simultaneously (Herrmann and Johnsrude, 2018b).

Age differences are investigated in 3 ways. First, we utilize a stimulus protocol that assesses the dynamics of neural adaptation in the auditory cortex because reduced inhibition and enhanced responsiveness in older people may manifest as faster adaptation recovery times (Herrmann et al., 2016b). Measures of loudness perception are used to explore whether cortical responsiveness as measured by adaptation is correlated with perceptual inferences about the loudness of sounds. Second, we assess the degree to which neural activity synchronizes with a sound's amplitude modulation because reduced inhibition and enhanced responsiveness in older individuals may also be reflected in enhanced neural synchronization (Goossens et al., 2016; Herrmann et al., 2017; Purcell et al., 2004; Presacco et al., 2016a; b). Third, we assess the magnitude of the sustained response to the same amplitude-modulated sounds that we utilize to assess neural synchronization.

## 2. Methods and materials

### 2.1. Participants

30 younger (mean: 23.7 years, range: 19–33 years, 18 female) and 26 older (mean: 67.1 years, range: 55–76 years, 16 female) adults participated in the present study. Participants reported no neurological disease or hearing problems and were naïve to the purposes of the experiment. None of the participants wore a hearing aid or reported having been prescribed a hearing aid. We focused on a typical sample of older individuals, allowing for the possibility of slight hearing impairment (measured using pure-tone audiometry, described below). Four additional participants were excluded: 2 because of extensive movement during the EEG recordings; one because of a Montreal Cognitive Assessment (Nasreddine et al., 2005) screening score that indicated mild cognitive impairment (<26) and which may affect neural activity in

sensory areas (Bidelman et al., 2017); and one because of severe hearing impairment as identified using audiometry.

Participants gave written informed consent before the experiment and were paid 5 CAD per half-hour for their participation. The study was conducted in accordance with the Declaration of Helsinki and the Canadian Tri-Council Policy Statement on Ethical Conduct for Research Involving Humans (TCPS2-2014) and was approved by the local Nonmedical Research Ethics Board of the University of Western Ontario (protocol ID: 106570).

## 2.2. Stimulation apparatus

Participants were seated in a comfortable chair within a sound-attenuating booth. Sounds were presented via Sennheiser (HD 25-SP II) headphones, using a Steinberg UR22 (Steinberg Media Technologies) external sound card controlled by a PC (Windows 7, 64 bit) running Psychtoolbox in MATLAB (R2015b).

## 2.3. Hearing assessment

Pure-tone audiometry was assessed for each participant for 6 frequencies: 0.25, 0.5, 1, 2, 4, and 8 kHz. All participants included in the present study had a low-frequency audiometric threshold smaller than or equal to 30 dB HL (average across 0.25, 0.5, 1, 2 kHz frequencies; average across thresholds from the left and right ear).

Participants filled out a detailed questionnaire to assess their subjective experience related to speech perception and loudness perception. We used a questionnaire made publically available in a previous study (Liberman et al., 2016). The questionnaire assessed self-rated speech perception in quiet (one question) and noise (4 questions), and spatial hearing (3 questions) (similar to SSQ questions; Gatehouse and Noble, 2004). Participants rated these questions on a 10-point scale (with 10 indicating “perfect” agreement). We also assessed the participants’ subjective sound loudness and annoyance experiences (twelve statements; e.g., “Lawn mower running next to you”) and sound avoidance behavior (ten statements; e.g., “Because sounds are too loud, you do not go out with your friends”). These statements were rated on a 100-point scale (with 100 indicating “unbearable loud,” “annoying,” and “avoiding,” respectively). The full questionnaire can be downloaded at <https://osf.io/7snrz/>.

## 2.4. Sensation level and loudness perception

Before the experiment, the sensation level (i.e., hearing threshold) was determined for each participant for a 1272-Hz sine tone using a method-of-limits procedure (Herrmann and Johnsrude, 2018b). The threshold was used as a reference point to assess each participant’s range for loudness perception. Thresholds were obtained as follows: Participants listened to 15-s sounds that changed continuously in intensity at 4.33 dB/s (either decreased [i.e., starting at suprathreshold levels] or increased [i.e., starting at subthreshold levels]). Participants pressed a button when they could no longer hear the tone (intensity decrease) or when they started to hear the tone (intensity increase). The sound intensity at the time of the button press was noted for 6 decreasing sounds and 6 increasing sounds (decreasing and increasing sounds alternated), and these were averaged to determine the individual hearing threshold.

Loudness perception was assessed using a category judgment procedure (Al-Salim et al., 2010; Epstein and Marozeau, 2006; Hebert et al., 2013; Oxenham and Bacon, 2003; Plack, 2014). Participants listened to 1272-Hz sine tones, one at a time, and indicated the perceived loudness of that tone using one of seven categories (“not heard,” “very soft,” “soft,” “comfortable,” “loud,” “very loud,”

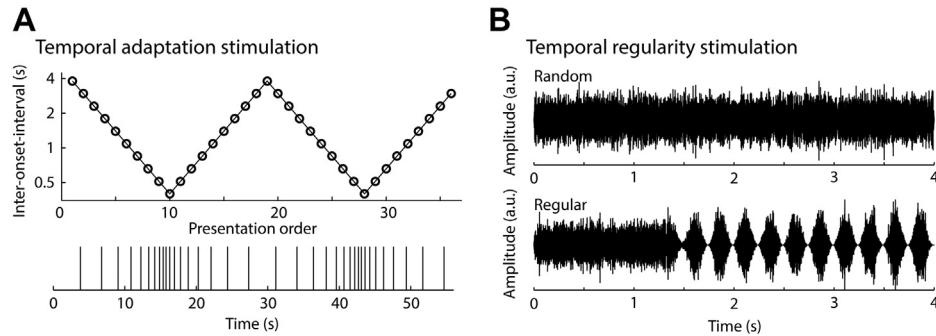
or “too loud”). Participants were instructed to judge the loudness of each tone subjectively, based on that presentation alone, and not to compare it with preceding tone presentations. Tones of 0.7-second duration were presented at one of 22 different sound levels ranging from −1.67 dB to 80 dB (step size: 3.89) relative to the average hearing threshold measured from a young, normal-hearing participant group ( $N > 100$ ) in a previous study (Herrmann and Johnsrude, 2018a). Hearing thresholds of normal-hearing ears relate to about 20 dB SPL (Moore et al., 1996). Each sound level was repeated 6 times and presented randomly. To quantify the range across which sound levels were perceived, we calculated the loudness range as (1) the difference in the mean level (in dB) for tones perceived as “very soft” relative to “very loud” and (2) the difference in the level between a participant’s hearing threshold (from the psychophysical method-of-limits procedure) and the mean level for tones perceived as “very loud.” We did not use the “too loud” category for the calculation of the loudness range because not all participants used this category. An independent samples *t*-test compared the loudness range between age groups.

## 2.5. Experimental sound materials for electrophysiological measurement of adaptation dynamics

We have previously shown that neural adaptation can provide a consistent marker for age-related enhancements in cortical responsiveness (Herrmann et al., 2016b, 2018). To demonstrate an increase in neural responsiveness in the current sample of older people, we closely followed the experimental adaptation design from our previous study (Herrmann et al., 2016b). To this end, sequences of 0.1-second pure tones (at 1272 Hz; 7 ms linear rise and 7 ms linear fall time) were presented, each 18 tones long. The onset-to-onset interval changed logarithmically, becoming progressively shorter (from 3.8 seconds to 0.4 seconds) in one half of the sequence and then progressively longer in the other half (to 2.959 seconds; see Fig. 1A). Twenty sequences were concatenated to make one long sequence. The duration of the onset-to-onset interval preceding a tone served as the independent variable by which trials were sorted into conditions. Presentation of the concatenated sequence was repeated 3 times in separate blocks (each approx. 9 minutes), and participants listened passively while watching a muted movie of their choice with subtitles on a battery-driven portable DVD player. Over the experiment, 1080 tones were presented ( $18 \text{ tones} \times 20 \text{ sequences} = 360 \times 3 \text{ repetitions} = 1080$ ). For 2 older participants, no data were recorded for this part of the study because the participants felt uncomfortable sitting for the extended period required by the experimental procedures. As a consequence, only 24 data sets from older people were available from which to examine the dynamics of adaptation.

## 2.6. Experimental sound materials for electrophysiological measurement of temporal regularity processing

Stimuli were narrow-band noises made by adding 50 amplitude-modulated pure-tone components of 4-second duration. For each of the 50 components, a random carrier frequency between 900 Hz and 1800 Hz was selected (starting phase was random). The amplitude of each component was modulated at a randomly changing rate between 2 Hz and 6 Hz (average rate of 4 Hz; different components were modulated at different rates). The 50 components were summed to obtain a narrow-band noise. We henceforth refer to this stimulus as the “random” condition (see Fig. 1B, top). A “regular” condition was created by manipulating the number of sound components with consistent phase. In this condition, the amplitude modulation of all 50 components aligned in phase at about 1.55 seconds after sound onset and the amplitude



**Fig. 1.** Experimental stimulation to measure temporal dynamics of neural adaptation (A) and temporal regularity processing (B).

modulation rate remained constant at 4 Hz for the rest of the sound. Stimuli were created such that there was no discontinuity at the transition from nonaligned to phase-aligned parts of the sound. The waveform of a “regular” example is displayed in Fig. 1B (bottom). The “random” condition was used as a control to investigate whether there were significant neural signatures of temporal regularity processing. Example stimuli for the regular and the random condition are available at <https://osf.io/ajpm2/>.

Participants listened passively to 150 trials of each condition (random, regular) while watching a muted movie of their choice with subtitles on a battery-driven portable DVD player. The experiment was divided into 3 blocks (each approx. 9 minutes long), separated by short breaks. During each block, 50 trials of each condition were randomly presented. Trials were separated by a 1.5-second interstimulus interval.

### 2.7. Intensity of sounds during EEG recording

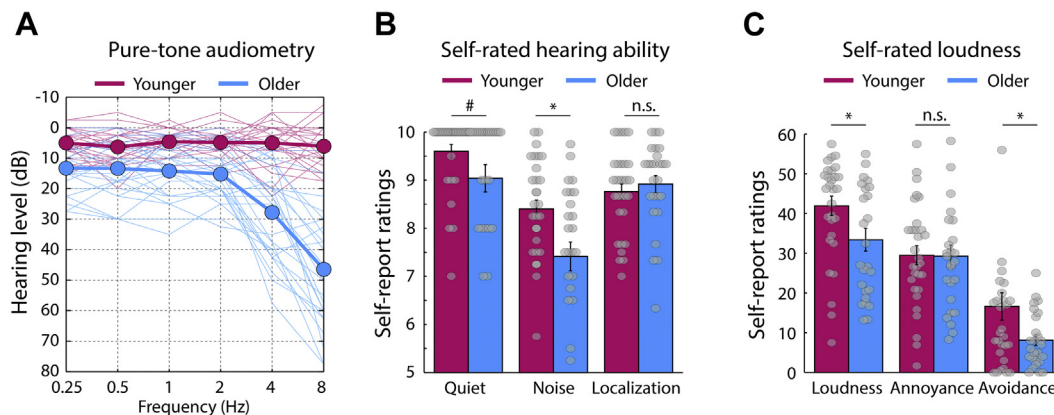
Sounds played in the 2 EEG experiments (one measuring adaptation dynamics and one measuring temporal regularity processing; the order was counterbalanced across participants) were presented at 60 dB above the level corresponding to the average hearing threshold for a group of young, normal-hearing adults ( $N > 100$ ) measured using the identical acoustic stimulus delivery system (Herrmann and Johnsrude, 2018a). Because of challenges with estimating the precise dB SPL level for our audio setup, we opted to use an arbitrary level corresponding to the averaged hearing threshold as a baseline for the participants in the present study and increased it by 60 dB to approximate 80-dB-SPL sound stimulation.

That is, because the average threshold for normally hearing listeners is 20 dB SPL (Moore et al., 1996), this approximates a stimulus presentation level of 80 dB SPL. For 10 of the 56 participants, sounds were presented at 60 dB relative to their own individual hearing threshold. Critically, we quantified the intensity of the sounds played during EEG recordings relative to each individual's hearing threshold (i.e., sensation level) and relative to each individual's comfortable listening level, which was derived from the categorical loudness judgments.

Relative to sensation level, sounds played to participants during the EEG recording were on average louder for younger compared with older participants ( $t_{53} = 4.097$ ,  $p < 0.001$ ,  $r_e = 0.490$ ). Furthermore, the intensity of sounds played during the EEG recording was perceived as louder relative to the comfortable sound level for younger participants ( $t_{29} = 3.147$ ,  $p = 0.004$ ,  $r_e = 0.505$ ), but not different from the comfortable sound level for older participants ( $t_{25} = 1.384$ ,  $p = 0.179$ ,  $r_e = 0.267$ ; the difference between age groups was not significant:  $t_{54} = 1.569$ ,  $p = 0.122$ ,  $r_e = 0.209$ ). The fact that the sounds presented during the EEG recordings were, on average, louder for younger compared with older participants works against our hypothesis that responsiveness to sound in the auditory cortex is enhanced in older people. Sound level is thus not a confounding factor in our study.

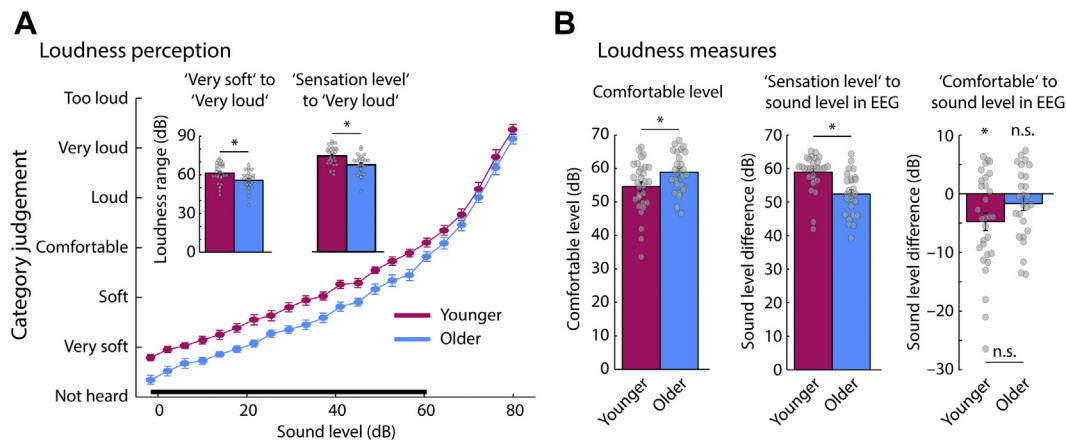
### 2.8. EEG recordings and preprocessing

Electroencephalography was recorded from 16 scalp electrodes (Ag/Ag-Cl electrodes; 10–20 placement) and from the left and right mastoids (BioSemi, Amsterdam, The Netherlands) at a sampling



**Fig. 2.** Hearing assessment measures. (A): Audiometric thresholds. Thin lines reflect individual participants. Thick solid lines reflect the average across participants. (B): Self-rated hearing ability for speech in quiet, speech in noise, and spatial hearing. (C): Self-rated loudness perception, sound annoyance, and avoidance of sound. Gray dots represent data points for individual participants. Error bars reflect the standard error of the mean. \* $p < 0.05$ , # $p < 0.1$ , n.s. – not significant.





**Fig. 3.** Results for loudness category judgments. (A): Shows the mean loudness judgments for a 1272-Hz sine tone, separately for each age group (the black solid line indicates a significant age group difference,  $p < 0.05$ ). The inset shows the 2 measures of loudness range ("very soft" to "very loud" and "sensation level" to "very loud"). Dynamic range for loudness was reduced in older compared with younger people. (B): Different loudness measures calculated from the loudness judgments: comfortable level, level of sounds during EEG recordings relative to sensation level, and level of sounds during EEG recordings relative to comfortable level. Gray dots represent data points for individual participants. Error bars reflect the standard error of the mean. \* $p < 0.05$ , n.s. — not significant.

rate of 1024 Hz. The online low-pass filter was set to 208 Hz. Electrodes were referenced to a monopolar reference feedback loop connecting a driven passive sensor and a common mode sense active sensor, both located posteriorly on the scalp.

Data were analyzed offline using the MATLAB software (v7.14; MathWorks, Inc). Data from one electrode ("O2") were excluded for all participants because the electrode broke over the course of the study. An elliptic filter was used to suppress line noise (60 Hz). Data were re-referenced to the average of the 2 mastoids. A high-pass filter with a cutoff of 0.7 Hz (2449 points, Hann window) and a low-pass filter with a cutoff of 30 Hz (111 points, Hann window) were applied. Activity related to blinks was suppressed using independent components analysis as implemented in Fieldtrip (Oostenveld et al., 2011; runica; Makeig et al., 1996; logistic infomax algorithm; Bell and Sejnowski, 1995). Data recorded in adaptation blocks (Fig. 1A) were divided into epochs ranging from  $-0.05$  to  $0.3$  seconds (time-locked to sound onset). Data recorded in temporal regularity blocks (Fig. 1B) were divided into epochs ranging from  $-0.6$  to  $4.6$  seconds (time-locked to sound onset). Epochs that exceeded a signal change of more than  $200 \mu V$  for any electrode were excluded from analyses. This pipeline was used to investigate neural adaptation and neural synchronization (see below).

To investigate sustained neural activity, the same analysis pipeline was calculated a second time, with the exception that high-pass filtering was omitted, because the sustained response is a very low-frequency DC shift (Barascud et al., 2016; Herrmann and Johnsrude, 2018b; Southwell et al., 2017). Activity related to blinks was suppressed using the identified components from the high-pass filtered data.

Finally, the signal for the broken "O2" electrode was interpolated by replacing it by the average signal across electrodes "Pz," "P4," and "O1." The interpolated signal was used only for the display of topographical distributions.

### 2.9. EEG data analysis: dynamics of neural adaptation

We calculated response time courses for unique onset-to-onset intervals. To this end, we binned single-trial time courses for a unique onset-to-onset interval and its direct neighbors (i.e., shorter and longer intervals; Ingham and McAlpine, 2005). Signals within each bin were averaged. For example, to obtain the average response for the  $0.514$ -s interval, we averaged all trials for the  $0.400$ -s,  $0.514$ -s,

and  $0.660$ -s ( $n-1$ ,  $n$ ,  $n+1$ ) onset-to-onset intervals. The overlap across intervals increased the signal-to-noise ratio by increasing the number of trials in the response average. This averaging procedure resulted in 8 logarithmically spaced onset-to-onset interval bins ( $0.514$ ,  $0.660$ ,  $0.847$ ,  $1.088$ ,  $1.397$ ,  $1.794$ ,  $2.304$ ,  $2.959$  seconds).

The analyses focused on N1 amplitudes for which neural adaptation has been reported previously (Hari et al., 1982; Herrmann et al., 2016b; Sams et al., 1993; Zacharias et al., 2012). We have shown that N1 amplitude adaptation can be used as a marker for age-related increases in neural responsiveness (Herrmann et al., 2016b, 2018). We did not analyze P1 and P2 amplitudes because they do not appear to reflect longer-term adaptation (Herrmann et al., 2016b, 2018; Roth et al., 1976; but see Supplemental Materials). Mean amplitudes for a broad electrode cluster (Fz, F3, F4, Cz, C3, C4, Pz, P3, P4) were extracted for the N1 time window ( $0.8$ – $0.11$  seconds; Herrmann et al., 2016b). The electrode cluster was selected because it covered the regions of the scalp for which it is known from previous work that the N1 response would be strongest (Herrmann et al., 2016b; Näätänen and Picton, 1987), and for reasons of consistency with the other analyses reported in the present study.

To investigate the sensitivity of neural responses to interval duration, a linear function was used to relate N1 amplitudes (averaged across the electrode cluster) to onset-to-onset intervals, separately for each participant. Onset-to-onset intervals were log-transformed before the linear function fit to linearize the intervals' logarithmic spacing. The estimated linear coefficient from the linear fit reflects the sensitivity of the N1 amplitude to interval duration.

To assess whether N1 amplitudes were sensitive to interval duration, linear coefficients from the function fits were tested against zero using a one-sample  $t$ -test (separately for the younger and the older participant group). Negative values index increasing N1 amplitudes with increasing interval duration. An independent samples  $t$ -test was used to compare linear coefficients between age groups. A larger negative coefficient for data from older compared with younger people would suggest faster recovery from adaptation over time in the auditory cortex of older people.

### 2.10. EEG data analysis: neural synchronization to temporal regularity

Neural synchronization was calculated as intertrial phase coherence (ITPC; Lachaux et al., 1999). Single-trial time courses

(high-pass filtered data) from the temporal regularity stimulation protocol (Fig. 1B) were transformed into the frequency domain by calculating a fast Fourier transform (including a Hann window taper and zero-padding) for each trial, regularity condition, and channel for the time window during which the temporal regularity (i.e., amplitude modulation) occurred in “regular” trials: 1.55–4 seconds. ITPC was calculated by dividing each complex number (from the fast Fourier transform) by its magnitude, averaging the resulting normalized complex numbers across trials and calculating the absolute value of this mean complex number. ITPC is bound between 0 (no coherence) and 1 (maximum coherence).

ITPC was calculated for frequencies ranging from 1 to 11 Hz (step size: 0.01 Hz). For statistical analyses, ITPC values were averaged across the fronto-central-parietal electrode cluster (Fz, F3, F4, Cz, C3, C4, Pz, P3, P4; Herrmann and Johnsrude, 2018b). ITPC values at the 4-Hz stimulation frequency were extracted by calculating the average across the 3.95– to 4.05-Hz frequency window. An analysis of variance (ANOVA) was carried out to compare neural synchronization strength (ITPC) between regularity conditions (within-subjects factor: random vs. regular) and age groups (between-subjects factor: younger vs. older).

### 2.11. EEG data analysis: sustained neural activity

Single-trial time courses (non-high-pass-filtered data) were averaged for each condition (random, regular) from the temporal regularity stimulation protocol (Fig. 1B). Response time courses were baseline corrected by subtracting the mean amplitude in the prestimulus time window (−0.6 to 0 seconds) from the amplitude at each time point. To investigate the sustained response, signals were averaged across the fronto-central-parietal electrode cluster (Fz, F3, F4, Cz, C3, C4, Pz, P3, P4; Herrmann and Johnsrude, 2018b) and, for both the random and regular conditions, the mean amplitude was calculated for the 1.55- to 4-second time window during which the temporal regularity occurred (on regular trials) (Barascud et al., 2016; Herrmann and Johnsrude, 2018b; Teki et al., 2016). An ANOVA was carried out to compare the amplitude of the sustained response between regularity conditions (within-subjects factor: random vs. regular) and age groups (between-subjects factor: younger vs. older).

### 2.12. Effect size

Throughout the manuscript, effect sizes are provided as partial eta squared ( $\eta_p^2$ ) for ANOVAs and  $r_e$  ( $r_{\text{equivalent}}$ ) (Rosenthal and Rubin, 2003) for t-tests.  $r_e$  is equivalent to a Pearson product-moment correlation for 2 continuous variables, to a point-biserial correlation for one continuous and one dichotomous variable, and to the square root of partial  $\eta^2$  for ANOVAs.

## 3. Results

### 3.1. Hearing assessment

Audiometric thresholds are depicted in Fig. 2A. All participants included in this study had an average hearing threshold below or equal to 30 dB HL in a low-frequency region (average across 0.25, 0.5, 1, 2 kHz frequencies; average across left and right ear) at which sounds were presented during EEG recordings. Low-frequency thresholds were elevated by 9 dB (on average) for older compared with younger listeners ( $F_{1,54} = 37.388$ ,  $p < 0.00001$ ,  $\eta_p^2 = 0.409$ ). Older participants also exhibited moderate-to-severe hearing loss at frequencies equal to and above 4 kHz. These audiometric changes are common in older adulthood (Plack, 2014). Please note that audiograms are not sensitive to all forms of peripheral decline.

Synapses connecting inner hair cells with auditory nerve fibers may also be damaged (Bharadwaj et al., 2014; Liberman and Kujawa, 2017) and/or spiral ganglion cells be lost (Bao and Ohlemiller, 2010) in older people, but audiograms likely miss this. For the purpose of the present study, we thus assume that the recruited older individuals had slight hearing impairment typical for the age range.

The results of a short version of the SSQ questionnaire (Gatehouse and Noble, 2004) assessing speech perception and spatial localization abilities are displayed in Fig. 2B. Older people reported experiencing greater challenges when listening to speech in noisy environments than did younger people ( $t_{54} = 2.873$ ,  $p = 0.006$ ,  $r_e = 0.364$ ; Fig. 2B, middle). There was also a marginal effect of age group on speech perception in quiet environments ( $t_{54} = 1.832$ ,  $p = 0.073$ ,  $r_e = 0.242$ ; Fig. 2B, left), with older adults reporting more difficulty. No effect of age was found for self-rated spatial localization abilities ( $t_{54} = 0.648$ ,  $p = 0.520$ ,  $r_e = 0.088$ ; Fig. 2B, right).

The results from the questionnaire that assessed loudness perception, annoyance, and avoidance are depicted in Fig. 2C. Unexpectedly, loudness ratings ( $t_{54} = 2.266$ ,  $p = 0.028$ ,  $r_e = 0.295$ ) and avoidance ratings ( $t_{54} = 2.160$ ,  $p = 0.035$ ,  $r_e = 0.282$ ) were lower for older compared with younger people. No age difference was found for annoyance ratings ( $t_{54} = 0.061$ ,  $p = 0.952$ ,  $r_e = 0.008$ ). These results are in contrast to previous work using the same questionnaire for the assessment of loudness, annoyance, and avoidance in younger participant groups with and without a history of noise exposure (Liberman et al., 2016). Older people may interpret the situations described for the self-rating differently than do younger people.

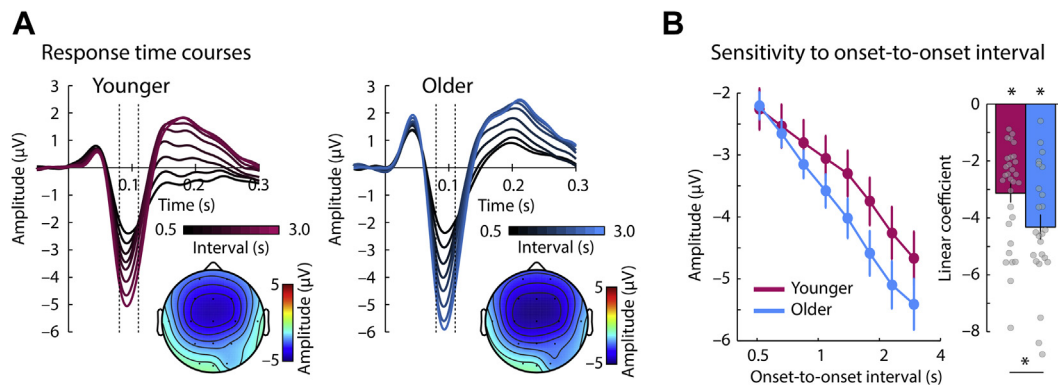
### 3.2. Loudness judgments

Loudness perception was assessed using a category judgment task (Epstein and Marozeau, 2006; Hebert et al., 2013). Participants classified the loudness of tones as belonging to one of seven categories. Fig. 3A shows the category judgment for each age group. Older participants perceived tones presented at low sound levels to be softer compared with younger participants. This is consistent and perhaps expected given the age-group difference in audiometric hearing thresholds for pure tones (Fig. 2A). The difference in perceived loudness between age groups at lower sound levels did not persist at higher levels (Fig. 3A). This is consistent with a reduced dynamic range for loudness in older compared with younger people (Hebert et al., 2013).

To test whether the loudness range differed between age groups, the perceptual loudness range was calculated. The loudness range for “very soft” relative to “very loud” percepts ( $t_{54} = 2.791$ ,  $p = 0.007$ ,  $r_e = 0.355$ ), as well as for the hearing threshold relative to “very loud” percepts ( $t_{53} = 3.361$ ,  $p = 0.001$ ,  $r_e = 0.419$ ), was smaller in older than younger individuals (Fig. 3A, inset). In addition, the comfortable sound level was more intense in older than younger people (difference: 4.33 dB;  $t_{54} = 2.328$ ,  $p = 0.024$ ,  $r_e = 0.302$ ; Fig. 3B, left).

### 3.3. Neural adaptation

Fig. 4A displays neural response time courses and topographical distributions for N1 responses (0.08- to 0.11-second time window; analyses for P2 responses are provided in Supplementary Materials). Topographical distributions are consistent with neural generators in the auditory cortex (Näätänen and Picton, 1987; Picton et al., 2003). The degree to which neural responses recover from adaptation over time was investigated by fitting a linear function to N1 amplitudes as a function of the interval duration



**Fig. 4.** Results from the temporal adaptation design. (A): Response time course for each onset-to-onset interval condition and age group. The vertical dashed lines mark the time interval of the N1 component (0.08–0.11 seconds). Topographies reflect the mean N1 response across interval conditions. (B): Mean N1 response for each onset-to-onset interval condition and age group. The bar graphs on the right shows the mean linear coefficient (across participants) from the linear function fit to N1 amplitudes as a function of onset-to-onset interval. Gray dots represent the linear coefficients for individual participants. Error bars reflect the standard error of the mean. \* $p < 0.05$ .

preceding a tone. The linear coefficient was significantly smaller than zero for younger ( $t_{29} = -9.752$ ,  $p < 0.001$ ,  $r_e = 0.875$ ) and older people ( $t_{23} = -9.990$ ,  $p < 0.001$ ,  $r_e = 0.902$ ), which shows that the N1 amplitude increases with increasing interval between 2 tones, consistent with recovery from adaptation. The linear coefficient was larger (i.e., more negative) for older than younger participants ( $t_{52} = 2.252$ ,  $p = 0.029$ ,  $r_e = 0.298$ ; Fig. 4B), which indicates that neurons in the auditory cortex of older people recover faster from adaptation over time. The overall amplitude of N1 (averaged over time bins) did not differ between age groups ( $t_{52} = 1.049$ ,  $p = 0.299$ ,  $r_e = 0.144$ ).

#### 3.4. Neural synchronization with amplitude modulation in sounds

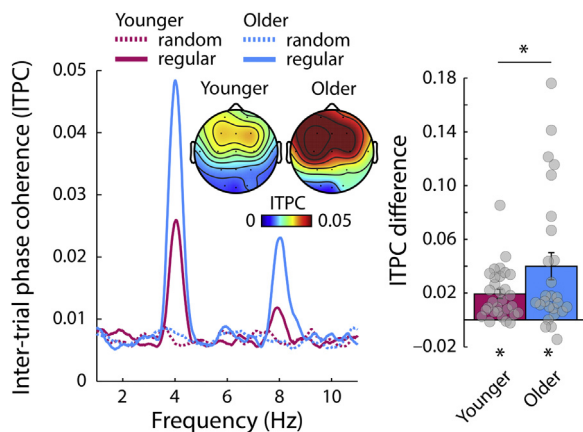
ITPC was calculated for stimuli that varied in phase coherence (i.e., random and regular condition). ITPC frequency spectra and topographies are depicted in Fig. 5. ITPC at the 4-Hz stimulation frequency was compared between regularity conditions and age groups. The ANOVA revealed a main effect of regularity ( $F_{1,54} = 34.633$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.391$ ) and a main effect of age group ( $F_{1,54} = 5.707$ ,  $p = 0.020$ ,  $\eta_p^2 = 0.096$ ). ITPC was larger for the “regular” condition (i.e., sounds with coherent amplitude modulation) than the “random” condition (i.e., sounds without coherent

amplitude modulation), and larger for older than younger people. The regularity  $\times$  age group interaction was also significant ( $F_{1,54} = 4.161$ ,  $p = 0.046$ ,  $\eta_p^2 = 0.072$ ). ITPC was larger for the regular than the random condition for younger ( $t_{29} = 5.666$ ,  $p < 0.001$ ,  $r_e = 0.725$ ) and older individuals ( $t_{25} = 3.956$ ,  $p < 0.001$ ,  $r_e = 0.621$ ; Fig. 5), but the difference in ITPC between the “regular” and the “random” condition was larger in older than younger individuals ( $t_{54} = 2.040$ ,  $p = 0.046$ ,  $r_e = 0.268$ ). This is consistent with previous work showing an enhancement of neural synchronization with low-rate amplitude modulation for older (>60 years) compared with younger people (<30 years) (Goossens et al., 2016; Presacco et al., 2016a; b). Topographical distributions are consistent with auditory cortex generators (Näätänen and Picton, 1987; Picton et al., 2003).

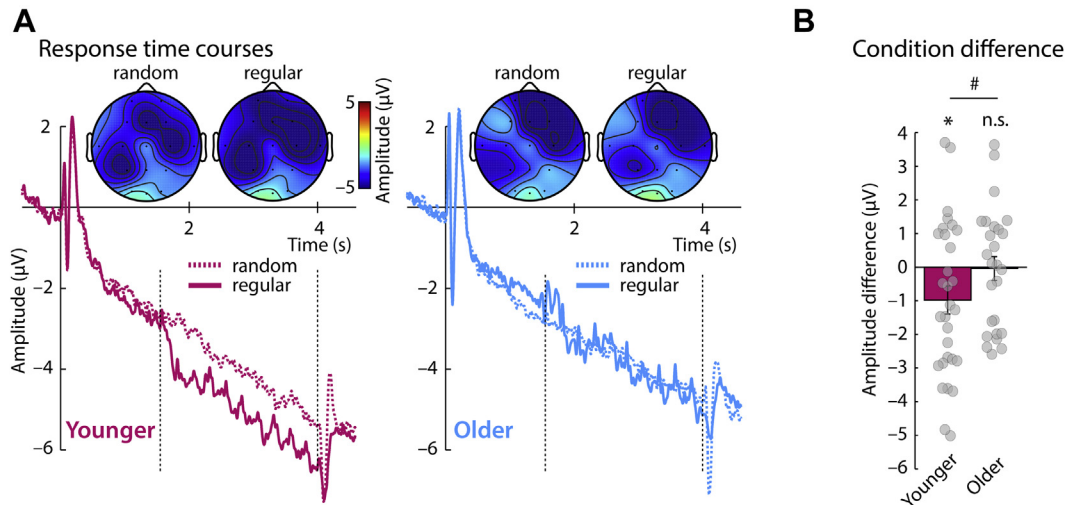
Notably, the difference in synchronization strength (regular minus random) was particularly prominent for a few older participants (~30%; Fig. 5, right). We thus tested whether the distributions’ median differed between age groups. There was no difference between age groups for the median neural synchronization ( $p = 0.379$ ,  $r_e = 0.120$ ). This suggests that the larger effect of regularity on neural synchronization in older compared with younger people may be due to the neural responses in a subset of older participants.

#### 3.5. Sustained neural activity to temporal regularity

Investigation of the sustained response focused on the time window during which the 4-Hz amplitude modulation occurred in “regular” sounds (1.55–4 seconds). Fig. 6A shows the response time courses and topographies for both regularity conditions (random, regular) and age groups (younger, older). The ANOVA revealed a marginally significant effect of regularity ( $F_{1,54} = 3.340$ ,  $p = 0.073$ ,  $\eta_p^2 = 0.058$ ), but no effect of age group ( $F_{1,54} = 0.325$ ,  $p = 0.571$ ,  $\eta_p^2 = 0.006$ ). The regularity  $\times$  age group interaction trended toward significance ( $F_{1,54} = 2.838$ ,  $p = 0.098$ ,  $\eta_p^2 = 0.050$ ; median test:  $p = 0.102$ ). We had planned tests of simple effects to directly investigate the magnitude of the sustained response in both age groups. Accordingly, paired t-tests (contrasting random vs. regular) were calculated separately for younger and older people. The sustained response was larger (i.e., more negative) in the “regular” than the “random” condition in younger individuals ( $t_{29} = 2.335$ ,  $p = 0.027$ ,  $r_e = 0.398$ ), but not in older individuals ( $t_{25} = 0.113$ ,  $p = 0.911$ ,  $r_e = 0.023$ ). As the regularity  $\times$  age group interaction indicates, the response difference between the “regular” and “random” conditions was marginally larger in younger than older people (Fig. 6B).



**Fig. 5.** Results for neural synchronization. Left: Inter-trial phase coherence (ITPC) as a function of neural frequency for the “regular” and the “random” condition. Topographical distributions reflect the mean ITPC for the regular condition. Right: ITPC difference between the “regular” and the “random” condition. Gray dots represent data points for individual participants. \* $p < 0.05$ .



**Fig. 6.** Results for sustained neural activity. (A): Neural activity time courses for random and regular conditions. Dashed vertical lines mark the time window of interest during which a regular pattern could occur (1.55–4 seconds) (B): Difference in sustained response between regular and random conditions. Gray dots represent data points for individual participants. Error bars reflect the standard error of the mean. \* $p \leq 0.05$ , # $p \leq 0.1$ , n.s. – not significant.

### 3.6. Temporal regularity index

Previous source localization studies indicate that the auditory cortex likely underlies neural synchronization to low-frequency temporal regularities in sounds (Herrmann et al., 2013b, 2016a; Keitel et al., 2017; Millman et al., 2017), whereas a network of auditory and higher-level cortices has been identified as underlying regularity-related sustained activity effects (Barascud et al., 2016; Gutschalk et al., 2002; Pantev et al., 1994; Teki et al., 2016; Tiitinen et al., 2012).

To contrast the effect of temporal regularity between neural synchronization and sustained neural activity, and thus potentially contrast the sensitivity to regularity of different networks, we subtracted the response to the “random” condition from the response to the “regular” condition, separately for the sustained response data and the ITPC data. Both differences were separately z-transformed (the sustained response data were also sign-inverted to match the sign of ITPC values). A regularity index was then calculated as the subtraction of the z-transformed ITPC effect from the z-transformed sustained response effect. A positive value of this regularity index indicates that the sustained response was more sensitive to regularity than neural synchronization. A negative value indicates that neural synchronization was more sensitive to regularity than the sustained response.

The regularity index was positive and significantly greater than zero for younger individuals ( $t_{29} = 2.052$ ,  $p = 0.049$ ,  $r_e = 0.356$ ), showing that the sustained response was more sensitive to regularity than neural synchronization, whereas the opposite was observed for older adults, though not significantly ( $t_{25} = -1.573$ ,  $p = 0.128$ ,  $r_e = 0.300$ ). Moreover, the regularity index differed significantly between age groups. It was significantly more positive for younger than older people ( $t_{54} = 2.505$ ,  $p = 0.015$ ,  $r_e = 0.323$ ; median test:  $p = 0.038$ ,  $r_e = 0.279$ ; Fig. 7), further highlighting the age-group difference in sensitivity to temporal regularity of the sustained response relative to neural synchronization.

### 3.7. Correlations between measures of hearing ability and neural responses

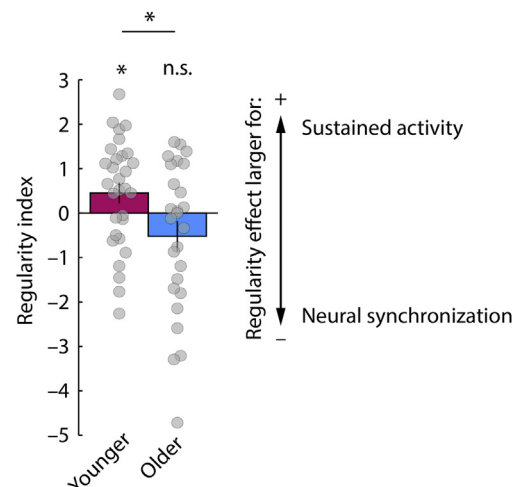
We calculated correlations between brain responses and measures of hearing. The following neural measures were used: the

linear coefficient from the adaptation paradigm, ITPC regularity effect (regular minus random), regularity effect for sustained activity (regular minus random), and the regularity index. The measures of hearing abilities were as follows: speech in noise score, loudness range (“very soft” to “very loud”), and averaged audiometric threshold for low frequencies ( $\leq 2000$  Hz). We controlled for multiple comparisons using false discovery rate (Benjamini and Hochberg, 1995; Genovese et al., 2002).

None of the correlations between neural measures and measures of hearing were significant when age was partialled out (all  $p > 0.1$ ). There were also no significant correlations when younger and older participant groups were analyzed separately (all  $p > 0.1$ ).

## 4. Discussion

In the present study, we investigated age differences in neural responsiveness and in the neural representation of temporally



**Fig. 7.** Regularity index reflecting the weighting between the regularity effects for neural synchronization versus the sustained response. Positive values indicate that the effect of regularity was larger for the sustained activity than neural synchronization, and vice versa for negative values. Gray dots represent data points for individual participants. Error bars reflect the standard error of the mean. \* $p \leq 0.05$ , n.s. – not significant.



regular amplitude modulations in sounds and whether age-related changes in adaptation might relate to changes in the representation of temporal regularity. Enhancements in cortical responsiveness to sound were assessed by neural response adaptation to sequences of tones in which the onset-to-onset intervals varied. We revealed faster recovery from adaptation in older compared with younger people, indicating an increase in responsiveness to sound in the aged auditory cortex.

Neural sensitivity to temporal regularity in sounds was assessed by neural synchronization and sustained neural activity to amplitude-modulated narrow-band noises. Neural synchronization to 4-Hz amplitude modulation—probably arising from the auditory cortex (Herrmann et al., 2013b; Keitel et al., 2017)—was more pronounced in older than younger people. In contrast, sustained neural activity—probably reflecting activity in higher-level brain regions in addition to auditory cortex (Barascud et al., 2016; Gutschalk et al., 2002; Pantev et al., 1994; Teki et al., 2016; Tiitinen et al., 2012)—was diminished in older people. A regularity index, contrasting the different neural signatures of regularity processing, suggests that despite enhanced responsiveness in the auditory cortex of older individuals, neural representations of temporal regularity in higher-level brain regions are weakened in the aging population.

#### 4.1. Subclinical impairments in hearing accompany aging

In the present study, we assessed the participants' hearing abilities using audiograms, self-rated reports of speech perception, and measures of loudness perception. Older (compared with younger) people had slightly increased audiometric thresholds for low- and mid-frequency pure tones ( $\leq 2000$  Hz; mean difference  $\sim 9$  dB). Sound stimulation in the present study was limited to this frequency range, and participants had no difficulty perceiving these sounds at suprathreshold levels (Fig. 3). However, older people had moderate-to-severe hearing loss at higher frequencies ( $\geq 4000$  Hz) and they reported having difficulty understanding speech in the presence of background sound (relative to younger people). Hearing abilities were also assessed using a loudness judgment task, during which participants categorized the perceived loudness of pure tones (Al-Salim et al., 2010; Epstein and Marozeau, 2006; Hebert et al., 2013). We observed that the loudness range over which older people perceive sounds was reduced compared with younger people (Fig. 3; Harris, 1953; Moore et al., 1996; Marozeau and Florentine, 2007; Steinberg and Gardner, 1937). Other peripheral damage, such as degradation of synapses connecting inner hair cells with auditory nerve fibers (Bharadwaj et al., 2014; Liberman and Kujawa, 2017) or spiral ganglion cell loss (Bao and Ohlemiller, 2010), may also be present in many older individuals. These changes, however, are not detectable with standard hearing assessment tools (e.g., audiometry) but would require additional peripheral measures (e.g., electrocochleography and otoacoustic emissions; Bharadwaj et al., 2015; Liberman et al., 2016). This is a new area of research, and it is not yet clear what best practice will be in this regard.

Elevated hearing thresholds, reduced speech perception in the presence of background sound, and a compressed loudness range suggest some hearing impairments in the sample of older people, compared with younger people, recruited for the present study. Such perceptual changes have been associated with a loss of cochlear compression, that is, with the loss of the active mechanism that in “normal” ears increases sensitivity to soft sounds (Moore et al., 1996; Moore and Glasberg, 1993; Oxenham and Bacon, 2003; Villchur, 1974). The consequences of impaired cochlear function for neural processing upstream in the brain stem and cortex can be profound. Changes include a loss of inhibition

(Caspary et al., 2008; Takesian et al., 2009, 2012), an increase in excitation (Salvi et al., 2017), and, in turn, an abnormal enhancement of neural responses to sounds (Herrmann et al., 2017; Hughes et al., 2010; Möhrle et al., 2016; Popelár et al., 1987; Salvi et al., 2017; Syka et al., 1994). Such “downstream” effects illustrate that the auditory system is highly integrated, and the enhancement of neural activity is compatible with perceptual effects such as a reduced loudness range and hypersensitivity to sound (Cai et al., 2009; Heinz et al., 2005; Knipper et al., 2013; Zeng, 2013). However, the absence of a correlation between loudness perception measures and neural measures in the present study may suggest that the relation between age-related changes in the auditory system and loudness perception are not straightforward and linear.

#### 4.2. Enhanced responsiveness to sound in the auditory cortex of older people

In the present study, neural adaptation was measured as the neural response to a tone in sequences with varying intertone intervals to assess age differences in neural responsiveness (Herrmann et al., 2016b). We observed that the sensitivity of neural responses to intertone interval was larger in older than younger people, particularly for longer intervals. The results—similar to our other findings (Herrmann et al., 2016b, 2018)—suggest that, between successive tone presentations, neurons recover faster from adaptation in the aged auditory cortex. Consistently, a reduced suppression of neural responses to tones presented in isochronous sequences has been observed in the auditory cortex of aged compared with young rats, also indicating faster recovery from adaptation between successive tone presentations in older animals (de Villers-Sidani et al., 2010). In sum, the current results demonstrate enhanced responsiveness to sound in the auditory cortex for our sample of older people.

Notably, the level at which sounds were played during EEG recordings was, on average, louder (relative to hearing threshold) for younger than older people and slightly above the comfortable loudness level for younger people (Fig. 3B). Hence, we observed an enhanced neural responsiveness in the auditory cortex of older compared with younger people despite the fact that sounds were slightly quieter for older individuals.

The current results are consistent with previous findings in humans and animals that show an age-related enhancement of sound-evoked responses in the auditory cortex (Anderer et al., 1996; Bidelman et al., 2014; Herrmann et al., 2018; Hughes et al., 2010; Sörös et al., 2009; Tremblay et al., 2003). Our results are also in line with the observation that damage to the auditory periphery in animals leads to hyper-responsiveness in the afferent auditory system (Gerken, 1979; Möhrle et al., 2016; Popelár et al., 1987; Salvi et al., 2017; Syka et al., 1994). In fact, denervation of any biological structure appears to lead to hyper-responsiveness (Cannon and Rosenblueth, 1949; Gerken, 1979; Larrabee, 1949) and the observed effects may reflect a general property of denervated tissue. For the auditory sensory modality, enhancements of responsiveness in mammalian brain structures may be the result of a loss of inhibition (Auerbach et al., 2014; Caspary et al., 2008; Llano et al., 2012; Takesian et al., 2009, 2012) and an increase in excitation (Salvi et al., 2017).

An enhanced gain in older people may have a variety of consequences. First, neuronal firing is metabolically expensive (Attwell and Laughlin, 2001) and an enhanced responsiveness may thus lead to increased energy consumption. Increased responsiveness also appears to be associated with altered neural adaptation to sound statistics, which may impair the flexible adjustment of perceptual systems to different acoustic environments, and may underlie the challenges older people experience with filtering out

irrelevant information (Herrmann et al., 2018). Critically, previous work suggests that enhanced neural synchronization in the auditory cortex may be related to impaired speech perception (Goossens et al., 2018; Millman et al., 2017). Although our findings do not directly speak to speech processing, they suggest that acoustic environments may not be represented accurately in the aged brain, despite enhanced responsivity to sound in the auditory cortex.

#### 4.3. Age differences in 2 different neural signatures of temporal regularity

We investigated the differences between younger and older listeners for 2 different neural signatures of temporal regularity in sounds—neural synchronization and sustained neural activity. We observed that neural synchronization was enhanced in older people and that this effect could be narrowed down to about 30% of our sample. Our data are consistent with previous observations of enhanced neural synchronization for sounds that contain low-frequency amplitude modulations (Goossens et al., 2016; Herrmann et al., 2017; Lai et al., 2017; Purcell et al., 2004; Presacco et al., 2016a; b, 2019). The fact that the effects of age group in the present study appear somewhat weaker than previous work may be due to the slightly perceptually quieter level used for older compared with younger adults (previous work either used more intense sounds for older people or sounds of equal intensity; see also Goossens et al., 2019). This was done to avoid biasing our results toward our hypothesis of increased responsiveness to sound in the auditory cortex of older people.

Previous source localizations suggest that synchronization of neural activity with low-frequency temporal regularities in sounds is strongest in the auditory cortex (Herrmann et al., 2013b, 2016a; Keitel et al., 2017; Millman et al., 2017). The finding of enhanced synchronization in the auditory cortex of older people is consistent with the age-related changes in adaptation that we observed. Although modeling work suggests that changes in neural synchronization can be due to changes in adaptation properties of neurons (Augustin et al., 2013; Ladenbauer et al., 2012), in our hands, increased synchronization, and changes in adaptation did not correlate with each other.

In contrast to neural synchronization, stronger sustained neural activity in response to the sound's amplitude modulation (compared to the control stimulus without temporal regularity) was present in younger individuals, but absent in older people (with the difference between age groups approaching significance; Fig. 6). Previous source localizations have shown that hippocampus and frontal cortex (Barascud et al., 2016; Teki et al., 2016; Tiitinen et al., 2012) in addition to the auditory cortex (Gutschalk et al., 2002; Keceli et al., 2012; Pantev et al., 1994, 1996) may underlie the pattern of sustained activity in response to regularity. The topographical distributions of the sustained activity were widespread (Fig. 6) and are consistent with involvement of brain regions beyond the primary auditory cortex.

The regularity index, which reflects the relative weight of sustained neural activity versus neural synchronization for the processing of temporal regularity (Fig. 7), was significantly larger in younger than older individuals. In other words, younger individuals showed a larger regularity effect for sustained activity than for neural synchronization, whereas the older individuals showed a smaller regularity effect for sustained activity than for neural synchronization. Previous source localizations have indicated that low-frequency neural synchronization likely originates from the auditory cortex (Herrmann et al., 2013b, 2016a; Keitel et al., 2017; Millman et al., 2017) and that sustained activity likely originates from the auditory cortex and higher-level cortices (including

hippocampus, parietal cortex, and frontal cortex; Barascud et al., 2016; Gutschalk et al., 2002; Pantev et al., 1994; Tiitinen et al., 2012; Teki et al., 2016). We thus suggest that the difference in the regularity index between younger and older individuals may indicate a change in how regularity in sounds are represented in the cortex of older people, with an over-representation of temporal regularity in the auditory cortex and an under-representation of temporal regularity in the network involving higher-level brain regions.

The age difference in the regularity index may further indicate that a reliable sensory representation may not be sufficient for the processing of temporal regularity but may be unhelpful. Others have demonstrated that hearing loss appears to increase the perceived magnitude of low-frequency amplitude modulation in sounds (Moore et al., 1996). Our results are consistent in demonstrating that neural activity in central auditory brain structures of older people appears fundamentally altered and that these changes include altered sensitivity to a sound's temporal regularity in the auditory cortex and beyond.

#### 4.4. Aging versus hearing loss

In the present study, we investigated differences between younger people, 19–33 years of age, and older people, 55–76 years, in neural responses to temporal regularity in sounds. Older participants were recruited from the local community, reflecting a typical sample of older adults, who reported having no diagnosed hearing loss. Nevertheless, typical older adults, on average, show raised audiometric hearing thresholds at low frequencies of about 9 dB and more severe threshold shifts at high frequencies compared with younger adults (Fig. 2; Herrmann et al., 2018; Plack, 2014; Presacco et al., 2019). From a diagnostic perspective, hearing is often considered to be clinically impaired when audiometric thresholds are higher than 20–30 dB HL (Alain et al., 2014; Presacco et al., 2019; Walker et al., 2013). In previous research, older participants have sometimes been separated into those having “normal” hearing (i.e., hearing thresholds equal to or below the clinical cutoff) or “impaired” hearing (i.e., hearing thresholds above the clinical cutoff) (e.g., Alain et al., 2014; Millman et al., 2017; Presacco et al., 2019). This categorization may be valuable to identify how different degrees of hearing loss affect neural processing (Goossens et al., 2019; Millman et al., 2017; Presacco et al., 2019), but it is not realistic to assume that elevation of audiometric thresholds below a clinical cutoff mean that hearing is entirely “normal” as cautioned by the British Society of Audiology (BSA, 2011), only that clinical intervention is not yet indicated. From a functional perspective, elevation of hearing thresholds appears to be a continuum (e.g., Fig. 2) rather than categorical (i.e., a bimodal distribution) for typical, aging adults without acute, traumatic noise exposure in their past.

Critically, recent work separating older adults into normal-hearing and hearing-impaired listeners found no difference in low-frequency neural synchronization in the cortex (Goossens et al., 2019; Presacco et al., 2019), only reporting differences between younger and older adults (Goossens et al., 2016; Presacco et al., 2016a). Consistent with this recent work, no correlations between audiometric thresholds and cortical responses were observed in the present study. This may suggest either (1) that other factors associated with aging, but not changes contributing to audiometric thresholds, are related to enhanced responsiveness and changes in neural signatures of temporal regularity processing, or (2) that the relation between audiometric thresholds and cortical processing is complex and potentially nonlinear, or (3) that other peripheral damage that is not captured by the audiogram, such as loss of synapses connecting hair cells to auditory nerve fibers

(Liberman and Kujawa, 2017) is linked to hyper-responsiveness and changes in neural signatures of temporal regularity processing in older people.

## 5. Conclusions

In the present study, we investigated differences between younger and older listeners in the sensitivity of cortical structures to temporal regularity—here, amplitude modulation—in sounds. Synchronization of auditory cortex activity with the amplitude modulation of narrow-band noises was enhanced in about 30% of older compared with younger people. Despite the reliable representation of temporal regularity in the auditory cortex (as indicated by neural synchronization), sustained neural activity—a neural signature of regularity processing that probably involves higher-order brain regions such as frontal and parietal cortex—was diminished in older people. The data may suggest a functional reorganization in older people that includes an over-representation of low-frequency amplitude modulation in the auditory cortex but diminished representations of amplitude modulation in higher-order cortical areas.

## Disclosure

All authors report no conflicts of interest.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neurobiolaging.2019.08.028>.

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