Reduced neural sensitivity to musical tempo despite enhanced neural tracking of musical features in older adults

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Keywords: neural tracking, electroencephalography, aging, music perception, temporal response function (TRF)

ABSTRACT

A substantial body of prior research has focused on how aging affects the neural processing of speech, whereas less is known about how older adults encode naturalistic music. Here, we investigated whether the neural tracking of different features in naturalistic music differs between age groups. Younger and older adults (both sexes) listened to excerpts of naturalistic music with different tempi (1-4 Hz) while electroencephalography (EEG) was recorded. The results show an age-related enhancement of neural responses to sound onsets, suggesting a loss of inhibition in the aged auditory cortex that is thought to arise from peripheral decline. This hyperresponsiveness generalized to the neural tracking of multiple features (amplitude envelope, onsets, beat, and spectral flux) in naturalistic music. Crucially, older adults showed reduced sensitivity of early brain responses (0-130 ms) to tempo: Unlike younger adults, whose neural tracking decreased systematically with increasing tempo, older listeners maintained uniformly enhanced tracking across tempi. Spectral flux best predicted tempo-related changes in EEG activity, but this was reduced in older compared to younger adults. In sum, the current study demonstrates that cortical hyperactivity in aging enhances the tracking of different features during naturalistic music listening but impairs the sensitivity to musical tempo. This dissociation highlights the complex changes and functional consequences of auditory aging related to the processing of naturalistic music.

SIGNIFICANCE STATEMENT

How aging affects the encoding of ecologically-valid, naturalistic music is not well understood, although music is an important part of older people's lives. Here, we used electroencephalography and temporal response function approaches to investigate how younger and older adults encode different features of naturalistic music at different tempi (1 to 4 Hz). The results reveal a fundamental trade-off in the aging auditory system: enhanced neural tracking of acoustic features coexists with declined sensitivity to musical tempo. This dissociation between hyperactivity for feature encoding and impaired temporal sensitivity highlights complex changes in the aged auditory system that can have implications for music perception in older adulthood.

INTRODUCTION

Aging is associated with a host of changes in auditory function, including reduced sensitivity to sound due to peripheral decline (Gratton and Vázquez, 2003; Jayakody et al., 2018) and aberrant plasticity in brain regions downstream, most prominently in auditory cortex (Ibrahim and Llano, 2019; Herrmann and Butler, 2021). Age-related changes in auditory function affect the processing of complex sound stimuli, with a large body of work focusing on changes in the perception and neural encoding of speech (Gordon-Salant and Fitzgibbons, 1999; Wöstmann et al., 2015). However, age-related changes in auditory function likely also impact music processing. For instance, older adults show different music preferences relative to their younger selves (Cohrdes et al., 2017), exhibit declines in pitch discrimination and chord categorization (Clinard et al., 2010; Bones and Plack, 2015), and experience challenges in processing mistuned harmonics of complex tones (Alain et al., 2012). Fundamentally, tracking dynamic temporal and spectral changes in music is vital for music perception (Stewart et al., 2006; Koelsch, 2011; Janata, 2015), but little is known about how aging affects the brain's ability to track features of naturalistic music over time.

Despite significant advances in understanding neural responses to music (Doelling and Poeppel, 2015; Norman-Haignere et al., 2015, 2022; Zuk et al., 2021), gaps remain in how the brain processes complex, naturalistic musical stimuli. Much research has focused on the neural processing of simplified music, such as tones or MIDI sound sequences. Analyses have typically relied on auditory evoked potentials (ERPs) to characterize fundamental processing mechanisms, including temporal coding fidelity via P1-N1-P2 components (Koelsch et al. 2000; Shahin et al. 2003) and deviance detection (encompassing spectral, temporal, or intensity changes) through the mismatch negativity (Näätänen et al., 1987; Tervaniemi et al., 2001). Despite the advantages in isolating specific acoustic features and establishing a relationship between stimulus properties and neural responses (Näätänen et al., 2007), these stimuli and ERP approaches are unable to capture the complexities and temporal evolution of real music.

Research addressing this ecological gap has focused on neural tracking, that is, the synchronization of neural activity (e.g., measured via EEG/MEG) with dynamic features of continuous stimuli (Lalor and Foxe, 2009; Lalor et al., 2009). Recent work has focused on the neural tracking of the amplitude envelope in naturalistic music (Di Liberto et al., 2020; Zuk et al., 2021; Keitel et al., 2025), inspired by speech-envelope tracking research (Luo and Poeppel, 2007; Ding and Simon, 2012). However, spectral features (e.g., timbre and melodic structure) are equally crucial in music. Research demonstrates that younger listeners track

spectral content more robustly than the amplitude envelope of naturalistic music, with strongest tracking at slower tempi (1-2 Hz; Bauer et al., 2015; Weineck et al., 2022). This tempo-effect may be linked to auditory event density, where sparser temporal structure allows more effective neural encoding (Näätänen et al., 1987). This research has thus far only focused on younger adults, whereas the extent to which aging affects the neural tracking of these features during naturalistic music listening is unknown.

Aging and hearing loss can lead to brain plasticity that may impact the neural encoding of music. Specifically, any peripheral damage that reduces acoustic inputs can lead to a loss of inhibition and an increase in excitation in the auditory cortex (Parry et al., 2018; Salvi et al., 2016; Herrmann and Butler, 2021). This, in turn, can manifest as hyperresponsiveness to sound, where, for example, simple tones or noise bursts often elicit larger ERP responses in the auditory cortex of older people compared to younger adults (Alain et al., 2012; Presacco et al., 2016). Moreover, older adults show increased neural tracking of amplitude and spectral features in simple continuous stimuli (e.g., tone sequences, modulated noise; Purcell et al., 2004; Goossens et al., 2016, 2019; Herrmann et al., 2019; but see Henry et al., 2017), suggesting that the loss of inhibition could also alter the neural tracking of features in naturalistic music.

A few studies have focused on the age-related changes in neural tracking of naturalistic auditory stimuli, namely the tracking of speech. The neural tracking of the amplitude envelope of speech is enhanced in older compared to younger adults (Presacco et al., 2016; Brodbeck et al., 2018; Decruy et al., 2019, 2020; Broderick et al., 2021; Panela et al., 2024), consistent with a loss of inhibition and an increase in excitation in the auditory cortex of older adults (Herrmann and Butler, 2021). However, hyperactivity may also impair the accurate encoding of features in music, which could underlie changes in music perception in older adulthood. In the current electroencephalography study, we investigate whether aging affects the neural tracking of different features (i.e., amplitude, spectral, beat) in naturalistic music at different tempi. Our multi-feature approach affords answering whether age-related hyperactivity is present during music encoding and whether it uniformly alters music tracking across different features and tempi.

MATERIALS AND METHODS

Participants

32 younger adults (22 females, 10 males; mean age: 24.4 years, age range: 19-34 years; data from our previous study; (Weineck et al., 2022)) and 34 older adults (16 females, 18 males, mean 66.2 years, 58-82 years of age) with self-reported normal hearing participated in the study. We reanalyzed the data from younger adults (Weineck et al., 2022) jointly with the new data from older adults that were recorded using the same experimental procedures. Data from 5 additional younger adults and 4 additional older adults were recorded but not included in further analyses, because a high number of trials contained artifacts in the EEG data (see below). Most participants self-reported normal hearing (4 participants reported occasional ringing in on or both ears and one reported hyperacusis since a young age). Participants' demographic background was obtained online through the LimeSurvey platform (LimeSurvey GmbH, Germany, https://www.limesurvey.org) prior to the main in-person session. Participants were remunerated for their online and in-person participation (Online: 2.50 €, EEG: 7 € per 30 min). All participants provided informed consent prior to the experiment. The study was approved by the Ethics Council of the Max Planck Society Ethics Council in compliance with the Declaration of Helsinki.

Pure-tone audiometry and estimation of sensation level

Participants underwent an audiogram hearing test (MA 25 Audiometer, Robert Bosch GmbH, Germany) at the beginning of the experiment. Audiogram data from younger participants were not available in our previous study (Weineck et al., 2022). Therefore, in the current study, we collected audiogram data from 18 new younger participants matched for age with the younger group in the original study from which the EEG data were taken (Weineck et al., 2022). Audiometric thresholds were assessed for pure tones at frequencies of 0.25, 0.5, 1, 2, 4, and 8 kHz (Figure 1A). The pure-tone average (PTA) was calculated as the average across the thresholds of 4 frequencies (0.5, 1, 2, and 4 kHz; Figure 1B). Compared to younger individuals, older adults showed elevated hearing thresholds ($t_{50} = 6.16$, $p = 1.23 \cdot 10^{-7}$, $\eta^2 = 1.80$), aligning with previous research (Peelle et al., 2011; Slade et al., 2020) and the prevalence of hearing thresholds in community-dwelling older adults (Cruickshanks et al., 1998; Feder et al., 2015; Goman and Lin, 2016).

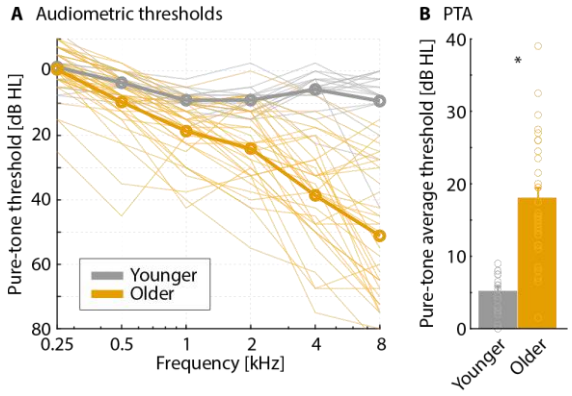

Figure 1. Audiograms and hearing thresholds for younger and older adults. A: Audiograms. Thick lines denote group-mean data and thin lines represent individual participant data. **B:** Pure-tone average (PTA) for both age groups (mean across 0.5, 1, 2, and 4 kHz). Individual data points are denoted by dots. *p < .05.

The sensation level was also determined for each person in MATLAB. To this end, participants listened to white-noise sounds of 12 s duration whose sound level continuously increased or decreased (6 trials each), and responded promptly upon detecting the presence of the noise (increasing sound level) or no longer hearing the noise (decreasing sound level) (Herrmann and Johnsrude, 2018). The sound level at which a participant pressed the button was averaged across the 6 trials to obtain the participant's sensation level. Note that sensation-level data from young adults were available from the previous study (Weineck et al., 2022). Sensation levels were lower for younger adults (-63.1 dB; MATLAB full scale) compared to older adults (-52.6 dB; $t_{64} = 6.95$, $p = 2.31 \cdot 10^{-9}$, $\eta^2 = 1.71$), as expected given the audiograms.

For younger adults, all music stimuli were presented at 50 dB above their individual sensational level (Weineck et al., 2022). Music stimuli for older adults were presented at a fixed sound level that corresponded to the mean level at which sounds were presented to younger adults. Hence, sounds were, on average, presented at the same sound-pressure level (SPL) for younger and older adults. We opted to present stimuli at the same SPL rather than at the same sensation level (that is, relative to individual thresholds), because the latter would have led to higher sound intensities for older compared to younger adults, given their elevated thresholds. Higher sound intensities can lead to larger brain responses (Woods et al., 2006; Sun et al., 2012). This could have confounded our main hypothesis that the neural tracking of music may be enhanced for older compared to younger adults, given previous age-related neural tracking enhancements for speech and modulated noise sounds (Alain, 2014; Herrmann et al., 2019). By presenting music stimuli at the same SPL across age groups (on average), we rather work against this hypothesis, while ensuring that stimuli were clearly audible for all participants. Using the same SPL also reflects more closely natural environments where the sound level is often not under control of a person. Moreover, older adults may have a compressed dynamic range, such that very soft sounds are not perceived, whereas sound at high levels can be perceived as being too loud (Slade et al., 2020; Shehabi

et al., 2022). Younger and older adults tend to perceive sounds as similarly loud for the mid-range sound levels used in the current study (Herrmann et al., 2019).

Stimuli

We adopted the same stimuli and procedures that we used to record the data for younger adults in our previous study (Weineck et al., 2022). The auditory materials initially consisted of 93 segments extracted from 39 full instrumental musical pieces spanning four primary genres: techno, rock, blues, and hip-hop, accessible for download from the Qobuz Downloadstore (https://www.qobuz.com/de-de/shop). Each segment was manually epoched at musical phrase boundaries, such as transitions between choruses and verses, resulting in musical segments with durations varying from 14.4 to 38 s. To determine the original tempo of each musical segment, we did not use beat counts from publicly available software, as its outputs lacked sufficient reliability for cross-genre tempo analysis. Instead, we asked a professionally trained percussionist to tap to the beat of each segment with a wooden drumstick on a MIDI drum pad. The tap tempo (BPMs, beats per minute) was extracted from the MIDI files. Each segment was repeated three times, and the final BPM was the average between the two takes with least difference.

Musical segments were then tempo-modulated to a range of 1 to 4 Hz in steps in 0.25 Hz increments (i.e., 13 tempi). The tempo manipulation was carried out using a customized MAX patch (MAX 8.1.0, Cycling ’74, CA, USA), which changes the tempo of music without changing the pitch. To ensure that stimuli had unambiguous, easily tappable beats, 8 individuals were asked to listen and tap to each segment on their computer keyboards for a minimum of 17 taps while their key strokes were recorded and analyzed using an online BPM tool (beats per minute; https://www.all8.com/tools/bpm.htm). 21 musical excerpts were excluded exhibiting high inter-tapper variability (>2 tappers diverging from the group) or poor sound quality. The process resulted in 703 music excerpts, varying in duration from 8.3 to 56.6 seconds across the 13 tempi conditions. While faster tempi resulted in shorter durations and slower tempi in longer durations for a unique musical piece, this ensures that the same number of rhythmic cycles are present for each condition.

To obtain a balanced distribution of stimulus conditions and avoid redundancy, the musical excerpts were pseudo-randomly allocated into four groups (Kaneshiro et al., 2020). Each group comprised 159 to 162 musical excerpts (trials). Each musical excerpt could repeat up to three times across different tempi within the same group, but was never repeated for a unique tempo (Weineck et al., 2022). All musical excerpts were mono WAV files with a sampling rate of 44,100 Hz. Each file featured a smooth linear-ramping fade-in and fade-out

phase of 500 ms, and underwent root-mean-squared normalization using custom MATLAB scripts. Auditory stimuli in the study were played through a Fireface sound card (RME Fireface UCX Audiointerface, Germany) via headphones (Beyerdynamics DT-770 Pro, Beyerdynamic GmbH & Co., Germany). Auditory and visual stimuli were delivered using custom-written MATLAB scripts with Psychtoolbox (PTB-3, Brainard, 1997) in MATLAB (R2021a; The MathWorks, USA).

Experimental design

The experimental procedures were conducted in an acoustically and electrically shielded booth. Verbal instructions for the experimental procedures were provided by the experimenter, complemented by written instructions displayed on the screen (BenQ Monitor XL2420Z, 144 Hz, 24”, 1920 × 1080). Each participant was assigned to one of the four groups of musical excerpts, with total trial numbers varying from 159 to 162. The study lasted approximately 2.5 hours.

The main task comprised eight blocks, and participants were allowed to take breaks between blocks as needed. Each block contained 19 to 21 trials, depending on the group of stimuli to which the participant assigned. Each trial comprised three phases: attentive listening (music stimulation without movement or responses), tapping (music stimulation with finger tapping) and rating. In the attentive listening phase, a fixation cross was presented on the computer screen and a music excerpt was presented to the participant. Participants were instructed to mentally identify the beat of the musical excerpt without any physical movement, devoting full attention to the music presentation. The duration of this phase varied for each trial, ranging from 8.3 to 56.6 seconds (depending on the duration of the musical excerpt). Following a 1-second interval after the music presentation ended, a visual cue (a cartoon picture of a hand) appeared on the screen, signaling the start of the tapping task. Simultaneously, the final 5.5 s segment of the previously heard musical excerpt was replayed, and participants were instructed to tap a finger in accordance with the beat. In the rating phase, participants were asked to assess the musical excerpt separately based on enjoyment/pleasure, familiarity, and ease of tapping to the beat using a visual analogue scale with the computer mouse. The scale ranged from -100 to +100, representing self-evaluations from ‘not at all’ to ‘very much’. Participants performed a brief three-trial training before the main task was performed. The aim of the current study was to investigate the degree to which the neural encoding of different features and tempi in naturalistic music differed between age groups. Analyses thus focused on the ‘attentive listening’ phase (i.e., phase 1) of the experiment.

EEG recording and pre-processing

EEG data were recorded using the BrainVision Recorder (v.1.21.0303, Brain Products GmbH, Gilching, Germany) and a Brain Products actiCAP system with 32 active electrodes attached to an elastic cap based on the international 10–20 placement (actiCAP 64Ch Standard-2 Layout Ch1-32, Brain Products GmbH, Germany). The EEG signals were sampled at a rate of 1000 Hz using an online low-pass filter at 250 Hz with electrode impedances consistently maintained below 10 kOhm. To ensure precise time alignment between the recorded EEG data and the auditory stimuli, a TTL trigger pulse was sent at both the onset and offset of each musical excerpt via a parallel port.

Offline data analysis was carried out using MATLAB software (R2021b; The MathWorks, Natick, MA, USA) with custom-written code combined with the Fieldtrip toolbox (Oostenveld et al., 2010). The continuous EEG data were bandpass filtered between 0.5 and 30 Hz (Butterworth and FIR two-pass filter), re-referenced to the average reference, and down-sampled to 500 Hz. EEG data were segmented into time series time-locked to the onset of each musical excerpt. Trials exhibiting a signal change of more than 1000 μV for any electrode were excluded from analyses to remove trials with huge artifacts that could bias Independent Component Analysis (ICA). ICA was calculated to identify and suppress activity related to eye blinks, horizontal eye movements, and cardiac artifacts. Following the transformation of data back from the ICA component space to the electrode space (after removing artifact components), trials with a signal change exceeding 400 μV in any electrode were excluded from analyses. Participants with less than 60% of valid trials were removed from analysis. Data from 5 younger adults and 4 older adults were excluded based on this criterion.

Data analysis

Analysis of neural response to music onset

We first examined the neural responses elicited by the onsets of the music stimuli. This analysis was conducted to investigate whether hyperactivity is present in older compared to younger adults (Anari et al., 1999; Herrmann and Butler, 2021). For each participant, EEG data were divided into epochs ranging from 100 ms before to 400 ms after the onset of each musical excerpt. Data were averaged across all trials. The averaged response was baseline-corrected by subtracting the mean amplitude in the pre-stimulus time window (-100 to 0 ms) from the amplitude at each time point. Data were averaged across 10 electrodes from a frontal-central cluster (F3, F4, Fz, FC5, FC6, FC1, FC2, C3, Cz, C4) that is known to be most sensitive to neural activity originating from auditory cortex (Näätänen et al., 1987; Picton et al., 2003). To examine the difference in onset responses between age groups, we conducted independent samples t-tests on the response amplitude at each time point. We identified the

time intervals indicative of group differences based on the adjusted p values (*p<.05) using the False Discovery Rate (FDR) method (Benjamini and Hochberg, 1995; Genovese et al., 2002).

Calculation of feature vectors in naturalistic music

We used the features adopted in our previous publication for all musical stimuli (Weineck et al., 2022). In total, four features were calculated: amplitude envelope, amplitude-onset envelope, beat, and spectral flux. The amplitude envelope was determined using a 128-channel gammatone filterbank between 60 to 6000 Hz (Patterson et al., 1987; Lopez-Poveda and Meddis, 2001). To calculate the amplitude-onset envelope, we applied half-wave rectification to the first derivative of the amplitude envelope, capturing the onsets and energy changes in the stimulus over time (Fiedler et al., 2017; Panela et al., 2024). The beat of each music segment was determined by a professional percussionist drumming in synchronization with the original tempo using drumsticks resulting in a binary-coded time series (0 for no beat and 1 for beat). The percussionist repeated each segment three times. The final beat vectors were determined by the average two takes with the minimal differences. Spectral flux was calculated by comparing the logarithmic amplitude spectrogram between consecutive time frames (each frame comprising 344 samples), reflecting the rate of power spectrum changes. All features in the naturalistic music were z-scored and down-sampled to 128 Hz. To ensure consistent sample sizes across stimulus features, the data were trimmed to match.

Analysis of neural tracking of features in music

We used temporal responses functions (TRFs) and EEG prediction accuracy to investigate whether the neural tracking of features in music differed between age groups. The temporal response function (TRF) is a system identification model that relates features of a sensory stimulus and the neural response based on regularized linear regression (Ding and Simon, 2012; Haufe et al., 2014). In this study, we adopted the TRF model to characterize how different features map onto the EEG signals (forward model) using the MATLAB toolbox “The multivariate Temporal Response Function (mTRF) Toolbox” (Crosse et al., 2016, 2021). To eliminate onset responses elicited by the start of the music excerpt, data from the first second following stimulus onset were excluded from further analysis. EEG data were down-sampled to 128 Hz for the TRF calculation.

For each of the 13 tempo conditions, EEG data from all trials and the corresponding time series for each feature were selected for model calculation using leave-one-trial-out cross-validation iterations. For each iteration, the EEG data and feature time series of one trial

served as the test dataset and was held out, whereas the EEG data and feature time series of the remaining trials served as the training dataset. The model training incorporated time lags ranging from 0 - 400 ms (using the functions *mTRFcrossval* and *mTRFtrain*). The model implemented ridge regularization to prevent overfitting, and the training process allowed us to determine the optimized ridge parameter (λ), maximizing the correlation between the actual and predicted neural response from the training outputs (λ range: 10^{-6} - 10^{6}). This process was repeated for each feature (Di Liberto et al., 2020). The primary output of the model training – that is, TRF weights assigned to each channel – reflects the modulation of the EEG signal in response to a change in a particular feature (Crosse et al., 2016, 2021) and was used for subsequent analysis. To obtain the accuracy with which the EEG response of the test dataset (i.e., the trial that was left out) could be predicted based on the TRF model, the feature time series of the test dataset was convolved with the TRF weights, resulting in a predicted EEG time series (separately for each feature). EEG prediction accuracy was then calculated as the Pearson correlation between the predicted and the actual EEG data (EEG prediction accuracy was calculated using the function *mTRFpredict*). TRF weights and EEG prediction accuracy were calculated for each participant separately for each of the 13 tempi. TRF weights and EEG prediction accuracy were averaged across the 10 electrodes of the frontal-central cluster (F3, F4, Fz, FC5, FC6, FC1, FC2, C3, Cz, C4) that are sensitive to neural activity from the auditory cortex.

We first assessed neural responses for each age group and age-group differences in neural responses independently of musical tempi. To this end, TRF time courses (weights) were averaged across the 13 tempi, separately for each feature and participant. We examined the TRF weights within each age group by calculating a one-sample test against zero, separately for each time point. FDR-thresholding was used to account for multiple comparisons. This analysis tests whether neural responses were modulated by a specific feature in music, separately for each age group. We then compared TRF weights between the two age groups using separate independent samples t-tests for each time point (including FDR-thresholding).

TRF time courses are characterized by positive and negative deflections (peaks), similar to the traditional event-related potential (Crosse et al. 2016; Crosse et al. 2021; Luck 2014). To examine response magnitude differences between age groups, analyses focused on the peaks in the TRF time courses. We analyzed the P1-N1 (first major positive peak minus first major negative peak) and P2-N1 amplitude differences in both age groups, separated by the four different features (see similar approaches for event-related potential analyses and TRF analyses: (Tremblay et al., 2001; Wagner et al., 2017; Herrmann, 2025). The P1, N1 and P2 amplitudes were determined by the local extrema (maximum for P1 and P2 components,

minimum for the N1 component) in the TRF weights within a 100-ms time window that included the corresponding component. The latencies of the P1, N1 and P2 components were thus identified by the time points corresponding to these extrema. For each participant, the P1, N1 and P2 amplitudes were determined by the local extreme values within a 30-ms time window centered at the averaged latencies of each component for each age group. Subsequently, the P1-N1 and P2-N1 amplitude differences were calculated by subtracting the amplitudes of the N1 from P1, and N1 from P2, respectively. Age-group differences in the P1-N1 and P2-N1 amplitude were assessed using independent samples t-tests for each feature.

In the previous study (Weineck et al., 2022), we found that the musical tempo affected TRF accuracy: TRF accuracy decreased as tempo increased, particularly for the spectral flux feature. Additionally, tempo also played a role on the TRF weights at different time points (ranging from 0 to 400 ms). Therefore, we conducted a nuanced analysis to investigate the 'sensitivity' of TRF weights to music pieces with different tempi. For each feature, we first defined a sliding time window of 62.5 ms (i.e., 9 samples) centered at each time point on the time courses of the TRF weights and averaged the weight values within each time window per participant. This sliding-window averaging procedure served to smooth data and mitigate local fluctuations at each data point prior to the musical-tempo analysis. Subsequently, we calculated a linear regression for each time point of the smoothed TRF, to linearly relate the 13 tempi to the TRF weights. The resulting slope value of this regression quantifies the degree of TRF weight change as a function of musical tempo (separately for each time point). Slope values were tested against zero using a one-sample t-test, separately for each age group (younger, older) and feature (amplitude envelope, onset envelope, beat, spectral flux), to examine whether musical tempo was associated with a change in the neural responses. The t-tests were performed for each time point within each age group and feature (FDR-thresholded). Age-group differences were examined using an independent samples t-test at each time point (FDR-thresholded).

In addition to the analysis of the TRF time courses (weights), we also analyzed the EEG prediction accuracy (i.e., TRF correlation: correlation between predicted and actual EEG) – another metric that reflects the strength of neural tracking. To examine age-group differences for EEG prediction accuracy without the tempi influences, we first averaged the prediction accuracy across 13 tempi separately for each of the four features. The averaged TRF correlations were submitted to a 2 × 4 mixed-design ANOVA, with 'Age Group' (younger, older) as a between-subjects factor and 'Feature' (envelope, amplitude-onset, beat, and spectral flux) as a within-subjects factor. Post-hoc pairwise comparisons were conducted using the Bonferroni correction. To evaluate how musical tempo affects EEG prediction accuracy, we

calculated a linear regression relating musical tempo to EEG prediction accuracy, separately for each participant and feature. The slope of the linear regression was tested against zero using a one-sample t-test for each feature and age group. Age-groups were compared using an independent samples t-test.

RESULTS

Auditory onset responses in older and younger adults

Figure 2 shows the neural responses to the onset of the musical excerpts for both age groups. Within the time range of 134-260 ms, responses significantly differed between age groups (FDR-thresholded). The response difference in this time window is the result of an enhanced and delayed N1 component, along with a diminished and delayed P2 component, in older compared to the younger adults. These results are consistent with previous research in auditory perception and aging, which may suggest differences in the information flow in auditory regions in response to complex acoustic features as well as with hyperactivity in auditory cortex of older adults (Friedman et al., 1993; Friedman, 2013; Henry et al., 2017b; Irsik et al., 2021; Herrmann et al., 2022).

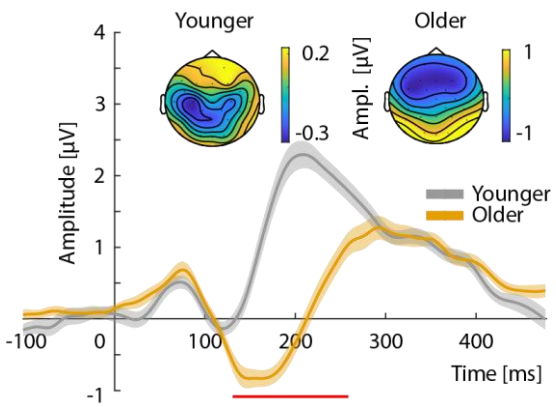

Figure 2. Neural responses to the onset of musical excerpts. Group-averaged time courses are displayed by the two colored curves. Shaded areas mark the standard error of the mean (SEM). The red line at the bottom marks the time window exhibiting a significant difference between age groups ($p_{FDR} < .05$). Topographies for the N1 component for the two age groups (based on the time window centered on the local minimum, separately for each age group).

Neural tracking of features in music is enhanced in older adults

We investigated the neural tracking of four different features in naturalistic music (amplitude envelope, amplitude-onset envelope, beat, and spectral flux) in younger and older adults. As shown in Figure 3, the averaged TRFs exhibited temporal patterns consistent with a canonical auditory P1-N1-P2 complex in both age groups (Martin et al., 2008; Picton, 2013). The N1 component was enlarged, and the P2 component was delayed in older adults compared to younger adults for the amplitude envelope, amplitude-onset envelope, and spectral flux, but not for the beat ($p_{FDR} <.05$).

To further investigate age-related differences in the P1-N1-P2 complex of the TRF weights, we calculated the P1-N1 and P2-N1 amplitude for each feature. Results showed that the P1-N1 amplitude was significantly larger in older adults compared to younger adults for all four features (envelope: $t_{64} = 3.29$, $p = .002$, $\eta^2 = .79$; onset: $t_{64} = 2.11$, $p = .04$, $\eta^2 = .49$; beat: $t_{64} = 3.64$, $p = 5.52 \cdot 10^{-4}$, $\eta^2 = .89$; spectral flux: $t_{64} = 3.33$, $p = .002$ $\eta^2 = .81$). In contrast, the P2-N1 amplitude difference was significantly larger for older adults for the envelope ($t_{64} = 3.29$, $p = .005$, $\eta^2 = .72$), and the beat ($t_{64} = 2.11$, $p = 2.44 \cdot 10^{-5}$, $\eta^2 = 1.12$). Unlike the other three features, the age-related enhancement of the N1-P1 and N1-P2 for the beat feature (Figure 3E and F) shows later latencies. These findings are consistent with the age-related enhancement of the neural responses to the stimulus onset in Figure 2.

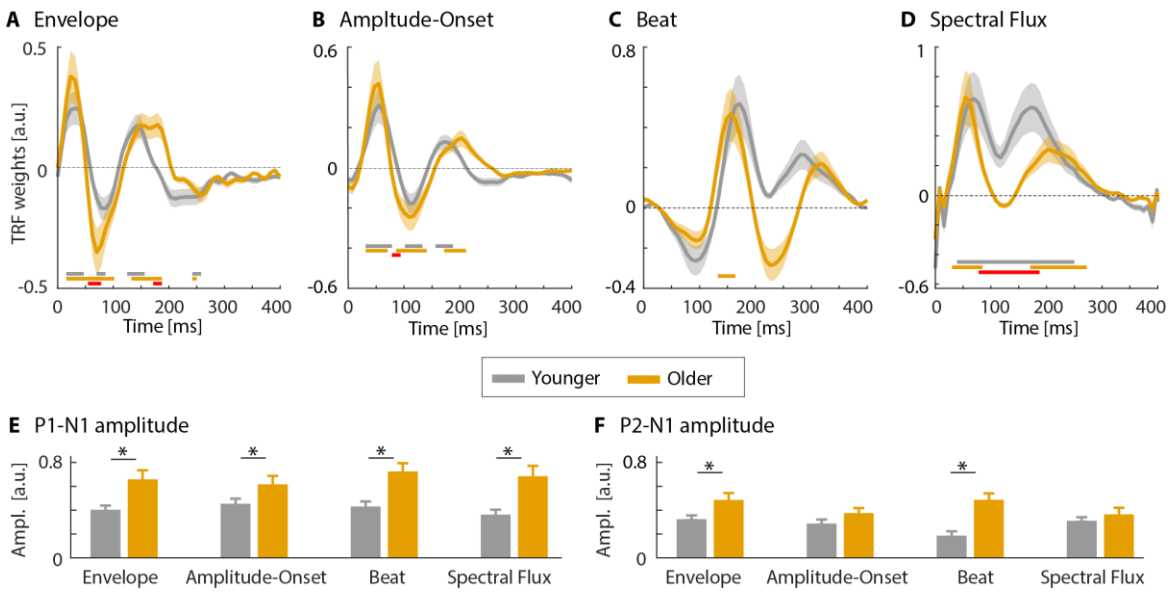

Figure 3. Neural tracking (TRF weights) for four features in naturalistic music and two age groups. A-D: Averaged TRF weights courses (shaded area around means reflects the SEM) for four features (averaged across tempi) and both age groups. Horizontal lines at the bottom mark the time window exhibiting a significant difference ($p_{FDR} < .05$) in TRF weights between age groups (red line) and within each group against 0 (younger adults: gray; older adults: yellow). **E-F:** P1-N1 and P2-N1 amplitude differences for TRF weights between age groups, separately for the four features. *p < 0.05

Sensitivity of neural tracking to musical tempo differs between age groups for early neural responses

Figure 4 shows the TRF time courses (weights) for each of the 13 different musical tempi. The sensitivity of TRF weights to musical tempo was assessed using the slope from the regression of TRF weight as a function of tempo steps at each time point of the time course (Figure 5).

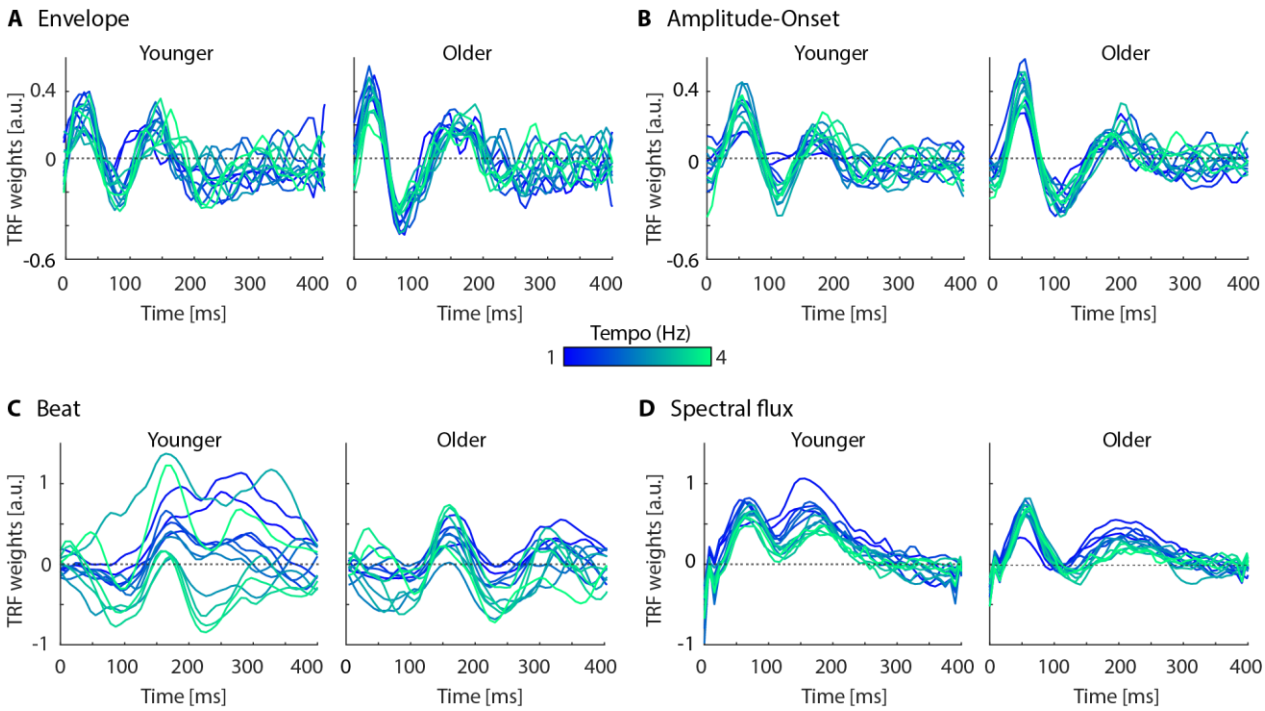

Figure 4. TRF time courses (weights) for each feature in music and music tempo. Each curve depicts the TRF weights from one musical tempo (13 tempi from 1 Hz to 4 Hz in steps of 0.25 Hz, blue to green).

Within each age group, we first examined the TRF sensitivity by comparing slope values against zero, separately for each feature (Figure 5). For this analysis, we were only interested in whether the slopes are different from zero, and were less concerned with the directionality of the effect because the positive and negative deflections in the TRF time courses can influence the slope's sign while reflecting a similar neural sensitivity to tempo. We evaluate the drivers of any slope effects subsequently in Figure 6 and the corresponding text.

For the amplitude envelope and onset-envelope, younger individuals showed effects of tempo modulation in two early time windows (Figure 5A and B): 100-133 ms (negative values) and 179-226 ms (positive values), but not for older adults. Age-group differences for the amplitude envelope were observed in the 62-102 ms and 164-211 ms ranges (Figure 5A). For spectral flux, younger adults show an extended effect of tempo (32-289 ms), such that TRF weights were larger for slower tempi, whereas older adults showed the effect only for a later time window (133-266 ms). Indeed, the effect was greater in younger compared to older adults in an early time window (47- 140 ms). No effects of tempo nor age group were observed for the beat. In sum, the results from these analyses show that early auditory cortex responses in

younger adults are sensitive to musical tempo, whereas only later responses are sensitive to tempo in older adults.

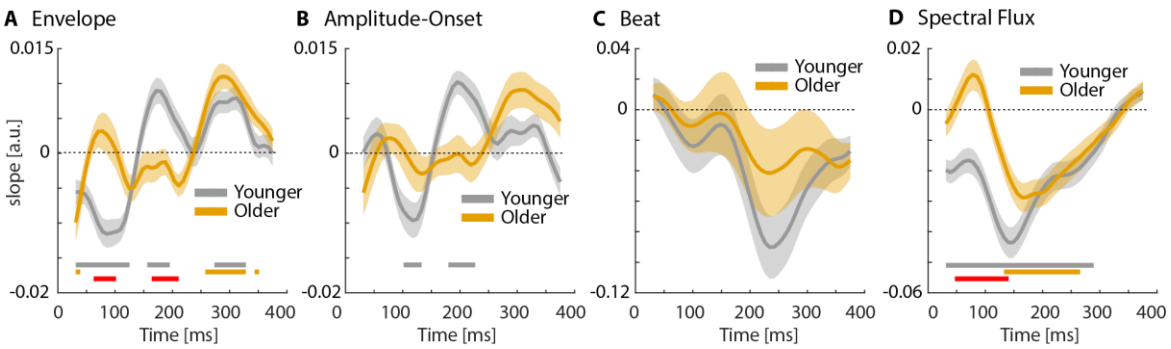

Figure 5. Slopes (linear coefficient) from the regression analysis relating musical tempo to TRF weights. Average slope time courses (shaded area: ±SEM). Horizontal lines at the bottom mark the time window exhibiting a significant difference (p_{FDR} <.05) in the slope between age groups (red line) and within each group against 0 (younger adults: gray; older adults: yellow).

The linear effects characterized by the slopes in Figure 5 reflect neural sensitivity to tempo, but the polarity of the slopes varied due to the TRF deflections in the time courses. To characterize in more detail the underlying structure of the neural tempo sensitivity, we overlaid the averaged TRF time courses across the slowest three tempi (1, 1.25, and 1.5 Hz) and the fastest three tempi (3.5, 3.75, and 4 Hz) with the slope time courses (Figure 6). This indicates that the tempo effect on the envelope and the amplitude-onset in younger adults, at least to some extent, results from a latency delay of the N1 and P2 components as tempo increases. Both age groups showed sensitivity to tempo for the envelope and spectral flux in a later time window, such that the envelope TRF weights were larger for faster tempos, whereas the spectral flux TRF weights were larger for slower tempos.

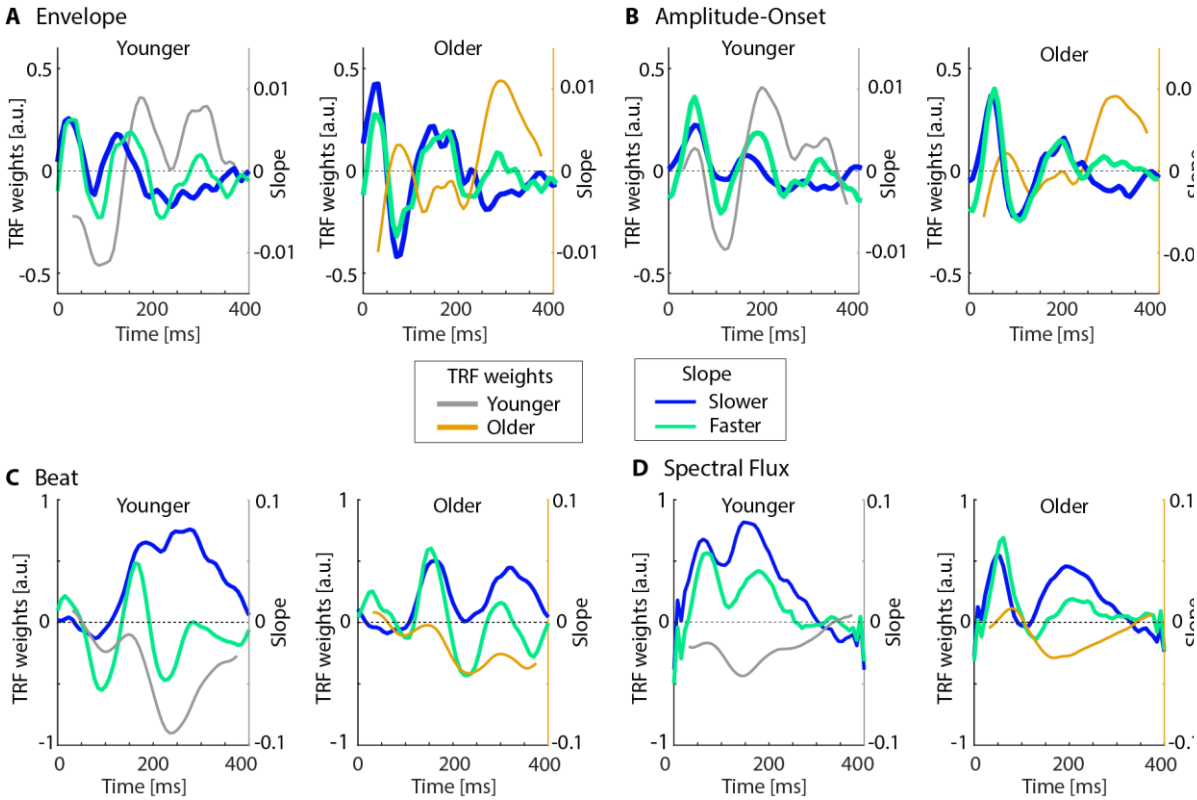

Figure 6. TRF weights for slower and faster tempi, overlaid by the slope (linear coefficient) from the regression model relating TRF weights to musical tempo. A: Average TRF weights across the slowest three tempi (1-1.5Hz; blue lines) and the fastest three tempi (3.5-4Hz; green lines) overlaid by the slope (linear coefficients) from the regression analysis of TRF weights as a function of 13 tempo steps in younger and older adults for the amplitude envelope. **B-D:** similar to panel A, but for the other three features: amplitude-onset envelope (panels B), beat (panel C) and spectral flux (panel D).

Age-groups differences in EEG prediction accuracy manifest strongest for spectral flux

Results for EEG prediction accuracy from both age groups are displayed in Figure 7. The mean prediction accuracy for the four features, independent of musical tempo, did not differ between age groups (main effect of Age Group: $F_{1,64}$ =.09, p =.77, η_p^2 =.001; Figure 7A). Averaged EEG prediction accuracy across all tempi was largest for spectral flux, relative to the other acoustic features (effect of Acoustic Feature: $F_{3,192}$ = 185.02, p = $2.17 \cdot 10^{-56}$, η_p^2 = .74), as indicated by post hoc tests (Bonferroni corrected) comparing prediction accuracy values from spectral flux to all three other features in both age groups (all p < .001). There was no Age Group × Feature interaction ($F_{3,192}$ = 2.14, p =.09, η_p^2 =.03).

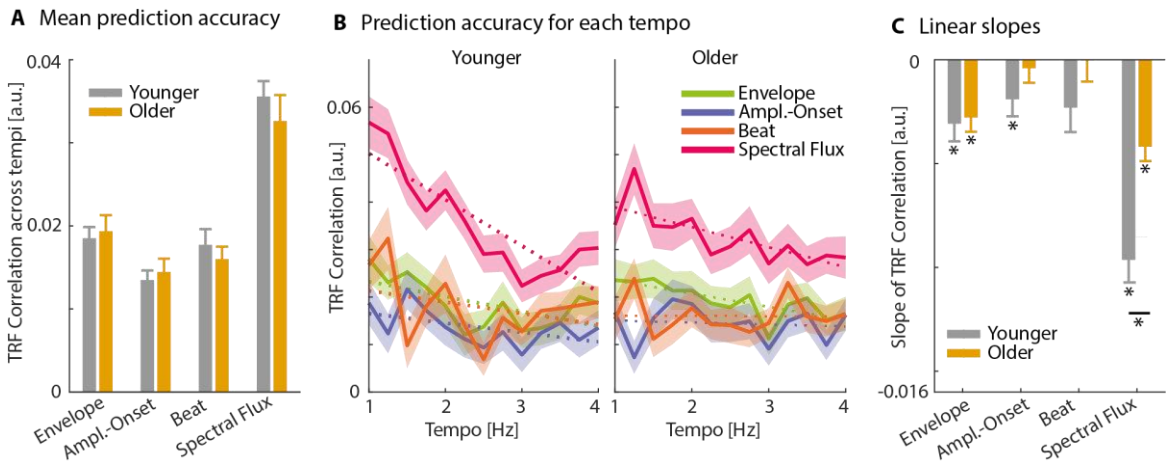

Figure 7. Results for EEG prediction accuracy. A: Mean TRF correlations (± SEM) across 13 tempi in both age groups, separated by four features in naturalistic music. **B:** Mean TRF (± SEM) correlations plotted against musical tempo separately for four features (represented by four colored lines and shaded areas). Dotted lines denote linear regression of TRF correlations as a function of 13 tempi for each feature. **C:** Group comparison of the slopes of linear regression for four features in two age groups. The gray and yellow bars represent slope values from younger and older adults, respectively. Asterisks near each bar data denote significant differences of slope values against 0, whereas asterisks above the straight lines denote significant differences between groups. *p<.05.

To explore the potential modulation of EEG prediction accuracy by musical tempo, we fitted a linear function (regression) to prediction accuracies as a function of tempo. Slopes were significantly smaller than zero for the amplitude envelope and spectral flux for both younger and older adults, and for the onset-envelope for younger adults (for all $p < .001$; Figure 7C), showing that EEG prediction accuracy decreased with increasing musical tempo. The slopes were submitted to an rmANOVA, yielding an effect of Feature ($F_{3,192} = 33.64$, $p = 1.61 \cdot 10^{-17}$, $\eta_p^2 = .35$), Age Group ($F_{1,64} = 6.02$, $p = .02$, $\eta_p^2 = .09$), and an interaction between Age Group and Feature ($F_{3,192} = 5.56$, $p = .001$, $\eta_p^2 = .08$). Post hoc Bonferroni-corrected tests revealed a more negative slope for younger compared to older adults for spectral flux ($t_{64} = 4.15$, $p = .002$, $\eta^2 = 1.02$), whereas there were no age-group differences for the other features (all $p \geq .10$).

DISCUSSION

In the present study, we examined age-related changes in neural tracking of naturalistic pieces of music that differed in tempo. We focused on features that encapsulate distinct temporal and spectral aspects of naturalistic music (envelope, onset-envelope, beat, and spectral flux). Our findings revealed several key points: spectral flux predicted EEG responses best in both younger and older adults, especially for slower music (1-2 Hz). Critically, older participants showed enhanced neural tracking of all features during early processing stages (0 to 200 ms). However, older adults showed reduced sensitivity to musical tempo compared to younger adults that was apparent for the neural tracking of the envelope, onset-envelope, and spectral flux. The current study suggests complex changes in the neural sensitivity to features in naturalistic music associated with aging.

Aging is associated with increased onset responses and neural tracking

Older participants exhibited overall larger neural responses to the onset of musical stimuli, particularly reflected in the N1 deflection of the event-related potential (Figure 2). The N1 component peaks between 90 and 130 ms after sound onset and originates from the auditory cortex (Näätänen and Picton, 1987; Scherg et al., 1989; Tremblay et al., 2001; Lyytinen et al., 2002). The observed enhancement of the N1 to sound onset is consistent with previous research showing hyperactivity to sound in older people (Anderer et al., 1996; Amenedo and Díaz, 1999; Herrmann et al., 2013), which is thought to result from increased neural excitability and reduced neural inhibition that follows the reduced sound input associated with peripheral deafferentation (Caspary et al., 2008; Auerbach et al., 2014; Ouellet and de Villers-Sidani, 2014; Zhao et al., 2016; Resnik and Polley, 2017; Herrmann and Butler, 2021). The age-related enhancement is unlikely due to attentional effects as it has been observed for a range of stimuli in the absence of attention in humans (Sörös et al., 2009; Herrmann et al., 2016, 2018) and also in anesthetized animal models (Herrmann et al., 2017; Parthasarathy et al., 2019). The current data may thus suggest that the auditory cortex in older adults exhibited reduced inhibition and heightened excitation levels compared to auditory cortex of younger adults.

Furthermore, the P2 deflection in auditory evoked potentials to music onset was delayed in older compared to younger adults (Figure 2). The P2 component, originating from the auditory association cortex (Wood and Wolpaw, 1982; Whiting et al., 1998; Sharma and Dorman, 1999), is sensitive to complex acoustic features (Bertoli and Probst, 2005; Herrmann et al., 2016). While the exact mechanism for the delayed P2 is unknown, it appears to be a consistent

with observations in studies examining the age-related changes in neural responses to sounds (Bertoli et al., 2005; Tremblay and Ross, 2007; Alain et al., 2022).

Our investigation of the TRF time courses revealed that older adults exhibited larger neural tracking for the envelope, amplitude-onset, and spectral flux (Figures 3 and 4), suggesting that hyperactivity also manifests in the neural tracking of relevant features of naturalistic music. This enhancement is also consistent with recent work showing increased neural synchronization of different sound features. For example, neural synchronization with the amplitude envelope and the amplitude-onset envelope of speech is often enhanced in older people compared to younger adults (Presacco et al., 2016; Karunathilake et al. 2023; Panela et al. 2024; McClaskey, 2024). Neural synchronization to low-frequency amplitude modulations of non-speech sounds, such as narrow-band noises, is also enhanced in older people (Purcell et al., 2004; Irsik et al. 2021; Herrmann et al. 2023). Less work exists with regards to the neural synchronization with frequency modulations in sounds, but the evidence that exists also points to enhanced synchronization in older adults (Herrmann et al., 2023), consistent with the results for spectral flux in the current study.

Age-groups did not differ in neural synchronization with the beat (Figure 3C; at least in the FDR-threshold time courses), but beat-based synchronization was the most variable in both age groups (Figure 3C and 4C). The beat may not be the most reliable feature for predicting neural responses in TRF models, possibly because the regular, discrete, and low-frequency nature of the beat occurrence might interfere with the model's calculations, particularly for the time-lags typically used < 500 ms. Moreover, the perception of the beat is subjective (Danielsen et al., 2024) and the beat identified by the professional percussionist may not necessarily align with the beat perceived by all participants, potentially contributing to the variability. Individual estimates for each participant were not available, but this could be explored further in future TRF work.

Overall, the current study reveals a generalized enhancement of neural responses and neural tracking of features in naturalistic music in older adults, indicating that individual features in music are overly represented in the aged auditory cortex.

Spectral flux best predicts EEG responses in younger and older adults

Both age groups showed the greatest EEG prediction accuracy (i.e., TRF correlation) for spectral flux, a measure of rapid spectral changes. This prominence likely arises because spectral changes are a key acoustic cue underlying timbre complexity (Alluri et al., 2011; McAdams, 2013) and melody (Zatorre et al., 1994; Janata et al., 2002). Consistent with this,

our current and previous work (Weineck et al., 2022) suggest that spectral flux better predicts EEG activity than amplitude features. Processing of spectral flux may dynamically engage tonotopically organized primary cortex (Formisano et al., 2003) and integrative non-primary areas (Norman-Haignere et al., 2015).

Older adults exhibit reduced sensitivity to tempo in naturalistic music

Both younger and older adults demonstrated greater neural tracking of the amplitude envelope and spectral flux at slower compared to faster tempi, evidenced by higher TRF correlations at 1-2 Hz (associated with the negative slope in Figure 7B and C). This finding aligns with previous research suggesting that slower tempos drive neural synchronization more strongly than higher tempos in music (Doelling and Poeppel, 2015; Weineck et al., 2022), that slow tempos are particularly relevant for the processing of music (Chang et al., 2024), and that slow tempos between 1-2 Hz reflect an optimal information sampling of auditory sequences (Zalta et al., 2020). The results are also consistent with work showing that slow temporal modulations in music are closely linked to the perception of temporal regularities and rhythms, which are essential for music perception (Drake and Botte, 1993; Large and Jones, 1999), and with the frequency at which individuals spontaneously tap (Burger et al., 2018).

Interestingly, older compared to younger adults showed attenuated modulation in EEG prediction accuracy (i.e., TRF correlations) across tempi for spectral flux, and this reduced tempo sensitivity stemmed primarily from reduced prediction accuracy at slower tempi (1-2 Hz; Figure 7B.). TRF temporal waveforms extended this pattern to the amplitude envelope, with age-related reductions in tempo sensitivity localized within early (<200 ms) sensory processing windows (Figures 5 and 6). These early components (N1 and P2), primarily generated in primary auditory cortex (Näätänen and Picton, 1987; Tremblay et al., 2001), may reflect an automatic encoding of acoustic features (Hillyard and Picton, 1978; Picton et al., 1978), and suggest reduced temporal sensitivity in early features extraction stages of the auditory system. The impairment in tempo sensitivity is particularly noteworthy given the older adults' enhanced responses in this early time window to the same features in naturalistic music (Figure 3). Neural activity from both age groups was similarly sensitive to musical tempo (for envelope and spectral flux) in later time windows (>200 ms), which is perhaps less automatic.

Previous work investigating age-related changes in neural sensitivity to spectral-temporal coherence, amplitude modulations, and frequency modulations in simpler sounds (e.g., narrow-band noises) observed a similar pattern of results for a different neural signature of regularity processing. That is, a low-frequency drift in neural activity – that has been shown to be sensitive to the detection of a regular pattern in sounds (Barascud et al., 2016; Teki et al.,

2016; Southwell et al., 2017) – was reduced in older compared to younger adults (Herrmann et al., 2019, 2022, 2023). This reduction in the neural signature of sound regularity processing was present despite the fact that neural responses to sound onsets were enhanced – suggesting hyperactivity – for older adults (Ross and Tremblay, 2009; Bidelman et al., 2014; Irsik et al., 2021). Thus, auditory cortex hyperactivity in aging enhances responses to various features in naturalistic music, but possibly at the cost of reduced sensitivity to acoustic dynamics, such as musical tempo. This neuro-computational tradeoff may limit temporal precision in complex listening environments.

Conclusions

The current study reveals how aging alters neural tracking of different features of naturalistic music. Older adults exhibited hyperactivity across multiple features, including sound onsets, amplitude envelope, and spectral flux, suggesting a generalized manifestation of a loss of inhibition in the auditory cortex of older people. Crucially, this hyperresponsiveness coexists with diminished neural sensitivity to musical tempo, particularly affecting early sensory processing (<200 ms). Paradoxically, while spectral flux remained the strongest neural predictor in both age groups, older adults showed reduced neural sensitivity of spectral flux to musical tempo (reduced tracking at slower tempi: 1-2 Hz) relative to younger adults. These findings demonstrate that age-related hyperactivity enhances feature encodings in music but may impair neural sensitivity to musical tempo, suggesting complex changes in the aged auditory system.

AUTHOR CONTRIBUTIONS

YR: Methodology, formal analysis, data curation, visualization, writing - original draft, writing - review and editing, project administration. **KW**: Conceptualization, methodology. **MJH**: Conceptualization, methodology, formal analysis, writing – review and editing, project administration, supervision, funding acquisition. **BH**: Conceptualization, methodology, formal analysis, writing – original draft, writing – review and editing, supervision, funding acquisition.

STATEMENTS AND DECLARATIONS

The authors have no conflicts or competing interests.

DATA AVAILABILITY

Data will be available to other researchers upon reasonable request to the corresponding author.

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