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

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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 adults (19-34 years) and older adults (58-82 years) 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. Although spectral flux best captured tempo-related changes in EEG activity, the effect was diminished 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 might imply that differences in music perception between younger and older adults result from hyperactive neurons in auditory cortex.

1. 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 event-related 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 (Avissar et al., 2013), these stimuli and ERP approaches are unable to capture how the brain processes naturalistic music. Naturalistic music contains multiple co-occurring acoustic features (rhythm, melody, amplitude) that fluctuate continuously over time, whereas simple tones or MIDI sound sequences used previously lack these important dynamics of music.

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An emerging approach to studying naturalistic sound processing is neural tracking, which captures the synchronization of brain activity measured via electroencephalography (EEG) or magnetoencephalography (MEG) with dynamic acoustic features, such as amplitude envelope of ongoing stimuli (Lalor and Foxe, 2009; Lalor et al., 2009). Unlike ERP analyses that require discrete, repeatable events, neural tracking methods can examine how neural responses follow the continuous dynamics of multiple acoustic features as they unfold simultaneously in naturalistic music. Recent work in younger adults has demonstrated neural tracking of the amplitude envelope in naturalistic music, showing that envelope tracking is modulated by temporal expectations and pitch predictability (Di Liberto et al., 2020; Zuk et al., 2021; Keitel et al., 2025), building on foundational speech-envelope tracking research (Luo and Poeppel, 2007; Ding and Simon, 2012). The amplitude envelope captures the temporal dynamics and rhythmic aspects of music, which are fundamental to the perception of the temporal structure and the beat (Deutsch, 2013). However, spectral features (e.g., timbre and melodic structure) are equally crucial in music. Research in younger adults (ages 18-36 years) demonstrates that 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 (Avissar et al., 2013). 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 neural responses in the auditory cortex of older people compared to younger adults (Alain et al., 2012; Presacco et al., 2016a). This phenomenon has been consistently observed across species and stimulus types in both active and passive listening conditions (Sörös et al., 2009; Herrmann et al., 2016, 2017, 2018; Parthasarathy et al., 2019). 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 differences 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, including syllable-level (4-8 Hz) and phrase-level (<2 Hz) amplitude modulations, with particularly strong enhancement for slower temporal modulations (Presacco et al., 2016b; Brodbeck et al., 2018; Decruy et al., 2019, 2020; Broderick et al., 2021; Panela et al., 2024). This pattern of enhanced neural tracking mirrors the hyperresponsiveness for more simple sounds and is thus thought to arise also from a loss of inhibition and an increase in excitation in the auditory cortex of older adults (Caspary et al., 2008; Auerbach et al., 2014; Herrmann and Butler, 2021). However, whether this hyperactivity extends to naturalistic music listening and affects the neural tracking of multiple acoustic features remains unknown. Moreover, although hyperactivity enhances the magnitude of neural responses, this may not translate into neural processing or perceptual benefits. Hyperresponsiveness may lead to better detection of a sound in quiet – essentially increasing loudness sensitivity – but seems to impair discrimination between sounds and speech (Chambers et al., 2016; Clayton et al., 2025; Herrmann and Butler, 2021; Resnik and Polley, 2021). Hence, hyperactivity may also impair the sensitivity to variations of musical features such as in musical tempo.

In the current electroencephalography study, we address these gaps by comparing the neural tracking of naturalistic music between younger and older adults. We reanalyzed EEG data from younger adults (N = 32) from Weineck et al. (2022) and collected new EEG data from older adults (N = 34). Specifically, we investigate: (1) whether older adults show hyperactivity during neural tracking of different acoustic features in music (amplitude envelope, onset-envelope, beat, spectral flux); (2) whether such hyperactivity manifests uniformly across features or shows feature-specific patterns; and (3) critically, whether older adults show altered sensitivity to musical tempo (1-4 Hz) compared to younger adults. Based on the literature on auditory aging, we hypothesized that: (1) older adults would show enhanced neural tracking of all acoustic features, consistent with auditory cortex hyperactivity; (2) this enhancement would be most pronounced for slower temporal modulations (<2 Hz), paralleling findings in speech; and (3) despite overall enhanced responses, older adults would show reduced modulation of neural tracking across tempi, reflecting impaired temporal precision. Our multi-feature, multi-tempo approach allows us to test whether age-related hyperactivity represents a uniform enhancement or whether it coexists with specific deficits in temporal processing.

2. Materials and methods

2.1. Participants

32 younger adults (22 females, 10 males; age range: 19-34 years; mean age: 24.4 years; data from our previous study (Weineck et al., 2022);) and 34 older adults (16 females, 18 males; age range: 58-82 years; mean age: 66.2 years) with self-reported normal hearing participated in the study. Participants were recruited from the general population and were not selected based on musical expertise or training. 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).

Additionally, 18 younger adults (7 females, 11 males; age range: 21-32 years, mean age: 27.1 years) completed only audiometric testing (see Audiometric Testing below), but did not participate in the EEG experiment. Audiometric data from this younger group were used as a reference point for the audiometric data from the older participants, because no audiometric data were recorded for the 32 participants in our previous study (Weineck et al., 2022).

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.

2.2. Pure-tone audiometry and estimation of sensation level

Older 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 the published study (Weineck et al., 2022). Therefore, in the current study, we collected audiogram data from 18 additional, age-matched younger participants drawn from the same population as the younger adults in Weineck et al. (2022). These data served as a descriptive baseline for characterizing age-group differences in hearing sensitivity in the current, as audiograms were not available for the younger participants included in the original EEG dataset. Importantly, the audiometric thresholds of this additional younger cohort were within the normal-hearing range and consistent with thresholds reported for younger adults in previous work (Herrmann et al., 2023, 2025; Panela et al., 2024), supporting the assumption that the younger EEG participants did not exhibit clinically relevant hearing loss.

Audiometric thresholds in younger and older adults were assessed for pure tones at frequencies of .25, .5, 1, 2, 4, and 8 kHz (Fig. 1A). The pure-tone average (PTA) was calculated as the average across the thresholds of 4 frequencies (.5, 1, 2, and 4 kHz; Catlin, 1979; Gurgel et al., 2012, Fig. 1B). Compared to younger individuals (mean PTA = 5.22 dB), older adults showed elevated hearing thresholds (mean PTA = 17.88 dB; $t_{50} = 6.16$, $p = 1.23 \bullet 10^{-7}$, $\eta^2 = 1.80$), 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).

The sensation level was also determined for each person in MATLAB. To this end, participants listened to white-noise sounds of 12 s duration for which the sound level continuously increased or decreased (6 trials each). Participants 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; $t_{64} = 6.95$, $p = 2.31 \bullet 10^{-9}$, $\eta^2 = 1.71$), 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 for both age groups 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 (Panela et al., 2024; Presacco et al., 2016a, 2016b). 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, thereby controlling for audibility (Herrmann et al., 2019).

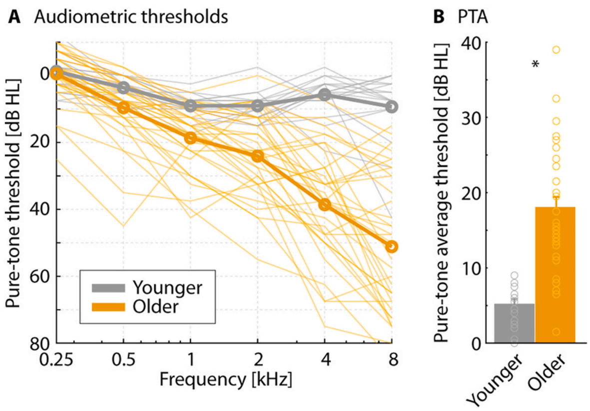

Fig. 1. Audiograms and hearing thresholds for younger and older adults. **A:** Audiograms. Thick lines denote group-mean data and thin lines represent individual participant data. **B:** Pure-tone average (PTA) for both age groups (mean across .5, 1, 2, and 4 kHz). Individual data points are denoted by dots. *$p < .05$.

2.3. Stimuli

We adopted the same stimuli and procedures that were used to record the data for younger adults in the previously published study (Weineck et al., 2022). Specifically, 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, due to the COVID-19 lockdown, the original tempo was assessed using an online method. Eight individuals listened to and tapped along with each segment on their computer keyboards for a minimum of 17 taps. The tap tempo (BPMs, beats per minute) was recorded using an online BPM estimation tool (https://www.all8.com/tools/bpm.htm). To ensure that stimuli had unambiguous, easily tappable beats, 21 musical segments were excluded because they exhibited high inter-tapper variability (>2 tappers diverging from the group) or poor sound quality. The remaining 72 segments, with original tempi ranging from 1.27 to 2.52 Hz (76-151 BPM), were retained for further processing (for details about all musical segments see appendix in Weineck et al., 2022).

As described in Weineck et al. (2022), musical segments were then tempo-modulated to a range of 1 to 4 Hz in steps in .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 stimulus quality after tempo manipulation, all tempo-shifted versions were systematically screened. Segments were eliminated if the tempo manipulation led to acoustic distortions, made individual notes indistinguishable, or resulted in excessively repetitive patterns. As a result, not all segments were stretched across the full 1-4 Hz range. Each segment was only stretched across tempo ranges where sound quality remained acceptable. This selective quality control process resulted in 703 music excerpts, varying in duration from 8.3 to 56.6 s across the 13 tempi conditions. Althougth 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 (cf. Weineck et al., 2022). All musical excerpts were mono WAV files with a sampling rate of 44,100 Hz. Each file comprised a linear fade-in and fade-out 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).

2.4. *Experimental design*

The experimental procedures were conducted in the EEG laboratory at the Max Planck Institute for Empirical Aesthetics, Frankfurt am Main, Germany, 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 h.

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 s (depending on the duration of the musical excerpt). Following a 1-s 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.

2.5. *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 .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.

2.6. *Data analysis*

2.6.1. *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).

2.6.2. *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 and 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.

2.6.3. *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 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. All feature time series were trimmed to have identical sample lengths (matching the shortest feature) to ensure proper temporal alignment with the EEG data for TRF analysis.

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 to 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) through nesting within the cross-validation, 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). Additionally, this procedure was repeated for all musical features together in a multivariate model. In contrast to single-feature TRF models that use one time-lag vector, the multivariate TRF approach combined all stimulus features by creating separate time-lag vectors for each of the four musical features, resulting in a combined predictor matrix (Time × 4 musical features × time lags). 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 traditional event-related potentials (Crosse et al. 2016, 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, 2024). 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), it was 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.

3. Results

3.1. *Auditory onset responses in older and younger adults*

Fig. 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

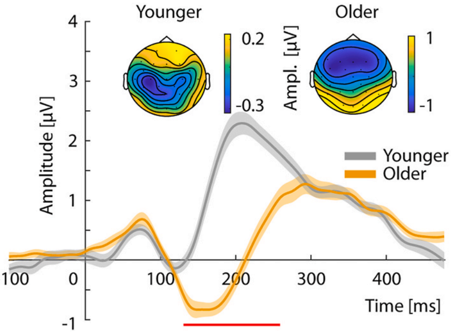

Fig. 2. Neural responses to the onset of musical excerpts. Group-averaged time courses are displayed by the two colored curves. Shaded areas mark the standard error of the mean (SEM). The red line at the bottom marks the time window exhibiting a significant difference between age groups ($p_{FDR} < .05$). 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). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

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.

3.2. *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 Fig. 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: $t_{64} = 3.64$, $p = 5.52 \bullet 10^{-4}$, $\eta^2 = .89$; 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 ($t_{64} = 2.11$, $p = 2.44 \bullet 10^{-5}$, $\eta^2 = 1.12$). Unlike the other three features, the age-related enhancement of the N1-P1 and N1-P2 for the beat feature shows later latencies (Fig. 3E and F). These findings are consistent with the age-related enhancement of the neural responses to the stimulus onset in Fig. 2.

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

Fig. 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 (Fig. 5).

Within each age group, we first examined the TRF sensitivity by comparing slope values against zero, separately for each feature (Fig. 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 Fig. 6 and the corresponding text.

For the amplitude envelope and onset-envelope, younger individuals showed effects of tempo modulation in two early time windows (Fig. 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 (Fig. 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.

The linear effects characterized by the slopes in Fig. 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 (Fig. 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.

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

Results for EEG prediction accuracy from both age groups are

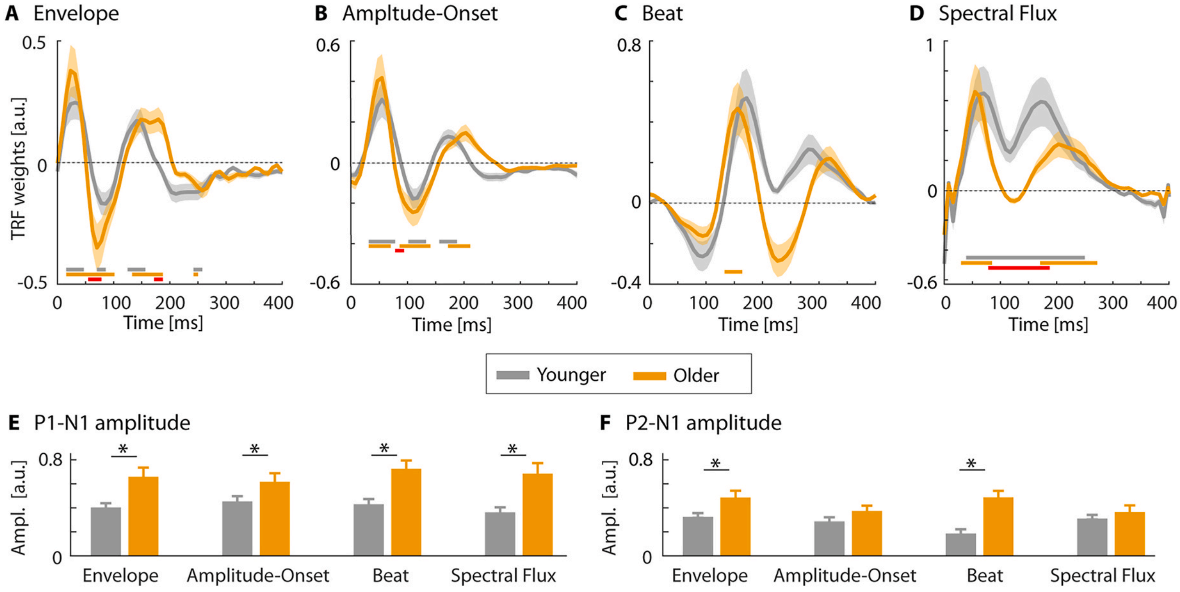

Fig. 3. Neural tracking (TRF weights) for four features in naturalistic music and two age groups. A-D: Averaged TRF weights courses (shaded area around means reflects the SEM) for four features (averaged across tempi) and both age groups. Horizontal lines at the bottom mark the time window exhibiting 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 < .05. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

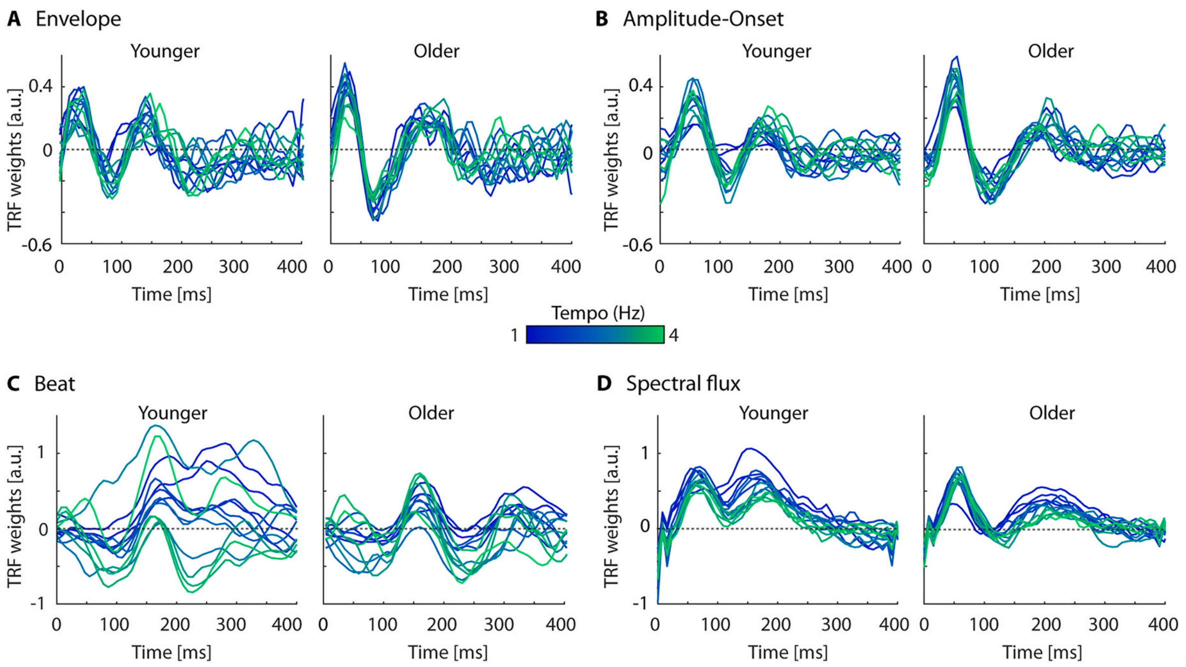

Fig. 4. TRF time courses (weights) for each feature in music and music tempo. Each curve depicts the TRF weights from one musical tempo (13 tempi from 1 Hz to 4 Hz in steps of .25 Hz, blue to green). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

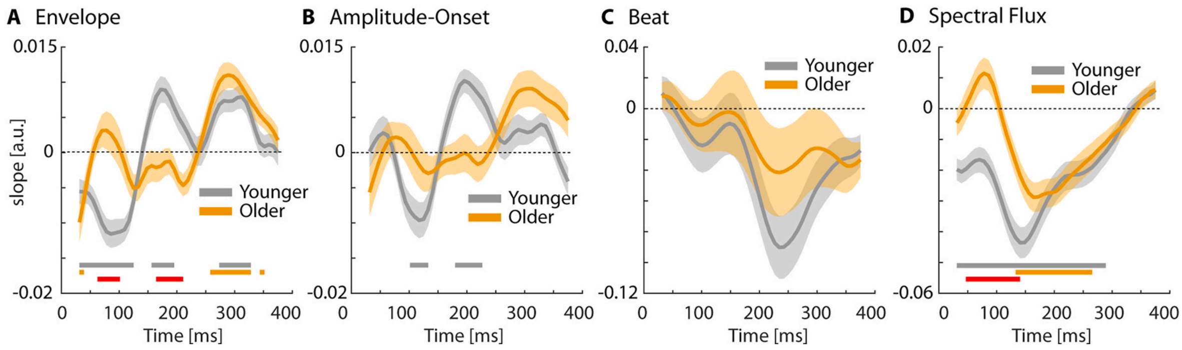

Fig. 5. Slopes (linear coefficient) from the regression analysis relating musical tempo to TRF weights. Average slope time courses (shaded area: ±SEM). Horizontal lines at the bottom mark the time window exhibiting a significant difference ($p_{FDR} < .05$) in the slope between age groups (red line) and within each group against 0 (younger adults: gray; older adults: yellow). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

displayed in Fig. 7. The mean prediction accuracy for the four features, independent of musical tempo, did not differ between age groups (main effect of Age Group: $F_{1,64} = .09$, $p = .77$, $\eta_p^2 = .001$; Fig. 7A). Averaged EEG prediction accuracy across all tempi was largest for spectral flux, relative to the other acoustic features (effect of Acoustic Feature: $F_{3,192} = 185.02$, $p = 2.17 \bullet 10^{-56}$, $\eta_p^2 = .74$), 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 ($F_{3,192} = 2.14$, $p = .09$, $\eta_p^2 = .03$).

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 $p < .001$; Fig. 7C), showing that EEG prediction accuracy decreased with increasing musical tempo. The slopes were submitted to an rmANOVA, yielding an effect of Feature ($F_{3,192} = 33.64$, $p = 1.61 \bullet 10^{-17}$, $\eta_p^2 = .35$), 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 $p \geq .10$). The multi-feature analysis mirrored the reported effects, also showing a significant difference in the slope between age groups ($t_{64} = 2.91$, $p = .005$, $\eta^2 = .12$).

4. Discussion

In the present study, we examined age-related differences in neural tracking of naturalistic 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 that spectral flux predicted EEG responses best in both age groups, 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 that was apparent for the neural tracking of the envelope, onset-envelope, and spectral flux. Together, these findings suggest that age-related hyperresponsiveness in auditory

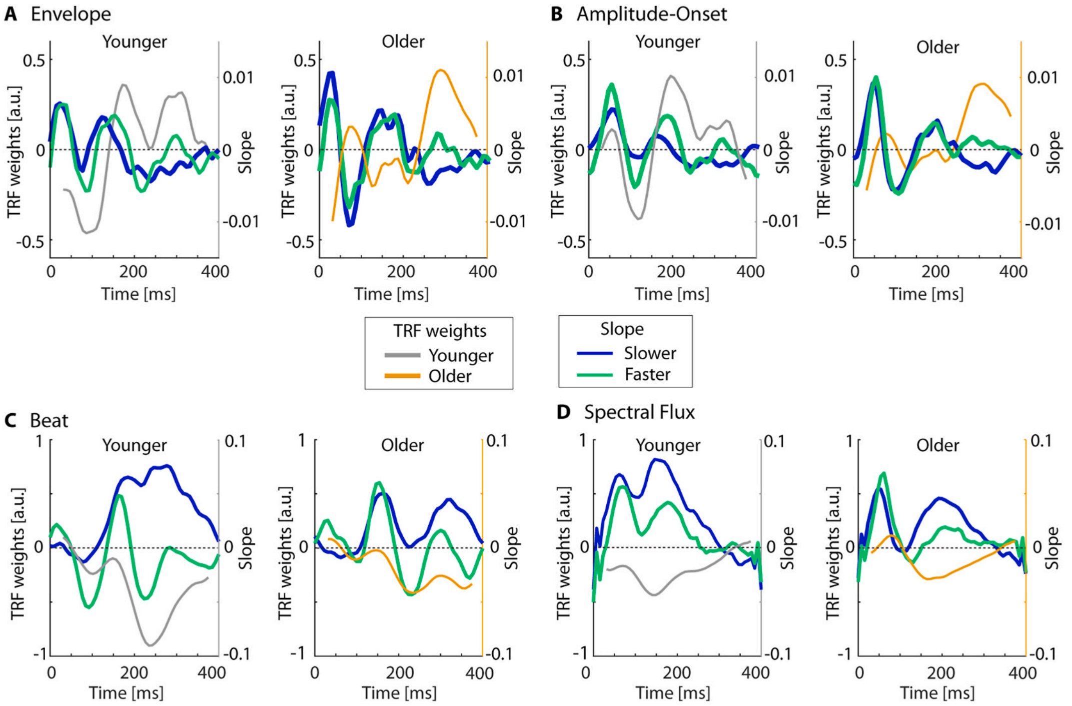

Fig. 6. TRF weights for slower and faster tempi, overlaid by the slope (linear coefficient) from the regression model relating TRF weights to musical tempo. A: Average TRF weights across the slowest three tempi (1-1.5Hz; blue lines) and the fastest three tempi (3.5-4Hz; green lines) overlaid by the slope (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). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

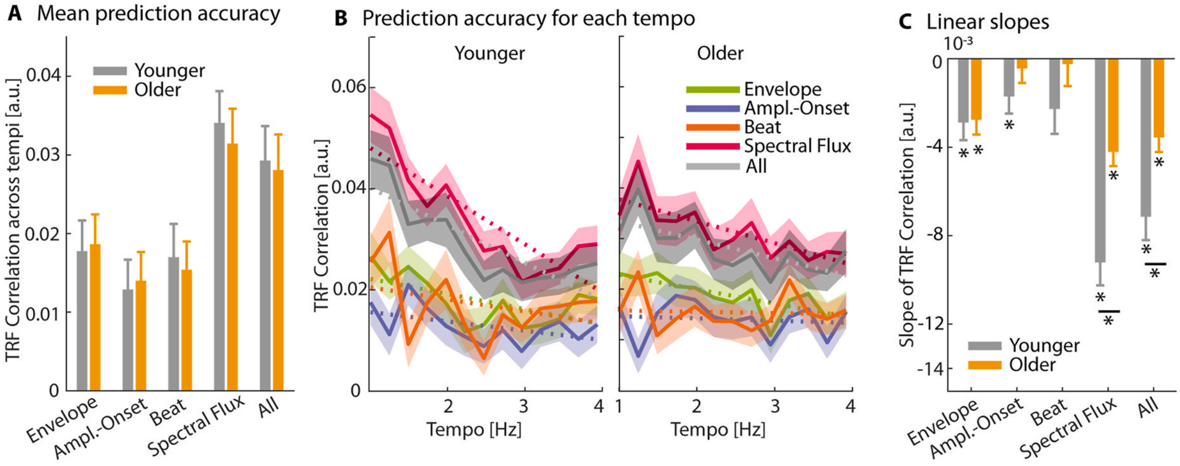

Fig. 7. Results for EEG prediction accuracy. A: Mean TRF correlations (±SEM) across 13 tempi in both age groups, separated by four features and all features combined (All) in naturalistic music. **B:** Mean TRF (±SEM) correlations plotted against musical tempo separately for four features (represented by four colored lines and shaded areas) and combined features (gray 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 and all features combined (All) 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. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

cortex to acoustic features of music may be maladaptive, indicating dysregulated neural processing in which increased activity is accompanied by reduced sensitivity to musical tempo.

4.1. Aging is associated with increased onset responses and neural tracking

Older participants exhibited larger neural responses to the onset of the music stimuli, particularly reflected in the enhanced N1 component (Fig. 2). This enhancement is consistent with previous research showing hyperresponsiveness to sound in older compared to younger adults (Anderer et al., 1996; Amenedo and Díaz, 1999). This hyperresponsiveness is thought to result from increased neural excitability and reduced neural inhibition following 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 across stimuli in passive listening 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 hyperresponsiveness 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 component in response to the onset of the music stimuli was delayed in older compared to younger adults (Fig. 2). The P2, 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). The pattern of enhanced and delayed N1 along with delayed P2 may reflect age-related differences in the temporal dynamics of information flow through auditory cortical regions (Friedman et al., 1993; Friedman, 2013; Henry et al., 2017; Irsik et al., 2021; Herrmann et al., 2022). While the exact mechanism for the delayed P2 is unknown, it appears to be consistent with observations in studies examining the age-related differences 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 (Figs. 3 and 4), suggesting that hyperactivity extends beyond simple onset responses to continuous features tracking in naturalistic music. This is 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., 2016b; 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 (Fig. 3C; at least in the FDR-threshold time courses), but beat-based synchronization was the most variable in both age groups (Fig. 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.

4.2. *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).

4.3. *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 Fig. 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 and 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; Fig. 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 (Figs. 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 feature-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 (Fig. 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 differences 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.

5. Conclusions

The current study reveals age-group differences in neural tracking of 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. This might suggest that differences in music perception between younger and older adults result from hyperactive neurons in auditory cortex, potentially affecting the efficiency of information processing of dynamically evolving music.

CRediT authorship contribution statement

Yue Ren: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation. **Kristin Weineck:** Data curation, Conceptualization. **Molly J. Henry:** Writing – review & editing, Supervision, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Björn Herrmann:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors have no conflicts or competing interests.

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Data availability

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

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