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Auditory Inference and Long-Term Modulation of Excitation and Inhibition

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ABSTRACT

Auditory event-related potential (ERP) analysis typically involves extraction of responses time-locked to each sound averaged together by auditory event type. In oddball sequences, a repetitious standard sound is occasionally interrupted by a low probability deviant. ERP component differences between standard and deviant ("oddball") events support the inference that humans rapidly and automatically extrapolate from patterns to predict the most likely structure and properties of upcoming sounds. A sound sequence composed of repeating patterns at multiple timescales was used to determine whether there is evidence of response normalization over long timescales, that is, reduced differences between standard and deviant responses over time. Two sounds (30 and 60 ms pure tones) were organized into four blocks in which the two sounds alternated in tone probability as rare deviants ($p = 0.125$) or common standards ($p = 0.875$). Continuous EEG was collected from 32 participants who heard four occurrences of this four-block alternating-oddball sequence. We extracted five-tone epochs centered on the deviant, exploiting a design principle of oddball sequences used in ERP studies that deviants are always separated by occurrences of the repeating standard, thus ensuring in this case that every deviant was preceded and followed by a minimum of three standards. The five-tone epoch analysis revealed that the occurrence of a deviant triggered a prolonged negative shift in the ERP that extended across the whole response of the deviant and the subsequent standard. The amplitude of this "deviant complex" (over 120–600 ms post deviant) and a mean "standard complex" amplitude (480–0 ms pre-deviant) were analyzed alongside conventional ERP components, assessing them for change over time. Results revealed convergence of the standard and deviant responses, such that differences reduced over long timescales. Findings are discussed with respect to being potential indices of excitatory/inhibitory homeostasis and evidence of pattern prediction over several 10s of minutes.

Modulation of the relative excitability of neurons is how learning is expressed and how we modify our experience of the world to filter the relative importance of information. The process of re-balancing excitation and inhibition (E/I) in the brain during learning is critical to efficient and effective function with disruption in E/I balance associated with numerous neurodevelopmental and neurodegenerative conditions (Zhang et al. 2021). According to the theory of efficient coding, neural computations should reflect an optimisation that maximizes information encoded about sensory stimuli while attempting to minimize the metabolic cost of neural activity (Abbott et al. 2016; Thalmeier et al. 2016). Sensory stimuli disrupt the "resting" dynamics of the brain and the present study involved the use of auditory event-related potentials (ERPs) to expose how this disruptive effect changes over time while learning patterned information.

ERPs recorded during exposure to patterned sound sequences are widely used to study perceptual learning (Naatanen et al. 2001) and it is well established that ERP components change over time in a manner consistent with the brain having formed an internal model, that is, a precision-weighted prediction about the most likely attributes of sound to follow (Winkler et al. 1996; Friston 2005). By extracting waveforms time-locked to the onset of a sound, it is possible to track the ways that responses differ as a function of physical attributes, probabilities and predictions (Alain and Winkler 2012). After only a few repetitions, response amplitudes are suppressed or inhibited to sounds that match predicted properties and disinhibited to sounds that deviate. More specifically, an increase in negativity (mismatch negativity or MMN) occurs when a sound deviates from a repetitive pattern. This is seen over fronto-central scalp sites approximately 100–250 ms after the deviation and forms part of the complex N2 waveform (Picton et al. 2000; Naatanen 2001). The relative suppression of responses to matching sounds, and enhancement to mismatching ones, increases over short timescales as the auditory system develops precise models of the acoustic patterns and probabilities (Lieder et al. 2013; Baldeweg 2007). Formalized under predictive coding treatments (Friston 2005, 2010; Lieder et al. 2013; Baldeweg 2007), this relative sensitivity is argued to help filter the relevance of sound and support efficient deployment of attention and cognitive resources (Winkler and Schroger 2015; Sussman et al. 2003; Escera et al. 2000). For example, if a mismatch becomes more frequent or is particularly large, this may signal that the environment has changed in an important way, requiring attention or a response, and may trigger remodeling of what is most likely to occur.

Time is an important factor in learning, particularly in processing sound where patterns evolve sequentially. Hierarchical models assume learning can occur simultaneously across multiple timescales, where learning about an underlying regularity is accompanied by the extraction of information about the stability of that regularity over time, and an even longer time course would enable learning about whether the stability itself changes over time (Mathys et al. 2011). Hierarchical learning is supported by a rostro-caudal gradient in the brain, with sensory areas extracting information over shorter periods (like 100s of milliseconds), and progressively longer periods of learning in association areas, with the longest periods (10s of minutes and beyond) engaging frontal cortices (Kiebel et al. 2008). When applied to ERPs, these different timescales of learning might be convolved into modulation on discrete components such as MMN. For example, studies exploring the effect of feature variability in repeating patterns have indeed observed MMN to be smaller when more variance is present (Winkler et al. 1990; Garrido et al. 2013; Todd and Cornwell 2018). In the present study, we take a much longer time course view to investigate what happens to the patterns of excitation and inhibition in response to regular "standard" sounds and rare "deviant" sounds when patterns change predictably over time in a way that is ultimately inconsequential to behavior. In other words, theoretically, learning in this case should help to minimize responses to sound to preserve attentional and cognitive resources from being depleted by changes that are ultimately not useful for goal-directed behavior. With this goal in mind, we consider longer timeframes of not only the acoustic patterning, but also the extended response in moving from conventional single-tone locked ERPs to a repeated multi-tone chain.

The present study featured a variant of typical oddball designs, beginning with two sounds, one common and one rare, and then, after a period, the sound that was rare started to repeat and the sound that was common became rare (Todd et al. 2011). These two "oddball" instances alternated back and forth at fixed periods, creating a larger-scale regularity and ultimately equal probability of the two sounds. Due to highly dynamic updating of internal models, the rare deviation from the current regularity always elicits the additional negativity (the MMN) within the alternating oddball blocks, consistent with the common sound being "predicted" by a relatively low-level internal model and the rare sound departing from the prediction eliciting a "prediction-error" (Friston 2005, 2010; Lieder et al. 2013; Baldeweg 2007). Therefore, the brain remains sensitive to the short-timescale difference in probability even when the sounds have equal probability over the longer term. This has been demonstrated whether the alternation in probabilities is slower (every 2.4 min) or more frequent (i.e., every 0.8 min) (Fitzgerald et al. 2021; Fitzgerald and Todd 2020; Frost et al. 2016). In such studies, sounds are not task-relevant, in that participants are asked to ignore them and focus attention on something else. In other words, the sounds have no relevance to behavior, and any benefit derived from modeling the sounds presumably relates to harnessing prediction to reduce responsiveness. The resultant diminished responsiveness should in turn limit the tendency for rare changes to divert attention from concurrent activity. Under the vernacular of predictive coding, we can "tune in" to goal-directed activity and "tune out" that which does not serve this purpose (Friston et al. 2016).

The traditional approach to studying oddball sequence processing involves comparing the averaged response to deviant sounds to the averaged response to the repeating standard sounds. The design principles of the alternating sequences enabled a less conventional approach, as it enforced a minimum of three of the locally common sounds between deviations. Thus, there were at least three common tones on either side of each deviant within the sequence. The present study took advantage of this design to extract a longer, deviant-centered five-sound epoch. The epoch enabled inspection of the amplitude and morphology changes to standards preceding a deviant, the deviant, and the subsequent standards after the deviant over time. It is well known that the response to the standard sound immediately following a deviant also differs relative to the response to standards that follow other standards (Winkler et al. 1996; Baldeweg 2007; Kujala et al. 2007). Studies that have explicitly measured standard-after-deviant responses have found an MMN-like increase in negativity that is typically substantially smaller than that to the deviant and has a somewhat different morphology than that of the deviant itself (Winkler et al. 1996; Sams et al. 1984). With respect to the long epoch ERP, we can therefore expect both the deviant and immediately following standard to disrupt the response amplitude and morphology to the string of regular sounds.

Using longer multi-tone epochs, we undertook to test the hypothesis that learning the patterning underlying behaviorally irrelevant sound would manifest not only as changes in the sensitivity to deviations, but potentially also as changes in E/I balance over time. If disruptions caused by the occurrence of locally rare deviations could be learned in the form of a generalized estimate of

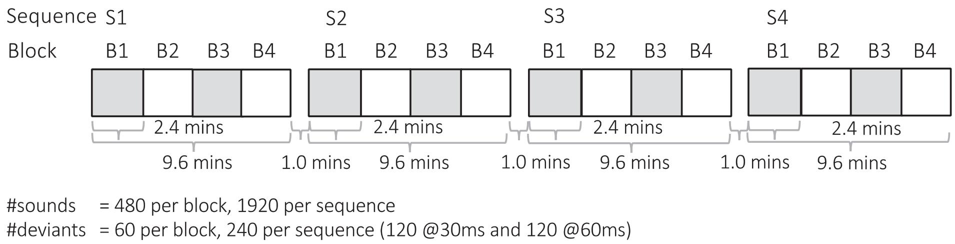

FIGURE 1 | Schematic representation of the four sound sequences (S1–S4) each containing four blocks of sound (B1–B4). The gray blocks represent periods in which the 30 ms sound was rare and the 60 ms sound was common and the white blocks where the probabilities were reversed.

the rate of disruption in a given pattern, learning may modulate the influence of such disruption over time (Mathys et al. 2014). This hypothesis, by extension, conforms to efficient encoding as defined by working towards the maximal information encoding with minimal effort (i.e., sparser neurons/reduced responding) and minimizing encoding error (see Zhou and Yu 2018). In the case of the alternating sequences, this should emerge as preservation of differentiation of local standards and deviants, while minimizing the differences in response between them over time.

1 | Methods

1.1 | Participants

The data featured in this paper is a combination of published data, reanalyzed for the current study, and new data. Published data was included from 17 participants recruited from undergraduate psychology students at the University of Newcastle (Todd et al. 2021) and unpublished data from 15 additional participants recruited from undergraduate psychology students at the University of Newcastle and community volunteers (only binary gender categories were collected at the time of testing, no data on race/ethnicity was collected, 13 M/19 F, mean age 28.9 years range 18–45 years). A sample size of 32 affords the analysis approximately 80% chance of observing standardized differences (effect sizes) of approximately 1 at an alpha level of $p = 0.05$, so the analysis was sufficient to detect large effects (Serdar et al. 2021). Inclusion criteria stipulated normal hearing (able to detect sounds between 500 and 4000 Hz at or below 20 dB HL), no history of head injury or neurological condition, no current mental illness or family history of psychosis and no alcohol or substance abuse. Remuneration was offered as course credit to students and monetary vouchers to community volunteers. All participants provided written informed consent in accordance with procedures approved by the university Human Research Ethics Committee (H-2012-0270).

1.2 | Sounds and Sequences

The sounds and sequence structure used are presented diagrammatically in Figure 1. All sequences contained two sounds: a 30 ms and a 60 ms long 1000 Hz pure tone (with a 5 ms onset and offset ramp using a cosine window) presented binaurally over stereo headphones at 75 dB SPL and at a regular 300 ms stimulus onset asynchrony. These two sounds were arranged into two block types: a 30 ms deviant and a 60 ms deviant block. In the 30 ms deviant blocks, the 60 ms sound was the repeating sound or "standard" ($p = 0.875$) and the 30 ms sound was the rare "deviant" ($p = 0.125$); in the 60 ms deviant blocks the probabilities were reversed. In each case, a block always commenced with five occurrences of the standard for that block (excluded from analyses), and there were always a minimum of three standard tones between successive deviant tone occurrences. Blocks contained 480 sounds and sequences contained four blocks: two of each deviant/standard composition as per Figure 1. Sequences were therefore 9.6 min in duration and each sequence was presented four times to each participant with a 1-min silent break between them. Previous studies using similar alternating probability sequences have shown effects of tone order on MMN in counter-balanced versions of this design (Mullens et al. 2016; Todd, Heathcote, Mullens, et al. 2014; Todd et al. 2011), and versions with other deviant sound properties (Fitzgerald et al. 2018; Todd, Heathcote, Whitson, et al. 2014). The present dataset was chosen for this analysis due to having the largest sample size with this to assess hypotheses about longer-term changes.

1.3 | ERP Recordings

Participants were fitted with a 64 Channel Neuroscan Quick Cap with Ag/AgCl electrodes arranged per the extended International 10–20 system including the nose as reference and bilateral mastoid electrodes. Electrooculogram was recorded from above and below the left eye and 1 cm lateral to the outer cantus of each eye. The impedance for all electrodes was reduced to < 5 kΩ prior to recording and data was acquired continuously at a 1000 Hz sampling rate (highpass 0.1 Hz, lowpass 70 Hz, notch filter at 50 Hz and a fixed gain of 2010) on a Synamps 2 Neuroscan system.

1.4 | Procedure

Participants read an information statement describing the purpose of the study and had the opportunity to ask questions before providing written informed consent if they wished to continue. A screening interview was administered to ensure inclusion criteria were met and a hearing test was conducted to determine thresholds for detection. All participants responded to stimuli at or below 20 dB HL according to a hearing test using an audiometer (Earscan ES3S), determining the lowest sound presentation level at which they could detect sound in the left and right ear for frequencies between 500 and 4000 Hz.

Once the electrode cap was fitted, participants watched a movie while sounds were presented to them over stereo headphones

(Sennheiser HD280pro), and continuous EEG data was acquired. Each participant was asked to focus attention on the silent, subtitled movie and it was explained that the process being measured was something that the brain does automatically and is best recorded when attempting to ignore the sounds and focus attention elsewhere as recommended (Kujala et al. 2007).

1.5 | Data Analysis

Data were processed in Neuroscan Edit (version 4.5) software. First, the continuous EEG was inspected for movement or other large artifacts and these were manually excluded. Second, an algorithm was run to model and mathematically eliminate eye-blink artifacts based on the vertical electrooculogram (Semlitsch et al. 1986). In the sequence structure, each deviant was preceded and followed by a minimum of three standards, which meant that each time a deviant occurred there would have been a seven-tone regularity: three standards, a deviant and three standards. On some of the trials, however, the first standard in this regularity would have immediately followed a deviant, and as explained earlier, the response to a standard after a deviant will be distorted by an adjustment in the model (Winkler et al. 1996). Therefore, the extracted long epochs only included two standards before the deviant. Two epochs were extracted: a five-tone and a six-tone epoch. The continuous EEG was segmented into both 1500 and 1800 ms time-locked epochs beginning 600 ms prior to each deviant and ending 900 or 1200 ms, respectively, after the onset of each deviant. In the sequence structure, each deviant was preceded and followed by a minimum of three standards. The epochs therefore captured a regular standard, standard, deviant, standard, standard (SSDSS) response with the longer epoch capturing a third standard after the deviant (SSDSSS). Both epochs were extracted to assess the feasibility of the approach, because longer epoching risks higher data loss due to the increased likelihood of an epoch including artifacts and therefore being lost in pre-processing. Indeed, the five-tone epochs yielded ~5%–10% higher trials per average; therefore, analysis in this paper has been applied to the five-tone epochs. Conventional analysis of single-tone epochs yielded an average of 91% of trials retained, while the five and six-tone epochs yielded an average of 65% and 60% data retention, respectively. The six-tone epochs are presented visually only to confirm observed trends in the data as described in the results section.

Epochs were baseline corrected to zero across the entire period and then epochs with amplitude variation that exceeded ±70 mV were rejected from further processing. Epochs were then averaged at different granularities to facilitate key comparisons. Firstly, the overall ERPs centred on the 30 ms deviant and the 60 ms deviant were averaged (see Figure 1, up to 480 trials per average, 60 per block and, therefore, nominally 120 per sequence for four occurrences of the sequence). These ERPs facilitated an inspection of the overall component structure and the disruption to the regular structure after the deviant tone. Next, the sub-averages for each block of each sequence were created (see Figure 1, up to 60 trials per average). These sub-averages were necessary for the analysis of change in the ERPs over different time courses. The dependent measures were not decided a priori given the intention to base the analysis upon an inspection of the disruptive effect of the deviant on the foregoing regular repetition in a novel, five-tone epoch of the time-locked response. Choice of measure and analysis is therefore detailed in the results section in relation to observed data. All statistical analyses were conducted using JASP (JASPTeam 2024). Outliers (> 2 standard deviations from the mean) were replaced by the mean for a given measure. This replacement occurred for 0.06% of measures. Where replacements were made (9 participants), data was analyzed with and without those participants. Effect sizes for main effects and interactions are reported with and without replacements as partial eta squared. Greenhouse–Geisser corrections were unnecessary as sphericity assumptions were met. The summary data that support the findings are openly available in OSF at http://osf.io, reference number dg63z.

2 | Results

In line with common practice (Kujala et al. 2007), the Fz site is presented for visualization of morphology and measurement of apparent modulations in the data. The frontal ERP at Fz averaged over all presentations of the five-tone SSDSS runs and centred on the 30 ms deviant and the 60 ms deviant is presented in Figure 2. The morphology showed a regular P1/N1/P2/N2 response evident to the first two tones that is disrupted by the occurrence of the deviant. The most negative response to the deviant peaked around 180 ms, which is later than the N1 peak elicited by standard tones (~120 ms) and much larger due to the influence of the enhanced-N2 and/or MMN component. This observation is consistent with that found with traditional single tone-locked epochs and will be hereafter referred to as the deviant response or deviant N2 (Todd et al. 2024, 2021; Yeark et al. 2022). Both ERPs also expose a negative component that begins slightly prior to, and peaks during the onset of, the standard immediately following the deviant (labeled "X" in Figure 2). Furthermore, both ERPs expose an additional negativity in the waveform that is triggered by the deviant and continues to influence the ERP over the duration of the deviant and the immediately following standard, thus leading to a prolonged negative shift in the ERP over the period marked with the white rectangle at the bottom of both panels of Figure 2. In other words, the response to the standard immediately after the deviant occurs before the negative shift in response to the deviant has returned to a regular baseline.

The disruption to the regular tone response was quantified by extracting the negative shift (hereafter referred to as the deviant complex) as the mean amplitude of activity from 120 to 600 ms post-deviant onset, with an equivalent period used to compare this negative shift to the preceding regular standard (hereafter referred to as the standard complex, −480 to 0 ms; the period is marked with a black rectangle on both panels of the figure). Several "components" were also extracted including measures of P1, N2, and component X. Measures of P1 and N2 were extracted to the standards preceding the deviant by averaging the means from 50 to 70 ms after a tone onset for P1 (−550 to −530 ms and −250 to −230 ms) and 200–220 ms after a tone onset for N2 (−400 to −420 ms and −100 to −80 ms). For the deviant, measures of P1 and the deviant N2 were extracted as the mean from 50 to 70 ms and 180 to 200 ms after the deviant tone onset, respectively. For the final standard in the 5-tone run, measures of

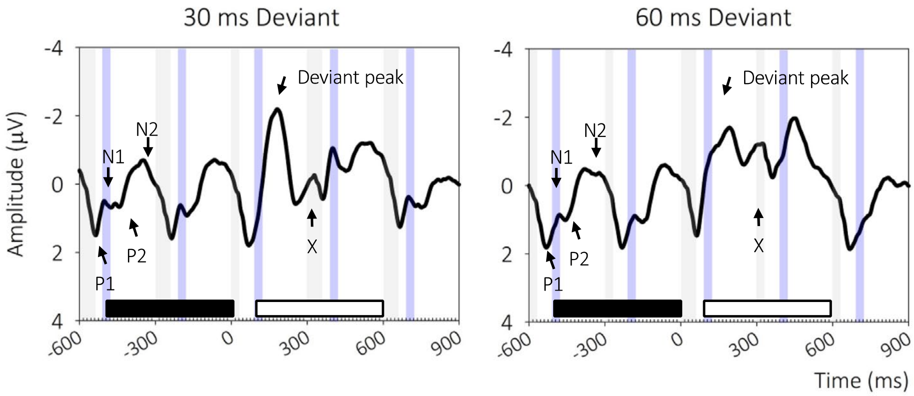

FIGURE 2 | The group-averaged five-tone frontal ERP at Fz centered on the occurrence of the 30 ms deviant (left) and 60 ms deviant (right). The gray vertical stripes indicate the onset and duration of each tone, and the blue vertical stripes indicate the regular N1 component to each sound (i.e., at the time that an N1 peak would be expected to a regular tone). Labels indicate the P1, N1, P2, N2 components to the first tone, the peak of the deviant response and the component labeled "X". The black rectangle marks the period (−480 to 0 ms) from which the amplitude of the standard complex was extracted, while the white rectangle (120 to 600 ms) marks that for the deviant complex (see main text for explanation of the two complexes).

P1 and N2 were extracted as the mean of the 50–70 ms interval after the tone onset (650–670 ms) and 200–220 ms after the tone onset (800–820 ms), respectively. Finally, the component labeled X in Figure 2 was quantified by extracting the mean amplitude from 300 to 330 ms.

2.1 | Deviant and Standard Complex

Figure 3A shows the five- and six-tone ERPs centred on the 30 and 60 ms deviant, with amplitude changes in responses evident between the first occurrence of an alternating sequence and the last occurrence of the alternating sequence. The sixth-tone ERPs provide further demonstration that the deviant complex resolves after the second standard following the deviant. Figure 3B depicts the same five-tone ERPs following the application of a 1 Hz low-pass filter to expose the apparent slow frequency change in these ERPs between repeats. The mean Fz amplitudes of the standard and deviant complex for the 30 ms and 60 ms deviant epochs are presented in Figure 3C, first averaged across all blocks (left) and then separately for each sequence and block (right).

Sequence repeats were the longest time course regularity in the experimental structure (see Figure 1), and a tendency is visible in both Figure 3A,C for the mean standard complex to become more negative while the mean deviant complex becomes less negative over sequence repeats. This pattern was confirmed in an omnibus repeated measures ANOVA with within-subject factors of oddball-role (standard, deviant), tone (30 ms, 60 ms), block (first-sequence occurrence [i.e., 1 and 2], second-sequence occurrence [i.e., 3 and 4]), and sequence (1–4). Main effects of oddball-role ($F(1,31)=54.624$, $p<0.001$, $\eta_p^2=0.638$; $\eta_p^2=0.715$ with replacement excluded), and sequence ($F(3,93)=2.937$, $p<0.037$, $\eta_p^2=0.083$; $\eta_p^2=0.117$ with replacement excluded) were modified by four two-way interactions. The effect of sequence differed as a function of the oddball-role ($F(3,93)=6.485$, $p<0.001$, $\eta_p^2=0.173$; $\eta_p^2=0.210$ with replacement excluded) and this was not further modified by tone type or block. Post hoc tests revealed that the deviant complex was always more negative than the standard complex, but as can be seen in Figure 3, this difference was largest for sequence 1 declining progressively over sequences. Polynomial contrasts confirmed a significant linear increase in negativity for the standard complex over sequence 1–4 ($t(31)=3.012$, $p<0.005$) and a significant linear decrease in negativity for the deviant complex over sequence 1–4 ($t(31)=5.442$, $p<0.001$). Thus, the disruptive effect caused by the deviant occurrence in sequence 1 lessens by sequence 4, which is evident both for the 30-ms and the 60-ms deviant ERPs (Figure 3A,B) and for the mean complex amplitudes (Figure 3C).

Oddball role was also modified by block ($F(3,93)=5.468$, $p<0.026$, $\eta_p^2=0.083$; n.s. $\eta_p^2=0.127$ with replacement excluded) with post hoc tests indicating that the change in the standard complex amplitude was not significant from early to later blocks but the deviant complex amplitude was less negative in later blocks ($t(31)=-2.935$, $p_{\text{Holm}}<0.006$). The mean amplitudes for the standard and the deviant complex are rearranged in Figure 3D to emphasize change from the first to the second occurrence of each block composition within each sequence, separately for 30-ms and 60-ms deviant runs. The amplitude modulation of the complexes was further explored by computing a change index through subtracting the amplitude for the second occurrence of each block from the first occurrence for each corresponding measure (e.g., standard complex block 1 minus standard complex block 3, etc.). These computations revealed that the average amplitude change in the corresponding standard and deviant complexes was highly negatively correlated. That is, the negative amplitude of the deviant complex and the positive amplitude of the standard complex proportionally declined (30 ms deviant blocks $r=-0.714$, $p<0.001$, 60 ms deviant blocks $r=-0.803$, $p<0.001$); that is, the absolute values of their amplitudes were attenuated together from the first to the second occurrence of the same type of block within the sequences. The change from early to later blocks within sequences was more pronounced for the 30 ms complex measures (tone by block interaction [$F(1,31)=7.546$, $p<0.010$, $\eta_p^2=0.196$; $\eta_p^2=0.124$ with replacement excluded]) with post hoc tests confirming a significant change by the later block for the 30 ms tone only ($t(31)=-2.900$, $p_{\text{Holm}}<0.041$). Finally, oddball role was modified by tone ($F(1,31)=6.497$, $p<0.016$, $\eta_p^2=0.173$; n.s. $\eta_p^2=0.153$ with replacement excluded) with post hoc tests indicating that

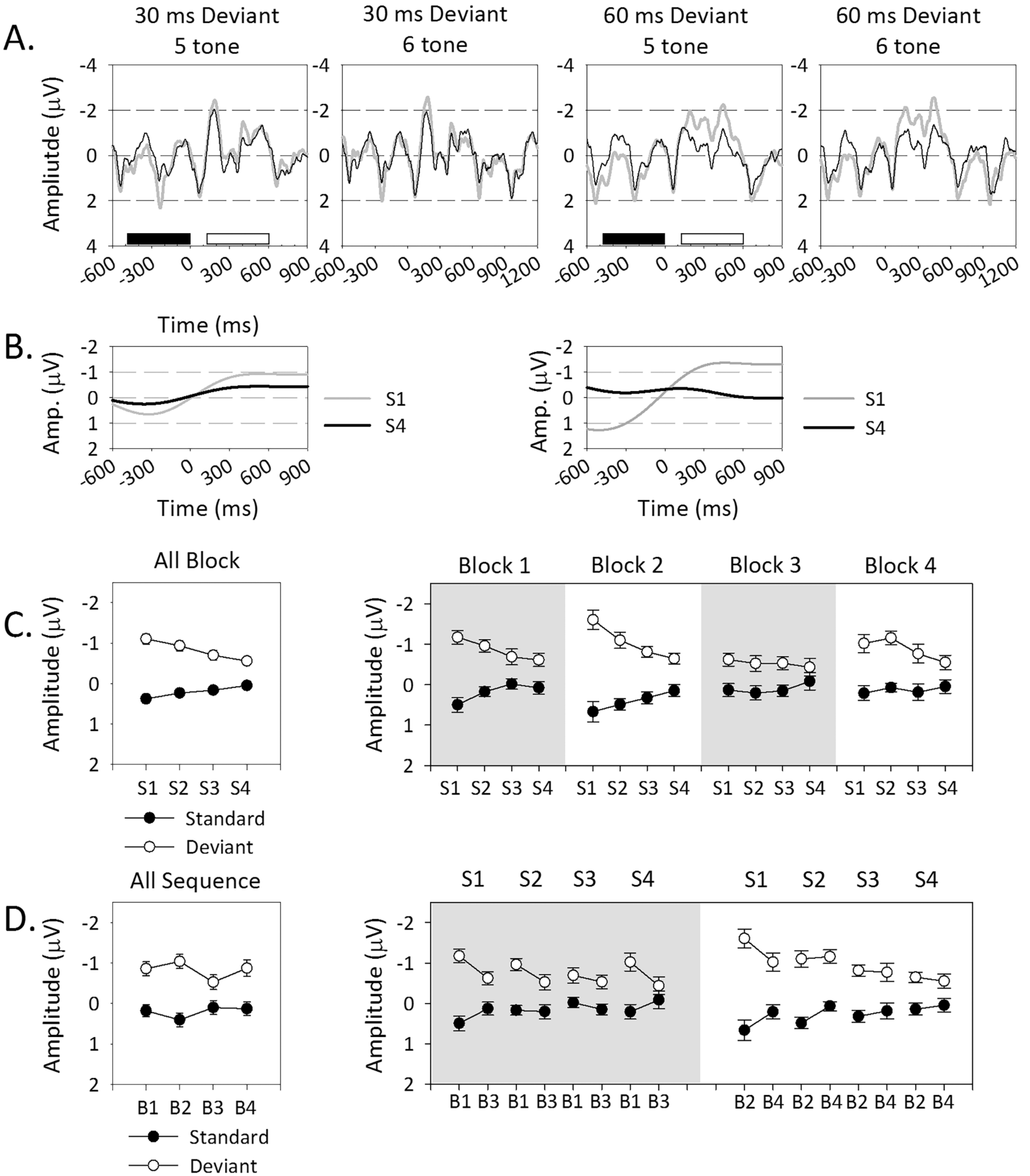

FIGURE 3 | (A) Group-averaged Fz five-tone and six-tone ERPs centred on the occurrence of the 30 ms and 60 ms deviant, for sequence 1 (gray/thick line) and sequence 4 (black/thick line). Six-tone ERPs are shown here to demonstrate that the deviant complex resolves after the second standard following the deviant, but not analyzed due to S/N issues—see Section 1. (B) Overplotting sequence 1 (gray) and 4 (black) waveforms for the five-tone ERP centred on the occurrence of the 30-ms (left) and the 60-ms deviant sequences (right) after a 1 Hz low-pass filter was applied (for illustration purposes, only). (C) The group averaged Fz standard (black circles) and deviant (white circles) complex means for each sequence (left) and separately for each block of each sequence (right). (D) The group averaged Fz standard (black circles) and deviant (white circles) complex means for each block (left) and separately for each block of each sequence (right). Error bars represent the standard error of the means.

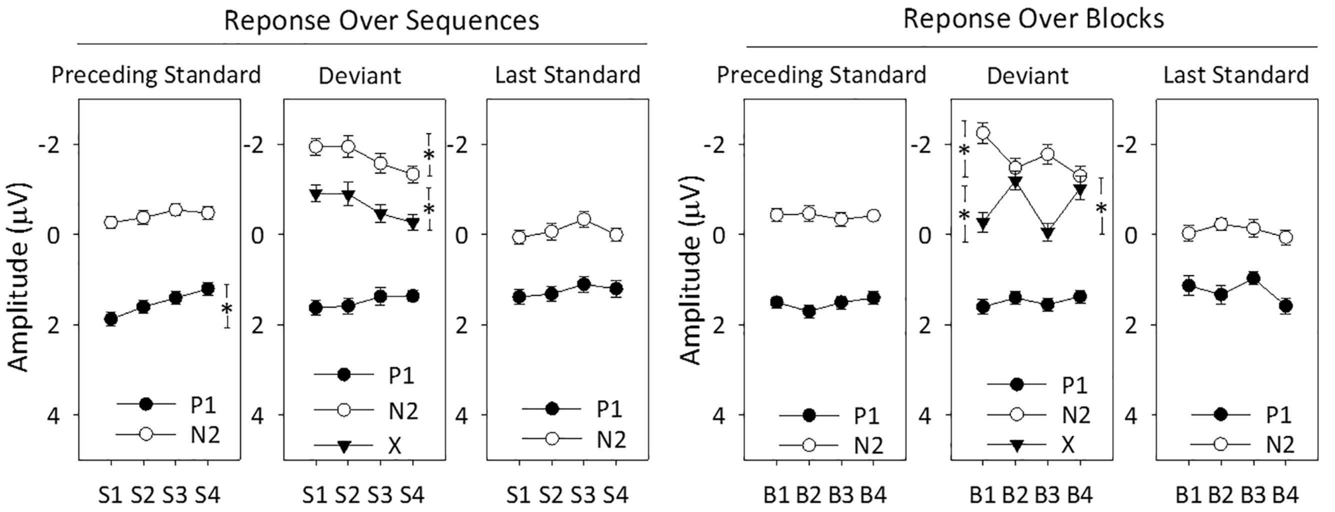

FIGURE 4 | The group averaged Fz means for P1 (black circles) and N2 (white circles) and X (black triangles) component means for each sequence (left) and, separately, for each block (right). Error bars represent the standard error of the means.

the interaction is due to the lack of difference in standard complex amplitudes between tones, while the deviant complex was larger to the 60 ms deviant overall ($t(31) = 2.530$, $p_{\text{Holm}} < 0.033$).

Finally, a difference value was computed for the change over the sequences by subtracting the amplitude for the fourth sequence from the first sequence for each corresponding block type (e.g., standard complex for the 30 deviant block type in sequence 1 minus standard complex for the 30 deviant block type in sequence 4, etc.). Once again, the absolute amplitude values of the deviant complex and the standard complex decreased proportionally together (30 ms deviant blocks $r = -0.622$, $p < 0.001$, 60 ms deviant blocks $r = -0.657$, $p < 0.001$). Taken together, the absolute values of the amplitudes of the deviant and the standard complex changed together across both sequences and between the first and the second occurrence of the same type of block within the sequence.

2.2 | Component Analyses

The component amplitudes extracted from each long epoch ERP are presented in Figure 4 and were assessed in repeated measures ANOVAs with factors of deviant context (30 ms, 60 ms), block (first occurrence, second occurrence) and sequence (1–4). In Figure 4, it would appear that the N2 and P1 amplitudes changed very little over blocks and sequences for the final standard, and this was supported in the ANOVA revealing no significant effects or interactions on N2, and a main effect of tone only for P1 (larger/more positive for 60 ms deviant blocks [$F(1,31) = 4.517$, $p < 0.042$, $\eta_p^2 = 0.127$; $\eta_p^2 = 0.241$ with replacement excluded]).

Figure 4 indicates minimal change in N2 for the standards preceding deviants which was also supported by no significant main effects or interactions in the ANOVA. However, the same ANOVA applied to P1 indicated a significant negative shift over sequences ($F(3,93) = 5.442$, $p < 0.002$, $\eta_p^2 = 0.149$; $\eta_p^2 = 0.270$ with replacement excluded) which was characterized by a significant linear increase in negativity in a polynomial contrast ($t(31) = -4.133$, $p_{\text{Holm}} < 0.001$). Sequence was modified by a tone by block by sequence interaction ($F(3,93) = 3.044$, $p < 0.033$, $\eta_p^2 = 0.089$; n.s. $\eta_p^2 = 0.022$ with replacement excluded). As can be seen in Figure 4, there was no generalized change in P1 over blocks overall for the standards preceding the deviant, but the three-way interaction occurred because P1 amplitude did become more negative from the first to second occurrence of a block in sequence 1 due to a change in the 60 ms deviant blocks only ($t(31) = 4.908$, $p_{\text{Holm}} < 0.001$).

Figure 4 shows the same pattern of change in deviant N2 and component X over sequences, but a different pattern of change in these components over blocks. The ANOVA on deviant N2 amplitude revealed significant main effects of tone (larger to 30 ms, $F(1,31) = 6.609$, $p < 0.015$, $\eta_p^2 = 0.176$; $\eta_p^2 = 0.163$ with replacement excluded), block (larger to early blocks, $F(3,93) = 8.957$, $p < 0.005$, $\eta_p^2 = 0.224$; n.s. $\eta_p^2 = 0.137$ with replacement excluded), and sequence ($F(3,93) = 5.063$, $p < 0.003$, $\eta_p^2 = 0.140$; $\eta_p^2 = 0.151$ with replacement excluded), with the decreasing negativity over sequence being characterized by a significant linear trend in a polynomial contrast ($t(31) = 3.785$, $p_{\text{Holm}} < 0.001$). This occurred in the absence of any significant main effects or interaction for the P1 component to deviant tones. Finally, the same ANOVA applied to component X confirmed a main effect of tone (more negative to 60 ms, $F(1,31) = 11.970$, $p < 0.002$, $\eta_p^2 = 0.279$; $\eta_p^2 = 0.320$ with replacement excluded) and sequence ($F(3,93) = 4.529$, $p < 0.005$, $\eta_p^2 = 0.127$; $\eta_p^2 = 0.152$ with replacement excluded), with the effect of sequence being significant for early blocks only (sequence by block, $F(3,93) = 3.736$, $p < 0.014$, $\eta_p^2 = 0.108$; n.s $\eta_p^2 = 0.098$ with replacement excluded). This larger amplitude for X after a 60 ms tone appears to be attributable to the sharper peak to the 30 ms tone while the X component "rides" on the unresolved negativity in response to the 60 ms tone (see Figure 2).

In summary, significant change over sequences was observed to standards preceding the deviant but only in the P1 component. Significant change over sequences was observed to deviants but only in the N2 component. Neither sequence nor block significantly altered the P1 and N2 to the last standard and component

X tended to vary similarly to the deviant N2 over sequences, with the changes being more marked for early blocks.

3 | Discussion

Participants in this study heard an unattended sound sequence which contained multiple levels of patterning: over the course of seconds it was a repeating standard tone, at the time scale of multiple minutes it was an alternating probability structure (alternating tone tendencies), and over 10s of minutes it was a repeating alternating probability sequence. The results suggest that the brain remains sensitive to violations of these learned patterns over time, but appears to reduce the overall distortion caused by these regularity violations in a manner consistent with the notion of both minimizing error signaling and restoring excitation/inhibition (E/I) balance over time (i.e., a kind of E/I homeostasis) (Chen et al. 2022).

The auditory ERPs extracted in this study differ from conventional analyses of auditory oddball-like paradigms by including five-tone SSDSS runs. In traditional auditory oddball analyses, the ERPs are time locked to the onset of each individual sound and typically baseline corrected to the activity immediately prestimulus to the sound onset (Kujala et al. 2007). This method enables a comparison of how the component structure and amplitude to each sound type differs, and it is well known that the response to a pattern deviant and the standard immediately after the deviant contain additional negativity relative to the repeating standard (Winkler et al. 1996; Sussman and Winkler 2001). Both differences have been attributed to evidence that the brain may be updating the prevailing internal model to accommodate the prediction-error; in the case of the deviant, it is the change from expected attributes, and in the case of the following standard, presumably the readjustment back in the direction of the standard or the rare transition from deviant to standard (Mittag et al. 2016; Winkler 2007). By extracting SSDSS runs in a single epoch, it appears that the additional negativity in the ERP to the deviant tone includes a longer-term disruption to the proceeding responsivity that, in this study, extends over the duration of the immediately following standard, but not beyond. This observation is supported by the visual return of the ERP to preceding amplitudes by the last standard (see Figures 2 and 4) and by the fact that the amplitude modulations observed to the deviant N2 and the deviant complex over sequences are not observed to the last standard.

An extended mean amplitude measurement was used to capture the prolonged deviant-induced negativity, and an equal-length mean amplitude over the preceding standards was used for comparison (hereafter, the deviant and standard complex, respectively). These measurements are therefore not component-specific but rather extract a mean over a longer window covering two tones. These measurements expose that the standard and deviant complex means appear to become more similar over time with experience with the sequence. This "normalizing" effect occurs both across sequences and within a sequence (the difference generally smaller for the second encounter of the given block type in Figure 3D). For both the 30 and 60 ms tones, the degree to which the standard and deviant complex changed between the earlier and later blocks is correlated implying that they change together (see Figure 3C). It would appear that familiarity with experience is important and not just time, as the differences do appear to reset with a composition change in the block type (i.e., the probability inversion between the two tones at block change points): the differences between block 1 and 2 in Figure 3C suggest that this resetting can be observed in both measurements; more negative for the deviant mean and more positive for the standard complex mean at the beginning of a standard-deviant reversal. At the component level, evidence of longer-term change over blocks of a sequence is restricted to the deviant N2, and to the earlier block occurrences of component X.

A "normalizing" change in complex measures was also evident over a longer time course with the deviant complex becoming less negative in parallel with the standard complex becoming more negative over sequence repeats. The start values differed less at the onset of a repeated sequence than for the onset of the sequences before that (i.e., the standard and deviant complex differ more for sequence 1 block 1 than sequence 2 block 1 and so on in Figure 3C). The change sensitivity reflected in the standard and deviant complex measures, therefore, seems to reduce with familiarity over multiple timescales. The opposing trends for the standard and deviant complex, however, could be influenced by the whole-epoch baseline correction applied. The tendency of the deviant complex to be much larger earlier in the recording could, on average, lead to a larger positive baseline correction to the whole epoch. A more pronounced baseline correction during earlier stages of the recording could explain the more positive standard complex measures in those recordings. While we cannot exclude the possibility that baseline correction is contributing to the opposing changes in standard and deviant complex over time, it seems equally possible that the distortion in both directions is changing over time, as the low pass filtered data in Figure 3B suggests. The component analysis offers some further support for this interpretation, in that the repeated sequences only change the deviant N2 amplitude, while changing the P1 only for the preceding standards. These selective changes are less likely to be explained by whole-epoch shifts due to baselining, and are more consistent with the kind of E/I change that might be expected in more efficient or sparse encoding (Zhou and Yu 2018).

Reductions in negative deviant response amplitude or MMN over long timeframes have been observed previously by our group using this alternating design in the counter-balanced order (starting with the 60 ms sound as deviant; Frost et al. 2016) and a non-alternating oddball design (Yeark et al. 2023). Using a traditional oddball sequence, one study looked for evidence that the brain comes to anticipate the occurrence of a deviant in a manner similar to a hazard function, observing a negative shift in the fourth repetition of a standard after the occurrence of a deviant in the form of a contingent negative variation (CNV) or stimulus-preceding negativity (SPN) visible as a shift in the baseline (Ford et al. 2010). The CNV is considered an indicator of expectancy typically observed in task-related ERPs between a cue and the target stimulus (Czenner et al. 1986). In task-independent ERPs, the negative shift is generally discussed as the SPN reflecting the stimulus anticipation element rather than the response preparation component of the CNV (Masaki et al. 2010). A similar CNV type response was observed to occur to an unattended sound when an expected sound was delayed using low probability long interstimulus interval deviants (Mento 2013). In the SSDSS averages used here, the two standards before the deviant will on average be at least the 6th and 7th standard in a row given that the probability of a deviant is 12.5% (1 in 8 tones). The significant linear correspondence between the negative shift in standard and the positive shift in deviant complex amplitudes over sequences and blocks could indicate support for the interpretation that the convergence of measures over time in the present study might reflect predictive activity. In other words, the higher the familiarity with the sequence, the larger the SPN as standards repeat, the higher the prediction that the stimulus is going to change, and the smaller the subsequent negativity elicited by that change. The presence of an SPN would also be consistent with the observation that the P1 to the last standard did not exhibit the sequence modulation as it occurs at the point where a deviant would be least probable. The concept of anticipating an upcoming deviation in the form of a local hazard function was not the intent of the experimental design which was instead to examine relative change in sensitivity to local deviants as a function of experience with the longer-term structure. This design may therefore not be ideal to examine SPN effects which ideally requires empirical support from a purposely designed study. A subset analysis conducted on the present data using shorter and longer standard strings (see supplementary text in Data S1) did not support this interpretation; however, the averaging over embedded patterning may limit the ability to see these established SPN effects.

The results of the present study are compatible with an extended notion of basing deviance detection on transitional probabilities by assuming that the auditory system creates statistics representing preceding micro-sequences beyond the immediately preceding transition. This interpretation is supported by mathematical models suggesting that the memory underlying MMN retains statistics from longer segments of the sequence preceding the deviant (Rubin et al. 2016) and it fully supports predictive utilization of the encoded information. Further, the predictive interpretation may only be the flip side of the notion of reestablishing the E/I balance, as for correctly predicting the future, the human brain must maintain context-dependent sensitivity to deviant events, which takes into account not only the immediate (low-level), but also the large-scale structural (higher-order) context. Previous studies (Mullens et al. 2016; Sussman and Winkler 2001; Auksztulewicz and Friston 2016; Fitzgerald et al. 2021; Todd et al. 2020, 2022; Todd and Mullens 2011) provide ample evidence that deviance detection is sensitive not only to the local, but also to the wider context. The predictive account of the behavior of the two complexes observed in the current study could be explicitly tested by varying the regularity of rare deviant occurrence by comparing, for example, the deviant and standard complex where a deviant occurs on average every 1 in 8 sounds (as it does here) with a separate condition in which it occurs exactly on every 8th tone. One might expect the difference in the standard and deviant complex to reduce faster or more in the more predictable environment.

The present analysis also exposed a component occurring simultaneously with the onset of the standard immediately after the deviant (labeled X in this paper). The amplitude of this component "rides on" the deviant complex given that there is no baseline correction to the pre-stimulus interval so the shift in X amplitude in Figure 4 largely resembles the change in deviant complex amplitude in Figure 3. Nonetheless it is clearly a distinct response that resolves with the onset of the P1 component to the standard after the deviant. This component is not typically seen in traditional analyses because the epoch ends before the onset of the next sound. The present study cannot disentangle whether this might be an offset response to the prior tone or an anticipatory response to the next sound. The X component peaks approximately 240–270 ms after the offset of the sounds and appears to peak at the same time for both the 30 ms and the 60 ms deviant sounds. This latency may be a little late for an offset response given observations of ~160 ms in younger adults (Horváth et al. 2017). Component X emerges before sound onset and may in fact be time locked to the rhythmic stimulus presentation every 300 ms. For the regular standards the component could be present but absorbed into the tail end of the N2. The larger N2 to the deviant appears to bring this component forward in time and into a sharper, narrower, morphology which may in turn lead to the exposure of the X component. The component may be useful in assessing how accurately the brain is tracking sound timing and may be related to the ability to entrain steady-state responses, in this case in the delta range. There is evidence that suggests that onset timing can be learned and predicted in oddball sequences. For example, using electrodes placed on the cortical surface it has been shown that there is neural activity occurring at the expected onset of a sound even when the expected sound is omitted (Cho et al. 2023). This suggestion requires further exploration, potentially with longer intervals between sounds that would separate component X from the N2 complex, and potentially with jittered sound timing which should lead to diminished amplitude or even abolish the component altogether. If component X remains visible and its latency does not change with such manipulations, then it would more likely reflect an offset response; conversely, if component X disappears under timing jitter, then it may be related to anticipatory activity.

The mean amplitudes based on long measurement intervals used in the present study could be argued to capture change in the slower dynamics in oddball sequence processing (Shymkiv et al. 2025). One of the strengths of this approach is the equality of signal-to-noise and the temporal proximity in measures of the standard and deviant given that the extraction is always from the same epoch and the same number of responses contributing to the averages. However, the limitation is that the standard complex amplitude may not fully represent how the brain responds to all standards in this period of the sound sequence given the potential presence of the SPN as reviewed above. Furthermore, the long-epoch analysis results in significant data loss relative to short-epoch analysis. In this data set for example the average trial count drops from 91% of coded deviants to 65% of coded deviants. Therefore, there is a reasonable amount of data loss even in very clean datasets. As noted in methods, the sound sequence design used to assess long-term changes was not counterbalanced. However, other shorter-term effects on standard and deviant processing have shown order dependence and not tone dependence in both conventional single-tone ERPs (e.g., Todd et al. 2021, 2014, 2011; Mullens et al. 2016) and in dynamic causal modeling observations of the data (Fitzgerald et al. 2021; Banaschewski et al. 2025). Tone type was not a significant interaction term to any of the longer-term effects that were the focus of this paper; however, additional studies would be required to confirm that the patterns generalize to the reverse order of tone duration and for other sound properties.

In conclusion, the present study introduces a new way to analyze oddball sequences to study how the brain builds internal models and weights the precision of these models over different timescales. The multi-tone epochs are essential to exposing the long-lasting perturbation of the ERP after the occurrence of a low probability deviant. The results conform to theory suggesting that whilst we may retain sensitivity to probabilistically rare events, the way these are expressed in neuronal response may change over time in a manner consistent with sparse encoding (Carandini and Heeger 2012). In scalp-recorded ERPs these changes are expressed as shifts in E/I balance normalization over time, evident in standard/deviant complex measures and standard P1 and deviant N2 components. In this particular study, predictability and time are confounded so future work would benefit from exploring whether varied predictability and/or the precision of information content affects these longer-term changes in ERPs. However, the potential to assess E/I balance in this manner opens the door to studying cross-species, developmental, age-related and illness-related changes in this process in a new way using task-independent learning as the paradigm.

Author Contributions

Juanita Todd: conceptualization, methodology, software, data curation, formal analysis, supervision, funding acquisition, writing – original draft, writing – review and editing. **Mattsen Yeark:** methodology, software, formal analysis, data curation, writing – review and editing, investigation, project administration. **Matthew Godfrey:** methodology, formal analysis, writing – review and editing. **Christoph Mathys:** methodology, writing – review and editing, funding acquisition. **Istvan Winkler:** methodology, funding acquisition, writing – review and editing.

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Ethics Statement

The study was approved by the university Human Research Ethics Committee (H-2012-0270).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in OSF at https://osf.io, reference number dg63z.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** psyp70193-sup-0001-DataS1.docx. **Table S1:** Group averaged standard and deviant complex measures and deviant peak component measures for the ERPs centred on the 30 and 60 ms deviant tones (mean 180–200 ms). Standard deviation presented in parentheses.