

The sound of silence: Predictive error responses to unexpected sound omission in adults

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Abstract

The human auditory system excels at detecting patterns needed for processing speech and music. According to predictive coding, the brain predicts incoming sounds, compares predictions to sensory input, and generates a prediction error whenever a mismatch between the prediction and sensory input occurs. Predictive coding can be indexed in EEG with the mismatch negativity (MMN) and P3a components, two ERP components that are elicited by infrequent deviant sounds (e.g., differing in pitch, duration, loudness) in a stream of frequent sounds. If these components reflect prediction error, they should also be elicited by omitting an expected sound, but few studies have examined this. We compared ERPs elicited by infrequent randomly occurring omissions (unexpected silences) in tone sequences presented at 2 tones/sec to ERPs elicited by frequent, regularly occurring omissions (expected silences) within a sequence of tones and resting state EEG (a constant silence). We found that unexpected silences elicited significant MMN and P3a, although the magnitude of these components was quite small and variable. These results provide evidence for hierarchical predictive coding, indicating that the brain predicts silences as well as sounds.

INTRODUCTION

Much of the information in auditory signals resides in their temporal dynamics. To extract relevant information, it is thought that the brain detects patterns by actively predicting incoming sounds based on the prior context (Arnal & Giraud, 2012; Bendixen, SanMiguel, & Schröger, 2012; Friston & Kiebel, 2009; Heilbron & Chait, 2017; Kumar et al., 2011). This process, termed predictive coding, is important for learning and understanding language (Romberg & Saffran, 2010; Ylinen, Bosseler, Junttila, & Huotilainen, 2017) and processing pitch and rhythm in music (Chang, Bosnyak, & Trainor, 2018; Háden, Németh, Török, & Winkler, 2015; He, Hotson, & Trainor, 2009; Trainor, 2012; Winkler, Haden, Ladinig, Sziller, & Honing, 2009; Winkler, 2007). When a stimulus violates a hypothesis, an error signal is generated, enabling updating of internal models. Models of predictive coding (Friston & Kiebel, 2009) suggest that any transient event-related potential (ERP) component could reflect prediction error response. For example, violations of self-action-generated auditory predictions have been shown to elicit an N1 response (Korka, Schröger, & Widmann, 2019, 2020; SanMiguel, Widmann, Bendixen, Trujillo-Barreto, & Schröger, 2013; Schröger, Marzecová, & Sanmiguel, 2015). When examining violations to purely auditory predictions the mismatch negativity (MMN: Näätänen, Gaillard, & Mantysalo, 1978; Näätänen, Kujala, & Winkler, 2011; Näätänen, Tervaniemi, Sussman, & Paavilainen, 2001; Winkler & Czigler, 2012) and P3a (Chang et al., 2018; Max, Widmann, Schröger, & Sussman, 2015) components are elicited. MMN typically occurs after a violation of expectation for an acoustic feature such as pitch, duration, or timbre, or a change in the pattern of sounds. However, if MMN represents all auditory expectation violations, then an omission of an expected stimulus (i.e., an unexpected silence) should also elicit MMN. Although

some previous work found MNN to unexpected silences (Horváth, Müller, Weise, & Schröger, 2010; Recasens & Uhlhaas, 2017; Shinozaki et al., 2003; Winkler et al., 2009; Yabe, Tervaniemi, Reinikainen, & Näätänen, 1997), most studies report an MMN-like response only when the tones are presented at a stimulus onset asynchrony (SOA) of 200 ms or less, which is within the brain's temporal integration window (Horváth, Czigler, Winkler, & Teder-Sälejärvi, 2007; Rüsseler, Altenmüller, Nager, Kohlmetz, & Münte, 2001; Shinozaki et al., 2003; Winkler et al., 2009; Yabe et al., 1997, 1998). Here we examine ERPs to tone omissions outside of the integration window at an SOA of 500 ms.

MMN is typically elicited by rare stimuli (deviants) embedded in a sequence of frequent stimuli called standards (Bartha-Doering et al., 2015; Näätänen, Astikainen, Ruusuvirta, & Huotilainen, 2010; Näätänen et al., 2011; Näätänen, Paavilainen, Rinne, & Alho, 2007; Näätänen et al., 2004; Sussman, Chen, Sussman-Fort, & Dinces, 2014; Winkler, 2007). The MMN response is a frontally negative deflection peaking between 150 and 250 ms that reverses polarity at the back of the scalp, consistent with a primary generator in auditory cortex (Näätänen, 2003; Paavilainen, 2013; Trainor, 2001, 2012). The amplitude and latency of the MMN are typically extracted from the local minimum in the difference wave formed by subtracting the deviant ERP from the standard ERP. MMN magnitude increases with increased deviant tone rarity and larger physical differences, such as larger pitch deviations (Näätänen et al., 2007). MMN can be elicited without attention, suggesting that detecting regularity and violations of regularity are automatic sensory processes (Max et al., 2015; Tervaniemi et al., 1999; Todd, Provost, Whitson, Cooper, & Heathcote, 2013).

MMN can be observed when the standard and deviant stimuli are physically identical, but where the deviant violates a rule in its context whereas the standard does not in its context

(Grimm, Escera, Slabu, & Costa-Faidella, 2011; Shestopalova, Petropavlovskaja, Vaitulevich, & Nikitin, 2015), or the stimulus is presented in different conditions, namely, an oddball paradigm and a condition that presents multiple stimuli all occurring with the same probability, thus controlling for context and occurrence rate (Jacobsen & Schröger, 2003; Ruhnau, Herrmann, & Schröger, 2012; Todd, Provost, & Cooper, 2011; Todd et al., 2013; Wiens, Szychowska, Eklund, & van Berlekom, 2019). Comparing the same stimulus under different context is essential when examining MMN responses to unexpected silences, because responses to a sound will contain auditory components not in the ERP responses to silence. Specifically, we compared the ERP waveforms to silence as a standard stimulus (i.e., an expected silence) to silence as a deviant (i.e., unexpected silence).

Despite decades of research, the mechanisms that elicit the MMN remain controversial. An alternate theory to predictive coding is neural adaptation (Garrido, Kilner, Stephan, & Friston, 2009; Gu, Wong, Hu, Zhang, & Tong, 2019; Jaaskelainen et al., 2004; May & Tiitinen, 2010). According to this theory, as a tone is repeated, neurons encoding its acoustic features habituate, leading to decreased neural firing. When the deviant tone is presented, the change elicits firing from new neurons not yet habituated. In this scenario, MMN represents the recruitment of neurons to encode the deviant stimulus features.

On the other hand, both empirical and modeling research supports a predictive coding view of MMN (Chennu et al., 2016; Trainor, 2012; Wacongne, Changeux, & Dehaene, 2012; Wacongne et al., 2011). MMN can be elicited by changes to abstract features or patterns (Bouwer, Van Zuijlen, & Honing, 2014; Moldwin, Schwartz, & Sussman, 2017; Paavilainen, 2013), differences in global and local probability (Basirat, Dehaene, & Dehaene-Lambertz, 2014), and disruptions to musical metric structure (Winkler et al., 2009). For example, infrequent

rising tone patterns in a sequence of descending tone patterns (Carral et al., 2005; Háden et al., 2015) and relative pitch changes in melodies presented in different pitch ranges (Fujioka, Trainor, Ross, Kakigi, & Pantev, 2004, 2005; Tew, Fujioka, He, & Trainor, 2009; Trainor, McDonald, & Alain, 2002) elicit MMN. In these cases, standards and deviants differ in pattern, not stimulus features such as pitch, suggesting that MMN cannot be a result of neural habituation to acoustic features. It is possible, however, that MMN might operate at a pattern or auditory object level, with habituation occurring at these higher levels of representation. (Costa-Faidella, Grimm, Slabu, Díaz-Santaella, & Escera, 2011).

Predictive coding has also been examined in relation to the P3a ERP component, which often follows the MMN, and is related to inadvertent capture of attention (Polich, 2007; Sussman, Horváth, Winkler, & Orr, 2007). P3a increases in amplitude with decreasing deviant predictability (Chang et al., 2018; Max et al., 2015; Sussman, Winkler, & Schröger, 2003). Furthermore, P3a amplitude is inversely correlated with the power of β band neural oscillations (Chang et al., 2018), which have been linked to auditory and motor predictive timing (Arnal & Giraud, 2012; Chang et al., 2018; Cirelli et al., 2014; Saleh, Reimer, Penn, Ojakangas, & Hatsopoulos, 2010). In sum, effects of predictive coding can be seen in various aspects of the EEG response. Here we focus on MMN and P3a.

The error signals generated by omission of an expected sound are an important, yet understudied, aspect of predictive coding. Finding MMN and P3a responses to an omission would be strong evidence against neural adaptation, as silence would not recruit any new sensory neurons. On the other hand, the absence of an MMN to unexpected silence would indicate that the neural signatures of an unexpected silence differ from those of unexpected feature or pattern deviations.

Early studies examining MMN to tone omissions only found a significant response with SOAs less than 200 ms (Yabe et al., 1997). Yabe and colleagues examined SOAs from 100 to 350 ms but did not find that omissions elicited a significantly different response from the sound stimulus at SOAs greater than 200 ms. Following this study, most studies used SOAs of less than 200 ms. Using depth electrodes, Hughes et al. (2001) found an MMN-like response to omissions in auditory sequences with an SOAs of 200 ms, but did not evaluate responses for larger SOAs because they “tended to produce responses that were dispersed in time” (p. 1078). Since these reports, most studies examining tone omissions, whether analyzing P1, N1, (Bendixen, Schröger, & Winkler, 2009) or MMN, (Bendixen, Scharinger, Strauss, & Obleser, 2014; Oeckl, Winkler, Sussman, & Alho, 2013; Recasens & Uhlhaas, 2017; Wacongne et al., 2012, 2011) used SOAs shorter than 200 ms. These studies interpret the omission MMN as evidence supporting predictive coding. However, the short SOAs used in these studies fall within the auditory integration window, in which two auditory events can be perceived as one event (Yabe et al., 1998). This window is often defined, and measured, as the time window over which intensity is summated, and it spans approximately 200 ms or less (Shinozaki et al., 2003; Yabe et al., 1998). Specifically, a 200 ms tone will sound louder than a 100 ms tone of equal amplitude, whereas a 2000 ms tone will sound equally loud as a 1000 ms tone of equal amplitude. Thus, at short SOAs, omission MMNs could result from the integration of successive sounds into single percept.

Furthermore, deviant tones can elicit MMN in sequences with SOAs of up to 2 seconds or more; in general the amplitude of the MMN decreases as SOA increases (Näätänen, Jacobsen, & Winkler, 2005; Näätänen et al., 2007), but the length of SOAs under which MMN can be observed varies greatly between individuals (Winkler, Schröger, & Cowan, 2001). Thus, if

MMN reflects predictive errors related to unexpected omissions, it would be expected to be observed at SOAs larger than 200 ms. Some models of the neural architecture predict MMN responses to omissions (Wacongne et al., 2012) particularly if attention is drawn to that point in time (Wacongne et al., 2011; Chennu et al., 2016). To our knowledge only one study using EEG has found what may be an MMN or P3a-like response to a stimulus using an SOA of 1 second, but the responses were small and variable, limiting the researchers' interpretation of the ERPs (Busse & Woldorff, 2003). However, intracranial recordings (Fonken et al., 2019; Halgren et al., 1995) have found specific responses, including increased high frequency power, to sound omissions, even with SOAs larger than 200 ms. Thus, it remains an open question whether MMN and P3a measured in EEG reflect predictive errors for unexpected omissions.

Salisbury et al. (2012) examined omission deviants in the context of discrete 6-tone patterns with SOAs of 330 ms between tones. They found significant MMN to omissions of the 4th or 6th tone and interpreted this as a gestalt pattern violation. One issue in Salisbury (2012), and most studies investigating the omission response, is that they calculated the MMN amplitude by either subtracting the omission response from the standard tone response or directly compared the two responses. This is problematic because the standard tone will elicit obligatory auditory components that the omission deviant will not. Thus, a difference waveform will show peaks related to the obligatory responses present in the standard waveforms but absent in the omission waveforms, which then could be mistaken for MMN. To our knowledge this potential confound has not been discussed in the literature to date (Bendixen et al., 2014; Moldwin et al., 2017; Recasens & Uhlhaas, 2017; Salisbury, 2012).

Given these questions and the importance of understanding neural responses to unexpected silences for predictive coding theories (Bendixen et al., 2014; Heilbron & Chait, 2017; Trainor,

2012), we investigated the response to unexpected silences (i.e., omission deviants), expected silences (i.e., during an expected interstimulus interval) and continuous silence (i.e., resting state). If silences that violate expectations elicit a different ERP response than silences that are expected, this would reflect predictive coding.

METHODS

Participants

Thirty adults (5 males; Age: $M = 18.7$, $SD = 1.23$) were recruited via the McMaster undergraduate participant pool and given course credit for their participation. All participants reported no known hearing impairments and normal or corrected to normal vision. 70% percent of participants spoke a language in addition to English and 67% had at least one year of musical training. All study procedures were approved by the McMaster University Research Ethics Board.

Stimuli

We used a C4 piano tone from the Iowa Musical Instrument Samples database (University of Iowa Electronic Music Studios). The tone was edited using Audacity to be 250 ms in duration, including 50 ms cosine rise and decay. The tone was presented through an AudioVideo Methods speaker (P730) placed 1 meter in front of the participants' head, at 60 dB SPL-C over a noise floor of 49.8 dB SPL-C (less than 30 dB SPL-A). The tone was presented in two separate conditions, one with unexpected silences (tone omissions) and one with expected silences (Figure 1a). During the unexpected silence condition, the stimulus onset asynchrony (SOA) between tones was set to 500 ms. The unexpected silences were created by omitting 10%

of tones pseudo-randomly within the sequence, with the constraint that at least two piano tones were presented between each unexpected silence.

For the expected silence condition, the same 250 ms piano tone was presented, but the SOA was doubled to 1000 ms. For this condition, the onset of the expected silence was defined as 500 ms after each tone (Figure 1a). Thus, we created two sequences with the same local context: silences occurred 500 ms after a tone onset and silences were followed by a tone occurring 500 ms after the silence onset. This ensured that the only difference between the silence conditions was the expectation of the silence from the global context of the sequence. A significantly different response to the unexpected silence compared to the expected silence would indicate a prediction violation for an unexpected stimulus omission. Finally, we also collected resting state EEG by not presenting any sound in blocks of 1 minute.

Three blocks of each of the unexpected silence condition, expected silence condition, and resting state were presented for a total of 9 blocks. Each block of the unexpected silence condition contained 600 trials (540 piano tones, 60 unexpected silences). Each block of the expected silence condition contained 60 trials (60 piano tones, 60 expected silences). Thus, we collected a total of 180 responses each of expected silences and unexpected silence.

Procedure

After obtaining consent, the participant completed a demographic questionnaire regarding language experience, musical training, hearing status, and handedness. The participant was then seated in a sound attenuating room, with the speaker presenting the sounds located 1 meter in front of their head. They were fitted with an EEG electrode net after it was soaked in a saline solution. Free field sound presentation was used to facilitate comparison to a subsequent infant

study. During the experiment, participants passively listened to the tones while watching a silent, subtitled movie of their choice.

For half the participants, the order of the first three blocks was unexpected silence, expected silence, resting state; for the other half, it was expected silence, unexpected silence, resting state. Whatever order participants received, that same order was repeated 3 times to comprise the 9 blocks in total. Between blocks there was 10 seconds of silence. After the EEG testing, participants completed the Goldsmith Musical Sophistication Index (Müllensiefen, Gingras, Musil, & Stewart, 2014).

Data Acquisition and Preprocessing

EEG data was collected using a 128-channel HydroCel GSN net with Electrical Geodesic NetAmps 200 amplifier, sampled at 1000 Hz and online referenced to Cz. Raw data was saved with NETSTATION software for offline analysis. Channel impedances were kept below 50 Ω . Any channel with impedance above 50 Ω was removed from the analysis. Channels displaying large fluctuations in amplitude, based on visual inspection during the EEG recording, were also removed during preprocessing. A total of 11 channels (see Figure 1b for details) were removed across all participants to keep the number of channels consistent for all participants.

The data were preprocessed with MATLAB 2016b (Mathworks Inc.) using the Fieldtrip Toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). The continuous EEG data was bandpass filtered between 0.5 and 20 Hz with a 4th order Butterworth filter using the zero-phase delay filtering technique. High amplitude artifacts were corrected using the artifact blocking algorithm (ABA; Fujioka, Mourad, He, & Trainor, 2011; Mourad, Reilly, De Bruin, Hasey, & MacCrimmon, 2007), with a threshold of + 75 μ V in 5 s windows, and then referenced to a common average. The data were then segmented into 750 ms segments from 250 ms before the

onset of the silence to 500 ms post-silence onset. These trials were then down sampled to 128 Hz. Any trial in either the expected or unexpected silence condition with an amplitude range larger than 75 μV was removed from the analysis. Blinks, saccades, and heartbeat artifacts were removed using independent component analysis (ICA). ICA components containing these artifacts were determined by visual inspection conducted by author DP. The remaining data were averaged per condition, per participant. Individual ERP waveforms were baseline corrected using a 100 ms pre-silence onset window. Difference waveforms were created by subtracting the expected silence from the unexpected silence ERP waveforms individually for each participant.

Event-related Potential (ERP) Data Analysis

The difference waveforms were separated and averaged based on six electrode groups (Figure 1b) based on laterality (left, midline, right) and centrality (frontal, central). To calculate MMN amplitude for each electrode group, we used the MATLAB function `findpeaks` and `max` to find the local minimum in each participant's difference waveform between 100 and 300 ms. We then averaged the amplitude in a 50 ms window centered around the peak (25 ms on either side). We also characterized the P3a using the same peak finding and averaging method, by finding the local maximum in the difference waveform between 250 ms and 400 ms post silence onset.

We analyzed the amplitudes from the difference waveforms using two separate 3x2 repeated measures ANOVAs for laterality (left, midline, right) and centrality (frontal, central) to determine if there was a difference in ERP activity between electrode regions. To assess the presence of an MMN or P3a response, the main goal of this study, we conducted a one-sample t-test against zero based on the ANOVA results. For example, if no difference was found between the electrode regions we conducted the t-test on the average across all six regions. If there was a

difference between frontal and central regions, but not between the left, mid or right regions, we conducted two t-tests, one averaged across the three central electrode regions and one averaged across the frontal regions.

For both 3x2 repeated measures ANOVAs, any violation of sphericity for main or interaction effects were corrected for using Greenhouse-Geisser correction, and only corrected p-values are reported. Significant main effects were followed up via post-hoc paired analysis. Significant interactions between laterality and centrality were followed up by one-way ANOVAs using laterality as a factor separately for the frontal regions and central regions. Significant effects in these follow-up ANOVAs were further analyzed using post-hoc paired analysis. Before conducting paired analyses, a Shapiro-Wilk test was used to assess the assumption of normality. If normality was not violated, we report values based on paired t-tests; however, if the assumption of normality was violated, we report values based on the Wilcoxon signed rank test. Multiple comparisons in the post-hoc analyses were corrected for using Holm-Bonferroni correction (Holm, 1978).

We further analyzed the power spectrum of the unexpected and expected silence conditions to assess whether potential oscillations at the stimulus presentation rates may have been present. During the expected silence condition, the SOA was 1000 ms, or 1 Hz, whereas during the unexpected silence condition the SOA was 500 ms or 2 Hz. To ensure this potential confound did not affect the ERP waveforms during the silence periods of both conditions we conduct two Bayesian repeated measures ANOVAs, one on power at 1 Hz and one on power at 2 Hz. Each included factors silence (unexpected, expected), laterality (left, midline, right) and centrality (central, frontal). Details regarding these analyses as well as the description of the results can be found in the supplemental materials. To briefly summarize, we found evidence for

no difference in power between the silence conditions at either frequency, suggesting the difference in presentation rate did not affect the processing of the silences.

Results

From the grand average ERPs (Figure 2) we can see a negative peak at approximately 125 ms. There is also a positive peak within the P3a window used for analysis, although it is more spread out in time in certain region along the scalp, likely due to high variability in the latency of peak amplitude responses (supplemental figure S1).

ERP Analyses of the MMN

The ANOVA comparing the MMN amplitude at different electrode regions revealed no significant difference in laterality ($F(2,58) = 2.19, p = 0.12, \eta^2_{\text{partial}} = 0.009$) or centrality ($F(1,29) = 0.27, p = 0.61, \eta^2_{\text{partial}} = 0.07$), nor an interaction ($F(2,58) = 1.94, p = 0.15, \eta^2_{\text{partial}} = 0.06$) suggesting a lack of difference between electrode regions analyzed (Figure 3a). Thus, to determine if there was a significant difference between the unexpected and expected silence conditions, we averaged the MMN amplitude across the 6 electrode regions for each participant and compared these averages against zero using a paired t-test. We found a significant difference ($t(29) = -3.76, p = 0.0007, CI = [-0.43, -0.126]$), such that the ERP of the difference waveform was significantly less than zero ($M = -0.277, SD = 0.404$). These analyses indicate a small, yet reliable MMN was elicited by the unexpected silences compared to expected silences.

ERP Analyses of the P3a

The ANOVA of the for the P3a component of the difference waveform revealed a significant main effect of centrality ($F(1,29) = 52.6, p < 0.001, \eta^2_{\text{partial}} = 0.645$), with larger P3a at frontal than central sites, a significant main effect of laterality ($F(2,58) = 23.92, p < 0.001, \eta^2_{\text{partial}} = 0.452$) as well as an interaction effect ($F(2,58) = 18.89, p < 0.001, \eta^2_{\text{partial}} = 0.394$). To further

investigate the interaction effect two one-way ANOVAs were conducted, one for the three frontal regions and one for the three central regions. We found no significant difference in P3a between the three central regions ($F(2,58) = 1.53, p = 0.22, \eta^2_{\text{partial}} = 0.05$), whereas the three frontal electrode regions differed significantly ($F(1.4, 39.6) = 94.12, p < 0.001, \eta^2_{\text{partial}} = 0.764$). Specifically, the right frontal electrode region had a smaller response compared to the frontal midline ($t(29) = 18.1, p < 0.001, CI = [0.653, 0.820]$) and the frontal left ($t(29) = 11.5, p < 0.001, CI = [0.495, 0.709]$), while the left and midline electrodes were not significantly different ($t(29) = 1.83, p = 0.23, CI = [-0.285, 0.015]$). This suggests that the P3a response to the unexpected silence was lateralized at frontal sites, such that it was stronger in the left hemisphere compared to the right (Figure 3b).

To test the significance of the P3a response we averaged the P3a response across the frontal left and midline regions for each individual and compared this average response against zero. We found there was indeed a significant difference from zero ($t(29) = 30.89, p < 0.001, CI = [0.972, 1.11], M = 1.04, SD = 0.18$). Conducting the same test for the right frontal region revealed a significant difference as well ($V = 465, p < 0.001, CI = [0.338, 0.421]$). Averaging across the three central regions, we did not find a significant P3a response ($t(29) = 1.17, p = 0.253, CI = [-0.077, 0.282]$), indicating the P3a response was limited to the frontal regions.

Discussion

Although most ERP studies investigating predictive coding examine violations of expected pitch, timbre, duration, or sound patterns, a full understanding of predictive coding requires characterizing neural responses to omissions of an expected stimulus. Here we investigated EEG responses to silence under different contexts. We hypothesized that stimulus omissions (unexpected silences) would generate significant MMN and P3a when compared to conditions of

expected silences. As predicted, we found an a significant MMN between 100 and 300 ms and a significant P3a response between 250 and 400 ms. Thus, we found evidence of predictive coding via the presence of MMN and P3a, suggesting multiple levels of predictive coding in response to unexpected silences. Our findings suggest that neural responses to unexpected stimulus omissions are reflected in ERP components that index auditory mechanisms of predictive coding.

Previous studies that have used unexpected stimulus omissions to investigate how MMN relates to predictive coding are limited in two respects. First, most previous studies only investigated an omission to auditory stimuli using an SOA of 200 ms or less (Bendixen et al., 2009; Chennu et al., 2016; Recasens & Uhlhaas, 2017; Salisbury, 2012; Todorovic & de Lange, 2012; Wacongne et al., 2012; Yabe et al. 1997, 1998). At such fast tempos, successive stimuli are presented within the window of temporal integration, meaning that the brain likely does not process each stimulus and silence as a fully separate events (Horváth et al., 2007; Shinozaki et al., 2003; Yabe et al., 1997, 1998). Second, previous studies compared deviant omissions (silence) to a standard tone. Tones will elicit obligatory ERP components that overlap in time with the MMN, such as the P1, N1 and P2, whereas silences do not elicit these components. Therefore, differences between the standard and difference waveform in this case are likely due to the presence of obligatory auditory ERP components (that overlap the time of possible MMN) in response to the standard (tone) stimuli but not the deviant (silence) stimuli. To our knowledge, ours is the only study to date to overcome these limitations by comparing silences under varying levels of expectation (expected, unexpected, resting state) rather than comparing responses to tones and silence in the auditory domain alone.

Under these novel conditions, we found small, but robust, MMN and P3a responses to unexpected silences. These results strongly support predictive coding as the mechanisms

underlying MMN and P3a rather than neural adaptation (Heilbron & Chait, 2018; Trainor, 2012; Wacongne et al., 2012, 2011). Furthermore, the results indicate that predictive errors can be generated without any stimulus present, and the mechanisms underlying prediction errors for stimulus feature or pattern violations are similar to those underlying the omission of an expected stimulus.

Our findings contrast with the few previous studies that examined MMN to stimulus omissions at tone sequence presentation rates larger than the temporal window of integration. Yabe et al. (1998) did not find a significant MMN to an omission with an SOA of 300 ms, although they did report a negative MMN-like ERP response under similar stimulus conditions in Yabe et al. (1997). However, both studies had very small sample sizes (less than 10) and therefore were likely insufficiently powered to observe a small effect size. The present study included 30 participants. Additionally, in the case of a stimulus omission, there may be temporal jitter from trial to trial and between participants as there is no stimulus to align the ERP responses precisely. This may tend to artificially diminish the size of ERP components in averaged data. Future studies could implement signal processing techniques such as temporal principal component analysis (Dien, 2012) to better align the MMN and P3a responses at the single trial level to improve overall signal to noise ratio.

Although we interpret the negative component we observed as an MMN, it is possible that it reflects a contribution of N1 or N2. Indeed, previous research has shown that when an action (button press) is associated with a sound, the omission of that sound after the action can elicit an N1 component, argued to reflect a top-down prediction signal (Korka et al., 2020; SanMiguel et al., 2013; Schröger et al., 2015). However, in the present auditory-only experiment, the mean peak latency for the negative ERP component is well beyond that of a typical N1 (see

Figure S3), making it unlikely that it reflects N1. It is possible that self-generated action provides a more powerful context for eliciting top-down expectations compared to auditory pattern expectations alone, as in the present study, making any N1 effects too small to observe. It is also possible that the negative component we observed reflects a contribution of an N2 component. This is unlikely, however, as N2 is typically associated with attention, whereas the present study used a passive protocol in which participants watched a silent subtitled movie while ignoring the auditory stimuli.

The P3a that we observed in response to unexpected stimulus omissions had the frontal left/midline distribution, although its latency was about 40 ms later than a typical P3a response to a sound stimulus (Escera & Corral, 2007; Polich, 2007). However, a latency delay might be expected due to difficulty in precisely locating the silence onset when there is no stimulus (Hughes et al., 2001) or a short delay before neural processes determine there is no stimulus. It is also possible that our observed response is a novelty P3 component which, like the P3a, is elicited when a novel stimulus is presented in a sequence of tones (Barry, Steiner, & De Blasio, 2016; Barry et al., 2020; Courchesne, Hillyard, & Galambos, 1975). The novelty P3 peaks little later than the P3a (between 300 and 400 ms: Dien, Spencer, & Donchin, 2003; Dien et al., 2004; Rushby et al., 2005). However, it remains controversial as to whether the P3a and the novelty P3 are actually distinct components (Escera & Corral, 2007; Simons, Graham, Miles, & Chen, 2001).

The P3a has been characterized as an inadvertent capture of attention that typically occurs when an unexpected sound is presented in an unattended stream (Combs & Polich, 2006; Masson & Bidet-caulet, 2018; Polich, 2007; Rushby et al., 2005). Thus, the P3a has been suggested to index a prediction error signal in oddball designs similar to the current experiment

(Max et al., 2015; Polich, 2007; Schröger et al., 2015). In a sense, our design could be thought of as examining temporal predictions, in that no stimulus occurred at an expected time for a stimulus. A recent study has shown that the degree of temporal prediction for the onsets of incoming sounds in a sequence (measured as the power of beta oscillations) is negatively correlated with the P3a amplitude following an unexpected pitch change. Thus, the less precise expectations are for event onsets, the greater the prediction error signals are for the deviant stimulus (Chang et al., 2018). Future studies could investigate whether individual differences in temporal tracking of tone onsets in a regular sequence, as indexed by beta power modulations, is related to the size of prediction errors as measured by P3a amplitude. This would help uncover whether predictive error responses in the case of unexpected stimulus omissions relate to temporal expectations.

During the unexpected silence condition, the standard tones were presented at a rate of 2 Hz, whereas during the expected silence condition they were presented at a rate of 1 Hz. We ruled out a possible confounding effect of neural entrainment at these rates with a Bayesian analysis that found evidence for no difference in 1 or 2 Hz power in the EEG between the silence conditions (see supplemental material and tables S1-S4 for results). However, a future study could be conducted in which the presentation rates of tones are the same across conditions with expected and unexpected omissions by having the omissions occur in either a random order (unexpected) or fixed order (expected). For example, the omissions could occur at a global rate of 20% in both conditions, but pseudo-randomly in the unexpected condition and predictably every 5th stimulus in the expected condition. We chose our current design because even though an unpredictable deviant stimulus leads to a stronger mismatch response compared to a predictable

deviant, if both stimuli are rare, they both elicit an MMN response (Basirat et al., 2014; Wacongne et al., 2011)

In summary, the present study expands our understanding of predictive coding in the brain by examining predictive error responses to unexpected silences. Through careful choice of tempos under which events are individuated, and by comparing silences that were unexpected (deviant) or expected (standard), rather than comparing silence to tones, we ensured that differences were not confounded by obligatory auditory components, regardless of expectations. We found that unexpected silences elicit both MMN and P3a error signals, providing empirical support for a framework involving a hierarchical model of predictive coding (Heilbron & Chait, 2017; Trainor, 2012) in which MMN may represent a prediction error signal at the level of sensory information and P3a may reflect a top-down prediction error signal at a higher level of information processing that is related to temporal attention orientation.

AUTHOR CONTRIBUTION

D.P helped design study, collect data, run the various analyses, draft all sections paper, and create the figures. D.H helped collect data and contributed to the discussion section of the paper. J.E.M helped with data collection and revision of the experiment. J.R. helped designed study. L.J.T. helped design the study, draft, and edit the various drafts of the paper. All authors have read and approved the manuscript.

Abbreviations: dB SPL, decibel sound pressure level; EEG, electroencephalography; ERP, event-related potential; ICA, independent component analysis; MMN, mismatch negativity; SOA, stimulus onset asynchrony.

DATA AVAILABILITY STATEMENT

Raw EEG data are stored on a private server and will be made available upon request.

Preprocessing and analysis scripts as well as spreadsheets containing the mean amplitude data used within the repeated measures ANOVA are stored on a public GitHub repository github.com/TrainorLab/Prete_Omissions_2022.

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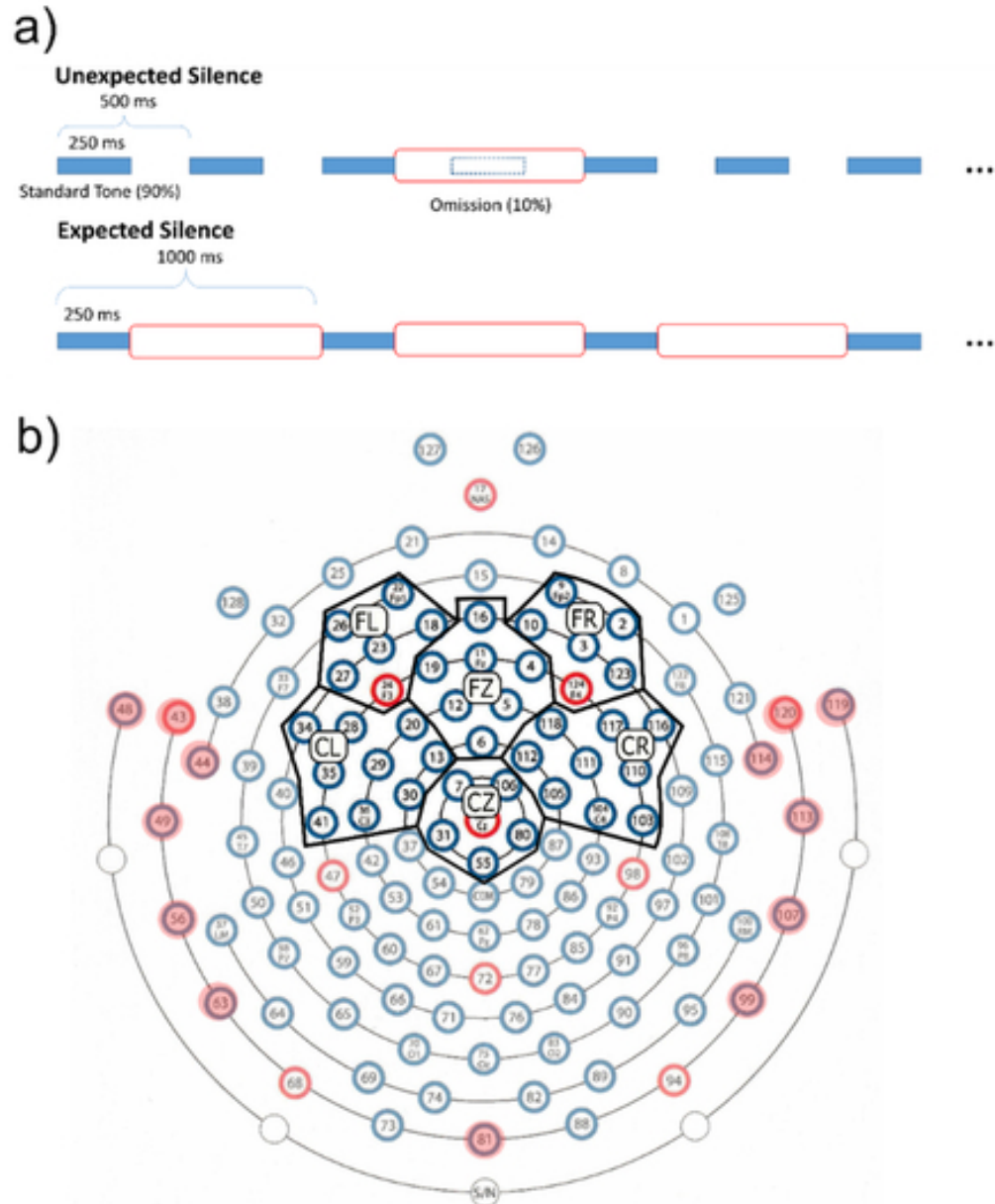


Figure 1. Experimental design and electrode placement. a) An example sequence presented during the unexpected and expected silence conditions. The filled blue rectangles represent the piano tone (C4). In the unexpected silence, the SOA between tones is 500 ms whereas in the expected silence condition it is 1000 ms. In the unexpected silence condition, 10% of tones were omitted to create the unexpected silences, represented by the blue dotted square. The rounded red rectangles represent the silences of interest for comparison between the two conditions. b) The placement of the 128 electrodes and the 6 electrode groupings used in the analysis: FL (frontal left), FZ (frontal midline), FR (frontal right); CL (central left); CZ (central midline), CR (central right). The light red shaded electrodes were removed from analysis for all participants. Specifically, they were 43, 44, 48, 49, 56, 63, 81, 99, 107, 113, 114, 119, 120.

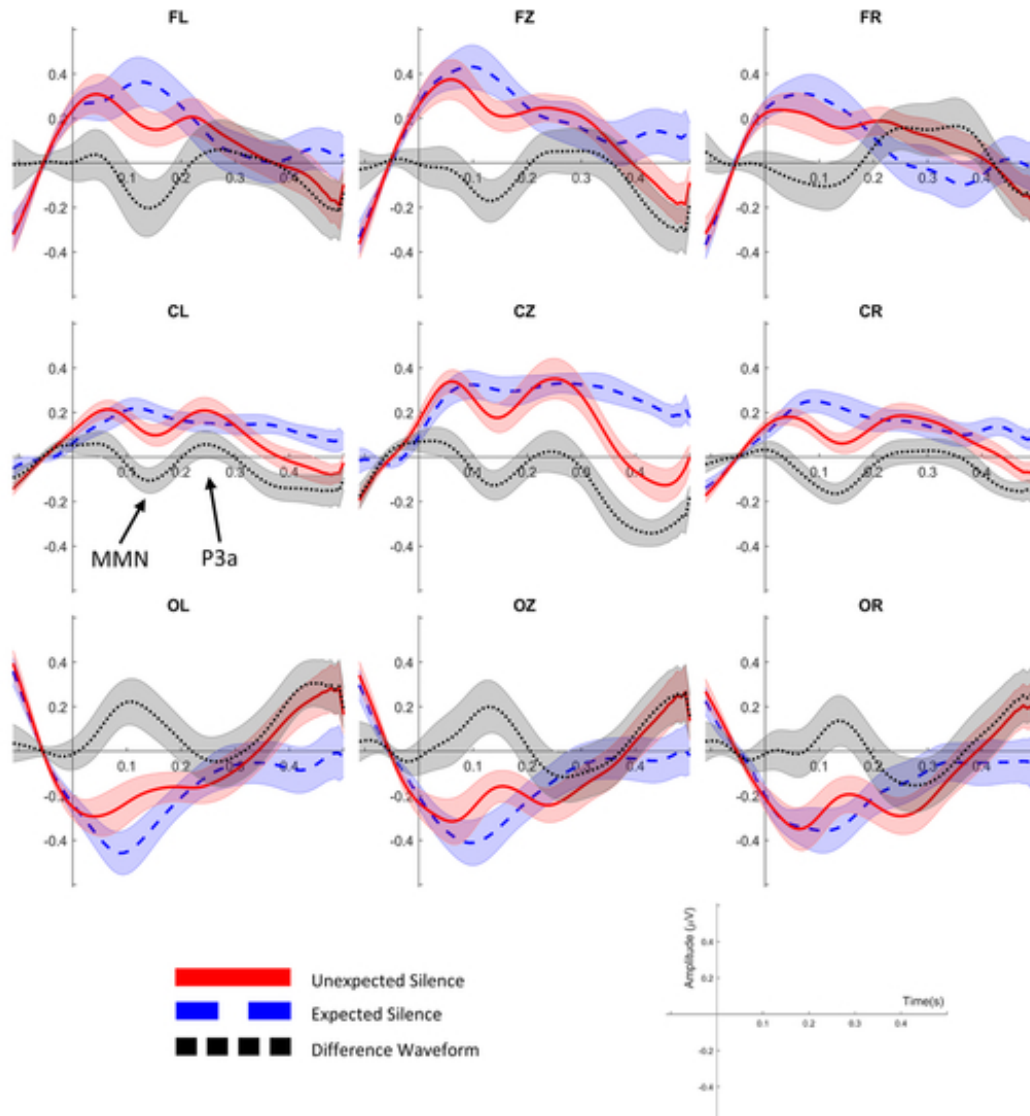


Figure 2. Grand Average ERP waveforms averaged across 9 regions of the scalp. These grand averages were filtered between 1 to 8 Hz, for visualization purposes. The unexpected waveform is displayed in a solid red line, the expected silence waveform is shown in a dashed blue line and the difference waveform is shown in the dotted black line. The axis labels are displayed in the bottom right showing amplitude in microvolts on the y-axis and time in seconds on the x-axis. The shaded region around the grand average represents 1 standard error of the mean. Frontal Left = FL, Frontal Midline = FZ, Frontal Right = FR, Central Left = CL, Central Midline = CZ, Central Right = CR, Occipital Left = OL, Occipital Midline = OZ, Occipital Right = OR. Only the Central and frontal regions were included in the ERP analyses, but the Occipital regions are shown for completeness.

338x190mm (72 x 72 DPI)

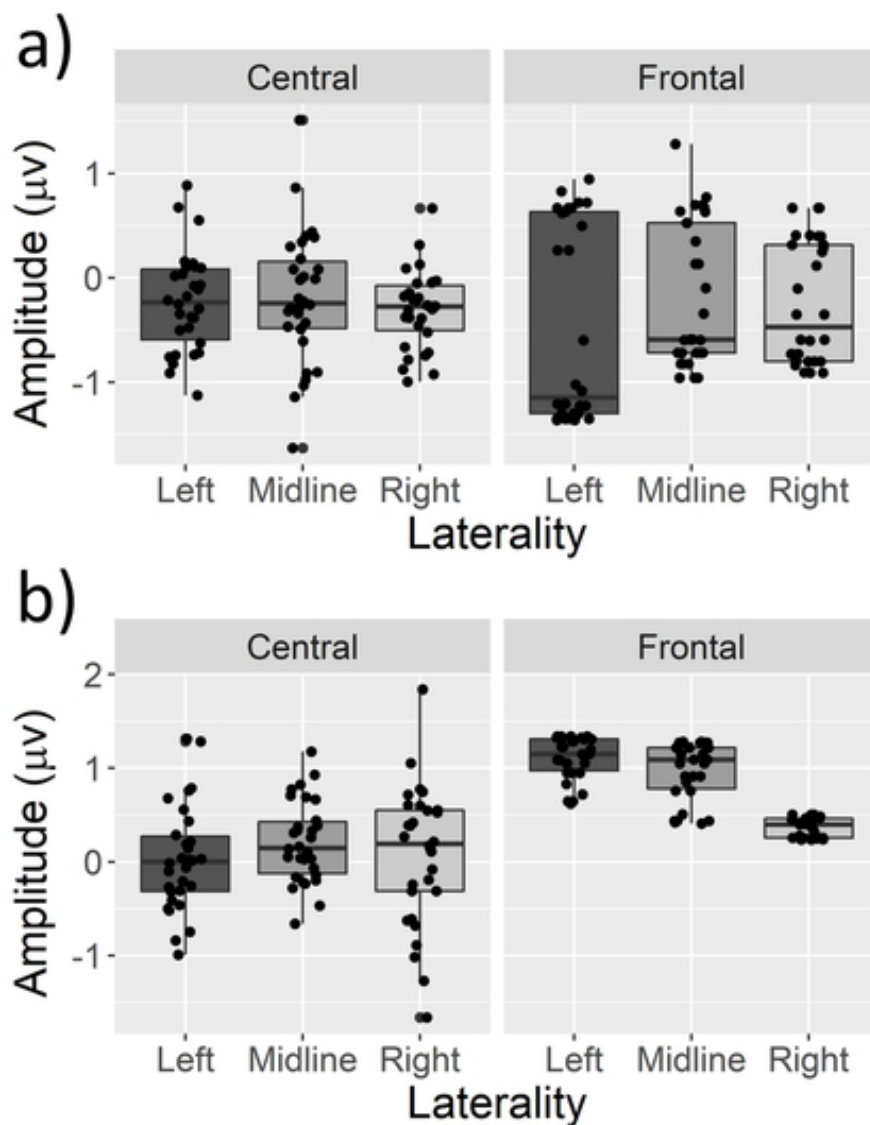


Figure 3. Amplitudes for the MMN and P3a. The MMN and P3a responses for each participant were calculated from the difference waves as the average amplitude in a 50 ms window centered on individual's peak MMN or P3a response found between 100 – 300 ms and 250 – 450 ms, respectively, for each of the six electrode regions. Individual participants are shown as black dots. The median is shown by the dark grey line within each box. The boxes and whiskers show the interquartile range and 1.5 times the interquartile range. a) The MMN peak amplitudes from each participant's difference waveform (black dots) across the left, midline, and right regions (darkest to lightest grey) of the central and frontal electrodes. There were no significant differences across regions and MMN was significantly different from zero overall ($p = 0.0007$). b) The P3a peak amplitudes from each participant (black dots) across the left, midline, and right regions (darkest to lightest grey) of the central and frontal electrodes. The P3a responses were significantly greater than zero for all three frontal regions ($p < .001$), and significantly greater for frontal left and frontal midline regions compared to the frontal right region ($p < 0.001$). P3a was not significantly different from zero for the central regions ($p = 0.22$).

Supplemental Materials.

Methods

Presentation Rates

Because the stimulus presentation rates were different in the expected silence condition (1 Hz) and the unexpected silence condition (2 Hz), we tested whether there was evidence for or against a difference in neural oscillation between the two conditions. Specifically, we wanted to ensure that ERP differences were due to whether the silence was expected or not rather than to potential lingering effects of processing the preceding tones. We computed the fast Fourier transform from -250 ms pre-silence onset to 500 ms post silence onset for each trial and channel individually, and zero padded the data to give a frequency resolution of 0.1 Hz. The trials were then averaged separately by silence condition, giving an average power spectrum for each channel per participant. The power at 1 Hz and 2 Hz was then extracted for each participant for each of the 6 electrode regions described in the main manuscript.

We then analyzed the power using a 2x2x3 Bayesian repeated measures ANOVA using JASP 0.14.1 (JASP 2020) with factors of silence (unexpected silence, expected silence), centrality (central and frontal) and laterality (left, midline, and right), separately for 1 Hz and 2 Hz power. We chose to use separate ANOVA for the two frequencies because we were not concerned about the direct comparison of the power between the two frequencies, but the comparison of power between the silence conditions and electrode regions used in our main analysis. Thus, we could compare if the two silence conditions were different for a specific presentation rate without adding more complexity to our analysis. We used the default prior distribution for an ANOVA suggested by Rouder et al. (2012), and the null hypothesis that there was no evidence for a difference in power between conditions.

Given the complexity of the analysis (as seen by the 18 models compared in Tables S1 and S3) we also computed the inclusion Bayes factor (BF_{incl}) for matched models (Mathôt, 2017; Van Den Bergh et al., 2020) (Tables S2 and S4). Match models for main effects are models that include the main effect of interest excluding models that contain an interaction with the effect of interest (e.g., for the main effect of silence, interaction effects with silence such as silence * laterality would be excluded). Matched models for interaction effects consists of averaging the probability for the interaction effect excluding models that contain the main effects of the predictors that make up the interaction (e.g., for the silence *laterality interaction, models that contain the main effect of silence or laterality would be excluded). This results in inclusion prior probability [P(incl)], exclusion prior probability [P(excl)], inclusion posterior probabilities [P(incl|data)] and exclusion posterior probabilities [P(excl|data)]. Finally, the inclusion Bayes factor is then calculated by dividing the inclusion posterior probability by the exclusion posterior probability [P(incl|data)/ P(excl|data)]. Thus, the BF_{incl} estimates the evidence for the alternative hypothesis for a main effect or interaction effect by comparing models including that effect of interest to models that do not include the effect of interest (Mathôt, 2017; Van Den Bergh et al., 2020). In other words, the BF_{incl} gives the unique estimate of evidence for an alternative hypothesis (i.e., that there is a difference between means) for a specific main effect or interaction effect across all the models within the repeated measures ANOVA.

Latencies

To demonstrate the variability in the latencies we have plotted the individual peak latencies of the MMN and P3a in Figure S1, overlaid with the boxplots to give a sense of the distribution of the peak latencies. For the MMN, the range of peaks spans about 200 ms and for the P3a, the range of peaks spans about 150 ms. This high variability in ERP responses and peak

latencies is similar to that of previous findings (Hughes et al., 2001), and is likely why the grand average difference waveforms show small or temporally spread out ERP components, especially for the P3a component.

Results

Presentation Rates

The results of the Bayesian analyses of the 1 Hz power are shown in Tables S1 and S2. From Table S1 we can see there is moderate evidence supporting the null hypothesis of no difference between silence conditions ($BF_{10} = 0.11$), strong evidence for a difference between left, midline and right regions ($BF_{10} = 12.52$) and strong evidence for a difference between the frontal and central regions ($BF_{10} = 3.10e^{33}$). A similar pattern of evidence is seen with the comparison for matched models (Table S2). There is strong evidence for effects of centrality, laterality, and the interaction between the two factors, suggesting differences in activity between the three frontal regions and the three central regions. This is similar to our analysis of the peak amplitudes which found differences between the central and frontal regions, and within the three frontal regions for the P3a activity (Figure 2). However, the matched model comparisons for the models that include a main effect of silence or an interaction with silence showed evidence in support of no difference in 1 Hz power between the expected and unexpected silence conditions ($BF_{incl} \leq 0.15$). Thus, models within table S1 that show evidence for a difference are most likely driven by differences in centrality, laterality, or both, not by differences between the silence conditions.

The results from the analyses of the 2 Hz power are shown in Tables S3 and S4. From Table S3 we can see there is moderate evidence in support of no difference in 2 Hz power between unexpected and expected silence conditions ($BF_{10} = 0.122$), but anecdotal evidence for a difference between left, midline and right electrodes ($BF_{10} = 1.27$) and strong evidence for a difference between central electrodes and frontal electrodes ($BF_{10} = 3.87e^{39}$). Examining the analysis of the matched models (Table S4), models including silence as a main effect or as an interaction demonstrated no evidence of a difference between the expected and unexpected silence conditions ($BF_{incl} < 0.15$). Strong evidence was found for an effect of laterality, centrality, and the interaction between the two factors ($BF_{incl} > 25.32$).

Taken together, the Bayesian analyses of 1 and 2 Hz power suggests there is little to no evidence that the difference in presentation rates led to differences in power spectrum between the expected and unexpected silence conditions. There was strong evidence to suggest the power differed based on the location on the scalp, but this did not interact with the silence condition.

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Table S1.
Bayesian Model Comparison of 1 Hz Frequency Response

Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
Null model (incl. subject)	0.053	2.28e -42	4.11e -41	1	
Silence	0.053	2.54e -43	4.57e -42	0.11	0.74
Centrality	0.053	7.06e -9	1.27e -7	3.10e +33	0.9
Laterality	0.053	2.86e -41	5.14e -40	12.52	1.24
Silence + Centrality	0.053	8.06e -10	1.45e -8	3.54e +32	2.54
Silence + Laterality	0.053	3.31e -42	5.96e -41	1.45	2.09
Laterality + Centrality	0.053	4.54e -6	8.17e -5	1.99e +36	1.57
Silence + Laterality + Centrality	0.053	5.02e -7	9.04e -6	2.20e +35	1.5
Silence + Centrality + Silence * Centrality	0.053	1.31e -10	2.36e -9	5.76e +31	3.6
Silence + Laterality + Silence * Laterality	0.053	1.8e -43	3.24e -42	0.08	2.42
Laterality + Centrality + Laterality * Centrality	0.053	0.87	118.23	3.80e +41	2.05
Silence + Laterality + Centrality + Silence * Centrality	0.053	7.61e -8	1.37e -6	3.34e +34	1.98
Silence + Laterality + Centrality + Silence * Laterality	0.053	2.85e -8	5.12e -7	1.25e +34	2.87
Silence + Laterality + Centrality + Laterality * Centrality	0.053	0.11	2.2	4.78e +40	8.72
Silence + Laterality + Centrality + Silence * Laterality + Silence * Centrality	0.053	4.84e -9	8.72e -8	2.12e +33	5.93
Silence + Laterality + Centrality + Silence * Centrality + Laterality * Centrality	0.053	0.02	0.3	7.17e +39	3.62
Silence + Laterality + Centrality + Silence * Laterality + Laterality * Centrality	0.053	0.006	0.1	2.50e +39	4.09
Silence + Laterality + Centrality + Silence * Laterality + Silence * Centrality + Laterality * Centrality	0.053	8.66e -4	0.02	3.80e +38	3.49

Silence + Laterality + Centrality + Silence					
* Laterality + Silence * Centrality +	0.053	1.05e -4	0.002	4.58e +37	13.44
Laterality * Centrality + Silence *					
Laterality * Centrality					

Note. All models include subject. $P(M|data)$ is the posterior probability, BF_M is the posterior odds. BF_{10} is the Bayes factor in terms of the evidence for the alternative hypothesis over the null hypothesis. Error % is an estimate of the error in computing the Bayes factor. The models are ordered from those with the largest BF_{10} to the smallest BF_{10} . $P(M)$ is the prior probability of the data. The error percentage indicates the percentage of error in estimating BF_{10} . For example, laterality has a BF_{10} of 12.52 and error of 1.24%. Thus, the estimation of the BF_{10} for centrality for this dataset ranges from approximately 12.36 to 12.66.

Table S2.
Analysis of Effects for the 1 Hz Frequency Response

Effects	P(incl)	P(excl)	P(incl data)	P(excl data)	BF _{incl}
Silence	0.263	0.263	0.11	0.87	0.13
Laterality	0.263	0.263	5.12e -6	7.99e -9	640.11
Centrality	0.263	0.263	5.08e -6	3.46e -41	1.47e +35
Laterality * Silence	0.263	0.263	0.01	0.13	0.05
Centrality * Silence	0.263	0.263	0.02	0.12	0.15
Centrality * Laterality	0.263	0.263	1	5.15e -6	194051
Centrality * Laterality * Silence	0.053	0.053	1.05e -4	8.66e -4	0.12

Note. Analysis of the various effect from the Bayesian repeated measures ANOVA of the power spectrum at 1 Hz. The analysis of effects allows us to determine the independent evidence for the alternative hypothesis for each main effect and interaction across matched model from table S5. This results in inclusion prior probability [P(incl)], exclusion prior probability [P(excl)], inclusion posterior probabilities [P(incl|data)] and exclusion posterior probabilities [P(excl|data)]. Inclusion Bayes factor is calculated by dividing the inclusion posterior probability by the exclusion posterior probability [P(incl|data)/ P(excl|data)], estimating the independent evidence for the alternative hypothesis for a specific main effect or interaction effect.

Table S3.
Bayesian Model Comparison of 2 Hz Frequency Response

Models	P(M)	P(M data)	BF _M	BF ₁₀	error %
Null model (incl. subject)	0.053	2.61e -47	4.69e - 46	1	
Silence	0.053	3.18e -48	5.72e - 47	0.122	5.12
Centrality	0.053	1.01e -7	1.82e - 6	3.87e +39	1.29
Laterality	0.053	3.30e -47	5.95e - 46	1.27	0.7
Silence + Centrality	0.053	1.12e -8	2.01e - 7	4.28e +38	1.7
Silence + Laterality	0.053	3.82e -48	6.88e - 47	0.15	1.4
Laterality + Centrality	0.053	2.55e -6	4.58e - 5	9.77e +40	1.21
Silence + Laterality + Centrality	0.053	2.92e -7	5.26e - 6	1.12e +40	2.4
Silence + Centrality + Silence * Centrality	0.053	1.93e -9	3.47e - 8	7.39e +37	3.89
Silence + Laterality + Silence * Laterality	0.053	2.23e -49	4.02e - 48	0.01	5.57
Laterality + Centrality + Laterality * Centrality	0.053	0.88	126.84	3.36e +46	2.66
Silence + Laterality + Centrality + Silence * Centrality	0.053	4.79e -8	8.62e - 7	1.84e +39	3.48
Silence + Laterality + Centrality + Silence * Laterality	0.053	1.65e -8	2.97e - 7	6.32e +38	2.98
Silence + Laterality + Centrality + Laterality * Centrality	0.053	0.10	2.06	3.94e +45	4.36
Silence + Laterality + Centrality + Silence * Laterality + Silence * Centrality	0.053	3.09e -9	5.56e - 8	1.18e +38	13.07
Silence + Laterality + Centrality + Silence * Centrality + Laterality * Centrality	0.053	0.02	0.28	5.90e +44	3.12
Silence + Laterality + Centrality + Silence * Laterality + Laterality * Centrality	0.053	0.01	0.09	2.05e +44	2.77

Silence + Laterality + Centrality + Silence *					
Laterality + Silence * Centrality + Laterality	0.053	8.27e -4	0.02	3.18e +43	11.88
* Centrality					
Silence + Laterality + Centrality + Silence *					
Laterality + Silence * Centrality + Laterality	0.053	9.72e -5	0.002	3.73e +42	12.76
* Centrality + Silence * Laterality *					
Centrality					

Note. All models include subject. $P(M|data)$ is the posterior probability, BF_M is the posterior odds. BF_{10} is the Bayes factor in terms of the evidence for the alternative hypothesis over the null hypothesis. Error % is an estimate of the error in computing the Bayes factor. The models are ordered from those with the largest BF_{10} to the smallest BF_{10} . $P(M)$ is the prior probability of the data. The error percentage indicates the percentage of error in estimating BF_{10} . For example, silence has a BF_{10} of 0.122 and error percentage of 5.12. Thus, the estimation of the BF_{10} for silence in this dataset ranges from approximately 0.116 to 0.128.

Table S4.
Analysis of Effects for the 2 Hz Frequency Response

Effects	P(incl)	P(excl)	P(incl data)	P(excl data)	BF _{incl}
Silence	0.263	0.263	0.1	0.88	0.12
Laterality	0.263	0.263	2.89e -6	1.14e -7	25.32
Centrality	0.263	0.263	2.97e -6	6.63e -47	4.48e +40
Laterality * Silence	0.263	0.263	0.01	0.12	0.05
Centrality * Silence	0.263	0.263	0.01	0.11	0.15
Centrality * Laterality	0.263	0.263	1	2.91e -6	3440044
Centrality * Laterality * Silence	0.053	0.053	9.72e -5	8.27e -4	0.12

Note. Analysis of the various effect from the Bayesian repeated measures ANOVA of the power spectrum at 2 Hz. The analysis of effects allows us to determine independent evidence for the alternative hypothesis for each main effect and interaction across matched model from table S3. This results in inclusion prior probability [P(incl)], exclusion prior probability [P(excl)], inclusion posterior probabilities [P(incl|data)] and exclusion posterior probabilities [P(excl|data)]. Inclusion Bayes factor is calculated by dividing the inclusion posterior probability by the exclusion posterior probability [P(incl|data)/ P(excl|data)] estimating the independent evidence for the alternative hypothesis for a specific main effect or interaction effect.

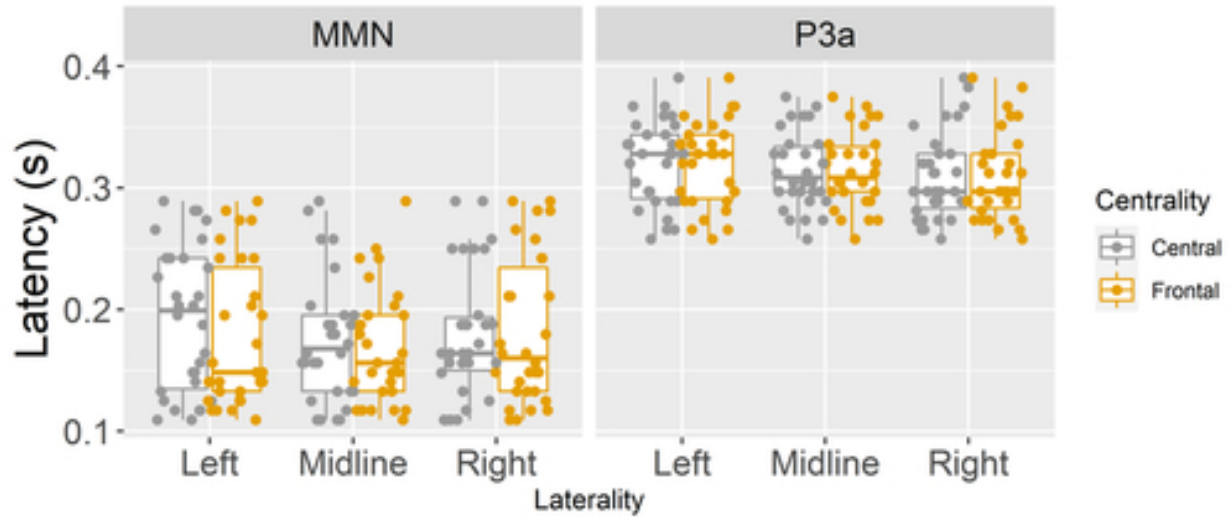
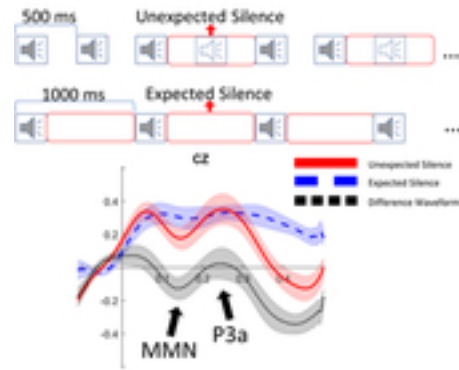


Figure S1. Individual Peak Latencies for The MMN and P3 ERP components.

Boxplots of the latencies for the individual peaks (shown as black dots) plotted for each ERP component (MMN on the left side of each figure; P3a on the right side of each figure) by centrality (Central on the left figure; frontal on the right figure) by laterality (Left, Center and Right). The line represents the median value, with the box representing interquartile range. The whiskers represent 1.5 times the interquartile range. This suggests a highly skewed distribution along with a wide variation in peak latencies.



Graphical Abstract. Unexpected silences in a sequence of tones at two tones/sec were compared to expected silences in sequences of one tone/sec. Unexpected silences produced EEG event-related potential components indicative of predictive coding, specifically the mismatch negativity (MMN) and P3a. Our results provide evidence that these components are not the product of neural adaptation to repeated tones but reflect the generation of prediction error signals to unexpected changes in auditory patterns, and that the brain is sensitive to unexpected silences.