



Predictable tones elicit stimulus-specific suppression of evoked activity in auditory cortex



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ABSTRACT

The auditory cortex is sensitive to many forms of acoustic regularity, resulting in suppressed neural activity for expected auditory events. It is unclear whether this activity reduction for expected events is the result of suppression of neurons that are tuned to the expected stimulus (i.e., dampening), or alternatively suppression of neurons that are tuned away from the expected stimulus (i.e., sharpening). In the present study, we adjudicated between these models by characterizing the effect of expectation on the ability to classify the identity of auditory stimuli from auditory neural activity patterns, using magnetoencephalography (MEG) in healthy human observers. Participants listened to pure tone pairs, in which the identity of the second tone was either expected or unexpected. The task of the participants was to detect a target tone, which deviated strongly from both the expected and unexpected tones. We found a strong suppression of the overall neural response in the expected condition compared to the unexpected condition. Linear classifiers showed a reduced ability to decode stimulus identity from event-related auditory fields in the expected condition compared to the unexpected condition. This suggests that stimulus-specific event-related activity is dampened for expected tones in auditory cortex.

1. Introduction

Sensory processing is not only dependent on the current stimulus, but also influenced by top-down factors like prior expectations (Lange et al., 2018; Summerfield and de Lange, 2014). Behavioral evidence shows that expected stimuli are associated with behavioral performance improvements in terms of accuracy, reaction time and sensitivity in perceptual decision-making (Rahnev et al., 2011; Stein and Peelen, 2015; Cheadle et al., 2014). Perhaps surprisingly, in terms of neural activity, expected events are usually not associated with increased neural activity. Rather, many studies show that valid expectation decreases the neural signals in single/multi-unit recordings (Kumar et al., 2017; Kaposvari et al., 2018; Meyer and Olson, 2011), electroencephalography (EEG)/magnetoencephalography (MEG) data (Todorovic et al., 2011; Todorovic and de Lange, 2012; Garrido et al., 2009) as well as in functional Magnetic Resonance Imaging (fMRI) data (Alink et al., 2010; Egner et al., 2010; Summerfield et al., 2008; Kok et al., 2012). This neural phenomenon is often referred to as expectation suppression.

The mechanisms of expectation suppression are still a topic of debate. One proposal is that neural representations of expected sensory signals are sharpened (Mumford, 1992; Kok et al., 2012). Under this account,

reduced activity when there is an expectation is caused by a suppression of the subset of the neurons that are less selective to the stimulus. In other words, neurons that are carrying the information about the stimulus maintain their level of activation (or are even enhanced), while neurons that are carrying the irrelevant information are suppressed, resulting in a better signal-to-noise ratio in the neural representation and thus facilitating perception (de-Wit et al., 2010; Murray et al., 2004; Lim et al., 2015). Alternatively, it has been proposed that the brain sends forward only the unexpected part of the sensory input while expected signals are suppressed (Blank and Davis, 2016; Rao and Ballard, 1999). In this account, reduced activity is the result of a relative deactivation of neurons that are selective to the stimulus, weakening the quality of the sensory input.

There is empirical support for both proposals. Studies that focused on orientation-selective responses in early visual cortex showed that prior expectations can induce a sensory template (Kok et al., 2014) around the time of onset of the stimulus (Kok et al., 2017; Gavornik and Bear, 2014), and thereby enhance the neural representation for the expected stimulus in primary visual cortex (Kok et al., 2012). On the other hand, studies that focused on object-selective representations in inferotemporal cortex showed a dampened neural representation for expected stimuli (Kumar

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et al., 2017; Meyer and Olson, 2011; Richter et al., 2018). This suggests that while expectation suppression may be a general phenomenon, its exact properties may depend on stimulus representation and location in the cortical hierarchy.

In this study, taking advantages of the high temporal and spatial resolution of MEG, we tried to adjudicate between the expectation sharpening model and expectation dampening model in the auditory domain by characterizing the effects of expectation on auditory evoked activity. We manipulated participants' stimulus expectation by assigning different occurrence probabilities to different tone pairs. We compared overall evoked activity and the fidelity of the neural representation between expected and unexpected conditions. To preview, we observed strong attenuation of auditory evoked activity for expected tones, consistent with previous studies. The fidelity of the neural representation was lower for expected tones suggesting a dampening of evoked responses for expected auditory events.

2. Materials and Methods

2.1. Participants

Twenty-six healthy participants enrolled in the experiment. Two participants were excluded from the analysis because of excessive measurement noise in the MEG data. The analyses were performed on the remaining twenty-four participants (15 female; age: 27.8 ± 8.2 years, mean $\pm$ SD; all right-handed). All participants had normal hearing and no history of neurological or psychiatric disorders. All participants gave their informed consent prior to the experiment in accordance with the Declaration of Helsinki and the study was approved by local ethics committee (Commissie Mensgebonden Onderzoek (CMO) Arnhem-Nijmegen, The Netherlands) under the general ethics approval (Imaging Human Cognition, CMO, 2014/288).

2.2. Data and code availability statement

All the data and code are available at https://data.donders.ru.nl/collections/di/dccn/DSC_3018035.01_533. The data and code used in the study are available in the public domain for its sharing or re-use. The data and code sharing adopted by the authors comply with the requirements of the institute, and comply with institutional ethics approval.

2.3. Experimental design

Participants were presented with pairs of pure tones. Each single tone

was 50 ms in duration including 2.5 ms on-ramp and 2.5 ms off-ramp and ~ 75 dB in loudness. The pitch of the first tone could be either 1046 Hz or 1174 Hz (Tone A or B, Fig. 1 AB). The pitch of the second tone could be 1318 Hz, 1396 Hz (Tone C, D) or 3520 Hz (target tone). For each trial, the pair of the two tones, separated by 400 ms, was presented using a PC running Presentation software (Neurobehavioral Systems) binaurally via MEG-compatible air tubes. The intertrial interval (defined as the interval between the second tone offset of current trial and the first tone onset of next trial) was set from 800 ms to 1200 ms.

Each participant performed 1600 trials, which were presented in 32 blocks (50 trials each). The identity of the first tone in all odd-numbered blocks was tone A, while the first tone was tone B in all even-numbered blocks. We manipulated the expectation by assigning different occurrence probabilities to the second tone. In the first 16 blocks, the tone pair A-C or tone pair B-D were assigned an occurrence probability of 70% (expected), while the tone pair A-D or tone pair B-C were assigned an occurrence probability of 20% (unexpected). In this way, tone C and D could be both expected and unexpected in the experiment, i.e. the expectation effect was independent from the stimulus identity. In order to further avoid any possible confounding effects of the stimulus identity of the first tone, in the other 16 blocks, the probability relationship was reversed: tone pair A-D and B-C were assigned a probability of occurrence of 70% and pair A-C and B-D were assigned 20%. In all 32 blocks, the target tone was assigned a probability of 10% and the participants were instructed to press a button with their right hand when they heard it.

2.4. MEG data acquisition and preprocessing

Brain activity was recorded using a whole-head MEG with 275 axial gradiometers (CTF MEG TM Systems Inc., Port Coquitlam, Canada) in a magnetically shielded room. Head localization was monitored continuously during the experiment using coils that were placed at the cardinal points of the head (nasion and left and right ear canals). As an aid for eye-blink rejection, an electrooculogram (EOG) was recorded from the supraorbital and infraorbital ridge of the left eye using 10-mm-diameter Ag-AgCl surface electrodes. All data were digitized at 1200 Hz and stored for offline analysis.

Data analysis was performed only on the trials containing the expected or unexpected tones, not on the trials containing the target tone, using FieldTrip (Oostenveld et al., 2011) with MATLAB (MathWorks) complemented by custom-written software. Epochs (i.e., trials) were extracted from all MEG channels surrounding each stimulus, extending from 500 before to 1500 ms after the first tone onset. Data epochs were

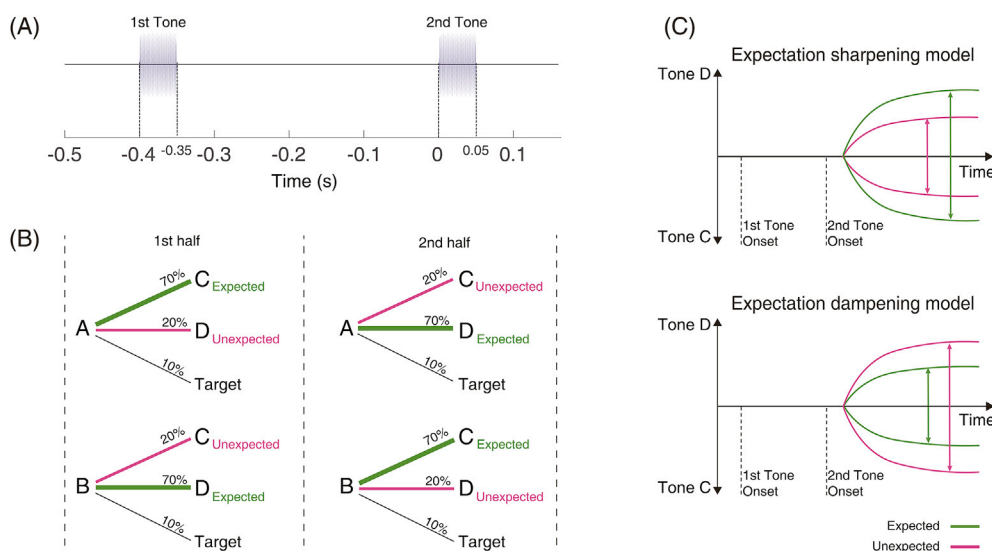


Fig. 1. (A) Auditory stimuli. Subjects were presented with two consecutive pure tones of 50 ms with an inter-stimulus interval of 400 ms. (B) Experimental design. Expectation was manipulated by assigning different occurrence probabilities to the second tone. Expected tone pairs occurred on 70% of trials and unexpected tone pairs on 20%. The relationship between first and second tones was reversed after half of the experiment. Subjects were instructed to press a button whenever a target tone occurred, and such a tone was very different from the expected and unexpected tones. Trials with a target tone were removed from the analysis. (C) Hypothesized fidelity of the neural representation of the tone identity under the expectation sharpening model and expectation dampening model.

checked for artifacts using a semiautomatic pipeline which was able to detect and reject trials containing muscle artifacts and jumps caused by the SQUID electronics. Furthermore, independent component analysis (A. J. Bell and Sejnowski, 1995) was performed to remove the artifacts attributable to eye blinks and heartbeat (Jung et al., 2000). Finally, based on visual inspection, trials containing any remaining artifacts were rejected manually. In the end, around 75% trials in each condition remained after the trial rejection and were selected for further analysis.

For the analysis, we further grouped all trials with tone C as the expected tone regardless of the identity of the first tone and labeled them as the “expected tone C” condition. Similarly, we also created “expected tone D”, “unexpected tone C” and “unexpected tone D” conditions. Since each condition contained an identical number of tone A and tone B, this cancels out any potential activity differences caused by the identity of the first tone.

Event-related field and global mean field

Before computing the event-related field (ERF) and global mean field (GMF), a 30Hz low-pass Butterworth IIR filter with a filter order of 6 was applied. ERFs were baseline corrected using an interval of 100 to 0 ms before the first tone onset. Without any assumption of the source location, GMF measures the overall activity by computing the mean standard deviation between the data in different channels (Lehmann and Skrandies, 1980). Unlike many techniques such as source modeling and event-related fields, GMF does not require a prior assumption on the source of the MEG signals or manual selection of interested channels, allowing a more direct and robust measure of overall brain activity. GMF in time t is defined as:

$$GMF_t = \sqrt{\frac{1}{m} \sum_{i=1}^m (u_{i,t} - \bar{u}_t)^2}$$

where $u_{i,t}$ is the ERF activity for channel i at time t , $\bar{u}_t$ is the mean activity over all channels at time t , and m is the number of channels. In the calculation of the topographic map of ERF, a planar gradient transformation was applied (Bastiaansen and Knösche, 2000). In this way, the interpretation of sensor-level data can be simplified since the planar gradient places the maximal signal above the source which allows for averaging across participants (Hämäläinen et al., 1993). To avoid differences in the amount of noise due to different trial numbers, we matched the number of trials for the expected and unexpected conditions by randomly selecting a subsample of trials (with the same amount of tone C and tone D trials) from the condition that contained more trials.

2.6. Decoding analysis

To investigate the fidelity of the neural representation of tone identity in different conditions, we created forward models from the MEG signal, which aimed to invert the encoding process in transforming the perceived tones into brain activity. Similar to previous studies (Kok et al., 2017; Mostert et al., 2015), we used a linear discriminant analysis approach (Fisher, 1936). We assumed that there is a linear combination of data from different MEG components that can best represent the characteristics of the perceived tones. Such a representation profile R at time t can be represented as:

$$R_t = \beta_{1,t} \cdot u_{1,t} + \beta_{2,t} \cdot u_{2,t} + \dots + \beta_{n,t} \cdot u_{n,t}$$

Where $\beta_{1,t}, \beta_{2,t}, \dots, \beta_{n,t}$ are the weights for the linear combination at time t . For the sake of being representative, the representation profiles should be similar from each other across different trials in one condition, but they also should be dissimilar from each other across trials in different conditions. Therefore, in order to best characterize tone C and tone D in our experiment, a score function can be created:

$$f(B) = \frac{\text{dist}(R_t^{\text{toneC}}, R_t^{\text{toneD}})}{\text{var}(R_t^{\text{toneC}}) + \text{var}(R_t^{\text{toneD}})}$$

where $B = [\beta_{1,t}, \beta_{2,t}, \dots, \beta_{n,t}]$, $\text{dist}(x,y) = (x-y)^2$ is the function for calculating the distance between the mean representation profiles of the two tones and is the function to calculate the variance within one condition. Mathematically, such score function will be maximal when:

$$B = \frac{\hat{u}_{\text{toneC}} - \hat{u}_{\text{toneD}}}{S_{\text{toneC}} + S_{\text{toneD}}}$$

where $\hat{u} = [\bar{u}_{1,t}, \bar{u}_{2,t}, \dots, \bar{u}_{n,t}]$, is the mean activity over trials in one condition for all components; S is the within-condition covariance. When such a score function is maximal, the combination weights B are the optimized ones.

Before performing the forward modeling, in order to improve the signal to noise ratio, the data were first averaged within a window of 20 ms centered on the time point of interest. Furthermore, we applied principal component analysis to further reduce the correlation within the data so that the data are simpler for the classifier and the noise and artifacts inside of the data can be separated out and then be suppressed by the classifier. (Edward Jackson, 2005; Grootswagers et al., 2017). To avoid differences in decoding resulting from a different numbers of trials, we matched the number of trials between tone C and D by randomly selecting a subsample of trials from the condition with more trials. In the comparison between the expected and unexpected conditions, we also matched the numbers of trials between the expected and unexpected conditions. We trained and tested the weights using a 10-fold cross-validation method for testing the learned weights in an independent dataset (Varoquaux et al., 2017) separately for the expected and unexpected conditions. Trials were divided into 10 subsets where each subset contained a balanced amount of trials from each tone. Weights were obtained using all-but-one subsets and then applied to the remaining subset. This process was repeated for all subsets for each time point. Weights obtained from one time point were also applied to other time points to generate the temporal generalization matrices (training time $\times$ testing time).

2.7. Statistical analysis

In order to statistically compare the evoked auditory activity in different conditions, we applied non-parametric cluster-based permutation tests (Maris and Oostenveld, 2007) across participants, which control the type I error rate in the context of multiple comparisons by identifying significant clusters. For GMF analyses, we first obtained the mean GMF in each condition for each participant. Random-effect statistics were obtained by computing paired t-statistics for every time point across all participants. Cluster-level statistics were then computed by taking the sum of the t-values within a cluster and comparing that with a null distribution generated by drawing 1000 random permutations of the observed data by shuffling the condition labels for each participant. Here, the clusters were defined as a group of contiguously above-threshold data points ($p < 0.05$) on the basis of temporal adjacency. A cluster was considered significant if the cluster-level statistics (sum of the t-statistics values within the cluster) were larger or smaller than 97.5% of the statistics in the null distribution (two tailed $\alpha < 0.05$). The cluster-based correction was applied in the time window from 0 to 600 ms relative to the second tone onset.

A similar approach was used for the statistical tests on the generalization matrices of the decoding analysis for both the expected and unexpected conditions. Here, since the data were two-dimensional, clusters were defined as the neighboring elements which were cardinally or diagonally adjacent. For the difference between the expected and unexpected condition, the t-statistics values were first calculated for each subject and then compared across subjects by applying similar cluster-level statistics. Additionally, the mean difference within the significant

cluster was calculated separately for the expected and unexpected conditions, and the neural representation difference was calculated by subtracting the mean difference in the expected condition from the difference in the unexpected condition.

Finally, to examine possible associations between (univariate) GMF differences and (multivariate) neural representation differences, we calculated the Pearson correlation coefficient between these measures within the same time window across subjects.

3. Results

3.1. Behavioral results

The participants' task was to press a button whenever the target tone was presented. Participants correctly and quickly responded to almost all target tones (hit rate: $95.6 \pm 1.9\%$, mean $\pm$ SD, reaction time: 375 ± 69 ms, mean $\pm$ SD) and correctly refrained from responding to almost all other tones (false alarm rate: $0.01 \pm 0.03\%$, mean $\pm$ SD).

3.2. Evoked activity is suppressed for expected tones

We compared the overall MEG evoked response between expected and unexpected tone pairs. The first tone of the pair elicited a strong global mean field (GMF) activity (Fig. 2A), which was maximal around 100 ms after stimulus onset. There were no differences in GMF between the expected and unexpected condition before the second tone onset ($p > 0.10$ for all time points). The second tone of the tone pairs evoked long-lasting GMFs with similar amplitude as the first tone, which was also maximal around 100 ms and sustained until ~ 600 ms after stimulus onset. The expectation of tone identity strongly modulated the evoked neural activity: GMF amplitude in the expected condition was lower than in the unexpected condition (Figs. 2A and 70–550 ms after second tone onset, cluster-based correction $p = 0.02$; post hoc paired t -test for mean GMFs from 0 to 600 ms: $p = 1.29 \times 10^{-7}$).

Furthermore, we obtained the topographic representation of the neural activity in the time window from 0 to 100 ms, 100–300 ms and 300–500 ms relative to the second tone onset using the planar-transformed ERF signals in different conditions (Fig. 2B). Tones elicited

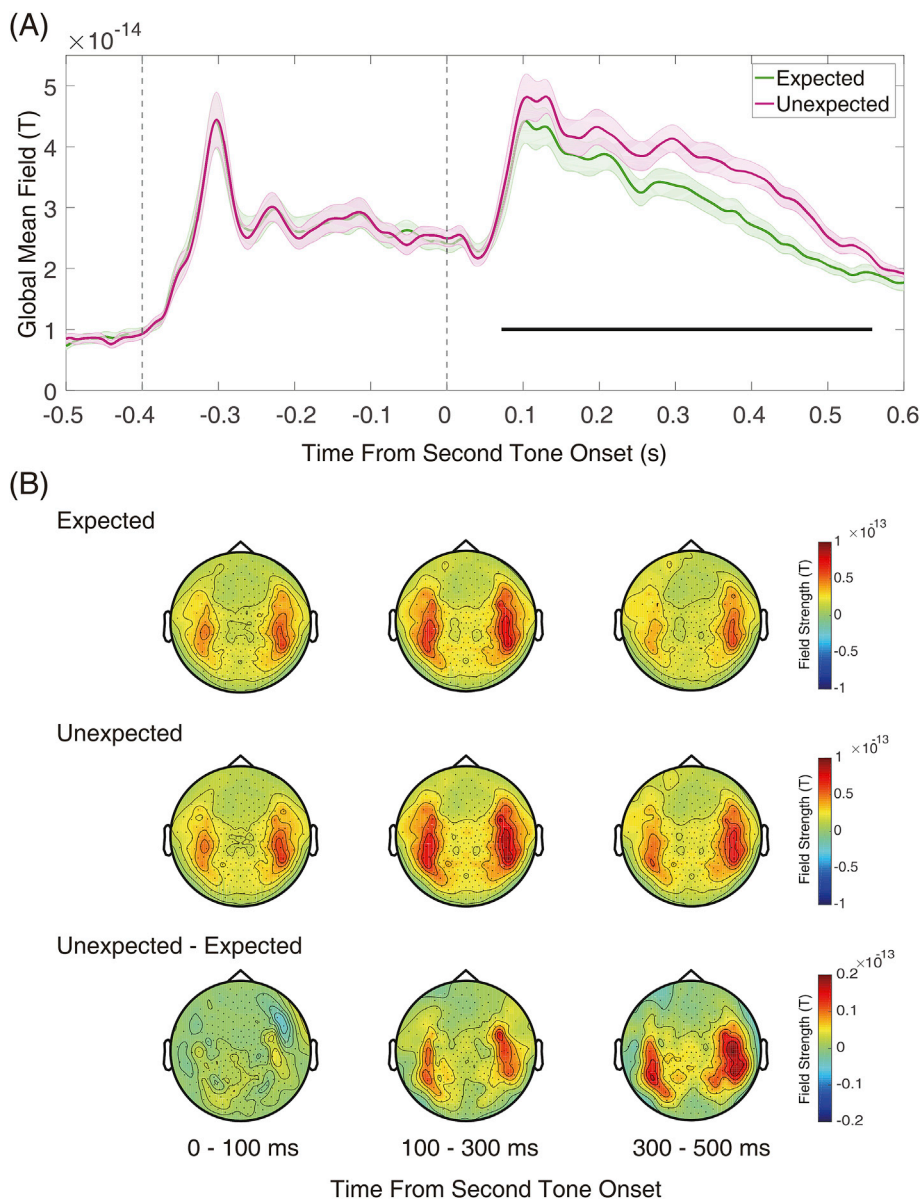


Fig. 2. (A) Comparison of the global mean field activity between the expected and unexpected conditions. Dashed lines indicate the onset time for the first tone (-0.4 s) and second tone (0 s). The black line indicates time points with a significant difference (cluster correction $p < 0.05$) in GMF between the expected and unexpected conditions. Shaded areas denote the standard errors of the mean (SEM) across participants. (B) Topographical representation of mean planar-transformed event-related field activity for different time windows in the expected condition (top), unexpected condition (middle) and the difference between the two conditions (bottom).

strong neural activity over bilateral temporal sensors for both expected and unexpected conditions in all three time windows and the difference between the two conditions shared a similar topographical pattern as the tone elicited activities.

Expected tones were repeated more frequently than unexpected tones within a block. Therefore, we ran a control analysis to determine whether repetition suppression was a relevant factor that could partly explain our experimental findings. To this end, we compared the global mean field activity between tone pairs that were preceded by the same tone pair (repeated tone pairs) and tone pairs that were preceded by a different tone pair (non-repeated tone pairs). There was no significant difference between these conditions (all $p > 0.10$, see Supplementary Material), suggesting that repetition suppression is an unlikely explanation for the observed findings.

3.3. Valid expectation of tone identity reduces the fidelity of neural representation

We adjudicated between the expectation sharpening model and expectation dampening model by investigating the neural representation fidelity in expected and unexpected conditions. Taking advantage of the cross-validation technique, we trained linear forward models to maximize the distance between Tone C and Tone D in the feature space using a large proportion of the data and obtained the representation profile (decoder signal) for the rest in different experimental conditions (see Materials and Methods). On this account, if the difference in decoder signals between Tone C and Tone D is larger in the expected condition than in the unexpected condition, the data favor the expectation sharpening model, while the opposite pattern favors the expectation dampening model (Fig. 1C).

We first investigated the decoder signals for expected and unexpected conditions (trial numbers were matched between conditions, see Materials and Methods) when performing the training and testing procedure in the same time bins. As a sanity check, for both the expected and unexpected conditions, we found no difference between the trials containing tone C and trials containing tone D before the second tone (tone C or D) onset. After the second tone onset, decoder signals corresponding to

tone C and D were distinguishable in the unexpected condition (post hoc paired t -test on the mean distance from boundary from 0 to 600 ms for tone C and D, $p = 3.8 \times 10^{-5}$), but not in the expected condition ($p = 0.14$ from 0 to 600 ms on the mean distance from boundary, Fig. 3A and B). Post hoc paired t -test between the distance from tone C to tone D in the unexpected condition and the distance in the expected condition also revealed a significant difference (from 0 to 600 ms, $p = 0.0048$). We further obtained the decoder signal difference between tone C and D in the form of a generalization matrix by training and testing on the same and different time bins. A paired t -test was performed on the difference separately for expected and unexpected conditions and then the statistical values were corrected for multiple comparison using a cluster-based permutation test (see Materials and Methods). A significant cluster of activity pattern difference between tone C and D was found from ~ 85 to 390 ms in the unexpected condition ($p = 0.023$) while no significant cluster was found in the expected condition ($p = 0.409$, Fig. 3C and D). We further statistically compared the difference between the expected and unexpected conditions and results showed that the difference in the unexpected condition was significantly larger than the expected condition (Fig. 3E, significant cluster from ~ 150 to 330 ms; $p = 0.021$).

A possible explanation is that ineffective decoding in the expected condition was caused by the linear forward modeling itself, i.e., this method was specific for the unexpected condition and the decoder signals between tone C and D were not distinguishable in all scenarios in the expected condition. In order to rule out this explanation, we performed the same forward modeling analysis on all trials in the expected condition (matched trial number for tone C and D) which contained ~ 3.5 times more trials than the previous analysis. By using this larger set of trials, we could observe a significant difference in decoder signals between tone C and D after the second tone onset (post hoc paired t -test from 0 to 600 ms, $p = 2.97 \times 10^{-4}$; significant cluster from ~ 100 to 450 ms, $p = 0.019$; Fig. 4A and B), indicating it is possible to distinguish different tone identities in the expected condition. Therefore, the ineffective decoding in the previous analysis should not be caused by the decoding technique itself. Rather, the data suggest that the neural activity patterns are less distinct during the expected condition, leading to a worse ability to classify its identity compared to the unexpected condition.

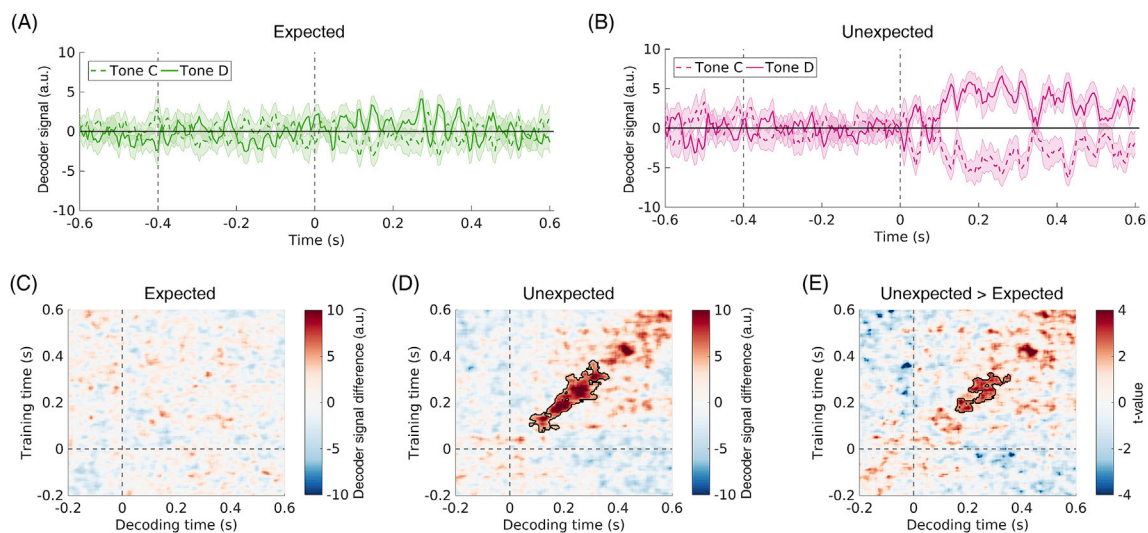


Fig. 3. (A) Decoder signals of tone C and tone D in the expected condition in different time bins. The dashed line is the mean decoder signal for tone C across participants and the solid line is for tone D. Shaded areas around the lines denote the standard errors of the mean. (B) Same as (A), but in the unexpected condition. (C) Temporal generalization matrix of the mean decoder signal difference between tone C and D in the expected condition. For each element inside of the matrix, the time of the row corresponds to the time bin (20 ms) that was used to train the linear forward model and the time of the column corresponds to the time bin that was used to obtain the decoder signal. The diagonal of the matrix corresponds to the difference of the decoder signal between tone D and C in (A). No significant clusters were found after cluster-based correction. (D) Same as (C), but in the unexpected condition. The diagonal of the matrix corresponds to (B). Black outlines indicated the significant cluster ($p < 0.05$) after multiple comparison correction using a cluster-based permutation. (E) Group-level t -statistics of the neural representation difference between the unexpected and expected conditions. Black outlines indicated the significant cluster (cluster-based correction, $p < 0.05$). For all analyses in (A–E), the number of trials was matched for tone C and D and also for the expected and unexpected conditions. Time 0 corresponds to the second tone onset.

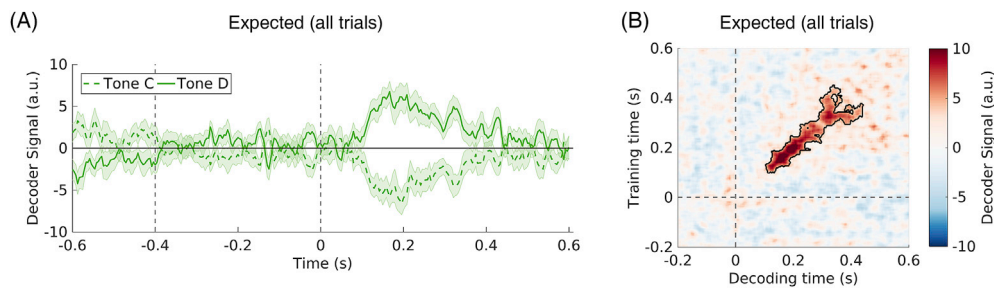


Fig. 4. (A) Decoder signals of tone C and tone D in the expected condition for all trials (~3.5 times more trials than in Fig. 3 A and C, matched trial numbers for tone C and D) in different time bins. (B) Temporal generalization matrix of the mean decoder signal difference between tone C and D in the expected condition for all trials. Black outlines indicated the significant cluster (cluster-based correction, $p < 0.05$).

In order to assess whether the difference in the neural representation fidelity between the expected and unexpected conditions was the direct result of the overall activity difference between the two conditions, we examined whether these two phenomena were correlated across subjects. A correlation analysis showed no reliable link between the mean neural representation difference within the significant cluster (Fig. 3 E) and the mean GMF difference within the time window from 150 to 330 ms (Fig. 5, $r = 0.037$, $p > 0.10$). This suggests that the reduced neural representation in the expected condition is potentially not simply the result of the smaller overall evoked activity.

4. Discussion

We investigated the effects of expectation suppression on the magnitude and fidelity of the neural representation in the auditory domain. We observed strong expectation suppression for expected, compared to unexpected, auditory events (Fig. 2). Linear forward modeling analysis showed that the difference between the decoder signals of the two different tones (tone C and D) was smaller in the expected condition than in the unexpected condition (Fig. 3), in line with an expectation dampening model.

Our data provide strong evidence for expectation suppression of auditory evoked activity, in line with several earlier studies showing suppression of expected stimuli in the auditory domain (Todorovic et al., 2011; Todorovic and de Lange, 2012; Wacongne et al., 2011; Näätänen et al., 1978; Bendixen et al., 2012). Our study extends these studies by

also investigating the fidelity of the neural representation, following up on previous research in the visual domain (St John-Saaltink et al., 2015; Meyer and Olson, 2011; Kumar et al., 2017; Kaposvari et al., 2018; Ramachandran et al., 2016; Richter et al., 2018; Kok et al., 2012). In our experiment, we manipulated expectation in a block-wise fashion, i.e. participants expected a particular tone pair during small blocks of trials. While this is different from studies using manipulations of conditional probability (Todorovic and de Lange, 2012), our experimental manipulation yielded highly similar activity differences between expected and unexpected tone pairs, suggestive of similar mechanisms. Furthermore, the expected and unexpected tones for which we observed expectation suppression were all task irrelevant and uninformative about the target tone. Therefore, it is unlikely that top-down attentional differences between the conditions are at play. On the other hand, one could argue that there is a difference in bottom-up attention caused by the violation of a statistical regularity. However, similar to earlier electrophysiological findings (Meyer and Olson, 2011), the latency of the expectation modulation is highly similar to the latency of the evoked activity, i.e. the suppression is visible from the onset of the auditory response. An attentional modulation that is generated down-stream from the sensory cortex would be expected to manifest itself only later in time. The observed expectation suppression may provide evidence for a specific neural coding strategy in the brain: since there is more overall redundant information in the expected condition than in the unexpected condition, the reduced neural activity in the expected condition is in line with the efficient coding principle (Barlow, 1961), which states that sensory systems should minimize the number of spikes to transmit a given signal.

Accompanied by expectation suppression, our data favored the expectation dampening model rather than the expectation sharpening model. When comparing the decoder signals in the expected and unexpected conditions, we matched trial number not only between the two tone identities but also between the two conditions in order to further remove any potential difference of history and noise (Friedman et al., 2001). Since expected and unexpected trials were randomly intermixed during the experiment, the amount of noise caused by the MEG acquisition should also be similar. Furthermore, since the tone identities could be successfully decoded in the unexpected condition or when we enhanced the signal-to-noise ratio by introducing more trials in the expected condition, we could indeed also distinguish neural representations for expected tone pairs. Therefore, the observed difference between the fidelity of the decoder signals in the expected and unexpected condition is likely resulting from a stimulus-specific attenuation of auditory activity. Moreover, since the neural activity difference and neural representation difference were not correlated with each other and were maximal in different time windows, the observed neural representation difference could not be simply explained by a boost in neural activation. Rather, the overall GMF amplitude difference, which was maximal around 300–500 ms, may reflect a more general surprise mechanism (Donchin, 1981; Sutton et al., 1965; Nieuwenhuis et al., 2005), whereas the decoding differences are related to an earlier sensory and stimulus-specific signal difference.

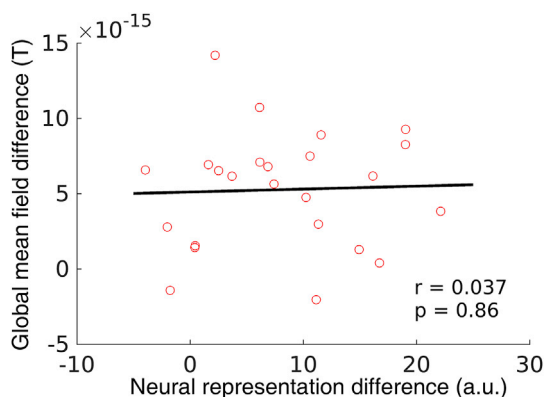


Fig. 5. Pearson correlation between the global mean field difference and neural representation difference across participants. The neural representation difference was calculated by subtracting the mean decoder signal difference between tone C and D within the significant cluster in Fig. 3E in the expected condition from the difference in the unexpected condition for each participant. The global mean field difference between the two conditions was averaged across the same time window (150–330 ms). Each red circle represents data from one participant and the line is the best linear fit of the data. No significant correlation was observed between the two measures ($r = 0.037$, $p = 0.86$).

In the current study, we did not observe a sharpened neural representation in the expected condition, in contrast to a previous study in the visual domain (Kok et al., 2012). There are obviously many differences between the current study and the previous one (e.g. MEG vs. fMRI), but we highlight some of the potentially most relevant differences below. Firstly, sharpening was found selectively in the primary visual cortex (Kok et al., 2012). However, electrophysiological (Meyer and Olson, 2011; Kumar et al., 2017) and fMRI (Blank and Davis, 2016; Richter et al., 2018) studies showed that in higher-order visual areas such as inferior temporal cortex in monkey and lateral occipital complex in humans, neural representations are dampened for expected visual object stimuli. Since our results are based on all MEG channels over the brain, it is impossible to know at which stage of the cortical hierarchy the observed dampening process has taken place in our study. Secondly, similar to many previous studies that observed dampening (Meyer and Olson, 2011; Kumar et al., 2017; Richter et al., 2018), the expected and unexpected tones were not the target stimuli in the current study. In comparison, discrimination judgments were required for all expected or unexpected stimuli in the study by Kok et al. (2012). Targets may be processed differently from distractors, possibly engaging different attentional selection processes that may sharpen stimulus representations (Serences et al., 2009).

In the framework of predictive coding, prior expectation generates a prediction feedback signal which is sent to the lower hierarchical area, where it interacts with the bottom-up input (Rao and Ballard, 1999). Current implementations of predictive coding as a model for cortical processing suggest the existence of two subpopulations of neurons: prediction units which represent the sensory input (which can be sharpened by matching prior expectation) and prediction error units which represent the difference between the sensory input and prediction (which can be dampened by matching expectation) (Friston, 2005; Spratling, 2008; Blank and Davis, 2016; Kok et al., 2012). One explanation for the different observations with respect to expectation sharpening and dampening is the notion that the observed neural signals may be from different subpopulation: sharpening effects occur in the prediction units and dampening effects occur in the prediction error units. At present, this is, however, pure speculation, and it will need to be specified under which circumstances, when and where activity modulations in these two hypothesized types of units are expected. Alternatively, the different observations may be caused by neural signals from different time windows. Prior expectation can preactivate the corresponding neurons and bias the neural representation toward the expected stimulus (Kok et al., 2017; A. H. Bell et al., 2016; Reddy et al., 2015). Therefore, sharpening and dampening operations may happen at different time windows. The resultant sharpening (Kok et al., 2012) or dampening (Richter et al., 2018) observed using fMRI is the integral of potentially different processes that happen at different stages of cortical processing.

In summary, our results showed that prior expectation of tone identity leads to suppressed overall neural activity over the auditory cortex. This suppression is accompanied by, but not correlated with a reduction of the neural representation fidelity of the tone identity, suggesting a dampening of the neural representation by expectation in the auditory domain.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuroimage.2019.06.033>.

Conflicts of interest

The authors declare no competing financial interests.

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