



Pre-stimulus brain state predicts auditory pattern identification accuracy

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ABSTRACT

Recent studies show that pre-stimulus band-specific power and phase in the electroencephalogram (EEG) can predict accuracy on tasks involving the detection of near-threshold stimuli. However, results in the auditory modality have been mixed, and few works have examined pre-stimulus features when more complex decisions are made (e.g. identifying supra-threshold sounds). Further, most auditory studies have used background sounds known to induce oscillatory EEG states, leaving it unclear whether phase predicts accuracy without such background sounds. To address this gap in knowledge, the present study examined pre-stimulus EEG as it relates to accuracy in a tone pattern identification task. On each trial, participants heard a triad of 40-ms sinusoidal tones (separated by 40-ms intervals), one of which was at a different frequency than the other two. Participants' task was to indicate the tone pattern (low-low-high, low-high-low, etc.). No background sounds were employed. Using a phase opposition measure based on inter-trial phase consistencies, pre-stimulus 7–10 Hz phase was found to differ between correct and incorrect trials ~200 to 100 ms prior to tone-pattern onset. After sorting trials into bins based on phase, accuracy was found to be lowest at around $\pm\pi$ relative to individuals' most accurate phase bin. No significant effects were found for pre-stimulus power. In the context of the literature, findings suggest an important relationship between the complexity of task demands and pre-stimulus activity within the auditory domain. Results also raise interesting questions about the role of induced oscillatory states or rhythmic processing modes in obtaining pre-stimulus effects of phase in auditory tasks.

1. Introduction

Increasingly, neurophysiological evidence suggests that ongoing brain states, indexed by frequency band-specific EEG features, shape perception and cognition (for review, see Buzsáki, 2006; Jensen and Mazaheri, 2010; VanRullen, 2016a). For example, suppressed pre-stimulus alpha (~8–13 Hz) power in the electroencephalogram has been associated with enhanced detection of faint flashes of light (Busch et al., 2009). That study also revealed that pre-stimulus EEG phase in the high theta/alpha range (~6–12 Hz) distinguished correct from incorrect trials, with a decreasing trend in accuracy from the most accurate phase to ~180° opposite. Similar reports have been made in other visual studies where oscillatory activity predicts perceptions (Dugué et al., 2011; Ergenoglu et al., 2004; Limbach and Corballis, 2016; Milton and Pleydell-Pearce, 2016; Samaha et al., 2017).

Findings from auditory studies are notably mixed (for review, see Zoefel and VanRullen, 2015). Some report less pre-stimulus alpha power

on correct relative to incorrect trials (e.g., Leske et al., 2015; Strauß et al., 2015), while others report a relative increase in alpha power on correct trials and power differences in other frequency bands (e.g., Bernasconi et al., 2011; Hermann et al., 2016; Kayser et al., 2016). Ng et al. (2012) found that missed detection of masked sounds was modulated by pre-stimulus phase, suggesting an important role of phase in the inhibition of background sounds. Pre-stimulus phase effects for lexical decision (Strauß et al., 2015), tone discrimination (Kayser et al., 2016), and gap detection (Henry et al., 2016) in non-rhythmic background sounds have also been observed. Further, oscillations induced by rhythmic input (i.e., entrained oscillations) have repeatedly produced phase-dependent auditory performances (Besle et al., 2011; Henry and Obleser, 2012; Stefanics et al., 2010). For instance, Henry and Obleser (2012) entrained delta oscillations with a tone modulated up and down in frequency at a rate of 3 Hz. Participants' task was to detect a short gap in the frequency-modulated sound. Gap detection hit rates were modulated by the phase of entrained oscillations. However, it has been demonstrated

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more than once that when near threshold tones are presented in silence, pre-stimulus phase fails to predict performance (Zoefel and Heil, 2013; VanRullen et al., 2014).

One possible reason for inconsistency is that the predictive capacity of pre-stimulus power and phase are dependent upon listeners being forced into a rhythmic processing mode (Henry and Obleser, 2012; Schroeder and Lakatos, 2009). Indeed, most works have entrained oscillations of a particular rate to measure how auditory perception is modulated by the phase of the entrained rhythm (e.g., Hermann et al., 2016; Neuling et al., 2012; Henry and Obleser, 2012; Stefanics et al., 2010); Zoefel et al. (2018). Pre-stimulus phase effects on auditory perception can be obtained without clear entrainment, but to date all studies demonstrating this have employed background sounds of some nature (e.g., Henry et al., 2016; Ng et al., 2012; Strauß et al., 2015). The presence of masking sounds often drives an increase in the power of oscillations even if those oscillations do not have clear phase consistency across trials. This is especially the case in the alpha range where many pre-stimulus phase effects have been reported (for review, see Strauß et al., 2015). There is evidence that the role of alpha phase is modulated by alpha power (for review, see Jensen and Mazaheri, 2010; Mathewson et al., 2011; also, see Hermann et al., 2016), and that alpha power is especially useful for inhibition during the presence of noise (Ng et al., 2012; Strauß et al., 2015). Pre-stimulus EEG may only relate to perceptual performances when background sounds are either driving oscillatory states through modulations of power, phase, or both. That most auditory studies have used background sounds may suggest that ongoing background stimulation (and perhaps associated entrainment) is assumed to be necessary (see Henry and Obleser, 2012; Peelle and Sommers, 2015; Wöstmann et al., 2016; Zoefel et al., 2018).

An additional possibility is that the level of cortical involvement is a critical factor (VanRullen et al., 2014). The visual and auditory systems differ architecturally in that auditory stimuli undergo more extensive processing prior to cortex. Frequency, envelope, spectrotemporal, and spatial information in auditory signals are well represented before reaching primary auditory cortex (Rees and Palmer, 2010). In contrast, in the visual system many simple features are coded in cortex itself (Hubel, 1988). Cortical oscillations may not matter if task-relevant information is processed well prior to cortex (e.g., in the envelope of a signal), but may matter at higher levels engaging cortical networks involved in assessing inter-stimulus relationships (Wisniewski et al., 2018) or extracting meaning (e.g., in a lexical decision task; Strauß et al., 2015). For instance, it could be that the reason that pre-stimulus phase matters for some tasks like lexical decision (Strauß et al., 2015) and tone comparison (Kayser et al., 2016) is not due to the background noise that was used. Rather, it is due to those tasks' dependencies on higher-level cortical areas. Unfortunately, the current literature does not disambiguate these possibilities.

Here, we examined how pre-stimulus power and phase relate to performance in a tone pattern recognition task when no background sounds are present. If pre-stimulus EEG is only predictive when background sounds are present, no relationships with accuracy should be seen (cf. Zoefel and Heil, 2013). Our task requires comparison of tones and classification, and thus should require cortical processing to a larger extent than simple detection (Chechik and Nelken, 2012). Pre-stimulus EEG may be predictive of accuracy if the level of cortical involvement is important. For EEG phase, results were consistent with the latter. For pre-stimulus power, no clear relationship with accuracy was found. Importantly, results show that background sounds are not necessary to observe pre-stimulus phase effects on auditory performance. Rather, it may be that task complexity is important.

2. Materials and methods

2.1. Listeners

Seventeen listeners (9 males, ages 19–33) were either paid for their participation or were unpaid volunteers. All participants reported normal

hearing. Three individuals were dropped from analysis due to excessively noisy EEG data.

2.2. Ethics statement

All listeners signed an informed consent form and underwent procedures approved by the Wright-Site Institutional Review Board.

2.3. Data and code availability statement

Data and analysis code can be obtained from the last author (M.G.W.) by emailing him at mgwisniewski@ksu.edu. Upon receipt of a request, M.G.W. will obtain the appropriate clearance to release the data to the requesting party.

2.4. Apparatus

Sounds were presented through Etymotic ER-2 earphones (Etymotic Research, Elk Grove Village, IL) at ~81 dB SPL (decibel of sound pressure level). All experimental procedures were carried out in MATLAB 2014a (Mathworks, Natick, MA) running on Windows 7. Responses were made via a computer keyboard. Listeners sat in a sound-attenuating booth throughout the experiment.

2.5. Stimuli, task, and procedures

A rapid auditory pattern identification task was used (see Fig. 1; cf. Tallal and Piercy, 1973; Warren, 1974). Stimuli were auditory pure tone sequences, each comprising a triad of 40-ms tones with 40-ms inter-tone-intervals. The frequencies of tones within a sequence were either “low” (L) or “high” (H), with the lowest tone selected randomly on every trial from a uniform distribution between 900 Hz and 1100 Hz. There were six possible sequence patterns with different L/H orders: LLH, LHL, LHH, HHL, HLH, & HLL. One pattern was selected at random with equal a priori probabilities across sequence types, and was presented on each trial. Two seconds after pattern onset, a response grid appeared on screen with the 6 different L/H patterns assigned to number keys 1–6. Response options were displayed in the same position and order as the first six digits of the numeric keypad located at the lower right of a standard desktop computer keyboard. (see Fig. 1). Key assignments were randomized from trial-to-trial. For instance, if “1” was paired with “LLH” on a given trial, “1” might be paired with “HLH” on the next trial. The randomization served to reduce any influence of motor preparations between correct and incorrect trials because the response could not be known until assignments were shown on screen. On-screen feedback (1000-ms) was presented after responses such that the word “Correct” was displayed after correct responses and the word “Wrong” was displayed after incorrect responses. If a participant pressed a key other than numbers 1 through 6, the words “WRONG KEY PRESS” were presented on the screen, and the trial was later discarded from analysis. There was no response deadline. Following response onset, the next trial was initiated after a variable inter-trial-interval (Gaussian distribution, $M = 4050$ -ms, $SD = 30$ -ms).

The full EEG session was preceded by a behavioral session designed to determine the frequency separation between H and L tones at which each individual could achieve ~50% accuracy. The task described above was run for three 50-trial blocks, in which the frequency separation between H and L started at 20% ($\Delta f = 100 \cdot (H-L)/L$). An adaptive 1-up 1-down procedure was used in which the frequency separation between the H and L tones was decreased after every correct response ($\Delta f \times 0.9$) and increased after every incorrect response ($\Delta f \times 1.1$). An individualized separation was taken to be the mean frequency separation across the last 5 trials of each block (i.e., mean across 15 trials total). The mean individualized frequency separation was $M = 5.9\%$ ($SD = 4.9$). The pre-experimental behavioral session and the EEG session were always conducted on separate days.

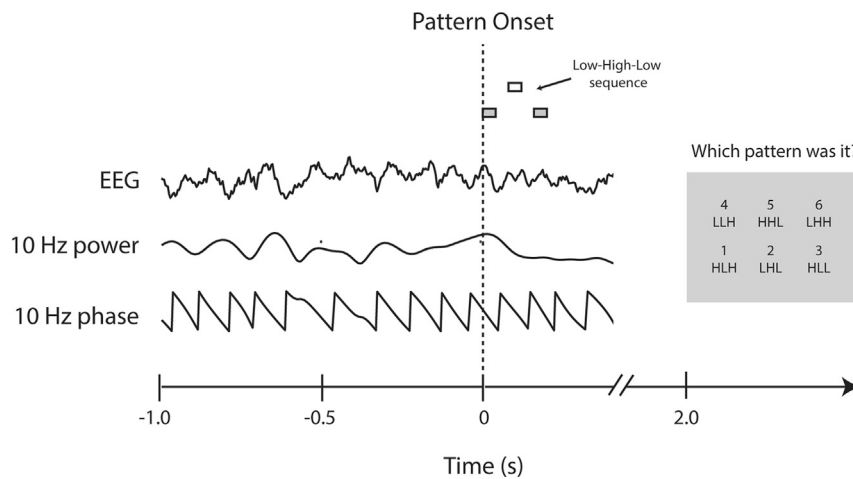


Fig. 1. A depiction of a single trial with traces of raw EEG, 10-Hz power, and 10-Hz phase. Grey inset box on right shows an example response option display.

For the EEG session, 5 blocks of 50 trials were run at individualized frequency separations (250 trials total). All other parameters were as outlined above.

2.6. EEG acquisition, preprocessing, and cleaning

EEG was recorded using a Biosemi Active II system recording at a 2048-Hz sample rate and 24-bit A/D resolution. A 70-channel array of electrodes was used. A cap with placements for 64 electrodes arranged according to the international 10–20 system was fitted to each participant's head. The remaining 6 electrodes were placed below each eye, lateral to each eye, and on each mastoid. Signals were referenced online to the Common-mode-sense/driven-right-leg (CMS/DRL) reference for the Biosemi system (see biosemi.com). DC offsets between CMS/DRL and each electrode were kept below 25 μ V or else an electrode was discarded from analysis.

Offline data processing, cleaning, and analysis of the results were conducted using the open-source EEGLAB toolbox (Delorme and Makeig, 2004) and custom MATLAB scripts/functions. Data were re-referenced to linked mastoids, resampled at 256 Hz (after applying an anti-aliasing filter), high-pass filtered (1691 point zero-phase finite impulse response (FIR); 0.25 Hz half amplitude cutoff), then low-pass filtered (69 point zero-phase FIR; 56.25 Hz half amplitude cutoff). Channels and portions of continuous data identified by visual inspection to be contaminated by noise or excessive movement artifacts were removed. Remaining data were submitted to independent component analysis (ICA). Components identified as artifactual based on their spectra and scalp projections were subtracted from the channel data (cf. Wisniewski et al., 2017; for review, see Jung et al., 2000). Missing channels were then interpolated (spherical interpolation method).

2.7. Statistical analysis

Epochs were extracted from –1500 ms to 1500 ms relative to sequence onset. Complex 3-cycle Morlet wavelets were used to yield single trial time-frequency decompositions spanning 2–20 Hz in 0.2 Hz increments at 200 time points (~7 ms increments). For power-based analyses, separate mean event-related spectra (ERS) for correct and incorrect trials were computed from the time-frequency decomposition of individual trials. Difference images were then generated using a percent relative power measure for each time-frequency point:

$$ERS_{diff} = 100 \times (ERS_{correct} - ERS_{incorrect}) / ERS_{incorrect}$$

Here, positive values of ERS_{diff} indicate greater power in the correct compared to incorrect trials. Negative values indicate the opposite.

For phase-based analyses, we used a phase opposition sum (POS) measure (for review, see VanRullen, 2016a,b) based on inter-trial phase consistencies (ITPCs). ITPC is large (closer to 1) when phase is consistently aligned across trials, and small (closer to 0) when phase is inconsistently aligned (for review, see Cohen, 2014). ITPCs were computed separately for correct trials, incorrect trials, and all trials combined. To compute the phase opposition sum we used the following formula:

$$POS = ITPC_{correct} + ITPC_{incorrect} - (2 \times ITPC_{all})$$

For POS images, if correct and incorrect trials tend to have opposing phases, POS will be large. A lower POS will result if correct and incorrect trials tend towards random phase, or if they align at similar phases. This is because when correct and incorrect trials are at random or similar phases, $ITPC_{all}$ will be similar to ITPC for correct and incorrect trials computed separately (i.e., similarly random, or similarly aligned). If the angle of phase alignment is different for correct and incorrect trials, ITPC will be low when those trials are combined. In contrast, ITPC will be high for correct and incorrect trials computed separately (for an extensive review, see VanRullen, 2016a,b).

We followed statistical analysis guidelines set by VanRullen (2016a, b) that are based on testing with real and simulated EEG data. Though this approach differs from some more standard permutation-based testing of pre-stimulus phase effects, note that this statistical procedure was chosen for empirical, not historical reasons. VanRullen (2016a, b) found the current approach to be more efficient and less susceptible to Type I errors compared to the standard. For both ERS_{diff} and POS images, correct and incorrect trial labels were shuffled for 100 iterations for each individual. An ERS_{diff} and POS image was recomputed for each iteration, creating a null hypothesis distribution with a mean and standard deviation for each time-frequency point. Each time-frequency point in an individual's actual ERS_{diff} and POS image was then converted to a z-score based on the mean and standard deviation of the null hypothesis distribution. These independent z-scores were combined across subjects using Stouffer's method (for review, see VanRullen, 2016a,b; Whitlock, 2005):

$$Z_s = \frac{\sum_{i=1}^k Z_i}{\sqrt{k}}$$

In this formula the combined z-score (Z_s) is the sum of the individual z-scores divided by the square root of the number of tests (k). These were then converted to p -values and interpreted using a false discovery rate (FDR) procedure to correct for multiple comparisons across time-frequency points and channels ($p < .05$; Benjamini & Hochberg, 1995).

3. Results

3.1. Pattern identification accuracy

Mean proportion correct across all trials in the experiment was $M = 0.50$ ($SD = 0.06$), confirming the appropriateness of individualized frequency separations determined for $\sim 50\%$ correct. Fig. 2a depicts accuracies broken up into the different tone pattern identities. There was a significant difference among means, $F(5,65) = 2.38$, $p = .048$, $\eta_p^2 = 0.15$, likely attributable to better than threshold level performance for the HLH identity and worse than threshold level performance for the LHL identity. In one-sample t -tests testing the null hypothesis of accuracy equal to 0.5 for each identity, only the HLH identity revealed significance, $t(13) = 2.59$, $p = .023$, Cohen's $d = 0.71$. The one-sample t -test for the LHL identity was not significant, $t(13) = 2.11$, $p = .055$, Cohen's $d = 0.50$.

Fig. 2b depicts accuracies broken up into 6 different linearly spaced bins according to the lowest frequency tone in a pattern. There was also a significant difference among these means, $F(5,65) = 3.58$, $p = .006$, $\eta_p^2 = 0.22$, trending such that frequencies nearer the center of the distribution (i.e., 1000 Hz) showed greater accuracy. Similar one-sample t -tests as above found only a significant lower than threshold accuracy for the 900–933 Hz frequency bin, $t(13) = 2.28$, $p = .04$, Cohen's $d = 0.61$.

It is important to note that even though there were apparent accuracy differences among trials with different pattern identities and frequencies, none of these differences can be related to the pre-stimulus EEG features we intended to analyze. That is, there is no way for a participant to have knowledge of any of these stimulus differences before they occur. Thus,

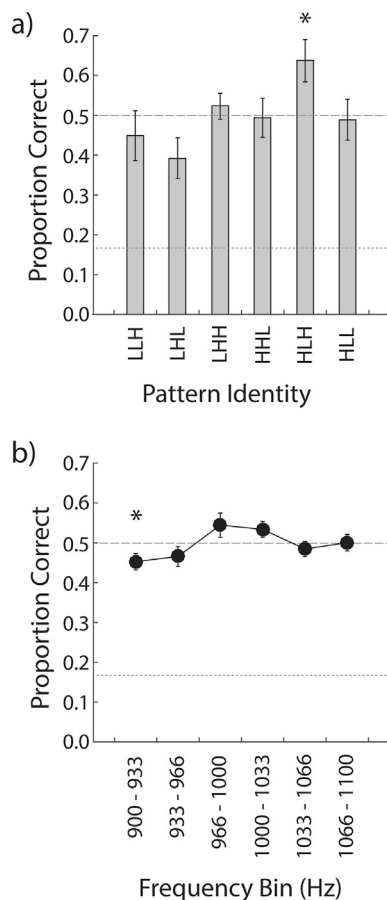


Fig. 2. Accuracy across different tone pattern identities (a) and different frequencies for the low frequency tone within a sequence (b). Note that the abscissa in (b) marks rounded bin edges (e.g., 933 Hz actually represents 933.33 Hz). The horizontal dashed lines represent the desired 50% correct threshold. The horizontal dotted lines represent chance performance.

stimulus-related effects may only serve to obscure a relationship between pre-stimulus EEG and pattern identification accuracy.

3.2. Pre-stimulus high-theta/low-alpha phase predicts accuracy

The upper panel in Fig. 3a shows POS for frontal electrode F3, where phase effects were strongest. Large values of POS (hot coloration in the figure) indicate stronger opposition of phases between correct and incorrect trials. The black line represents the last possible data point before pattern onset that included any post-stimulus onset data points in the time-frequency decomposition. There was strong POS between approximately -200 to -100 -ms relative to the onset of tone patterns, between approximately 7–11 Hz. The white outline in this region of the figure depicts the edge of significance of this effect (FDR corrected, $p < .05$), indicating that phases for correct and incorrect trials at these time-frequency points tended to align at opposing phase positions. For FDR corrected POS at all other scalp electrodes, see Fig. S1. The effect was not restricted to electrode F3. The bottom panel in Fig. 3a shows individual traces of POS at 8.2 Hz (thin black lines), along with the combined POS (thick red line). Though there were latency differences among individuals regarding when POS reached its peak, most individuals show evidence of increased POS in the time range between -200 and -100 ms relative to tone sequence onset. The scalp map of POS at a point in the center of this region of significance ($-15s$, 8.2 Hz) is shown in Fig. 3b. Similar to the visual work (Busch et al., 2009) and other auditory work (Strauß et al., 2015), the scalp map shows a frontal distribution of POS, though slightly left lateralized. Fig. 3c plots the phase difference values (correct minus incorrect). Note that most individuals show a phase difference greater than 90° (cf. Strauß et al., 2015).

To further characterize how pre-stimulus phase was related to accuracy, we binned individual trials into 9 different phase bins at electrode F3, time point $-0.15s$, and frequency 8.2 Hz (cf. Busch et al., 2009; Ng et al., 2012). This time-frequency point was chosen because it was in the center of the significant region of POS shown in Fig. 3. Bin sizes were $2\pi/9$ (non-overlapping). Proportion correct was computed using trials falling into each bin; we will refer to the bin associated with the greatest proportion correct as the “most accurate” bin. These bins were then sorted such that each individual’s “most accurate bin” was aligned at 0 radians. Critically, this allowed us to examine a relationship between pre-stimulus phase and accuracy even if different individuals had different preferred phases (cf. Busch et al., 2009; Ng et al., 2012). These data are depicted in Fig. 4. It is not surprising that the most accurate bin is at 0, since the data were aligned this way. Interestingly, when pre-stimulus phase differs more from the phase associated with this “most accurate” bin, approaching the opposite phase ($\pm\pi$), accuracy decreases. Accuracy is lowest at bins nearest to $\pm\pi$ relative to the most accurate bin. A repeated measures ANOVA was run on binned accuracy, excluding bin 0. A significant effect of phase was observed, $F(7, 91) = 2.84$, $p = .01$, $\eta_p^2 = 0.18$.

To probe this effect, we compared mean accuracy for the bins closest to the most accurate bin (red markers in Fig. 4a) to those furthest from that most accurate bin (blue markers in Fig. 5a). This difference was significant, as revealed by a paired-sample t -test, $t(13) = 4.23$, $p < .001$, Cohen's $d = 0.79$. This effect was remarkably consistent across individuals. Fig. 4b presents a scatterplot of accuracy for far (x-axis) in relation to close (y-axis) bins. Points falling in the red portion of the plot represent individuals with greater accuracy for those bins closer to the most accurate bin than those bins farther from the most accurate bin. All but one individual showed better performance for the closest bins. The advantage across individuals ranged from 26.5% to -4.7% with a mean of $M = 10.3\%$ ($SD = 9.1$). Of further note, a supplemental analysis revealed no significant differences in the number of any pattern type falling into the highest and lowest accuracy phase bins by chance, making it unlikely that the observed effects are stimulus-related (see Fig. S2 and supplemental data). Overall, the results support a relationship

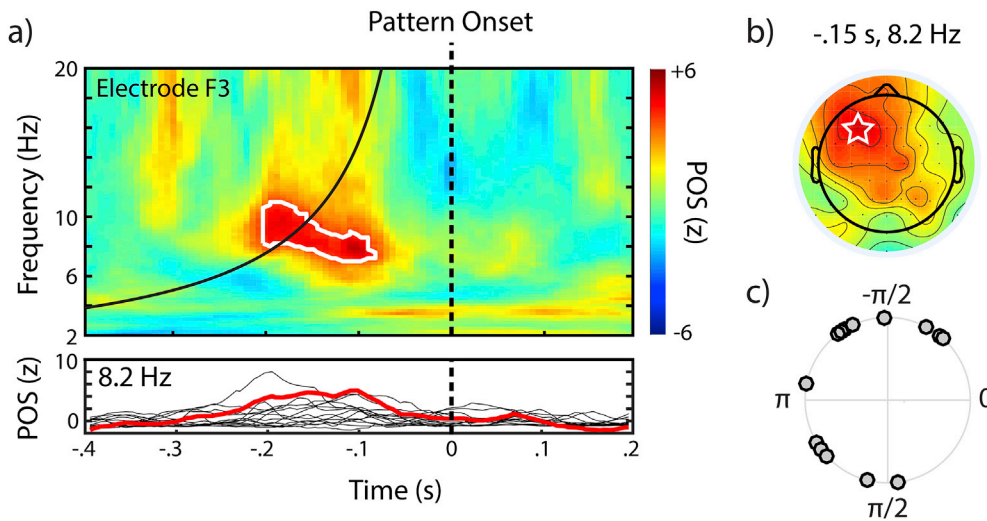


Figure 3. (a) POS at left frontal electrode F3. The upper panel shows POS at multiple time-frequency points. The white outline indicates the area of significance after FDR correction. Any point in the image to the left of the black line contains no post pattern onset data points. The lower panel shows traces of individual POS in z-score units (thin black lines) and combined z for POS across individuals (thick red line). (b) Scalp map of POS at a time-frequency point in the center of the region of significance (-0.15 s, 8.2 Hz). The star highlights electrode F3. (c) Phase difference values at -0.15 s and 8.2 Hz for each subject at electrode F3.

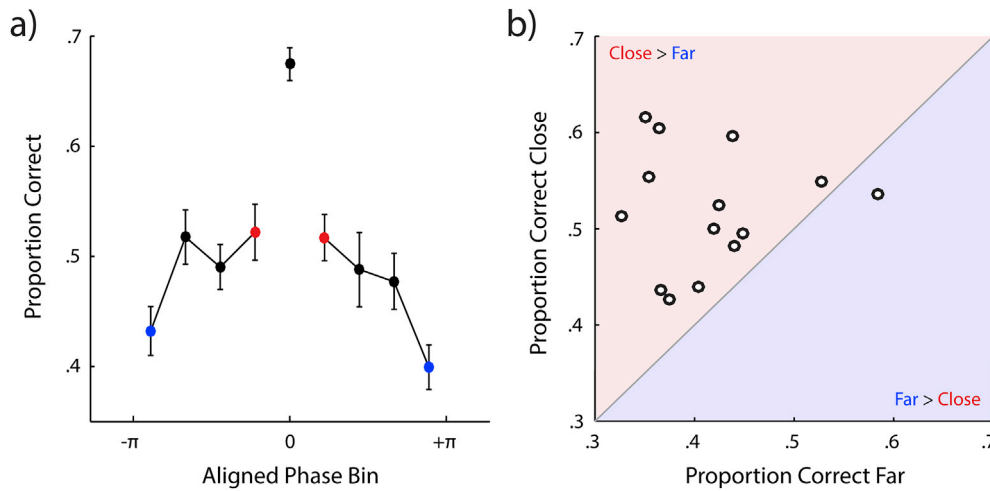


Fig. 4. (a) Proportion correct for phase bins centered around the bin associated with the greatest number of correct responses (“most accurate bin”). For clarity, red markers depict bins closest to the most accurate bin. Blue markers represent bins furthest from the most accurate bin. (b) Scatterplot depicting individual proportion correct for the far bins (y-axis) and close bins (x-axis). Points in the red area indicate higher accuracy for the close over far bins. The opposite is true for the blue area.

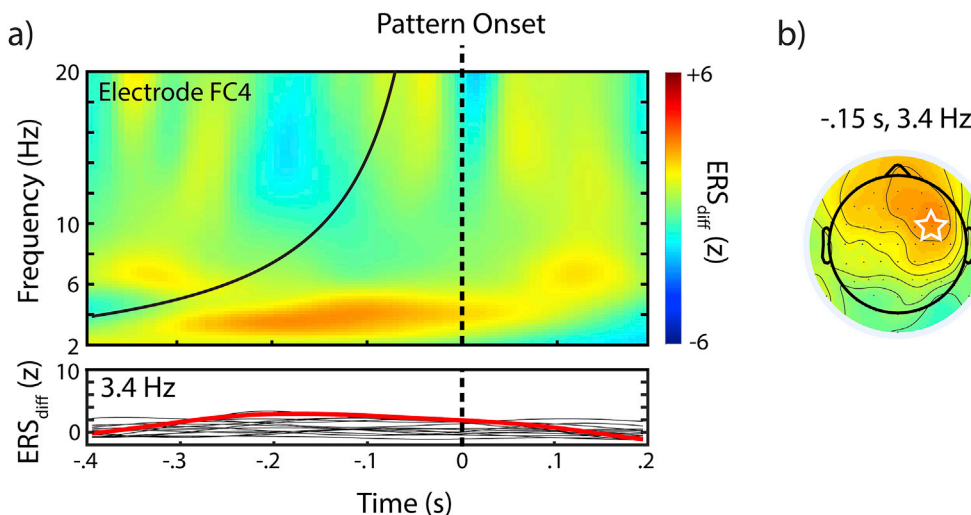


Fig. 5. (a) ERS_{diff} at right frontal electrode FC4. The upper panel shows ERS_{diff} at multiple time-frequency points. ‘Hot’ colors indicate greater power for correct compared to incorrect trials. ‘Cool’ colors indicate the opposite. Any point in the image to the left of the black line contains no post pattern onset data points. The lower panel shows traces of individual ERS in z-score units (thin black lines) and combined z for ERS across individuals (thick red line). Note that although there appeared to be a trend for enhanced delta/low-theta on correct compared to incorrect trials, this did not reach significance after correcting for multiple comparisons. (b) Scalp map of ERS_{diff} at a time-frequency point in the center of the apparent delta/low-theta difference (-0.15 s, 3.4 Hz). The star highlights electrode FC4.

between pre-stimulus oscillatory phase and auditory pattern identification, even without concurrent background sounds.

3.3. No pre-stimulus power differences between correct and incorrect trials

No significant pre-stimulus power differences were revealed by statistical analyses of ERS_{diff} after FDR correction. There was a trend for greater delta/low-theta power on correct trials. In the interest of transparent presentation of the data, and since some other work has revealed similar pre-stimulus effects in the delta band (Hermann et al., 2016; Kayser et al., 2016), the top panel of Fig. 5a shows an image of ERS_{diff} (combined z-scores; for review, see VanRullen, 2016a,b) at electrode FC4 where this effect appeared strongest. Individual traces of power at 3.4 Hz are shown in the bottom panel of Fig. 5a. Though some individuals showed greater pre-stimulus delta power on correct trials, most individuals showed little effect. The scalp map in Fig. 5b shows a right frontal distribution of ERS_{diff} at -0.15 s and 3.4 Hz. However, even when a less stringent statistical criterion was applied (FDR correction including channel FC4 only), ERS_{diff} failed to reach significance at any time-frequency point.

3.4. Pre-stimulus phase effects cannot be explained by post-stimulus activity

Due to the temporal smearing that can occur during time-frequency analysis, there is the possibility that the results of such analyses on pre-stimulus time windows are influenced by post-stimulus activity. In our case, such influences may come from event-related potentials (ERPs) that differ in amplitude or phase between conditions. We therefore conducted two additional analyses to rule out the possibility that the pre-stimulus phase-related effects observed above are related to post-stimulus activity in the EEG. First, we compared post-stimulus ERPs for correct and incorrect trials. Were an influence of post-stimulus activity present, we may have seen a difference in ERPs for the two types of trials. However, this analysis revealed that the ERPs were virtually indistinguishable for correct versus incorrect trials at F3 (Fig. 6a). No time points were significantly different between correct and incorrect trials, $ps > .10$ (uncorrected).

In a second control check, we conducted an analysis of POS on time-frequency transforms using shorter 1-cycle wavelets with poorer frequency, but better temporal precision. If our results were due to differences in post-stimulus activity, we would expect an absence of the noted POS effect with this shorter wavelet in the -200 to -100 ms time-window. We found that POS was apparent at similar time-frequency points, even though these points in the transform were generated without the inclusion of any post-stimulus onset data. In Fig. 6b these points are those that fall to the left of the solid black line. Significance ($p < .05$; fdr corrected) is highlighted by the regions outlined with white outlines.

4. Discussion

4.1. General discussion

The current study was designed as a novel test of pre-stimulus EEG effects on subsequent auditory task performance. We employed an auditory pattern identification task in which sounds were presented well above detection threshold. Importantly, there were no background sounds utilized for masking, and the task was sufficiently complex to involve cortical processing beyond that needed for simple detection in silence. We found strong phase opposition between correct and incorrect trials in a high theta/low alpha region shortly before stimulus onset (~ 200 to -100 ms). When trials were binned according to pre-stimulus phase, a clear relationship with accuracy was observed such that bins opposite an individual's most accurate bin displayed the lowest accuracy. Further, analyses of ERPs and an alternative time-frequency

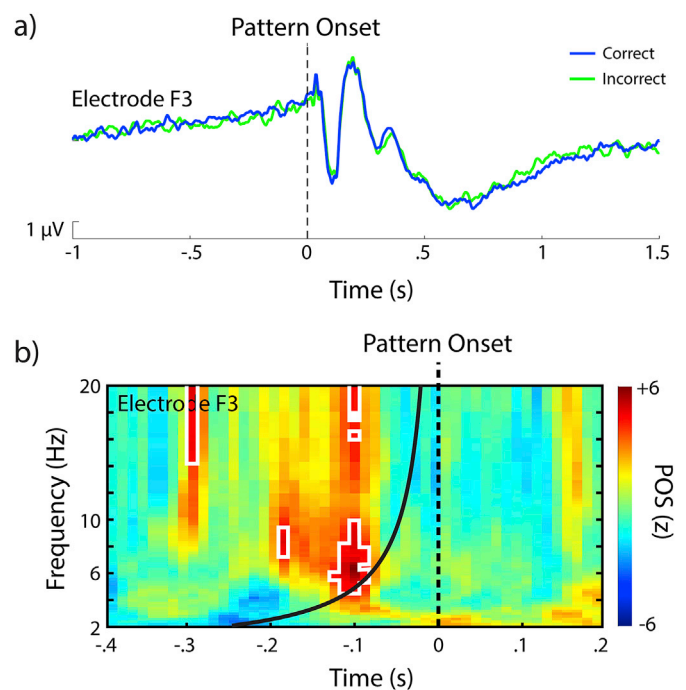


Fig. 6. (a) ERPs for correct and incorrect trials at electrode F3 where pre-stimulus phase effects were strongest. (b) POS computed at electrode F3 using shorter 1 cycle wavelets than the 3 cycle wavelets used in original analyses of POS (Fig. 3). Note here that any point to the left of the solid black line cannot possibly be corrupted by post-stimulus activity, yet strong POS still exists. The regions outlined in white were significantly significant after correcting for multiple comparisons across time-frequency points and channels ($p < .05$; fdr corrected).

decomposition using 1-cycle wavelets ruled out the possibility that the effects observed were related to post-stimulus activity. The data show that the phase of ongoing brain oscillations prior to stimulus presentation can predict auditory performance even without background masking or confounding post-stimulus differences between correct and incorrect trials.

So why have we found effects of pre-stimulus phase without background sounds, while others have not? We suggest that the complexity of the task at hand matters in a substantial way for auditory perception. The auditory system differs from the visual system in that a large amount of processing occurs prior to cortex (e.g., processing of frequency and envelope information; for review, see Pratt, 2011; Rees and Palmer, 2010). Oscillations in EEG largely reflect cortical activity (for review, see Buzsáki, 2006; Luck, 2005) and there is considerable evidence that they are related to excitatory and inhibitory states in cortex (for review, see Buzsáki, 2006; Jensen and Mazaheri, 2010; Schroeder and Lakatos, 2009). This may explain why detection tasks with no background masking, which have been used in examinations of pre-stimulus phase effects in the visual domain (e.g. Busch et al., 2009), may not reveal pre-stimulus phase effects in audition. Our task required listeners to discriminate pitch differences, identify a pattern (e.g., High-Low-High), and assign labels to what they heard. This higher complexity task is likely to be more cortically intensive than detection of simple tones, which likely is based on processing of stimulus envelope in regions prior to cortex (Rees and Palmer, 2010; Scharf, 1998). One other recent work supports this position. Ten Oever and Sack (2015) found that identification of ambiguous syllables was influenced by the pre-stimulus phase in the high theta/low alpha range. In that study (Experiment 1), pre-stimulus phase predicted whether the ambiguous syllable was going to be perceived as a/da/or a/ga/. No background or entraining sounds were employed, yet pre-stimulus phase effects were seen. This may be because speech is also a complex stimulus that receives extensive cortical

processing (Hickok and Poeppel, 2007; Wisniewski et al., 2017). The observance of pre-stimulus phase effects on detection may require either entrainment, or stimulus induced increases in oscillatory power (e.g., with detection of gaps in ongoing stimulation, or detection of sounds in noise).

Several theories posit that the natural rhythms associated with speech features at different levels (i.e. phonemic attributes, syllabic rate, lexical and phrasal units) are fundamental for organizing incoming verbal information into the temporal units (Giraud and Poeppel, 2012; Luo and Poeppel, 2007). These theories have supported the idea that pre-stimulus oscillations only matter when the auditory system is forced into an entrained state or a state of enhanced oscillatory power (e.g., VanRullen, 2016b). In two earlier studies using background stimulation in their methods, pre-stimulus phase also appeared to modulate performance for lexical decision (Strauß et al., 2015) and consecutive tone comparison on dimensions of frequency and amplitude (Kayser et al., 2016). However, the current results reframe this earlier work and suggest that finding pre-stimulus phase effects in such studies may result from task complexity. Future work should aim to explore further how task-related attributes affect the predictive capacity of pre-stimulus EEG.

Another intriguing feature of the current data, which is concurrent with earlier work (e.g., Busch et al., 2009; Kayser et al., 2016; Strauß et al., 2015), is that effects were strongest at frontal electrodes. Kayser et al. (2016) used two auditory discrimination tasks in an attempt to dissociate oscillatory state influences on earlier sensory processes from those on higher-level decision processes. They also compared activity in both auditory cortical networks and frontoparietal areas across the two task conditions. In auditory networks, phase did not influence decision-making, but power affected encoding of sensory information. Over frontal and parietal regions, theta and alpha phase appeared to influence decision-making, but was not involved in the accumulation of sensory evidence. The study suggests that there are two consistent mechanisms by which pre-stimulus activity affects perception, and the time scales depend on the specific brain regions engaged by the respective task. The effects we observed were distributed frontally. It is possible that our results, and those of other researchers seeing similar frontal distributions, are related to effects of pre-stimulus phase on decision processes rather than sensory-based processes.

The absence of any effects for pre-stimulus power is consistent with recent explorations into the role of alpha oscillations more generally. Alpha band activity has been suggested to have a negative correlation with overall baseline activity; that is, reduced alpha power is associated with global baseline excitability, rather than affecting signal sensitivity (Iemi et al., 2017). In such a scenario, alpha power influences detection criterion, but may have no effect on discrimination task outcomes. Our task relied on pitch discrimination, rather than detection. Also, decision confidence appears to correlate similarly with alpha power, for both detection and discrimination (Samaha et al., 2017; Wöstmann et al., 2019). We did not obtain subject confidence ratings in the current study, but this may be a useful addition in further studies (cf. Zakrzewski et al., 2019).

4.2. Considerations

We did discover some stimulus-related behavioral effects in the current paradigm. Participants performed variably depending upon the particular pattern that was presented and the frequency range of stimuli. Frequency range and pattern were selected randomly on each trial, and a participant had no way of knowing before presentation what these selections were. These behavioral effects likely only serve to obscure a relationship between pre-stimulus EEG and pattern identification accuracy. Additionally, a supplementary analysis (see Fig. S2) yielded no systematic relationship between pattern type with binned phase (e.g., if most high-low-high trials fell near the optimal phase bin by chance), making it unlikely that observed effects were due to the differences among pattern types. We expect that if we were able to correct for these

differences in stimuli, the overall phase opposition effect would quite possibly be stronger than the effect observed in the current study, not weaker. It is possible that these stimulus differences could account for the lack of significant relationships between pre-stimulus power and accuracy. There are many studies that demonstrate effects of pre-stimulus power (Bernasconi et al., 2011; Ergenoglu et al., 2004; Hermann et al., 2016; Kayser et al., 2016; Leske et al., 2015; Limbach and Corballis, 2016; Samaha et al., 2017; Strauß et al., 2015), and we cannot refute that pre-stimulus power relates to the accuracy of perceptual decisions.

Because of the short jitter in the inter-stimulus interval in the current study (see Methods), we cannot rule out a role of entrainment underlying the phase effects seen here. Our study differs from the previous work using entrainment, in that we did not use stimuli intended to induce entrainment specifically in the frequency ranges we were investigating. If there was entrainment to the inter-trial interval, this would occur in a lower frequency band than that observed. However, the stimuli we employed were inherently rhythmic tone triplets. Participants could have reset the phase of alpha oscillations based on a rough global rhythm (e.g., ~ 0.25 Hz with some noise from variable response times) such that alpha would align to as much relevant information in the stimulus as possible. Note, however, that this reset of alpha would be more likely an experience-based reset, not stimulus driven. This is because there was no present rhythmic stimulation in the alpha range in the pre-stimulus interval where effects manifested. Nevertheless, we cannot unequivocally rule out that some sophisticated rhythmic processing mode was at play (Schroeder and Lakatos, 2009). It would be interesting to examine the possibility of such a learned entrainment of alpha phase to lower frequency delta rhythms.

4.3. Future directions

The findings reported here, and other related work in the literature, have important ramifications for work in applied research domains. For instance, aircraft operators often have many signals to attend to, both visual and auditory. While much work has been done exploring the perceptual and cognitive effects of longer-term brain states such as drowsiness or acute stress (Thomas et al., 2000; Hermans et al., 2011; Yuen et al., 2009; Arnsten, 2009), understanding the influences of short-term shifts in brain state may allow for optimizing the conditions under which an operator can detect, identify, and understand crucial signals. There are many cases in which one might hope to use pre-stimulus EEG information to augment performance (e.g., identification of cockpit warning sounds; Nees and Walker, 2011). Being able to present signals in alignment with these short-term states may be one approach for achieving such optimization; inducing oscillatory entrainment in the operator herself may be another. With advances in real-time EEG data analysis (Lotte et al., 2018) and interventions with brain stimulation (Thut et al., 2012; Zoefel et al., 2018), it may in the future be possible to use pre-stimulus measures as gauges of ongoing brain state in real time. This could be useful in human-system interactions in which an operator is performing a monitoring function that does not require a behavioral response. Pre-stimulus measures could provide an index of performance when overt action is absent.

This work directs us towards a deeper investigation of pre-stimulus phase effects in audition. Though it for the first time demonstrates a relationship between pre-stimulus phase and accuracy in an auditory perceptual task without background or masking sounds, there are a number of unanswered questions for future research. A logical next step is to test the impact of task complexity by varying task demands within an experiment. One way this could be done is by presenting listeners with identical sounds between conditions, but have different degrees of necessary cortical involvement. For instance, in one condition listeners might have to decide on the lateralization of a sound source, but in the other make a decision about whether or not that sound was something they heard previously. It will also be useful in future studies to manipulate the presence of background sounds. This approach would allow a

more direct assessment of the impacts of background noise on the capability of pre-stimulus EEG to predict perceptual accuracy.

5. Conclusion

The present work supports and extends the growing understanding that ongoing brain-states significantly influence how we perceive and respond to incoming stimuli. We found strong evidence for phase-based prediction of task performance in the auditory domain, in the absence of background sound. Importantly, these predictions appear to rely on a relatively high level of task complexity; how the level of complexity alters the predictive ability more specifically is a question for future work. Higher order entrainment processes (e.g., resetting of alpha phase based on lower-frequency entrainment) also deserve further exploration.

Declarations of interest

None.

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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.2019.05.054>.

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