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Word repetition priming induced oscillations in auditory cortex: a magnetoencephalography study

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Abstract

Magnetoencephalography was used in a passive repetition priming paradigm. Words in two frequency bins (high/low) were presented to subjects auditorily. Subjects' brain responses to these stimuli were analyzed using synthetic aperture magnetometry. The main finding is that single word repetition of low frequency word pairs significantly attenuated the post-second word event related desynchronization in the theta-alpha (5–15Hz) bands, 200–600ms post second word stimulus onset. Peak significance between repeated high and low frequency words was evident at ~365–465ms post target onset. This finding has implications for (i) the role of theta-alpha ERD in lexical representation and access; (ii) the study of repetition suppression in the spectral-temporal domain; and (iii) the connection of neuronal repetition suppression with behavioral effects of repetition priming.

Keywords

MEG; SAM; event related desynchronization (ERD); repetition priming; auditory; theta-band; alpha-band; speech

Introduction

This study uses magnetoencephalography (MEG) to examine the brain's response to spoken words presented in a passive repetition priming paradigm. The primary goal is to use the neural response suppression associated with repetition—in this case, of spoken words—as a tool to probe the spectral-temporal characteristics of language processing in the brain.

The picture of language emerging from recent spectral-temporal studies of language reveals distinct stages of representation and computation across a number of distinct time-frequency intervals [1–4]. Among these, it appears that the neural representation and access of words is connected with theta-alpha event related desynchronization (ERD), as well as with gamma-band event related synchronization (ERS) [4,5]. In this study, we analyze the brain's response to repeated and non-repeated auditory presented words using synthetic aperture magnetometry (SAM), a beamforming approach to magnetic source imaging that has been successfully applied to spatiotemporal characterization of cortical oscillations without the need for time-locked averaging of the type that is performed in more tightly stimulus locked responses [6].

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One of the goals of this study is to provide a basic spectral-temporal picture of the repetition priming effect. In addition, the study is designed to identify the effects of priming in two different types of words. An important finding in the behavioral literature is that low-frequency words benefit from repetition more than high-frequency words, where the increased benefit is understood as increased priming (i.e., a greater reduction in reaction time); this is the *Frequency Attenuation Effect* [7,8]. Based on this, the words employed in the study were divided into high and low lexical frequency categories.

Our study employs a passive repetition priming paradigm, and places the emphasis on the neurobiological side of priming: in particular, on the phenomenon of *response suppression*. Suppressed responses associated with repetition have been reported in a number of different imaging techniques (for reviews see [9,10]), and may in fact be affected by whether or not subjects perform active tasks [11]. Concentrating on EEG/MEG, the repetition priming has been studied along two dimensions: in the temporal domain, with respect to evoked responses (the N400 in ERP, e.g. [12]; in MEG, [13–15]); and in the spectral-temporal domain, where suppressed activity in induced MEG has been found with repetition of words [16,17].

Based on earlier findings showing theta-alpha ERD to be sensitive to lexicality [3,4], we hypothesized that repetition suppression with word stimuli would be manifested in this spectral range.

Methods

Eighteen healthy adult human subjects (MEAN $\pm$ SD age 32 ± 9 yrs, 8 males; self-reported right-handed) volunteered for the experimental procedure after giving written informed consent. The study was approved by the Institutional Review Board of The Children's Hospital of Philadelphia, Pennsylvania USA.

The stimulus material were identical to stimuli in [4], namely words ranging from 397–623 ms in duration read by a single native English female speaker, and presented binaurally at 45dB above individual SL. For each frequency bin (high = 60, low = 60), words were randomly paired (ISI=500ms) into two repetition conditions: identical (same word) and non-identical (different word). Each subject encountered a given word four times throughout data acquisition, in order to minimize semantic relatedness. Subjects watched a self-selected silent movie to ensure constant alertness during the passive paradigm. Anatomic, 1 mm isotropic resolution T1-weighted structural MR images (MP-RAGE) were obtained for each subject using a 3.0 T Magnetom VerioTM system (Siemens, Erlangen, Germany).

Auditory cortex source localization was based on single equivalent current dipole modeling of word onset evoked (M100) response. Raw MEG data pre-processing, and bilateral auditory source modeling, and ERD/ERS analysis were performed according to procedures described in [4]. In each subject, dipole locations were used as virtual sensors for the SAM linearly constrained minimum variance beamformer. Differential ERD was computed using SAM applied to the raw MEG trial data band-passed between 1.5–80 Hz (3.2s epochs, 0.6s pre-stimulus). Extending the epoch ensured the necessary length of baseline used to compute the signal covariance for each stimulus type at the virtual sensors. To visualize the activation induced by stimuli, time-frequency representation (TFR) plots (spectrograms) were computed as described in [4].

The time-course of auditory oscillations in the TFR were characterized by sample-wise parametric testing in order to determine effects of repetition (identical v. non-identical) and word-frequency (high vs. low) on induced activation. Post-stimulus spectrotemporal blocks of interest were identified by paired t-test (two-tailed). Based on visual inspection of the

distribution of significant spectrotemporal blocks, and on previous results reported in [4], we computed the mean power in the theta-alpha range. Power modulation was evaluated by repeated measures ANOVA with factors hemisphere (left, right), repetition (identical, non-identical), frequency (high, low), applied to power measurements following each stimulus (prime, target) for each subject. All reported significance levels for post-hoc tests were corrected for multiple comparisons using the Bonferroni adjustment.

Results

Figure 1a,b show auditory evoked neuromagnetic fields for the repetition priming paradigm, and M100 equivalent current dipole source localizations for a representative individual participant. Peak dipole field strengths of stimuli onset responses showed a remarkable habituation effect between first and second word presentation. Of the 18 subjects, 13 had bilateral dipole fits accounting for 80–90% of variance in the fit interval. In 5 subjects, single equivalent dipole fits were not possible for both hemispheres due to weak and/or noisy responses, thus they were not considered in the analysis of word position effect on dipole field strengths. Word position affected peak onset responses in the signal filtered between 1–40 Hz ($F_{(1,12)}=31.718, p<0.001, \eta^2=.73$) such that responses to the second word ($14.64\pm1.79\text{nAm}$) were significantly attenuated as compared to those following the first word ($22.49\pm2.55\text{nAm}$). Figure 1c shows the grand average—collapsed across subjects and hemispheres—time frequency representation (TFR) plots of ERD/ERS in the two repetition conditions (identical/non-identical) for each word frequency bin (high frequency words/low frequency words). Generally, oscillatory activity was characterized by a dynamic pattern of ERS and ERD. The initial response was an evoked low frequency ERS at approximately 100 ms post-stimulus onset, lasting approximately up to 200 ms following primes. Although dipole model peaks showed a habituation effect due to rapid stimulus repetition, the mean 1–40 Hz power in the interval of the ERS was not significantly affected by other factors ($p>.05$).

The evoked ERS was followed by prolonged differential ERD in the upper-theta and alpha ranges. The onset of this low frequency ERD was approximately 200 ms following stimuli onsets; it lasted throughout the duration of the stimulus, with peak ERD approximately 400 ms post-stimuli onsets. The TFRs indicated differential ERD that was modulated by word repetition and frequency (fig. 1c). Sample wise interrogation of the ERD in the TFRs indicated that power modulation occurred in the theta-alpha frequency range between 5–15 Hz. The time course of this 5–15 Hz power modulation showed a maximal difference between repetition conditions at approximately 415 ms following target onset. As such, separate repeated measures ANOVA of 5–15 Hz power were carried out in the interval 365–465 post stimuli—prime and targets—onsets. Critically, 5–15 Hz ERD power modulation in the interval 365–465 post prime (first word) onset was unaffected by factors repetition and frequency, $p>.05$.

Results from the analysis of target (second word) induced 5–15 Hz ERD in the interval 365–465 post stimulus onset revealed a marked effect of word frequency ($F_{(1,17)} = 9.965, p<.01; \eta^2=.37$). Post-hoc comparisons of cell means indicated a difference between high-frequency ($-11.40\pm1.30\text{nAm}$), as compared to low-frequency ($-9.41\pm.97\text{nAm}$) words, $p<.05$. Furthermore, 5–15 Hz power following targets was significantly affected by the factor repetition ($F_{(1,17)} = 4.911, p<.05; \eta^2=.22$). Post-hoc comparisons showed repetition suppression, where repetition ($-9.44\pm1.07\text{nAm}$) resulted in an attenuation of the auditory ERD, as compared to non-identical word pairings ($-11.36\pm1.29\text{nAm}$), $p<.05$. We show the grand averaged—collapsed across hemispheres and subjects—time course of 5–15 Hz power for each frequency bin in the two repetition conditions in figure 1d. In the figure a clear difference is discerned from the time course of low and high frequency words between

the two repetition conditions. Following targets, the ERD in the identical repetition condition for low frequency words was markedly attenuated relative to low frequency words when not repeated. Therefore, we carried out sample wise paired t-tests (uncorrected) on the waveforms for low and high frequency targets in both the repetition conditions. In figure 1d right panel, we highlighted in grey the region where low frequency targets resulted in significantly ($p < .001$) attenuated ERD in the identical as compared to the non-identical condition. This difference was absent in the high-frequency waveforms. The significant difference in ERD attenuation for low frequency words during identical repetition began at 355 ms, lasting approximately 70 ms following target stimulus onset.

Discussion

The main result of this study is the finding that theta-alpha band ERD following the target word in a repetition priming experiment is sensitive to word frequency. While significant ERD is noted after the first (prime) word, as previously reported in single word studies [4], the magnitude of this ERD following the second (target) word is sensitive to repetition effects and to word frequency in the following way. Target word ERD is not significantly diminished in non-identical word pairs, nor in paired (repeated) high frequency words. It is, however, significantly diminished in the repeated word condition for low frequency words. This ERD modulation is statistically significant for approximately 70ms, between 355 and 425ms post target word onset. This finding appears to be bilateral, appearing in both left and right STG responses.

A very slight and non-significant trend towards a brief period of differential ERD modulation (reduced ERD in repeated, paired, words) appears to be evident in the high frequency words too, suggesting ERD suppression may be an indicator of repetition priming, and that the magnitude of such ERD suppression may be an index of word frequency.

The finding of theta-alpha band (5–15Hz) suppression during repeated word trials is in agreement with activity attenuation results in the fMRI literature [10,20]. However, direct comparison of our results to electrophysiological studies is problematic as these studies were carried out in the visual domain and/or multi-modal priming across visual and auditory domains focusing on evoked responses, which are time and phase locked to stimulus onset [21–24].

Taken together, the findings of this paper yield two primary results for further investigation. First, the primary findings center on the role of ERD following the presentation of words, and show that this activity is differentially affected by words of different types. This finding provides further evidence for the idea that theta-alpha ERD plays an important role in lexical representation and access. Second, our findings show theta-alpha ERD to be affected directly by repetition, further (i) strengthening the case for an important role of ERD in lexical processing, and (ii) providing evidence about the nature of spectro-temporal repetition suppression. Moreover, the fact that repetition suppression is driven primarily by the low-frequency words resonates in suggestive ways with the behavior literature, and with the Frequency Attenuation Effect (the finding that facilitation is enhanced with low frequency words) in particular. In sum, while our findings in this domain do not allow for the formulation of specific hypotheses about the precise role of theta-alpha ERD, they show this activation to be sensitive to psycholinguistically significant properties of words in a way that provides a foundation for further study of linguistic computations in the brain.

Conclusion

The present findings show that theta-alpha ERD originating in auditory cortex does indeed show suppression in repeated versus non-repeated words, and that this suppression is differentially affected by word frequency. Specifically 5–15Hz ERD elicited in auditory cortex approximately 200–600ms following hearing a word is significantly attenuated in the context of priming by an identical word, when that word is of lower lexical frequency.

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Figure 1.

(A) Word average evoked response data. Cursors indicate maximal dipolar activity elicited by word onsets. (B) auditory source localization results in a typical individual subject. (C) Time-frequency representation (TFR) plots for increases (yellow/red) and decreases (blue) in auditory cortical source power following high and low lexical frequency words for identical and non-identical repetition conditions. The stimulus data for were averaged over all trials, hemispheres, and subjects ($n=18$) in units of percent change with respect to a 200 ms baseline. (D) Time-course of grand-average mean 5–15 Hz activity defined by the spectral-temporal region of interest based on sample-wise t-tests of conditional TFRs. Activity is plotted throughout paired-word trials, and the shaded area (right panel) indicates interval where mean source power significantly differed for low lexical frequency target stimuli across repetition conditions. $**p<.001$ (uncorrected).