

A right-ear bias of auditory selective attention is evident in alpha oscillations

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Abstract

Auditory selective attention makes it possible to pick out one speech stream that is embedded in a multispeaker environment. We adapted a cued dichotic listening task to examine suppression of a speech stream lateralized to the nonattended ear, and to evaluate the effects of attention on the right ear's well-known advantage in the perception of linguistic stimuli. After being cued to attend to input from either their left or right ear, participants heard two different four-word streams presented simultaneously to the separate ears. Following each dichotic presentation, participants judged whether a spoken probe word had been in the attended ear's stream. We used EEG signals to track participants' spatial lateralization of auditory attention, which is marked by interhemispheric differences in EEG alpha (8–14 Hz) power. A right-ear advantage (REA) was evident in faster response times and greater sensitivity in distinguishing attended from unattended words. Consistent with the REA, we found strongest parietal and right frontotemporal alpha modulation during the attend-right condition. These findings provide evidence for a link between selective attention and the REA during directed dichotic listening.

Descriptors: Attention, Auditory processes, Alpha rhythm, EEG

The “cocktail party problem” refers to the perceptual challenge of selectively listening to a single speaker amid competing speakers (Cherry, 1953). In a laboratory version of this real-world perceptual challenge, the dichotic listening task presents different streams of speech to the right and left ears simultaneously. Results from this task have illuminated how the brain resolves the cocktail party problem. For example, when listeners to dichotic speech are instructed to freely report when they hear a target in either ear, a right-ear advantage (REA) is observed. Kimura (1961) associated the REA with the left hemisphere's usual specialization for language processing. She described the REA as a consequence of structural asymmetries in the brain, including faster conduction along the contralateral pathways (Kimura, 1967). Although Kimura's structural model continues to influence many investigations of speech processing, it fails to account for some more recent observations with the REA (Hiscock & Kinsbourne, 2011). For example, a purely structural account of the REA does not explain why cued or directed dichotic listening (DDL) to the left ear can overcome the REA, or why attention directed to the right ear can amplify the

REA (Hugdahl et al., 2009). Despite the social importance of being able to pick out a single speaker from a crowded acoustic environment and the neurological significance of auditory asymmetry, our understanding of the mechanisms of the REA remain incomplete. In particular, does the REA reflect a hard-wired, perceptual asymmetry, or does it include some flexible rightward attentional bias for verbal processing?

The present study will use EEG alpha (8–14 Hz) activity as a marker of selective attention. Auditory selectivity during DDL is believed to include enhancement of the attended stream and suppression of the unattended stream (Chait, de Cheveigné, Poeppel, & Simon, 2010; Choi, Rajaram, Varghese, & Shinn-Cunningham, 2013; Golumbic et al., 2013). Cortical oscillations within the alpha band are a key marker of selective attention thought to reflect suppression of task-irrelevant information in several sensory modalities (Payne & Sekuler, 2014). Although the majority of evidence regarding the alpha band comes from the visual and somatosensory systems, there is a suggestion that alpha rhythms signify an inhibitory process in auditory attention as well (Banerjee, Snyder, Molholm, & Foxe, 2011; Dubé, Payne, Sekuler, & Rotello, 2013). The difference in alpha power across hemispheres indicates the lateralization of auditory attention (Ahveninen, Huang, Belliveau, Chang, & Hämmäläinen, 2013; Frey et al., 2014; Kerlin, Shahin, & Miller, 2010). The relative increase in alpha power contralateral to unattended stimuli supports the interpretation that alpha activity represents reduced processing. Moreover, alpha power lateralization predicts the selective enhancement of the attended auditory stimuli (Kerlin et al., 2010). Importantly, no link between alpha oscillations during DDL and the REA has been previously established.

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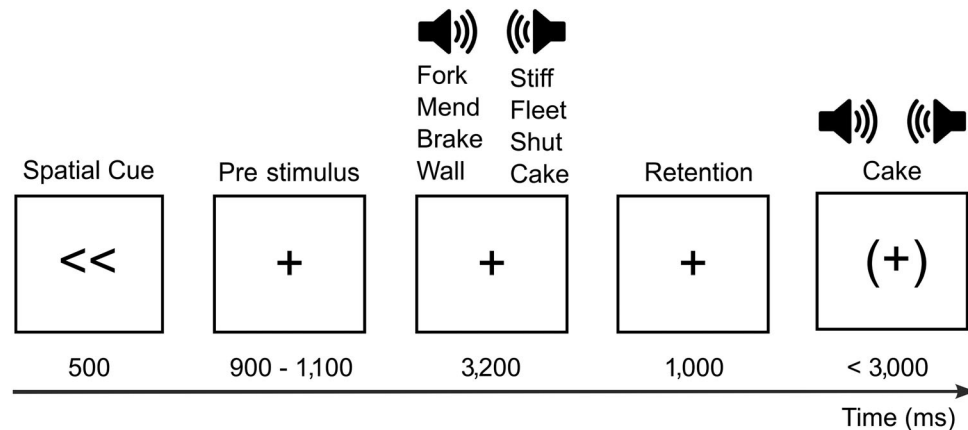


Figure 1. Schematic diagram illustrating a directed dichotic listening trial's event structure. Each trial began with a fixation cross that oriented the participant to the region of the computer display at which the trial's cues would be centered. An arrow cued the subject to attend to either their right (>) or left (<) ear. Then, two simultaneous streams of four spoken words were presented, one stream to each ear. After a brief retention interval, a probe word was presented binaurally. Participants reported via keyboard key press whether or not the probe word had been a member of the to-be-attended word stream.

In order to assess the effects of directed attention on the ability to distinguish between the attended and unattended stream, we extended the basic DDL task (Broadbent, 1952; Cherry, 1953; Treisman, 1960) to include a trial-by-trial test of short-term recognition, and a delayed recognition test following the completion of all DDL trials. If the unattended stream were genuinely suppressed during dichotic listening, words in that unattended stream would be less memorable than words in the attended stream. The REA would be evident in greater accuracy during dichotic listening and faster reaction times for words heard in the right ear when attending to the right. Right-ear biased auditory attention would be evident in asymmetrical modulation of alpha power when attending to the right versus left. We propose that right-ear biased modulation of alpha power during DDL will demonstrate that selectivity is the connection between attention and the REA.

Method

Participants

Sixteen adults gave written informed consent and were paid for participation in the experiment. Of these, two participants' data were excluded from our analysis because of excessive EEG artifacts (epoch rejection rate > 50%). The age range of the remaining 14 participants was from 18–22 years (mean = 20, $SD = 1.20$) and eight were female. All were right-handed as determined by the Edinburgh Handedness Inventory (Oldfield, 1971), and had normal or corrected-to-normal visual acuity as determined by a logarithm of the minimum angle of resolution chart (ETDRS 2000 Series 2, www.good-lite.com). All participants met a criterion of clinically normal hearing defined as a pure tone threshold average across 500, 1000, and 2000 Hz of less than 25 dB HL (Hall & Mueller, 1997). There was no significant difference in acuity between the two ears (left ear mean = 6.77 dB HL, $SD = 5.18$; right ear mean = 7.5 dB HL, $SD = 4.67$; $F < 1$, *n.s.*). All participants were native English speakers. Participants denied any psychological or neurological disorders.

Stimuli and Apparatus

A total of 689 monosyllabic words spoken by a male native speaker of American English were recorded using an Audio Technica

AT2045 microphone and SoundEdit software (Macromedia, Inc., San Francisco, CA). Recordings were digitized using a Presonus Audiobox USB audio interface at a sampling rate of 44.1 kHz. A cosine-squared amplitude ramp of 5 ms rise/fall time was applied to the beginning and end of each word to avoid popping noise from sudden onsets or offsets. Words were divided into three groups that were balanced for Kucera-Francis word frequency (Kucera & Francis, 1967) and assigned to one of the three experimental conditions (attended, unattended, new). In each trial of the DDL task, two streams of four words were presented simultaneously, one stream to each ear, through Etymotic Research ER1 insert earphones. Durations for the spoken words were between 422–758 ms (mean = 617 ms, $SD = 72$ ms). Stimuli were concatenated into two streams of four words (i.e., left and right), and synchronized so that each word pair began simultaneously at 0, 800, 1,600 and 2,400 ms.

Procedure

Each participant completed one experimental session that included the DDL phase followed by a delayed recognition phase.

Directed dichotic listening. Figure 1 illustrates the DDL procedure. Each participant completed 210 trials. The first 18 trials were practice trials that were not included in further analysis, resulting in 192 final trials. For each trial, a visually displayed arrow presented for 500 ms directed participants to attend to either their right or left ear. Participants were cued to attend to the left ear on half of the trials; on the remaining trials, they were cued to attend to the right ear. The order of cues was randomly intermixed. Then, 900–1,100 ms (mean = 1,000) later, simultaneous streams of four words were presented to the right and left ears through insert earphones. The duration of each four-word stream was 3,200 ms. In order to populate the two simultaneous, four-word streams, the 560 words were presented three times each. Half of these words were only presented in attended streams, and the other half were presented only in unattended streams. The words were organized across the three repetitions such that any given pair of words across a trial's attended and unattended streams did not repeat. The order of attended and unattended word-pair presentations was randomly shuffled for each participant, with the constraint that all word pairs

had to be presented in each condition before a given word could be repeated.

Following a brief, 1,000-ms retention period, parentheses were displayed around the fixation cross, and a single probe word was presented binaurally. For the 96 attend-left trials and 96 attend-right trials, respectively: half of the probes ($N = 48$) were a target word from the attended stream (target), 24 were from the unattended stream (unattended probe), and 24 were new words (new probe) that were otherwise not presented during DDL. The order of target, unattended probe, and new probe trials was randomized. If the probe was from the attended or an unattended stream, it was equally likely to have appeared at each of the four positions in that trial's word set.

Participants rested two fingers from their right hand on a computer keyboard and responded via a key press whether the probe was or was not a member of the current trial's attended stream. Participants had up to 3,000 ms to make a response and were instructed to respond as quickly and as accurately as possible. During the 18 practice trials, feedback was provided after each trial in the form of a green fixation cross for correct responses (attended hit, unattended correct rejection, or new correct rejection) or red for incorrect responses (attended miss, unattended false alarm, or new false alarm). In each case, the color was displayed for a 600-ms feedback interval. No feedback was given during the final 192 experimental trials retained for analysis.

Delayed recognition. Delayed recognition instructions were given after DDL trials and after the EEG cap had been removed. The time between the end of DDL trials and the start of delayed recognition ranged from 3 to 7 min (mean = 5). Participants completed the delayed recognition phase in less than 10 min. During delayed recognition, words were presented binaurally through the insert earphones. The recognition test was comprised of 120 "old" words randomly drawn from the DDL trials and 72 "new" words that were not previously heard in the experiment, presented in random order. To distinguish the effects of attention during dichotic listening from the effects of attention to a single probe word, whether a word was used as a probe in the earlier DDL task was systematically varied. There were 24 old words from each of the following five categories: words from the attended stream that had not served as probe words, words from the attended stream that had served as probe words, words from the unattended stream that had not served as probe words, words from the unattended stream that had served as probe words, and words that had been presented as new probes. Participants rested two fingers from their right hand on a computer keyboard. Following each word, the question, "Old or new?" was displayed on the computer screen. Participants were instructed to respond "Old" to any word that was presented in the DDL phase of the experiment, regardless of whether it was attended or not. They had up to 3,000 ms to make a response and were instructed to respond as quickly and as accurately as possible. The attended words and unattended words were counterbalanced for whether they had been presented to the left or right ear, and the position they had held within the stream.

Behavioral Analysis

Directed dichotic listening. For the DDL task, participants' sensitivity to attended words was measured using d' (Green & Swets, 1966), which was calculated as the difference between z -transformed hit rates to probes of attended items (target hit) and z -transformed false alarm rates to probes that were new (FA new) and

from the unattended stream (FA unattended). This yielded two d' estimates: d' new—an index of participants' ability to distinguish attended words from new items, and d' unattended—an index of the extent to which participants distinguished between words that were in the attended and unattended streams. Both d' estimates were calculated using the same hit rate, but different FA rates (FA new, FA unattended). To avoid undefined values of d' when hit or false alarm rates equaled 1.00 or 0.00, we applied the log-linear rule recommended by Hautus (1995). Latencies to correct responses included attended hits, new correct rejections (CR new), and unattended correct rejections (CR unattended). To attenuate the undue influence of outliers on mean latencies, latencies outside 2.5 standard deviations of the mean were considered outliers and excluded from latency analysis for each participant and for each condition. A total of 80 trials were excluded from the latency analysis in accordance with this criterion (3% of trials). There were 41 trials excluded from the attend-right condition and 39 from the attend-left condition.

Delayed recognition. The delayed recognition task was meant to assess indirect effects of auditory attentional control processes on words during the attention task. Words that served as probes during the DDL task might be remembered better because of their binaural presentation and additional processing at the time of short-term recognition. In order to control for this potential concern, we limited our analysis only to words that were not probed during the DDL task. Two values of d' were calculated using hit rates to attended words, hit rates to unattended words, and FA rates to new words. Latencies to correct responses included attended hits and unattended hits. A total of seven attended hits and six unattended hits were excluded from the latency analysis (2% of trials) as described in the Directed Dichotic Listening section.

EEG Recording and Analysis

EEG signals were recorded from the scalp using a high-density, 129-electrode array (Electrical Geodesics Inc., Eugene, OR) and high-impedance amplifiers. All channels were adjusted for scalp impedance < 50 k Ω . Sensor signals were sampled at 250 Hz with a 0–125 Hz analogue band-pass filter, and stored for offline analysis. Bipolar periocular channels were recorded from above and below each eye and from a location near the outer canthus of each eye.

EEG signals were preprocessed using the EEGLAB toolbox (Delorme & Makeig, 2004) for MATLAB (The Mathworks, Inc., Natick, MA). The recorded signals were rereferenced to the grand-averaged voltage. A 0.5 Hz Butterworth high-pass filter and a 60 Hz Parks-McClellan notch filter were applied. Trial epochs were segmented from $-2,200$ to $+4,400$ ms surrounding the onset of the dichotic stimuli. An initial visual inspection was performed to remove epochs containing gross artifacts and to identify bad channels. Bad channels that exceeded more than 10% of trials were excluded from independent component analysis (ICA). The ICA was performed with EEGLAB's extended infomax ICA decomposition. Components clearly containing blinks, muscle artifacts, eye movements, electrical heartbeat, or singular artifacts were manually identified and subtracted from the data. Two bad channels in one participant's data and one bad channel in a second participant's data were then interpolated using EEGLAB's spherical spline interpolation. A final visual inspection was performed to reject any remaining epochs with artifacts.

Finally, incorrect trials were also excluded from analysis. The number of artifact-free, correct trials remaining totaled 995 trials in

the attend-left condition and 1,030 trials in the attend-right condition. All subsequent analyses and plotting were performed using the FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2010) for MATLAB.

Induced alpha power. Induced (nonphase-locked) time-frequency power during DDL was computed. Separately for every subject, electrode, and condition, the ERP was calculated, and this evoked (phase-locked) activity was subtracted from the EEG for each trial (Kalcher & Pfurtscheller, 1995). Following this single trial subtraction of the ERP, time-frequency representations were computed using Morlet wavelets with a width of four cycles per wavelet at center frequencies between 1 and 40 Hz, in 1 Hz steps.

Statistical analysis. For each participant, alpha amplitude (8–14 Hz) for attend-right and attend-left trials was averaged separately and then normalized by calculating $\frac{\text{attendRight} - \text{attendLeft}}{\text{attendRight} + \text{attendLeft}}$. Note that positive values will signify stronger alpha power in the attend-right condition, and negative values will signify stronger alpha power in the attend-left condition. To establish the effect of directional attention on alpha power, the normalized difference between attend-right and attend-left trials was compared to zero using a within-subject, nonparametric clustering approach (Maris & Oostenveld, 2007). For each electrode and time point between –900 and 3,200 ms, a dependent samples *t* value was calculated. All comparisons for which the *t* value exceeded the $p < .05$ significance level were clustered based on spatial adjacency. For each cluster, the *t* scores of its member electrodes and time points were summed, giving a cluster score that reflected both the extent of the cluster (in space and time) and the magnitude of the difference between the lateralization index and zero. A reference distribution of test statistics was generated by randomly permuting the data across the two conditions being compared (the normalized difference and zero), computing such scores for each resulting cluster, and taking the largest cluster score on each of 1,000 permutations. Where clusterwise *p* values are reported, they have been derived by comparing the empirically obtained cluster score to the permuted reference distribution. A cluster was deemed significant if less than 5% of the proportion of randomized values exceeded the observed test statistic.

Results

Behavior

Unless otherwise indicated, we only report effects significant at the $p < .05$ significance level that were not involved in a higher-order interaction. After an interaction was revealed to be significant, we used post hoc *F* tests that applied the Bonferroni correction for reduction of Type I error. Mauchly's test of sphericity and Levene's test for homogeneity of variance were also calculated. If the assumption of sphericity was violated, the Greenhouse-Geisser correction for mean squared error (*MSE*) and degrees of freedom was applied. If homogeneity of variance was violated, degrees of freedom were adjusted.

Directed dichotic listening. Participants' sensitivity to attended words was assessed with a 2 (Ear: left, right) \times 2 (*d'* Type: *d'* new, *d'* unattended) repeated measures analysis of variance (ANOVA). This analysis revealed significant main effects of ear, $F(1,13) = 9.59$, $MSE = 4.60$, $p < .01$, $\eta_p^2 = .43$, and *d'* type, $F(1,13) = 38.38$, $MSE = 9.70$, $p < .001$, $\eta_p^2 = .75$. The interaction of *d'* type and attended ear was not significant ($F < 1$). The results

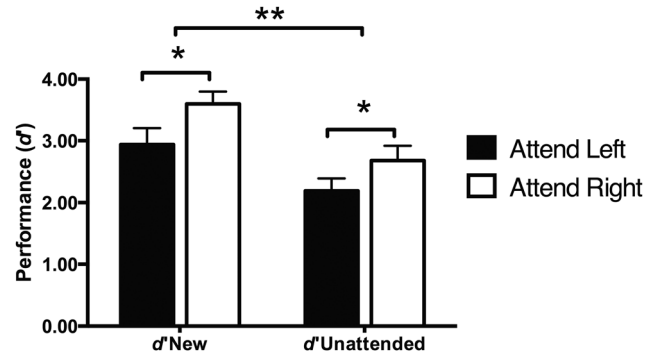


Figure 2. Performance in the directed dichotic listening task as measured using *d* prime (*d'*). Participants made more false alarms to unattended words than to new words, driving the difference between *d'* new and *d'* unattended. In addition, performance was worse when attending to the left ear. Error bars are \pm one within-subject standard errors of the mean. Significant differences $*p < .05$, $**p < .001$.

are displayed in Figure 2, which shows that participants' sensitivity was greater when attention was directed to the right ear rather than the left, thus replicating the REA. Also, *d'* new estimates were higher than *d'* unattended estimates, indicating that participants distinguished attended targets from unattended probe words less well than they distinguished attended targets from new probe words.

We also examined participants' latencies to correct responses on the DDL task. There were three types of correct responses in this task: target hits (target hit), correct rejections of new probes (CR new), and correct rejections of unattended probes (CR unattended). We submitted the latencies to these responses to a 2 (Ear: left, right) \times 3 (Response: target hit, CR new, CR unattended) repeated measures ANOVA, which revealed significant main effects of ear, $F(1,13) = 14.32$, $MSE = 0.14$, $p < .01$, $\eta_p^2 = .52$, and response, $F(1.7,26) = 20.33$, $MSE = 0.14$, $p < .001$, $\eta_p^2 = .61$. The interaction between ear and response was not statistically significant, $F(1.61,20.98) = 1.45$, $MSE = 0.01$, $p = .26$. Post hoc tests of the main effect of response revealed CR unattended responses to be significantly slower than target hit and CR new responses, which were not significantly different from each other. This pattern of results is depicted in Figure 3, which shows that participants made target hits and rejected new probes with similar latency, but were

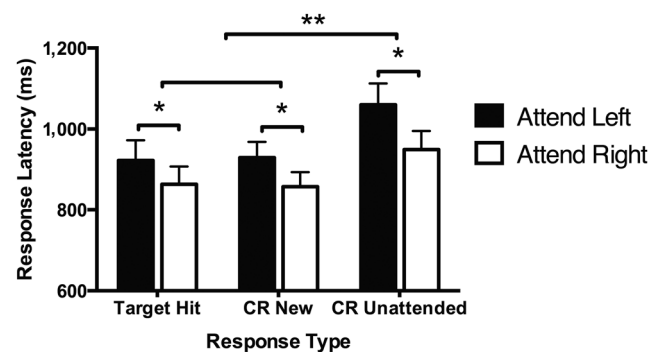


Figure 3. Time to correct responses in the directed dichotic listening task. Participants were slower on correct rejections of probe words presented in the unattended speech stream than correct rejections of new probes or hits on target probes. In addition, latencies to all types of correct responses were slowest when attending to the left ear. Error bars are \pm one within-subject standard errors of the mean. Significant differences $*p < .01$, $**p < .001$.

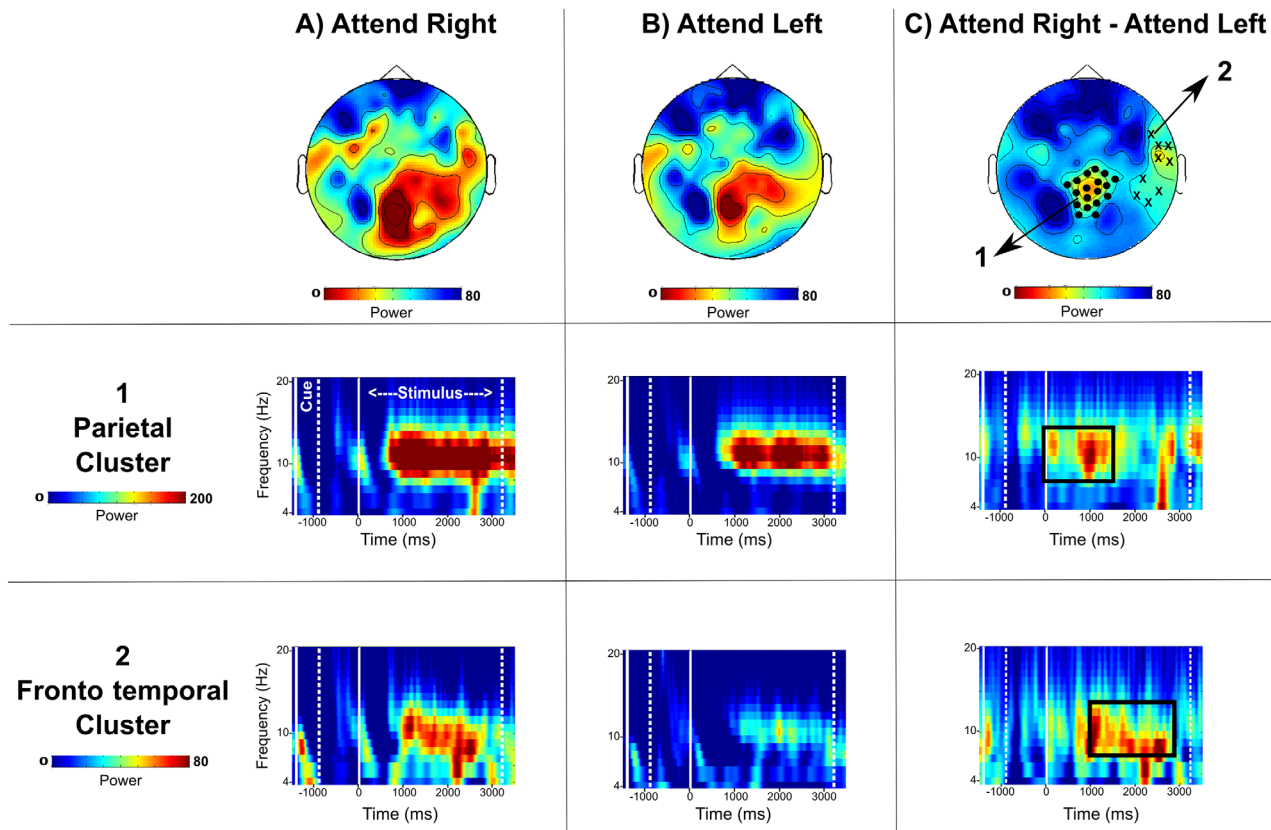


Figure 4. Induced alpha power modulation during dichotic listening. A: Attend-right condition. B: Attend-left condition. C: Attend-right minus attend-left. Top row: Grand-averaged, topographical display of alpha power (8–14 Hz) across the 3,200-ms duration of the dichotic speech streams relative to baseline. In column (C), sensor locations for Cluster 1 (os) and Cluster 2 (xs) have been superimposed on the attend-right minus attend-left topography. Bottom rows: Time-frequency representations averaged across the cluster of parietal electrodes (middle panel) and frontotemporal electrodes (bottom panel) relative to baseline. Stimulus onset at Time = 0 is marked by a solid white line. The dashed line at Time = 3,200 marks the stimulus offset. The black boxes on the difference time-frequency representations in column (C) depict the time intervals of maximum difference between attend-right and attend-left conditions.

considerably slower making correct rejections of unattended probes. As can also be seen in Figure 3, participants were faster in making correct responses when attending to the right side rather than the left side, confirming the presence of the REA.

Delayed recognition. Delayed recognition to words that were attended versus unattended was assessed by a repeated measures ANOVA (d' type: d' attended, d' unattended). The analysis revealed a significant main effect, $F(1,13) = 9.80$, $MSE = 0.85$, $p < .01$, $\eta_p^2 = .45$. A greater number of words that had been attended during the dichotic listening trials were recognized (d' attended $M = 0.43$, $SEM = 0.13$) than words that had been unattended (d' unattended $M = 0.07$, $SEM = 0.08$). It is worth noting that d' for unattended words did not differ from zero, $t(12) = 0.90$, $p = .39$, indicating that performance was at chance; however, d' for attended words was significantly greater than zero, $t(12) = 3.29$, $p < .01$. Calculation of a repeated measures ANOVA for response latencies (attended hit, unattended hit) did not reveal a significant effect of response ($F < 1$).

Alpha Power

To establish the effect of directional attention on alpha power, the normalized difference between attend-right and attend-left trials was compared to zero. Results of the cluster-based permutation test

revealed two clusters of electrodes for which alpha power was greater in attend-right trials than attend-left trials throughout the duration of the dichotic word streams (Figure 4). No clusters were identified in which electrodes' alpha power was greater in attend-left trials than in attend-right trials. The attend-right bias in alpha power can be seen in an 18-electrode cluster located over midline parietal cortex ($p < .01$) that showed maximum differentiation for the epoch from -0.068 ms to 1,472 ms poststimulus onset (average t score of cluster = 3.6). An additional nine-electrode cluster over right frontotemporal brain areas ($p < .05$) had maximal differentiation from 1,064 ms to 2,880 ms poststimulus onset (average t score of cluster = 2.7). Time-frequency transforms were averaged separately across the two electrode clusters, and a baseline period of -900 to 0 ms was subtracted in order to illustrate the alpha modulation across the duration of the dichotic word streams (Figure 4, bottom two rows).

Discussion

In the present study, we characterized the effect of directed dichotic listening on the ability to distinguish between attended and unattended words on short-term and delayed recognition tests. Using modulation of alpha oscillations as a marker of selective attention, we also investigated whether the right-ear advantage for speech processing includes a rightward attentional bias.

In the trial-by-trial test of short-term recognition, the effects of the unattended stream were evidenced by reduced sensitivity in distinguishing between attended and unattended words compared to distinguishing between attended and new words. This finding is consistent with evidence that unattended speech is represented in low-level auditory areas (Golombic et al., 2013). Early representation of information arriving in the unattended ear is also exhibited by faster response times to a target word in the attended ear if that word follows that same word presented to the unattended ear (Dupoux, Kouider, & Mehler, 2003), or if a target word follows a semantically related word presented to the unattended ear (Bentin, Kutas, & Hillyard, 1995). More directly, our finding of slowed reaction times for correct rejection of unattended words than for correct rejection of new words corroborates the notion of early representation. Despite indications of their intrusion into short-term memory, unattended words were less memorable than attended words during the delayed recognition test that followed the DDL trials. Together, these results support the suggestion of a progressive top-down bias toward the representation of attended stimuli and degradation of unattended stimuli across the hierarchy of auditory processing (Lakatos et al., 2013; Mesgarani & Chang, 2012).

Consistent with the REA, when attention was directed to our participant's right ear rather than the left, they were faster to make correct responses, and showed greater sensitivity in distinguishing attended from both unattended and new words. In addition, during directed attention to words heard in the right ear, participant's EEG exhibited greater alpha power over parietal and ipsilateral frontotemporal brain regions. Our findings of greater attend-right modulation of alpha activity during DDL and greater accuracy for words heard in the right ear support previous behavioral evidence that the REA and selective attention are intricately linked. For example, when participants are directed to attend to the right ear, accuracy scores near perfection and performance is even greater than during free-report dichotic listening to either ear. When participants attend to the left, they show significantly greater accuracy; however, accuracy for attend-left is still worse than for attend-right (Hiscock & Kinsbourne, 2011; Hugdahl et al., 2009). The REA observed during free-report dichotic listening has been attributed to structural asymmetries in the brain that include left hemisphere dominance for language processing (Kimura, 1961, 1967). Our study reveals that the benefits of directed dichotic listening to the right ear are marked by asymmetrical modulation of alpha oscillations.

Parietal Alpha and the REA

We found that parietal alpha power increased during DDL consistent with evidence that these rhythms reflect sensory selective attention (for review, Payne & Sekuler, 2014). fMRI studies have shown that nonvisuotopic regions in the lateral and anterior intraparietal sulcus are involved in auditory spatial attention (Kong et al., 2014; Wu, Weissman, Roberts, & Woldorff, 2007). Moreover, posterior alpha oscillations have been associated with auditory spatial attention when participants are presented with two simultaneous auditory streams (Ahveninen et al., 2013; Kerlin et al., 2010; Wöstmann, Herrmann, Maess, & Obleser, 2016). More specifically, the lateralization of parietal alpha oscillations has been shown to index the direction of attention; that is, alpha power increases in the hemisphere ipsilateral to the attended side and decreases contralateral to the unattended side.

Uniquely, when we directed attention to streams of words, the increase in alpha power was greater when attention was directed to the right ear. Despite employing a DDL task for linguistic stimuli,

Kerlin et al. (2010) found neither a behavioral REA nor a right-ear bias of parietal alpha oscillations. In their design, two sentences were each attended 480 times, minimizing unique speech processing on each trial. In our study, participants attended and identified 256 individual words, presented in four-word sets, thus maximizing unique speech processing per trial. This difference is important because the REA is associated with identification of speech features (Shankweiler & Studdert-Kennedy, 1967; Studdert-Kennedy & Shankweiler, 1970) and, more specifically, with identification of the leading syllable (Morais & Bertelson, 1975). Given the significance of the leading syllable in speech identification, it could be surmised that early deployment of spatial attention is an important factor of directed dichotic listening. Indeed, the maximal difference in parietal alpha power between our attend-right and attend-left conditions began at the onset of the presentation of dichotic streams. Although our results do not distinguish whether differential alpha power causes the REA or reflects an underlying mechanism of the REA, it does illustrate a bias in spatial attention when attending to words heard in the right ear.

Right Hemisphere Frontotemporal Alpha and the REA

The present finding of asymmetric increases in alpha oscillations over right frontotemporal brain regions is in agreement with modulation of alpha power described in recent studies of directed dichotic listening (Frey et al., 2014; Müller & Weisz, 2012). Using streams of tones, Müller and Weisz (2012) demonstrated a right hemispheric dominance of auditory attention-related magnetoencephalographic (MEG) alpha power that was localized to the auditory cortex. The dominance of the right auditory cortex for neural encoding of speech stimuli (Ding & Simon, 2012) is believed to reflect an asymmetry in auditory processing wherein the left auditory cortex is specialized for localizing sounds within the contralateral, right side of egocentric space, while the right auditory cortex is involved in localizing sounds across the whole space (Spierer, Bellmann-Thiran, Maeder, Murray, & Clarke, 2009; Zatorre & Penhune, 2001). Given the specialization of the right auditory cortex in processing information from both the left and right ears, greater modulation would seem necessary toward resolving the two competing pieces of information during dichotic listening.

In addition to this asymmetry in sound localization, the contralateral pathway to the auditory cortex has an anatomical and physiological advantage over the ipsilateral pathway (Hall & Goldstein, 1968; Rosenzweig, 1951). Together with evidence that during dichotic listening information from the ipsilateral ear is inhibited relative to information from the contralateral ear (Brancucci et al., 2004; Milner, Taylor, & Sperry, 1968), it may be that, during attention to the right ear, suppression of the right auditory cortex serves to reduce processing of input from the competing left ear. This interpretation would certainly be in line with the view that alpha oscillations represent the suppression of noise in speech during challenging listening situations (for review, Strauß, Wöstmann, & Obleser, 2014). Our results, however, do not indicate that rightward attention was related to preferentially improved suppression of the unattended stream. Instead, when attending toward the right, participants showed greater sensitivity in distinguishing between attended words and both unattended and new words, indicating a general improvement in selective listening.

Wöstmann and colleagues (2016) recently reported a correlation between the strength of hemispheric modulation of alpha power and the number of errors participants made in selecting the attended stimuli. In light of this recent discovery, we explored

potential relationships in our data. Each participant's alpha lateralization index was averaged for each cluster of sensors (parietal and right lateral) across the entire stimulus duration and also across the epoch of greatest differences between attend-left and attend-right conditions. Pearson correlations were calculated between these values and d' new, d' unattended, latency to target hits, CR new, CR unattended, and false alarm rates to unattended probe words. Each of these measures was calculated for attend-right, attend-left, and the average of attend-right and left conditions. These correlations did not reach significance, likely due to ceiling and floor effects on behavioral scores. For example, target hits for attend-left and attend-right conditions were extremely high (attend-left $M = .89$, attend-right $M = .91$), while false alarm rates were very low (FA new left $M = .09$, FA new right $M = .01$, FA unattended-left $M = .21$, FA unattended-right $M = .15$).

In the task used by Wöstmann and colleagues (2016), separate streams of four spoken digits were presented simultaneously to the two ears following a cue to attend toward one stream or the other. Participants then selected from a visual array the four numbers that had been members of the attended stream. Unlike our results, Wöstmann and colleagues (2016) did not report a REA despite also using DDL to speech-based information in combination with short-term recognition. A couple of differences could account for this discrepancy. First, it has been shown that digits can be recognized at a lower signal-to-noise ratio than for other types of words (McArdle, Wilson, & Burke, 2005) and also may be easier to rehearse than words (Cantor, Engle, & Hamilton, 1991). The relative ease of selectively attending and rehearsing digits may reduce the interaction between attention and the REA. Their results are similar to ours, however, in that participants made more errors by selecting numbers from the unattended stream than from numbers that had not been presented. It was the combination of these two types of errors that was predicted by the amplitude of the stimulus onset-modulated alpha lateralization. Thus, the fact remains that relative increases in auditory alpha power that occur in the hemisphere contralateral to the unattended stream of information during DDL have yet to be directly linked to increased suppression of the unattended stream of information.

It is important to recognize that the right lateral increases in alpha oscillations that we observed during DDL may originate

outside of the auditory cortex in nearby brain regions. During directed dichotic listening, MEG alpha has been localized to the right inferior parietal and right inferior frontal regions in addition to the auditory cortices (Wöstmann et al., 2016). The insula is also a neighboring area believed to play many roles in sensory processing, including the allocation of auditory attention (for review, Bamiou, Musiek, & Luxon, 2003). Of special interest to the current study is a case report of a female who suffered a stroke that damaged her right insula (Habib et al., 1995). Following the stroke, after her audiometric thresholds had returned to normal, she still showed almost complete left-ear extinction on a dichotic task. The insular cortex has also emerged as a candidate structure for mediating the processing of degraded speech (Erb, Henry, Eisner, & Obleser, 2013; Wilsch, Henry, Herrmann, Maess, & Obleser, 2014). Although the dichotic streams of words used in our study were not degraded, the overarching similarity can be described as an adverse listening condition. During adverse listening conditions, the insula has been observed to function both in processing the task-relevant auditory feature and in attenuating the task-irrelevant feature (Henry, Herrmann, & Obleser, 2013). Furthermore, MEG alpha activity was localized to the right insula during a task using speech in noise and interpreted to indicate the suppression of irrelevant information (Wilsch et al., 2014). This discovery of alpha activity generated from the insula supports the role of this structure in auditory selective attention as well as the possibility that the right frontotemporal alpha effects that we observed during DDL are functionally related to structures outside of the auditory cortex.

Conclusion

In summary, using a combination of DDL and short-term recognition, we have shown concurrent attention-modulated alpha power and the REA for speech stimuli. Our novel finding of a greater increase in parietal and frontotemporal alpha power when attention was directed to speech heard in the right ear indicates that the processes that underlie the REA include preferential modulation of selective attention. We suggest that this asymmetrical modulation of alpha activity can serve as a guide for understanding the connection between selective attention and the REA.

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