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Bilinguals at the "cocktail party": Dissociable neural activity in auditory–linguistic brain regions reveals neurobiological basis for nonnative listeners' speech-in-noise recognition deficits

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ABSTRACT

We examined a consistent deficit observed in bilinguals: poorer speech-in-noise (SIN) comprehension for their nonnative language. We recorded neuroelectric mismatch potentials in mono- and bi-lingual listeners in response to contrastive speech sounds in noise. Behaviorally, late bilinguals required ~10 dB more favorable signal-to-noise ratios to match monolinguals' SIN abilities. Source analysis of cortical activity demonstrated monotonic increase in response latency with noise in superior temporal gyrus (STG) for both groups, suggesting parallel degradation of speech representations in auditory cortex. Contrastively, we found differential speech encoding between groups within inferior frontal gyrus (IFG)–adjacent to Broca's area—where noise delays observed in nonnative listeners were offset in monolinguals. Notably, brain-behavior correspondences double dissociated between language groups: STG activation predicted bilinguals' SIN, whereas IFG activation predicted monolinguals' performance. We infer higher-order brain areas act compensatorily to enhance impoverished sensory representations but only when degraded speech recruits linguistic brain mechanisms downstream from initial auditory-sensory inputs.

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1. Introduction

Bilingualism is an intrinsic part of modern culture. It is believed that nearly half the world is bilingual (Grosjean, 2010) and that in the U.S. alone, more than 20% of the population speaks multiple languages (U.S. Census Bureau, 2010). Indeed, increased demand for a multi-lingual society has influenced recent educational practice and public policy (Wiese & Garcia, 2010). Consequently, there is substantial interest in understanding how language experiences sculpt brain function and potentially enhance perceptual-cognitive skills (Bialystok, Craik, & Luk, 2012; Costa & Sebastian-Galles, 2014; Ressel et al., 2012).

By virtue of interacting with multiple languages, non-native speakers experience an enriched auditory–linguistic environment atypical of their monolingual peers. The joint activation of two competing language systems (Kim, Relkin, Lee, & Hirsch, 1997) forces bilinguals to regulate, manipulate, and suppress multiple streams of lexical information (Bialystok, 2009; Bialystok et al.,

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Shorek, & Cohen-Mansfield, 2008). Indeed, early bilingualism is now linked to enriched perceptual abilities and protection against age-related decline in cognitive control. The human brain is a limited capacity system whose neural resources are allocated according to the functional demands of the environment (Marois & Ivanoff, 2005). Moreover, experience-

2012). As a consequence of managing two languages (Crinion et al., 2006), bilinguals develop more effective inhibitory control

than their monolingual peers (Bialystok et al., 2012; Costa &

Sebastian-Galles, 2014; Crinion et al., 2006; Krizman, Marian,

Shook, Skoe, & Kraus, 2012). While usually more pronounced in

late-onset bilinguals, the increased cognitive demands of bilingual-

ism, in turn, yield physical (Ressel et al., 2012) and functional

(Bialystok et al., 2012; Costa & Sebastian-Galles, 2014; Li, Legault,

& Litcofsky, 2014) changes in brain networks that confer advan-

tages in complex human behaviors including sustained attention,

conflict monitoring, and executive functions (Bialystok, 2009;

Bialystok et al., 2012; Krizman et al., 2012). Intriguingly, these

behavioral benefits garnered through lifelong, early multilingual

experience may act to boost "cognitive reserve" and ultimately

postpone or even protect against cognitive decline over the lifespan (Bialystok, Craik, & Freedman, 2007; Craik, Bialystok, &

Freedman, 2010; Gold, Johnson, & Powell, 2013; Kave, Eyal,







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dependent plasticity is an inherently competitive process and plastic changes that produce beneficial behavioral adaptations are equally accompanied by those which hinder behaviors (i.e., "maladaptive" or "negative plasticity") (Kolb & Gibb, 2014; Mahncke et al., 2006). Thus, while it is clear that speaking multiple languages yields neural reorganization that influences perceptualcognitive skills (Krizman et al., 2012; Ressel et al., 2012), bilinguals' gains in certain abilities may have detrimental consequences for other, equally important functions. Indeed, developmental studies reveal that bilinguals control a smaller vocabulary (Oller & Eilers, 2002) and show deficiencies in verbal fluency (Portocarrero, Burright, & Donovick, 2007) relative to their monolingual peers, providing evidence for neuroplastic tradeoffs. Here, we examined the neurobiological basis of another prominent and pervasive limitation of speaking multiple languages: bilinguals' poorer speech-in-noise (SIN) comprehension for their nonnative language (Hervais-Adelman, Pefkou, & Golestani, 2014; Rogers, Lister, Febo, Besing, & Abrams, 2006; Tabri, Smith, Chacra, & Pring, 2010; von Hapsburg, Champlin, & Shetty, 2004; Zhang, Stuart, & Swink, 2011). In the current study, we chose to examine late-onset bilinguals in order to maximize the possibility of identifying a neural correlate of nonnative listeners' SIN perception deficits. However, while speech in noise deficits are more prominent in late bilinguals, even relatively early bilinguals [i.e., second language (L2) onset prior to age 6] can show behavioral deficits in speech in noise listening (Rogers et al., 2006; Shepherd & Bent, 2014; Tabri et al., 2010).

Natural listening environments typically contain interferences (which can be both acoustic and linguistic in nature), making successful extraction of speech from noise a fundamental skill for effective communication. In this regard, understanding nonnative listeners' SIN recognition deficits is among the many broad and widespread interests to understand how human experiences influence auditory scene analysis and figure-ground perception (e.g., Alain, Zendel, Hutka, & Bidelman, 2014; Bidelman & Krishnan, 2010). Characterizing nonnative listeners' noise-exclusion deficits is particularly germane for understanding communication in modern classrooms, which are inherently noisy (Knecht, Nelson, Whitelaw, & Feth, 2002) and increasingly bilingual environments (Chin, Daysal, & Imberman, 2013). It also has important ramifications for establishing normative measures in nonnative speakers for speech testing in the audiology clinic.

To elucidate the neurobiological basis of nonnative listeners' SIN deficits, we recorded neuroelectric mismatch negativity (MMN) potentials in monolingual and late bilingual listeners in response to contrastive speech sounds presented in various levels of noise. The MMN is a scalp-recorded component of the auditory event-related potentials (ERP), indexing cortical registration of acoustic deviancy in the absence of attention or a behavioral engagement (Naatanen, Paavilainen, Rinne, & Alho, 2007). Previous studies have shown earlier latency mismatch activity is correlated with more accurate behavioral speech discrimination, indicating the response provides a neural correlate of speech perception abilities (e.g., Dehaene-Lambertz et al., 2005; Tremblay, Kraus, & McGee, 1998). A constellation of neural generators contributes to the MMN including sources in the superior temporal plane (bilateral auditory cortices) and frontal lobes (Giard, Perrin, Pernier, & Bouchet, 1990; Naatanen et al., 2007; Yago, Escera, Alho, & Giard, 2001). Both temporal and frontal MMN sources are thought to contribute to normal speech perception; sources in superior temporal gyrus (STG) are thought to play a role in initial sound analysis in auditory sensory cortex while those near inferior frontal gyrus (IFG) likely reflect higher-order (i.e., linguistic) analysis of speech information downstream (for review, see Myers, 2014). Relevant to the current report, previous studies have shown that inferior frontal sources (proximal to Broca's area and the insula) show particular sensitivity when listening to ambiguous or noise degraded speech (Diaz, Baus, Escera, Costa, & Sebastian-Galles, 2008; Du, Buchsbaum, Grady, & Alain, 2014).

Here, we applied distributed source analysis to these neural responses to evaluate cross-language and region-specific differences in the brain's differentiation of degraded speech. Comparing listeners' electrical brain responses to their perception allowed us to assess the degree to which different neural substrates (i.e., those subserving auditory sensory vs. linguistic processes) contribute to behavioral SIN abilities. We predicted parallel noise-related changes in both groups within auditory cortical regions, consistent with progressive masking of neural speech representations in sensory brain areas (e.g., Binder, Liebenthal, Possing, Medler, & Ward, 2004; Du et al., 2014; Eisner, McGettigan, Faulkner, Rosen, & Scott, 2010). Furthermore, we hypothesized monolinguals would show additional recruitment of frontal sources (cf. Diaz et al., 2008: Eisner et al., 2010). These findings would suggest that higher-order linguistic brain regions act in a compensatory manner to improve noise-degraded speech representations output from the sensory cortices in native (monolingual) but not nonnative (late bilingual) listeners.

2. Methods

2.1. Participants

Ten monolingual (Mono) and ten bilingual (Bi) young adult listeners (age range: 21-34 years) were recruited from the University of Memphis graduate student body to participate in the experiment. A language history questionnaire assessed linguistic background (Bidelman, Gandour, & Krishnan, 2011; Li, Sepanski, & Zhao, 2006). Monolinguals were native speakers of American English unfamiliar with a L2 of any kind. Bilingual participants were classified as late sequential bilinguals having not received formal instruction in English, on average, before age 10.1 ± 3.9 years. We chose to recruit late bilinguals to be consistent with previous work in this area (von Hapsburg et al., 2004; Zhang et al., 2011) and to maximize the possibility of identifying a neural correlate of the bilingual SIN deficit. However, it should be noted that even early bilinguals (i.e., L2 onset well before age 6) can show a behavioral disadvantage in speech in noise listening (Rogers et al., 2006; Shepherd & Bent, 2014; Tabri et al., 2010). All reported using their first language 46 ± 33% of their daily use. Self-reports of L2 language aptitude indicated that all were fluent in English reading, writing, speaking, and more critically, listening proficiency [1(very poor)-7(native-like) Likert scale; reading: 5.9(0.73); writing: 5.2(0.62); speaking: 5.2(0.62); listening: 5.7(0.94)]. We specifically recruited bilinguals with diverse language backgrounds (e.g., Spanish, Hindi, Korean, and Japanese) to increase external validity/generalizability of our study.

Participants were otherwise matched in right handedness [Mono: 73.8 ± 62%; Bi: 88 ± 19%; $t_{18} = 0.67$, p = 0.49] and formal education [Mono: 18.4 ± 1.8 years; Bi: 20 ± 2.3 years; $t_{18} = 1.73$, p = 0.09]. Musical training amplifies the auditory evoked potentials (Bidelman et al., 2011; Musacchia, Strait, & Kraus, 2008; Zendel & Alain, 2009) and improves SIN listening skills (Bidelman & Krishnan, 2010; Parbery-Clark, Skoe, Lam, & Kraus, 2009). Hence, all participants were required to have minimal (\leq 3 years) formal musical training. Air conduction audiograms confirmed normal hearing (i.e., \leq 25 dB HL) at octave frequencies (250–8000 Hz). Subjects reported no history of neuropsychiatric disorders. Each gave written informed consent in compliance with a protocol approved by the University of Memphis Institutional Review Board and were reimbursed monetarily for their time.

2.2. Behavioral speech-in-noise task

We measured listeners' speech reception thresholds in noise using the QuickSIN test (Killion, Niquette, Gudmundsen, Revit, & Banerjee, 2004). The QuickSIN provides an efficient means to measure noise-degraded speech understanding and provides a standardized behavioral measure of SIN listening abilities. The QuickSIN contains 12 equivalent lists (6 sentences per list) available for measuring behavioral SIN. Participants heard two lists (selected at random) embedded in four-talker babble noise containing five key words. Noise-degraded sentences were presented at 70 dB SPL using pre-recorded signal-to-noise ratios (SNRs) which decreased in 5 dB steps from 25 dB (easy) to 0 dB (difficult). After each sentence presentation, participants repeated the utterance and were given one point for each correctly recalled key word. "SNR loss" (computed in dB) was determined by subtracting the total number of words correctly identified from 25.5. This number represents the SNR required to correctly recognize 50% of the key words among target sentences (Killion et al., 2004). SNR loss was measured separately in both the left and right ears. However, the better of the two ears was taken as a singular measure of participants' behavioral SIN perception-which in all cases was the right ear.

2.3. Stimulus presentation

Neuroelectric activity was recorded in response to the English minimal pair /tɑt/ (e.g., "tot") and /tɔt/ (e.g., "taught") (Fig. 1). This speech contrast was chosen given its common confusion by non-native listeners (Shafiro, Levy, Khamis-Dakwar, & Kharkhurin, 2013). However, informal pilot testing indicated that these sounds were clearly discriminable (in quiet) by both mono- and bilinguals. Stimulus tokens were natural productions recorded by a male speaker. Mismatch responses were recorded in a passive auditory oddball paradigm (standard: /tot/; oddball (deviant): /taught/) with an interstimulus interval of 750 ms and standard/deviant ratio of 85/15%, respectively. Standards (680 trials) and deviants (120 trials) were presented in a pseudo-random order such that at least two standard tokens intervened between subsequent deviants.

In addition to this "clean" speech contrast (i.e., $SNR = +\infty dB$), stimuli were presented in three noise conditions (randomized

order). Degraded speech was achieved by adding multitalker noise babble (Nilsson, Soli, & Sullivan, 1994) during oddball sequences at SNRs of +10, 0, and -5 dB. Importantly, we manipulated SNR by changing the level of the masker rather than the level of the signal which ensured that SNR was inversely correlated with overall sound intensity (Binder et al., 2004). The babble was presented continuously throughout the experimental runs, i.e., noise was never time-locked to stimulus presentation. Continuous babble is desirable because (i) it has a larger effect on the MMN than other maskers (e.g., white noise) (Kozou et al., 2005), (ii) it more closely mimics real-world listening situations where listeners must extract target signals from a blanket of background interference (e.g., cocktail party scenario), and (iii) it ensures engagement of the relatively sluggish medial olivocochlear (MOC) efferent system whose presumed role is one of "antimasking" and signal-in-noise enhancement (de Boer & Thornton, 2008; Guinan, 2006), Engagement of the MOC pathway therefore allows us to assess the physiological response to speech in noise under the auditory system's normal mode of operation.

Participants reclined comfortably in an electro-acoustically shielded booth to facilitate recording of neurophysiological responses. They were instructed to ignore the auditory stimuli and were allowed to watch a muted, subtitled movie to maintain a calm yet wakeful state. Stimuli were controlled by MATLAB (The MathWorks), presented through a TDT RP2 interface (Tucker-Davis Technologies), and delivered binaurally at an intensity of 80 dB SPL through shielded (Campbell, Kerlin, Bishop, & Miller, 2012) ER-2 insert earphones (Etymotic Research).

2.4. Electrophysiological recordings

2.4.1. MMN recording and preprocessing

Neuroelectric activity was recorded from 64 sintered Ag/AgCl electrodes at standard 10–20 locations around the scalp using standard procedures from our lab (Bidelman & Grall, 2014). EEGs were digitized using a sampling rate of 500 Hz (SynAmps RT amplifiers; Compumedics Neuroscan) using an online passband of DC-200 Hz. Electrodes placed on the outer canthi of the eyes and the superior and inferior orbit were used to monitor ocular activity. During acquisition, electrodes were referenced to an additional sensor placed ~1 cm posterior to Cz. Data were then re-referenced



Fig. 1. Speech stimuli used to probe cross-language differences in SIN perception. Acoustic time-waveforms (*top row*) and spectrograms (*bottom row*) of the speech contrast / tot/ (as in "tot") vs. /tot/, (as in "taught"), commonly confused by non-native English listeners (Shafiro et al., 2013). Stimulus tokens were natural productions recorded by a male speaker equated in duration, intensity, and amplitude profile; only formant frequencies differed. Electrical mismatch potentials (MMNs) were recorded in response to this minimal speech pair in a passive auditory oddball paradigm [standard (85%): /tot/; oddball (15%): /taught/].

off-line to a common average reference. Contact impedances were maintained ${\leqslant}10~k\Omega.$

Subsequent preprocessing was performed in Curry 7 (Compumedics Neuroscan) and custom routines coded in MATLAB. Data visualization and scalp topographies were computed using EEGLAB (Delorme & Makeig, 2004). EEGs were first digitally filtered (3–15 Hz; zero-phase filters). Ocular artifacts (saccades/blink artifacts) were then corrected in the continuous EEG using a principal component analysis (PCA) (Wallstrom, Kass, Miller, Cohn, & Fox, 2004). PCA decomposition provided a set of independent components which best explained the topography of the blink/saccadic artifacts. Scalp projections of the first two PCA loadings were subtracted from the continuous EEG traces to nullify ocular contamination in the final ERPs. Cleaned EEGs were then epoched (–200 to 600 ms), baseline-corrected, and subsequently averaged in the time domain to obtain ERPs for each stimulus condition per participant.

MMNs were derived by subtracting ERPs to the standard stimuli from their corresponding deviant ERPs (of the same SNR condition), resulting in a total of four difference waves for each listener (i.e., clean, +10, 0, -5 dB SNR). Following visual inspection of the grand average waveforms, MMN was quantified as the peak negativity between 175 and 350 ms. Earlier latency MMNs at certain SNRs or between language groups would indicate better, more efficient neural differentiation of speech information.

2.4.2. MMN source analysis

Neuronal sources of evoked potentials must be inferred given the volume conducted nature of the scalp-recorded EEG and "cross-talk" between adjacent sensor measurements. To more directly assess generator characteristics underlying speech-evoked MMNs, we performed a distributed source analysis. Source reconstruction was implemented in the MATLAB package Brainstorm (Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011) using a 3-shell spherical volume conductor head model and the well-established sLORETA inverse solution (Pascual-Margui, 2002). sLORETA allowed us to estimate the distributed neuronal current density underlying the measured sensor data. This algorithm models the inverse solution as a large number of elementary dipole generators distributed over nodes on a mesh of the cortical surface. When constrained to neocortical layers, the aggregate strength of source activity can be projected spatiotemporally onto the neuroanatomy, akin to functional maps in fMRI (e.g., Fig. 4). The resultant activation maps represent the transcranial current source density underlying the scalp-recorded potentials as seen from the cortical surface. We used the default settings in Brainstorm's implementation of sLORETA (Tadel et al., 2011). Source activity was derived for each MMN time course (per subject and noise condition) and projected onto the standardized Montreal Neurological Institute (MNI) brain (Collins, Zijdenbos, Kollokian, et al., 1998) for subsequent group-level analysis.

From each activation map (e.g. Fig. 4), we extracted the timecourse of source activity in two predefined regions of interest (ROI) averaged across the two hemispheres: (1) Insula/Broca's area (i.e., BA44/45) in inferior frontal gyri (IFG); (2) primary auditory cortex (i.e., Heschl's gyrus, BA41) in superior temporal gyri (STG). These ROIs were chosen to directly contrast source activity in brain regions subserving lower-order auditory processing (i.e., primary auditory areas in STG) and higher-order linguistic functions (i.e., Ins/Broca's area in IFG) (e.g., Du et al., 2014). Averaging hemispheres was used as a data reduction technique and to improve the SNR of neural responses. Pooling hemispheres is also justified based on prior studies which demonstrate that the MMN is largely bilateral in response to noise-degraded speech (e.g., Shtyrov et al., 1998). ROI parcellation was based on anatomical segmentations (Tzourio-Mazoyer, Landeau, Papathanassiou, et al., 2002) as implemented in Brainstorm (Tadel et al., 2011). Resulting source waveforms reflect the neural activity (current, measured in μ Amm) as seen within each anatomical ROI. As with sensor data, amplitude and latency were then measured from each MMN source waveform in a 175–350 ms analysis time window. Spearman's correlations were used to explore correspondences between MMN ROI source activity and behavioral SIN scores. For each ROI, multiple correlation testing was corrected via false-discovery rate (FDR) on the family of contrasts under investigation (α = 0.05) (Benjamini & Hochberg, 1995).

3. Results

3.1. Behavioral speech-in-noise performance

On average, monolingual listeners achieved QuickSIN scores ~10 dB lower (i.e., better) than their bilingual peers (Fig. 2). The monolingual advantage for SIN perception was confirmed by an independent samples *t*-test which revealed a significant group effect QuickSIN scores [$t_{18} = -6.75$, p < 0.0001]. Associations between bilinguals' poorer SIN performance could be mediated by length of exposure to their L2. However, we found no association between bilinguals' perceptual QuickSIN scores and ESL age [r = 0.35, p = 0.31]. However, L2 listening proficiency was negatively correlated with QuickSIN scores [r = -0.75, p = 0.03], implying that bilinguals with longer experience with their nonnative language have improved noise degraded speech perception.

3.2. MMN responses to noise-degraded speech in monolinguals and bilinguals

For electrode-level data, MMN waves appeared as negativities, distributed maximally over fronto-central regions of the scalp (Fig. 3). Guided by prior work (Naatanen et al., 2007) and the observed topography of the MMN (Fig. 3), we restricted analysis of sensor data to the FCz electrode. MMN amplitude was variable and did not differ between groups [$F_{1,18} = 3.14$, p = 0.09] nor SNRs [$F_{3,54} = 1.77$, p = 0.16]. In contrast, we found that MMN latency was modulated by speech SNR [$F_{3,54} = 12.60$, p < 0.0001]. The sole effect of SNR indicates that MMN latency (at the electrode level) was modulated by stimulus noise across the board. Indeed, MMNs



Fig. 2. Monolingual advantage for speech-in-noise listening. Monolinguals (\Box) achieve QuickSIN scores ~10 dB smaller (i.e., better) than their bilingual (\blacksquare) peers. That is, bilinguals require a much more favorable signal-to-noise ratio to achieve speech recognition comparable to monolinguals' performance. errorbars = ±1 s.e.m.



Fig. 3. Early cortical speech processing is more resilient to noise in monolinguals compared to bilinguals. Grand average mismatch negativity (MMN) responses (i.e., difference waves) recorded in monolinguals (A) and bilinguals (B) elicited by speech stimuli presented with (dotted lines) and without (solid lines) noise babble. Triangles mark the onset of the time-locking speech stimulus. Time traces reflect potentials recorded at the FCz electrode. Scalp maps illustrate the topography of MMNs to clean and noise-degraded speech (+10 dB SNR). A polarity inversion is observed in the MMN's topography between frontal-temporal electrode sites, consistent with bilateral neural generator(s) in the superior temporal plane (Naatanen et al., 2007). Mismatch responses emerge ~250 ms after the onset of the stimulus and reflect early cortical discrimination of speech. Both groups show stronger MMN in the presence of minimal noise (+10 dB SNR) relative to clean speech, consistent with the notion that low-level noise facilitates cortical speech processing (Alain, McDonald, & Van Roon, 2012). Relative to monolinguals, bilinguals show more prolonged cortical speech responses with noise interference.

were systematically prolonged with increasing noise in both groups (monolinguals: t_{54} = 3.49, p = 0.0039; bilinguals: t_{54} = 4.15, p = 0.0005; Bonferroni adjusted linear trend contrasts).

3.3. MMN source and ROI analysis

Functional source activation maps underlying the MMN response to speech are shown in Fig. 4. Early source activity appeared in focal regions localized to the primary auditory cortices within bilateral STG (Fig. 4A). Paralleling electrode data, MMN source latency within the STG generator increased systematically with increasing noise level [$F_{3,54}$ = 42.31, p < 0.0001; poorer SNR prolonged cortical speech differentiation in both groups (monolinguals: t_{54} = 7.08, p < 0.0001; bilinguals: t_{54} = 6.60, p < 0.0001; Bonferroni adjusted linear trend contrasts). No group [$F_{1,18}$ = 0.27, p = 0.61] nor interaction [$F_{3,54}$ = 0.31, p = 0.82] effects were observed indicating that noise equally affected STG speech coding regardless of language experience.

In contrast, MMN source activity localized to inferior frontal brain regions (Ins./Broca) showed differential SIN encoding between monolingual and bilingual listeners (Fig. 4B). This was confirmed by main effects of both group [$F_{1,18} = 4.91$, p = 0.0398] and stimulus SNR [$F_{3,54} = 30.56$, p < 0.0001] on MMN source latency [group × SNR: $F_{3,54} = 2.12$, p = 0.11]. These results suggest faster MMNs in monolingual compared to late bilinguals across the board. Interestingly, MMN activity in the IFG occurred ~25 ms earlier in monolinguals compared to bilinguals at higher noise levels (-5 dB: p = 0.0101). By group, regional comparisons indicated a

similar source latency MMN for nonnative listeners across brain regions [$F_{1,63} = 1.08$, p = 0.302]. However, in monolinguals, MMNs occurred ~15 ms early in IFG compared to STG [main effect of region: $F_{1,63} = 4.44$, p = 0.0391]. Follow-up contrasts indicated this effect was mainly driven by monolingual's earlier responses in IFG relative to STG in the -5 dB SNR condition (p = 0.028). Collectively, these results suggest that in nonnative listeners, speech processing degrades systematically with noise as in sensory brain regions (i.e., STG) but that noise-related changes are offset (i.e., compensated) in higher brain areas (IFG) in native listeners. As with electrode-level data, we found no reliable differences in MMN source amplitude in either STG or IFG.

3.4. Brain-behavior correlations

We examined the degree to which neural source activity in the STG and Ins/Broca's predicted each group's behavioral SIN perception via correlational analyses. QuickSIN scores were regressed against MMN source waveform latencies extracted from each ROI (average MMN latency of noise conditions: +10, 0, -5 dB SNR). We found a double dissociation in the explanatory power of each brain area in predicting monolinguals' and bilinguals' SIN perception (Fig. 5). Within STG, earlier MMN responses were associated with better SIN perception in bilinguals [r = 0.69, $p_{FDR} = 0.028$] but not in monolinguals' STG responses and their SIN perception remained significant even after partialling out ESL age [r = 0.74, p = 0.023] but not L2 listening proficiency [r = 0.62, p = 0.10]. These



Fig. 4. Differential speech encoding in frontal and temporal brain regions accounts for bilinguals' deficits in SIN recognition. (bottom) Distributed source activity underlying the scalp-recorded MMN response computed using an sLORETA inverse solution (Pascual-Marqui, 2002) projected onto the inflated cortical surface of the normalized MNI anatomy (Collins et al., 1998). Scalp maps illustrate the monolingual group average in the +10 dB SNR condition, 250 ms after the time-locking speech token. (A) Source activation shows neural activity localized to the traverse gyrus of the superior temporal plane, consistent with early auditory generators of the mismatch response. Averaged across hemispheres, MMN source latencies increase monotonically with decreasing SNR; increasing levels of noise systemically degrade neural speech representation in primary-secondary auditory cortices in both groups. (B) MMN activity emerging from inferior frontal brain regions (STG). In contrast, noise-related changes are offset in monolingual listeners suggesting that higher-order frontal brain areas act in a compensatory manner to aid degraded speech listening. Differential speech encoding between groups implies that compensatory processing is only available when speech recruits linguistic brain mechanisms as reflected in mono-but not bilinguals' cortical response to speech. STG, superior temporal gyrus; Ins, insula; SNR, signal-to-noise-ratio; errorbars = ±1 s.e.m.



Fig. 5. Double dissociation in brain-behavior correlations underlying cross-language differences in SIN perception. Faster speech-evoked responses in STG (but not IFG) predict bilinguals' behavioral SIN performance (A), whereas IFG (but not STG activity) predicts monolinguals' SIN perception (B). The double dissociation in brain-behavior correlations suggests that different cortical areas drive monolinguals' and bilinguals' SIN recognition; in nonnative listeners, successful SIN recognition is determined based on the quality of neural representations in auditory cortex whereas linguistic brain areas determine monolinguals' SIN abilities. Solid lines, significant correlations; dotted lines, *n.s.* relationships. STG, superior temporal gyrus; Ins, insula; * *p*_{FDR} < 0.05.

results suggest that late bilinguals' poorer neural encoding of noisy speech might be at least partially driven by the extent of their nonnative language experience.

Notably, we found the opposite brain-behavior relationship for the frontal ROI. Source latencies within Ins./Broca's area predicted monolinguals' [r = 0.73, $p_{FDR} = 0.02$] but not bilinguals' [r = 0.22, $p_{FDR} = 0.27$] SIN performance. Collectively, these findings suggest (i) earlier neural mismatch responses support better perceptual speech-in-noise recognition, (ii) speech representations in primary auditory brain areas (STG) dictate bilinguals' perceptual SIN deficits, but (iii) higher-order linguistic regions (IFG) govern monolinguals' SIN perception.

4. Discussion

Bilingualism has been associated with improved cognitive control (Bialystok, 2009; Bialystok et al., 2007, 2012; Crinion et al., 2006) and sustained attention (Krizman et al., 2012), executive functions that may boost cognitive reserve and offset behavioral declines during aging (Bialystok et al., 2007; Craik et al., 2010; Gold et al., 2013; Kave et al., 2008). Often neglected are the negative consequences of bilinguals' neuroplastic effects—adaptations that are maladaptive rather than beneficial to behavior (Kolb & Gibb, 2014; Mahncke et al., 2006). Our data provide a neurobiological account for nonnative listeners' deficits in SIN perception and illustrate that juggling multiple languages produces neuroplastic changes in brain function that can hinder, rather than benefit, speech-listening abilities.

At a behavioral level, we found that nonnative listeners showed much poorer SIN recognition of their nonnative language, requiring ~10 dB more favorable SNR to achieve the performance of their monolingual peers. These data corroborate a growing number of studies which show that speaking multiple languages creates substantial deficiency in SIN listening within the nonnative language, inhibiting analysis of the auditory scene and proper extraction of signals from noise (Hervais-Adelman et al., 2014; Rogers et al., 2006; Shepherd & Bent, 2014; Tabri et al., 2010; von Hapsburg et al., 2004; Zhang et al., 2011). Our findings also underscore the importance of documenting language background in speech audiometry and SIN testing and establishing separate norms for bilingual listeners, regardless of their L2 onset or length of experience.

At a neural level, we found that cortical responses to noise-degraded speech were delayed in bilinguals relative to monolingual speakers. These findings imply that the late bilingual brain is less efficient at processing nonnative speech signals amidst noise. Analysis of region-specific brain activity further revealed that speech processing became progressively weaker in superior temporal gyri regardless of language experience. Parallel STG degradation between language groups suggests that noise has a similar effect on speech representations within auditory cortex. In stark contrast, noise-related changes were less pronounced within inferior frontal regions (near Broca's area) of monolinguals. Starting at moderate noise levels (e.g., SNRs = 0 dB), monolinguals' mismatch potentials were offset in IFG compared to those generated within STG. The contrastive pattern of responses between auditory and linguistic brain regions (in native listeners) suggests that spatially distinct areas of cerebral cortex are differentially vulnerable to noise (i.e., STG > IFG). The greater resilience of linguistic (Ins/Broca's) compared to auditory speech representations (STG) aligns well with both theoretical (Rauschecker & Scott, 2009) and recent neuroimaging evidence (Du et al., 2014; Wong, Ettlinger, Sheppard, Gunasekera, & Dhar, 2010; Wong et al., 2009) which posits that compensatory mechanisms from higher-order brain areas act to mitigate degraded speech processing.

Presumably, in optimal listening conditions (i.e., no noise), sensory representations within the auditory system are sufficient to support speech perception; however, during adverse listening situations that degrade sensory inputs, additional neural resources must be deployed to compensate for impoverished speech signals (Du et al., 2014). In the current study, we provide compelling evidence that linguistic brain regions (IFG/Broca's) may partly perform this compensatory role, helping to counteract/interpret poor signal quality output from STG and aid spoken word recognition in noise. Our data closely align with recent neuroimaging studies which demonstrate that non-auditory brain mechanisms, including sensorimotor system, contribute to phonological processing (Du et al., 2014; Kuhl, Ramírez, Bosseler, Lin, & Imada, 2014) and compensate for lost specificity in the auditory system when it is stressed by adverse listening conditions (Du et al., 2014; current study) or has impaired peripheral input (e.g., hearing loss) (Campbell & Sharma, 2013). The fact we observe these effects in the absence of an overt speech task or attentional engagement further implies that noise-induced compensation is largely automatic. In this sense, our results agree well with data linking aspects of complex auditory scene analysis to pre-attentive and "primitive" levels of brain processing (Alain et al., 2014; Bidelman & Krishnan, 2010).

Critically, native listeners' neural compensation for speech in noise was not observed in nonnative listeners. Whereas IFG responses in late bilinguals became progressively weaker with decreasing SNR (i.e., increasing noise), monolinguals' differentiation of speech in this same region was more resilient to noise. These results indicate distinct brain signatures between native and nonnative listeners, driven by each group's differential encoding of SIN in auditory and language networks. We infer that when listening to L2 speech in challenging listening environments, nonnative listeners fail to engage critical linguistic brain mechanisms that perform top-down compensation on the degraded speech input. This notion is supported by the double dissociation observed in brain-behavior predictions. In bilinguals, STG (but not Ins/Broca's) activity predicted perceptual SIN performance whereas in monolinguals, degraded speech recognition was predicted by regional activation of Ins/Broca's rather than primary auditory structures (STG). Taken together, our findings provide convincing evidence that nonnative listeners process noise-degraded speech in a "nonlinguistic" mode (Best, McRoberts, & Goodell, 2001), recruiting more auditory rather than lexical brain mechanisms.

In the absence of neural compensation, successful SIN perception for nonnative listeners might be determined primarily by the quality of phonemic representation at a sensory level. This interpretation is supported by (i) the positive correlation observed in our data between bilinguals' neurophysiological responses in STG and QuickSIN scores and (ii) previous work from our lab and others which has demonstrated enhanced, more faithful encoding of noise-degraded speech in bilinguals as early as the level of the brainstem (Krishnan, Gandour, & Bidelman, 2010; Krizman et al., 2012). However, our data here indicate that bilingual's sensory gains in auditory processing are, by themselves, insufficient to improve their perceptual abilities, particularly for SIN listening (cf. Krishnan et al., 2010; Krizman et al., 2012). Instead, our findings reveal that robust and successful SIN analysis requires additional engagement of higher-order cortical brain areas specialized for language processing (Hickok & Poeppel, 2007). Recent volumetric imaging studies indicate that successful SIN perception depends on neuroanatomical properties of inferior frontal brain areas (proximal to our IFG ROI) including the morphology and thickness of cortical tissue (Wong et al., 2010). Coupled with our electrical recordings, these studies confirm the importance of brain regions downstream from primary auditory centers (i.e., IFG) in achieving robust speech-in-noise recognition.

It is useful to examine additional characteristics of this SIN compensatory mechanism. Enhanced excitement of auditory cortex has been observed when processing less meaningful sounds or those requiring a further layer of analysis (Skipper, 2014). In this regard, degraded speech is thought to necessitate further hypothesis testing beyond primary sensory cortices for effective processing. The increased activation in monolinguals' frontal brain areas we find for degraded speech follows this premise. Our data are also consistent with studies showing that individual variability in learning degraded speech information is predicted by differences in the recruitment of higher-level linguistic brain regions including IFG (Binder et al., 2004; Diaz et al., 2008; Eisner et al., 2010). They are also consistent with the notion that speech networks undergo an increase in functional connectivity between higher cortical areas (remote from auditory cortex) to facilitate degraded speech comprehension (Obleser, Wise, Dresner, & Scott, 2007). Our data corroborate these studies by demonstrating similar recruitment of higher-order linguistic areas when processing impoverished (native) speech sounds.

Interestingly, we found that monolinguals' (but not bilinguals') mismatch responses were slightly earlier (10-15 ms) in IFG relative to the STG. While seemingly paradoxical prima face-one would expect a causal flow of information from auditory cortex (STG) to IFG-this finding is consistent with the notion that higher order speech centers produce an inhibitory influence on concurrent auditory representations in order to prevent interference from nonlinguistic cues (Dehaene-Lambertz et al., 2005; Liberman, Isenberg, & Rakerd, 1981). The magnitude of this latency effect is also consistent with previously reported "top-down" (e.g., attentional) influences on the MMN latency (Pfingst & McKenzie, 2012). Such "top-down" inhibition (i.e., IFG \rightarrow STG)-or alternatively, IFG facilitation-might therefore account for native listeners' slightly slower responses in auditory sensory cortex relative to more frontal linguistic brain regions. Our data also underscore the notion that speech operations are not entirely serial, but rather, the brain uses multiple routes for lexical access that are implemented in parallel processing channels (Hickok & Poeppel, 2007).

The differential recruitment of frontal vs. auditory cortex between native and nonnative listeners also aligns closely with the notion of the reverse hierarchy theory (RHT) (Ahissar & Hochstein, 2004). Originally applied to the visual domain, RHT is a theoretical framework that posits that with increasing task demand, the brain performs a progressive backward search from higher-order information to lower-level inputs in search of representations with more optimal signal-to-noise ratio. Under RHT, high-order linguistic representations in late bilinguals may be too weak given their non-native stature, forcing a backward search toward the sensory input (i.e., auditory cortex) in order to arrive at more favorable speech representations. This interpretation is supported by recent work showing that poorer perceivers of nonnative speech contrasts have attenuated mismatch responses in frontal cortex relative to good perceivers (Diaz et al., 2008). This may explain the differential activation of IFG and STG between monolingual and late bilingual listeners and the fact that the latter group seems to rely more heavily on acoustic-phonetic representations in temporal brain areas (Figs. 4 and 5).

Unlike other salient human experiences that offer benefits to brain and behavioral functions [e.g., musical training (Bidelman & Krishnan, 2010; Bidelman et al., 2011; Moreno & Bidelman, 2014; Parbery-Clark et al., 2009; Zendel & Alain, 2009)], bilinguals are not self-selected (Bialystok et al., 2012; Ressel et al., 2012). Bilingual participants in our study began learning their second language in school settings during childhood. Importantly, they did not become bilingual because they self-selected to do so nor because they were especially gifted at learning foreign languages. Accordingly, our data provide clear demonstration that second language experience is likely a causal factor in bilinguals' SIN listening deficits (Ressel et al., 2012).

Limitations of the current study are worth noting. Our investigation of bilinguals' deficits in SIN were limited to late-onset bilinguals who acquired their L2 sequentially after age ~ 10 . Some studies have suggested that early (L2 onset well before age 6) and simultaneous (i.e., L1 and L2 onset prior to age 1) bilinguals can achieve similar SIN performance to monolinguals and may differ in degraded speech perception from their late bilingual counterparts (Calandruccio, Gomez, Buss, & Leibold, 2014). However, other studies report the opposite, showing that early bilinguals can similarly show a behavioral disadvantage in speech in noise listening (Rogers et al., 2006; Shepherd & Bent, 2014; Tabri et al., 2010). While equivocal, it is clear that SIN perception in a nonnative language depends on both the specific characteristics of an individual's language experience(s) and the age of acquisition of their nonnative tongue. It remains to be seen whether the neural correlates of late bilinguals' SIN processing observed here apply to all bilinguals across the board. For example, it is entirely plausible that late bilinguals' SIN deficits are mitigated (or entirely absent) in simultaneous bilinguals. Additionally, our study employed a single English speech contrast. While we have no reason to believe that the observed effects are idiosyncratic to our specific stimuli, future studies are needed to determine if the noise processing deficits we observe for nonnative speakers generalize to other nonnative speech sounds.

In summary, the current study establishes a neurobiological basis for a prominent disadvantage observed in late bilinguals, degraded speech perception of the nonnative language. Our study also offers compelling evidence for tradeoffs in experiencedependent plasticity (Mahncke et al., 2006); bilinguals' gains in certain cognitive traits (Krizman et al., 2012; Ressel et al., 2012) are accompanied by detrimental consequences for signal-in-noise extraction, a necessary ability for accurate auditory scene analysis. More broadly, late bilinguals' impaired "cocktail party" listening has implications for understanding communication in modern classrooms, which are inherently noisy soundscapes (Knecht et al., 2002) and increasingly multilingual environments (Chin et al., 2013). Current standards in architectural acoustics recommend an optimal SNR of +15 dB between the teacher and classroom noise for effective learning (ANSI/ASA, 2010). Our data suggest that at comparable noise levels (+10 dB SNR), nonnative listeners already show dramatic impairment in both their behavioral and neurobiological processing of speech information. Given that noise levels often exceed recommended standards (Knecht et al., 2002), our findings emphasize that classroom acoustics warrant special attention when demographics include bilingual pupils. Of interest to futures studies is whether bilinguals' SIN deficits can be alleviated with training or mere long-term experience with their second language. Longer exposure to their nonnative language would tend strengthen L2 processing so that it becomes more resistant to potential interference. This proposition is supported by the correlation we observed between bilinguals' L2 (i.e., English) listening proficiency and behavioral SIN. Indeed, partial correlations demonstrated that the link between bilinguals' (STG) neural responses and their SIN perception was driven, at least in part, by their L2 experience. It is possible that ESL or L2 experience might prove to be even more predictive of SIN listening abilities with a more heterogeneous sample of bilinguals with larger variation in L2 experience. Future work is needed to reveal if bilinguals raised speaking two languages concurrently (i.e., simultaneous bilinguals) can obtain similar brain architecture and SIN compensation as found in monolinguals.

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