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Research Paper

Brainstem-cortical functional connectivity for speech is differentially challenged by noise and reverberation

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ABSTRACT

Everyday speech perception is challenged by external acoustic interferences that hinder verbal communication. Here, we directly compared how different levels of the auditory system (brainstem vs. cortex) code speech and how their neural representations are affected by two acoustic stressors: noise and reverberation. We recorded multichannel (64 ch) brainstem frequency-following responses (FFRs) and cortical event-related potentials (ERPs) simultaneously in normal hearing individuals to speech sounds presented in mild and moderate levels of noise and reverb. We matched signal-to-noise and direct-to-reverberant ratios to equate the severity between classes of interference. Electrode recordings were parsed into source waveforms to assess the relative contribution of region-specific brain areas [i.e., brainstem (BS), primary auditory cortex (A1), inferior frontal gyrus (IFG)]. Results showed that reverberation was less detrimental to (and in some cases facilitated) the neural encoding of speech compared to additive noise. Inter-regional correlations revealed associations between BS and A1 responses, suggesting subcortical speech representations influence higher auditory-cortical areas. Functional connectivity analyses further showed that directed signaling toward A1 in both feedforward cortico-collicular (BS→A1) and feedback cortico-cortical (IFG→A1) pathways were strong predictors of degraded speech perception and differentiated “good” vs. “poor” perceivers. Our findings demonstrate a functional interplay within the brain’s speech network that depends on the form and severity of acoustic interference. We infer that in addition to the quality of neural representations within individual brain regions, listeners’ success at the “cocktail party” is modulated based on how information is transferred among subcortical and cortical hubs of the auditory-linguistic network.

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1. Introduction

In natural listening environments, noise and reverberation hinder the successful extraction of speech information (for review, see Bidelman, 2017). Although both are acoustic interferences, each has a distinct effect on speech signals (Helfer and Wilber, 1990; Nabelek and Dagenais, 1986). Noise is caused by the addition of external competing sounds that mask target speech. Contrastively, reverberation is the persistence of reflected acoustic energy in the sound field caused by internal room acoustics (Kinsler et al., 2000). Reverberation produces an overlap between direct and indirect

sounds that “smears” a signal’s spectrum. Natural reverberation also acts to low-pass filter speech compared to the overall flattening of modulations produced by noise. Conveniently, the degree of noise and reverberation superimposed on a target signal can be quantified by similar metrics. For noise, the relative contribution of “noise” and “signal” are characterized via the signal-to-noise ratio (SNR). Similarly, the proportions of acoustic energy attributable to signal and reverberant energy are characterized (in dB) by the direct-to-reverberant energy ratio (D/R), or less commonly, “wet-to-dry” ratio (von Békésy, 1938; Zahorik, 2002).

While both acoustic stressors hinder intelligibility, behavioral studies reveal that human listeners show a differential sensitivity when perceiving signals in noise vs. reverberation (Larsen et al., 2008; McShefferty et al., 2015; Zahorik, 2002). That is, even when the relative intensities between signal and interference are matched in severity (i.e., $SNR \approx D/R$), noise and reverberation

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impact speech perception in different manners. While each interference reduces speech understanding by ~15–20%, vowel confusion patterns can differ under these two acoustic backdrops (Nabelek and Dagenais, 1986). Interestingly, reverb also induces less listening effort than noise during speech comprehension, even at similar levels of behavioral performance (Picou et al., 2016). This suggests that while there is a comparable tax on speech intelligibility, noise and reverberation might uniquely impact the underlying neural representations for speech (cf. White-Schwoch and Kraus, 2017). To our knowledge, this possibility has not been formally tested.

It is now well-established that speech-in-noise (SIN) understanding is determined by more than audibility or peripheral hearing status (Middelweerd et al., 1990; Song et al., 2011) (but see Humes and Roberts, 1990). The fact that SIN performance is not reliably predicted from the audiogram (Killion and Niquette, 2000) and varies among even normal-hearing listeners (Song et al., 2011) has led to the notion that central brain mechanisms play a critical role in supporting successful cocktail party listening (e.g., Alain et al., 2014; Bidelman and Howell, 2016; Billings et al., 2009; Billings et al., 2010; Billings et al., 2013; Parbery-Clark et al., 2011; Song et al., 2011). In this regard, electrophysiological studies have been important in elucidating the central factors of speech sound processing.

The brain's neuroelectric response to speech reflects an aggregate of activity generated from both brainstem and cortical structures. By exploiting properties of each response (e.g., spectral bandwidth), one can isolate their contributions within the scalp EEG and examine sound encoding within various structures of the auditory hierarchy (Bidelman et al., 2013). The cortical ERPs are composed of several "waves" (e.g., P1-N1-P2), reflecting activation of auditory thalamus, cortex, and associative areas (Picton et al., 1999). ERPs are sensitive to the acoustic features of speech (Agung et al., 2006; Chang et al., 2010; Kraus and Cheour, 2000; Sharma and Dorman, 1999) and correlate with listeners' perceptual skills (Bidelman et al., 2014b; Ross and Tremblay, 2009; Tremblay et al., 2001). The *subcortical* component, or frequency-following response (FFR), is a sustained potential emitted dominantly from the upper brainstem that closely mirrors acoustic stimuli with high fidelity (Bidelman, 2018; Krishnan, 2007; Skoe and Kraus, 2010). FFR activity similarly correlates with listeners' SIN perception (Anderson et al., 2010; Parbery-Clark et al., 2009a; Song et al., 2011). Yet, few studies have examined FFRs to reverberant speech (Bidelman and Krishnan, 2010; Fujihira and Shiraishi, 2015), and we unaware of any directly contrasting the effects of noise and reverb on speech FFRs. Moreover, while a number of studies have investigated the independent contributions of brainstem (e.g., Bidelman, 2016; Bidelman and Krishnan, 2010; Billings et al., 2013; Krishnan et al., 2010; Parbery-Clark et al., 2009a; Song et al., 2011) and cortical neurophysiology (e.g., Alain et al., 2014; Bidelman and Howell, 2016; Billings et al., 2010; Billings et al., 2013; Shtyrov et al., 1998) to degraded speech processing, examining these functional levels simultaneously (within individual listeners) would offer a more comprehensive, systems-level characterization of the biological mechanisms underlying cocktail party listening in different acoustic scenarios and possible interplay between stages of the neuroaxis.

To this end, our recent studies have championed the use of concurrent FFR-ERPs recordings to examine hierarchical auditory processing (e.g., Bidelman, 2015; Bidelman and Alain, 2015b; Bidelman et al., 2013; Bidelman et al., 2014b) (see also Bellier et al., 2015; Slugocki et al., 2017). Dual FFR-ERP paradigms have provided important insight into how lower vs. higher tiers of the neuroaxis code complex sounds and interact during early perception when object-based representations of speech are still in their nascent

stages (e.g., Bidelman et al., 2013). Translational applications have further shown how brainstem vs. cortical functions are uniquely strengthened by plasticity (Bidelman and Alain, 2015a; Bidelman et al., 2014a; Musacchia et al., 2008), are differentially compromised by hearing loss (Bidelman et al., 2014b), and are altered in neurocognitive disorders (Bidelman et al., 2017). This approach emphasizes a growing body of work that advocates speech processing as an integrative and dynamic network (Kraus and White-Schwoch, 2015; Obleser et al., 2007; Scott et al., 2009) which includes possible interactions and/or signal transformations between brainstem-cortex (Gao and Suga, 1998; Suga et al., 2002) and auditory-linguistic brain areas downstream (Du et al., 2014). Given that early brainstem-cortical and later auditory-linguistic interplay can presumably vary on an individual basis, we hypothesized these individual differences might modulate cocktail party perception. Here, we exploited dual FFR-ERPs to further investigate the neural encoding of impoverished (noisy and reverberant) speech and define the functional connectivity between subcortical and cortical hubs of the auditory system.

The aims of the present study were thus twofold. First, we directly compared how subcortical and cortical levels of the auditory system encode different forms of degraded speech information. While previous reports have investigated relations between brainstem and cortical auditory processing (e.g., Bidelman et al., 2013; Bidelman et al., 2017; Krishnan et al., 2012; Musacchia et al., 2008; Slugocki et al., 2017), studies have focused exclusively on scalp (electrode-level) recordings and therefore, can only *infer* contributions of sub- and neo-cortex from volume conducted mixtures of EEG signals. Here, source analysis of brainstem FFRs and cortical ERPs allowed us to parse region-specific activity with higher granularity and more definitively reveal how neural processing *within* each tier of the neuroaxis coordinate during speech processing. Functional connectivity analysis evaluated the directed, causal signaling between brainstem and cortical regions and how inter-regional neural communication might predict listeners' speech perception skills. We also measured source FFR/ERPs elicited by noisy and reverberant speech. This allowed us to directly assess how neural speech representations are affected by different acoustic stressors common to the auditory scene. To anticipate, our data reveal that degraded speech perception is governed by intra- and inter-regional brainstem-cortical activity including cortico-collicular (brainstem-cortical) and cortico-cortical (fronto-temporal) signaling.

2. Methods

2.1. Participants

Eleven adults (age: 24.7 ± 2.7 years) participated in the experiment. All had obtained a similar level of formal education (at least an undergraduate degree), and were monolingual speakers of American English. Musical training is known to enhance auditory evoked responses (e.g., Bidelman et al., 2011; Musacchia et al., 2008; Zendel and Alain, 2009) and improve degraded speech-listening skills (Bidelman and Krishnan, 2010; Parbery-Clark et al., 2009a, 2009b). Hence, all participants were required to have <3 years formal musical training (1.3 ± 1.8 years) and none within the past 5 years. Audiometric screening confirmed normal hearing (i.e., thresholds < 25 dB HL) at octave frequencies (250–8000 Hz). All participants reported no history of neuropsychiatric disorders. Participants gave written informed consent in compliance with a protocol approved by the University of Memphis Institutional Review Board and were compensated monetarily for their time.

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