



Functional connectivity in the dorsal stream and between bilateral auditory-related cortical areas differentially contribute to speech decoding depending on spectro-temporal signal integrity and performance



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ABSTRACT

Speech processing relies on the interdependence between auditory perception, sensorimotor integration, and verbal memory functions. Functional and structural connectivity between bilateral auditory-related cortical areas (ARCAs) facilitates spectro-temporal analyses, whereas the dynamic interplay between ARCAs and Broca's area (i.e., dorsal pathway) contributes to verbal memory functions, articulation, and sound-to-motor mapping. However, it remains unclear whether these two neural circuits are preferentially driven by spectral or temporal acoustic information, and whether their recruitment is predictive of speech perception performance and learning. Therefore, we evaluated EEG-based intracranial (eLORETA) functional connectivity (lagged coherence) in both pathways (i.e., between bilateral ARCAs and in the dorsal stream) while good- (GPs, $N = 12$) and poor performers (PPs, $N = 13$) learned to decode natural pseudowords (CLEAN) or comparable items (speech-noise chimeras) manipulated in the envelope (ENV) or in the fine-structure (FS). Learning to decode degraded speech was generally associated with increased functional connectivity in the theta, alpha, and beta frequency range in both circuits. Furthermore, GPs exhibited increased connectivity in the left dorsal stream compared to PPs, but only during the FS condition and in the theta frequency band. These results suggest that both pathways contribute to the decoding of spectro-temporal degraded speech by increasing the communication between brain regions involved in perceptual analyses and verbal memory functions. Otherwise, the left-hemispheric recruitment of the dorsal stream in GPs during the FS condition points to a contribution of this pathway to articulatory-based memory processes that are dependent on the temporal integrity of the speech signal. These results enable to better comprehend the neural circuits underlying word-learning as a function of temporal and spectral signal integrity and performance.

1. Introduction

Speech constitutes a unique human faculty that is dependent on the dynamic interplay between auditory perception, articulation, and cognitive operations (Bornkessel-Schlesewsky and Schlesewsky, 2013; Friederici, 2012; Hagoort, 2014; Hickok and Poeppel, 2007). For example, learning to distinguish the speech sounds of a new language constitutes an inalienable prerequisite for an accurate articulation (Kuhl, 2004; Smith, 1975). In addition, the integration of auditory and motor information has previously been shown to facilitate speech perception (Liberman and Mattingly, 1985), as well as to promote verbal

short-term- and working memory functions (Aboitiz, 2012; Schulze et al., 2012). Although current biologically grounded frameworks of speech processing (Bornkessel-Schlesewsky and Schlesewsky, 2013; Friederici, 2009, 2012; Hagoort, 2014; Hickok and Poeppel, 2007; Rauschecker and Scott, 2009) diverge somewhat in their linguistic and neurological conceptualizations, they conjointly emphasize the contribution of auditory-related cortical areas (i.e., ARCAs) to spectro-temporal analyses, and of the dorsal stream to sound-to-motor mapping (in the left hemisphere), articulation (in the left hemisphere), and verbal memory functions (bilateral).

From a histological perspective, humans (Galuske et al., 2000;

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Harasty et al., 2001), but not monkeys and macaques (Buxhoeveden and Casanova, 2000; Buxhoeveden et al., 2001), exhibit an asymmetric columnar organization of ARCAs. In particular, left ARCAs are interspersed with micro-columns that are more widely spaced and are more strongly myelinated than those situated in the right hemisphere (Harasty et al., 2001; Seldon, 1981a, 1981b). These micro-anatomical peculiarities possibly form the basis of the often reported asymmetry of the planum temporale (PT) (Galaburda et al., 1978; Jancke and Steinmetz, 1993; Shapleske et al., 1999; Steinmetz, 1996). Based on this asymmetrical columnar organization of ARCAs, it has been proposed that left-sided parts are preferentially driven by fast-changing acoustic cues, whereas the right-sided counterparts are functionally advantaged in extrapolating spectral, prosodic, and slow acoustic information (Griffiths and Warren, 2002; Zaehle et al., 2008, 2004; Zatorre and Belin, 2001).

Recently, both MRI (Elmer et al., 2016) and EEG (Kuhnis et al., 2014) studies have contributed to a better understanding of the division of labor between left and right ARCAs by taking into account functional and structural connectivity. In a multimodal MRI study, Elmer et al. (2016) uncovered a relationship between the ability to discriminate consonant-vowel (CV) syllables manipulated in the voice-onset time (VOT), the activity of the left PT, and myelin integrity in the transcallosal projection linking the left and right PT. In another study using EEG Kuhnis et al. (2014) provided further evidence for a relationship between the brain activity generated by ARCAs while passively listening to vowels and intracerebral phase synchronization between left and right ARCAs, however, this effect was only observed in musicians. Taken together, these results suggest that faithful impulse transmission and temporal alignment of neural oscillations between left and right ARCAs fundamentally contribute to spectro-temporal speech processing.

According to a hierarchical processing mode of the brain (Bornkessel-Schlesewsky and Schlesewsky, 2013; Rauschecker, 1998), after the completion of spectro-temporal analysis in ARCAs, the speech signal is transmitted in parallel along two functionally distinct processing streams. A bilaterally organized ventral stream, projecting from ARCAs toward the temporal pole, is involved in mapping sensory and phonological representations onto conceptual lexical representations (Hickok and Poeppel, 2007). By contrast, a dorsal stream stretching from ARCAs toward the premotor cortex (via the dorsal part of the superior longitudinal fasciculus, SLF) and to Broca's area (via the long segment of the arcuate fasciculus) has been proposed to support articulation (Hickok and Poeppel, 2007), sensory-to-motor coupling mechanisms (Hickok and Poeppel, 2007), and verbal memory functions (Catani et al., 2007). Within this parallel network, Broca's area constitutes a point of convergence of the two processing streams (Bornkessel-Schlesewsky and Schlesewsky, 2013; Friederici, 2009, 2012; Hickok and Poeppel, 2007). Broca's area supports a variety of linguistic (i.e., semantic and syntax) and cognitive (i.e., attention, short-term memory, working memory) functions (Fedorenko et al., 2012), and therefore constitutes an optimal candidate for orchestrating the two processing streams via top-down control mechanisms (Bornkessel-Schlesewsky and Schlesewsky, 2013).

Both MRI and EEG studies have demonstrated a functional and structural contribution of the dorsal stream to language expertise (Elmer and Kühnis, 2016; Vandermosten et al., 2015) and word learning mechanisms (Catani et al., 2007; Lopez-Barroso et al., 2013), but with a differential hemispheric involvement depending on the lexical status of the stimulus material. By using diffusion tensor imaging (DTI), Catani et al. (2007) found a relationship between the degree of asymmetry of the arcuate fasciculus and verbal memory functions. In particular, individuals with more symmetrical manifestations of this fiber bundle were better at remembering previously learned words than those with a strong left-hemispheric asymmetry. In a second multimodal MRI study, Lopez-Barroso et al. (2013) investigated the relationship between functional and structural connectivity in the left

dorsal stream and the learning of pseudowords presented in the form of concatenated speech. Such an experimental approach is particularly fruitful in that it enables to artificially “knock out” the ventral stream, while at the same time forcing sensory-to-motor coupling mechanisms which are required for creating the motor codes of new phonological sequences (Rauschecker and Scott, 2009; Rodriguez-Fornells et al., 2009) as well as for keeping phonetic information in short-term- and working-memory (Aboitiz, 2012; Schulze et al., 2012). Lopez-Barroso et al. (2013) revealed that the individuals who were better at remembering the previously heard pseudowords exhibited increased functional as well as structural connectivity in the left hemisphere.

In the present study, we evaluated EEG-based intracranial functional connectivity between the bilateral ARCAs, as well as between ARCAs and Broca's region (i.e., bilaterally), while good (GPs) and poor performers (PPs) learned to decode pseudowords manipulated in the envelope (ENV, the time course of the signal amplitude) or in the fine-structure (FS, the time course of the spectral information). We predicted that the higher perceptual and mnemonic demands associated with the processing of degraded speech (Kuhnis et al., 2013b) would be accompanied by increased functional connectivity in both processing streams. Furthermore, based on previous work, we hypothesized that GPs would be characterized by increased functional connectivity between left- and right-sided ARCAs (Elmer et al., 2016; Kuhnis et al., 2014), as well as between left ARCAs and Broca's area, compared to PPs (Lopez-Barroso et al., 2013). Finally, by using an assumption-free approach, we also evaluated the preferential recruitment of both neural circuits as a function of temporal and spectral signal integrity. Thereby, we assessed whether the reduction of spectral and temporal speech information might influence functional connectivity between the regions of interest.

2. Methods

2.1. General remarks

In the present work, we re-evaluated the data collected in the context of a previous study of our group (Kuhnis et al., 2013b). However, based on specific a-priori hypotheses, here we evaluated intracranial functional connectivity instead of microstates. Based on the fact that the “stimulus material” and the “experimental procedure” were exactly the same, here we partially resumed these sections from our previous work.

2.2. Participants

The 25 participants enrolled in this study were all non-musicians, in the age range of 19–45 years (mean age 26.4 ± 7.5 SD), had a normal audiological status, and no history of neurological or psychiatric disease. All participants were native Swiss-German or German speakers, and consistently right-handed, as revealed by a standard handedness questionnaire (Annett, 1970). The subjects were paid for participation, the local ethics committee approved the study (in accordance with the Helsinki declaration), and written consent was obtained from all participants. In order to elucidate the functional mechanisms beyond GPs and PPs, the original pool of 25 subjects was split into two sub-groups (GPs, $N = 12$, 5 female, mean age = 24.6, SD = 4.8; PPs, $N = 13$, 7 female, mean age = 28.1, SD = 9.2) according to the median of the percent correct trials across all three experimental conditions consisting of identifying natural pseudowords (i.e., not manipulated or CLEAN) or comparable items manipulated in the fine-structure (FS) or envelope (ENV).

2.3. Cognitive capability

In order to rule out differences in intelligence between GPs and PPs, all subjects performed the KAI test (<http://www.testzentrale.ch/>). This

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