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Sensorimotor Modulations by Cognitive Processes During Accurate Speech Discrimination: An EEG Investigation of Dorsal Stream Processing

Abstract

Internal models mediate the transmission of information between anterior and posterior regions of the dorsal stream in support of speech perception, though it remains unclear how this mechanism responds to cognitive processes in service of task demands. The purpose of the current study was to identify the influences of attention and working memory on sensorimotor activity across the dorsal stream during speech discrimination, with set size and signal clarity employed to modulate stimulus predictability and the time course of increased task demands, respectively. Independent Component Analysis of 64-channel EEG data identified bilateral sensorimotor mu and auditory alpha components from a cohort of 42 participants, indexing activity from anterior (mu) and posterior (auditory) aspects of the dorsal stream. Time frequency (ERSP) analysis evaluated task-related changes in focal activation patterns with phase coherence measures employed to track patterns of information flow across the dorsal stream. ERSP decomposition of mu clusters revealed event-related desynchronization (ERD) in beta and alpha bands, which were interpreted as evidence of forward (beta) and inverse (alpha) internal modeling across the time course of perception events. Stronger pre-stimulus mu alpha ERD in small set discrimination tasks was interpreted as more efficient attentional allocation due to the reduced sensory search space enabled by predictable stimuli. Mu-alpha and mu-beta ERD in peri- and post-stimulus periods were interpreted within the framework of Analysis by Synthesis as evidence of working memory activity for stimulus processing and maintenance, with weaker activity in degraded conditions suggesting that covert rehearsal mechanisms are sensitive to the quality of the stimulus being retained in working memory. Similar ERSP patterns across conditions despite the differences in stimulus predictability and clarity, suggest that subjects may have adapted to tasks. In light of this, future studies of sensorimotor processing should consider the ecological validity of the tasks employed, as well as the larger cognitive environment in which tasks are performed. The absence of interpretable patterns of mu-auditory coherence modulation across the time course of speech discrimination highlights the need for more sensitive analyses to probe dorsal stream connectivity.

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**Sensorimotor Modulations by Cognitive Processes During Accurate Speech
Discrimination: An EEG Investigation of Dorsal Stream Processing**

A Dissertation
Presented for
The Graduate Studies Council
The University of Tennessee
Health Science Center

In Partial Fulfillment
Of the Requirements for the Degree
Doctor of Philosophy
From The University of Tennessee

By
David E. Jenson
May 2018

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DEDICATION

This dissertation is dedicated to my wife Allison and my daughters Norah, Callie, and Eve. Thank you for your love, encouragement, and support. You have sustained me through this process, and I would not have been able to do this without you.

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ABSTRACT

Internal models mediate the transmission of information between anterior and posterior regions of the dorsal stream in support of speech perception, though it remains unclear how this mechanism responds to cognitive processes in service of task demands. The purpose of the current study was to identify the influences of attention and working memory on sensorimotor activity across the dorsal stream during speech discrimination, with set size and signal clarity employed to modulate stimulus predictability and the time course of increased task demands, respectively. Independent Component Analysis of 64-channel EEG data identified bilateral sensorimotor mu and auditory alpha components from a cohort of 42 participants, indexing activity from anterior (mu) and posterior (auditory) aspects of the dorsal stream. Time frequency (ERSP) analysis evaluated task-related changes in focal activation patterns with phase coherence measures employed to track patterns of information flow across the dorsal stream. ERSP decomposition of mu clusters revealed event-related desynchronization (ERD) in beta and alpha bands, which were interpreted as evidence of forward (beta) and inverse (alpha) internal modeling across the time course of perception events. Stronger pre-stimulus mu alpha ERD in small set discrimination tasks was interpreted as more efficient attentional allocation due to the reduced sensory search space enabled by predictable stimuli. Mu-alpha and mu-beta ERD in peri- and post-stimulus periods were interpreted within the framework of Analysis by Synthesis as evidence of working memory activity for stimulus processing and maintenance, with weaker activity in degraded conditions suggesting that covert rehearsal mechanisms are sensitive to the quality of the stimulus being retained in working memory. Similar ERSP patterns across conditions despite the differences in stimulus predictability and clarity, suggest that subjects may have adapted to tasks. In light of this, future studies of sensorimotor processing should consider the ecological validity of the tasks employed, as well as the larger cognitive environment in which tasks are performed. The absence of interpretable patterns of mu-auditory coherence modulation across the time course of speech discrimination highlights the need for more sensitive analyses to probe dorsal stream connectivity.

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LIST OF ABBREVIATIONS

BCI	Brain Computer Interface
BOLD	Blood Oxygen Level Dependent
DIVA	Directions Into Velocities of Articulators
EEG	Electroencephalography
ERD	Event Related Desynchronization
ERS	Event Related Synchronization
ERSP	Event Related Spectral Perturbations
fMRI	Functional Magnetic Resonance Imaging
ICA	Independent Component Analysis
IFG	Inferior Frontal Gyrus
IPL	Inferior Parietal Lobule
MEG	Magnetoencephalography
MEP	Motor Evoked Potential
MMN	Mismatch Negativity
PMBS	Post-Movement Beta Synchronization
PMC	Premotor Cortex
pMTG	Posterior Middle Temporal Gyrus
pSTG	Posterior Superior Temporal Gyrus
rTMS	Repetitive Transcranial Magnetic Stimulation
SFC	State Feedback Control
SIS	Speech Induced Suppression
SNR	Signal to Noise Ratio
spTMS	Single Pulse Transcranial Magnetic Stimulation
STG	Superior Temporal Gyrus

CHAPTER 1. INTRODUCTION

Anterior (i.e., motor/premotor cortices) and posterior (i.e., primary and association auditory cortices) portions of the dorsal stream sensorimotor speech network, linking sound to action (Hickok and Poeppel, 2000; 2004; 2007), activate during speech production, facilitating online monitoring of speech by internal modeling (Jenson et al., 2014; Jenson et al., 2015). Activation of this same network also occurs during speech perception (Callan et al., 2006a; Osnes et al., 2011; Bowers et al., 2014), though the level of activity appears task specific (Sato et al., 2009; Fowler and Xie, 2016) and is thought to be correlated with task demands (Alho et al., 2012a; Deng et al., 2012; Peschke et al., 2012; Alho et al., 2014) and task goals (Wostmann et al., 2017). In contrast to passive perception, active discrimination tasks require subjects to attend to stimuli, perform some sensory processing, and retain the stimuli in working memory prior to response. However, it remains unclear how these cognitive demands affect sensorimotor processing. In order to address this question, it is necessary to consider dorsal stream activation in speech perception in light of the tasks that elicit it. Specifically, dorsal stream activity must be examined with respect to the contributions of attention (Mottonen et al., 2014) and working memory (Heald and Nusbaum, 2014; Ritz, 2016; Thornton et al., 2017) to task demands and goals (Wostmann et al., 2017).

To delineate the contributions of cognitive process such as attention (i.e., focus of processing) and working memory to sensorimotor processing, it is necessary to consider how dorsal stream activity unfolds over time. While attention is required for all perceptual tasks, early dorsal stream activity may be linked to the heightened attentional demands (Alho et al., 2014) imposed by difficult tasks through both predictive and inhibitory processes. Predictive Coding (Rao and Ballard, 1999; Kilner et al., 2007; Sohoglu et al., 2012) emerges during heightened attentional states (e.g., expectation) and relays motor-based predictions to sensory regions through forward internal models (i.e., motor to sensory projections) to instill production-based constraints on upcoming sensory analysis (Skipper et al., 2017). Concurrent with Predictive Coding processes, early inhibitory processes mediate attentional demands through resource allocation (Brinkman et al., 2014; van Diepen and Mazaheri, 2017). Activity emerges in cortical regions processing the stimuli of interest, while regions processing other types of information are inhibited (Jensen and Mazaheri, 2010; Haegens et al., 2012). For example, in dichotic listening paradigms, inhibitory activity emerges over the hemisphere processing information to be ignored (Frey et al., 2014), thus preferentially allocating cognitive resources to the region processing the target sensory stream. Thus, dorsal stream activity while awaiting a stimulus may represent both predictive and inhibitory contributions to sensorimotor processing. Dorsal stream activity can also occur during stimulus presentation. This activity may index automatic sensory to motor mapping (i.e., inverse models), consistent with reports of dorsal stream recruitment in passive perception tasks that can be achieved with minimal attention (Pulvermuller et al., 2006; Wilson and Iacoboni, 2006; Santos-Oliveira, 2017). Dorsal stream activity may also occur following speech perception, such as in discrimination tasks requiring categorization or decision-making (Callan et al., 2010; Bowers et al., 2013). This activity may reflect the retention

and processing of stimuli in phonological working memory (Baddeley, 2003; Hickok and Poeppel, 2007). This aligns with previous reports that working memory mediates dorsal stream contributions to perceptual tasks (Lutzenberger et al., 2002; Hickok and Poeppel, 2004; Buchsbaum et al., 2005; Herman et al., 2013). In light of the time-varying contributions of cognitive processes to sensorimotor processing, temporally precise neural data is necessary to address the critical question of when the dorsal stream activates during speech perception tasks (Skipper et al., 2017).

The precise temporal resolution of electroencephalography (EEG) makes it a prime avenue for charting the temporal profile of dorsal stream activity in speech perception tasks. EEG is sensitive to the sensorimotor mu rhythm, typically recorded over anterior dorsal stream regions (Tamura et al., 2012; Jenson et al., 2014; Denis et al., 2017) and consisting of peaks in alpha (~10 Hz; sensory) and beta (~20 Hz; motor) frequency bands (Hari, 2006). Event related spectral perturbations (ERSP) are time-frequency analyses that can be applied to the mu rhythm to reveal patterns of enhancement (event related synchronization; ERS) and suppression (event related desynchronization; ERD) corresponding to cortical inhibition and disinhibition, respectively. While generally linked to motor processing, early mu beta ERD in perception tasks has been considered a measure of motor-based prediction (Arnal and Giraud, 2012), serving to focus attention on relevant stimulus features (Alho et al., 2014; Schwager et al., 2016). When characterized by ERS, early mu alpha activity has been linked to inhibitory sensory gating (Klimesch et al., 2007; Jensen and Mazaheri, 2010; Schroeder et al., 2010) and maximizing resource allocation (Brinkman et al., 2014), both processes that enhance attention. Mu alpha ERD has been reported during perception of biologically relevant movements (Muthukumaraswamy and Johnson, 2004; Oberman et al., 2005; Crawcour et al., 2009; Frenkel-Toledo et al., 2013) and sounds (Pineda et al., 2013), suggesting sensory to motor processing. These findings have been interpreted to suggest a contribution of alpha activity to inverse modeling (Sebastiani et al., 2014). Both alpha and beta bands of the mu rhythm have a demonstrated sensitivity to speech (Bowers et al., 2013; Bartoli et al., 2016; Mandel et al., 2016; Saltuklaroglu et al., 2017), and thus ERSP analysis of the mu rhythm may capture the contributions of internal modeling and inhibitory processes across the time course of speech processing. The dynamics of mu alpha and mu beta activity across the time course of speech perception may identify early predictive coding/inhibitory activity, peri-stimulus sensory processing, and late activity corresponding to working memory maintenance.

To assess the contributions of these processes in speech perception, Jenson et al. (2014) employed Independent Component Analysis (ICA; Stone, 2004) to identify the mu rhythm during accurate discrimination of /ba/ /da/ syllable pairs in quiet and noisy backgrounds. Discrimination accuracy was high (above 95%) and did not differ between quiet and noisy backgrounds. ERSP decomposition of data from correctly discriminated trials revealed activity characterized by beta ERD and alpha ERS in the pre-stimulus period and persisting through stimulus presentation. While present in both quiet and noisy backgrounds, alpha ERS appeared stronger in the presence of noise. Post-stimulus activity was marked by the emergence of robust alpha and beta ERD. The authors interpreted these findings as evidence of predictive coding (beta) and inhibitory control

(alpha) during the pre-stimulus window, followed by working memory maintenance via covert rehearsal in the post-stimulus window. However, questions remain regarding how early and late activity reflects the contributions of sensorimotor activity to cognitive processes in the service of task demands.

First, the relationship between stimulus predictability and pre-stimulus beta activity remains unclear. Pre-stimulus mu activity from both quiet and noisy discrimination tasks was characterized by beta ERD, which Jenson et al. (2014) interpreted under the framework of Analysis by Synthesis (Stevens and Halle, 1967; Bever and Poeppel, 2010) as evidence of predictive coding. It should be noted that as the study required discrimination of /ba/ /da/ syllable pairs, only four stimulus combinations were possible, and the stimuli employed in Jenson et al. (2014) were thus highly predictable. Pre-stimulus beta ERD was therefore considered evidence of a motor-based hypothesis, derived on the basis of context (e.g., predictability) and constituting a forward model projection to auditory regions for comparison with the incoming acoustic signal. This aligns with previous reports that context modulates sensory processing (Skipper et al., 2007b; Sohoglu et al., 2012; Kleinsorge and Scheil, 2016; Sohoglu and Davis, 2016), and that the selective attention enabled by this predictive activity (Alho et al., 2014) is mediated by the beta band (Arnal and Giraud, 2012; Bastos et al., 2012; Bressler and Richter, 2015; Gao et al., 2017). In contrast to Jenson et al. (2014), Thornton et al. (2017) employed 18 possible stimulus combinations in a pseudo-word discrimination task that required segmentation. Thornton et al. (2017) did not observe pre-stimulus mu beta ERD, raising the possibility that the larger stimulus set size made individual stimulus pairs less predictable, thus reducing subjects' ability to predictively code. This aligns with notions that the demands associated with correcting an erroneous prediction (Philipp et al., 2008) constrain predictive coding to situations in which predictions are likely to be reliable (Kleinsorge and Scheil, 2016). However, as Jenson et al. (2014) and Thornton et al. (2017) differed in regard to stimulus length/complexity and the presence of a segmentation requirement, it is necessary to examine pre-stimulus mu beta ERD in tasks employing large and small set sizes in the same study to clarify the effect of stimulus predictability on predictive coding. A difference between small and large set sizes suggests that stimulus predictability modulates predictive coding, while the absence of an effect may be interpreted to suggest that set size does not modulate stimulus predictability.

The second problem pertains to the interpretation of early alpha activity. Jenson et al. (2014) identified pre-stimulus mu alpha ERS persisting through stimulus presentation in both quiet and noisy discrimination conditions, though it appeared stronger in the presence of noise. As alpha activity is associated with attentional modulation (Pesonen et al., 2006; Sadaghiani et al., 2010; Wostmann et al., 2017), Jenson et al. (2014) interpreted pre-stimulus alpha ERS as an index of inhibitory control (Klimesch et al., 2007; Jensen and Mazaheri, 2010; Schroeder et al., 2010) over sensorimotor processing in the service of task demands. Since alpha ERS was present in quiet, some portion of this pre-stimulus activity may be interpreted as the allocation of cognitive resources (Perry and Bentin, 2010; Brinkman et al., 2014) to achieve successful discrimination. However, it must be noted that noise masking was present throughout the

pre-stimulus period in Jenson et al. (2014). It therefore remains unclear whether the increased alpha ERS in noisy discrimination reflects additional resource allocation to meet the increased processing demands associated with degraded stimuli (Downs and Crum, 1978) or represents the inhibition of noise via sensory gating (Stenner et al., 2014). Inhibition of information detrimental to task goals (Wostmann et al., 2017) via sensory gating has been linked with alpha ERS across sensory modalities (Mathewson et al., 2011; Haegens et al., 2012; Hartmann et al., 2012), suggesting that the increased alpha ERS in noisy discrimination may represent gating of the noise masking. Removing bands of spectral information from the speech signal (Gilbert and Lorenzi, 2010; Ramos de Miguel et al., 2015) provides a way to control the time course of increased task demands without introducing a competing signal, thereby delineating the contributions of resource allocation and sensory gating to pre-stimulus alpha ERS. Increased alpha ERS throughout the pre-stimulus period in band-removed discrimination tasks supports interpretations of increased resource allocation, while the emergence of increased alpha ERS during stimulus presentation suggests an attempt to inhibit irrelevant information via sensory gating. A clearer understanding of the role of pre-stimulus alpha activity is critical to clarifying the way in which activity across alpha and beta channels of the mu rhythm cooperate to support speech perception (Bastos et al., 2012; Brinkman et al., 2014).

The third problem pertains to the interpretation of activity following stimulus offset. Post stimulus activity in Jenson et al. (2014) was marked by robust ERD in both alpha and beta bands of the mu rhythm. This finding has been observed in speech discrimination tasks across multiple studies (Bowers et al., 2013; Saltuklaroglu et al., 2017; Thornton et al., 2017), suggesting that late mu ERD may characterize neural responses to speech discrimination. Based on the similarity of these patterns to those reported in overt speech production (Gunji et al., 2007; Tamura et al., 2012; Jenson et al., 2014) as well as previous reports of alpha and beta ERD in working memory (Tsoneva et al., 2011; Behmer and Fournier, 2014) and motor imagery tasks (Brinkman et al., 2014; Li et al., 2015), the authors interpreted post-stimulus mu activity as evidence of covert rehearsal to retain the stimuli in working memory (Hickok et al., 2003). This is consistent with the notion of covert production being instantiated by paired forward and inverse models (Pickering and Garrod, 2013) and the association of beta and alpha mu frequency bands with these models, respectively. However, it should be noted that when asked, subjects did not report covertly replaying the stimuli and interpretations of covert rehearsal therefore require further validation. As the forward internal models involved in covert production (Tian and Poeppel, 2010; 2012; Pickering and Garrod, 2013; Tian and Poeppel, 2013) are known to have an inhibitory effect on posterior dorsal stream (i.e., auditory) activity (Kauramaki et al., 2010; Tian and Poeppel, 2015), this suggests that analysis of temporally sensitive data from auditory regions during speech discrimination may clarify interpretations regarding post-stimulus mu activity. Specifically, activity in posterior dorsal stream regions may be viewed alongside anterior dorsal stream activity to validate notions of covert rehearsal.

To investigate activity in posterior dorsal stream regions, Jenson et al. (2015) employed ICA/ERSP to identify and decompose the auditory alpha rhythm from the same

dataset as Jenson et al. (2014). The auditory alpha is an oscillatory rhythm localized over posterior dorsal stream regions (i.e., posterior superior temporal gyrus; pSTG) and responsive to auditory stimulation (Tiihonen et al., 1991; Lehtela et al., 1997; Weisz et al., 2011). Auditory alpha responses are characterized by ERD during perception of speech (Weisz et al., 2011; Muller et al., 2015), and have been linked to cortical disinhibition to facilitate stimulus processing (Lehtela et al., 1997; Muller and Weisz, 2012). In contrast, auditory alpha ERS emerges during active inhibition of distractors (Muller and Weisz, 2012; van Diepen and Mazaheri, 2017; Wostmann et al., 2017). This alpha inhibitory effect has been documented across sensory modalities (Foxe et al., 1998; Worden et al., 2000; Mathewson et al., 2009; Hartmann et al., 2012), suggesting a contribution of amodal attentional mechanisms (Haegens et al., 2012) to acoustic stimulus processing. Jenson et al. (2015) identified auditory alpha ERS following stimulus offset, which was interpreted through the framework of Gating by Inhibition (Jensen and Mazaheri, 2010) as a marker of functional deactivation of auditory regions. Based on the temporal alignment of auditory alpha ERS and the mu ERD in Jenson et al. (2014), the authors suggested that a forward model arising from covert production (Tian and Poeppel, 2010; 2013) inhibited auditory activity akin to speech-induced suppression reported in overt speech tasks (Curio et al., 2000; Houde et al., 2002; Heinks-Maldonado et al., 2005). However, this interpretation is circumstantial, based on patterns of temporal concordance between mu ERD and auditory alpha ERS. In order to more fully interrogate Jenson et al. (2015) interpretation of post-stimulus activity as forward model inhibition of auditory regions during covert rehearsal, it is necessary to consider interactions between mu and auditory alpha rhythms across the time course of speech perception.

Despite evidence of motor-auditory communication during speech perception (Gow Jr and Segawa, 2009; Park et al., 2015), interpretation is hampered by two primary weaknesses. First, data from alpha and beta bands is lacking, a critical omission given the spectral profile of mu and auditory alpha rhythms and the proposed role of alpha and beta bands in mediating sensorimotor transformations between them. Second, the way in which patterns of information flow unfold over time remains unclear, a critical weakness considering timing and direction of information flow respond dynamically to tasks (Fontolan et al., 2014). Temporally sensitive measures of connectivity between mu and auditory alpha rhythms within alpha and beta bands may be viewed alongside focal time-frequency activation patterns to supplement interpretations regarding dorsal stream dynamics during speech perception. Phase synchronization (i.e., coherence) constitutes the principal method for inter-areal communication across the cortex (Fries, 2005; Weisz and Obleser, 2014), and has been successfully measured with ICA decomposed EEG data (Hong et al., 2005), suggesting its suitability to the mu and auditory alpha source signals to be identified by ICA in the current study. While phase coherence is a measure of functional connectivity (Friston, 2011), agnostic to the direction of information flow, theoretical interpretations of beta and alpha bands as indices of forward and inverse modeling, respectively, may enable the interpretation of directionality. Specifically, forward modeling should be revealed by mu-auditory coherence in the beta band, while inverse modeling will be revealed by mu-auditory coherence in the alpha band. This potential for the assessment of directionality allows testing of hypotheses regarding

forward and inverse internal model contributions to dorsal stream activation in speech perception.

The overarching goal of the current study is to better understand early and late dorsal stream activity in light of the cognitive demands imposed by speech discrimination tasks. The specific goals are to address the questions highlighted above by 1) determining the effect of set size on predictive coding, 2) clarifying the contributions of resource allocation and sensory gating to pre-stimulus inhibitory mu alpha by manipulating the time course of increased task demands, and 3) better understanding the role of sensorimotor activity while stimuli are held in working memory. Consistent with predictive coding accounts, it is first hypothesized that pre-stimulus mu beta ERD will be stronger in conditions with a smaller stimulus set size, and that pre-stimulus coherence measures will demonstrate beta band coupling between mu and auditory alpha rhythms. In accord with the notion that pre-stimulus alpha is sensitive to both resource allocation and sensory gating, it is hypothesized that differences in alpha ERS will be found between quiet, noise masked, and filtered discrimination tasks. Finally, in line with the notion that internal models mediate dorsal stream contributions to sensorimotor processing, it is hypothesized that coherence measures will identify patterns of forward and inverse internal models across the time course of speech perception. Support of these hypotheses will clarify dorsal stream contributions to perceptual processes and their relationship to the underlying cognitive demands.

CHAPTER 2. LITERATURE REVIEW

The Dorsal Stream

The dorsal stream network consists of anterior motor (i.e., premotor/primary motor cortices) and posterior sensory (i.e., auditory and somatosensory cortices) regions (Hickok and Poeppel, 2000; 2004; 2007). The dynamics of this dorsal stream network have been thoroughly investigated in speech production paradigms (Houde and Nagarajan, 2011; Kell et al., 2011; Gehrig et al., 2012; Hickok, 2012; Rauschecker, 2012; Herman et al., 2013; Cogan et al., 2014; Tian and Poeppel, 2015; Ylinen et al., 2015) and tied to the process of internal modeling. Forward internal models constitute a mapping from the motor domain to the sensory domain and have been considered a mechanism for the motor control system to predict the sensory consequences of an upcoming motor plan (Blakemore et al., 2000; Wolpert and Flanagan, 2001). Conversely, inverse internal models constitute a mapping from the sensory domain to the motor domain and have been considered a mechanism for implementing corrective motor commands based on detected (Tourville and Guenther, 2011; Guenther and Vladusich, 2012) or predicted (Houde and Nagarajan, 2011; Houde and Chang, 2015) sensory discrepancies. These internal model sensorimotor transformations are vital to efficient speech production as motor control is implemented in the motor domain yet gives rise to a signal in the sensory domain. Co-activation of anterior and posterior dorsal stream regions during speech production has thus been considered a reliable index of internal modeling.

Activation of this dorsal stream network has also been reported in a variety of speech perception tasks (Davis and Johnsrude, 2003; Giraud et al., 2004; Callan et al., 2010), and interpreted to suggest an essential contribution of motor regions to speech perception. However, this interpretation has been questioned by authors who either fail to find anterior dorsal stream activity (Menenti et al., 2011), or have found that such activation is not specific to speech (LoCasto et al., 2004; Agnew et al., 2011; Rogalsky et al., 2014). The role of the dorsal stream in speech perception is thus hotly debated (Meister et al., 2007; Möttönen and Watkins, 2009; Bever and Poeppel, 2010; Hickok et al., 2011b; Fowler and Xie, 2016). Central to these equivocal findings is the diversity of tasks that have been employed, each imposing distinct task demands requiring differential contributions of underlying cognitive processes. Given reports that cortical networks dynamically reorganize in response to task (Skipper et al., 2017), it may be proposed that differential task demands underlie the equivocal findings regarding anterior dorsal stream involvement in speech perception. It is therefore critical to consider experimental findings in light of the tasks that elicit them.

Necessity of Considering Cognitive Processes in Speech Perception

Passive speech perception tasks provide a unique window into dorsal stream processing of speech, as neural responses are uncontaminated by decision-making and response selection. A number of functional magnetic resonance imaging (fMRI) studies

have reported anterior dorsal stream activation during the passive perception of speech. Wilson et al. (2004) reported that bilateral motor and premotor regions active during the production of meaningless CV syllables also activate during perception of the same syllables, which the authors interpreted as evidence for the mapping of acoustic input to a phonetic code. Similarly, Callan et al. (2006b) identified bilateral premotor cortex (PMC) activity to the passive perception of both spoken and sung speech, with greater right hemisphere activity noted for sung speech in accord with notions of right hemisphere processing of prosodic features (Poeppel, 2003). Wilson and Iacoboni (2006) investigated responses to auditory presentation of native and non-native syllables. PMC activity was reported to all stimuli, with greater activity noted for non-native syllables. This elevated response to non-native stimuli was interpreted to suggest that motor regions respond dynamically to stimuli even in the absence of directed attention. Taken together, these findings suggest that anterior motor regions reliably activate during the passive perception of speech. However, as Binder et al. (2008) reported bilateral PMC activation during passive perception of both syllables and tones, it remains unclear whether anterior dorsal stream activations during perception tasks are speech specific.

Evidence for a speech specific activation profile for the anterior dorsal stream comes from studies demonstrating somatotopic specificity during passive tasks. Pulvermüller et al. (2006) identified /p/ and /t/ specific regions of motor cortex with fMRI during overt production, reporting that regions involved in production of /p/ or /t/ activated preferentially to the passive presentation of compatible stimuli (though see Arsenault and Buchsbaum, 2016 for a failure to replicate this finding). An alternative line of evidence demonstrating somatotopic activation of motor regions comes from a set of studies employing single pulse transcranial magnetic stimulation (spTMS) to assess articulator-specific motor evoked potentials (MEP) during speech perception. Fadiga et al. (2002) employed spTMS over tongue motor cortex during the passive perception of disyllabic (CVCV) stimuli in which the second syllable was initiated by either an alveolar trill (i.e., /r/) or labiodental fricative (i.e., /f/). MEPs recorded from anterior tongue muscles were larger for stimuli with embedded alveolar trills, with the authors suggesting that the greater tongue tip mobilization required for production of an alveolar trill gave rise to the enhanced MEPs through mediation by the human mirror neuron system (Rizzolatti and Craighero, 2004; Fadiga et al., 2005). In a similar vein, Watkins et al. (2003) assessed the modulation of MEPs from the orbicularis oris by spTMS to bilateral labial motor cortex during the passive perception of auditory speech, non-speech auditory signals, visual speech, and non-speech facial movements. Enhanced MEPs were noted to both auditory speech and visual speech (see Sundara et al., 2001 for reports of modality-specific MEP modulation), with the authors tying this finding to motor resonance, akin to the mirror neuron interpretation of Fadiga et al. (2002). While evidence of somatotopic activation suggests speech specific response properties for the anterior dorsal stream, it remains unclear whether this represents a coarse articulator-specific effect or a precise articulatory-kinematic effect. D'Ausilio et al. (2014) paired spTMS of tongue motor cortex with Doppler ultrasound of the oral cavity during passive perception of /ki/, /ko/, /ti/, and /to/ syllables, with lingual motor synergies paralleling those generated by production of the same syllables. This finding suggests that anterior dorsal stream

activation in passive perception is specific to the articulatory kinematics of the perceived stimulus.

The presence of this articulatory-kinematic specific activation of motor regions during passive speech perception has been interpreted to suggest that anterior dorsal stream activity represents an inverse mapping from acoustic stimulus to a phoneme-specific motor code (Correia et al., 2015). This notion aligns with the tenets of Direct Realism, which proposes that motor activation is a default concomitant of perception, rooted in the embodied nature of language and cognition (Fowler, 1986; Fowler et al., 2003; Fowler and Xie, 2016). That is, these anterior motor regions do not actively contribute to speech perception but represent an automatic acoustic-articulatory inverse mapping that occurs irrespective of task. While this interpretation for anterior dorsal stream activity is consistent with the results from passive tasks reviewed above, an alternative explanation is needed to account for the results of studies demonstrating behavioral effects when activity in anterior dorsal stream regions is externally modulated (Grabski et al., 2013).

Disruption of anterior dorsal stream activity through repetitive transcranial magnetic stimulation (rTMS) is known to lead to decreased performance in syllable identification and discrimination tasks. Möttönen and Watkins (2009) applied rTMS to lip motor cortex during the identification of ambiguous phonemes along a place of articulation continuum as well as discrimination of unambiguous syllable pairs. A reduced category boundary slope was noted for the ambiguous phonemes and discrimination accuracy was impaired in discrimination, though these effects only emerged in the presence of bilabial sounds. In a follow up task evaluating the mismatch negativity (MMN) to trains of syllables and tones under rTMS to lip motor cortex, Mottonen et al. (2013) confirmed the specificity of the effect to speech stimuli, though it should be noted that this effect only emerges when attention is directed to the auditory stimuli (Möttönen et al., 2014). Similar effects have been noted with stimulation of the PMC. Meister et al. (2007) applied rTMS to left PMC or left superior temporal gyrus (STG) while subjects discriminated voiceless stop consonants, noting decreased performance for syllable discrimination with PMC stimulation only. The authors interpreted these findings to suggest that PMC is essential for speech perception. However, this interpretation has been questioned by Sato et al. (2009) who applied rTMS or sham stimulation to left PMC during phoneme identification, syllable discrimination, and phoneme discrimination requiring segmentation. There was an increase in reaction time with stimulation on the phoneme discrimination task only, suggesting that contributions of PMC may be task specific.

The notion of task specific contributions of the dorsal stream is also suggested by D'Ausilio et al. (2012) who monitored the effect of spTMS to lip and tongue motor cortex on identification of alveolar and bilabial syllables in quiet and noisy backgrounds. No effect was noted in quiet, while faster reaction times were noted during somatotopic stimulation (relative to stimuli) in the presence of noise (though see Bartoli et al., 2015 for reports of somatotopic response facilitation in quiet). The authors advanced the notion of task demands as a mediating factor on anterior dorsal stream activation during

speech perception, suggesting that degraded stimuli impose increased processing demands that must be addressed through attentional processes. A similar role of task demands was proposed by Sato et al. (2009) to explain the presence of an rTMS effect only in phoneme discrimination requiring segmentation, suggesting that working memory processes required for segmentation recruited anterior dorsal stream regions (Burton et al., 2000; LoCasto et al., 2004; Burton and Small, 2006). The presence of both attentional and working memory modulation of anterior dorsal stream activity is consistent with the view of speech perception as an active cognitive process (Heald and Nusbaum, 2014).

In summary, the available evidence suggests that anterior dorsal stream activity reported during speech perception is speech specific and occurs in the absence of active task demands. This may reflect the instantiation of an inverse internal model, consistent with the tenets of Direct Realism, or may also reflect the activity of an intrinsic speech-motor rhythm rooted in the underlying neural architecture (Assaneo and Poeppel, 2018). However, variable performance decrements following disruption to the anterior dorsal stream suggest that anterior motor activity contributes to perception, and that this contribution is mediated by the engagement of cognitive processes including attention and working memory to achieve task goals (Wostmann et al., 2017). Yet, the precise manner in which attentional and working memory processes mediate dorsal stream contributions to speech processing remains unclear, and thus further investigation is warranted.

Attentional Modulation of Dorsal Stream Activity in Speech Perception

In contrast to passive tasks, active tasks with increased attentional demands elicit higher levels of activation in the anterior dorsal stream (Binder et al., 2008; Osnes et al., 2011; Du et al., 2014), particularly in the left hemisphere. These increased activations may reflect the implementation of two distinct yet complementary processes, Predictive Coding (Rao and Ballard, 1999; Kilner et al., 2007; Sohoglu et al., 2012) and inhibitory control (Brinkman et al., 2014), for the purpose of accomplishing task demands (Wostmann et al., 2017). While they operate in tandem, both predictive and inhibitory processes are sensitive to distinct characteristics of the perceptual environment and must be considered individually.

Predictive Coding Contributions to Attention

Predictive coding is a component of Constructivist Analysis by Synthesis (Stevens and Halle, 1967; Bever and Poeppel, 2010; Poeppel and Monahan, 2011) theories, which propose that early motor-based predictions are generated in anterior dorsal stream regions on the basis of the available context and relayed via forward internal models to posterior sensory regions for comparison with the incoming stimulus (Poeppel et al., 2008). Following a comparison of prediction and afference, any mismatch (i.e., prediction error) is propagated up the cortical hierarchy via an inverse

internal model for hypothesis revision (Sohoglu et al., 2012). This hypothesis-test-refine process continues in an iterative manner until the sensory mismatch is reconciled and the stimulus is identified. Involvement of motor regions within this paradigm is deemed necessary based on the paucity of the acoustic signal and the lack of invariant phoneme-specific cues for perception (Liberman, 1957; Liberman et al., 1967; Galantucci et al., 2006). Predictive coding refers to the active generation of motor-based hypotheses within this framework, which is thought to focus attention on relevant stimulus features (Schwager et al., 2016).

This predictive coding mechanism was initially described in visual perception (Srinivasan et al., 1982), and much of its empirical validation has come through the visual modality (Rao and Ballard, 1999; Schellekens et al., 2016; Schindler and Bartels, 2017). However, behavioral evidence suggests that this predictive coding mechanism is both active in the auditory domain and sensitive to context across multiple sources. Perhaps the most well-known example is the McGurk-MacDonald effect, in which simultaneous presentation of an auditory /pa/ and visual /ka/ leads the perception of /ta/ (McGurk and MacDonald, 1976). This effect is thought to be mediated by the earlier arrival of visual cues, which provide viseme-based hypotheses (i.e., context) that constrain upcoming analysis of acoustic information (van Wassenhove et al., 2005; Skipper et al., 2007b). This interpretation aligns with experimental evidence demonstrating superior perception in noise for audio-visual compared to auditory only speech (Sumby and Pollack, 1954). Somatosensory stimulation is also known to mediate perception of speech, as demonstrated by Ito et al. (2009). Participants identified ambiguous syllables on the continuum of /həd/ to /hæd/ while their facial skin was stretched in a manner consistent with production of /həd/ or /hæd/. The psychometric profile was shifted by tactile perturbation, with subjects more likely to perceive stimuli in a manner consistent with the direction of skin stretching. Taken together, these studies suggest that auditory processing of speech may be influenced by the sensory context in which stimuli are presented. That is, predictions formulated on the basis of available context are relayed to sensory cortices, with the final percept resulting from the fusion of sensory streams. However, while visual and auditory concomitants of speech elicit sensory predictions, it remains unclear what other sources of context may be sufficient to elicit predictive coding.

Emerging evidence suggests that even non-articulatory context is sufficient to elicit predictive coding. For example, orthographic representations, which elicit abstract phonological forms and semantic concepts, have been shown to alter perception of aurally presented speech (Sohoglu et al., 2014). Sohoglu and Davis (2016) asked subjects to rate the perceptual clarity of monosyllabic words degraded through noise vocoding (Shannon et al., 1995), with each stimulus preceded by presentation of a matched, mismatched, or neutral orthographic representation. Matched orthographic primes enhanced the perceived clarity of stimuli, suggesting that they were mapped onto articulatory constraints to facilitate subsequent auditory processing. Predictions may also be based on syntactic constraints, as demonstrated by DeLong et al. (2005) through analysis of the N400 response as an index of prediction error in high cloze probability sentences. In addition to the expected effect of a greater N400 response for unpredicted

words, the authors reported an effect for the indefinite article associated with the predicted item. These findings may be interpreted to suggest that predictions are sensitive to both semantic and syntactic components of linguistic context (Pickering and Garrod, 2007). While the studies reviewed above provide ample support for the existence of predictive coding processes during speech perception and their sensitivity to a wide variety of contextual cues, it remains necessary to demonstrate that this hypothesis generation occurs in the anterior dorsal stream.

Several fMRI studies have linked elevated activity in anterior dorsal stream regions to predictive coding. Davis and Johnsrude (2003) required subjects to rate the intelligibility of degraded and non-degraded sentences, identifying increased activity over left inferior frontal gyrus (IFG) and PMC for degraded sentences. The authors interpreted these findings as the use of context to recover content that cannot be decoded from the sensory signal. Similarly, Clos et al. (2014) found increased left PMC and IFG activity while subjects discriminated a degraded target sentence and a degraded or non-degraded prior. PMC activity was found in all trials, while non-degraded trials were associated with stronger activity in IFG. Results were interpreted as support for predictive coding, with propositional (i.e., non-degraded) priors providing context for degraded targets. Blank and Davis (2016) presented subjects with degraded and non-degraded monosyllabic words preceded by a matched or mismatched orthographic cue, interpreting elevated activity in left PMC during presentation of degraded speech as a marker of predictive coding. Taken together, these studies suggest that left hemisphere anterior dorsal stream regions contribute to predictive coding. However, this interpretation is necessarily tentative based on the inability of fMRI to clearly delineate the time course of activity, and the sensitivity of these regions to task-related factors (Blank and von Kriegstein, 2013) such as decision-making and response selection (Binder et al., 2004).

A clear link between anterior dorsal stream activity and predictive coding may be derived from Skipper et al.'s (2007b) fMRI investigation of the McGurk-MacDonald effect. Skipper and colleagues identified a set of cortical regions (i.e., inferior frontal, premotor, and primary motor cortices) responsive to both perception and production of syllables that elicit the McGurk-MacDonald effect in participants who were and were not susceptible to the McGurk-MacDonald effect. Anterior motor responses from subjects who reported hearing the fusion percept (i.e., /ta/ to A_PV_K) were most like their responses to the veridical audio-visual /ta/ stimulus. In contrast, anterior responses from subjects prone to visual capture (i.e., /ka/ to A_PV_K) were most similar to their responses to the veridical audio-visual /ka/ stimulus. The authors interpreted these findings to suggest that frontal motor areas formulate early hypotheses rather than directly encoding sensory information. While clarifying the role that anterior motor regions play in perception, the results of Skipper et al. (2007b) still leave the time course of the observed effect unresolved. Sohoglu et al. (2012) addressed the lack of temporal specificity in predictive coding studies by employing joint EEG-magnetoencephalography (MEG) while subject rated the perceptual clarity of parametrically degraded words preceded by matching or mismatching orthographic primes, identifying differential effects of sensory detail and prior knowledge. Sensory detail modulated activity over posterior auditory regions (i.e.,

pSTG), while prior knowledge modulated activity over a patch of cortex encompassing left IFG, premotor, and motor cortices. The anterior effect temporally preceded the posterior effect, which the authors interpreted as evidence that top down predictions are compared against the incoming signal, and only unexplained information is propagated up the cortical hierarchy (Todorovic et al., 2011). Taken together, these studies provide strong support for the notion that anterior dorsal stream regions engage in active hypothesis generation during speech perception.

In summary, there is compelling behavioral evidence to suggest that the predictive coding mechanism described in the visual system also operates in the auditory system. These motor-based predictions may be elicited by context across a variety of areas including both the sensory concomitants of speech and more abstract phonological and linguistic cues. Both neuro- and electro-physiologic studies implicate anterior dorsal stream regions in the generation of these early motor-based hypotheses, which are thought to enhance attention by directing processing to relevant stimulus features (Schwager et al., 2016). A description of cortical processes supporting attention would not be complete, however, without considering the role of inhibitory control.

Inhibitory Contributions to Attention

Concurrent with implementation of predictive coding, attentional demands are also mediated by early inhibitory processes. fMRI studies have reported reduced activation of sensory cortex processing the unattended sensory modality in cross-modal attention studies. Johnson and Zatorre (2005) required subjects to identify target stimuli in unimodal (audio or visual) and bimodal (audiovisual) tasks, identifying reduced blood oxygen level dependent (BOLD) activity in the sensory cortex processing the non-presented modality in unimodal tasks and the non-target modality in bimodal tasks. The authors suggested this reduced activity was a gating of sensory input, enhancing the processing of one modality at the expense of the other. Similar findings were reported by Regenbogen et al. (2012), in which subjects completed a visual n-back task while being instructed to ignore a concurrent auditory oddball paradigm. Decreased activity over bilateral auditory cortices with increased visual working memory load was interpreted as allocation of cognitive resources to regions processing primary tasks when the brain is under high cognitive demands. While it is apparent that information in one sensory modality may be preferentially attended at the expense of another, it still remains to be demonstrated that such preferential processing occurs within the same sensory modality. In support of this notion, Amaral and Langers (2013) identified stronger BOLD activity in auditory cortex contralateral to the attended ear in a dichotic n-back task, interpreting their results as evidence of increased resource allocation. While these studies are consistent with notions of attentional modulation through inhibitory control, two primary questions remain. First, due to the limited temporal resolution of fMRI, the observed inhibitory activity cannot be clearly allocated to the pre-stimulus period. Second, as all studies included a distractor, it is not possible to determine whether this inhibitory activity reflects the gating of irrelevant information or the allocation of additional cognitive resources (Brinkman et al., 2014) to the target sensory stream.

The time course of inhibitory activity may be assessed by oscillatory dynamics, as activity within the alpha band (~10 Hz) is inversely correlated with the BOLD signal (Laufs et al., 2003; Brookes et al., 2005; Mayhew et al., 2013; Scheeringa et al., 2016), rendering alpha enhancement a temporally sensitive proxy for inhibition. The majority of the work investigating the role of alpha activity in selective attention has been performed in the visual modality. Bonnefond and Jensen (2012) recorded MEG during a modified Sternberg task with strong and weak distractors, interpreting greater occipital alpha enhancement preceding strong distractors than weak distractors as a gating of information detrimental to task performance. Both Rihs et al. (2007) and Worden et al. (2000) required subjects to respond with a button press to a visual stimulus in a cued location while recording EEG. In both studies, alpha enhancement was noted in the occipital lobe over the hemisphere processing the non-attended hemi-field. As no distractors were present, it was proposed that all information irrelevant to task performance is inhibited, not only stimuli specifically detrimental to task completion. The results of van Dijk et al. (2008), however, suggest a slightly more nuanced interpretation. Subjects discriminated pairs of visual stimuli of the same color or with barely detectable color differences (i.e., difference limen), with incorrectly discriminated trials characterized by greater occipital alpha power than correct trials. The authors interpreted this as a mechanism of gain control over the incoming sensory signal, and it must therefore be acknowledged that inhibitory control is likely more nuanced than a binary on/off mechanism. It remains to be demonstrated, however, that such an inhibitory gain control mechanism operates in the auditory domain.

Much of the evidence for inhibitory attentional control in the auditory modality is based on dichotic tasks. Muller and Weisz (2012) asked participants to identify target tones in a visually cued ear while recording the MEG signal. Alpha enhancement was noted over the auditory cortex ipsilateral to the cued ear (processing information from the unattended ear), which was interpreted as active gating of the non-target sensory stream. Similar results of a hemispheric laterality effect were reported by Frey et al. (2014) during a cued auditory identification task. However, based on the nature of dichotic tasks, it is not possible to determine whether the hemisphere effect indicates gating of irrelevant information or increased resource allocation to the target sensory stream. The results of van Diepen and Mazaheri (2017), in which subjects identified a target in a cued modality (auditory or visual) with or without a cross-modal distractor, suggests that these two effects may operate in concert. Conditions with a cross-modal distractor exhibited an early increase in alpha activity over the sensory cortex processing the non-cued modality, while conditions without a distractor did not elicit this alpha enhancement, suggestive of sensory gating. However, there was no difference in the absolute level of alpha power between these two conditions, leading the authors to interpret these findings as evidence of early top-down modulation of cognitive resource allocation in a task-dependent manner. Thus, it may be that early inhibitory activity in active perception tasks reflects the contributions of paired sensory gating and resource allocation processes to attention.

In summary, it is apparent that attentional demands are supported by early inhibitory activity to focus attention on relevant sensory information. This attentional

focus operates both between and within sensory modalities, including the auditory domain. Evidence suggests that both resource allocation and sensory gating processes may operate in concert to facilitate rapid and efficient stimulus processing. As these inhibitory processes are concurrent with the predictive coding mechanisms described above, it may be proposed that predictive and inhibitory attentional mechanisms function in tandem and are employed dynamically on the basis of task demands (Wostmann et al., 2017), characterizing early dorsal stream contributions to speech perception.

Working Memory Contributions to Dorsal Stream Activity in Speech Perception

In addition to a role in attention, it has been proposed that dorsal stream activation in speech perception tasks may be mediated by working memory processes (Hickok et al., 2003; Hickok et al., 2011b). This notion has been advanced in support of the perspective that anterior portions of the dorsal stream are not essential for speech perception, but that their activation simply represents an effect of task (Hickok et al., 2011a). Late dorsal stream activity in speech perception tasks may therefore be representative of the phonological loop component of Baddeley (2003)'s working memory model. Wilson (2001) reviewed the literature on working memory, deeming sensory only and motor only explanations insufficient to account for the diversity of experimental findings. Instead, Wilson (2001) proposed a sensorimotor coding scheme in which items are maintained in phonological storage but refreshed through articulatory rehearsal. This is consistent with the perspective of Buchsbaum et al. (2005), who dissociated an echoic memory system subject to rapid decay from an articulatory rehearsal mechanism, which can be updated endlessly. An articulatory rehearsal account of working memory is consistent with the findings of Ellis and Hennessey (1980), who performed digit span tasks with Welsh-English bilinguals. Within the same subject pool, memory span was longer for English than Welsh numbers, which the authors suggested was due to the longer articulation time for Welsh numbers. Similar results have been reported in other cross-language studies (Stigler et al., 1986), albeit not in within groups contrasts. While these studies suggest that working memory maintenance relies on articulatory processes, it remains unclear whether this articulatory rehearsal is responsible for dorsal stream activation in some speech perception tasks. To resolve this ambiguity, it is necessary to consider the imaging literature linking articulatory rehearsal processes to dorsal stream regions.

Both Burton et al. (2000) and LoCasto et al. (2004) required subjects to discriminate initial sounds in words and tone sequences both with and without segmentation requirements, noting increased hemodynamic activity in left IFG during trials requiring segmentation. This was considered evidence of motor recruitment to accomplish working memory demands through rehearsal mechanisms, though interpretations were tentative as the patterns of activity were not speech specific. Buchsbaum et al. (2001) required subjects to covertly produce pseudowords during a silent retention period, noting increased BOLD activity compared to passive perception in left IFG and PMC. IFG activation was considered evidence of articulatory rehearsal, with the authors stating that the role of PMC was less clear. Hickok et al. (2003)

employed a similar design, including a set of conditions with tonal stimuli. PMC and IFG activations were noted for both tonal and speech stimuli, and the authors proposed that both anterior motor regions participate in the process of articulatory rehearsal. Thus, while there appears to be consensus regarding involvement of the IFG in articulatory rehearsal, the inconsistent activation of the PMC in working memory tasks deserves further consideration.

The variable findings of PMC versus IFG activation in working memory tasks may be due to slightly different functions which are differentially recruited based on the demands of the specific task. Henson et al. (2000) required subjects to perform symbol matching, letter matching, letter probe, and sequence probe tasks while recording fMRI. Letters elicited greater activation than symbols in both IFG and PMC, consistent with previous reports implicating these regions in articulatory rehearsal. However, PMC was additionally associated with the sub-vocal rehearsal of serial order, a necessary process for the sequence probe task. A similar interpretation was advanced by Chein and Fiez (2001) to account for their results from a delayed pseudoword recall task with a prolonged retention period. Delayed recall elicited increased hemodynamic activity in left IFG and PMC, with IFG demonstrating a decreased activation profile along the time course of retention, while PMC activity was stable across this window. The authors interpreted their results to propose a two-stage mechanism for articulatory rehearsal, with the first stage capitalizing on the capacity of the IFG for articulatory recoding to generate an articulatory plan. In the second stage, this articulatory plan is continually executed, instantiated in PMC activity. This mechanism for articulatory rehearsal accounts for the ubiquitous activation of IFG in working memory tasks, as well as the more equivocal findings regarding PMC activity. Taken together these reports suggest a dynamic contribution of anterior dorsal stream regions to working memory processes in speech perception, though such an interpretation would be bolstered by a clear link between activation of these regions and working memory capacity.

In order to lend credence to this proposed articulatory rehearsal network for working memory, it is imperative to demonstrate a contribution to behavioral performance. Romero et al. (2006) employed rTMS over IFG, inferior parietal lobule (IPL), or the vertex while subjects performed digit span, phonological judgment, and visual judgment tasks, noting increased reaction times and decreased accuracy for digit span and phonological judgment tasks during rTMS to both IFG and IPL, while no effects were noted for vertex stimulation. The decreased performance corresponding to IFG stimulation was considered evidence for a role in articulatory rehearsal, while performance modulation associated with IPL activation was considered evidence that the phonological store must also be intact to enable effective rehearsal. Liao et al. (2014) applied rTMS and sham stimulation to left motor cortex while subjects performed modified Sternberg tasks with pseudowords, words, and Chinese characters, reporting slowed reaction times compared to sham stimulation for pseudowords and Chinese characters. As subjects reported employing articulatory recoding for pseudowords and covert tracing for Chinese characters, the authors suggested that motor representations are activated during retention when working memory demands increase, especially for stimuli that may benefit from a motor-based encoding scheme. The performance

decrement observed during exogenous inhibition of anterior dorsal stream activations during working memory tasks therefore suggests a role in stimulus retention via articulatory rehearsal.

In summary, there is strong support for the existence of a sensorimotor coding scheme for working memory maintenance implemented through articulatory rehearsal, an interpretation consistent with the phonological loop of Baddeley (2003). This articulatory rehearsal mechanism reliably activates anterior dorsal stream regions, though this likely indicates the recruitment of paired articulatory recoding and rehearsal mechanisms rather than a unitary process. Further bolstering the link between anterior dorsal stream activations and articulatory rehearsal based working memory maintenance is the performance decrease elicited by deactivation of anterior dorsal stream regions. When considered alongside the findings implicating the anterior dorsal stream in early attentional modulation through paired predictive and inhibitory processes, it becomes evident that the role of the dorsal stream in speech perception is multifaceted. Specifically, the contributions of the dorsal stream are dynamic across the time course of speech perception rooted in the rapidly fluctuating contributions of cognitive processes including attention and working memory to task demands. Thus, in order to clearly determine the contributions of each of these processes to speech perception, a temporally sensitive metric is needed which is capable of identifying the dynamic patterns of dorsal stream activation across the time course of perception events.

Electroencephalography and the Mu Rhythm

Temporally sensitive neural data reflecting the dynamic contributions of anterior dorsal stream regions to speech perception may be garnered through consideration of the sensorimotor mu rhythm. The mu is an oscillatory rhythm typically recorded over anterior dorsal stream regions (Tamura et al., 2012; Hauswald et al., 2013; Jenson et al., 2014; Friedrich et al., 2015; Denis et al., 2017) which captures sensorimotor contributions to both motor and non-motor (i.e., cognitive) tasks. While early descriptions of the mu rhythm focused on activity within the alpha (~10 Hz) band (see Fox et al., 2016 for a comprehensive review), multiple lines of evidence suggest that a complete characterization of the mu rhythm must consider activity across both alpha and beta (~20 Hz) frequency bands.

First, MEG work has identified unified mu rhythms with spectral peaks in both alpha and beta bands localized over anterior motor regions (Hari et al., 1997; Hari, 2006; Tiihonen et al., 1989). Second, the use of blind source separation techniques to decompose scalp-recorded EEG signals into a series of independent sources has revealed similar unified mu rhythms which can be localized to a point source over the anterior dorsal stream across a variety of tasks (Bowers et al., 2013; 2014; Cuellar et al., 2016; Jenson et al., 2014; 2015; Seeber et al., 2014). Finally, recent work demonstrates that while activity in alpha and beta bands may be highly correlated (Carlqvist et al., 2005; de Lange et al., 2008), there is evidence of dissociation (Brinkman et al., 2014), suggesting that they index distinct processes (Jurgens et al., 1995; Sugata et al., 2014). In support of

this notion, alpha and beta bands demonstrate different response profiles, with activity in the beta band sensitive to motor processes (Hari, 2006; Kilavik et al., 2013) and activity in the alpha band considered an index of sensory processing across modalities (Arroyo et al., 1993; Cheyne et al., 2003; Kuhlman, 1978; Tamura et al., 2012). Given these considerations, it is critical to consider activity within both bands of the mu rhythm in order to accurately describe the participation of anterior dorsal stream regions in speech perception.

The mu rhythm can be recorded through temporally sensitive instrumentation such as EEG and MEG and decomposed across time and frequency via ERSP to track the activity of the underlying neuronal assemblies across both alpha and beta bands. Increases in spectral power compared to baseline (ERS; enhancement) are considered a marker of cortical inhibition, while reduced spectral power (ERD; suppression) compared to baseline represents cortical disinhibition. By tracking the time course of ERS and ERD across alpha and beta frequency bands of the mu rhythm, it is therefore possible to ascertain the time-varying contributions of motor and sensory processes to speech perception tasks.

Mu Alpha

Despite the dual peak nature of the mu rhythm, a large number of studies probing sensorimotor dynamics have focused exclusively on the alpha band. In addition to the sensitivity of alpha oscillations to inhibitory gating and resource allocation discussed above, suppression of the alpha band of the mu rhythm has also been investigated as a proxy for the engagement of the mirror neuron system (Arnstein et al., 2011; Braadbaart et al., 2013), thought to provide the link between perception and action (Gallese et al., 1996; Rizzolatti et al., 1996; Rizzolatti and Craighero, 2004; Iacoboni, 2005; Iacoboni and Dapretto, 2006). Muthukumaraswamy and Johnson (2004) recorded EEG over central electrodes while subjects viewed a hand engaged in a neutral position, a precision grip, or a grasping motion, interpreting greater mu alpha suppression during perception of precision grip and grasping motions as preferential engagement of the mirror neuron system for goal-direction actions (Gallese et al., 1996). Similarly, Frenkel-Toledo et al. (2013) reported greater mu alpha suppression over central regions for the perception of grasping/reaching movements compared to non-biologic movements, suggesting that it represented a mirroring response. Ulloa and Pineda (2007) also reported greater mu alpha suppression during the perception of biologic versus scrambled point light representations, proposing that humans have a stored set of motor patterns that can be engaged by the mirror neuron system during the perception of familiar sequences. This interpretation is supported by Cannon et al. (2014), who identified greater mu alpha suppression during action observation for observers who had executed the action than for observers who had only observed the action. Results were interpreted to suggest that the mirror neuron system is more readily engaged when the observer is skilled at the observed task. This aligns with the findings of greater mu alpha ERD in experienced than novice tennis players during the perception of tennis shots reported by Denis et al.

(2017). In sum, these findings suggest that mu alpha ERD is sensitive to activity of the mirror neuron system.

Even though a clear relationship exists between mu alpha ERD and engagement of the mirror neuron system, few authors have extrapolated beyond mirror neuron accounts to propose a role for mu alpha as a marker for inverse modeling. Engagement of the mirror neuron system involves mapping from a sensory signal to a corresponding motor representation, with these sensory to motor mappings constituting an inverse model projection. In support of this notion, Sebastiani et al. (2014) presented subjects with videos of finger tapping movements, identifying alpha ERD in the MEG signal across the dorsal stream. The emergence of alpha ERD in a posterior to anterior direction was interpreted to suggest that mu alpha encodes an inverse model in action observation. This proposal is additionally consistent with reports of mu alpha suppression during passive limb movement (Kuhlman, 1978; Arroyo et al., 1993), in which inverse model transformations may be used to update the current state of the motor system. Thus, while it has been proposed that mu alpha is a reliable index of the mirror neuron system (Fox et al., 2016) (though see Hobson and Bishop, 2017 for a contrasting account), it must be considered that mu alpha ERD during perception tasks may be more parsimoniously interpreted as evidence of inverse modeling.

In summary, the alpha band of the mu rhythm is a rich source of information sensitive to a variety of cognitive processes engaged during speech perception. Specifically, mu alpha ERS is considered a metric of inhibitory contributions to attention, which may be engaged for the purpose of sensory gating or resource allocation processes. In contrast, mu alpha ERD during perception tasks likely reflects sensory to motor inverse model projections, a process commonly interpreted as evidence for engagement of the mirror neuron system. Given that inverse models may play a role in covert production (Pickering and Garrod, 2007; Pickering and Garrod, 2009; Pickering and Garrod, 2013) akin to the articulatory rehearsal mechanism underlying working memory, consideration of the temporal dynamics of mu alpha is expected to illuminate the contribution of attention and working memory across the time course of speech perception.

Mu Beta

In contrast to the role of mu alpha in inverse modeling, the beta band of the mu rhythm is typically considered to correspond to motor processing (Hari, 2006). It has been proposed that activity within the beta band of the mu rhythm during perception tasks may be involved in the generation of sensory predictions (Arnal et al., 2011; Arnal and Giraud, 2012), a process potentially mediated by forward internal models. This is consistent with various reports implicating beta oscillations in inter-areal communication encoding top-down signals (Kopell et al., 2000; von Stein and Sarnthein, 2000; Wang, 2010). However, in order to draw a clear connection between beta oscillations and forward models, it is necessary to consider the way in which mu beta responds during production tasks, as this is the environment in which forward models are often

considered. Beta suppression is a ubiquitous finding in tasks requiring a motor response, and does not appear to be effector specific, emerging over anterior motor regions during the movement of fingers (Stancak, 2000; Gaetz et al., 2010), wrist (Alegre et al., 2006), shoulder (Stancak et al., 2000), foot (Pfurtscheller and Lopes da Silva, 1999), and tongue (Crone et al., 1998; Cuellar et al., 2016). Of note, this effect also emerges during isometric contraction, when there is no overt displacement of the target effector (Nasser-oleslami et al., 2014). The pervasive nature of beta suppression during movement tasks has been interpreted to suggest a role in motor execution (Zaepffel et al., 2013), an assertion consistent with reports that an individual-specific threshold of absolute beta power must be reached before movement can be initiated (Heinrichs-Graham and Wilson, 2016). This also aligns with the role proposed for beta oscillations by Engel and Fries (2010), who suggested that it facilitated maintenance of the current sensorimotor state, while reduction in beta power facilitates a change in the status quo, enabling movement. While these findings clearly implicate beta oscillations in motor execution, the role proposed for mu beta ERD in perception necessitates disambiguation of neural responses corresponding to execution and forward modeling. Compelling evidence exists to suggest that mu beta ERD is sensitive to forward modeling.

First, beta ERD has been reported in motor imagery tasks, in which no motor act is executed. Di Nota et al. (2017) reported beta ERD over bilateral PMC when subjects engaged in kinesthetic motor imagery of a previously displayed ballet dance. Additionally, Yi et al. (2016) observed beta ERD over contralateral motor regions during the mental imagery of manual movement sequences. Similarly, Brinkman et al. (2014) reported beta ERD over contralateral sensorimotor cortex during a decision task based on manual motor imagery. As greater ERD was noted in trials with more possible responses, they suggested that larger cell assemblies were disinhibited on the basis of task difficulty. Krautner et al. (2014) employed execution and motor imagery of button press sequences, identifying beta ERD over contralateral motor regions during both tasks with stronger ERD during execution. They proposed that computation of movement parameters and execution of the motor act may both influence sensorimotor beta oscillations, consistent with a review by Kilavik et al. (2013). Despite apparent interpretational difficulties due to its sensitivity to multiple processes, the presence of beta ERD over motor regions during motor imagery suggests that it is not tied directly to motor execution but may also reflect motor planning.

Further support for the notion that mu beta ERD encodes motor planning arises from delayed response paradigms demonstrating beta suppression during the delay period. Zaepffel et al. (2013) required subjects to perform a grasping motion with a precision or non-precision grip and differential force magnitudes following cues about grip type, force load, both, or neither. Beta ERD emerged during the delay period only when the cue indicated the grip type, which the authors interpreted as contingent motor planning in motor/premotor regions, in which force cannot be encoded without the movement parameters. Critically, as subjects were anticipating movement in all trials, the beta ERD cannot be considered a general effect of movement expectation and is most parsimoniously considered planning for the specific movement. A similar interpretation was advanced by Alegre et al. (2006) to account for the beta ERD during the delay period

in a go/no-go paradigm involving wrist extension. Further confirming the preparatory/planning nature of mu beta ERD are the results of Kaiser et al. (2001), who instructed participants to perform finger-lifting movements upon hearing a response tone with the response side cued by either a spatially lateralized tone or phonological evaluation of a cue vowel. Beta ERD emerged earlier during the delay period for trials cued by lateralized tones than for trials cued by phonological analysis, which was interpreted as earlier response preparation based on the earlier availability of movement parameters. While beta ERD in motor imagery and delayed movement tasks is consistent with a role in motor preparation and planning, theoretical models of speech production must be considered in order to propose a role in forward modeling.

The anterior motor regions over which the mu rhythm is recorded (particularly PMC; (Hauswald et al., 2013; Cuellar et al., 2016), are integral to both the Directions Into Velocities of Articulators (DIVA; Guenther, 2016) and State Feedback Control (SFC; Houde and Chang, 2015) models of speech production. In DIVA, projections from the speech sound map in ventral PMC to primary auditory and somatosensory cortices encode the sensory predictions (i.e., forward models) defining the auditory and somatosensory target maps (Guenther, 2016). In contrast, SFC proposes that the PMC contains the predicted state of the vocal tract, with projections (i.e., forward models) to auditory and somatosensory cortices encoding sensory predictions against which refference is compared (Houde et al., 2014; Houde and Chang, 2015). In both DIVA and SFC, the issuance of these forward models occurs concurrent with motor execution, which aligns with the interpretations of Kraeutner et al. (2014) and Kilavik et al. (2013) regarding the sensitivity of beta ERD to multiple motor-based processes. The presence of beta ERD in delayed execution and motor imagery tasks additionally coheres with a simplified model presented by Tian and Poeppel (2012) in which they propose a role for forward models in mental imagery (i.e., covert production). It may be proposed then that in addition to a role in motor execution, beta ERD is sensitive to the generation of forward models in anterior dorsal stream regions. This is consistent with interpretations of reduced pre-movement beta ERD as weak forward modeling in clinical populations including those with Parkinson's Disease (Delval et al., 2006; Degardin et al., 2009; Heinrichs-Graham et al., 2014; Moisello et al., 2015), amyotrophic lateral sclerosis (Bizovicar et al., 2014), and schizophrenia (Bickel et al., 2012; Dias et al., 2013). Thus, while it is plausible based on empirical data and computational models to suggest that mu beta ERD reflects motor to sensory predictions (Arnal and Giraud, 2012) in perception tasks (though see Hickok, 2013 for a dissenting opinion), it is necessary to consider direct evidence from perception tasks for a role of forward internal models.

Despite the proposal of Arnal and Giraud (2012), clear evidence demonstrating a role for beta in sensory predictions during perception tasks is limited (Sedley et al., 2016). Haegens et al. (2012) recorded MEG while requiring subjects to discriminate near-threshold tactile stimuli in the presence of a contralateral tactile distractor, interpreting bilateral pre-stimulus beta ERD over somatosensory cortex as a predictive mechanism serving to enhance active stimulus processing. Schubert et al. (2009) employed a similar tactile discrimination task, with detected stimuli preceded by beta ERD first over frontal followed by central electrodes. The authors proposed that central

beta ERD represented a downstream measure of expectancy mediated by frontal beta activity. A similar predictive interpretation for beta ERD during perception was proposed by Sebastiani et al. (2014), who recorded MEG while subjects observed and performed complex finger tapping sequences. Beta ERD was identified over sensorimotor cortex during both execution and observation, with the authors suggesting that this activity reflected the predictive activation of forward internal models during action observation (Press et al., 2011; Leveque and Schon, 2013). While these studies suggest a role for mu beta ERD in forward model generation during perception tasks, it is not yet apparent that such a mechanism is engaged during auditory perception.

Few studies have directly assessed the predictive role of beta ERD in auditory perception, though the evidence that exists is consistent with the generation of forward models. Fujioka et al. (2012) presented subjects with isochronous stimulus trains, noting beta band phase synchrony between auditory cortices and anterior motor regions, consistent with the inter-areal communication effected by a forward model. In a follow up study, Fujioka et al. (2015) presented subjects with unaccented beats, instructing them to imagine them as either a march (2 step) or waltz (3 step) pattern, identifying stronger beta ERD prior to the onset of the first beat in each sequence. They proposed that beta modulation during the perception of rhythm reflects the transformation of timing information into a sensorimotor code. Under this framework beta ERD in perception may reflect timing-based predictions, in contrast to other authors who consider beta ERD an updating of the content of sensory predictions (Sedley et al., 2016). Thus, while there is compelling evidence to consider pre-stimulus beta ERD as a marker for forward model generation, further work is necessary to clarify the precise nature of the sensory prediction instantiated by this forward model.

In summary, as alpha and beta bands of the mu rhythm are reliable markers of inverse and forward modeling, respectively, reports that speech perception modulates activity within both bands (Bowers et al., 2013; Bartoli et al., 2016; Mandel et al., 2016; Saltuklaroglu et al., 2017) may be considered support for Constructivist proposals that predictive internal processes contribute to speech perception. ERSP analysis of the mu rhythm may be employed to ascertain the time course of forward and internal modeling contributions to speech perception in the service of task demands. Specifically, mu beta ERD across the time course of speech perception may index early predictive coding/inhibitory activity, peri-stimulus sensory processing, and post-stimulus activity reflective of working memory maintenance. Mu alpha activity, in contrast, may be interpreted to reflect sensory gating, resource allocation, and inverse modeling across the time course of perception events.

Internal Modeling in Speech Perception

To assess the contributions of internal modeling processes to speech perception, Jenson et al. (2014) recorded 64-channel EEG data while subjects discriminated /ba/ /da/ syllable pairs in quiet and noisy backgrounds. Discrimination accuracy was high (above 95%), and neural data from correctly discriminated trials were submitted to Independent

Component Analysis (ICA; Stone, 2004) to extract bilateral mu rhythms from the scalp recorded signal. ERSP decomposition of mu rhythms revealed distinct patterns of task-related power modulation in both alpha and beta bands. In both quiet and noisy discrimination conditions, pre-stimulus and peri-stimulus periods were characterized by beta ERD and alpha ERS. Pre-stimulus alpha ERS appeared stronger in the presence of noise, though this was not tested by direct statistical comparison. The post-stimulus period was characterized by robust ERD in both frequency bands of the mu rhythm in both quiet and noisy conditions. Patterns of mu rhythm modulation were similar bilaterally, though appeared stronger in the left hemisphere. Based on both this power difference and the well-documented left hemisphere preference for speech (Specht, 2014), only left mu activity was considered further. Pre- and peri-stimulus results were interpreted within the framework of Analysis by Synthesis, with beta ERD considered a measure of predictive hypothesis generation during the pre-stimulus window. Peri-stimulus beta ERD, in contrast, was interpreted as hypothesis testing against the afferent signal. Alpha ERS across the pre- and peri-stimulus epochs was interpreted as a measure of inhibitory control. Post-stimulus mu ERD was interpreted as evidence of internal modeling contributions to working memory maintenance (Baddeley, 2003) through covert rehearsal. However, it must be acknowledged that several pertinent questions remain regarding how early and late mu activity reflect the influence of cognitive processes on sensorimotor activity in the service of task demands.

Pre-stimulus Beta and Predictability

First, the relationship between pre-stimulus beta activity and stimulus predictability deserves further investigation. The interpretation of early beta ERD as predictive coding in Jenson et al. (2014) under the framework of Analysis by Synthesis was based on its presence prior to stimulus onset and the previously reviewed evidence implicating mu beta ERD in forward internal models. However, it should be noted that Analysis by Synthesis is generally considered in perceptual paradigms providing strong contextual cues. For example, discourse (Poeppel et al., 2008; Pickering and Garrod, 2009; Bever and Poeppel, 2010) and sentence-level comprehension tasks (Bendixen et al., 2014; Lewis and Bastiaansen, 2015; Lewis et al., 2016) provide robust semantic and syntactic cues. Audiovisual speech tasks (Skipper et al., 2007b; Olasagasti et al., 2015; Peelle and Sommers, 2015) provide early viseme-based cues, which invoke articulatory constraints regarding the auditory stimulus (Dubois et al., 2012). Orthographic (Sohoglu et al., 2012; 2014; Sohoglu and Davis, 2016) or pictorial (Kay et al., 1996; Cole-Virtue and Nickels, 2004; McKelvey et al., 2010) primes provide robust phonological and semantic contextual cues, respectively. It is unclear, however, what contextual cues are available to facilitate predictive coding during the discrimination of syllable pairs in isolation.

Context for prediction may have arisen from the nature of the task (i.e., /ba/ /da/ discrimination), in which only four syllable combinations were possible across the 160 trials (80 trials per condition). Moreover, each individual syllable could be predicted with 50% accuracy. Thus, it may be proposed that due to the small set size, stimulus

predictability was high enough to compensate for the lack of other contextual cues, thereby enabling predictive coding. This notion is plausible considering similar interpretations of pre-stimulus beta ERD as predictive coding during the discrimination/identification of syllable pairs drawn from small sets. Callan et al. (2010) identified pre-stimulus beta ERD over left PMC during the correct identification of /b/ and /d/ phonemes in noise, though not for either incorrect trials or for /a/ and /o/ phonemes. The authors interpreted pre-stimulus beta ERD within the framework of predictive coding, proposing that the absence of an effect during the identification of vowels was rooted in task difficulty, as background noise degrades consonant information more than vowel information. Task demands were also proposed as a mediating factor in the emergence of pre-stimulus mu beta ERD by Bowers et al. (2013) during the passive perception and active discrimination of syllable pairs and tone sweeps at low (-6 dB) and high (+4 dB) signal to noise ratios (SNR). Pre-stimulus beta ERD was present during active discrimination of syllable pairs, regardless of SNR, while it was absent during the active discrimination of tones as well as all passive tasks. The absence of pre-stimulus beta activity in the passive tasks suggests that predictions are only generated when required by the task, while the lack of an effect during tone discrimination precludes interpretation as a general attentional mechanism. Instead, the authors proposed that internal models are deployed in a predictive fashion to tune neural assemblies to expected stimulus features. Taken together, these studies suggest that, when using a small set, sufficient context exists to enable predictive coding with syllable stimuli, and that this predictive coding activity is encoded in the mu beta band.

Further support for the notion of a set size effect comes from the results of Thornton et al. (2017), who failed to find evidence of predictive coding during the discrimination of pseudo-word pairs with and without a segmentation requirement. In contrast to the studies discussed above, no pre-stimulus beta ERD was present in any condition. The authors suggested that based on the larger set size (18 distinct pseudo-word pairs), individual stimuli were less predictable (Kleinsorge and Scheil, 2016). This interpretation is consistent with the results of Tan et al. (2016), who investigated post-movement beta synchronization (PMBS) during a manual reaching task under rotational perturbation which was preceded by a priming period with either a random or stable rotational perturbation. Reduced PMBS in participants exposed to random priming environments was interpreted to suggest that in periods of elevated uncertainty, (i.e., when sensory consequences cannot be predicted), implementation and updating of internal models is reduced. In a series of studies investigating switch costs, Kleinsorge and Scheil have demonstrated a performance cost in terms of both speed and accuracy when an incorrect prediction must be corrected (Kleinsorge and Scheil, 2014; 2015; 2016). Paired with the reduced predictability of individual stimuli in Thornton et al. (2017), it may be proposed that the cost of correcting erroneous predictions constrains the implementation of predictive coding to situations in which predictions are expected to be reliable (Philipp et al., 2008), such as discrimination tasks involving a small stimulus set.

It should be noted, that in addition to stimulus set size, Thornton et al. (2017) and Jenson et al. (2014) differed in regard to stimulus length/complexity (CV syllables vs. CVC pseudo-words), the presence of a segmentation requirement, and the presence of

background noise, all parameters that exert a modulatory effect on task difficulty. As the contributions of anterior dorsal stream regions to speech perception are thought to be sensitive to task difficulty (Callan et al., 2010; Osnes et al., 2011; Alho et al., 2012a; Peschke et al., 2012; Alho et al., 2014), it may be proposed that the lack of pre-stimulus beta ERD in Thornton et al. (2017) represented differential dorsal stream recruitment by a parameter other than set size. It is unlikely, however, that different levels of dorsal stream recruitment are responsible for the difference in pre-stimulus beta activity between the two studies, considering the robust modulation of mu power during the peri- and post-stimulus periods in both studies. However, as the effect of large and small set sizes on predictive coding has not been investigated in the same study, it is necessary to demonstrate an effect of set size on pre-stimulus mu beta activity in the absence of other differential stimulus parameters. A pre-stimulus beta difference between small and large set sizes may be interpreted to suggest that set size modulates predictive coding through stimulus predictability, while the absence of an effect suggests that set size does not sufficiently modulate stimulus predictability to alter predictive coding.

Early Alpha ERS and Inhibitory Control

Second, the interpretation of early mu alpha activity in Jenson et al. (2014) remains unclear. Discrimination in both quiet and noisy backgrounds was characterized by ERS in the mu alpha band beginning prior to stimulus onset and persisting through stimulus presentation. Alpha ERS appeared stronger in the noisy discrimination condition, though this was not tested with direct statistical comparison. Alpha activity was interpreted as a form of active sensing (Schroeder et al., 2010), similar to that employed in the cocktail party effect, where selective attention to relevant speech cues filters out competing sensory signals (Bidet-Caulet et al., 2007; Zion Golumbic et al., 2012). The increased ERS in noise was considered sensory gating of the noise masker to enable accurate discrimination (Stenner et al., 2014). However, an alternative account must be considered as alpha ERS has also been linked to the allocation of additional cognitive resources (Brinkman et al., 2014) in service of task demands (see “Attentional Modulation Across the Dorsal Stream”). It may therefore be proposed that the increased alpha ERS in the presence of noise represents the allocation of additional cognitive resources to meet the increased processing demands associated with degraded stimuli (Downs and Crum, 1978; Wostmann et al., 2017).

A cognitive resource allocation account for increased mu alpha ERS suggests that additional processes outside of PMC, which compete for resources, are recruited during the discrimination of syllables in noise. Such an interpretation aligns with Giraud et al. (2004), who presented subjects with clear and noise degraded sentences, requiring them to judge whether the stimuli contained speech or noise. Following an intervening condition, in which subjects heard clear and degraded pairs of the same sentences together, subjects repeated the perceptual judgment task. Greater hemodynamic activity was found over left IFG when compared to the first exposure, which the authors interpreted as the implementation of an additional cognitive mechanism after subjects learned that noisy trials might contain meaningful cues. Similarly, Wild et al. (2012b)

reported a noise-elevated BOLD response over left IFG during the presentation of degraded over clear speech in the presence of auditory and visual distractors. Critically, this response only emerged when subjects were cued to attend to the speech stimuli; it was absent when subjects were cued to attend to either of the distractors. This was interpreted as evidence that additional cognitive processes are engaged when subjects are attending to degraded speech, a finding supported by a differential attention effect on recognition performance for clear and degraded stimuli. As the left IFG is thought to house a ‘mental syllabary’ containing speech sound motor programs (Tourville and Guenther, 2011; Guenther and Vladusich, 2012), these reports of increased left IFG during the perception of degraded speech may be interpreted as greater recruitment of the mental syllabary. Given the proximity between IFG and PMC, alpha ERS over PMC may be a necessary mechanism to minimize competition for metabolic and cognitive resources. Of note, resource allocation levels may be set in advance of task initiation (van Diepen and Mazaheri, 2017), which gives rise to a conundrum regarding interpretations of increased alpha ERS during noisy discrimination in Jenson et al. (2014).

Specifically, based on the presence of noise masking throughout the pre- and peri-stimulus windows in Jenson et al. (2014), the time courses of increased alpha ERS predicted by both sensory gating and resource allocation mechanisms are identical. Consequently, it is not possible to unequivocally ascribe a function to the increased alpha activity present during syllable discrimination in a noisy background. Doing so requires a task in which resource allocation and sensory gating would elicit differential temporal patterns of alpha ERS. Robust filtering, in which some frequency bands are removed from the signal, provides an avenue to degrade the stimulus without introducing a masking signal which must be gated (i.e., inhibited) during the pre-stimulus period. Filtering has been employed to assess neural (Carter et al., 2013; Easwar et al., 2015a; b) and behavioral (Ardoint and Lorenzi, 2010; Martin et al., 2012; Freyman et al., 2013) responses to degraded stimuli in both clinical (Vinay and Moore, 2010; Goswami et al., 2016) and non-clinical (Martin et al., 2012; Leibold et al., 2014; Ramos de Miguel et al., 2015) populations. As robust filtering elicits differences in the intelligibility of resulting stimuli (Gilbert and Lorenzi, 2010), it may provide a means of signal degradation that does not depend on a competing stimulus (i.e., noise). By degrading speech stimuli with both filtering and noise masking methods, it is possible to disentangle resource allocation and sensory gating explanations for the increased early alpha ERS present during discrimination in noise. No difference between filtered and noise masked conditions is most consistent with allocation of additional cognitive resources secondary to the increase in task difficulty, while an alpha power difference in the pre-stimulus window is most consistent with sensory gating accounts. Clarifying the role that pre-stimulus alpha activity plays during the perception of degraded speech is critical to understanding the way in which alpha and beta bands of the mu rhythm cooperate to support speech perception (Bastos et al., 2012; Brinkman et al., 2014). Mu rhythm dynamics during the perception of degraded speech are an especially salient issue given reports that speech is degraded during most normal communication (Wild et al., 2012b), and degraded speech tasks are therefore the most ecologically valid means for probing dorsal stream contributions to perceptual processes.

Late Mu Activity and Covert Rehearsal

Finally, the relationship between late mu activity and the cognitive demands associated with discrimination tasks deserves further clarification. Activity following stimulus offset in Jenson et al. (2014) was characterized by robust ERD across both frequency bands of the mu rhythm. This finding of late mu ERD has now been reported in a number of studies employing syllable discrimination tasks (Bowers et al., 2013; Saltuklaroglu et al., 2017; Thornton et al., 2017), suggesting that it may characterize sensorimotor responses to the cognitive demands imposed by the task. As this activity was found during the time period prior to the response cue, the authors tentatively proposed that subjects were engaging in covert rehearsal to maintain the stimuli in working memory, possibly via Baddeley's phonological loop (Baddeley, 2003). This interpretation of concurrent alpha and beta mu ERD as evidence of covert rehearsal supporting working memory maintenance was based on several factors.

First, alpha and beta ERD are commonly reported during working memory tasks and may serve as an index of stimulus retention. Tsoneva et al. (2011) identified robust alpha and beta ERD across central and parietal electrodes while subjects completed a visual n-back task, proposing that sustained activity served to integrate freshly encoded information with that already in working memory. Similarly, Erickson et al. (2017) observed that control subjects exhibited alpha and beta ERD throughout both encoding and retention periods during a visual change tasks, while patients with schizophrenia produced ERD only during stimulus encoding. Greater ERD during the maintenance window was associated with superior task performance, suggesting that alpha and beta ERD are essential for successful retention. Scharinger et al. (2017) employed digit span, n-back, and a complex operations span tasks, observing stronger alpha and beta ERD in the n-back and complex operations span task than the digit span. The authors proposed that ERD magnitude scales with working memory load, suggesting that task difficulty is a mediating factor in working memory processes. Behmer and Fournier (2014) advanced a similar proposal to account for higher levels of mu alpha and beta ERD during a retention period for low memory span subjects than high span subjects. Results were interpreted through the framework of neural efficiency (Grabner et al., 2004; Del Percio et al., 2008) to suggest elevated working memory engagement based on increased task difficulty. Taken together, these studies demonstrate that concurrent alpha and beta ERD reliably emerge during working memory tasks, consistent with the proposal of Jenson et al. (2014) that subjects were engaged in working memory maintenance following stimulus offset.

It should be noted, however, that working memory in tasks employing real words may be supported by activity in both dorsal and ventral streams (Majerus, 2013). To unambiguously ascribe a role for the dorsal stream in working memory maintenance, it is therefore necessary to consider tasks involving non-words, free from semantic associations and the consequent ventral stream activation. Herman et al. (2013) employed a delayed syllable sequence repetition task in which subjects repeated an

aurally presented two or four syllable sequences upon the presentation of a visual cue. The authors identified alpha and beta ERD over anterior motor regions during the stimulus retention window, which was interpreted as evidence that interactions across the dorsal stream may serve as a maintenance buffer for storing syllable representations within the phonological loop. The authors additionally proposed that at least once cycle of this internal feedback loop may be necessary for successful speech production. However, despite clear evidence implicating the dorsal stream in working memory maintenance, it still remains to be demonstrated that subjects employed covert rehearsal to facilitate stimulus retention.

In addition to working memory tasks, concurrent alpha and beta mu ERD have additionally been reported during overt speech production and are thought to characterize normal sensorimotor processing for speech. Mandel et al. (2016) identified robust alpha and beta ERD over left sensorimotor regions from dyads engaged in natural conversation. Similarly, Gunji et al. (2007) recorded alpha and beta ERD over bilateral PMC during speech, song, and humming. While investigating speech related sensorimotor differences in people who stutter, Mersov et al. (2016) identified concurrent alpha and beta ERD over premotor cortex in their control subjects, interpreting it as normal sensorimotor function serving to integrate motor networks for speech. Additionally, while the discussion of Jenson et al. (2014) thus far has pertained to their speech perception data, it should be noted that they also included overt production of syllable pairs and words, which produced similar patterns of mu ERD to that found in the late perception window. Despite the diverse focuses of the aforementioned studies, the factor most relevant to the current line of inquiry is that all studies interpreted concurrent alpha and beta ERD over motor regions as indicative of normal sensorimotor activity for speech. Given that mu activity during the post-stimulus period in Jenson et al. (2014) consists of patterns characteristic of sensorimotor control for speech, notions of articulatory rehearsal are tenable. However, it still remains to be demonstrated that similar patterns of mu alpha and beta ERD are produced during covert speech.

Much of the evidence comparing neural responses to overt and covert tasks comes from brain computer interface (BCI) applications, as the ability to recover movement parameters from the neural signal in the absence of overt movement is critical to effective BCI (Yuan et al., 2010a). To date we are unaware of any studies investigating time-frequency decomposed, scalp-recorded activity over anterior motor regions during covert speech production, with the literature consequently disproportionately weighted towards gait and limb control. This notwithstanding, there is compelling evidence that covert movement produces similar patterns of neural activity across alpha and beta bands as overt movement. Holler et al. (2013) reported reduced alpha and beta ERD over central electrodes during imagination and execution of hand clenching movements, suggesting that similar sensorimotor mechanisms underlie both processes. However, as results were referenced to a control condition rather than a pre-stimulus baseline, interpretations regarding task-related dynamics are unclear. Yuan et al. (2010b) evaluated neural responses to overt and imagined clenching of the hands at different rates, training a linear classifier to recover movement parameters from alpha and beta ERD over central electrodes during both overt and imagined tasks. Results were interpreted to suggest that

neural activity in covert tasks encodes similar parameters as that arising from execution. Similarly, de Lange et al. (2008) observed concurrent alpha and beta ERD during the mental imagery of hand rotation, suggesting that motor imagery entails an internally executed motor program with a similar temporal and spectral profile to that observed during execution. While these studies did not specifically compare time-frequency patterns underlying overt and covert speech, they provide compelling evidence that similar patterns of activity support both overt and covert movement.

The recovery of speech-based motor parameters from the neural signal is significantly more challenging than limb movement parameters based on the elevated motoric complexity of speech production (Ackermann, 2008; Kent, 2000). This consideration notwithstanding, emerging evidence using electrocorticography (ECoG) suggests such decoding may be possible (Blakely et al., 2008). Kellis et al. (2010) collected ECoG data in the gamma band from face motor cortex during overt speech production, training a classifier to identify the spoken word from a set of ten possibilities on the basis of the neural data. The ability of the classifier to identify targets significantly above chance was interpreted as evidence of the feasibility of recovering speech motor parameters from the ECoG signal. Guenther and colleagues (2009) demonstrated the efficacy of a similar technique for covert speech decoding by training a patient with locked in syndrome to control a speech synthesizer through an electrode implanted in left precentral gyrus. The patient was able to mimic formant transitions characterizing different vowels, suggesting that covert speech generates movement parameters that can be used to duplicate overt speech. However, the authors provided no information about the frequency range used, thus it remains unclear whether alpha and beta bands contributed to the observed effect. Pei et al. (2011) recorded ECoG from a series of pre-operative epileptic patients with subdural electrode grids over left perisylvian cortex during overt and covert production of CVC words. The authors trained a classifier to identify both the vowel and consonant pair in each utterance from the neural signal, identifying premotor and primary motor cortices as the regions with the highest discriminability in both overt and covert conditions. The authors stated that activity in alpha, beta, and high gamma bands were used, but did not provide any information about the contributions of individual frequency bands to classification accuracy. While the results of Pei et al. (2011) may be interpreted to suggest that similar patterns of neural activity from the anterior dorsal stream may support overt and covert speech production, a limitation must be addressed. While above chance level, classification accuracy did not exceed 38% in the covert speech tasks, suggesting that the recorded signal does not allow for complete decoding. Despite this limitation, when considered alongside previously discussed reports that alpha and beta ERD emerge during overt speech, the similarity of neural responses to overt and covert movement further supports Jenson et al. (2014)'s interpretation of covert rehearsal to facilitate working memory maintenance.

In summary, late (i.e., post-stimulus) mu activity in Jenson et al. (2014) was characterized by concurrent mu alpha and beta ERD, a pattern that is known to emerge during working memory maintenance, overt speech, and covert (i.e., imagined) movement. It is therefore logical to suggest that subjects engaged in covert replay to retain stimuli in working memory prior to discrimination response. Such a proposal is

consistent with interpretations of alpha and beta bands of the mu rhythm as indices of forward and inverse modeling, respectively. The involvement of forward models in covert production is uncontroversial (Tian and Poeppel, 2010; Poeppel and Monahan, 2011; Tian and Poeppel, 2012; Tian et al., 2016), and it has been proposed that covert speech may be instantiated by paired forward and inverse models (Pickering and Garrod, 2013). However, it should be noted that when probed, subjects in Jenson et al. (2014) did not report engaging in covert rehearsal. Such an interpretation of the neural data therefore requires further validation, potentially via examination of speech induced suppression (SIS), the process whereby auditory responses are attenuated during speech production (Numminen et al., 1999; Curio et al., 2000; Heinks-Maldonado et al., 2005; Sitek et al., 2013). SIS has been tied to the inhibitory effect that forward models exert on posterior sensory regions (Blakemore et al., 2000; Wolpert and Flanagan, 2001), and it has additionally been demonstrated that the same inhibitory mechanism is active during covert speech (Kauramaki et al., 2010; Tian and Poeppel, 2015). Interpretations regarding late mu activity in Jenson et al. (2014) may therefore be validated by analysis of temporally sensitive data from the posterior dorsal stream, as inhibition of auditory regions concurrent with mu ERD is a necessary consequence of covert rehearsal accounts.

Auditory Alpha as an Index of Posterior Dorsal Stream Activity

The contributions of posterior dorsal stream (i.e., auditory) regions to task demands may be reliably evaluated by time-frequency decomposition of the auditory alpha rhythm. As addressed above (see “Electroencephalography and the Mu Rhythm”), alpha oscillations are ubiquitous across the brain, having been implicated in a variety of cognitive and sensory processes. However, emerging evidence supports the existence of a distinct oscillatory generator located over posterior superior temporal regions with response properties specific to auditory stimulation (Tiihonen et al., 1991; Lehtela et al., 1997; Weisz et al., 2011; Hartmann et al., 2012). Disambiguation of this auditory alpha rhythm from other more widely known alpha generators such as the sensorimotor mu and the occipital alpha rhythm governing visual processing (Pollen and Trachtenberg, 1972) is based on two primary factors. First, the auditory alpha rhythm is localized close to the source of the N100/M100 auditory response (Hari, 1990; Tiihonen et al., 1991), consistent with a role in auditory processing. Second, the fact that it does not respond to closing of the eyes or clenching of the fist (Tiihonen et al., 1991; Lehtela et al., 1997), tasks known to modulate the occipital alpha and sensorimotor mu rhythms, suggests its distinct nature. Given this selective (i.e., auditory only) response profile and general interpretations of alpha power as an index of the excitatory/inhibitory balance of the underlying neural tissue (Jensen and Mazaheri, 2010; Weisz et al., 2011; Mazaheri et al., 2014), time frequency decomposition of the may be employed to track auditory alpha activity across a variety of sensory processes and cognitive functions.

Auditory alpha ERD is generally considered to reflect disinhibition of auditory neuronal assemblies for the purpose of stimulus processing (Muller and Weisz, 2012). Lehtela et al. (1997) identified bilateral temporal alpha ERD during the perception of

transient tones, suggesting that the auditory alpha rhythm is sensitive to the processing of exogenous auditory stimuli. Leske et al. (2015) confirmed the behavioral relevance of this activity, noting that detected trials in a near-threshold detection paradigm were marked by significantly reduced auditory alpha power. In addition to a role in the bottom-up processing of exogenous input, auditory alpha ERD has also been implicated in subjective, rather than veridical, perceptual experiences such as tinnitus (Weisz et al., 2011) and the illusory perception of music in noise (Muller et al., 2013). Taken together, these findings suggest that while the auditory alpha exhibits a bottom-up, stimulus driven response profile, it may also be prone to top-down modulation as evidenced by alpha ERD during non-veridical perception. Reduced alpha power over auditory regions in advance of expected auditory stimulation (Bastiaansen et al., 2001; Bastiaansen and Brunia, 2001) has been interpreted to suggest a role for attention in top-down modulation. This is corroborated by the results of Hartmann et al. (2012), who demonstrated stronger auditory alpha ERD for salient than non-salient stimuli. Thus, while alpha ERD may represent the influence of attention on sensory processing, top-down attentional effects may also exert inhibitory influence on the auditory alpha rhythm.

Auditory alpha ERS has often been interpreted as a measure of top down inhibitory modulation of auditory responses. Muller and Weisz (2012) identified alpha ERS over auditory cortex ipsilateral to the cued ear in dichotic stimulation, which was interpreted as gating of the unattended sensory stream. Similar results and interpretations arise from Payne et al. (2017), who identified alpha ERS over auditory cortex contralateral to the non-cued ear in a modified dichotic Sternberg task. In both of these studies, this inhibitory effect was dominated by the right hemisphere, which was proposed to represent the processing of stimuli from both ears in the right hemisphere (Zatorre and Penhune, 2001; Spierer et al., 2009), necessitating a stronger inhibitory signal for the competing sensory stream. The sensitivity of this effect to task demands is demonstrated by the results of Wostmann et al. (2017), in which the magnitude of alpha ERS elicited by a dichotic distractor scaled parametrically with the spectral detail of the distractor. Stronger auditory alpha ERS in the presence of less degraded distractors was interpreted to suggest that more salient distractors must be more strongly inhibited in order to achieve task goals. The effectiveness of this top down inhibitory control is suggested by studies demonstrating that the conscious modulation of auditory alpha power through neurofeedback has clinical efficacy for reducing (Dohrmann et al., 2007a; Hartmann et al., 2014) or abolishing (Dohrmann et al., 2007b) the tinnitus percept. Two critical points emerge from the synthesis of these experimental findings. First, the auditory alpha rhythm is subject to top-down modulation. Second, auditory alpha ERS may be interpreted as evidence of inhibitory control over auditory responses. This inhibitory interpretation constitutes a prime avenue for testing the presence of covert rehearsal in the post-stimulus window in Jenson et al. (2014), as auditory alpha ERS constitutes an oscillatory marker for the speech induced suppression predicted by covert rehearsal accounts.

Jenson et al. (2015) identified the auditory alpha rhythm from the same subjects performing the same tasks as Jenson et al. (2014), employing ERSP analysis to identify task-related patterns of enhancement and suppression. Alpha ERD lagged slightly behind

stimulus onset, persisting slightly beyond stimulus offset. The late portion of the trial epoch was marked by the transition from ERD to ERS in the alpha band, suggesting functional inhibition of auditory regions. As the timelines were identical between the two studies (Jenson et al., 2014; 2015), mu and auditory alpha ERSP data could be viewed alongside each other to assess auditory activity in the wider context of dorsal stream processing. Based on the temporal concordance of alpha and beta mu ERD and the emergence of auditory alpha ERS, the authors suggested that a forward model arising from covert production attenuated activity in posterior auditory regions. This interpretation is additionally consistent with reports that auditory attenuation via speech-induced suppression occurs during covert production. Specifically, Kauramaki et al. (2010) identified reduced amplitude of the N100 response to probe tones during covert vowel production. This suppression of activity was localized to auditory regions bilaterally by a follow up study employing fMRI with the same tasks (Balk et al., 2013). As Tian and Poeppel (2015) identified reduced modulation of auditory responses to pitch-shifted and temporally delayed feedback compared to unperturbed feedback, it must be considered that the observed effect is not a generalized attenuation of auditory responses, but rather a specific modulation driven by the content of the forward model. Thus, the results of (Jenson et al., 2014) may be cautiously interpreted as evidence of auditory attenuation via forward model delivery during covert articulatory rehearsal for the purpose of working memory maintenance.

While the temporal alignment of mu ERD and auditory alpha ERS during the late post-stimulus period in Jenson et al. (2015) is consistent with what would be predicted by covert rehearsal accounts, it must be acknowledged that no causal link can be established on the basis of temporal concordance alone. Establishing such a link is necessary to validate covert rehearsal accounts given that alternative explanations exist for auditory alpha ERS which are reliant on supramodal attentional mechanisms and do not invoke speech-specific processes. van Dijk et al. (2010) identified auditory alpha ERS over the left hemisphere during the retention period in a delayed tone matching task, suggesting that alpha ERS served to allocate cognitive resources towards the functionally relevant right hemisphere (Herholz et al., 2008). A similar explanation was offered by Leiberg et al. (2006) to account for the presence of right auditory alpha ERS with increasing memory load during a Sternberg task using syllables. Post-stimulus activity in Jenson et al. (2015) may therefore be interpreted as an index of resource allocation processes. However, as Wostmann et al. (2016) reported that alpha ERS over the non-attended hemisphere during dichotic stimulation was modulated in synchrony with the speech rate, attentional modulation by the inhibition of distractors (Strauss et al., 2014) must also be considered. As participants in Jenson et al. (2015) were engaged in working memory maintenance prior to the response cue, it is plausible that either distractor inhibition or resource allocation may account for the functional inhibition of auditory regions indicated by alpha ERS. In order to demonstrate that a speech specific mechanism reliant on forward models is responsible for auditory attenuation during the post-stimulus window, it is critical to demonstrate information flow between anterior and posterior aspects of the dorsal stream during the post-stimulus period.

Connectivity Across the Dorsal Stream in Speech Perception

A large number of studies have demonstrated communication between motor and auditory regions during speech perception tasks (Husain et al., 2006; Patel et al., 2006; Skipper et al., 2007a; Londei et al., 2010; Osnes et al., 2011; Wild et al., 2012a; Sharda et al., 2015; Li et al., 2017), an unsurprising finding considering their connection via arcuate and superior longitudinal fasciculi (Specht, 2014). However, the majority of these studies have employed fMRI, which limits the ability to interpret connectivity patterns for two primary reasons. First, fMRI does not possess sufficient temporal resolution to identify the timeline of the observed connectivity, critical considering reports that the timing and directionality of information flow respond dynamically to tasks (Fontolan et al., 2014). Second, the reported findings do not indicate the direction of information flow (Friston, 2011). As the current study is concerned primarily with forward and inverse models, which encode opposite directions of information flow across the dorsal stream, it is critical to ascertain the direction of information flow between motor and auditory regions across the time course of speech perception.

Temporally sensitive analyses of speech perception have identified patterns of effective connectivity across the dorsal stream consistent with bidirectional auditory-motor information flow. Gow Jr and Segawa (2009) employed Granger Causality (Granger, 1969; 1988) analysis of multimodal imaging data while subjects perceived word pairs with an ambiguous final consonant, interpreting information flow from PMC to bilateral pSTG as evidence of forward model delivery. Giordano et al. (2017) interpreted bidirectional Directed Information (Massey, 1990; Amblard and Michel, 2011) between motor regions and auditory regions during an audiovisual speech perception task as evidence of recurrent processing of speech, consistent with the dynamics of both forward and inverse internal models within the Analysis by Synthesis paradigm. However, while it is clear that anterior and posterior dorsal stream regions reciprocally communicate during speech perception, it should be noted that interpretations of these two studies were hampered by the lack of spectral detail. As it has been previously argued that the anterior dorsal stream encodes forward and inverse internal models in the beta and alpha bands, respectively, it may be proposed that a similar spectral differentiation is employed for internal model delivery. Specifically, auditory-motor interactions in the beta band may be interpreted as evidence of forward modeling, and auditory-motor alpha band connectivity may represent inverse modeling. It is therefore necessary to consider evidence that that anterior and posterior aspects of the dorsal stream communicate along alpha and beta frequency channels.

Studies implementing spectrally detailed measures of information flow have provided weak, but consistent support for the notion that beta band connectivity encodes forward model transformations across the dorsal stream. Park et al. (2015) assessed dorsal stream connectivity during the passive perception of intelligible and unintelligible speech with Transfer Entropy (Schreiber, 2000). Activity in the left PMC was shown to modulate the phase of activity in left auditory cortex, which the authors interpreted as evidence of top-down signaling of motor regions during speech perception. While the study focused primarily on lower delta/theta bands, the authors did note that a similar

top-down effect existed in the beta band and was consistent with general notions of beta oscillations encoding descending information (Bastos et al., 2012; Fontolan et al., 2014; Bastos et al., 2015). Alho et al. (2014) confirmed a role for beta band connectivity in dorsal stream processing by computing the weighted phase lag index (Vinck et al., 2011; Ortiz et al., 2012) between PMC and auditory sources during a syllable identification task, with beta connectivity noted approximately 100 ms following stimulus onset. Although it was not possible to determine the direction of information flow in Alho et al. (2014), the results of these two studies may be taken together to suggest that beta band connectivity across the dorsal stream encodes forward model predictions.

Despite evidence supporting a role for beta band connectivity in internal modeling across the dorsal stream, scant evidence is available regarding the role of alpha band dorsal stream connectivity in speech perception. Evidence does exist, however, suggesting that PMC communicates with sensory cortices in the alpha band across a variety of tasks. Pollok et al. (2009) identified alpha band phase synchrony between left STG and dorsal PMC when subjects performed an aurally paced, but not visually paced, finger-tapping task, suggesting a role in relaying sensory information necessary for motor planning. Palva et al. (2010) identified a network of regions involved in visual working memory, including PMC and visual cortex, during a delayed match to sample task exhibiting alpha band synchrony, suggesting that interareal alpha phase synchronization may constitute a method for regulating the maintenance of sensory objects in working memory (Ono et al., 2013). While lacking directional specificity, these studies do suggest that PMC communicates with sensory regions in the alpha band. Kujala et al. (2007) identified a network including visual cortex, left STG, and anterior motor regions while subjects performed a reading task, with Granger causality analysis indicating a posterior to anterior direction of information flow in the alpha band, consistent with the dynamics of an inverse sensory to motor mapping. While none of these studies directly assessed alpha band connectivity across the dorsal stream during speech perception, the results confirm that anterior and posterior aspects of the dorsal stream communicate along the alpha frequency channel, with results consistent with a role in inverse modeling. This bolsters the notion that the frequency band of cortical interactions may serve as a proxy for directional information, with beta connectivity suggestive of top-down forward modeling influences and alpha band connectivity indexing sensory-driven inverse modeling.

In summary, anterior and posterior aspects of the dorsal stream communicate bidirectionally across alpha and beta frequency channels, consistent with the notion that the same spectral differentiation of forward and inverse models employed in the anterior dorsal stream governs information flow across the dorsal stream. However, no studies to date have examined communication across the dorsal stream within these frequency bands together during speech perception. Such connectivity data would supplement current understandings of the role that internal models play in speech perception, the mechanism of their transmission, and the manner in which they are modulated by cognitive processes such as attention and working memory. In order to ensure the sensitivity and specificity of this analysis, two primary factors must be considered when selecting the connectivity metric. First, it must possess sufficient temporal resolution to

track the rapid fluctuations in information flow arising from task-dependent network reorganization (Fontolan et al., 2014; Skipper et al., 2017). Second, it must be sensitive to interactions across distinct frequency bands. This is critical given the proposal that the frequency of auditory-motor interactions may serve as a proxy for directional information. Analysis of dorsal stream connectivity with a spectrally and temporally sensitive metric is critical to accurate classification of the role of sensorimotor processing in speech perception and its modulation by cognitive processes such as attention and working memory.

Phase coherence analysis of time-frequency decomposed EEG data from anterior and posterior aspects of the dorsal stream has the potential to identify connectivity modulations in response to task demands. The use of phase coherence to probe connectivity is based on the notion that neural ensembles instantiate communication through alignment of their oscillatory phase (Fries, 2005; Weisz and Obleser, 2014). Phase coherence is a well-established method for probing interactions between cortical sites, having been employed in a variety of motor (Leocani et al., 1997; Abdul-latif et al., 2004; Melgari et al., 2013) and cognitive tasks including working memory (Yokota and Naruse, 2015; Wiesman et al., 2016), attention, (van Schouwenburg et al., 2016; Hasan et al., 2017), response inhibition (Muller and Anokhin, 2012), nociception (Drewes et al., 2006), and speech perception (Sengupta et al., 2016; Steinmann et al., 2018). As anterior and posterior dorsal stream regions are directly connected via the arcuate fasciculus (Specht, 2014), it is proposed that phase coherence will capture the interactions between them given its maximal sensitivity to direct connections (Friston, 2011). Also, critical for the current study, which will employ ICA to identify the sensorimotor mu and auditory alpha rhythms from a larger complex of scalp recorded signals, it has been shown to be suitable for use with ICA decomposed EEG data (Hong et al., 2005). The spectral and temporal detail afforded by coherence analysis is expected to reliably identify fluctuations in information flow over alpha and beta frequency bands across the time course of perceptual events, with frequency specificity serving as a proxy for directionality. Time periods characterized by forward modeling should demonstrate mu-auditory coherence in the beta band, while periods of inverse modeling should be characterized by mu-auditory coherence in the alpha band.

In summary, the aims of the current study are to characterize the influence of cognitive processes such as attention and working memory on the contributions of dorsal stream processing to speech perception. By considering ERSP decomposed data from anterior and posterior aspects of the dorsal stream alongside measures of phase coherence across the dorsal stream, it is possible to probe the dynamics of internal modeling across the time course of speech perception. Specifically, early activity is expected to reveal the contributions of predictive and inhibitory processes to attentional modulation of dorsal stream activity. Late activity is anticipated to reveal covert articulatory rehearsal mechanisms to facilitate working memory maintenance prior to discrimination response. Validation of these hypotheses has the potential to disambiguate diverse theoretical orientations regarding the contributions of anterior motor regions to speech perception, as well as clarifying how cognitive processes such as attention and working memory modulate internal modeling across the dorsal stream in light of task demands.

CHAPTER 3. METHODOLOGY

Participants

42 female native English speakers (mean age = 24.1; 3 left handed) with no history of cognitive, communicative, or hearing impairment recruited from the University of Tennessee student body participated in the current study. Handedness was assessed via the Edinburgh Handedness inventory (Oldfield, 1971). Prior to participation all subjects provided informed consent, approved by the University of Tennessee Institutional Review Board.

Stimuli

The stimuli consisted of pairs of monosyllabic CV syllables initiated by a voiced consonant (i.e., /b/, /d/, /g/, /l/) and followed by a vowel (/i/, /a/, /ε/) recorded by a male native English speaker. Fully crossing consonant and vowels yielded twelve syllables. However, in order to eliminate potential effects of lexicality (Pratt et al., 1994; Chiappe et al., 2001; Kotz et al., 2010; Ostrand et al., 2016), two syllables (/bi/, /li/) were not used for generation of syllable pairs. Ten tokens of each syllable were recorded with an AKG C520 microphone using a Mackie 402-VLZ3 pre-amp and a Krohn-Hite Model 3384 amplifier implementing a Butterworth bandpass filter from 20 Hz – 20 kHz, then digitized at 44.1 kHz. From this corpus, the best exemplar of each syllable was selected for use in the discrimination tasks on the basis of overall duration, vowel clarity, and consonant clarity. Selected syllable tokens were then filtered from 300 to 3400 Hz (Callan et al., 2010) and normalized for intensity and duration in Audacity 2.0.6. The duration of all syllables was pruned to 200 ms, and intensity was set to approximately 70 dB SPL.

From the normalized speech tokens, syllable pairs were generated and 200 ms of silence was inserted between the syllables. An additional 1400 ms of silence was inserted after the offset of the second syllable so that the total length of stimuli was two seconds. While not necessary for successful discrimination, it should be noted that segmentation is known to recruit anterior dorsal stream regions (Burton et al., 2000; LoCasto et al., 2004; Sato et al., 2009; Thornton et al., 2017). To mitigate against this potential confound, pairs of syllables differed only by the initial consonant. Subject to this constraint, 36 syllable pairs were possible.

The initial syllable pairs with a quiet background were subjected to two distinct methods of signal degradation, yielding three forms of each syllable pairing. In the Masked conditions, syllable pairs were embedded in white noise at +4 dB SNR. This signal to noise ratio was chosen as it has been shown to reliably elicit sensorimotor activity while still allowing discrimination with a high degree of accuracy (Osnes et al., 2011; Bowers et al., 2013; Jenson et al., 2015). In the Filtered conditions, stimuli were filtered into 24 bands according to the Bark frequency scale (Smith and Abel, 1999)

using custom Matlab scripts. The amplitude of frequency bands ranging from 20 – 400 Hz and 1480 – 2700 Hz were retained, while the amplitude of all other frequency bands was set to zero. The resulting frequency bands were then combined into a single signal, and syllable pairs were normalized for RMS amplitude. A pilot study confirmed both the discriminability of the resulting syllable pairs as well as similar levels of discrimination accuracy for Masked and Filtered syllable pairs.

Design

The experiment consisted of a seven condition within-subjects design. The conditions were derived by crossing set size with signal clarity. The conditions were:

- a) Passive listening to white noise (PasN);
- b) Discrimination of small set in quiet (SQuiet);
- c) Discrimination of small set in noise (SMask);
- d) Discrimination of small bandpass filtered set (SFilt);
- e) Discrimination of large set in quiet (LQuiet);
- f) Discrimination of large set in noise (LMask); and
- g) Discrimination of large bandpass filtered set (LFilt).

Condition 1 was used as a control condition and conditions 2 – 7 were active discrimination conditions. To control for the presence of a button press in the discrimination conditions, a button press was included in the PasN condition. The stimulus set for the S- conditions (2 – 4) used syllable pairs consisting of /ba/ and /da/ (i.e., four possible pairings). The stimulus set for the L- conditions (5 – 7) contained all permissible syllable pairs subject to the one phoneme difference constraint described above (i.e., 36 possible pairings). Stimuli were randomly in a block design with an equal number of same and different trials in each block to mitigate the potential effects of response bias (Venezia et al., 2012; Smalle et al., 2015).

Procedures

The experiment was conducted in an electromagnetically shielded, double-walled, sound-treated booth fit with a faraday cage. Participants were seated in a comfortable chair with their head and neck well supported. Stimuli were presented, and button press responses recorded by a computer running Compumedics NeuroScan Stim 2, version 4.3.3. All stimuli were presented binaurally at 70 dB SPL through Etymotic ER3-14A insert earphones. The response cue for all conditions was a 100 ms 1000 Hz tone presented 3000 ms following stimulus onset. Given reports that anticipatory motor planning can occur up to 2000 ms before movement onset (Graumann and Pfurtscheller, 2006), this timeline was chosen to eliminate the potential contamination of discrimination-related neural activity by motor planning for the button press. In addition to controlling for anticipatory neural activity corresponding to motor planning, the inclusion of a button press response in the PasN condition ensured that subjects were

attending to stimuli (Alho et al., 2012b; Alho et al., 2015). In the PasN condition subjects were instructed to press the button when they heard the response cue. In the discrimination conditions, subjects were instructed to press one of two buttons based on whether the syllables were judged to be the same or different. Handedness of button press responses was counterbalanced within subjects.

All trial epochs were five seconds in length, ranging from -3000 to +2000 ms around time zero, defined as the onset of the syllable pair. All epochs contained a baseline consisting of 1000 ms of silence (i.e., -3000 -> -2000 ms) to allow subsequent time-frequency decomposition. In the PasN and Masked conditions (1, 3, 6) white noise began 1500 – 2000 ms prior to syllable onset (i.e., -2000 -> -1500 ms) and persisted until 1400 ms following syllable offset (i.e., +2000 ms). The temporal jitter of noise onset was implemented to reduce the temporal cues provided to participants. Each of the conditions was presented in 2 blocks of 40 trials each, yielding fourteen blocks (2 blocks x 7 conditions). The order of block presentation was randomized across subjects. The timeline for trial epochs is illustrated in **Figure 3-1**.

Neural Data Acquisition

Whole head EEG data was recorded from 68 channels, with 64 neural channels will supplemented with four EMG channels to capture the electrocardiogram, electro-oculogram, and peri-labial muscle movement. The electro-oculogram was captured by means of two channel pairs placed above and below the orbit of the left eye (VEOU, VEOL) and on the lateral canthi of the left and right eyes (HEOL, HEOR) to measure vertical and horizontal eye movement, respectively. Two surface EMG electrodes were placed over the medial and lateral portions of the orbicularis oris muscle to capture peri-labial muscle movement. The EKG channels were placed over the left and right carotid complex. All data were recorded from an unlinked, sintered NeuroScan Quik Cap arranged according to the extended 10 – 20 system (Jasper, 1958). In order to increase the precision of source localization, and consequently the proportion of contributing subjects, individual channel locations were recorded via a Polhemus Patriot 3D digitizer. A source generation was held in place on the forehead, while a stylus was used to identify 3D locations for each recording electrode relative to the source. Individual channel locations were recorded following cap placement but prior to neural data acquisition and stored offline for later use during individual data pre-processing.

EEG data were acquired using Compumedics NeuroScan Scan 4.3.3 software coupled with the Synamps 2 system. During signal acquisition, data were band-pass filtered (0.15 – 100 Hz) and digitized with a 24-bit analog to digital converter at a sampling rate of 500 Hz. Data were time locked to the onset of syllable presentation in all discrimination conditions. Thus, time zero corresponds to stimulus onset in the discrimination conditions and to a random point in the middle of white noise in the PasN condition.

Figure 3-1. Timeline for single trial epochs.

Top line corresponds to Quiet and Filtered conditions, while bottom line corresponds to Masked conditions.

Data Processing

Data processing was performed in EEGLAB 12.0.2.6b (Brunner et al., 2013), an open source toolbox for electro-physiologic data running on Matlab 8.2. Data were processed at the individual level to identify the oscillatory rhythms of interest. Subsequent group analyses identified condition differences in both focal time-frequency and inter-regional connectivity patterns. The processing pipeline listed here is discussed in greater detail below:

- Individual processing:
 - a) Pre-processing of all 14 data files per subject;
 - b) ICA of concatenated data files per subject to identify neural components common across conditions; and
 - c) Localization of all independent components for each subject.
- Group processing:
 - a) Pre-processed data files from all subjects and conditions were submitted to the EEGLAB STUDY module;
 - b) Independent components common across subjects clustered via Principal Component Analysis (PCA);
 - c) Bilateral mu and auditory alpha clusters were identified from the results of PCA;
 - d) ERSP analysis performed to achieve time-frequency decomposition of bilateral mu and auditory alpha clusters;
 - e) Mu and auditory alpha clusters were localized through ECD techniques; and
 - f) Paired mu and auditory alpha components per subject were submitted to coherence analyses via custom Matlab scripts.

Pre-processing

Both raw EEG data files from each condition were appended to create a single data file containing 80 trials. This aggregate data file was then downsampled from the original sample rate (500 Hz) to 256 Hz to reduce the computational demands of further processing steps. All channels were then referenced to the mastoids (M1 M2) for the reduction of common mode noise. Following this step, any channels deemed to be noisy were removed from the data. Additionally, correlation coefficients were computed for all channel pairs to monitor salt-bridging across channels (Greischar et al., 2004; Alschuler et al., 2014), with correlations of .99 or higher considered evidence of salt bridging. For salt bridged channel pairs, one channel was removed to eliminate signal redundancy. To enable successful comparison across conditions, the identified channels were removed from all condition datasets for a given subject. Five-second epochs ranging from -3000 ms to +2000 ms around stimulus onset were extracted from the continuous signal, yielding 80 epochs per condition. Trial epochs were visually inspected and removed

from the data if they contain gross artifact. Additionally, all trials in which subjects did not discriminate syllables accurately or failed to respond within 2000 ms of the response cue were excluded. All usable trials were then submitted to further processing steps.

Independent Component Analysis

Prior to ICA decomposition all pre-processed datasets for each subject were concatenated, allowing ICA to extract a single set of channel weights common to all conditions. This step enabled the comparison of component activations across conditions. The concatenated datasets were then decorrelated through the use of an extended Infomax algorithm (Lee et al., 1999). The data were subjected to ICA training via the extended “runica” algorithm with an initial learning weight of .001 and a stopping weight of 10⁻⁷. As the number of independent components (ICs) returned corresponds to the number of channels submitted, a maximum of 66 components (68 recording channels – 2 reference channels) were returned for each subject. The true number of resultant components differed across subjects, however, depending on the number of channels excluded during pre-processing. Scalp maps, corresponding to coarse estimates of component scalp distribution, were then generated by the projection of the inverse weight matrix (W^{-1}) back onto the original channel montage.

Dipole Localization

An equivalent current dipole (ECD) model (i.e., point source estimate) was generated in the DIPFIT toolbox (Oostenveld and Oostendorp, 2002) for each component identified by ICA. Individual digitized channel locations for each subject were referenced to the extended 10-20 system (Jasper, 1958) and warped to the BESA (spherical) head model. This process minimizes the distance between the digitized channel locations and the 10-20 channel locations while retaining the true arrangement of the recording channels on the scalp. Due to an equipment error, individual channel locations were not available for four subjects, and standard 10-20 channel locations were used instead. Automated coarse and fine fitting to the head model resulted in a single dipole model for each of the 2205 components. The resulting ECD models represent physiologically plausible solutions to the inverse problem, which were then projected onto the original channel configuration (Delorme et al., 2012). The residual variance (RV%), considered a measure of “goodness of fit” for the dipole model, was determined by the mismatch between this projection to the scalp and the original scalp-recorded signal.

Study Module

Group level analyses were performed in the EEGLAB STUDY module, which enables the analysis of ICA data across subjects and conditions. Data files from all subjects and conditions were loaded into the STUDY module. Any component with RV

higher than 20% or an ECD model localized outside the cortical volume was excluded from further analysis. The RV threshold of 20% was chosen as higher levels are likely indicative of artifact or noise.

PCA Clustering

Component pre-clustering was implemented on the basis of similarities in component spectra, scalp maps, and ECD model localizations. The K-means statistical toolbox was used to group similar components on the basis of the specified criteria via PCA. Components were assigned to 40 clusters, from which bilateral mu and auditory alpha clusters were identified. Final component attribution to clusters of interest was based predominantly on the results of PCA. However, all clusters were visually inspected to ensure that each member of the clusters of interest met the inclusion criteria, and that no components meeting cluster membership had been omitted. Inclusion criteria for the mu clusters were a characteristic mu spectrum (i.e., peaks at ~10 Hz and ~20 Hz), $RV < 20\%$, and source localization to Brodmann's area 1-4 or 6. Inclusion criteria for the auditory alpha cluster were an alpha spectrum, $RV < 20\%$, and source localization to pSTG or posterior middle temporal gyrus (pMTG). Any mis-allocated components were re-allocated to correct clusters.

Source Localization

Once final designation to component clusters of interest was complete, bilateral mu and auditory alpha clusters were localized through ECD methods. The ECD cluster localization is the mean of the Talairach coordinates (x, y, z) of all dipoles contributing to the cluster. These stereotactic coordinates were converted to anatomic locations with the Talairach Client, yielding estimates of most likely cortical locations and Brodmann's areas.

ERSP Analysis

ERSP analysis was employed to investigate fluctuations in spectral power (in normalized dB units) over time across the frequency range of interest (7 – 30 Hz). Component activations were decomposed with a Morlet wavelet expanding linearly from 3 cycles at 7 Hz to 6.4 cycles at 30 Hz. ERSP data were referenced to a 1000 ms silent baseline extracted from the inter-trial interval with a surrogate distribution generated from 200 randomly sampled time points within this baseline window (Makeig et al., 2004). Calculation of individual ERSP changes across time employed a bootstrap resampling method ($p < .05$, uncorrected). Single trial data between 7 and 30 Hz from all conditions were submitted for time-frequency decomposition.

Statistical analyses employed permutation statistics (2000 permutations) with an FDR correction for multiple comparisons (Benjamini and Hochberg, 1995) to assess

differences across conditions. A 2 x 3 Repeated Measures ANOVA was performed to decompose the 1 x 7 omnibus test. As no interaction term was present in the 2 x 3 design, subsequent statistical comparisons collapsed across variables. As direct comparison of small and large set size conditions did not reveal significant differences, both sets of conditions were compared to PasN separately, and the differences were compared. Additionally, a 1 x 3 ANOVA was performed to test the effect of Signal Clarity, with paired *t*-tests performed to decompose the Signal Clarity effect.

Connectivity

Analysis of coherence between mu and auditory component clusters was performed using custom Matlab scripts. Pairs of mu and auditory alpha components contributed by the same subjects were identified from the STUDY module in EEGLAB, extracted from the larger datasets per condition, and submitted to coherence analysis. Separate analyses were completed for left and right hemispheres. The steps in the phase coherence pipeline are listed here, and explained in greater detail below:

- a) Extraction of matching mu and auditory alpha components for all subjects, conditions, and hemispheres;
- b) Removal of phase-locked activity;
- c) Wavelet decomposition;
- d) Coherence estimation; and
- e) Statistical comparisons.

Extraction of Component Pairs

Subjects contributing matched pairs of mu and auditory alpha components to either hemisphere were identified from the STUDY module. For each identified subject, mu and auditory alpha component activations were extracted from the larger dataset in each condition, yielding seven pruned datasets per subject. Component extraction was performed to reduce the computational demands of subsequent processing steps and was deemed appropriate based on the nature of the coherence measures employed in the current study. Specifically, as phase coherence exclusively probes bivariate relationships, and does not distinguish direct from indirect interactions, there was no benefit to retaining additional components in the coherence analysis. Based on the number of contributing subjects (27 – left hemisphere, 28 – right hemisphere), 385 pruned datasets were generated (55 pairs x 7 conditions), with separate analyses performed for left and right hemispheres.

Removal of Phase Locked Activity

The focus of the current study was on intrinsic connectivity between mu and auditory alpha rhythms, and it was therefore necessary to exclude coherence resulting

from synchronization to an external event. To accomplish this, the ERP was removed from all mu and auditory alpha components by subtracting the mean across trials from each component activation, with the resulting signals passed on to further analysis.

Wavelet Decomposition

To enable the recovery of phase information from the time-domain signals, a family of 25 complex Morlet wavelets linearly spaced between 7 and 30 Hz was generated, ranging from 3 cycles at 7 Hz to 19 at 30 Hz. Wavelet decomposition was performed by element-wise multiplication of the fft from each wavelet with the fft of mu and auditory alpha rhythms, with the inverse Fourier transform performed to convert results back to the time domain. Phase angles (in radians) were extracted from the decomposed data, yielding matrices of size 2 (components) x 25 (frequencies) x 1280 (time points) x number of trials.

Coherence Estimation

Coherence at every time frequency point for each trial was computed using Euler's formula (e^{ik}) with k representing the pair of phase angles from mu and auditory alpha rhythms. The coherence value across trials for each dataset was calculated as the mean across trials of the absolute value of the coherence estimates. As coherence was evaluated separately for each condition, there were seven 25 x 1280 (frequencies x time points) matrices for each subject per hemisphere.

Statistical Comparisons

Coherence estimates were concatenated across subjects, yielding seven (one per condition) 27 x 25 x 1280 matrices for the left hemisphere, and 28 x 25 x 1280 matrices for the right hemisphere. Statistical comparisons of coherence differences across conditions employed permutation statistics (2000 permutations) with FDR corrections for multiple comparisons (Benjamini and Hochberg, 1995). Analyses were performed with the *statcond()* function included in EEGLAB. 1 x 7 omnibus ANOVAs were performed separately for each hemisphere in addition to paired *t*-tests between PasN and all discrimination conditions.

CHAPTER 4. RESULTS

One subject was excluded from the study for failure to comply with instructions, as she reported that she only used one hand for all button press responses. Consequently, data from only 41 subjects was submitted to further analysis.

Condition Accuracy

A multivariate repeated measures ANOVA with Greenhouse-Geisser corrections for violations of sphericity [$\epsilon = .86$, $p = .034$] was computed on arcsine transformed discrimination accuracy for subjects contributing to neural clusters of interest. Significant effects of set size [$F(1,39) = 112.82$, $p < .01$], signal clarity [$F(2,78) = 66.8$, $p < .05$], and a set size x signal clarity interaction [$F(1.77,67.1) = 15.69$, $p < .05$] were noted. Discrimination accuracy was higher in small set size [mean = 1.42, se = .012] than large set size [mean = 1.31, se = .014], and differed across all three levels of signal clarity with Quiet [mean = 1.48, se = .014] higher than Masked [mean = 1.27, se = .016], which was higher than Filt [mean = 1.34, se = .017]. Decomposition of the interaction term by paired t -tests revealed that accuracy was lower [$t(39) = -6.55$, $p < .05$] in LMask [mean = 1.16, sd = .1] than LFilt [mean = 1.3, sd = .14], but did not differ [$t(39) = .16$, $p > .05$] between SMask and SFilt (See **Figure 4-1**).

Number of Usable Trials

For the subjects contributing to neural clusters of interest, the average number of usable trials per condition were: PasN = 58 (SD = 6.9), SQuiet = 56.5 (SD = 9.2), SMask = 54.4 (SD = 8.8), SFilt = 54.9 (SD = 5.6), LQuiet = 53.5 (SD = 6.9), LMask = 49.5 (SD = 6.5), and LFilt = 51.1 (SD = 6.6).

Cluster Characteristics

Figure 4-2 and **Figure 4-3** show the distribution of components contributing to left and right mu and auditory alpha clusters, respectively. Of the 41 subjects whose data was submitted to neural analysis, 40 contributed to the clusters of interest. Specifically, 31 contributed to the left mu cluster, 35 contributed to the left auditory cluster, 34 contributed to the right mu cluster, and 32 contributed to the right auditory cluster. 27 and 28 subjects contributed matching mu and auditory components in the left and right hemisphere, respectively, which were used for the analysis of connectivity. **Table 4-1** shows the contributions of each subject to clusters of interest.

Figure 4-1. Mean discrimination accuracy for active discrimination conditions.

Figure 4-2. Left mu cluster characteristics.

A) Left mu spectra. B) Mean scalp map for components contributing to left mu cluster. C) Equivalent current dipole localization for contributing components. D) Dipole density function for contributing components.

Figure 4-3. Right mu cluster characteristics.

A) Right mu spectra. B) Mean scalp map for components contributing to right mu cluster. C) Equivalent current dipole localization for contributing components. D) Dipole density function for contributing components.

Table 4-1. Subject contribution to neural clusters of interest.

Subject ID	Left Mu	Left Auditory	Right Mu	Right Auditory
1	X			
2				
3	X	X		X
4	X	X	X	X
5				
6	X	X	X	X
7		X	X	
8	X	X	X	X
9		X	X	
10	X	X	X	X
11			X	X
12		X		X
13		X		X
14	X	X	X	X
15	X	X	X	X
16	X	X	X	X
17	X	X	X	X
18	X	X	X	
19	X	X	X	X
20	X	X	X	X
21	X	X	X	X
22		X		X
23	X	X	X	X
24	X	X	X	X
25	X	X	X	X
26	X	X	X	
27	X	X	X	X
28	X	X	X	X
29	X	X	X	
30		X	X	X
31		X	X	
32	X	X	X	X
33	X	X	X	X
34	X			
35	X	X	X	X
36	X	X	X	X
37	X		X	X
38	X	X	X	X
39		X	X	X
40	X	X	X	X
41	X		X	X
42	X	X	X	X

Left Mu

The mean ECD location for the left mu cluster was at Talairach [-41, -8, 41] in the precentral gyrus (BA – 6) with an unexplained residual variance of 3.73%.

Left Auditory

The mean ECD location for the left auditory cluster was at Talairach [-50, -43, 4] in the middle temporal gyrus (BA – 22) with an unexplained residual variance of 4.02%.

Right Mu

The mean ECD location for the right mu cluster was at Talairach [45, -4, 38] in the precentral gyrus (BA – 6) with an unexplained residual variance of 3.86%.

Right Auditory

The mean ECD location for the right mu cluster was at Talairach [51, -45, 7] in the middle temporal gyrus (BA – 21) with an unexplained residual variance of 4.39%.

ERSP Characteristics

Omnibus

Left Mu. ERSP data from the left hemisphere mu rhythm was characterized by ERD across both alpha and beta bands in all discrimination conditions, with no activity noted during the control condition. Alpha / beta mu ERD emerged during stimulus presentation, persisting across the late trial epoch. An omnibus 1 x 7 ANOVA employing permutation statistics with FDR corrections for multiple comparisons revealed significant differences from ~280 ms following stimulus onset until the end of the trial in the alpha band and from ~200 ms post stimulus onset through the end of the trial in the beta band. **Figure 4-4** shows the ERSP data from the left and right mu clusters alongside the results of the omnibus tests.

Right Mu. ERSP data from the right hemisphere was characterized by alpha and beta ERD lagging slightly behind stimulus onset in all active discrimination conditions, with no activity noted during the control condition. An omnibus 1 x 7 ANOVA employing permutation statistics with FDR corrections for multiple comparisons revealed significant differences from ~400 ms post stimulus onset through the end of the trial in the alpha band, and from ~350 ms post stimulus onset through the end of the trial in the beta band. Patterns from the right hemisphere were similar to those observed in the left

Figure 4-4. Time-frequency decomposition of left and right mu clusters.

Top row corresponds to left mu cluster and bottom row corresponds to right mu cluster. Columns correspond to experimental conditions, with right-most column displaying results of the omnibus F -test across conditions with FDR corrections for multiple comparisons. Red voxels indicate time-frequency bins displaying condition differences at $\alpha = .05$.

hemisphere, albeit with weaker spectral power, consistent with reports that sensorimotor transformations for speech are bilateral (Cogan et al., 2014) yet left hemisphere dominant (Hickok and Poeppel, 2000; 2004; 2007). As the right hemisphere results did not reveal different significance patterns from those found in the left hemisphere, statistical contrasts for the purpose of testing were restricted to the left hemisphere.

Factorial Design

The results of a 2 x 3 repeated measures ANOVA with FDR corrections for multiple comparisons did not reveal a significant interaction term. Consequently, the statistical contrasts for hypothesis testing reported below were collapsed across factors to increase statistical power.

Results Pertaining to Hypothesis 1

In contrast to the first hypothesis that stronger pre-stimulus mu beta ERD would be present in small set than large set size conditions, the results of a paired t-test employing permutation statistics with FDR corrections for multiple comparisons did not reveal a set size effect in bilateral mu clusters. Additionally, only weak pre-stimulus beta ERD was observed in both small and large set sizes.

Despite the absence of a pre-stimulus set size effect in direct comparison of the discrimination conditions, comparison of small and large set size conditions to the control condition individually revealed interesting differences in the left hemisphere (**Figure 4-5**). While similar patterns of robust alpha and beta mu ERD were present in the post-stimulus window for both small and large set discrimination, patterns were different in the pre- and peri-stimulus windows. The comparison of small set discrimination to the control condition in the left hemisphere revealed robust differences in the alpha band across the pre- and peri-stimulus windows, with robust differences in peri-stimulus beta. In contrast, comparison of large set discrimination to the control condition in the left hemisphere revealed only weak, transient alpha differences early in the pre-stimulus window, with weak beta differences in the peri-stimulus window. Additionally, the onset of peri-stimulus beta differences in large set discrimination was ~200 ms later than in small set discrimination.

Results Pertaining to Hypothesis 2

In accord with the second hypothesis that differences would be found between quiet, masked, and filtered discrimination conditions, a 1 x 3 ANOVA employing permutations stats with FDR corrections for multiple comparisons revealed significant differences between degradation levels. Differences were present in the alpha band from ~350 to ~1200 ms post stimulus onset, and in the beta band from ~300 ms post stimulus

Figure 4-5. Set size effects.

The top and bottom rows represent the statistical comparison of Small and Large set conditions, respectively, to the PasN condition, with significantly different time-frequency bins indicated by red in the right column ($p\text{FDR} < .05$). The middle row indicates time-frequency bins significant in Small but not Large set discrimination conditions.

onset through the remainder of the epoch. In order to decompose the source of these effects, a series of paired *t*-tests employing permutations stats with FDR corrections for multiple comparisons were conducted between the levels of stimulus degradation.

Figure 4-6 displays the results of the ANOVA and the *t*-tests.

The contrast between Masked and Filtered conditions revealed significant differences in the beta band from ~1200 ms following stimulus onset through the end of the trial epoch, comprising the late post-stimulus window. The contrast between Quiet and Masked conditions revealed differences in the alpha band from ~400 to ~750 ms following stimulus onset, encompassing the late peri-stimulus and early post-stimulus windows. The contrast of Quiet and Filtered conditions revealed robust differences in both alpha and beta bands. Alpha differences were present from ~400 to ~950 ms post stimulus onset, while beta differences were present from ~400 to ~1200 ms post stimulus onset, encompassing the late peri-stimulus and early post-stimulus windows.

Results Pertaining to Hypothesis 3

The results from the mu-auditory coherence analysis failed to support the third hypothesis that patterns of forward and inverse modeling would be present across the trial epoch. No clearly discernable pattern of coherence between mu and auditory clusters was observed across conditions in either hemisphere. The results of the coherence analysis for left and right hemispheres are displayed in **Figure 4-7** and **Figure 4-8**, respectively. The omnibus ANOVA did not reveal any differences surviving corrections for multiple comparisons. Additionally, a series of paired *t*-tests employing permutation statistics with FDR corrections for multiple comparisons comparing coherence values between PasN and each of the discrimination conditions failed to demonstrate significant differences across the trial epoch.

Figure 4-6. Signal clarity effects.

The top row corresponds to the F -test across levels of signal clarity with significantly different time-frequency bins indicated in red in the right-most column. The remaining rows display the results of paired t -tests to decompose the signal clarity effect. All differences significant at $p\text{FDR} < .05$.

Figure 4-7. Left hemisphere mu-auditory alpha phase coherence.

Columns correspond to experimental conditions, with the right-most column representing the uncorrected F values for the omnibus test across conditions. No differences survived corrections for multiple comparisons.

Figure 4-8. Right hemisphere mu-auditory alpha phase coherence.

Columns correspond to experimental conditions, with the right-most column representing the uncorrected F values for the omnibus test across conditions. No differences survived corrections for multiple comparisons.

CHAPTER 5. DISCUSSION

In the current study, ICA identified bilateral sensorimotor mu and auditory alpha components from a cohort of typical speakers across an array of speech discrimination tasks. Consistent with other studies employing similar inclusion criteria for cluster membership (Bowers et al., 2014; Jenson et al., 2015; Cuellar et al., 2016; Saltuklaroglu et al., 2017), 88% and 93% of subjects contributed to mu and auditory alpha clusters, respectively (see **Table 4-1** for full description of cluster contribution). ECD models localized mu clusters to premotor cortex (BA-6) bilaterally, consistent with accepted generator sites of the mu rhythm (Pineda, 2005; Hari, 2006). Auditory alpha component clusters were localized to posterior middle temporal gyrus bilaterally (left: BA-22; right: BA-21) in accord with previous localizations of the auditory alpha rhythm (Muller and Weisz, 2012; Herman et al., 2013; Bowers et al., 2014). Critical to the investigation of mu to auditory coherence, matching mu and auditory alpha components were contributed by 66% and 68% of subjects in left and right hemispheres, respectively. Given the high proportion of subjects contributing neural components, it was possible to test experimental hypotheses regarding set size, stimulus degradation, and covert rehearsal.

Set Size Differences

In contrast to the first hypothesis that small set conditions would produce stronger pre-stimulus mu beta ERD than large set conditions, set size effects were present in pre-stimulus alpha and peri-stimulus alpha and beta activity when compared to PasN. While not in direct support of the first hypothesis, these differences from PasN may be tentatively interpreted to inform regarding the influence of stimulus predictability on sensorimotor processes. Stronger pre- and peri-stimulus alpha ERD was noted in small set discrimination, with peri-stimulus beta differences emerging ~200 ms earlier in small set than large set discrimination. Thus, rather than stimulus predictability moderating attention by predictive generation of forward models as hypothesized, an alternative mechanism must be considered. Pre-stimulus alpha ERD in perception tasks is typically interpreted as a measure of increased attentional allocation to a target sensory stream (Jones et al., 2010; Muller and Weisz, 2012; Frey et al., 2014). However, as none of the discrimination tasks employed in the current study required preferential processing of a target sensory stream, the nature of differential attentional allocation based on set size requires further consideration.

In visual search tasks, the reduction of the search space by prior knowledge leads to increased performance (Barrett et al., 2016) as well as pre-stimulus alpha ERD (Worden et al., 2000; Rihs et al., 2007; Bonnefond and Jensen, 2012). As alpha ERD tracks the spatial locus of attention (Foster et al., 2017) and reflects the cortical prioritization of memory representations serving as the current selection filter (de Vries et al., 2017), it may be proposed that the a priori narrowing of the search space enables increased attentional allocation to relevant stimulus parameters. A corollary mechanism in the auditory domain, akin to the perceptual narrowing experienced by infants (Pons et

al., 2009; Fava et al., 2014; Ortiz-Mantilla et al., 2016), may have enabled a similar sensory narrowing in the small set tasks employed in the current study. That is, since the sub-region of the auditory signal necessary to perform the discrimination task is known a priori in small set discrimination, the brain may constrain sensory analysis to a task-relevant subsection of the incoming signal. Rather than enacting predictive forward models, the repetitive nature of the discrimination tasks may have enabled subjects to narrow the auditory search space by probabilistic (Clayards et al., 2008; Kleinschmidt and Jaeger, 2015) or statistical (Maye et al., 2008; Virtala et al., 2018) learning methods. This sensory narrowing may account for the earlier onset of mu alpha and beta ERD in the peri-stimulus window, as more efficient attentional allocation would enable the earlier extraction of relevant stimulus parameters and their mapping onto articulatory gestures.

It must also be considered that stronger early alpha ERD in small set conditions may represent an effect of repetition priming. Under this interpretation, recently presented items possess a residual level of activity and are more readily activated. However, several factors render this interpretation untenable. First, as the current analysis pipeline entails referencing ERSP data to a pre-stimulus baseline, residual activation from previous trials is present in the baseline. Consequently, selection of a recently activated item would be expected to elicit weaker, rather than stronger activity. Second, data from ERP studies demonstrate weaker processing of primed compared to unprimed items (Holcomb et al., 2005; Grainger and Holcomb, 2015; Grisoni et al., 2016; Rommers and Federmeier, 2018). To date, no studies have examined repetition priming effects on the sensorimotor mu rhythm, though Tavabi et al. (2011) examined the oscillatory consequences of repetition priming over auditory regions, identifying reduced alpha ERD for primed compared to unprimed words. Taken together, these results preclude a priming explanation for the set size differences reported in the current study, lending credence to interpretations of more efficient attentional allocation based on reduced sensory search space. However, given the absence of significant condition differences in direct comparison of small and large set conditions, it must also be considered that set size may not constitute a meaningful experimental manipulation of stimulus predictability. Consequently, future studies probing the role of stimulus predictability on dorsal stream activity should employ a variety of experimental manipulations to ensure robust predictability changes.

Signal Clarity Differences

In contrast to the second hypothesis that pre-stimulus alpha differences would be found between Quiet, Masked, and Filtered discrimination conditions, differences were found across alpha and beta bands in the peri- and post-stimulus windows (i.e., during and following stimulus presentation). The absence of pre-stimulus alpha differences was unexpected given the findings of Jenson et al. (2014) and may reflect an adaptation to the task based on the large number of discriminations (i.e., 480) employed in the current study. Weaker alpha ERD compared to Quiet conditions was present in the late peri- and early post-stimulus windows in both degraded conditions, persisting later in the Filtered condition. Due to the similar time course of reduced alpha ERD in the current study and

alpha ERS in Jenson et al. (2014), results may be considered evidence of relative inhibition of the anterior dorsal stream in degraded compared to Quiet conditions. That is, considering reports that alpha ERD indexes a release from inhibition (Klimesch et al., 2007; Klimesch, 2012), results may be interpreted to suggest a reduced release from inhibition in degraded conditions. In light of the research question, such an interpretation suggests a resource allocation account of early inhibitory activity since no pre- or peri-stimulus differences were found between Masked and Filtered conditions. This interpretation is made tentatively however, as theoretical models linking alpha activity to inhibitory function generally consider inhibition from baseline rather than a relative effect between conditions (Klimesch et al., 2007; Jensen and Mazaheri, 2010; Schroeder et al., 2010; Strauss et al., 2014).

An alternate account emerges when results are considered within the framework of Analysis by Synthesis (Stevens and Halle, 1967; Poeppel and Monahan, 2011), which proposes that early motor-based hypotheses from a quick sketch of the stimulus are subjected to iterative loops of hypothesis testing and revision until the stimulus is identified (Bever and Poeppel, 2010). As mu alpha corresponds to sensory processing, the reduced peri-stimulus alpha ERD in degraded conditions may be considered evidence of a weak early sketch based on the low fidelity of the auditory signal. While this may appear to contradict reports of elevated dorsal stream activity during perception in noise (Osnes et al., 2011; Cuellar et al., 2012), it is critical to consider the timeline of activity. During Masked conditions, weak alpha ERD resolves quickly, with similar patterns of late activity as found in Quiet tasks. This normalization of late activity may be explained through the hypothesis-test loops in Analysis by Synthesis. While the source signal is degraded by the presence of noise, it still contains all of the information necessary to confirm forward model transformations of motor-based hypotheses. That is, sufficient detail exists in the source signal to confirm or revise hypotheses, allowing the sensorimotor system to converge on the stimulus identity and replay it in working memory.

In contrast, Filtered conditions were characterized by reduced alpha and beta ERD across the peri- and post-stimulus windows when compared to Quiet conditions. Reduced beta activity has been linked to weak forward models (Delval et al., 2006; Bickel et al., 2012; Bizovicar et al., 2014), suggesting that insufficient information exists to compensate for the weak early sketch of the stimulus. Since the mode of signal degradation in Filtered conditions entailed the removal of spectral information, hypothesis testing through forward model transformations specifies acoustic consequences that can neither be verified nor refuted. The inability of the sensorimotor system to effectively test and revise hypotheses may lead to a failure to converge on the stimulus identity, resulting in the persistence of weak internal modeling across the trial epoch. Given previous interpretations of late post-stimulus activity as working memory maintenance via covert rehearsal (Jenson et al., 2014; Saltuklaroglu et al., 2017; Thornton et al., 2017), this suggests that the ability to encode and maintain stimuli in working memory is mediated by the quality of the source signal. Support for this notion comes from evidence of decreased working memory capacity in normal aging (Cervera et al., 2009) and hearing impaired (Nittrouer et al., 2013; AuBuchon et al., 2015; Bharadwaj et

al., 2015) populations, both of whom have reduced access to spectral detail in the source signal. Taken together, these results suggest that articulatory rehearsal is not a modular process deployed identically across working memory tasks, but is sensitive to stimulus characteristics (Gathercole, 1995; Gathercole et al., 2001), and may additionally contribute to stimulus processing.

However, as increased working memory load typically elicits stronger beta ERD (Behmer and Fournier, 2014; Scharinger et al., 2017) (c.f. Schneider et al., 2017), an alternative interpretation must be considered. Reduced beta has been linked to increased levels of uncertainty (Tan et al., 2014; Tan et al., 2016), while weaker responses to sensory mismatches (encoded in the alpha band) have been reported under conditions of reduced confidence (Acerbi et al., 2017). It may then be proposed that the weaker activity in alpha and beta bands during Filtered tasks constitutes a neural marker for uncertainty. Under this interpretation, the reduced late beta ERD in Filtered conditions compared to Masked conditions suggests a mediating effect of confidence/uncertainty on the strength of covert rehearsal. However, as uncertainty is likely mediated by the paucity of the source signal, it remains unclear whether this constitutes a truly alternative interpretation. Further work is therefore necessary to clarify the contributions of working memory load, signal clarity, and uncertainty to late mu beta activity in discrimination tasks.

Coherence

The results of the mu-auditory coherence analysis failed to support the third hypothesis that patterns of forward and inverse modeling would be present across the trial epoch. While differences were present in the omnibus test across conditions in the alpha and beta bands, none of these differences survived corrections for multiple comparisons. Subsequent post hoc tests also did not reveal significant differences between the control condition and any of the discrimination conditions. This result was unexpected for several reasons. First, ERSP data replicated the findings from Jenson et al. (2015) demonstrating temporal concordance between the onset of mu ERD and the emergence of auditory alpha ERS (see **Figure 5-1**). Second, theoretical interpretations of alpha and beta bands as sensory feedback and forward modeling channels, respectively, suggest oscillatory coupling within those frequencies. Finally, recent evidence suggests that anterior and posterior dorsal stream regions communicate in alpha and beta bands during speech perception (Alho et al., 2014; Park et al., 2015; Elmer et al., 2017).

Several factors may have contributed to the failure to identify mu-auditory coherence in the current study. First, passive listening to noise may not have been an effective control condition. While it does not elicit activity in the anterior dorsal stream (Bowers et al., 2013; Jenson et al., 2014), little is known about its effects on dorsal stream connectivity, and its use as a control condition may have obscured discrimination-related effects. Second, while anterior and posterior aspects of the dorsal stream are directly connected via the arcuate and superior longitudinal fasciculi, it remains unclear whether communication entails intermediate processing stages. As coherence is

Figure 5-1. Temporal concordance between left hemisphere mu and auditory alpha rhythms.

The top row corresponds to sensorimotor mu activity across conditions, while the bottom row corresponds to the auditory alpha rhythm. The first column depicts the dipole density function from clusters of interest, while the remaining columns depict time-frequency activity across experimental conditions.

maximally sensitive to direct connections, intermediate processing may have reduced the sensitivity of the analysis. Third, alpha and beta bands may not constitute the primary channel of communication across the dorsal stream, as recent evidence suggests auditory-motor coupling in the theta band (von Stein and Sarnthein, 2000; Giraud et al., 2007; Park et al., 2015) consistent with the syllabic rate. Finally, it may be that patterns of dorsal stream coherence vary considerably across individuals and are not interpretable at the group level. In support of this notion, a high degree of inter-subject variability was noted in the ERSP data from auditory alpha components in the current study. As these results suggest that phase coherence in the alpha and beta ranges is not an effective means for probing auditory-motor interactions, future dorsal stream investigations should employ connectivity measures capable of addressing the weaknesses in the current paradigm.

General Discussion

The current study leveraged the temporal sensitivity of EEG to investigate the dynamic influences of cognitive demands including attention and working memory on sensorimotor processing. The temporal and spectral detail afforded by the current methodology enabled the tracking of multiple concurrent processes over the time course of speech perception events, with set size and stimulus clarity employed to modulate attentional demands through predictive and inhibitory mechanisms, respectively. Accordingly, the presence of stronger mu alpha ERD throughout the pre- and peri-stimulus windows coupled with earlier peri-stimulus beta ERD in small set discrimination is interpreted as evidence of more efficient attentional allocation based on the reduced sensory search space. Such an interpretation aligns with findings of preparatory attentional allocation during speech perception (Wostmann et al., 2015) and the role of attention in filtering and weighting sensory information according to task demands (Forschack et al., 2017). However, the manner in which these data correspond to the extant literature demonstrating elevated anterior dorsal stream activity during more difficult perception tasks (Osnes et al., 2011) remains unclear.

It must be considered that subjects may have adapted to the tasks, employing similar processing strategies across conditions despite the differences in stimuli. This is suggested by the failure to replicate previously reported pre-stimulus mu alpha ERS and mu beta ERD in speech discrimination tasks (Bowers et al., 2013; Jenson et al., 2014). In contrast to those studies, which employed a small number of speech discrimination tasks among a larger set of conditions, the current study consisted entirely of speech discrimination tasks. Similarly, the lack of robust pre-stimulus activity in Thornton et al. (2017) may be attributed to the exclusive use of active discrimination tasks. Under this interpretation, novel tasks may elicit processing strategies optimal for successful performance, while over time repetitive tasks may elicit processing strategies designed for maximum efficiency (i.e., minimal energy expenditure) while still allowing task completion. This proposal expands upon previous concerns regarding the ecological validity of tasks employed to probe dorsal stream processing (Hickok et al., 2011a).

Specifically, not only do tasks need to be considered in regard to naturalness, but also the larger experimental environment in which tasks are completed.

Concurrent alpha and beta mu ERD in the late trial epoch has now been reported in a large corpus of speech and non-speech discrimination studies (Bowers et al., 2013; Jenson et al., 2014; Jenson et al., 2015; Saltuklaroglu et al., 2017; Thornton et al., 2017; Thornton et al., In Prep), and appears to characterize sensorimotor responses to discrimination tasks. Based on its presence in the post-stimulus window and its similarity to patterns emerging during overt speech, this pattern has been interpreted as evidence of covert rehearsal to support working memory maintenance. The data from the current study, however, suggest a more nuanced interpretation. While subjects were able to perform the discrimination task with degraded stimuli, patterns of covert rehearsal were weaker in Filtered conditions than in both Quiet and Masked conditions. One possible explanation for this is that subjects were unable to recover the articulatory features required for covert rehearsal from the Filtered signal. As covert rehearsal mechanisms serve to refresh the sensory trace in working memory (Wilson, 2001; Buchsbaum et al., 2005), it may be proposed that while access to articulatory features is not necessary to perform the discrimination task, it is necessary to refresh the sensory trace in working memory through articulatory rehearsal. Weaker late activity in Filtered conditions may additionally represent uncertainty resulting from the inability to confirm forward model predictions. While in agreement with previous suggestions that late mu ERD corresponding to covert rehearsal characterizes discrimination tasks, the results of the current study suggest that this articulatory rehearsal is not a modular phenomenon deployed similarly in all cases. Rather, it is a dynamic process sensitive to both uncertainty and the quality of the signal being retained in working memory.

Limitations

While the current study identified robust effects of cognitive demands on sensorimotor processing during speech perception, some limitations should be addressed. First, only 88% and 93% of subjects contributed to mu and auditory clusters, with only 66% and 68% contributing to both clusters in left and right hemispheres, respectively. Reduced participant contribution is common in EEG research (Nystrom, 2008; Bowers et al., 2013), and has been linked to the use of standard head models. While subject specific electrode locations were used in the current study to mitigate this, mapping of these individualized locations to a standard head model yielded reduced participant contribution. Second, as the cohort consisted exclusively of female participants, it remains unclear how the findings of the current study apply to the larger population. Such a consideration is critical given reports that males and females may employ different sensorimotor processing strategies (Popovich et al., 2010; Kumari, 2011; Thornton et al., In Prep).

Conclusions and Future Directions

The current study exploited the temporal and spectral detail afforded by time-frequency decomposed EEG data to track the contributions of attentional and working memory processes to dorsal stream sensorimotor processing across the time course of speech discrimination. The differences emerging upon manipulation of set size and stimulus clarity confirmed the sensitive of dorsal stream processing to task demands. Specifically, the increased pre- and peri-stimulus mu alpha ERD in small set conditions was considered evidence of more efficient attentional allocation on the basis of a reduced sensory search space. Differences among the levels of stimulus clarity were considered support for Constructivist Analysis by Synthesis models, with motor-based hypotheses derived from an early sketch of the stimulus being an essential step for loading and maintaining the stimuli in working memory to enable task completion. Additional work, however, is necessary to validate this interpretation. Further confirmation and elucidation of the dynamic contributions of task demands to dorsal stream processing should consider the larger cognitive environment in which tasks are being completed. The cost-effective nature of the methodology employed in the current study supports its continued use to probe the dynamic influences of cognitive processes on dorsal stream processing.

LIST OF REFERENCES

- Abdul-Latif, A.A., Cosic, I., Kumar, D.K., Polus, B., Pah, N., and Djuwari, D. (2004). EEG coherence changes between right and left motor cortical areas during voluntary muscular contraction. *Australas Phys Eng Sci Med* 27, 11-15.
- Acerbi, L., Vijayakumar, S., and Wolpert, D.M. (2017). Target Uncertainty Mediates Sensorimotor Error Correction. *PLoS One* 12, e0170466.
- Ackermann, H. (2008). Cerebellar contributions to speech production and speech perception: psycholinguistic and neurobiological perspectives. *Trends Neurosci* 31, 265-272.
- Agnew, Z.K., Mcgettigan, C., and Scott, S.K. (2011). Discriminating between auditory and motor cortical responses to speech and nonspeech mouth sounds. *J Cogn Neurosci* 23, 4038-4047.
- Alegre, M., Imirizaldu, L., Valencia, M., Iriarte, J., Arcocha, J., and Artieda, J. (2006). Alpha and beta changes in cortical oscillatory activity in a go/no go randomly-delayed-response choice reaction time paradigm. *Clin Neurophysiol* 117, 16-25.
- Alho, J., Lin, F.H., Sato, M., Tiitinen, H., Sams, M., and Jaaskelainen, I.P. (2014). Enhanced neural synchrony between left auditory and premotor cortex is associated with successful phonetic categorization. *Front Psychol* 5, 394.
- Alho, J., Sato, M., Sams, M., Schwartz, J.L., Tiitinen, H., and Jaaskelainen, I.P. (2012a). Enhanced early-latency electromagnetic activity in the left premotor cortex is associated with successful phonetic categorization. *Neuroimage* 60, 1937-1946.
- Alho, K., Salmi, J., Koistinen, S., Salonen, O., and Rinne, T. (2015). Top-down controlled and bottom-up triggered orienting of auditory attention to pitch activate overlapping brain networks. *Brain Res* 1626, 136-145.
- Alho, K., Salonen, J., Rinne, T., Medvedev, S.V., Hugdahl, K., and Hamalainen, H. (2012b). Attention-related modulation of auditory-cortex responses to speech sounds during dichotic listening. *Brain Res* 1442, 47-54.
- Alschuler, D.M., Tenke, C.E., Bruder, G.E., and Kayser, J. (2014). Identifying electrode bridging from electrical distance distributions: a survey of publicly-available EEG data using a new method. *Clin Neurophysiol* 125, 484-490.
- Amaral, A.A., and Langers, D.R. (2013). The relevance of task-irrelevant sounds: hemispheric lateralization and interactions with task-relevant streams. *Front Neurosci* 7, 264.

- Amblard, P.O., and Michel, O.J. (2011). On directed information theory and Granger causality graphs. *J Comput Neurosci* 30, 7-16.
- Ardoint, M., and Lorenzi, C. (2010). Effects of lowpass and highpass filtering on the intelligibility of speech based on temporal fine structure or envelope cues. *Hear Res* 260, 89-95.
- Arnal, L.H., and Giraud, A.L. (2012). Cortical oscillations and sensory predictions. *Trends Cogn Sci* 16, 390-398.
- Arnal, L.H., Wyart, V., and Giraud, A.L. (2011). Transitions in neural oscillations reflect prediction errors generated in audiovisual speech. *Nat Neurosci* 14, 797-801.
- Arnstein, D., Cui, F., Keysers, C., Maurits, N.M., and Gazzola, V. (2011). mu-suppression during action observation and execution correlates with BOLD in dorsal premotor, inferior parietal, and SI cortices. *J Neurosci* 31, 14243-14249.
- Arroyo, S., Lesser, R.P., Gordon, B., Uematsu, S., Jackson, D., and Webber, R. (1993). Functional significance of the mu rhythm of human cortex: an electrophysiologic study with subdural electrodes. *Electroencephalogr Clin Neurophysiol* 87, 76-87.
- Arsenault, J.S., and Buchsbaum, B.R. (2016). No evidence of somatotopic place of articulation feature mapping in motor cortex during passive speech perception. *Psychon Bull Rev* 23, 1231-1240.
- Assaneo, M.F., and Poeppel, D. (2018). The coupling between auditory and motor cortices is rate-restricted: Evidence for an intrinsic speech-motor rhythm. *Sci Adv* 4, eaao3842.
- Aubuchon, A.M., Pisoni, D.B., and Kronenberger, W.G. (2015). Short-Term and Working Memory Impairments in Early-Implanted, Long-Term Cochlear Implant Users Are Independent of Audibility and Speech Production. *Ear Hear* 36, 733-737.
- Baddeley, A. (2003). Working memory and language: an overview. *J Commun Disord* 36, 189-208.
- Balk, M.H., Kari, H., Kauramaki, J., Ahveninen, J., Sams, M., Autti, T., and Jaaskelainen, I.P. (2013). Silent lipreading and covert speech production suppress processing of non-linguistic sounds in auditory cortex. *Open J Neurosci* 3.
- Barrett, D.J., Shimozaki, S.S., Jensen, S., and Zobay, O. (2016). Visuospatial working memory mediates inhibitory and facilitatory guidance in preview search. *J Exp Psychol Hum Percept Perform* 42, 1533-1546.

- Bartoli, E., D'ausilio, A., Berry, J., Badino, L., Bever, T., and Fadiga, L. (2015). Listener-speaker perceived distance predicts the degree of motor contribution to speech perception. *Cereb Cortex* 25, 281-288.
- Bartoli, E., Maffongelli, L., Campus, C., and D'ausilio, A. (2016). Beta rhythm modulation by speech sounds: somatotopic mapping in somatosensory cortex. *Sci Rep* 6, 31182.
- Bastiaansen, M.C., Bocker, K.B., Brunia, C.H., De Munck, J.C., and Spekreijse, H. (2001). Event-related desynchronization during anticipatory attention for an upcoming stimulus: a comparative EEG/MEG study. *Clin Neurophysiol* 112, 393-403.
- Bastiaansen, M.C., and Brunia, C.H. (2001). Anticipatory attention: an event-related desynchronization approach. *Int J Psychophysiol* 43, 91-107.
- Bastos, A.M., Usrey, W.M., Adams, R.A., Mangun, G.R., Fries, P., and Friston, K.J. (2012). Canonical microcircuits for predictive coding. *Neuron* 76, 695-711.
- Bastos, A.M., Vezoli, J., Bosman, C.A., Schoffelen, J.M., Oostenveld, R., Dowdall, J.R., De Weerd, P., Kennedy, H., and Fries, P. (2015). Visual areas exert feedforward and feedback influences through distinct frequency channels. *Neuron* 85, 390-401.
- Behmer, L.P., Jr., and Fournier, L.R. (2014). Working memory modulates neural efficiency over motor components during a novel action planning task: an EEG study. *Behav Brain Res* 260, 1-7.
- Bendixen, A., Scharinger, M., Strauss, A., and Obleser, J. (2014). Prediction in the service of comprehension: modulated early brain responses to omitted speech segments. *Cortex* 53, 9-26.
- Benjamini, Y., and Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, 289-300.
- Bever, T.G., and Poeppel, D. (2010). Analysis by synthesis: a (re-) emerging program of research for language and vision. *Biolinguistics* 4, 174-200.
- Bharadwaj, S.V., Maricle, D., Green, L., and Allman, T. (2015). Working memory, short-term memory and reading proficiency in school-age children with cochlear implants. *Int J Pediatr Otorhinolaryngol* 79, 1647-1653.
- Bickel, S., Dias, E.C., Epstein, M.L., and Javitt, D.C. (2012). Expectancy-related modulations of neural oscillations in continuous performance tasks. *Neuroimage* 62, 1867-1876.

- Bidet-Caulet, A., Fischer, C., Besle, J., Aguera, P.E., Giard, M.H., and Bertrand, O. (2007). Effects of selective attention on the electrophysiological representation of concurrent sounds in the human auditory cortex. *J Neurosci* 27, 9252-9261.
- Binder, J.R., Liebenthal, E., Possing, E.T., Medler, D.A., and Ward, B.D. (2004). Neural correlates of sensory and decision processes in auditory object identification. *Nat Neurosci* 7, 295-301.
- Binder, J.R., Swanson, S.J., Hammeke, T.A., and Sabsevitz, D.S. (2008). A comparison of five fMRI protocols for mapping speech comprehension systems. *Epilepsia* 49, 1980-1997.
- Bizovicar, N., Dreo, J., Koritnik, B., and Zidar, J. (2014). Decreased movement-related beta desynchronization and impaired post-movement beta rebound in amyotrophic lateral sclerosis. *Clin Neurophysiol* 125, 1689-1699.
- Blakely, T., Miller, K.J., Rao, R.P., Holmes, M.D., and Ojemann, J.G. (2008). Localization and classification of phonemes using high spatial resolution electrocorticography (ECoG) grids. *Conf Proc IEEE Eng Med Biol Soc* 2008, 4964-4967.
- Blakemore, S.J., Wolpert, D., and Frith, C. (2000). Why can't you tickle yourself? *Neuroreport* 11, R11-16.
- Blank, H., and Davis, M.H. (2016). Prediction Errors but Not Sharpened Signals Simulate Multivoxel fMRI Patterns during Speech Perception. *PLoS Biol* 14, e1002577.
- Blank, H., and Von Kriegstein, K. (2013). Mechanisms of enhancing visual-speech recognition by prior auditory information. *Neuroimage* 65, 109-118.
- Bonnefond, M., and Jensen, O. (2012). Alpha Oscillations Serve to Protect Working Memory Maintenance against Anticipated Distracters. *Current Biology* 22, 1969-1974.
- Bowers, A., Saltuklaroglu, T., Harkrider, A., and Cuellar, M. (2013). Suppression of the micro rhythm during speech and non-speech discrimination revealed by independent component analysis: implications for sensorimotor integration in speech processing. *PLoS One* 8, e72024.
- Bowers, A.L., Saltuklaroglu, T., Harkrider, A., Wilson, M., and Toner, M.A. (2014). Dynamic modulation of shared sensory and motor cortical rhythms mediates speech and non-speech discrimination performance. *Front Psychol* 5, 366.

- Braadbaart, L., Williams, J.H., and Waiter, G.D. (2013). Do mirror neuron areas mediate mu rhythm suppression during imitation and action observation? *Int J Psychophysiol* 89, 99-105.
- Bressler, S.L., and Richter, C.G. (2015). Interareal oscillatory synchronization in top-down neocortical processing. *Curr Opin Neurobiol* 31, 62-66.
- Brinkman, L., Stolk, A., Dijkerman, H.C., De Lange, F.P., and Toni, I. (2014). Distinct roles for alpha- and beta-band oscillations during mental simulation of goal-directed actions. *J Neurosci* 34, 14783-14792.
- Brookes, M.J., Gibson, A.M., Hall, S.D., Furlong, P.L., Barnes, G.R., Hillebrand, A., Singh, K.D., Holliday, I.E., Francis, S.T., and Morris, P.G. (2005). GLM-beamformer method demonstrates stationary field, alpha ERD and gamma ERS co-localisation with fMRI BOLD response in visual cortex. *Neuroimage* 26, 302-308.
- Brunner, C., Delorme, A., and Makeig, S. (2013). Eeglab - an Open Source Matlab Toolbox for Electrophysiological Research. Biomed Tech (Berl).
- Buchsbaum, B.R., Hickok, G., and Humphries, C. (2001). Role of left posterior superior temporal gyrus in phonological processing for speech perception and production. *Cognitive Science* 25, 663-678.
- Buchsbaum, B.R., Olsen, R.K., Koch, P., and Berman, K.F. (2005). Human dorsal and ventral auditory streams subserve rehearsal-based and echoic processes during verbal working memory. *Neuron* 48, 687-697.
- Burton, M.W., and Small, S.L. (2006). Functional neuroanatomy of segmenting speech and nonspeech. *Cortex* 42, 644-651.
- Burton, M.W., Small, S.L., and Blumstein, S.E. (2000). The role of segmentation in phonological processing: an fMRI investigation. *J Cogn Neurosci* 12, 679-690.
- Callan, A.M., Callan, D.E., Tajima, K., and Akahane-Yamada, R. (2006a). Neural processes involved with perception of non-native durational contrasts. *Neuroreport* 17, 1353-1357.
- Callan, D., Callan, A., Gamez, M., Sato, M.A., and Kawato, M. (2010). Premotor cortex mediates perceptual performance. *Neuroimage* 51, 844-858.
- Callan, D.E., Tsytsarev, V., Hanakawa, T., Callan, A.M., Katsuhara, M., Fukuyama, H., and Turner, R. (2006b). Song and speech: brain regions involved with perception and covert production. *Neuroimage* 31, 1327-1342.

- Cannon, E.N., Yoo, K.H., Vanderwert, R.E., Ferrari, P.F., Woodward, A.L., and Fox, N.A. (2014). Action experience, more than observation, influences mu rhythm desynchronization. *PLoS One* 9, e92002.
- Carlqvist, H., Nikulin, V.V., Stromberg, J.O., and Brismar, T. (2005). Amplitude and phase relationship between alpha and beta oscillations in the human electroencephalogram. *Med Biol Eng Comput* 43, 599-607.
- Carter, L., Dillon, H., Seymour, J., Seeto, M., and Van Dun, B. (2013). Cortical auditory-evoked potentials (CAEPs) in adults in response to filtered speech stimuli. *J Am Acad Audiol* 24, 807-822.
- Cervera, T.C., Soler, M.J., Dasi, C., and Ruiz, J.C. (2009). Speech recognition and working memory capacity in young-elderly listeners: effects of hearing sensitivity. *Can J Exp Psychol* 63, 216-226.
- Chein, J.M., and Fiez, J.A. (2001). Dissociation of verbal working memory system components using a delayed serial recall task. *Cereb Cortex* 11, 1003-1014.
- Cheyne, D., Gaetz, W., Garnero, L., Lachaux, J.P., Ducorps, A., Schwartz, D., and Varela, F.J. (2003). Neuromagnetic imaging of cortical oscillations accompanying tactile stimulation. *Brain Res Cogn Brain Res* 17, 599-611.
- Chiappe, P., Chiappe, D.L., and Siegel, L.S. (2001). Speech perception, lexicality, and reading skill. *J Exp Child Psychol* 80, 58-74.
- Clayards, M., Tanenhaus, M.K., Aslin, R.N., and Jacobs, R.A. (2008). Perception of speech reflects optimal use of probabilistic speech cues. *Cognition* 108, 804-809.
- Clos, M., Langner, R., Meyer, M., Oechslin, M.S., Zilles, K., and Eickhoff, S.B. (2014). Effects of prior information on decoding degraded speech: an fMRI study. *Hum Brain Mapp* 35, 61-74.
- Cogan, G.B., Thesen, T., Carlson, C., Doyle, W., Devinsky, O., and Pesaran, B. (2014). Sensory-motor transformations for speech occur bilaterally. *Nature* 507, 94-98.
- Cole-Virtue, J., and Nickels, L. (2004). Why cabbage and not carrot?: An investigation of factors affecting performance on spoken word to picture matching. *Aphasiology* 18, 153-179.
- Correia, J.M., Jansma, B.M., and Bonte, M. (2015). Decoding Articulatory Features from fMRI Responses in Dorsal Speech Regions. *J Neurosci* 35, 15015-15025.
- Crawcour, S., Bowers, A., Harkrider, A., and Saltuklaroglu, T. (2009). Mu wave suppression during the perception of meaningless syllables: EEG evidence of motor recruitment. *Neuropsychologia* 47, 2558-2563.

- Crone, N.E., Miglioretti, D.L., Gordon, B., Sieracki, J.M., Wilson, M.T., Uematsu, S., and Lesser, R.P. (1998). Functional mapping of human sensorimotor cortex with electrocorticographic spectral analysis. I. Alpha and beta event-related desynchronization. *Brain* 121 (Pt 12), 2271-2299.
- Cuellar, M., Bowers, A., Harkrider, A.W., Wilson, M., and Saltuklaroglu, T. (2012). Mu suppression as an index of sensorimotor contributions to speech processing: evidence from continuous EEG signals. *Int J Psychophysiol* 85, 242-248.
- Cuellar, M., Harkrider, A.W., Jenson, D., Thornton, D., Bowers, A., and Saltuklaroglu, T. (2016). Time-frequency analysis of the EEG mu rhythm as a measure of sensorimotor integration in the later stages of swallowing. *Clin Neurophysiol* 127, 2625-2635.
- Curio, G., Neuloh, G., Numminen, J., Jousmaki, V., and Hari, R. (2000). Speaking modifies voice-evoked activity in the human auditory cortex. *Hum Brain Mapp* 9, 183-191.
- D'ausilio, A., Bufalari, I., Salmas, P., and Fadiga, L. (2012). The role of the motor system in discriminating normal and degraded speech sounds. *Cortex* 48, 882-887.
- D'ausilio, A., Maffongelli, L., Bartoli, E., Campanella, M., Ferrari, E., Berry, J., and Fadiga, L. (2014). Listening to speech recruits specific tongue motor synergies as revealed by transcranial magnetic stimulation and tissue-Doppler ultrasound imaging. *Philos Trans R Soc Lond B Biol Sci* 369, 20130418.
- Davis, M.H., and Johnsrude, I.S. (2003). Hierarchical processing in spoken language comprehension. *J Neurosci* 23, 3423-3431.
- De Lange, F.P., Jensen, O., Bauer, M., and Toni, I. (2008). Interactions between posterior gamma and frontal alpha/beta oscillations during imagined actions. *Front Hum Neurosci* 2, 7.
- De Vries, I.E., Van Driel, J., and Olivers, C.N. (2017). Posterior alpha EEG Dynamics Dissociate Current from Future Goals in Working Memory-Guided Visual Search. *J Neurosci* 37, 1591-1603.
- Degardin, A., Houdayer, E., Bourriez, J.L., Destee, A., Defebvre, L., Derambure, P., and Devos, D. (2009). Deficient "sensory" beta synchronization in Parkinson's disease. *Clin Neurophysiol* 120, 636-642.
- Del Percio, C., Rossini, P.M., Marzano, N., Iacoboni, M., Infarinato, F., Aschieri, P., Lino, A., Fiore, A., Toran, G., Babiloni, C., and Eusebi, F. (2008). Is there a "neural efficiency" in athletes? A high-resolution EEG study. *Neuroimage* 42, 1544-1553.

- Delong, K.A., Urbach, T.P., and Kutas, M. (2005). Probabilistic word pre-activation during language comprehension inferred from electrical brain activity. *Nat Neurosci* 8, 1117-1121.
- Delorme, A., Palmer, J., Onton, J., Oostenveld, R., and Makeig, S. (2012). Independent EEG sources are dipolar. *PLoS One* 7, e30135.
- Delval, A., Defebvre, L., Labyt, E., Douay, X., Bourriez, J.L., Waucquier, N., Derambure, P., and Destee, A. (2006). Movement-related cortical activation in familial Parkinson disease. *Neurology* 67, 1086-1087.
- Deng, Y., Guo, R., Ding, G., and Peng, D. (2012). Top-down modulations from dorsal stream in lexical recognition: an effective connectivity fMRI study. *PLoS One* 7, e33337.
- Denis, D., Rowe, R., Williams, A.M., and Milne, E. (2017). The role of cortical sensorimotor oscillations in action anticipation. *Neuroimage* 146, 1102-1114.
- Di Nota, P.M., Chartrand, J.M., Levkov, G.R., Montefusco-Siegmund, R., and Desouza, J.F. (2017). Experience-dependent modulation of alpha and beta during action observation and motor imagery. *BMC Neurosci* 18, 28.
- Dias, E.C., Bickel, S., Epstein, M.L., Sehatpour, P., and Javitt, D.C. (2013). Abnormal task modulation of oscillatory neural activity in schizophrenia. *Front Psychol* 4, 540.
- Dohrmann, K., Elbert, T., Schlee, W., and Weisz, N. (2007a). Tuning the tinnitus percept by modification of synchronous brain activity. *Restor Neurol Neurosci* 25, 371-378.
- Dohrmann, K., Weisz, N., Schlee, W., Hartmann, T., and Elbert, T. (2007b). Neurofeedback for treating tinnitus. *Prog Brain Res* 166, 473-485.
- Downs, D.W., and Crum, M.A. (1978). Processing demands during auditory learning under degraded listening conditions. *J Speech Hear Res* 21, 702-714.
- Drewes, A.M., Sami, S.A., Dimcevski, G., Nielsen, K.D., Funch-Jensen, P., Valeriani, M., and Arendt-Nielsen, L. (2006). Cerebral processing of painful oesophageal stimulation: a study based on independent component analysis of the EEG. *Gut* 55, 619-629.
- Du, Y., Buchsbaum, B.R., Grady, C.L., and Alain, C. (2014). Noise differentially impacts phoneme representations in the auditory and speech motor systems. *Proc Natl Acad Sci U S A* 111, 7126-7131.

- Dubois, C., Otzenberger, H., Gounot, D., Sock, R., and Metz-Lutz, M.N. (2012). Visemic processing in audiovisual discrimination of natural speech: a simultaneous fMRI-EEG study. *Neuropsychologia* 50, 1316-1326.
- Easwar, V., Purcell, D.W., Aiken, S.J., Parsa, V., and Scollie, S.D. (2015a). Effect of Stimulus Level and Bandwidth on Speech-Evoked Envelope Following Responses in Adults With Normal Hearing. *Ear Hear* 36, 619-634.
- Easwar, V., Purcell, D.W., Aiken, S.J., Parsa, V., and Scollie, S.D. (2015b). Evaluation of Speech-Evoked Envelope Following Responses as an Objective Aided Outcome Measure: Effect of Stimulus Level, Bandwidth, and Amplification in Adults With Hearing Loss. *Ear Hear* 36, 635-652.
- Ellis, N.C., and Hennessey, R. (1980). A bilingual word-length effect: Implications for intelligence testing and the relative ease of mental calculation in Welsh and English. *British Journal of Psychology* 71, 43-51.
- Elmer, S., Kohns, J., Rauch, P., Abolfazl Valizadeh, S., and Jancke, L. (2017). 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. *Neuropsychologia* 106, 398-406.
- Engel, A.K., and Fries, P. (2010). Beta-band oscillations--signalling the status quo? *Curr Opin Neurobiol* 20, 156-165.
- Erickson, M.A., Albrecht, M.A., Robinson, B., Luck, S.J., and Gold, J.M. (2017). Impaired suppression of delay-period alpha and beta is associated with impaired working memory in schizophrenia. *Biol Psychiatry Cogn Neurosci Neuroimaging* 2, 272-279.
- Fadiga, L., Craighero, L., Buccino, G., and Rizzolatti, G. (2002). Speech listening specifically modulates the excitability of tongue muscles: a TMS study. *Eur J Neurosci* 15, 399-402.
- Fadiga, L., Craighero, L., and Olivier, E. (2005). Human motor cortex excitability during the perception of others' action. *Curr Opin Neurobiol* 15, 213-218.
- Fava, E., Hull, R., and Bortfeld, H. (2014). Dissociating Cortical Activity during Processing of Native and Non-Native Audiovisual Speech from Early to Late Infancy. *Brain Sci* 4, 471-487.
- Fontolan, L., Morillon, B., Liegeois-Chauvel, C., and Giraud, A.L. (2014). The contribution of frequency-specific activity to hierarchical information processing in the human auditory cortex. *Nat Commun* 5, 4694.

- Forschack, N., Nierhaus, T., Muller, M.M., and Villringer, A. (2017). Alpha-Band Brain Oscillations Shape the Processing of Perceptible as well as Imperceptible Somatosensory Stimuli during Selective Attention. *J Neurosci* 37, 6983-6994.
- Foster, J.J., Sutterer, D.W., Serences, J.T., Vogel, E.K., and Awh, E. (2017). Alpha-Band Oscillations Enable Spatially and Temporally Resolved Tracking of Covert Spatial Attention. *Psychol Sci* 28, 929-941.
- Fowler, C. (1986). An event approach to the study of speech perception from a direct-realist perspective. Status Report on Speech Research, edited by IG Mattingly and N. O'Brien, Haskins Laboratories, New Haven, CT, 139-169.
- Fowler, C.A., Brown, J.M., Sabadini, L., and Weihing, J. (2003). Rapid access to speech gestures in perception: Evidence from choice and simple response time tasks. *J Mem Lang* 49, 396-413.
- Fowler, C.A., and Xie, X. (2016). "Involvement of the speech motor system in speech perception," in *Speech motor control in normal and disordered speech: Future developments in theory and methodology*, ed. P. Van Lieshout, Maassen, B., & Terband, H. (Rockville, MD: ASHA Press), 1-24.
- Fox, N.A., Bakermans-Kranenburg, M.J., Yoo, K.H., Bowman, L.C., Cannon, E.N., Vanderwert, R.E., Ferrari, P.F., and Van, I.M.H. (2016). Assessing human mirror activity with EEG mu rhythm: A meta-analysis. *Psychol Bull* 142, 291-313.
- Foxe, J.J., Simpson, G.V., and Ahlfors, S.P. (1998). Parieto-occipital approximately 10 Hz activity reflects anticipatory state of visual attention mechanisms. *Neuroreport* 9, 3929-3933.
- Frenkel-Toledo, S., Bentin, S., Perry, A., Liebermann, D.G., and Soroker, N. (2013). Dynamics of the EEG power in the frequency and spatial domains during observation and execution of manual movements. *Brain Res* 1509, 43-57.
- Frey, J.N., Mainy, N., Lachaux, J.P., Muller, N., Bertrand, O., and Weisz, N. (2014). Selective modulation of auditory cortical alpha activity in an audiovisual spatial attention task. *J Neurosci* 34, 6634-6639.
- Freyman, R.L., Griffin, A.M., and Macmillan, N.A. (2013). Priming of lowpass-filtered speech affects response bias, not sensitivity, in a bandwidth discrimination task. *J Acoust Soc Am* 134, 1183-1192.
- Friedrich, E.V., Sivanathan, A., Lim, T., Suttie, N., Louchart, S., Pillen, S., and Pineda, J.A. (2015). An Effective Neurofeedback Intervention to Improve Social Interactions in Children with Autism Spectrum Disorder. *J Autism Dev Disord* 45, 4084-4100.

- Fries, P. (2005). A mechanism for cognitive dynamics: neuronal communication through neuronal coherence. *Trends Cogn Sci* 9, 474-480.
- Friston, K.J. (2011). Functional and effective connectivity: a review. *Brain Connect* 1, 13-36.
- Fujioka, T., Ross, B., and Trainor, L.J. (2015). Beta-Band Oscillations Represent Auditory Beat and Its Metrical Hierarchy in Perception and Imagery. *J Neurosci* 35, 15187-15198.
- Fujioka, T., Trainor, L.J., Large, E.W., and Ross, B. (2012). Internalized timing of isochronous sounds is represented in neuromagnetic beta oscillations. *J Neurosci* 32, 1791-1802.
- Gaetz, W., Macdonald, M., Cheyne, D., and Snead, O.C. (2010). Neuromagnetic imaging of movement-related cortical oscillations in children and adults: age predicts post-movement beta rebound. *Neuroimage* 51, 792-807.
- Galantucci, B., Fowler, C.A., and Turvey, M.T. (2006). The motor theory of speech perception reviewed. *Psychonomic bulletin & review* 13, 361-377.
- Gallese, V., Fadiga, L., Fogassi, L., and Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain* 119 (Pt 2), 593-609.
- Gao, Y., Wang, Q., Ding, Y., Wang, C., Li, H., Wu, X., Qu, T., and Li, L. (2017). Selective Attention Enhances Beta-Band Cortical Oscillation to Speech under "Cocktail-Party" Listening Conditions. *Front Hum Neurosci* 11, 34.
- Gathercole, S.E. (1995). Is nonword repetition a test of phonological memory or long-term knowledge? It all depends on the nonwords. *Mem Cognit* 23, 83-94.
- Gathercole, S.E., Pickering, S.J., Hall, M., and Peaker, S.M. (2001). Dissociable lexical and phonological influences on serial recognition and serial recall. *Q J Exp Psychol A* 54, 1-30.
- Gehrig, J., Wibrall, M., Arnold, C., and Kell, C.A. (2012). Setting up the speech production network: how oscillations contribute to lateralized information routing. *Front Psychol* 3, 169.
- Gilbert, G., and Lorenzi, C. (2010). Role of spectral and temporal cues in restoring missing speech information. *J Acoust Soc Am* 128, E1294-299.
- Giordano, B.L., Ince, R.a.A., Gross, J., Schyns, P.G., Panzeri, S., and Kayser, C. (2017). Contributions of local speech encoding and functional connectivity to audio-visual speech perception. *Elife* 6.

- Giraud, A.L., Kell, C., Thierfelder, C., Sterzer, P., Russ, M.O., Preibisch, C., and Kleinschmidt, A. (2004). Contributions of sensory input, auditory search and verbal comprehension to cortical activity during speech processing. *Cereb Cortex* 14, 247-255.
- Giraud, A.L., Kleinschmidt, A., Poeppel, D., Lund, T.E., Frackowiak, R.S., and Laufs, H. (2007). Endogenous cortical rhythms determine cerebral specialization for speech perception and production. *Neuron* 56, 1127-1134.
- Goswami, U., Cumming, R., Chait, M., Huss, M., Mead, N., Wilson, A.M., Barnes, L., and Fosker, T. (2016). Perception of Filtered Speech by Children with Developmental Dyslexia and Children with Specific Language Impairments. *Front Psychol* 7, 791.
- Gow Jr, D.W., and Segawa, J.A. (2009). Articulatory mediation of speech perception: A causal analysis of multi-modal imaging data. *Cognition* 110, 222-236.
- Grabner, R.H., Fink, A., Stipacek, A., Neuper, C., and Neubauer, A.C. (2004). Intelligence and working memory systems: evidence of neural efficiency in alpha band ERD. *Brain Res Cogn Brain Res* 20, 212-225.
- Grabski, K., Tremblay, P., Gracco, V.L., Girin, L., and Sato, M. (2013). A mediating role of the auditory dorsal pathway in selective adaptation to speech: a state-dependent transcranial magnetic stimulation study. *Brain Res* 1515, 55-65.
- Graimann, B., and Pfurtscheller, G. (2006). Quantification and visualization of event-related changes in oscillatory brain activity in the time-frequency domain. *Prog Brain Res* 159, 79-97.
- Grainger, J., and Holcomb, P.J. (2015). An ERP investigation of dichotic repetition priming with temporally overlapping stimuli. *Psychon Bull Rev* 22, 289-296.
- Granger, C.W. (1969). Investigating causal relations by econometric models and cross-spectral methods. *Econometrica: Journal of the Econometric Society*, 424-438.
- Granger, C.W. (1988). Some recent development in a concept of causality. *Journal of econometrics* 39, 199-211.
- Greischar, L.L., Burghy, C.A., Van Reekum, C.M., Jackson, D.C., Pizzagalli, D.A., Mueller, C., and Davidson, R.J. (2004). Effects of electrode density and electrolyte spreading in dense array electroencephalographic recording. *Clin Neurophysiol* 115, 710-720.
- Grisoni, L., Dreyer, F.R., and Pulvermuller, F. (2016). Somatotopic Semantic Priming and Prediction in the Motor System. *Cereb Cortex* 26, 2353-2366.

- Guenther, F.H. (2016). "Neural control of speech". Mit Press).
- Guenther, F.H., Brumberg, J.S., Wright, E.J., Nieto-Castanon, A., Tourville, J.A., Panko, M., Law, R., Siebert, S.A., Bartels, J.L., Andreasen, D.S., Ehirim, P., Mao, H., and Kennedy, P.R. (2009). A wireless brain-machine interface for real-time speech synthesis. *PLoS One* 4, e8218.
- Guenther, F.H., and Vladusich, T. (2012). A Neural Theory of Speech Acquisition and Production. *J Neurolinguistics* 25, 408-422.
- Gunji, A., Ishii, R., Chau, W., Kakigi, R., and Pantev, C. (2007). Rhythmic brain activities related to singing in humans. *Neuroimage* 34, 426-434.
- Haegens, S., Luther, L., and Jensen, O. (2012). Somatosensory anticipatory alpha activity increases to suppress distracting input. *J Cogn Neurosci* 24, 677-685.
- Hari, R. (1990). The neuromagnetic method in the study of the human auditory cortex. *Advances in audiology* 6, 222-282.
- Hari, R. (2006). Action-perception connection and the cortical mu rhythm. *Prog Brain Res* 159, 253-260.
- Hartmann, T., Lorenz, I., Muller, N., Langguth, B., and Weisz, N. (2014). The effects of neurofeedback on oscillatory processes related to tinnitus. *Brain Topogr* 27, 149-157.
- Hartmann, T., Schlee, W., and Weisz, N. (2012). It's only in your head: expectancy of aversive auditory stimulation modulates stimulus-induced auditory cortical alpha desynchronization. *Neuroimage* 60, 170-178.
- Hasan, R., Srinivasan, R., and Grossman, E.D. (2017). Feature-based attentional tuning during biological motion detection measured with SSVEP. *J Vis* 17, 22.
- Hauswald, A., Weisz, N., Bentin, S., and Kissler, J. (2013). MEG premotor abnormalities in children with Asperger's syndrome: determinants of social behavior? *Dev Cogn Neurosci* 5, 95-105.
- Heald, S.L., and Nusbaum, H.C. (2014). Speech perception as an active cognitive process. *Front Syst Neurosci* 8, 35.
- Heinks-Maldonado, T.H., Mathalon, D.H., Gray, M., and Ford, J.M. (2005). Fine-tuning of auditory cortex during speech production. *Psychophysiology* 42, 180-190.

- Heinrichs-Graham, E., and Wilson, T.W. (2016). Is an absolute level of cortical beta suppression required for proper movement? Magnetoencephalographic evidence from healthy aging. *Neuroimage* 134, 514-521.
- Heinrichs-Graham, E., Wilson, T.W., Santamaria, P.M., Heithoff, S.K., Torres-Russotto, D., Hutter-Saunders, J.A., Estes, K.A., Meza, J.L., Mosley, R.L., and Gendelman, H.E. (2014). Neuromagnetic evidence of abnormal movement-related beta desynchronization in Parkinson's disease. *Cereb Cortex* 24, 2669-2678.
- Henson, R.N., Burgess, N., and Frith, C.D. (2000). Recoding, storage, rehearsal and grouping in verbal short-term memory: an fMRI study. *Neuropsychologia* 38, 426-440.
- Herholz, S.C., Lappe, C., Knief, A., and Pantev, C. (2008). Neural basis of music imagery and the effect of musical expertise. *Eur J Neurosci* 28, 2352-2360.
- Herman, A.B., Houde, J.F., Vinogradov, S., and Nagarajan, S.S. (2013). Parsing the phonological loop: activation timing in the dorsal speech stream determines accuracy in speech reproduction. *J Neurosci* 33, 5439-5453.
- Hickok, G. (2012). Computational neuroanatomy of speech production. *Nat Rev Neurosci* 13, 135-145.
- Hickok, G. (2013). Predictive coding? Yes, but from what source? *Behav Brain Sci* 36, 358.
- Hickok, G., Buchsbaum, B., Humphries, C., and Muftuler, T. (2003). Auditory-motor interaction revealed by fMRI: speech, music, and working memory in area Spt. *J Cogn Neurosci* 15, 673-682.
- Hickok, G., Costanzo, M., Capasso, R., and Miceli, G. (2011a). The role of Broca's area in speech perception: evidence from aphasia revisited. *Brain Lang* 119, 214-220.
- Hickok, G., Houde, J., and Rong, F. (2011b). Sensorimotor integration in speech processing: computational basis and neural organization. *Neuron* 69, 407-422.
- Hickok, G., and Poeppel, D. (2000). Towards a functional neuroanatomy of speech perception. *Trends Cogn Sci* 4, 131-138.
- Hickok, G., and Poeppel, D. (2004). Dorsal and ventral streams: a framework for understanding aspects of the functional anatomy of language. *Cognition* 92, 67-99.
- Hickok, G., and Poeppel, D. (2007). The cortical organization of speech processing. *Nat Rev Neurosci* 8, 393-402.

- Hobson, H.M., and Bishop, D.V. (2017). The interpretation of mu suppression as an index of mirror neuron activity: past, present and future. *R Soc Open Sci* 4, 160662.
- Holcomb, P.J., Anderson, J., and Grainger, J. (2005). An electrophysiological study of cross-modal repetition priming. *Psychophysiology* 42, 493-507.
- Holler, Y., Bergmann, J., Kronbichler, M., Crone, J.S., Schmid, E.V., Thomschewski, A., Butz, K., Schutze, V., Holler, P., and Trinka, E. (2013). Real movement vs. motor imagery in healthy subjects. *Int J Psychophysiol* 87, 35-41.
- Hong, B., Acharya, S., Thakor, N., and Gao, S. (2005). Transient phase synchrony of independent cognitive components underlying scalp EEG. *Conf Proc IEEE Eng Med Biol Soc* 2, 2037-2040.
- Houde, J.F., and Chang, E.F. (2015). The cortical computations underlying feedback control in vocal production. *Curr Opin Neurobiol* 33, 174-181.
- Houde, J.F., and Nagarajan, S.S. (2011). Speech production as state feedback control. *Front Hum Neurosci* 5, 82.
- Houde, J.F., Nagarajan, S.S., Sekihara, K., and Merzenich, M.M. (2002). Modulation of the auditory cortex during speech: an MEG study. *J Cogn Neurosci* 14, 1125-1138.
- Houde, J.F., Niziolek, C., Kort, N., Agnew, Z., and Nagarajan, S.S. (Year). "Simulating a state feedback model of speaking", in: 10th International Seminar on Speech Production), 202-205.
- Husain, F.T., Mckinney, C.M., and Horwitz, B. (2006). Frontal cortex functional connectivity changes during sound categorization. *Neuroreport* 17, 617-621.
- Iacoboni, M. (2005). Neural mechanisms of imitation. *Curr Opin Neurobiol* 15, 632-637.
- Iacoboni, M., and Dapretto, M. (2006). The mirror neuron system and the consequences of its dysfunction. *Nat Rev Neurosci* 7, 942-951.
- Ito, T., Tiede, M., and Ostry, D.J. (2009). Somatosensory function in speech perception. *Proc Natl Acad Sci U S A* 106, 1245-1248.
- Jasper, H.H. (1958). The ten twenty electrode system of the international federation. *Electroencephalography and Clinical Neurophysiology* 10, 371-375.
- Jensen, O., and Mazaheri, A. (2010). Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front Hum Neurosci* 4, 186.

- Jenson, D., Bowers, A.L., Harkrider, A.W., Thornton, D., Cuellar, M., and Saltuklaroglu, T. (2014). Temporal dynamics of sensorimotor integration in speech perception and production: independent component analysis of EEG data. *Front Psychol* 5, 656.
- Jenson, D., Harkrider, A.W., Thornton, D., Bowers, A.L., and Saltuklaroglu, T. (2015). Auditory cortical deactivation during speech production and following speech perception: an EEG investigation of the temporal dynamics of the auditory alpha rhythm. *Front Hum Neurosci* 9, 534.
- Johnson, J.A., and Zatorre, R.J. (2005). Attention to simultaneous unrelated auditory and visual events: behavioral and neural correlates. *Cereb Cortex* 15, 1609-1620.
- Jones, S.R., Kerr, C.E., Wan, Q., Pritchett, D.L., Hämäläinen, M., and Moore, C.I. (2010). Cued Spatial Attention Drives Functionally Relevant Modulation of the Mu Rhythm in Primary Somatosensory Cortex. *The Journal of Neuroscience* 30, 13760-13765.
- Jurgens, E., Rosler, F., Henninghausen, E., and Heil, M. (1995). Stimulus-induced gamma oscillations: harmonics of alpha activity? *Neuroreport* 6, 813-816.
- Kaiser, J., Birbaumer, N., and Lutzenberger, W. (2001). Event-related beta desynchronization indicates timing of response selection in a delayed-response paradigm in humans. *Neurosci Lett* 312, 149-152.
- Kauramäki, J., Jaaskelainen, I.P., Hari, R., Mottonen, R., Rauschecker, J.P., and Sams, M. (2010). Lipreading and covert speech production similarly modulate human auditory-cortex responses to pure tones. *J Neurosci* 30, 1314-1321.
- Kay, J., Lesser, R., and Coltheart, M. (1996). Psycholinguistic assessments of language processing in aphasia (PALPA): An introduction. *Aphasiology* 10, 159-180.
- Kell, C.A., Morillon, B., Kouneiher, F., and Giraud, A.L. (2011). Lateralization of speech production starts in sensory cortices--a possible sensory origin of cerebral left dominance for speech. *Cereb Cortex* 21, 932-937.
- Kellis, S., Miller, K., Thomson, K., Brown, R., House, P., and Greger, B. (2010). Decoding spoken words using local field potentials recorded from the cortical surface. *J Neural Eng* 7, 056007.
- Kent, R.D. (2000). Research on speech motor control and its disorders: a review and prospective. *J Commun Disord* 33, 391-427; quiz 428.
- Kilavik, B.E., Zaepffel, M., Brovelli, A., Mackay, W.A., and Riehle, A. (2013). The ups and downs of beta oscillations in sensorimotor cortex. *Exp Neurol* 245, 15-26.

- Kilner, J.M., Friston, K.J., and Frith, C.D. (2007). Predictive coding: an account of the mirror neuron system. *Cogn Process* 8, 159-166.
- Kleinschmidt, D.F., and Jaeger, T.F. (2015). Robust speech perception: recognize the familiar, generalize to the similar, and adapt to the novel. *Psychol Rev* 122, 148-203.
- Kleinsorge, T., and Scheil, J. (2014). Effects of reducing the number of candidate tasks in voluntary task switching. *Front Psychol* 5, 1555.
- Kleinsorge, T., and Scheil, J. (2015). Incorrect predictions reduce switch costs. *Acta Psychol (Amst)* 159, 52-60.
- Kleinsorge, T., and Scheil, J. (2016). Guessing versus Choosing an Upcoming Task. *Front Psychol* 7, 396.
- Klimesch, W. (2012). alpha-band oscillations, attention, and controlled access to stored information. *Trends Cogn Sci* 16, 606-617.
- Klimesch, W., Sauseng, P., and Hanslmayr, S. (2007). EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res Rev* 53, 63-88.
- Kopell, N., Ermentrout, G.B., Whittington, M.A., and Traub, R.D. (2000). Gamma rhythms and beta rhythms have different synchronization properties. *Proc Natl Acad Sci U S A* 97, 1867-1872.
- Kotz, S.A., D'ausilio, A., Raettig, T., Begliomini, C., Craighero, L., Fabbri-Destro, M., Zingales, C., Haggard, P., and Fadiga, L. (2010). Lexicality drives audio-motor transformations in Broca's area. *Brain Lang* 112, 3-11.
- Kraeutner, S., Gionfriddo, A., Bardouille, T., and Boe, S. (2014). Motor imagery-based brain activity parallels that of motor execution: evidence from magnetic source imaging of cortical oscillations. *Brain Res* 1588, 81-91.
- Kuhlman, W.N. (1978). Functional topography of the human mu rhythm. *Electroencephalogr Clin Neurophysiol* 44, 83-93.
- Kujala, J., Pammer, K., Cornelissen, P., Roebroek, A., Formisano, E., and Salmelin, R. (2007). Phase coupling in a cerebro-cerebellar network at 8-13 Hz during reading. *Cereb Cortex* 17, 1476-1485.
- Kumari, V. (2011). Sex differences and hormonal influences in human sensorimotor gating: implications for schizophrenia. *Curr Top Behav Neurosci* 8, 141-154.

- Laufs, H., Kleinschmidt, A., Beyerle, A., Eger, E., Salek-Haddadi, A., Preibisch, C., and Krakow, K. (2003). EEG-correlated fMRI of human alpha activity. *Neuroimage* 19, 1463-1476.
- Lee, T.W., Girolami, M., and Sejnowski, T.J. (1999). Independent component analysis using an extended infomax algorithm for mixed subgaussian and supergaussian sources. *Neural Comput* 11, 417-441.
- Lehtela, L., Salmelin, R., and Hari, R. (1997). Evidence for reactive magnetic 10-Hz rhythm in the human auditory cortex. *Neurosci Lett* 222, 111-114.
- Leiberg, S., Lutzenberger, W., and Kaiser, J. (2006). Effects of memory load on cortical oscillatory activity during auditory pattern working memory. *Brain Res* 1120, 131-140.
- Leibold, L.J., Hodson, H., McCreery, R.W., Calandruccio, L., and Buss, E. (2014). Effects of low-pass filtering on the perception of word-final plurality markers in children and adults with normal hearing. *Am J Audiol* 23, 351-358.
- Leocani, L., Toro, C., Manganotti, P., Zhuang, P., and Hallett, M. (1997). Event-related coherence and event-related desynchronization/synchronization in the 10 Hz and 20 Hz EEG during self-paced movements. *Electroencephalogr Clin Neurophysiol* 104, 199-206.
- Leske, S., Ruhnau, P., Frey, J., Lithari, C., Muller, N., Hartmann, T., and Weisz, N. (2015). Prestimulus Network Integration of Auditory Cortex Predisposes Near-Threshold Perception Independently of Local Excitability. *Cereb Cortex* 25, 4898-4907.
- Leveque, Y., and Schon, D. (2013). Listening to the human voice alters sensorimotor brain rhythms. *PLoS One* 8, e80659.
- Lewis, A.G., and Bastiaansen, M. (2015). A predictive coding framework for rapid neural dynamics during sentence-level language comprehension. *Cortex* 68, 155-168.
- Lewis, A.G., Schoffelen, J.M., Schriefers, H., and Bastiaansen, M. (2016). A Predictive Coding Perspective on Beta Oscillations during Sentence-Level Language Comprehension. *Front Hum Neurosci* 10, 85.
- Li, B., Cui, L.B., Xi, Y.B., Friston, K.J., Guo, F., Wang, H.N., Zhang, L.C., Bai, Y.H., Tan, Q.R., Yin, H., and Lu, H. (2017). Abnormal Effective Connectivity in the Brain is Involved in Auditory Verbal Hallucinations in Schizophrenia. *Neurosci Bull* 33, 281-291.
- Li, L., Wang, J., Xu, G., Li, M., and Xie, J. (2015). The Study of Object-Oriented Motor Imagery Based on EEG Suppression. *PLoS One* 10, e0144256.

- Liao, D.A., Kronemer, S.I., Yau, J.M., Desmond, J.E., and Marvel, C.L. (2014). Motor system contributions to verbal and non-verbal working memory. *Front Hum Neurosci* 8, 753.
- Liberman, A.M. (1957). Some results of research on speech perception. *The Journal of the Acoustical Society of America* 29, 117-123.
- Liberman, A.M., Cooper, F.S., Shankweiler, D.P., and Studdert-Kennedy, M. (1967). Perception of the speech code. *Psychological review* 74, 431.
- Locasto, P.C., Krebs-Noble, D., Gullapalli, R.P., and Burton, M.W. (2004). An fMRI investigation of speech and tone segmentation. *J Cogn Neurosci* 16, 1612-1624.
- Londei, A., D'ausilio, A., Basso, D., Sestieri, C., Gratta, C.D., Romani, G.L., and Belardinelli, M.O. (2010). Sensory-motor brain network connectivity for speech comprehension. *Hum Brain Mapp* 31, 567-580.
- Lutzenberger, W., Ripper, B., Busse, L., Birbaumer, N., and Kaiser, J. (2002). Dynamics of gamma-band activity during an audiospatial working memory task in humans. *J Neurosci* 22, 5630-5638.
- Majerus, S. (2013). Language repetition and short-term memory: an integrative framework. *Front Hum Neurosci* 7, 357.
- Makeig, S., Debener, S., Onton, J., and Delorme, A. (2004). Mining event-related brain dynamics. *Trends Cogn Sci* 8, 204-210.
- Mandel, A., Bourguignon, M., Parkkonen, L., and Hari, R. (2016). Sensorimotor activation related to speaker vs. listener role during natural conversation. *Neurosci Lett* 614, 99-104.
- Martin, J.S., Gibson, K.Y., and Huston, L.C. (2012). Dichotic listening performance in young adults using low-pass filtered speech. *J Am Acad Audiol* 23, 192-205.
- Massey, J. (Year). "Causality, feedback and directed information", in: *Proc. Int. Symp. Inf. Theory Applic.(ISITA-90)*, 303-305.
- Mathewson, K.E., Gratton, G., Fabiani, M., Beck, D.M., and Ro, T. (2009). To see or not to see: prestimulus alpha phase predicts visual awareness. *J Neurosci* 29, 2725-2732.
- Mathewson, K.E., Lleras, A., Beck, D.M., Fabiani, M., Ro, T., and Gratton, G. (2011). Pulsed out of awareness: EEG alpha oscillations represent a pulsed-inhibition of ongoing cortical processing. *Front Psychol* 2, 99.

- Maye, J., Weiss, D.J., and Aslin, R.N. (2008). Statistical phonetic learning in infants: facilitation and feature generalization. *Dev Sci* 11, 122-134.
- Mayhew, S.D., Ostwald, D., Porcaro, C., and Bagshaw, A.P. (2013). Spontaneous EEG alpha oscillation interacts with positive and negative BOLD responses in the visual-auditory cortices and default-mode network. *Neuroimage* 76, 362-372.
- Mazaheri, A., Van Schouwenburg, M.R., Dimitrijevic, A., Denys, D., Cools, R., and Jensen, O. (2014). Region-specific modulations in oscillatory alpha activity serve to facilitate processing in the visual and auditory modalities. *Neuroimage* 87, 356-362.
- Mcgurk, H., and Macdonald, J. (1976). Hearing lips and seeing voices. *Nature* 264, 746-748.
- Mckelvey, M.L., Hux, K., Dietz, A., and Beukelman, D.R. (2010). Impact of personal relevance and contextualization on word-picture matching by people with aphasia. *Am J Speech Lang Pathol* 19, 22-33.
- Meister, I.G., Wilson, S.M., Deblieck, C., Wu, A.D., and Iacoboni, M. (2007). The essential role of premotor cortex in speech perception. *Curr Biol* 17, 1692-1696.
- Melgari, J.M., Zappasodi, F., Porcaro, C., Tomasevic, L., Cassetta, E., Rossini, P.M., and Tecchio, F. (2013). Movement-induced uncoupling of primary sensory and motor areas in focal task-specific hand dystonia. *Neuroscience* 250, 434-445.
- Menenti, L., Gierhan, S.M., Segaert, K., and Hagoort, P. (2011). Shared language: overlap and segregation of the neuronal infrastructure for speaking and listening revealed by functional MRI. *Psychol Sci* 22, 1173-1182.
- Mersov, A.M., Jobst, C., Cheyne, D.O., and De Nil, L. (2016). Sensorimotor Oscillations Prior to Speech Onset Reflect Altered Motor Networks in Adults Who Stutter. *Front Hum Neurosci* 10, 443.
- Moisello, C., Blanco, D., Lin, J., Panday, P., Kelly, S.P., Quartarone, A., Di Rocco, A., Cirelli, C., Tononi, G., and Ghilardi, M.F. (2015). Practice changes beta power at rest and its modulation during movement in healthy subjects but not in patients with Parkinson's disease. *Brain Behav* 5, e00374.
- Mottronen, R., Dutton, R., and Watkins, K.E. (2013). Auditory-motor processing of speech sounds. *Cereb Cortex* 23, 1190-1197.
- Mottronen, R., Van De Ven, G.M., and Watkins, K.E. (2014). Attention fine-tunes auditory-motor processing of speech sounds. *J Neurosci* 34, 4064-4069.

- Möttönen, R., and Watkins, K.E. (2009). Motor representations of articulators contribute to categorical perception of speech sounds. *Journal of Neuroscience* 29, 9819-9825.
- Muller, N., Keil, J., Obleser, J., Schulz, H., Grunwald, T., Bernays, R.L., Huppertz, H.J., and Weisz, N. (2013). You can't stop the music: reduced auditory alpha power and coupling between auditory and memory regions facilitate the illusory perception of music during noise. *Neuroimage* 79, 383-393.
- Muller, N., Leske, S., Hartmann, T., Szebenyi, S., and Weisz, N. (2015). Listen to Yourself: The Medial Prefrontal Cortex Modulates Auditory Alpha Power During Speech Preparation. *Cereb Cortex* 25, 4029-4037.
- Muller, N., and Weisz, N. (2012). Lateralized auditory cortical alpha band activity and interregional connectivity pattern reflect anticipation of target sounds. *Cereb Cortex* 22, 1604-1613.
- Muller, V., and Anokhin, A.P. (2012). Neural synchrony during response production and inhibition. *PLoS One* 7, e38931.
- Muthukumaraswamy, S.D., and Johnson, B.W. (2004). Changes in rolandic mu rhythm during observation of a precision grip. *Psychophysiology* 41, 152-156.
- Nasserouleslami, B., Lakany, H., and Conway, B.A. (2014). EEG signatures of arm isometric exertions in preparation, planning and execution. *Neuroimage* 90, 1-14.
- Nittrouer, S., Caldwell-Tarr, A., and Lowenstein, J.H. (2013). Working memory in children with cochlear implants: problems are in storage, not processing. *Int J Pediatr Otorhinolaryngol* 77, 1886-1898.
- Numminen, J., Salmelin, R., and Hari, R. (1999). Subject's own speech reduces reactivity of the human auditory cortex. *Neurosci Lett* 265, 119-122.
- Nystrom, P. (2008). The infant mirror neuron system studied with high density EEG. *Soc Neurosci* 3, 334-347.
- Oberman, L.M., Hubbard, E.M., McCleery, J.P., Altschuler, E.L., Ramachandran, V.S., and Pineda, J.A. (2005). EEG evidence for mirror neuron dysfunction in autism spectrum disorders. *Brain Res Cogn Brain Res* 24, 190-198.
- Olasagasti, I., Bouton, S., and Giraud, A.L. (2015). Prediction across sensory modalities: A neurocomputational model of the McGurk effect. *Cortex* 68, 61-75.
- Oldfield, R.C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9, 97-113.

- Ono, Y., Nanjo, T., and Ishiyama, A. (2013). Pursuing the flow of information: connectivity between bilateral premotor cortices predicts better accuracy in the phonological working memory task. *Conf Proc IEEE Eng Med Biol Soc* 2013, 7404-7407.
- Oostenveld, R., and Oostendorp, T.F. (2002). Validating the boundary element method for forward and inverse EEG computations in the presence of a hole in the skull. *Hum Brain Mapp* 17, 179-192.
- Ortiz, E., Stingl, K., Munssinger, J., Braun, C., Preissl, H., and Belardinelli, P. (2012). Weighted phase lag index and graph analysis: preliminary investigation of functional connectivity during resting state in children. *Comput Math Methods Med* 2012, 186353.
- Ortiz-Mantilla, S., Hamalainen, J.A., Realpe-Bonilla, T., and Benasich, A.A. (2016). Oscillatory Dynamics Underlying Perceptual Narrowing of Native Phoneme Mapping from 6 to 12 Months of Age. *J Neurosci* 36, 12095-12105.
- Osnes, B., Hugdahl, K., and Specht, K. (2011). Effective connectivity analysis demonstrates involvement of premotor cortex during speech perception. *Neuroimage* 54, 2437-2445.
- Ostrand, R., Blumstein, S.E., Ferreira, V.S., and Morgan, J.L. (2016). What you see isn't always what you get: Auditory word signals trump consciously perceived words in lexical access. *Cognition* 151, 96-107.
- Palva, J.M., Monto, S., Kulashekhar, S., and Palva, S. (2010). Neuronal synchrony reveals working memory networks and predicts individual memory capacity. *Proc Natl Acad Sci U S A* 107, 7580-7585.
- Park, H., Ince, R.A., Schyns, P.G., Thut, G., and Gross, J. (2015). Frontal top-down signals increase coupling of auditory low-frequency oscillations to continuous speech in human listeners. *Curr Biol* 25, 1649-1653.
- Patel, R.S., Bowman, F.D., and Rilling, J.K. (2006). Determining hierarchical functional networks from auditory stimuli fMRI. *Hum Brain Mapp* 27, 462-470.
- Payne, L., Rogers, C.S., Wingfield, A., and Sekuler, R. (2017). A right-ear bias of auditory selective attention is evident in alpha oscillations. *Psychophysiology* 54, 528-535.
- Peelle, J.E., and Sommers, M.S. (2015). Prediction and constraint in audiovisual speech perception. *Cortex* 68, 169-181.

- Pei, X., Barbour, D.L., Leuthardt, E.C., and Schalk, G. (2011). Decoding vowels and consonants in spoken and imagined words using electrocorticographic signals in humans. *J Neural Eng* 8, 046028.
- Perry, A., and Bentin, S. (2010). Does focusing on hand-grasping intentions modulate electroencephalogram mu and alpha suppressions? *Neuroreport* 21, 1050-1054.
- Peschke, C., Ziegler, W., Eisenberger, J., and Baumgaertner, A. (2012). Phonological manipulation between speech perception and production activates a parieto-frontal circuit. *Neuroimage* 59, 788-799.
- Pesonen, M., Bjornberg, C.H., Hamalainen, H., and Krause, C.M. (2006). Brain oscillatory 1-30 Hz EEG ERD/ERS responses during the different stages of an auditory memory search task. *Neurosci Lett* 399, 45-50.
- Pfurtscheller, G., and Lopes Da Silva, F.H. (1999). Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clin Neurophysiol* 110, 1842-1857.
- Philipp, A.M., Kalinich, C., Koch, I., and Schubotz, R.I. (2008). Mixing costs and switch costs when switching stimulus dimensions in serial predictions. *Psychol Res* 72, 405-414.
- Pickering, M.J., and Garrod, S. (2007). Do people use language production to make predictions during comprehension? *Trends Cogn Sci* 11, 105-110.
- Pickering, M.J., and Garrod, S. (2009). Prediction and embodiment in dialogue. *European Journal of Social Psychology* 39, 1162-1168.
- Pickering, M.J., and Garrod, S. (2013). An integrated theory of language production and comprehension. *Behav Brain Sci* 36, 329-347.
- Pineda, J.A. (2005). The functional significance of mu rhythms: translating "seeing" and "hearing" into "doing". *Brain Res Brain Res Rev* 50, 57-68.
- Pineda, J.A., Grichanik, M., Williams, V., Trieu, M., Chang, H., and Keysers, C. (2013). EEG sensorimotor correlates of translating sounds into actions. *Front Neurosci* 7, 203.
- Poeppel, D. (2003). The analysis of speech in different temporal integration windows: cerebral lateralization as 'asymmetric sampling in time'. *Speech communication* 41, 245-255.
- Poeppel, D., Idsardi, W.J., and Van Wassenhove, V. (2008). Speech perception at the interface of neurobiology and linguistics. *Philos Trans R Soc Lond B Biol Sci* 363, 1071-1086.

- Poeppel, D., and Monahan, P.J. (2011). Feedforward and feedback in speech perception: Revisiting analysis by synthesis. *Language and Cognitive Processes* 26, 935-951.
- Pollen, D.A., and Trachtenberg, M.C. (1972). Some problems of occipital alpha block in man. *Brain Res* 41, 303-314.
- Pollok, B., Krause, V., Butz, M., and Schnitzler, A. (2009). Modality specific functional interaction in sensorimotor synchronization. *Hum Brain Mapp* 30, 1783-1790.
- Pons, F., Lewkowicz, D.J., Soto-Faraco, S., and Sebastian-Galles, N. (2009). Narrowing of intersensory speech perception in infancy. *Proc Natl Acad Sci U S A* 106, 10598-10602.
- Popovich, C., Dockstader, C., Cheyne, D., and Tannock, R. (2010). Sex differences in sensorimotor mu rhythms during selective attentional processing. *Neuropsychologia* 48, 4102-4110.
- Pratt, H., Erez, A., and Geva, A.B. (1994). Lexicality and modality effects on evoked potentials in a memory-scanning task. *Brain Lang* 46, 353-367.
- Press, C., Cook, J., Blakemore, S.J., and Kilner, J. (2011). Dynamic modulation of human motor activity when observing actions. *J Neurosci* 31, 2792-2800.
- Pulvermuller, F., Huss, M., Kherif, F., Moscoso Del Prado Martin, F., Hauk, O., and Shtyrov, Y. (2006). Motor cortex maps articulatory features of speech sounds. *Proc Natl Acad Sci U S A* 103, 7865-7870.
- Ramos De Miguel, A., Perez Zaballos, M.T., Ramos Macias, A., Borkoski Barreiro, S.A., Falcon Gonzalez, J.C., and Perez Plasencia, D. (2015). Effects of high-frequency suppression for speech recognition in noise in Spanish normal-hearing subjects. *Otol Neurotol* 36, 720-726.
- Rao, R.P., and Ballard, D.H. (1999). Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. *Nat Neurosci* 2, 79-87.
- Rauschecker, J.P. (2012). Ventral and dorsal streams in the evolution of speech and language. *Front Evol Neurosci* 4, 7.
- Regenbogen, C., De Vos, M., Debener, S., Turetsky, B.I., Mossnang, C., Finkelmeyer, A., Habel, U., Neuner, I., and Kellermann, T. (2012). Auditory processing under cross-modal visual load investigated with simultaneous EEG-fMRI. *PLoS One* 7, e52267.

- Rihs, T.A., Michel, C.M., and Thut, G. (2007). Mechanisms of selective inhibition in visual spatial attention are indexed by alpha-band EEG synchronization. *Eur J Neurosci* 25, 603-610.
- Ritz, H. (2016). The Effects of Concurrent Cognitive Load on the Processing of Clear and Degraded Speech. The University of Western Ontario.
- Rizzolatti, G., and Craighero, L. (2004). The mirror-neuron system. *Annu Rev Neurosci* 27, 169-192.
- Rizzolatti, G., Fadiga, L., Gallese, V., and Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Brain Res Cogn Brain Res* 3, 131-141.
- Rogalsky, C., Chen, K.-H., Poppa, T., Anderson, S.W., Damasio, H., Binder, J.R., Love, T., and Hickock, G. (2014). Relative Contributions of the Dorsal vs. Ventral Speech Streams to Speech Perception are Context Dependent: a lesion study. *Front. Psychol. Conference Abstract: Academy of Aphasia -- 52nd Annual Meeting*.
- Romero, L., Walsh, V., and Papagno, C. (2006). The neural correlates of phonological short-term memory: a repetitive transcranial magnetic stimulation study. *J Cogn Neurosci* 18, 1147-1155.
- Rommers, J., and Federmeier, K.D. (2018). Predictability's aftermath: Downstream consequences of word predictability as revealed by repetition effects. *Cortex* 101, 16-30.
- Sadaghiani, S., Scheeringa, R., Lehongre, K., Morillon, B., Giraud, A.L., and Kleinschmidt, A. (2010). Intrinsic connectivity networks, alpha oscillations, and tonic alertness: a simultaneous electroencephalography/functional magnetic resonance imaging study. *J Neurosci* 30, 10243-10250.
- Saltuklaroglu, T., Harkrider, A.W., Thornton, D., Jenson, D., and Kittilstved, T. (2017). EEG Mu (micro) rhythm spectra and oscillatory activity differentiate stuttering from non-stuttering adults. *Neuroimage* 153, 232-245.
- Santos-Oliveira, D.C. (2017). Automatic Activation of Phonological Templates for Native but Not Nonnative Phonemes: An Investigation of the Temporal Dynamics of Mu Activation. The University of Tennessee Health Science Center.
- Sato, M., Tremblay, P., and Gracco, V.L. (2009). A mediating role of the premotor cortex in phoneme segmentation. *Brain Lang* 111, 1-7.
- Scharinger, C., Soutschek, A., Schubert, T., and Gerjets, P. (2017). Comparison of the Working Memory Load in N-Back and Working Memory Span Tasks by Means of EEG Frequency Band Power and P300 Amplitude. *Front Hum Neurosci* 11, 6.

- Scheeringa, R., Koopmans, P.J., Van Mourik, T., Jensen, O., and Norris, D.G. (2016). The relationship between oscillatory EEG activity and the laminar-specific BOLD signal. *Proc Natl Acad Sci U S A* 113, 6761-6766.
- Schellekens, W., Van Wezel, R.J., Petridou, N., Ramsey, N.F., and Raemaekers, M. (2016). Predictive coding for motion stimuli in human early visual cortex. *Brain Struct Funct* 221, 879-890.
- Schindler, A., and Bartels, A. (2017). Connectivity Reveals Sources of Predictive Coding Signals in Early Visual Cortex During Processing of Visual Optic Flow. *Cereb Cortex* 27, 2885-2893.
- Schneider, D., Barth, A., and Wascher, E. (2017). On the contribution of motor planning to the retroactive cuing benefit in working memory: Evidence by mu and beta oscillatory activity in the EEG. *Neuroimage* 162, 73-85.
- Schreiber, T. (2000). Measuring information transfer. *Physical review letters* 85, 461.
- Schroeder, C.E., Wilson, D.A., Radman, T., Scharfman, H., and Lakatos, P. (2010). Dynamics of Active Sensing and perceptual selection. *Curr Opin Neurobiol* 20, 172-176.
- Schubert, R., Haufe, S., Blankenburg, F., Villringer, A., and Curio, G. (2009). Now you'll feel it, now you won't: EEG rhythms predict the effectiveness of perceptual masking. *J Cogn Neurosci* 21, 2407-2419.
- Schwager, S., Gaschler, R., Runger, D., and Frensch, P.A. (2016). Tied to expectations: Predicting features speeds processing even under adverse circumstances. *Mem Cognit.*
- Sebastiani, V., De Pasquale, F., Costantini, M., Mantini, D., Pizzella, V., Romani, G.L., and Della Penna, S. (2014). Being an agent or an observer: different spectral dynamics revealed by MEG. *Neuroimage* 102 Pt 2, 717-728.
- Sedley, W., Gander, P.E., Kumar, S., Kovach, C.K., Oya, H., Kawasaki, H., Howard, M.A., and Griffiths, T.D. (2016). Neural signatures of perceptual inference. *Elife* 5, e11476.
- Seeber, M., Scherer, R., Wagner, J., Solis-Escalante, T., and Muller-Putz, G.R. (2014). EEG beta suppression and low gamma modulation are different elements of human upright walking. *Front Hum Neurosci* 8, 485.
- Sengupta, R., Shah, S., Gore, K., Loucks, T., and Nasir, S.M. (2016). Anomaly in neural phase coherence accompanies reduced sensorimotor integration in adults who stutter. *Neuropsychologia* 93, 242-250.

- Shannon, R.V., Zeng, F.G., Kamath, V., Wygonski, J., and Ekelid, M. (1995). Speech recognition with primarily temporal cues. *Science* 270, 303-304.
- Sharda, M., Midha, R., Malik, S., Mukerji, S., and Singh, N.C. (2015). Fronto-temporal connectivity is preserved during sung but not spoken word listening, across the autism spectrum. *Autism Res* 8, 174-186.
- Sitek, K.R., Mathalon, D.H., Roach, B.J., Houde, J.F., Niziolek, C.A., and Ford, J.M. (2013). Auditory cortex processes variation in our own speech. *PLoS One* 8, e82925.
- Skipper, J.I., Devlin, J.T., and Lametti, D.R. (2017). The hearing ear is always found close to the speaking tongue: Review of the role of the motor system in speech perception. *Brain Lang* 164, 77-105.
- Skipper, J.I., Goldin-Meadow, S., Nusbaum, H.C., and Small, S.L. (2007a). Speech-associated gestures, Broca's area, and the human mirror system. *Brain Lang* 101, 260-277.
- Skipper, J.I., Van Wassenhove, V., Nusbaum, H.C., and Small, S.L. (2007b). Hearing lips and seeing voices: how cortical areas supporting speech production mediate audiovisual speech perception. *Cereb Cortex* 17, 2387-2399.
- Smalle, E.H., Rogers, J., and Mottonen, R. (2015). Dissociating Contributions of the Motor Cortex to Speech Perception and Response Bias by Using Transcranial Magnetic Stimulation. *Cereb Cortex* 25, 3690-3698.
- Smith, J.O., and Abel, J.S. (1999). Bark and ERB bilinear transforms. *IEEE Transactions on speech and Audio Processing* 7, 697-708.
- Sohoglu, E., and Davis, M.H. (2016). Perceptual learning of degraded speech by minimizing prediction error. *Proc Natl Acad Sci U S A* 113, E1747-1756.
- Sohoglu, E., Peelle, J.E., Carlyon, R.P., and Davis, M.H. (2012). Predictive top-down integration of prior knowledge during speech perception. *J Neurosci* 32, 8443-8453.
- Sohoglu, E., Peelle, J.E., Carlyon, R.P., and Davis, M.H. (2014). Top-down influences of written text on perceived clarity of degraded speech. *J Exp Psychol Hum Percept Perform* 40, 186-199.
- Specht, K. (2014). Neuronal basis of speech comprehension. *Hear Res* 307, 121-135.

- Spierer, L., Bellmann-Thiran, A., Maeder, P., Murray, M.M., and Clarke, S. (2009). Hemispheric competence for auditory spatial representation. *Brain* 132, 1953-1966.
- Srinivasan, M.V., Laughlin, S.B., and Dubs, A. (1982). Predictive coding: a fresh view of inhibition in the retina. *Proc R Soc Lond B Biol Sci* 216, 427-459.
- Stancak, A., Jr. (2000). Event-related desynchronization of the mu rhythm in extension and flexion finger movements. *Suppl Clin Neurophysiol* 53, 210-214.
- Stancak, A., Jr., Feige, B., Lucking, C.H., and Kristeva-Feige, R. (2000). Oscillatory cortical activity and movement-related potentials in proximal and distal movements. *Clin Neurophysiol* 111, 636-650.
- Steinmann, S., Meier, J., Nolte, G., Engel, A.K., Leicht, G., and Mulert, C. (2018). The Callosal Relay Model of Interhemispheric Communication: New Evidence from Effective Connectivity Analysis. *Brain Topogr* 31, 218-226.
- Stenner, M.P., Bauer, M., Haggard, P., Heinze, H.J., and Dolan, R. (2014). Enhanced alpha-oscillations in visual cortex during anticipation of self-generated visual stimulation. *J Cogn Neurosci* 26, 2540-2551.
- Stevens, K.N., and Halle, M. (1967). Remarks on analysis by synthesis and distinctive features. *Models for the perception of speech and visual form*, ed. W. Walthen-Dunn, 88-102.
- Stigler, J.W., Lee, S.Y., and Stevenson, H.W. (1986). Digit memory in Chinese and English: evidence for a temporally limited store. *Cognition* 23, 1-20.
- Stone, J.V. (2004). Independent component analysis. *Wiley Online Library*.
- Strauss, A., Wostmann, M., and Obleser, J. (2014). Cortical alpha oscillations as a tool for auditory selective inhibition. *Front Hum Neurosci* 8, 350.
- Sugata, H., Hirata, M., Yanagisawa, T., Shayne, M., Matsushita, K., Goto, T., Yorifuji, S., and Yoshimine, T. (2014). Alpha band functional connectivity correlates with the performance of brain-machine interfaces to decode real and imagined movements. *Front Hum Neurosci* 8, 620.
- Sumby, W.H., and Pollack, I. (1954). Visual contribution to speech intelligibility in noise. *The journal of the acoustical society of america* 26, 212-215.
- Sundara, M., Namasivayam, A.K., and Chen, R. (2001). Observation-execution matching system for speech: a magnetic stimulation study. *Neuroreport* 12, 1341-1344.

- Tamura, T., Gunji, A., Takeichi, H., Shigemasu, H., Inagaki, M., Kaga, M., and Kitazaki, M. (2012). Audio-vocal monitoring system revealed by mu-rhythm activity. *Front Psychol* 3, 225.
- Tan, H., Jenkinson, N., and Brown, P. (2014). Dynamic neural correlates of motor error monitoring and adaptation during trial-to-trial learning. *J Neurosci* 34, 5678-5688.
- Tan, H., Wade, C., and Brown, P. (2016). Post-Movement Beta Activity in Sensorimotor Cortex Indexes Confidence in the Estimations from Internal Models. *J Neurosci* 36, 1516-1528.
- Tavabi, K., Embick, D., and Roberts, T.P. (2011). Word repetition priming-induced oscillations in auditory cortex: a magnetoencephalography study. *Neuroreport* 22, 887-891.
- Thornton, D., Harkrider, A., Jenson, D., and Saltuklaroglu, T. (In Prep). Sex Differences in Early Sensorimotor Processing for Speech Discrimination. *Cereb Cortex*.
- Thornton, D., Harkrider, A.W., Jenson, D., and Saltuklaroglu, T. (2017). Sensorimotor activity measured via oscillations of EEG mu rhythms in speech and non-speech discrimination tasks with and without segmentation requirements. *Brain and Language*.
- Tian, X., and Poeppel, D. (2010). Mental imagery of speech and movement implicates the dynamics of internal forward models. *Front Psychol* 1, 166.
- Tian, X., and Poeppel, D. (2012). Mental imagery of speech: linking motor and perceptual systems through internal simulation and estimation. *Front Hum Neurosci* 6, 314.
- Tian, X., and Poeppel, D. (2013). The effect of imagination on stimulation: the functional specificity of efference copies in speech processing. *J Cogn Neurosci* 25, 1020-1036.
- Tian, X., and Poeppel, D. (2015). Dynamics of self-monitoring and error detection in speech production: evidence from mental imagery and MEG. *J Cogn Neurosci* 27, 352-364.
- Tian, X., Zarate, J.M., and Poeppel, D. (2016). Mental imagery of speech implicates two mechanisms of perceptual reactivation. *Cortex* 77, 1-12.
- Tiihonen, J., Hari, R., Kajola, M., Karhu, J., Ahlfors, S., and Tissari, S. (1991). Magnetoencephalographic 10-Hz rhythm from the human auditory cortex. *Neuroscience letters* 129, 303-305.

- Tiihonen, J., Kajola, M., and Hari, R. (1989). Magnetic mu rhythm in man. *Neuroscience* 32, 793-800.
- Todorovic, A., Van Ede, F., Maris, E., and De Lange, F.P. (2011). Prior expectation mediates neural adaptation to repeated sounds in the auditory cortex: an MEG study. *J Neurosci* 31, 9118-9123.
- Tourville, J.A., and Guenther, F.H. (2011). The DIVA model: A neural theory of speech acquisition and production. *Lang Cogn Process* 26, 952-981.
- Tsoneva, T., Baldo, D., Lema, V., and Garcia-Molina, G. (2011). EEG-rhythm dynamics during a 2-back working memory task and performance. *Conf Proc IEEE Eng Med Biol Soc* 2011, 3828-3831.
- Ulloa, E.R., and Pineda, J.A. (2007). Recognition of point-light biological motion: mu rhythms and mirror neuron activity. *Behav Brain Res* 183, 188-194.
- Van Diepen, R.M., and Mazaheri, A. (2017). Cross-sensory modulation of alpha oscillatory activity: suppression, idling and default resource allocation. *Eur J Neurosci*.
- Van Dijk, H., Nieuwenhuis, I.L., and Jensen, O. (2010). Left temporal alpha band activity increases during working memory retention of pitches. *Eur J Neurosci* 31, 1701-1707.
- Van Dijk, H., Schoffelen, J.M., Oostenveld, R., and Jensen, O. (2008). Prestimulus oscillatory activity in the alpha band predicts visual discrimination ability. *J Neurosci* 28, 1816-1823.
- Van Schouwenburg, M.R., Zanto, T.P., and Gazzaley, A. (2016). Spatial Attention and the Effects of Frontoparietal Alpha Band Stimulation. *Front Hum Neurosci* 10, 658.
- Van Wassenhove, V., Grant, K.W., and Poeppel, D. (2005). Visual speech speeds up the neural processing of auditory speech. *Proc Natl Acad Sci U S A* 102, 1181-1186.
- Venezia, J.H., Saberi, K., Chubb, C., and Hickok, G. (2012). Response Bias Modulates the Speech Motor System during Syllable Discrimination. *Front Psychol* 3, 157.
- Vinay, and Moore, B.C. (2010). Psychophysical tuning curves and recognition of highpass and lowpass filtered speech for a person with an inverted V-shaped audiogram (L). *J Acoust Soc Am* 127, 660-663.
- Vinck, M., Oostenveld, R., Van Wingerden, M., Battaglia, F., and Pennartz, C.M. (2011). An improved index of phase-synchronization for electrophysiological data in the

- presence of volume-conduction, noise and sample-size bias. *Neuroimage* 55, 1548-1565.
- Virtala, P., Partanen, E., Tervaniemi, M., and Kujala, T. (2018). Neural discrimination of speech sound changes in a variable context occurs irrespective of attention and explicit awareness. *Biol Psychol* 132, 217-227.
- Von Stein, A., and Sarnthein, J. (2000). Different frequencies for different scales of cortical integration: from local gamma to long range alpha/theta synchronization. *Int J Psychophysiol* 38, 301-313.
- Wang, X.J. (2010). Neurophysiological and computational principles of cortical rhythms in cognition. *Physiol Rev* 90, 1195-1268.
- Watkins, K.E., Strafella, A.P., and Paus, T. (2003). Seeing and hearing speech excites the motor system involved in speech production. *Neuropsychologia* 41, 989-994.
- Weisz, N., Hartmann, T., Muller, N., Lorenz, I., and Obleser, J. (2011). Alpha rhythms in audition: cognitive and clinical perspectives. *Front Psychol* 2, 73.
- Weisz, N., and Obleser, J. (2014). Synchronisation signatures in the listening brain: a perspective from non-invasive neuroelectrophysiology. *Hear Res* 307, 16-28.
- Wiesman, A.I., Heinrichs-Graham, E., Mcdermott, T.J., Santamaria, P.M., Gendelman, H.E., and Wilson, T.W. (2016). Quiet connections: Reduced fronto-temporal connectivity in nondemented Parkinson's Disease during working memory encoding. *Hum Brain Mapp* 37, 3224-3235.
- Wild, C.J., Davis, M.H., and Johnsrude, I.S. (2012a). Human auditory cortex is sensitive to the perceived clarity of speech. *Neuroimage* 60, 1490-1502.
- Wild, C.J., Yusuf, A., Wilson, D.E., Peelle, J.E., Davis, M.H., and Johnsrude, I.S. (2012b). Effortful listening: the processing of degraded speech depends critically on attention. *J Neurosci* 32, 14010-14021.
- Wilson, M. (2001). The case for sensorimotor coding in working memory. *Psychon Bull Rev* 8, 44-57.
- Wilson, S.M., and Iacoboni, M. (2006). Neural responses to non-native phonemes varying in producibility: evidence for the sensorimotor nature of speech perception. *Neuroimage* 33, 316-325.
- Wilson, S.M., Saygin, A.P., Sereno, M.I., and Iacoboni, M. (2004). Listening to speech activates motor areas involved in speech production. *Nat Neurosci* 7, 701-702.
- Wolpert, D.M., and Flanagan, J.R. (2001). Motor prediction. *Curr Biol* 11, R729-732.

- Worden, M.S., Foxe, J.J., Wang, N., and Simpson, G.V. (2000). Anticipatory biasing of visuospatial attention indexed by retinotopically specific-band electroencephalography increases over occipital cortex. *J Neurosci* 20, 1-6.
- Wostmann, M., Herrmann, B., Maess, B., and Obleser, J. (2016). Spatiotemporal dynamics of auditory attention synchronize with speech. *Proc Natl Acad Sci U S A* 113, 3873-3878.
- Wostmann, M., Lim, S.J., and Obleser, J. (2017). The Human Neural Alpha Response to Speech is a Proxy of Attentional Control. *Cereb Cortex*, 1-11.
- Wostmann, M., Schroger, E., and Obleser, J. (2015). Acoustic detail guides attention allocation in a selective listening task. *J Cogn Neurosci* 27, 988-1000.
- Yi, W., Qiu, S., Wang, K., Qi, H., He, F., Zhou, P., Zhang, L., and Ming, D. (2016). EEG oscillatory patterns and classification of sequential compound limb motor imagery. *J Neuroeng Rehabil* 13, 11.
- Ylinen, S., Nora, A., Leminen, A., Hakala, T., Huotilainen, M., Shtyrov, Y., Makela, J.P., and Service, E. (2015). Two distinct auditory-motor circuits for monitoring speech production as revealed by content-specific suppression of auditory cortex. *Cereb Cortex* 25, 1576-1586.
- Yokota, Y., and Naruse, Y. (2015). Phase coherence of auditory steady-state response reflects the amount of cognitive workload in a modified N-back task. *Neurosci Res* 100, 39-45.
- Yuan, H., Liu, T., Szarkowski, R., Rios, C., Ashe, J., and He, B. (2010a). Negative covariation between task-related responses in alpha/beta-band activity and BOLD in human sensorimotor cortex: an EEG and fMRI study of motor imagery and movements. *Neuroimage* 49, 2596-2606.
- Yuan, H., Perdoni, C., and He, B. (2010b). Relationship between speed and EEG activity during imagined and executed hand movements. *J Neural Eng* 7, 26001.
- Zaepffel, M., Trachel, R., Kilavik, B.E., and Brochier, T. (2013). Modulations of EEG beta power during planning and execution of grasping movements. *PLoS One* 8, e60060.
- Zatorre, R.J., and Penhune, V.B. (2001). Spatial localization after excision of human auditory cortex. *J Neurosci* 21, 6321-6328.
- Zion Golumbic, E.M., Poeppel, D., and Schroeder, C.E. (2012). Temporal context in speech processing and attentional stream selection: a behavioral and neural perspective. *Brain Lang* 122, 151-161.

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