BEYOND BROCA: NEURAL ARCHITECTURE AND EVOLUTION OF A DUAL MOTOR SPEECH COORDINATION SYSTEM

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1. Introduction and preview

Classical neural architecture models of speech production propose a single system coordinating all the vocal articulators from lips to larynx. Here we propose a dual coordination system in which laryngeal control of pitch-related aspects of prosody and song are controlled by a dorsal precentral gyrus system while supralaryngeal articulation at the phonetic/syllabic level is controlled by a ventral precentral system. The separability of these neural systems supports models of the evolution of speech and language in which song-based communication was an early foundational stage.

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2.0 Evidence for distinct two systems

Evidence for the existence of two speech coordination systems comes from functional imaging (Hickok, Buchsbaum, Humphries, & Muftuler, 2003; Price et al., 1996; Wilson, Saygin, Sereno, & Iacoboni, 2004), direct cortical stimulation mapping (Lu et al., 2021), and post stroke apraxia of speech (Graff-Radford et al., 2014; Hickok et al., 2014), all of which have identified speech-related regions in both the ventral and more dorsal central gyrus. We refer to these as the dorsal and ventral precentral speech areas (dPCSA and vPCSA).

3.0 Evidence for a voice pitch-related coordination in the dPCSA

Two recent published findings argue for a functional distinction between the two speech areas, specifically that the dPCSA, but not vPCSA is involved in voice pitch coordination for prosody and song. One is an intracranial recording study showing that neural activity in the dPCSA (but not vPCSA) is correlated with

control of voice pitch and when stimulated elicits vowel-like vocalization (Dichter, Breshears, Leonard, & Chang, 2018). The other is an fMRI study showing that the dPCSA (but not vPCSA) has *auditory* spectrotemporal receptive fields that code pitch-related information (Venezia, Richards, & Hickok, 2021). We also provide new functional connectivity evidence: dPCSA has greater connectivity to auditory cortex and vPCSA has greater connectivity to secondary somatosensory cortex.

4.0 The Dual Speech Coordination Model

The observations described above led us to the following dual coordination model:

The dPCSA is part of a sensorimotor control circuit for pitch-related vocalization, which would include prosodic aspects of speech as well as song, and predominantly acts on the laryngeal effector via the dorsal laryngeal motor cortex.
The vPCSA is part of a sensorimotor control circuit for syllabic and phonetic-related speech features and acts on supralaryngeal effectors as well as voicing-related control of the larynx via the ventral laryngeal motor cortex.

We further propose and provide evidence for the following secondary hypotheses.

-Both the dPCSA and vPCSA are part of hierarchy of speech control networks in frontal cortex with both situated between lower-level primary motor systems posteriorly and higher-level systems anteriorly, extending into the posterior middle frontal gyrus and inferior frontal gyrus (Broca's area), respectively.
-The location of the dPCSA can be explained in evolutionary terms, having evolved out of a voluntarily controllable goal-directed orienting hub in premotor cortex, which is present in both human and non-human primates, and which makes use of pitch and other acoustic cues.
-The vPCSA evolved out of voluntarily controlled supralaryngeal effectors, used extensively for mastication, oral-grasping behaviors, and non-vocal oral communication (e.g., lip smacking) with the major advance for speech being the coordination of open-close jaw cycles (the syllabic frame) with articulatory gestures (the phonetic content), as proposed in MacNeilage's frame/content model speech production evolution (MacNeilage, 1998).
-The dPCSA and its associated circuit for controlling vocal pitch, prosody, and song evolved prior to the vPCSA system's control over phonetic articulatory gestures and represented an early stage of the evolution of language, as originally proposed by Darwin (Darwin, 1871).

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