Beyond Broca: Neural Architecture and Evolution of a Dual Motor Speech Coordination System

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Abstract

Classical neural architecture models of speech production propose a single system centered on Broca's area coordinating all the vocal articulators from lips to larynx. Modern evidence has challenged both the idea that Broca's area is involved in motor speech coordination and that there is only one coordination network. Drawing on a wide range of evidence, here we propose a dual speech coordination model in which laryngeal control of pitch-related aspects of prosody and song are coordinated by a hierarchically organized dorsolateral system while supralaryngeal articulation at the phonetic/syllabic level is coordinated by the classic ventrolateral speech/language system. We argue further that these two speech production subsystems have distinguishable evolutionary histories and discuss the implications for models of language evolution.

0. Introduction

In a series of reports in the 1860s, Paul Broca famously implicated a single area in the posterior portion of the left inferior frontal gyrus—now called Broca's area—as the seat of the “faculty of articulated language” (Berker et al., 1986; Broca, 1861b, 1865). Broca was clear about what he meant by “articulated language”: “...it is not the faculty of language, it is not the memory for words, nor is it the action of the nerves and muscles corresponding to phonation and to articulation”, rather, it is “*the faculty that coordinates the proper movement of articulated language*” (Broca, 1861b) (p. 332, emphasis original; translation from (Green, 2000)). Just over a century later, Norman Geschwind endorsed Broca's claims: “Broca's area, which is adjacent to the region of the motor cortex that controls the movement of the muscles of the lips, the jaw, the tongue, the soft palate and the vocal cords, apparently incorporates programs for the coordination of these muscles in speech” (Geschwind, 1972)(p. 78).

Modern evidence, however, has challenged both the idea that Broca's area is involved in motor speech coordination and that there is only one coordination network. Regarding Broca's area, typically defined as the pars opercularis and pars triangularis of the inferior frontal gyrus, we now appreciate that it is not functionally or anatomically monolithic (Amunts et al., 1999; Conner et al., 2019; Fedorenko and Blank, 2020; Rogalsky et al., 2008) and that this heterogeneity has been linked not to aspects of lower-level articulatory coordination but to

various higher-level processes including syntax (Fedorenko et al., 2012; Grodzinsky and Santi, 2008; Matchin and Hickok, 2020; Schell et al., 2017), lexical selection (Conner et al., 2019; Novick et al., 2005), working memory (Buchsbaum and D'Esposito, 2008; Rogalsky et al., 2008), and sequencing (Fiebach and Schubotz, 2006; Peeva et al., 2010; Rong et al., 2018). In contrast, lower-level speech coordination deficits of the sort Broca described, such as those found in apraxia of speech (Strand et al., 2014), have been associated primarily with lateral premotor cortex, the anterior insula, and primary sensorimotor cortex (Chang et al., 2020; Dronkers, 1996; Graff-Radford et al., 2014; Hickok et al., 2014; Itabashi et al., 2016; Ogar et al., 2006; Patira et al., 2017). Regarding the idea of a single speech coordination network, many studies have reported not only ventral areas involved in speech tasks, but also a more dorsal speech region, which is consistently activated in simple receptive and expressive speech tasks (Hickok et al., 2003; Price et al., 1996; Rong et al., 2018; Wilson et al., 2004) and when directly stimulated can induce speech arrest (Lu et al., 2021) and vocalization (Dichter et al., 2018), making this more dorsal premotor speech zone an additional candidate for a speech coordination area. The possibility of a dual speech coordination architecture is the topic of this article.

In the following sections we motivate a new neural architecture model, which parcels speech coordination into two parallel systems, one for pitch-related vocalization (prosody, song) predominantly involving laryngeal control, and the other for phonetic/syllabic articulation involving the supralaryngeal vocal tract. Our discussion is divided into two main parts. Part 1 reviews the evidence for two separable speech areas on the precentral gyrus, which motivates our hypothesized functional distinction. Part 2 considers the evolutionary origins of these systems with an emphasis on the more recently appreciated dorsal network.

PART 1: TWO SPEECH COORDINATION AREAS AND A HYPOTHESIS

1.1 Two speech areas in the lateral precentral gyrus

Evidence for a more dorsal speech area emerged as early as 1861 when Broca presented the neuroanatomical findings from his second case, Lelong, of speech dyscoordination or *aphemia* as he called it (Broca, 1861a). Lelong's lesion was more focal than Broca's first case as it involved only the most posterior part of the pars opercularis and extended dorsally to include the posterior middle frontal gyrus (Dronkers et al., 2007). Broca took note of this fact: "The integrity of the third frontal convolution (*and perhaps of the second*) seems indispensable to the exercise of the faculty of articulate language" (emphasis added, translation from (Dronkers et al., 2007)). Modern day evidence from a variety of sources provides strong support for the existence of two speech coordination areas in the precentral gyrus, which we summarize next.

Functional imaging

Functional imaging evidence began emerging in the 1990s for two speech areas in the posterior-lateral frontal cortex, a ventral site corresponding to the pars opercularis portion of Broca's area and a more dorsal site in the precentral gyrus, likely premotor cortex, just posterior to the middle frontal gyrus (Hickok et al., 2003; Price et al., 1996; Wilson et al., 2004) (Figure 1). This evidence was consistent enough to feature the two zones in modern dual stream models of

speech processing (Hickok and Poeppel, 2004, 2007; Rauschecker and Scott, 2009), although the functional roles of the two regions were and remain unclear.

Figure 1. Brain maps from a range of studies implicating a dorsal precentral gyrus region in speech processing (red arrows). A. PET study showing activation associated with repeating words minus saying “crime” after hearing a reversed word. B. fMRI study showing activation associated with both auditory (listening to nonsense sentences) and motor (silently rehearsing nonsense sentences) speech. C. fMRI study showing activation associated with listening to syllables (heat map) and producing the same syllables (black outline). D. Myelin (left) and fMRI task activation (right) map from the Human Connectome Project database showing area 55b. E. Schematic diagram of the dual stream model of speech processing showing two frontal regions associated motor speech-related processes.

Neurosurgical stimulation mapping

Further evidence for two lateral precentral gyrus speech coordination zones comes from a recent multisite retrospective study of the anatomical distribution of speech disruption during direct cortical stimulation mapping (Lu et al., 2021). Disruption was classified as either (i) *speech arrest*, defined by “complete interruption while counting, without obvious oral, facial, mandibular, and laryngeal muscle movement” (p. 5), which corresponds most closely to Broca’s aphemia, or (ii) *anomia*, defined as the “inability to name the object in a picture, or misnaming by using the wrong word (e.g. using ‘cat’ instead of ‘dog’), while still being able to speak the leading word [e.g. ‘This is a(n) . . .]’” (p. 5). Examining data from nearly 600 patients, four clusters associated with speech arrest were identified. The two most dense clusters were ventral posterior frontal cortex (green, cluster #1) and dorsolateral posterior frontal cortex (yellow, cluster #2), each of which had centroids in the precentral gyrus. The other two clusters involved the supplementary motor area and the posterior superior temporal lobe (Figure 2A). Classical Broca’s area, including the pars opercularis, was not consistently implicated in speech arrest, but was implicated in anomia, consistent with other evidence suggesting a higher-level linguistic function for Broca’s area.

Figure 2. Neurosurgical and stroke-based evidence for dorsal and ventral speech coordination systems. A. Map of locations eliciting speech arrest (see text) during direct cortical stimulation. Colors represent the results of a cluster analysis. The yellow and green clusters have density distributions centered on the dorsal and ventral precentral gyrus, respectively. From (Lu et al., 2021). B. Map of white matter connections predictive of speech repetition deficits in post-stroke aphasia implicating both dorsal and ventral connectivity. From (Baboyan et al., 2021).

Apraxia of speech

Apraxia of speech (AOS) is a motor speech disorder that is argued to reflect an impairment in the planning and/or programming of speech, situated on a functional hierarchy in between higher-level aphasia and lower-level dysarthrias (Duffy, 2013; Strand et al., 2014). As such, AOS is the modern-day disorder that most closely fits Broca's and Geschwind's definition of a speech coordination deficit. There are persistent debates about the underlying neuroanatomy of AOS but it is noteworthy in the present context that some investigators emphasize ventral regions and the anterior insula (Dronkers, 1996; Ogar et al., 2006), while others have found evidence for a more dorsal premotor focus (Chang et al., 2020; Itabashi et al., 2016; Patira et al., 2017), or both (Graff-Radford et al., 2014; Hickok et al., 2014), thus mirroring the dual zone neurosurgical and functional imaging observations. There are further debates about whether there are subtypes of apraxia of speech (Mailend and Maas, 2020). One proposal that is gaining support is a distinction between phonetic (predominantly phoneme distortions, substitutions, additions) versus prosodic (predominantly suprasegmental distortions of rate, segmentation, prosody) variants (Mailend and Maas, 2020). Perhaps these different subtypes correlate with relative ventral versus dorsal brain damage, respectively. Indeed, a recent case report indicates that surgical resection of the posterior middle frontal gyrus can result in a chronic pure apraxia of speech with prosodic dysfunction (Chang et al., 2020).

Speech repetition

Speech repetition has long been used as a diagnostic test for the integrity of auditory-motor speech circuits as it reduces the demand on lexical access and selection, while placing higher loads on more direct sensorimotor interaction (Rogalsky et al., 2015). In the classical model, the neuroanatomy underlying this ability involves the arcuate fasciculus, a major white matter pathway thought to connect Wernicke's area with Broca's area (Geschwind, 1965). However, it

has become clear that the picture is more complicated (Buchsbaum et al., 2011; Catani et al., 2005) with connectivity from various posterior temporal and parietal regions to both dorsal and ventral speech zones (Chang et al., 2015). A recent data-driven, machine learning study directly assessed the region-to-region connectivity underlying speech repetition deficits in post-stroke aphasia reporting that repetition deficits were predicted by disruption of white matter connectivity to both the ventral and dorsal frontal speech areas (Baboyan et al., 2021). Neither of these connectivity patterns implicated an arcuate fasciculus-mediated connection between Wernicke’s and Broca’s area. Instead, the critical connection to the ventral speech region was with inferior parietal secondary somatosensory cortex in the anterior supramarginal gyrus, while the critical connections (there were several) to the dorsal speech area were with auditory cortical areas in the superior temporal gyrus (Figure 2B).

Section summary and definitions

Evidence from various task-based functional imaging paradigms in healthy people, direct cortical stimulation in neurosurgical populations, and post-stroke lesion and white matter connection patterns all point to two lateral precentral gyrus speech areas, one ventral and one more dorsal. The existence two speech-related zones has been appreciated for a while, but more recent neurosurgical and stroke-based connectivity studies (reviewed above) have clarified that neither of the two areas are centered on classical Broca’s area and instead are situated more on the precentral gyrus. Figure 3 shows the location of the two regions, which we will call the *dorsal precentral speech area* (dPCSA) and the *ventral precentral speech area* (vPCSA), in schematic form (left panel) and more precisely localized from functional imaging and stimulation mapping studies (right panel, Figure S1). By using these terms, we are not claiming speech selectivity (indeed, we believe the dPCSA is also strongly involved in song); rather, the terms merely highlight their prominent role in speech coordination. The dPCSA aligns with premotor cortex on precentral gyrus (cytoarchitonic area 6) while the vPCSA is mostly posterior to area 44 in a region that is also likely premotor cortex (Zilles and Amunts, 2018), but does not yet appear in the Jülich-Brain probabilistic atlas. We also assume that each PCSA is an intermediate zone between lower-level primary motor systems and higher-level linguistic/cognitive systems (see Section 1.3). When referring to the precentral speech areas themselves, we will use the acronyms dPCSA and vPCSA; when referring more broadly to the networks in which they are situated we will use descriptors such as “dorsal/ventral speech coordination networks” or the like.

Figure 3. Left: A schematic of the location of the dorsal and ventral precentral speech areas in relation to other major anatomical landmarks. Pars Tri. = Pars Triangularis; Pars Op. = Pars Opercularis. Right: Inflated brain map showing dPCSA (blue outline) and vPCSA (yellow outline) ROIs in relation to the dorsal laryngeal motor cortex (red outline), ventral laryngeal motor cortex (maroon outline), area 55b (orange outline), and maximal probability maps for cytoarchitectonic areas (color shaded areas) from the Jülich-Brain atlas (Amunts et al., 2020), supplemented by a thresholded probability map of premotor area 6 (Geyer., 2004). dPCSA and vPCSA ROIs are estimated from functional imaging activation peaks on the precentral gyrus from (Rong et al., 2018), which align with coordinates from the speech arrest stimulation study (Lu et al., 2021)(see Figure S1). The dLMC and vLMC were defined by performing an activation likelihood estimate (ALE) meta-analysis (Eickhoff et al., 2012) of fMRI studies that explicitly refer to laryngeal motor cortex in their results (see Table S1). ALE values were thresholded at $p < 0.00001$ (cluster correction at $p < 0.00001$) and the resulting clusters were projected onto the fsaverage surface using registration fusion with Advanced Normalization Tools (Wu et al., 2018). The vPCSA and dPCSA ROIs were projected onto the fsaverage surface in the same way. Area 55b was extracted from the Human Connectome Project's (HCP) Multimodal Parcellation 1.0 atlas (Glasser et al., 2016) and resampled from the fs_LR mesh to the fsaverage mesh using the HCP's connectome workbench (Marcus et al., 2013). Maximal probability maps for motor areas 4a and 4p, somatosensory areas 3a, 3b, 1, and 2, opercular areas Op6 and OP4, and area 44 were all extracted from the Jülich-Brain atlas (Amunts et al., 2020; version 2.9), which provides its own fsaverage projections of volume-based maps (see Mangin, Rivière & Amunts, 2021 for procedure). The probability map for premotor area 6 (Geyer., 2004), which is largely unmapped in the Jülich-Brain atlas, was projected onto the fsaverage surface using the RF-ANTs transformations, then thresholded to show vertices that were at least 40% likely to be area 6.

Reference	x-coordinate	y-coordinate	z-coordinate	Space	Sample size	Task
				TAL		Speech recitation (read aloud; but activity compared to contrasts like lip and tongue movement as well)
Brown et al., 2009	-40	12	30		16	
	-44	10	30			
	-55	4	37			
	44	-6	33			
Brown et al., 2008	-38	-14	32	MNI	16	Phonation (schwa vowel) and glottal stops
	-53	0	42			
	-40	-10	30			
	-51	0	44			
	44	-10	34			
	53	4	42			
	44	-8	24			
	50	-2	37			
				TAL		Phonation (syllable with glottal stop followed by vowel)
Loucks et al., 2007	-44	-10	39		12	
	36	-8	28			
Olthoff et al., 2008	-52.2	0.8	22.9	TAL	16	Phonation (humming without intonation)
	55.2	1.5	20.5			
	-46.9	-11.6	45.2			
	45.5	-9.2	43.9			

Terumitsu et al., 2006	-56	-2.8	21	MNI	18	Phonation with (vowel) and without (syllable) tongue movement
	-40	-19	42			
Simonyan et al., 2009	-50	-14	40	MNI	13	Syllable repetition
	51	-15	41			
	-52	-13	40			
	50	-14	40			
Grabski et al., 2012	-60	-4	18		13	Vowel vocalization
	52	-6	32			
	-60	-4	36			
	54	-6	38			
Belyk et al., 2021	-59	-16	13	MNI	13	imitate melody by singing or whistling
	65	-4	14			
	61	-15	20			
	-41	-16	39			
	-51	-11	49			
	47	-9	38			
	41	-14	38			
	-49	-11	36			
	53	-7	47			
	51	-6	49			
	43	-13	37			
				MNI		
Eichert et al., 2020	-58	-2	18		20	Syllable and vowel production (controlled for breathing)
	-58	-2	20			
	-40	-16	36			
	-42	-16	40			
	60	-2	16			
	58	-4	18			
	43	-13	38			
	50	-6	40			

Table S1. Studies referring to laryngeal motor cortex that were analyzed to generate dLMC. Talairach coordinates were transformed to MNI space using the Brett Transform (Brett et al., 2002).

Figure S1: Alignment between dPCSA and vPCSA ROIs derived from an fMRI study of syllable perception and covert (imagined) production (Rong et al., 2018) (outlines) versus ROIs derived from a direct cortical stimulation mapping study of speech arrest (Lu et al., 2021) (solid color patches). Areas represent 8mm spheres around reported coordinates projected onto a common surface template.

1.2 Functional Differentiation of the Dorsal and Ventral Precentral Speech Areas

In this section, we review three relatively recent findings that provide important clues to the unique role of the dPCSA and which motivate a new hypothesis: that the dPCSA coordinates pitch-related vocalization (prosody/song) while the vPCSA coordinates phonetic/syllabic speech features.

The dPCSA codes voice pitch during vocalization

One set of observations comes from an intracranial recording and stimulation study aimed at mapping motor cortex related to vocal pitch control (Dichter et al., 2018). The primary task involved producing the same sentence repeatedly but with emphasis (higher pitch) on different words (I never SAID she stole my money; I never said SHE stole my money). After controlling for supralaryngeal articulation and intensity, a region on the mid lateral precentral gyrus was identified that showed neural activity time locked with the pitch accents. When the same sentences were played back to the participant, pitch-correlated auditory responses were recorded in the same region. A similar result was obtained with a non-speech singing task, showing that

the effect is not speech specific, consistent with a previous fMRI study of speech and melody repetition (Hickok et al., 2003). Direct cortical stimulation of this zone produced involuntary vocalization. More ventral precentral cortical regions were not strongly pitch-tuned and instead were shown to be more related to control of voicing (which involves different muscles). The authors claim to have identified dorsal laryngeal motor cortex (dLMC), which serves to control vocal pitch. While we agree with their functional conclusion regarding this region's role in pitch control, it is debatable whether it is dLMC or a higher-level coordination area with input to dLMC. Specifically, since recordings were made on the gyral surfaces using implanted electrode grids, the investigators were more likely recording from premotor rather than primary motor cortex, the latter being mostly buried in the central sulcus (Figure 3) and where dLMC is argued to be located (Eichert et al., 2020). Thus, we suggest instead that the authors have uncovered some critical properties of the dPCSA.

The dPCSA codes pitch features during perception

Further evidence for pitch-related sensitivity of the dPCSA comes from a completely different angle, an fMRI study aimed at mapping the speech-related spectrotemporal receptive field (STRF) properties of regions outside of auditory cortex (Venezia et al., 2021). The study involved participants listening to speech that was filtered so that on different trials, portions of the spectrotemporal modulation spectrum were excised from the signal (Venezia et al., 2016). Neural activity was then correlated with the presence or absence of signal in different regions of spectrotemporal modulation space enabling the estimation of regional STRFs (Venezia et al., 2019). Relevant to the present discussion, robust speech-related STRFs were found in a dorsal precentral location that aligns spatially with the dPCSA (Figure 4). The vPCSA was not among the regions with mappable STRFs, although a more anterior site in the pars triangularis region of Broca's area did prove partly auditory responsive. The dorsal premotor site exhibited an STRF profile similar to that of early auditory cortex in that it showed tuning not only to regions of spectrotemporal modulation space relevant to intelligibility (typical of higher-order auditory cortex) but also to regions related to voice pitch (*atypical* of higher-order auditory cortex). Further, the dorsal premotor region showed strong functional connectivity with early auditory cortex, converging with the stroke connectivity result noted above. A recent intracranial cortical recording study provides evidence that auditory information engaging this dorsal premotor region has functional relevance for speech coordination: under conditions of fluency-disrupting delayed auditory speech feedback, activity in the dorsal precentral region was enhanced as part of a network that included auditory areas and the supramarginal gyrus (Ozker et al., 2022).

In contrast, the STRF profile in the Broca's area site was selectively responsive to intelligible speech, was not tuned to pitch, and showed functional connectivity with higher-order regions in the superior temporal sulcus and middle temporal gyrus, not early auditory cortex, strongly suggesting that it is receiving inputs from higher-level (e.g., lexical) networks.

Figure 4. Distribution of mappable spectrotemporal receptive fields (STRF) (right brain image) and plots of the STRF maps associated with the two lateral frontal STRF regions (left images, A & B), one in dorsal precentral gyrus and one on the pars triangularis. The dorsal precentral site exhibits significant tuning to the pitch-related region of STRF space (black oval). Colored dots correspond to the coordinates of three separate fMRI study activations, two which map auditory-motor speech responses (green and blue; (Buchsbaum et al., 2001; Wilson et al., 2004)), and one that mapped laryngeal motor cortex (Brown et al., 2008), coordinate is on “gyral portion” (see text).

Persistent developmental stuttering implicates ventral sensorimotor cortex

Developmental stuttering persists into adulthood in approximately 1% of the population (Prasse and Kikano, 2008; Yairi and Ambrose, 2013) and results in sound and syllable repetitions, sound prolongations, and blocks, suggesting a deficit in the ability to initiate, control, and terminate speech gestures (Guenther, 2016). Fluency among adults who stutter has been reported to improve substantially during singing (Andrews et al., 1982; Wan et al., 2010), suggesting a relative sparing of the more dorsal speech coordination system while disrupting the ventral speech coordination system at some level. This question was examined in a recent study of white matter structural connectivity of the dorsal and ventral speech systems using seeds for the dorsal and ventral laryngeal motor areas, respectively (Neef et al., 2021) (see section 1.3 for discussion of these two laryngeal areas). The ventral network was found to have weaker connectivity than the dorsal network in adults who stutter compared to controls and the connectivity profile of the ventral (but not dorsal) network predicted stuttering severity. This work suggests that the ventral network plays a critical role in speech coordination at the sound and syllable level and can be impaired while sparing song. It should be noted that prosodic abnormalities have also been reported in stuttering (Neumann et al., 2018), but relatively preserved singing ability in adults who stutter argue against a primary deficit in pitch-related voice coordination.

Section summary

The studies described above indicate that the dPCSA is involved both in the control of voice pitch and capable of coding pitch-related cues in acoustic signals via functional connectivity with relatively early auditory areas. This contrasts with the vPCSA, which appears to lack these pitch-related properties and instead is more involved in speech coordination at the phonetic and syllable level. Given that a hallmark of sensorimotor control circuits is neural coding of corresponding sensory and motor features (e.g., corresponding codes for object shape and grip type in grasping (Jeannerod et al., 1995)), these findings suggest that the dPCSA (but not vPCSA) is part of an auditory-motor circuit for learning and feedback control of pitch-related vocalization.

1.3 The Dual Speech Coordination Model

We propose that dPCSA and vPCSA are part of distinguishable, parallel (but interacting) networks for coordinating pitch-related and syllabic/phonetic related speech features, respectively. Specifically,

- **The dPCSA** is part of an auditory-weighted sensorimotor control circuit for pitch-related vocalization, which includes 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 somatosensory-weighted 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.

In the following sections we discuss the broader networks in which the two speech coordination areas are situated.

Parallel frontal motor hierarchies for speech coordination

Motor control systems are hierarchically organized (Uthol et al., 2012) and there is no reason to think that speech coordination systems are any different. What is less clear is whether the dPCSA and vPCSA are at a similar level in parallel hierarchical streams, as we will argue here, or whether one is subordinate to the other. (A third possibility is that the dorsal and ventral precentral speech regions are one undifferentiated zone (Jarvis, 2019) but this paper argues against this view.) One source of evidence for the parallel hierarchical claim is that both speech areas appear to be at the same level of the general cortical hierarchy somewhere between higher-order linguistic processing and low-level motor implementation, as suggested by the cortical stimulation mapping data discussed earlier. Another source of evidence is the apparently tight relation between the dPCSA and dorsal laryngeal motor cortex (dLMC), which we turn to next.

dLMC is the lowest level in the cortical hierarchy for vocal pitch-related coordination

Humans have two spatially separable regions related to laryngeal control, one more ventral and thought to be in *premotor* cortex, which is shared with other primates, and one more dorsal and thought to be in *primary* motor cortex in the central sulcus, which is phylogenetically younger and not shared with other primates (Eichert et al., 2020; Eichert et al., 2021; Jarvis, 2019;

Simonyan, 2014). We will refer to these regions as dLMC and vLMC. Functional differences between the dLMC and vLMC are yet to be mapped in detail but one major distinction is the differential effects of cortical stimulation mapping: stimulating regions in the vicinity of dLMC elicits vowel-like phonation whereas more ventral stimulation does not, eliciting grunt-like behaviors instead (Belyk et al., 2021; Breshears et al., 2015).

While the existence of two areas involved in laryngeal control is unique to humans among primates, multiple motor maps for a given effector (e.g., the hand) has been observed in many species, and is thought to reflect an organization of motor cortex around adaptive behaviors or functional domains—such as reaching, grasping, hand-to-mouth, defensive postures, and so on—rather than a simple somatotopy (Graziano and Aflalo, 2007; Graziano et al., 2002; Kaas et al., 2013). Given that the same effector can be involved in multiple functional domains, multiple representations of the same effector is expected, as the data indeed show (Kaas, 2012). Applying this thinking to the larynx, the existence of two areas in humans suggests two functional domains associated with laryngeal control. The existing evidence strongly points to the dLMC as part of a functional domain for pitch-related vocalization and which includes other motor systems that are important for this functional domain, such as respiratory control (Chan et al., 2022; McKay et al., 2003). The functional domain(s) of the vLMC is less clear for speech, although some role in initiation, timing, and cessation may be involved (Neef et al., 2021). In non-human primates, the vLMC likely plays a role in nonvocal functions (Simonyan and Jurgens, 2005) such as ingestion (Huang et al., 1988; Yamada et al., 2005). The broader ventral orofacial motor system in which the monkey vLMC is situated involves functions including oral grasping (Ferrari et al., 2003; Rizzolatti et al., 1988) and communicative oral gestures such as lip-smacking (Shepherd and Freiwald, 2018). It should be noted that limited voluntary control over innate vocalizations has been reported in monkeys, with ventral motor-related cortex implicated (Coude et al., 2011; Hage and Nieder, 2013), consistent with a possible role of human vLMC in voicing initiation. However, damage to monkey ventral motor regions does not affect the ability to generate innate calls (Kirzinger and Jurgens, 1982), showing that the ventral orofacial motor system does not contain the neural codes for monkey vocalizations but rather a mechanism for voluntarily eliciting the vocalization “subroutines” coded elsewhere (Jurgens, 2009).

The proposed framework is consistent with the hypothesis that vocal pitch control is the functional domain associated with dLMC. We make this inference on the basis of the spatial relation between the pitch-related dPCSA and the dLMC, which partially overlap in group-based studies (Figure 3). In fact, some investigators refer to two subdivisions of the dLMC, sulcal and gyral LMC (Brown et al., 2021). The gyral LMC partially overlaps our dPCSA, which we propose to be hierarchically dominant to the sulcal dLMC based on (i) the probabilistic location of dPCSA in premotor cortex and sulcal LMC in primary motor cortex (Figure 3), (ii) dPCSA activation for imagined speech production (suggestive of a planning process) (Hickok et al., 2003; Rong et al., 2018), and (iii) the acoustic response properties of the dPCSA in the absence of any expressive speech task (Venezia et al., 2021), which is consistent with the previous observation of an anterior (auditory-motor) to posterior (more purely motor) gradient in this region (Figure 1C) (Wilson et al., 2004). Note that although we are framing our hypotheses around a rather strict hierarchy, it is likely that the boundaries reflect a gradient of hierarchical control rather than a sharply delineated hierarchy.

A higher-order language area anterior to the dPCSA in the posterior middle frontal gyrus

Anterior to the dPCSA lies a higher-level language region in the posterior middle frontal gyrus, area 55b (Figure 1D and 3) (Glasser et al., 2016). It is relatively unmyelinated and sandwiched between the two moderately myelinated lateral eye fields. Posterior to 55b is the heavily myelinated primary motor cortex (Glasser et al., 2016), which includes the (sulcal) dLMC. The dPCSA overlaps the posterior portion of area 55b, while the anterior portion of 55b extends into the posterior middle frontal gyrus. Evidence for a language function associated with anterior 55b comes from the very definition of the area, which is derived in part from the Human Connectome Project’s functional activation language task, story listening, which shows a peak activation focus in the anterior portion of the 55b parcellation (Glasser et al., 2016). Further evidence comes from a recent study showing a role for the posterior middle frontal gyrus in expressive agrammatism (an acquired deficit of syntactic production) (Matchin et al., 2020) as well as from an automated meta-analysis of “syntactic” processing that we conducted using the Neurosynth database (Yarkoni et al., 2011) (Figure 6).

Figure 6. An automated meta-analysis of functional imaging studies on the term “syntactic” (heat map) using neurosynth.org. Note the relation to area 55b (yellow outline).

What function(s) might be served by the higher-order level of the dorsal speech coordination network? This is an open question, but one hypothesis that is consistent with existing data is that it plays a role in prosodic planning, which is known to correlate with syntactic features and has been proposed as a planning frame for speech production (Shattuck-Hufnagel, 2015; Shattuck-Hufnagel and Turk, 1996). One may wonder whether dysfunction of a prosodic planning system can impact expressive syntactic processing sufficiently to contribute to expressive agrammatism, as described above, a rather severe deficit of syntax. But if “the prosodic structure of an utterance provides the representational ‘spine’ that governs ... the serial ordering of lexical elements and their sub-constituents” (p. 11) (Shattuck-Hufnagel and Ren, 2018), then it seems quite possible that the disruption of this planning “spine” could lead to significant deficits in the serial ordering of syntactic elements (Matchin and Hickok, 2020).

The ventral speech coordination hierarchy

The proposed hierarchy in the dorsal system parallels a similar hierarchy in more classic ventral speech and language areas with the vPCSA lying between primary oromotor cortex posteriorly and Broca's area anteriorly in the posterior inferior frontal gyrus (Figure 3). We have argued that the vPCSA coordinates phonetic articulation within the syllabic frame (Fitch, 2019; MacNeilage, 1998) and we follow previous hypotheses that higher levels of the ventral speech coordination system play a role in *sequencing* of syllables (*pars opercularis*) (Fitch, 2019; Rong et al., 2018) and morphosyntactic elements (*pars triangularis*) (Matchin and Hickok, 2020) (see also (Hagoort, 2005)). As the existence of a ventral frontal speech- and language-related hierarchy is widely accepted, we will not further review or argue the details of its internal organization, which is an active topic of research.

Connectivity

Results from the connectome mapping study of repetition deficits in stroke aphasia (Section 1.1, Figure 2B) indicate different patterns of connectivity associated with the dPCSA and vPCSA with the dorsal region more strongly connected to auditory cortex and the ventral region more strongly connected to inferior parietal/secondary somatosensory cortex. The spectrotemporal receptive field mapping study described in Section 1.2 also included a functional connectivity analysis that showed connectivity between the dPCSA and auditory cortex. Here we present two new analyses of functional connectivity of the two speech areas. Both use seed ROIs corresponding to the dPCSA and vPCSA defined from (Rong et al., 2018) (Figures 3, S1).

The first functional connectivity analysis is from a task fMRI study of speech-based spectrotemporal receptive field mapping (Herrera Ortiz, C., Whittle, N., Leek, M. R., Brodbeck, C., Lee, G., Barcenas, C., ... Venezia, J. H. (2021, July 29). Cortical Networks for Recognition of Speech with Simultaneous Talkers. <https://doi.org/10.31234/osf.io/vea5y>) using similar methods to the study described in Section 1.2. The second functional connectivity analysis draws on previously published and publicly available multi-echo resting state fMRI data (Kundu et al., 2013; Power et al., 2018), but adds an additional 48 participants for whom data was collected in the same way by the same group (courtesy of Peter Bandettini). The results of both functional connectivity analyses are presented in Figure 7, which confirms the hypothesized pattern of stronger auditory cortex connectivity for the dPCSA and strongly higher-level somatosensory connectivity for the vPCSA.

Figure 7. (Left) Resting state functional connectivity map for the dPCSA (cool colors) and vPCSA (warm colors). Whole brain maps were generated for each ROI (defined in Figure 3) in each participant ($N = 137$) using multi-echo independent components regression (Kundu et al., 2013). Voxelwise paired t -tests were then performed to determine brain regions where resting functional connectivity was significantly higher to either dPCSA or vPCSA in the group. Familywise error was controlled at $p < 0.01$ using threshold free cluster enhancement (TFCE) with 5000 permutations (Smith & Nichols, 2009). The resulting t -map was projected onto the fsaverage surface using registration fusion with Advanced Normalization Tools (Wu et al., 2018). (Right) Task fMRI-based, functional connectivity maps. Beta time series functional connectivity analyses ($N = 34$) were conducted using data from 400 trials of a receptive competing speech task (Herrera Ortiz et al., 2021; “Competing” condition). Data were projected onto a cortical surface model of the MNI152 template and surface-node-wise estimates of functional connectivity (Least-Squares-Separate beta time series; Pearson correlation) were obtained using the average time series within dPCSA and vPCSA ROIs defined as in Figure 3 as seeds. A second-level contrast t -map (dPCSA connectivity vs. vPCSA connectivity) was obtained and thresholded at FDR-corrected $p < 0.01$, then projected onto the fsaverage surface using registration fusion with Advanced Normalization Tools (Wu et al., 2018)

Section summary

This section argued for parallel hierarchical networks, one ventral and one more dorsal in lateral posterior frontal cortex, supporting speech coordination. Each involves a primary motor cortical zone at the lowest level, an intermediate level corresponding to the two precentral speech areas, and one or more higher-order linguistic region(s). The ventral hierarchy corresponds to the familiar inferior frontal speech/language network with Broca’s area at the top of the hierarchy, with an internal hierarchical organization of its own. The dorsal hierarchy involves dLMC, the

dPCSA, and the posterior middle frontal gyrus (pMFG) language area, which we suggest is a core region involved in prosodic planning. The precentral speech areas differ in terms of the sensory input they receive with the dPCSA more strongly auditory-weighted and the vPCSA more strongly somatosensory-weighted. Figure 8 provides a graphical sketch of the proposed architecture.

Figure 8. Schematic depiction of the dual speech coordination system model. Input labels (purple arrows) are intended to reflect a bias toward the named input type, not exclusivity, and are not intended to reflect anatomical locations of white matter pathways. For detailed arguments regarding the morphosyntactic pathway, see (Matchin and Hickok, 2020). Anatomical localizations are approximate. Location of orofacial motor cortex ventral to dLMC is based on a meta-analysis from (Guenther, 2016).

PART 2: EVOLUTION OF THE DUAL SPEECH COORDINATION ARCHITECTURE

The evolutionary origin of human speech and language ability has been a topic of deep interest and much debate since Darwin (Darwin, 1871; Fitch, 2010). The dual speech coordination model proposed here sheds some light on this issue by more clearly describing the subcomponents of the neural phenotype that evolved, which both motivates some new hypotheses and contributes a new framework in which to interpret evidence relevant to existing proposals. In terms of new hypotheses, the auditory nature of the dPCSA along with its location near the frontal eye fields suggest the hypothesis that it evolved from a premotor orienting system, which also makes extensive use of similar kinds of auditory cues (section 2.1). The existence of separable pitch/prosody/song-related and phonetic/syllabic-related networks suggests the possibility of differentiable evolutionary histories and aligns (i) with the hypothesis that song evolved at an early stage in our vocal communication ability related to the emergence of voluntary laryngeal control and song-like vocal production learning (Darwin, 1871; Fitch, 2010), and (ii) with the

hypothesis that phonetic/syllabic coordination emerged from orofacial actions (mastication and lip-smacking) (Fitch, 2019; Ghazanfar et al., 2012; MacNeilage, 1998).

Next we evaluate the evolutionary precursors of first the dorsal and then the ventral speech coordination systems, followed by a discussion of their sequence of emergence, and conclude with a consideration of the relation between our proposal and theories of the evolution of language.

2.1 The dPCSA evolved from a premotor goal-directed orienting system

We argue that there is a relation between auditory inputs to premotor cortex that are used in the service of goal-directed orienting and the evolution of the dorsal speech coordination system (see (Martins and Boeckx, 2014) for more general discussion of the evolutionary relation between language and attention systems). The logic of this argument is that motor coordination systems require the right kinds of sensory inputs to enable feedback control (Guenther, 2016; Hickok, 2012); control of vocal pitch features requires input from auditory pitch-related codes; the only cortical motor network in the non-human primate brain known to use pitch-related codes is the orienting system, which involves the dorsal precentral region. Therefore, if a motor coordination system for pitch-related vocalization were to evolve, it should be in the vicinity of networks that already have the relevant sensory input signals, which is dorsal premotor cortex. We elaborate this argument next.

Spatial orienting systems and the dPCSA are adjacent

In macaque, the dorsolateral premotor cortex, including the frontal eye field, is part of the dorsal, sensorimotor stream and receives input from caudal non-primary auditory areas that are thought to play a role in spatial localization of auditory signals (Hackett et al., 1999; Romanski et al., 1999). The frontal eye field in particular has a large population of auditory responsive cells (Caruso et al., 2016) and is well-suited to guiding sensory-driven orienting responses and covert spatial attention (Thompson et al., 2005). The fact that the frontal eye field utilizes not only visual but also auditory inputs and is part of the orienting system is key, given that human area 55b and the dPCSA are situated in between the human frontal eye field dorsally and premotor eye field ventrally (Glasser et al., 2016). Human fMRI work has also identified auditory-driven spatial attention networks in the dorsolateral premotor cortex (Tobyne et al., 2017).

Spatial orienting uses spectral auditory cues including pitch

While auditory spatial localization in the horizontal plane relies primarily on sound level and time delay differences in acoustic signals reaching the two ears, localizing sounds in the vertical plane relies strongly on spectral acoustic features (Brown et al., 1982) including pitch (Cabrera and Morimoto, 2007). Natural auditory scene statistics exhibit an elevation-based frequency gradient with higher-pitched sounds tending to have sources at higher elevations (Parise et al., 2014). Human listeners use these cues to modulate spatial orienting and inform sound source elevation judgments (Cabrera and Morimoto, 2007; Chiou and Rich, 2012; Parise et al., 2014; Roffler and Butler, 1968). Use of spectral cues in spatial orienting must be adaptive given that the filtering properties of the human outer ear have evolved to amplify this vertical pitch gradient (Parise et al., 2014). The ability to detect these cross-modal correspondences between auditory

pitch and visuospatial elevation has also been reported in human neonates (Walker et al., 2018) as well as in domestic dogs (Korzeniowska et al., 2019), arguing against a cultural explanation. More generally, given that vocalized spectral cues are correlated with animal size (Fitch, 2000) and that modulation of these cues are used for social communication in a variety of mammals (Pisanski et al., 2016), it should be no surprise that such information is salient to listeners and used by the orienting/attention system (Kayser et al., 2005) beyond its relevance as a cue to spatial location (Pisanski et al., 2017). Relatedly, the human frontal eye field exhibits “ultra rapid” responses to both auditory and visual stimuli, which are modulated by sensory features, including pitch, as opposed to simply the presence or absence of stimulation (Kirchner et al., 2009). These ultra rapid responses are likely useful for rapid orienting and suggest that relatively low-level auditory features are transmitted in this signal, as opposed to higher-level object-based features, which would require more processing and thus longer latencies.

Auditory-responsive regions have also been identified in more ventral prefrontal (Romanski and Goldman-Rakic, 2002; Romanski et al., 1999) and premotor cortex (Graziano et al., 1999; Hage, 2018) in monkeys. However, in the prefrontal case, inputs come from rostral auditory cortex, are part of the ventral “what” stream, and code more complex information. Audio-motor responses have been recorded in this region, involving the execution and perception of species-specific calls (Hage, 2018). These responses, however, likely reflect the ability to modulate innate calls in response to external stimulation rather than using auditory features to code the calls themselves (Hage, 2018; Loh et al., 2017). In the premotor case, one study reported neurons that are spatially selective for proximal locations near the body, but which are not tuned to pitch, instead preferring broadband sounds, and with somatosensory receptive fields around the ears or back of the head, ideal for guiding actions toward objects (e.g., insects) around the head (Graziano et al., 1999).

Thus, dorsal premotor cortex, by virtue of the auditory orienting networks located there, but not ventral premotor cortex, was arguably prewired in our ancestral species to receive a rich array of acoustic information, including pitch-related cues, which would have been critical for an evolving auditory-motor, pitch-related vocal production-learning circuit. Comparative evidence from the evolution of song in birds indicates that brain areas with pre-song auditory inputs are targets for the evolution of song (Brenowitz, 1991).

The premotor cortex as a hub for a broader goal-directed orienting system

Auditory cues can drive goal-oriented action beyond eye-based spatial localization and again dorsolateral premotor areas are implicated in this ability in human and non-human primates. For example, some studies have reported that auditory rhythmic entrainment engages dorsal premotor cortex while visually-paced entrainment does not, the latter involving more ventral premotor regions (Chen et al., 2006; Jancke et al., 2000; Pollok et al., 2009). Instrumental musicians, who have stronger auditory-manual associations, exhibit stronger activation in dorsal premotor cortex than non-musicians (Baumann et al., 2007). And monkeys, when trained to reproduce pitch sequences via a “monkey piano”, tend to activate more dorsal motor and premotor arm-related areas while passively listening to the auditory sequences they previously learned to “play” (Archakov et al., 2020).

Research on the frontal eye fields also points to a broader orienting and attention network (Vernet et al., 2014). Indeed, while the name “eye field” implies eye-selective activity, research in human and nonhuman primates that examined both eye and head orienting behavior, has found evidence that the frontal “eye” field is involved in control and coordination of both effectors (Petit and Beauchamp, 2003; Tu and Keating, 2000).

Building on modern thinking regarding the “functional domain” organization of motor systems, we suggest that the frontal eye fields are part of a hub for a broader orienting network (Posner, 2016; Posner and Niell, 2019) that coordinates multiple effectors (eyes, head, arms) in the service of voluntary goal-directed action. Thus, we propose that it is out of this dorsal premotor, auditory-responsive, goal-directed orienting system that voluntary laryngeal control and the dPCSA evolved, perhaps initially serving a song-based adaptive function related to social bonding (Savage et al., 2021).

Behavioral evidence for a link between vocal pitch control and non-vocal orienting

If the dPCSA and its associated network evolved from a more general orienting system, we might expect to see correlations between vocal and non-vocal gestures due to coactivation of related networks. Such correlations have been observed both in musical and linguistic contexts.

Behavioral studies have found a strong correlation between laryngeal pitch control and head/face movements. Singers, for example, raise their head and eyebrows with an amplitude that strongly correlates with the size of ascending pitch intervals (Thompson and Russo, 2007). This cannot be explained as a strategy for improving singing quality as head movement is not advantageous for pitch-related vocal production (Knight and Austin, 2020). Head movements during talking are also correlated with prosodic pitch (Munhall et al., 2004) and lexical tone (Burnham et al., 2022). These non-vocal head and eye movements are correlated strongly enough with pitch to provide observers with redundant visual cues to pitch information. Pitch accents in speech are also correlated with co-speech manual gestures (Loehr, 2012) and may be causally related: two expressions of the same prosodic frame for speech planning (Shattuck-Hufnagel and Ren, 2018). All of this points to a correspondence between laryngeal pitch control and non-vocal gesturing, which is consistent with the hypothesis of a phylogenetic connection between them.

2.2 Coordination of the supralaryngeal vocal tract evolved from ventral orofacial control systems

Frame-content theory

MacNeilage’s frame-content theory of the evolution of speech production provides an account of how the ability to articulate phonological segments within syllabic frames might have evolved (Fitch, 2019; MacNeilage, 1998). The basic idea is that syllables are formed by the cyclic opening and closing of the jaw, into which various phonetic gestures are articulated to form different vowels (open phase) and consonants (closed phase). Syllabic jaw cycles, according to the frame-content theory, evolved from cyclic jaw actions characteristic of mastication and observed in communicative lip-smacking in non-human primates. Lip-smacking in particular, while unaccompanied by vocalization (but see below), involves speech-like gestures including

synchronized lip, jaw, and tongue movements with jaw oscillation cycles in the speech frequency range (Ghazanfar et al., 2012). Thus, lip-smacking is a very strong candidate for a pre-adaptation preceding supralaryngeal speech coordination (Fitch, 2019; Ghazanfar and Takahashi, 2014; MacNeilage, 1998).

Lip-smacking implicates ventral frontal premotor regions

Although MacNeilage (MacNeilage, 1998) argued for the medial motor system (e.g., the SMA) as the neural source of cyclic jaw movement, recent work in macaques has pointed to the lateral ventral motor network for both ingestive actions and lip-smacking behavior. Ferrari, et al. (Ferrari et al., 2003), for example, identified neurons in F5, a presumed homologue of human Broca's area, that responded during a range of executed mouth actions including grasping, sucking, chewing, and lip-smacking (among others). Ingestion-related action responses were the most commonly recorded. About half (48.7%) of the neurons also had visual-response properties. Auditory responses were not studied. A more recent fMRI study of macaques producing lip-smacking gestures reported activation in a broad motor network including primary motor cortex and ventral (but not dorsal) premotor cortex, which overlapped that for non-communicative facial movement control (Shepherd and Freiwald, 2018). This strongly suggests that lip-smacking communicative gestures developed from ventral orofacial motor control networks.

The ventral motor regions that are activated during the generation of lip-smacking actions do not seem to respond to social communicative auditory signals. In one unit-recording study, macaque F5 neurons were reported to respond to object-action-related sounds such as paper being torn or a stick being dropped, but no responses to monkey calls were found (Kohler et al., 2002). In another study (Coude et al., 2011), macaques were trained to elicit "coo" calls in response to the presentation of food. A population of F5 cells responded prior to or around the onset of cued calls but they did not respond to auditory recordings of the calls nor during spontaneous call generation (consistent with the view that ventral motor areas do not house the codes for innate calls but play a role in voluntarily initiating them).

These studies provide evidence for ventral orofacial motor networks as the basis for the evolution of supralaryngeal vocal tract coordination and reinforces the view that this system was not particularly sensitive to vocal auditory signals in our pre-human ancestors.

Alternative hypotheses regarding the function and location of the dorsal and ventral systems

Brown and colleagues have proposed an alternative theory of the location of dLMC (and by extension the dPCSA) arguing that it is related to the more dorsal distribution of motor cortex for jaw opening (Brown et al., 2021). However, a close examination of the distribution of jaw opening motor areas in the monkey do not provide strong support for this claim, with responses during jaw-open and jaw-close occurring both ventrally and more dorsally (Huang et al., 1988). Belyk et al. (Belyk et al., 2021) suggest that both dLMC and vLMC play a role in integrating respiration with phonation during vocalization, but hint that functional differences between vLMC and dLMC may reflect the fact that (i) only vLMC seems to respond to somatosensory stimulation of the larynx and (ii) vLMC appears to be cytoarchitecturally intermediate to primary

motor and primary somatosensory cortex. We view this hypothesis as broadly consistent with ours in that it supports the view that a primary organizing feature of dorsal and ventral speech coordination circuits is their relative sensitivity to different sensory inputs (i.e., auditory vs. somatosensory), and argues against an organization based on motor somatotopy.

2.3 Evolutionary sequence of dorsal and ventral speech coordination systems

The vLMC is generally believed to be phylogenetically older than the dLMC and voluntary control of the orofacial articulators, including the capacity for communicative lip-smacking gestures, predates the evolution of voluntary laryngeal control. Nonetheless, we suggest, following proponents of the song-first hypothesis (Darwin, 1871; Fitch, 2019; Mithen, 2005), that in the domain of speech coordination, the evolution of laryngeal pitch-related coordination preceded the (co)evolution of supralaryngeal phonetic/syllabic coordination beyond the stage of lip-smacking gestures. This hypothesis runs into immediate apparent complications, however.

One is that monkeys can, with much effort and explicit training, gain partial voluntary control over the elicitation of innate calls, as the study summarized in section 2.2 shows. If simple vocalizations could be brought under full voluntary control to initiate or cease, then this would provide a vocal source signal enabling further evolution of auditory-guided coordination of the supralaryngeal filter. A pitch coordination system, on this scenario, is an add-on rather than a prerequisite. An apparent existence proof showing perhaps a first step in such an evolutionary trajectory comes from the vocalized lip smack or “wobble” of the gelada (*Theropithecus gelada*), which appears to involve overlaying lip-smacking on a “moan” vocalization, both of which are separately present in their repertoire (Bergman, 2013). From that stage, all that would be needed for speech is to evolve complex vocal production learning (Fitch, 2019). This doesn’t explain the evolution of pitch coordination, but it does complicate the claim that the pitch coordination system evolved first.

A second complication comes from vocal convergence in great apes (e.g., (Watson et al., 2015))—a simple form of vocal learning where vocalization of individuals in a group become similar—or the apparent ability of orangutans to modify the pitch (higher vs. lower) of an existing call in response to a higher or lower pitch cue (Lameira et al., 2016). Both kinds of results seem to challenge the view that vocal learning is unique to humans among primates. But these results themselves have been challenged on methodological grounds (Fitch, 2019) and even if valid are not much removed from the range of the vocal control ability of many mammalian species, for example, in modulating spectral features, including pitch, under some conditions (Charlton and Reby, 2016).

So, while it may be true that observations such as these complicate the claim that pitch-related laryngeal coordination predates supralaryngeal coordination by raising the possibility that much can be accomplished without the dorsal pitch-related system, neither do they provide compelling evidence against it. Next, we turn to the evidence that supports a pitch coordination-first model.

Four pieces of evidence support the hypothesis that pitch coordination preceded phonetic coordination. The first is that pitch control is a simpler engineering task in that it can be modeled as a simple linear system using only auditory feedback; in contrast, controlling the

multidimensional supralaryngeal system for speech articulation is nonlinear and dependent on somatosensory feedback (Parrell et al., 2019). Second, prosody, which prominently includes pitch melody and accents, plays an important role in word learning (Thorson, 2018) and, as noted, functions as an important planning frame for speech. Thus, if pitch coordination evolved first it could potentially facilitate the more computationally complex task of developing supralaryngeal vocal tract control. This leads to our third piece of evidence: pitch control in the form of song has evolved in multiple song species (Nieder and Mooney, 2020), but the ability to articulate speech by coordinating both the sound source and filtering organs (“high vocal learning”) is exceedingly rare, found only in parrots and humans (Patel, 2021; Petkov and Jarvis, 2012), both of which also have pitch control. Based on the first two points and given this pattern of vocal learning ability, it may be that song is a necessary preadaptation for high vocal learning. Fourth, the development of vocalization in infants progresses from cooing, a song-like vocalization, to a later syllable-like babbling stage (Nathani et al., 2006). Interestingly, direct cortical recordings of a 10-month-old during cooing and babbling vocalizations showed neural activation in distinct dorsal (cooing) and ventral (babbling) precentral gyrus locations (Cho-Hisamoto et al., 2012). Thus, the fact that (i) pitch control is computationally simpler, (ii) a pitch-related component of language (prosody) eases the computational burden of full-blown speech/language acquisition, (iii) pitch control exists without complex supralaryngeal/syringeal coordination in many species, while the reverse does not, and (iv) pitch-based vocalizations develop earlier in human infants, all point to an earlier evolution of the dorsal pitch-related system prior to the ventral system.

2.4 Relation to Theories of the Evolution of Language

Darwin proposed that an early step in the evolution of language was the emergence of a song-based musical protolanguage, analogous to birdsong, prior to the evolution of articulate speech (Darwin, 1871), a hypothesis that remains viable today (Fitch, 2010, 2017; Mithen, 2005). Our proposal of a distinguishable vocal pitch/prosody/song system in dorsal premotor cortex and surrounds, which preceded the evolution of the ventral system, is consistent with the song protolanguage account and provides additional support in two ways. First, it identifies a circuit, distinct from that proposed to be involved in syllabic/phonetic coordination, that could have been the target of this first stage of language evolution enabling voluntary control of the larynx and vocal production learning. Second, it provides a viable means for the evolution of such a system via the relation between vocal pitch-related prosody/song coordination to the goal-directed orienting system.

Other authors have argued for an early mimetic or gestural protolanguage stage in the evolution of language (Arbib, 2005; Corballis, 2010; Donald, 2017; Molesti et al., 2019). Although vocal and gestural foundations of language are often pitted against one another, both could serve foundational roles as part of an integrated system (de Boer, 2017; Goldin-Meadow, 2017; Kendon, 2017). Indeed, they appear to do so developmentally: both gestural and prosodic communication emerge early in human development and both are argued to play foundational roles in lexical, syntactic, and pragmatic aspects of language acquisition (Hubscher and Prieto, 2019). The possibility of the coordinated evolution of song and gesture systems as a foundation for language evolution is reinforced by the present hypothesis in that it provides a plausible

neural link between pitch-related vocal coordination and non-vocal gesture, both of which are associated with a dorsal, premotor orienting system as argued above.

While our hypothesis of two speech coordination systems does not suggest a new model of the evolution of language, it does support and tie together several ideas currently being debated. Specifically, our claim that voice pitch-related coordination is a separable neural system from syllabic/phonetic coordination supports the hypothesis that song communication has very deep roots in our evolutionary history. The proposal that voice-pitch coordination evolved from a more general orienting system involving eye, head, and limbs—which itself plays an important role in social communication—also supports the hypothesis that gestural communication has similarly deep evolutionary roots. It is on this foundation, we propose, that the ability to modulate vocalizations via the coordination of open-close jaw cycles with phonetic articulation evolved.

3.0 Summary and outstanding questions

Many questions remain to be addressed. For example, coordination *between* the two systems is clearly necessary and disruption of such coordination is surely a cause of speech coordination deficits such as apraxia of speech. This will be a critical topic for future work. Additionally, rhythm is an important feature in prosodic and song production and can be disrupted in speech coordination deficits. Given that rhythmic timing also plays an important role in phonetic planning, it will be crucial to determine whether and to what extent vocal rhythm production depends on dorsal vs. ventral speech coordination circuits (or their interaction). Respiratory control is yet another important component of speech coordination that needs to be considered in future investigations, though it seems likely that control over respiration must be integrated with prosodic and phonetic aspects of production, and thus also with dorsal and ventral speech coordination circuits (Belyk et al., 2021). There are also more detailed functional-anatomic questions to answer, such as the precise boundaries of these systems and their hierarchical levels.

Finally, there are important questions about lateralization that need to be answered. As part of the dorsal sensorimotor stream, we would predict relatively strong left-dominance for both of the hypothesized speech coordination systems (Hickok and Poeppel, 2007). But there is also evidence for a possible hemispheric dissociation of song/prosody production versus production of other aspects of speech and language that remain to be sorted (Ozdemir et al., 2006; Royal et al., 2015). Moreover, several recent direct cortical stimulation/recording studies suggest responses to acoustic speech features and laryngeal production in left *and* right dPCSA/dLMC (Belkhir et al., 2021; Berezutskaya et al., 2020; Dichter et al., 2018; Hamilton et al., 2018). We leave these and other questions to future study.

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