Revisiting human language and speech production network: A meta-analytic connectivity modeling study

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ARTICLE INFO

ABSTRACT

In recent decades, converging evidence has reached a consensus that human speech production is carried out by large-scale hierarchical network comprising both language-selective and domain-general systems. However, it remains unclear how these systems interact during speech production and the specific contributions of their component regions. By utilizing a series of meta-analytic approaches based on various language tasks, we dissociated four major systems in this study: domain-general, high-level language, motor-perception, and speech-control systems. Using meta-analytic connectivity modeling, we found that while the domain-general system is coactivated with high-level language regions and speech-control networks, only the speech-control network at the ventral precentral gyrus is coactivated with other systems during different speech-related tasks, including motor perception. In summary, this study revisits the previously proposed language models using meta-analytic approaches and highlights the contribution of the speech-control network to the process of speech production independent of articulatory motor.

1. Introduction

Language production is a complex process that involves conceptualization, words selection, syntactic encoding, articulatory processes, and speech feedback, which is also a key component of human language (Levelt et al., 1999). This process requires the orchestration of multiple brain regions at the network level and has been traditionally considered from two perspectives: the psycholinguistic view and the motor control view. From the perspective of psycholinguistics, three linguistic processing phases are typically focused on: acoustic-phonological level, syntactic and semantic level, and sentence level (Dell, 1986; Fitch and Hauser, 2004

brain region or network responsible for the interaction between linguistic processing and motor control remains unclear (Baldo et al., 2008; Buchsbaum et al., 2011).

Emerging perspectives emphasize the interplay bwtween motor and perceptual processes in speech production, yet the boundaries between motor-specific functions and integrative cognitive control remain understudied. The Hierarchical State Feedback Control (HSFC) model (Hickok, 2012) provides a framework for motor speech control, where primary motor cortex (M1) and BA44 manage phoneme and syllable programs, integrating sensory feedback to ensure articulatory precision. This model highlights the hierarchical organization linking motor execution with higher-order planning. Building upon this, the somato-cognitive action network (SCAN) further expands the HSFC by incorporating sensory feedback into multi-effector motor planning and linking motor actions to cognitive goals, playing a pivotal role in aligning localized motor processes with broader cognitive demands (Gordon et al., 2023). On the other hand, previous studies have shown that during speech perception and comprehension, the Multiple Demand (MD) system, as a domain-general network, facilitates high-level integration between language production and cognitive demands such as working memory, executive control, and task switching (Fedorenko et al., 2011a; 2013; Silbert et al., 2014). Neuroimaging studies support this framework, showing coactivation of traditional language regions (Broca′s area, Wernicke′s area, inferior parietal and angular gyrus) with non-typical brain regions (e.g., precentral and middle frontal gyri) during language production tasks (Crosson, 2013; Hebb and Ojemann, 2013; Price, 2012). While evidence indicates the involvement of a broader networks in language production—where SCAN supports localized integration between motor and cognitive systems, and MD facilitates cross-domain

compared with a control condition. (2) Participants were healthy adults, and studies of patients or aging populations were excluded. (3) Using wholeY)

preparation and control. (2) Articulation tasks activate both control and motor execution areas. (3) The conjunction of these tasks reveals areas that are active in both conditions, which we hypothesize to be crucial for speech control but not motor execution. By using this conjunction, we can identify regions that are involved in speech control processes regardless of whether overt articulation occurs. This allows us to distinguish the speech control system from the pure motor system, as the latter would not be strongly activated during covert reading. We used conjunction analysis to reveal the coactivated regions between articulation and reading covert tasks, and define these as the speech control system.

(3) Domain general system (WG ∩ SR ∩ WM)

To extract the domain-general system that serves non-specific or general cognitive functions such as memory from tasks, we used conjunction analysis to reveal the co-activation brain regions shared by word generation, syntax discrimination, and n-back tasks. Our use of n-back tasks is based on studies that have employed this paradigm to investigate domain-general cognitive processes in language contexts (e.g., Fedorenko et al., 2013; Chein et al., 2011). While this approach may not capture all aspects of domain-general cognition involved in language, it focuses on processes crucial for language processing, particularly cognitive control. Recent meta-analyses (e.g., Bulut, 2023) further support the validity of using n-back tasks to identify domain-general systems involved in language processing, while also highlighting the complex interactions between domain-specific and domain-general networks.

(4) High-level language system (WG ∩ SR - WM)

Syntax and semantics are the key components of human language; the rearrangement of the words in sequences can produce multiple complex meanings(Fitch and Hauser, 2004). Unlike simple articulation task, higher-level language tasks (such as syntax or semantics) are likely to recruit language-specific areas in the dominant hemisphere, and damage to these areas can result in semantic or phonological anomiR

Table 2

Summary of studies selected for the meta-analysis.

Category / Included paper	Imaging method	N	Foci	Task and contrast
Articulation				
Lotze et al. (2000)	fMRI	17	8	/Pa/ vs. Rest
Braun et al. (1997)	PET	20	10	Orolaryngeal Motor - Rest, Controls
Bookheimer et al. (2000)	PET	8	20	Phoneme vs. Rest
Heim et al. (2002b)	fMRI	12	5	BASE - NULL, Activations
Riecker et al. (2000a)	fMRI	18	6	Overt Speech vs. Rest
Sörös et al. (2006)	fMRI	9	28	Vowel Sound vs. Rest
Wilson et al. (2004)	fMRI	10	6	Producing Speech
Kemeny et al. (2005)	fMRI	6	6	Syllable Generation vs. Rest, ASSIST
Bohland and Guenther. (2006)	fMRI	13	41	Simple Syllable, Go vs. Fixation
Riecker et al. (2000b)	fMRI	10	6	"Ta" Repetition vs. Rest
Brown et al. (2008)	fMRI	16	28	Phonation > Fixation
Grabski et al. (2012)	fMRI	13	26	Vowel Vocalization - Rest
Luc et al. (2008)	fMRI	15	8	Repeat minus Baseline, Healthy Controls
Brendel et al. (2010)	fMRI	16	23	Motor prepareness (NCT>BL)
Loucks et al. (2007)	fMRI	12	8	Vocalization > Rest
Pinto et al. (2004)	PET	10	7	?

(Fig. 2A and Table 4).

3.2.2. Contrast: motor and perception system

Results of contrast analysis (reading overt and reading covert) showed significant co-activations in the bilateral superior temporal gyrus, bilateral declive, left precentral gyrus, and left lingual gyrus. (Fig. 2B and Table 4).

3.2.3. Conjunction: speech control system

The conjunction analysis revealed co-activations in the left precentral gyrus and left IFG for both articulation and reading tasks. (Fig. 2C and Table 5).

3.2.4. Conjunction: domain-general system

The conjunction analysis among word genR   .   vyvinO

gyrus (BA32), right lentiform nucleus, and left superior frontal gyrus (BA6) were more activation peaks for processing of word generation (Fig. 1D and Table 3).

3.1.5. Syntax discrimination

For the process of syntax discrimination, 108 contrasts with 611 foci. The results revealed significant convergence of peaks at the left IFG (BA39), left superior temporal gyrus (BA22), left inferior parietal lobule (BA39), left medial frontal gyrus (BA6), right insula (BA13), and right precentral gyrus (BA6) (Fig. 1E and Table 3).

3.1.6. N-Back

For the process of n-back, 136 contrasts with 1152 foci. The results revealed more activation peaks at the right precuneus (BA7), bilateral middle frontal gyrus (BA6), and left insula (BA13) (Fig. 1F and Table 3).

3.2. Conjunction and contrast analyses

3.2.1. Contrast: high-level language system

Results of contrast analysis (word generation and syntax > n-back) showed significant differences in the left IFG, left cingulate, left middle temporal gyrus, left precentral gyrus, and left superior frontal gyrus

Table 3

Result from ALE analysis of language task, including articulation, reading overt, reading covert, word generation, syntax discrimination and N-back categories.

	Cluster size (mm3)	Side	Location	BA	MNI coordinates			ALE max values
					x	y	z	
Articulation								
	22,432	L	Superior					

systems, while shared language comprehension-related terms with high-level language system. The domain-general, speech-control, and high-level language systems converge on language-related terms, including semantic, language, words, reading, phonological, and verbal. The speech-control and motor systems converge on sound, pitch, and music terms. It is worth noting that neither the high-level language nor the domain-general system shared cognitive terms with the motor and perception system independently; terms related to speech-production were mostly overlapped with the speech-control system.

4. Discussion

In this study, we employed a series of meta-analytic approaches using a wide range of language-related tasks based on the model proposed by Fedorenko (2014) and spatially mapped the four cognitive components supporting language processing, including high-level language, motor and perception, domain-general, and speech-control networks. Unlike previous studies that primarily relied on task-specific fMRI, our meta-analytic approach integrates co-activation patterns across a diverse range of tasks, providing a finer-grained view of the language network's components. Our findings both support and extend the framework proposed by Fedorenko and Thompson-Schill (2014), addressing critical gaps in the hierarchical organization of language production networks. We found convergence in the identification of

high-level language regions, recognition of domain-general involvement, and inclusion of motor and perception components. Our study extends their model by distinguishing a separate speech control system and providing empirical evidence for interactions among these systems through ALE and MACM analyses. These extensions align with hierarchical state feedback control model, emphasizing sensorimotor integration in language processing (Hickok, 2012). Using MACM, we identified the potential intermediate role of the speech control network between domain-general, high-level language, and speech motor/perception functions. The MACM findings support the hierarchical organization of the language networks and the possible existence of a "key" region regulating the recruitment of neural resources during language task processing. The broad ALE cluster and potential anatomical overlap reflect the distributed nature of brain function, aligning with contemporary views of brain function as a dynamic system.

We defined the high-level language network as the conjunction of word generation and syntax discrimination while excluding brain regions involved in working memory. Classical language-specific brain regions were observed as expected, including the left IFG, left cingulate, left middle temporal gyrus, left precentral gyrus (dorsal part), and left superior frontal gyrus. These lateralized functional regions were also reported in the work by Friederici (2011) and are well known to be critical for phonology, semantics, and other language-selective functions (Fitch and Hauser, 2004; Friederici, 2002; 2011; Price, 2012). The
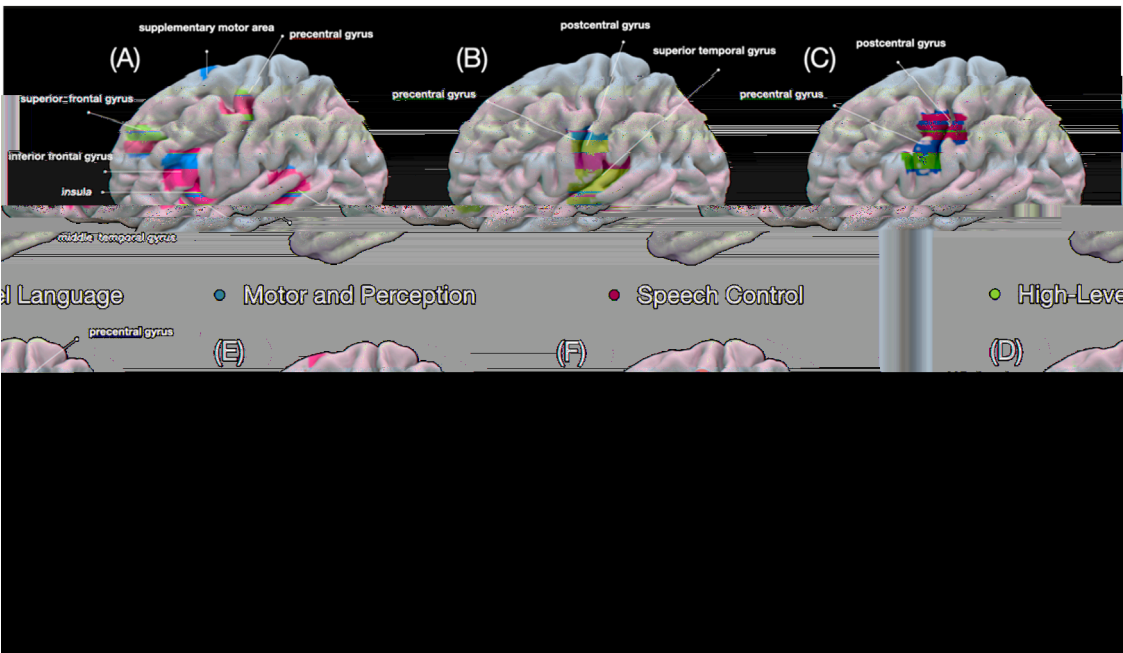
Fig. 2. The overview of four language-related region from meta-analysis. The contrast activation including (A) high-level language and (B) motor and perception. (A) High-Level language presents more activation for word generation and syntax discrimination > n-back. (B) Motor and perception shows greater activation for reading overt > reading covert; The conjunction activation includes (D) domain-general and (C) speech control. (D) Domain general presents the conjunctions activations in both word generation, syntax discrimination, and n-back. The (C) Speech control presents co-activations between articulation and reading covert. ($P < 0.01$ using 5000 permutations and minimum volume 200 mm³). (E) The four systems are merged into one for comparison with (F) systems proposed by Fedorenko and Thompson-Schill (2014).

Table 4
Result from ALE analysis (contrast analysis) of high-level language and motor perception.

Cluster size (mm3)	Side	Location	BA	MNI coordinates			Z-Score
				x	y	z	
High-Level Language (Conjunction of word generation and syntax > n-back)							
3944	L	Inferior Frontal Gyrus	44	-46	25	13	3.23
2992	L	Middle Cingulum Gyrus	24	-3	9	35	3.15
2152	L	Middle Temporal Gyrus	22	-54	-37	6	3.54
840	L	Dorsal Precentral Gyrus	4	-44	-8	52	2.70
712	L	Superior Frontal Gyrus	9	-26	50	30	3.15
614	L	Medial Superior Frontal Gyrus	6	-4	0	54	1.28
537	L	Insula	13	-39	13	6	3.52
Motor and Perception (Reading overt > reading covert)							
4952	R	Superior Temporal Gyrus	41	56	-22	9	2.76
4896	L	Superior Temporal Gyrus	41	-48	-21	6	3.81
3624	L	Postcentral Gyrus	6	-51	-10	26	3.54
2888	R	Cerebellum 6	[a]	10	-64	-16	3.23
2280	L	Cerebellum 6	[a]	-18	-61	-17	3.71
752	L	Lingual Gyrus	18	-22	-85	-6	2.28
344	R	Vermis 4,5	[a]	29	-58	-12	2.17
324	R	Insula	13	49	-9	2	2.09

Notes: $p < 0.05$ (FDR corrected), minimum cluster volume of 200 mm³. BA: Broadmann area; Side represent the location of left (L) or right(R) hemisphere.
[a] there is no correspondimg Brodmann area.

Table 5
Result from ALE analysis (conjunction analysis) of domain general and speech control.

Cluster size (mm³)	Side	Location	BA	MNI coordinates			ALE Max values
				x	y	z	
Domain General (Conjunction of high-level language and n-back)							
10,456	L	Inferior Frontal Gyrus	45	-39	29	22	0.0171
6201	L	Dorsal Precentral Gyrus	6	-43	13	23	0.0259
4232	L	Supplementary Motor Area	6	-0.9	11	47	0.0218
1800	L	Insula	48	-33	19	3	0.0332
Speech Control (Conjunction of articulation and reading overt)							
1440	L	Postcentral Gyrus	4	-49	-13	41	0.0162
864	L	Ventral Precentral Gyrus	6	-51	2	23	0.0142

Notes: $p < 0.05$ (FDR corrected), minimum cluster volume of 200 mm³. BA: Broadmann area; Side represent the location of left (L) or right(R) hemisphere. [a] there is no correspondimg Brodmann area.

identified brain regions that are involved in language-related motor/-perception system mostly align with previous evidence, including the left postcentral gyrus, left Rolandic operculum, bilateral superior temporal gyrus, bilateral declive in the cerebellum, right insula, and left lingual gyrus. Co-activations in the Rolandic operculum and postcentral gyrus during tongue and mouth movement have been reported in previous studies (Heim et al., 2002a; Herbster et al., 1997), and bilateral superior temporal gyrus activated was found to be evoked during overt reading (Cheung et al., 2016). Our findings also support the notion of left-lateralized articulation function, as demonstrated by the contrast map between reading covert and reading overt (Keller and Kell, 2016).

Notably, shared activation in the left anterior part of the ventral precentral gyrus (vPCG; or ventral premotor cortex, vPMC) was found
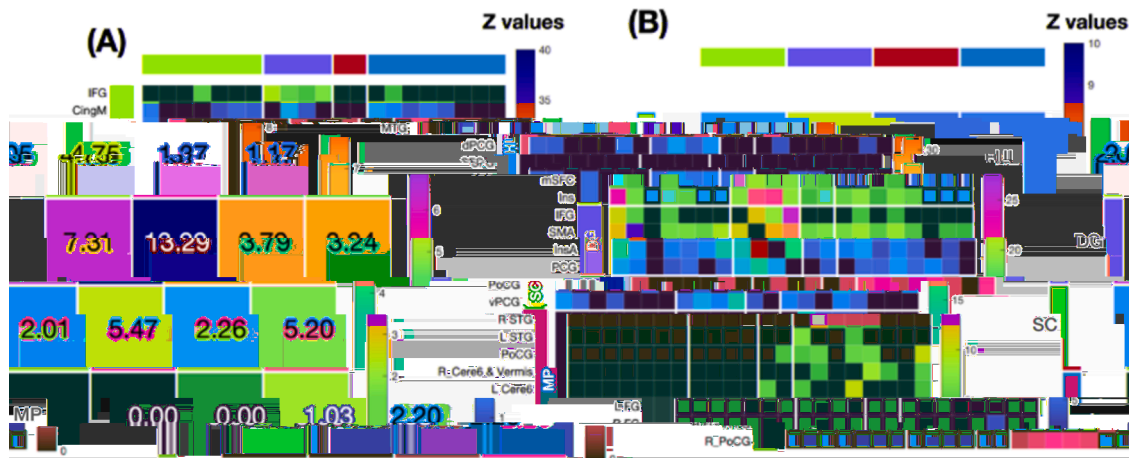
Fig. 3. Seed-to-whole brain meta-analytic connectivity modelling (MACM). (A) MACM connectivity matrix. ($P < 0.001$ corrected for multiple comparisons). (B) MACM connectivity matrix of the four domains with a threshold of z values > 3.48 (Gifuni et al., 2017). IFG, inferior frontal gyrus; MCG, middle cingulum gyrus; MTG, middle temporal gyrus; dPreCG, dorsal precentral gyrus; vPreCG, ventral precentral gyrus; SFG, superior frontal gyrus; mSFG, medial superior frontal gyrus; IN, insula; SMA, suplementary motor area; PostCG, postcentral gyrus; TPOsup, superior temporal gyrus;CER6, cerebellum 6; LING, lingual gyrus; VER45, vermis 4,5; L, left; R, right; HL,High-level language system; Dom, Domain general system; SC, Speech control system; Mp, Motor and perception system.
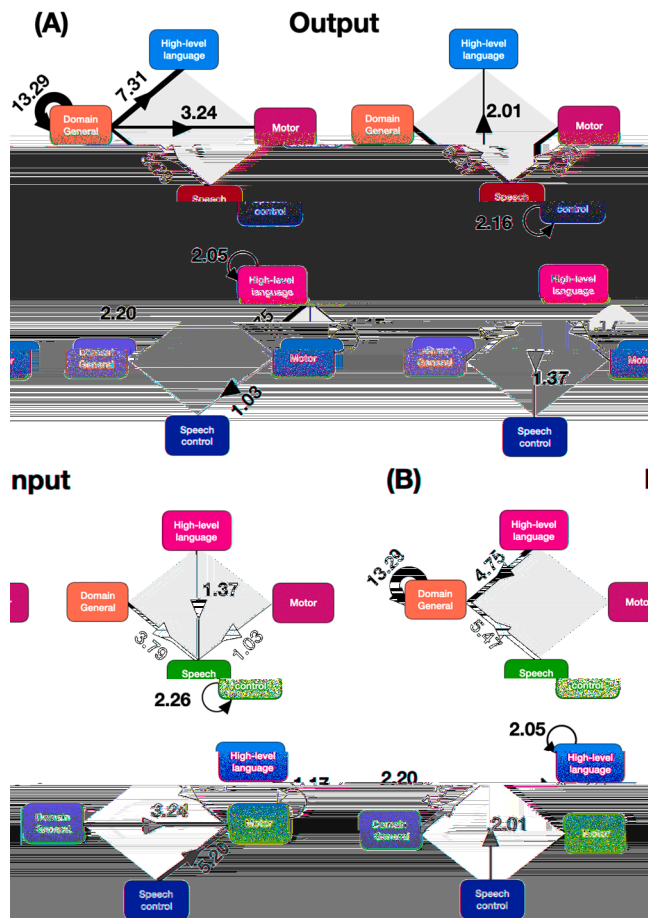
Fig. 4. Meta-Analytic Connectivity Modeling (MACM) Analysis. Fig. 4 illustrates the co-activations among the four systems using MACM. Output connections show co-activation in other regions when a specific region is activated, while input connections show co-activation in a specific region when other regions are activated. The figure highlights significant connections between the domain-general, speech-control, and motor and perception systems.

not only in simple articulation but also in both overt and covert reading tasks. This finding supports the speech sound map proposed in the Directions Into Velocities of Articulators (DIVA) model, which explains how the brain produces speech sounds and controls various speech articulators during actual speech production. Importantly, our study expands upon this by demonstrating the speech control system's integrative role beyond simple articulation, linking it with higher-level cognitive functions and domain-general networks. This evidence emphasizes the distinctiveness of the ventral precentral gyrus (vPCG) in coordinating hierarchical processes of language production, highlighting its unique role as a functional nexus between linguistic and motor domains, which was previously underexplored in theoretical models (Guenther and Hickok, 2016; Hickok and Poeppel, 2007; Kearney and Guenther, 2019). It is worth noting that, in this study, we deliberately isolated the motor component from the broader speech control network to clarify the distinct roles played by higher-order integrative functions beyond motor execution. This approach prevents conflating motor execution with higher-order processes, such as goal-oriented planning, error monitoring, and linguistic coordination, which are essential for understanding the broader integrative functions of the speech control network. Building on the framework proposed by Gordon et al. (2023) our findings offer further evidence for a functional distinction between effector-specific motor regions and the somato-cognitive action network (SCAN). By isolating motor processes, our MACM analysis revealed that regions within the speech control network are not only connected to motor areas but also to domain-general cognitive systems and high-level language regions. This supports the SCAN model's premise that the speech control network functions as an integrative hub bridging linguistic, cognitive, and motor domains, supporting both task-specific and domain-general coordination. Furthermore, our results underscore the importance of disentangling these components to better understand how distinct processes—such as motor execution and cognitive control—interact dynamically within the speech production network. While this study emphasizes the control and coordination aspects of the speech network, it also highlights the indispensable role of motor execution as part of the broader integrative framework.

From the perspective of speech production, recent studies have suggested that the damage to vPMC may result in complete and long-standing speech arrest, but no such effect was observed with damage to Broca's area (Gajardo-Vidal et al., 2021). This distinction highlights the unique role of vPMC in speech control, separate from the motor
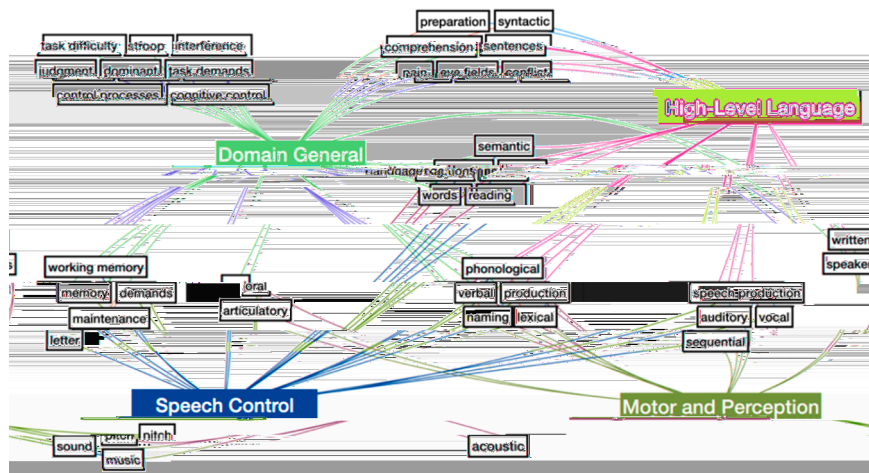
Fig. 5. Metadata characterization of functional preference in four system via Neurosynth. Word clouds were generated base on the correlation coefficient greater than 0.075 is preserved and assigned intersection between the system.

execution system. Empirical evidence from both lesion and tumor studies has linked speech motor programming disorders to damage in the left vPMC, rather than to pure phonation and laryngeal control dysfunction typically associated with motor system damage (Hillis et al., 2004; Robin et al., 2008; Zhao et al., 2023). Additionally, a recent study employing direct electrical stimulation on the vPMC and somatosensory cortex demonstrated distinct outcomes, revealing that motor arrest without awareness occurred exclusively during left vPMC stimulation (Fornia et al., 2020). These findings suggest that the vPMC is engaged in higher-level speech control processes rather than merely motor execution. In our recent study, we compared the cortical projection of dorsal language pathways with the positive sites identified by direct cortical stimulation. We found that the speech arrest sites overlapped significantly with the termination of the arcuate fasciculus and superior longitudinal fasciculus converging at the vPMC, instead of Broca's area in IFG (Zhao et al., 2023). The above evidence suggests that the left vPMC plays a critical role in the implicit aspect of motor awareness and planning, distinct from the explicit motor execution system. Thus, we define it as a speech control system, emphasizing its distinctiveness from pure articulatory movement. This conceptualization aligns with our methodological approach of using coactivation in both articulation and covert reading tasks, which allows us to isolate regions involved in speech control processes regardless of overt motor execution.

Another issue to consider is whether the speech control system is distinct from the domain-general system. Do these regions merely serve as extraneous neural resources recruited due to task demands, or is the multiple-demand network intrinsically capable of supporting core operations in language production? Recent work by Diachek et al. (2020b) has demonstrated that the brain regions of domain-general multiple demand network respond exclusively to language comprehension. Their results suggest that the domain-general system is engaged more in extraneous task demands rather than the core aspects of language comprehension, thus ruling it out as a central component of speech output. On the other hand, research by Wright et al. (2011) utilized a passive listening paradigm and a covert experimental design to demonstrate that the left IFG plays a key role in the neural language system during lexical decision task and in response to complex words, even without making an overt response. Our own research builds upon these findings, revealing that the speech control system operates as a latent core mechanism supporting the language production network. In contrast, the domain-general system recruits different brain regions primarily mediated by working memory resources when faced with varying levels of task difficulty (Chein et al., 2011; Fedorenko et al., 2012). Taken together, these findings suggest that while the domain-general system may be involved in managing the cognitive and

executive demands associated with language production, it likely does not serve as the central region for this function. Instead, regions like the left IFG appear to support the core aspects of language processing even during covert tasks. Therefore, we propose that dissociating the speech control system from both the domain-general system and the core language regions may fill the gap in our understanding between language and speech production.

By conjoining the meta-analysis findings across word generation, syntax discrimination, and working memory, we found that the domain-general network is left-lateralized and mainly lies in the left pars opercularis (BA44), middle frontal cortex, and anterior supplementary motor area (SMA), aligning with previous theories (Fedorenko and Thompson-Schill, 2014). Our use of the n-back task to define the domain-general system is grounded in its established utility for capturing verbal working memory processes, which are tightly integrated with language production and comprehension(Fedorenko et al., 2013). The n-back task effectively engages regions like BA44, which exhibit overlapping activation patterns for verbal working memory and linguistic tasks, making it particularly suitable for exploring the interaction between domain-general and language-specific systems. While we acknowledge that the n-back paradigm does not encompass all domain-general cognitive functions, such as attentional control or task switching, it provides a robust framework for investigating the interaction between domain-general and language-specific systems, particularly in tasks requiring the maintenance and manipulation of linguistic information. This choice aligns with the findings of Campbell and Tyler (2018),which suggest that task paradigms can introduce extraneous cognitive demands, leading to the engagement of domain-general systems even in language-specific tasks. Although our approach has considered this issue, by defining the high-level language system as the intersection of word generation and syntax discrimination while subtracting working memory activations, it may still oversimplify the nuanced interplay between language-specific and domain-general processes. Future research could address this limitation by incorporating additional tasks that engage broader domain-general functions, such as passive comprehension or attentional modulation paradigms, to capture the dynamic interactions across different stages of language processing. This integration could further refine our understanding of how domain-general networks support linguistic functions without reducing their role to task-specific demands.

Despite these limitations, our findings showed consistent left-lateralized coactivations in classical language regions for the high-level language network. Notably, our results support the posterior localization of language-related SMA activity (Hiroshima et al., 2014), with higher-order cognitive control involved anteriorly (Hertrich et al.,

2016). Synthesizing these findings, we postulate that the domain-general network is spatially distinct from both the high-level language and speech control networks(Fedorenko et al., 2012). The speech control system defined here appears to be different from the domain-general system and might occupy an intermediate position in both anatomical and functional hierarchies among the domain-general, high-level language, and motor control systems. Future studies should investigate these dynamic interactions across various linguistic contexts and processing stages, potentially refining current models of language processing in

coordination during the production process. While our study identified four main systems within the language network, we acknowledge that this classification is not definitive. The number and nature of these systems could potentially vary with different analytical approaches or levels of granularity. Future studies might explore alternative classifications or finer subdivisions within these systems. Our approach provides a framework based on current theoretical understanding, which can be further refined in future research.

Data and code availability

All data for meta-analysis are available at the BrainMap (https://www.brainmap.org/sleuth/) and NeuroSynth (https://neurosynth.org) websites. Code for the meta-analysis and plotting are available from the corresponding author via email on reasonable request.

CRediT authorship contribution statement

Chun-Wei Hsu: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation. **Chu-Chung Huang:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Conceptualization. **Chih-Chin Heather Hsu:** Methodology, Formal analysis, Data curation. **Yanchao Bi:** Writing – review & editing. **Ovid Jyh-Lang Tzeng:** Supervision, Conceptualization. **Ching-Po Lin:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Data availability

Data will be made available on request.

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