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

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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; Friederici, 2011; Skeide and Friederici, 2016). In contrast, the motor control aspect focuses on kinematic forces and feedback control involved in speech production (Guenther and Hickok, 2016; Kearney and Guenther, 2019). Although these two aspects have generally been studied separately, recent research has argued for a large hierarchical network architecture encompassing both concepts to support complex human language functions (Hickok, 2012). Nevertheless, the

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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 coordination—it suggests the necessity to extend the current understanding of the language network and incorporate the roles of other systems that orchestrate different brain regions.

Fedorenko and Thompson-Schill (2014) proposed a language network model that disassociated the core language system from the hierarchical course of language production processing (Friederici, 2011). The model divided the language network into five key components: the "high-level" language, speech perception, visual word form area (vWFA), articulation, and cognitive control regions. The cognitive control regions, synonymous with the MD network or domain-general system, play a crucial role in coordinating cognitive control and working memory processes in language production, as well as in non-language goal-directed behaviors (Fedorenko et al., 2011a; 2012; 2013; Fedorenko and Thompson-Schill, 2014). Recent research has emphasized the complexity of the language network, particularly the role of cognitive control in integrating motor-perceptual processes and feedback control in speech production. Hierarchical State Feedback Control model supports this concept, highlighting the intricate connection between motor and perceptual processes in language processing and underscoring the importance of integrating motor planning, execution, and corresponding perceptual feedback (Hickok, 2012). This perspective suggests a refinement of the general cognitive control system to include not only the domain-general system responsible for broader cognitive functions but also a specialized speech control system dedicated to motor-level control and modulation in language production. Recently, Diachek et al. (2020a) found that the MD network can be dissociated from language comprehension and may serve as a regulator between language-specific and cognitive control functions. However, the identification of participating networks and core operations in language production remains debated. Integrating motor-perceptual processes and speech-specific control mechanisms is crucial for a more comprehensive understanding of the neural architecture supporting both language comprehension and production.

Given the hierarchical nature of the network system and the substantial overlap of functions across high-level brain regions, decomposing complex language networks into components at different levels during the dynamic language production process is highly challenging and may require a large-scale investigation using a wide range of task fMRI combinations. In this regard, the meta-analytic framework offers promising opportunities to uncover the network patterns across diverse tasks. Vigneau et al. (2006) used meta-analysis to review findings reported in language studies across the previous 13 years, reinforcing and refining our understanding of the left-brain hierarchical language process of phonology, semantics, and sentence, as well as suggesting a crossroad region that overlaps phonological and semantic functional area. Price (2012) integrated the research of the previous 20 years and further subdivided language processing into seven processing levels: auditory processing of speech and nonspeech sounds, speech selective auditory processing, speech comprehension, word retrieval, speech production, covert and overt planning, auditory-motor feedback and visual word processing. Nevertheless, the conclusions made in these previous meta-analysis studies relied heavily on manual review, which could be limited by research focus, potential biases in study selection, or a lack of proper statistical inference, thus hindering the comprehensive exploration of language networks and their integration with domain-general cognitive systems (Kohn et al., 2014; Price, 2012; Vigneau et al., 2006). The recent large-scale meta-analysis databases, such as BrainMap and NeuroSynth, allow us to overcome these limitations. Using automatic methods to collate fMRI studies from the literature, a much larger number of studies can be included, allowing for proper statistical testing. Such large datasets also enable a fully data-driven approach, offering the potential to uncover patterns beyond specific hypotheses and addressing the underexplored relationship between language production and cognitive control networks. The activation-likelihood estimation (ALE) method can be used not only to contrast between different paradigms to distinguish functional processes (Cieslik et al., 2013; Laird et al., 2009), but also to apply a meta-analytic connectivity modeling (MACM) approach to examine the brain-wide co-activation pattern of a given brain region across a set of functional tasks. This dual-method approach ensures that specific task-driven activations can be systematically linked to broader network interactions, offering a novel framework to disentangle the relationship between hierarchical networks of language production (Kohn et al., 2014; Molenberghs et al., 2016; Ran et al., 2018).

In this study, we aim to refine the model of language network through meta-analytic approaches. Building upon Fedorenko and Thompson-Schill (2014) framework, which encompasses both perception and production aspects of language processing, we analyze studies that address diverse language processing levels. By utilizing the ALE and MACM algorithms in BrainMap, we study the hierarchical relationships among these subcomponents, capturing both language production and perception processes. This approach allows us to explore aspects of the language network that might be underrepresented in purely perception-focused studies. Additionally, we use the NeuroSynth meta-analysis to explore the interplay between language-related cognition and different neural networks. Our study aims to deepen the understanding of the neurological model of language production and its interaction with cognitive control, highlighting the interconnectedness between different subcomponents across both production and comprehension processes.

2. Methods

2.1. Literature selection

Literature research was conducted through the BrainMap database using Sleuth (Version 2.4, http://www.brainmap.org/sleuth/) to identify articles containing the terms "Language" in the behavioral domain and satisfying the following search criteria: "activation only", "Imaging", and "Not disease or Not aging (context)". As of June 2024, 972 articles were identified, and the presented meta-analysis consisted of 132 studies. The following four major criteria were used for further screening: (1) Reporting an activation during language processing compared with a control condition. (2) Participants were healthy adults, and studies on patients or aging populations were excluded. (3) Using whole-brain imaging scanning or reporting complete coordinates of the activation in standardized anatomical space, thereby excluding articles using a region-of-interest (ROI). Those studies' coordinates published in Talairach space were converted to MNI space using the algorithm implemented in GingerALE 3.0.2 (Eickhoff et al., 2012). (4) Participants' native language was English (to minimize variability associated with different languages). This decision to focus on English speakers was based on two key methodological considerations. First, our primary aim was to refine existing models of language processing, not to investigate cross-linguistic differences. Focusing on a single language allowed us to control for linguistic variables, ensuring a more homogeneous dataset for analysis. Second, English-language studies provided the largest available sample size in the neuroimaging literature, enhancing the statistical power and reliability of our meta-analysis. In addition, to minimize the confounding effect of gender difference in the included literature, any study using only female or male participants was excluded.

The concept of the current meta-analysis was based on the model proposed by Fedorenko and Thompson-Schill (2014), which parcellate the language network into four systems: high-level language regions, speech perception regions, articulation regions, and cognitive control regions. To test this model, we categorized the identified literature into the following five task groups for the meta-analysis: (1) reading overt (RO); (2) reading covert (RC); (3) word generation (WG); (4) syntax reading (SR); 5) articulation (tasks repeating non-word sounds) (Table 1). In addition, literatures using n-back task were also included to reveal the brain regions involved in general working memory (WM). It's important to note that while we started with this four-system framework, our analysis was not constrained to this number. The identification of these four systems (high-level language, motor and perception, domain-general, and speech control) as distinct functional components emerged from our meta-analytic results, aligning with theoretical predictions.

2.2. Activation-likelihood estimation (ALE) analysis

The meta-analyses were performed using the revised algorithm of the activation likelihood estimation (ALE) approach, which is a coordinate-based meta-analysis method provided in BrainMap (https://www.brainmap.org/) (Turkeltaub et al., 2002). This method identifies areas with a convergence of foci reported from different neuroimaging studies and uses a random-effects analysis to form co-activation clusters across studies. The foci reported in the studies are treated as three-dimensional Gaussian probability distributions which take into account spatial uncertainly (Eickhoff et al., 2009). Furthermore, the width of probability distributions (i.e., full-width half-maximum, FWHM) estimate the spatial uncertainly between-subject variances. An ALE map is calculated by combining the modeled activation (MA) map, and the ALE scores are computed voxel-by-voxel, representing significantly activated peaks.

In the present study, we use a cluster-level family-wise error (FWE) correction at $P < 0.05$ with a cluster-defining threshold of $P < 0.005$ (cluster-forming threshold at voxel level) and 5000 permutations to threshold for significant findings. Furthermore, conjunction analysis and subtraction analysis were conducted to dissociate the differences between language network components. Conjunction analysis was performed to identify common language processing while subtraction analysis was used to identify different language processing ($P < 0.05$, 5000 permutations, cluster extend > 200 voxels).

2.3. Contrast and conjunction analyses

In our study, we aimed to explore the similarities and differences in brain activations among language tasks. To examine brain regions that are consistently reported in different language tasks, we utilized conjunction analyses to identify areas of overlap between two corrected ALE results. To further investigate differences between language tasks, we performed contrast analyses by computing cluster-wise differences between separate ALE maps for each task. Additionally, we conducted permutation tests to compare ALE values for any two randomly assembled groups, which allowed us to obtain a null distribution of differences in ALE values between two tasks. By repeating this process 1000 times, we were able to obtain a robust and reliable estimate of the null distribution. We then tested the true difference in the ALE values against the voxel-wise null distribution of label-exchangeability, setting a threshold at a probability greater than >95 % for true differences, to ensure that any differences we observed were statistically significant and unlikely to have occurred by chance.

To dissociate the language network components involved in studies that may include more than two language processing components, we applied contrast and conjunction analyses based on the functional components shown in (Table 1). The framework is as follows:

(1) Motor and perception system (RO - RC)

The integration of motor and sensory systems into a single component is based on Hickok's (2012) Hierarchical State Feedback Control (HSFC) model, which emphasizes the intricate interplay between auditory and somatosensory feedback and motor output in speech production. Current speech production paradigms make it challenging to completely separate motor and sensory processes due to the inherent auditory feedback in speech production.Given that the only difference in involved functional components between reading overt and reading covert tasks is motor and perception. Contrast analysis was conducted to isolate the motor and perception system, which should reflect activation during articulation but are less likely to be contaminated by speech compared to a simple articulation task. This contrast reflects the inherent overlap of perception and production in speech processes.

(2) Speech control system (Articulation ∩ RC)

To isolate the speech control system from the motor system, we utilized the coactivation of reading covert and articulation tasks. This approach is based on the following rationale: (1) Reading covert engages speech planning and control mechanisms without overt motor execution, thus activating regions involved in speech

Table 1
The contrast table of language components. This table demonstrates the definition of contrast examined in this study, and the involved functional components during the processes of language production (marked with symbol V) based on the model proposed by Fedorenko and Thompson-Schill (2014).

	Task - Control (Contrast)		Involved Functional Component			
			High-level language	Cognitive control	Articulatory motor	perception
1	Articulation	Resting		V	V	Sound
2	Reading Overt (RO)	Resting	V	V	V	Visual and sound
3	Reading Covert (RC)	Resting	V	V		visual
4	Word Generation (WG)	Word Reading	V			
5	Syntax Reading (SR)	Non-Syntax Reading	V			
6	Working Memory(WM)	Non-working memory		V		

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 anomia (Ralph et al., 2002). Given that high-demand sentence comprehension tasks may engage more extensive brain regions more strongly involving working memory, we defined the conjunction region between high-level language (syntax and semantics) and working memory tasks (n-back) as the domain-general and the contrast region as the high-level language system. This definition aligns with psycholinguistic models distinguishing lexical-semantic and syntactic processing.

2.4. Task-based connectivity: meta-analytic connectivity modeling analysis

Meta-analytic connectivity modeling (MACM) was conducted to examine the co-activation patterns of the motor and perception, speech control, domain-general, and high-level language systems using a connectivity approach. Significant clusters obtained from contrast and conjunction analyses were used as regions of interest (ROIs) to search for coactivated regions across studies in the BrainMap database. This study utilized entire activation patterns as ROIs, rather than solely peak coordinates. This approach captures broader functional associations, reflecting the integrated nature of brain function. While this may result in some overlap between networks, it allows for examination of functional integration between regions, which is critical for understanding complex cognitive processes such as language. Only whole-brain neuroimaging analytic approaches were included in this analysis, and ROI-based studies were excluded to avoid selection bias. Coordinates of studies reporting functional co-activation were processed using GingerALE 2.3.6, with a family-wise error (FWE) corrected threshold of $P < 0.05$ and 5000 permutations, and a minimum cluster volume of 200 mm^3. Z-scores were derived for each ROI and reported in an ROI-to-projection table of Z values [32]. An ROI-to-projection coefficient, or edge, is the Z value obtained from the centroid voxel of the ROI. If reciprocal significance was present, the co-directionality of edges was determined. It is important to note that while ALE and MACM analyses use different sets of studies, this approach is intentional and reflects the complementary nature of these methods. ALE identifies consistently activated regions under specific conditions, while MACM explores their co-activation patterns across a broader range of tasks. This strategy allows us to first identify key language-related regions and then explore their role within broader brain functional networks, enhancing the reliability and generalizability of our results.

2.5. Decoding analysis using Neurosynth database

We utilized Neurosynth as a complementary analysis to provide additional context for the cognitive involvement of the four systems identified within BrainMap and Neurosynth repositories. To identify the involved cognition of the co-activation regions found in the meta-analytic maps using BrainMap database, we uploaded the calculated contrast and conjunction maps in MNI standard space to the Neurosynth image decoder (https://neurosynth.org/decode/) to quantitatively compare the similarity between the obtained brain regions of each language component with the coactivation maps of each term in the Neurosynth (de la Vega et al., 2016; Wang et al., 2020). Any term showing a correlation coefficient greater than 0.075 was preserved and assigned to each of the corresponding language components (Váša et al., 2020). The intersection between the terms assigned to the components was visualized using a connectivity manner approach. To focus our analysis and address potential limitations, we removed brain anatomy-related terms, eliminated non-informative terms (e.g., numbers, generic words), and retained cognition-related terms not limited to language. This approach aimed to capture broader functional characteristics of the identified systems.

3. Result

3.1. ALE analysis: language-related tasks

The meta-analysis of all studies involving language processing consisted of six ALE analyses: articulation, reading overt, reading covert, word generation, syntax discrimination, and n-back tasks. The results are reported in Table 2 and Fig. 1.

3.1.1. Articulation

For the process of articulation, 21 contrasts with 350 foci. The results revealed more activation peaks at the left superior temporal gyrus (BA41), Left precentral Gyrus (BA6), left medial frontal gyrus (BA6), bilateral culmen, bilateral lentiform Nucleus, and bilateral thalamus (Fig. 1A and Table 3).

3.1.2. Reading overt

For the process of reading overt, 20 contrasts with 197 foci. The results revealed significant convergence of peaks at the bilateral superior temporal gyrus(BA6), bilateral inferior occipital gyrus (BA18), bilateral declive, left precentral(BA6), and left medial frontal gyrus (BA6) (Fig. 1B and Table 3).

3.1.3. Reading covert

For the process of reading covert, 16 contrasts with 88 foci. The results revealed more activation peaks at the left inferior frontal gyrus (IFG) (BA9), left precentral (BA4), and fusiform gyrus (BA37) (Fig. 1C and Table 3).

3.1.4. Word generation

For the process of word generation, 34 contrasts with 188 foci. The results showed that the left middle frontal gyrus (BA9), left cingulate

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	7	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	Speech Production - Rest, Healthy Controls
Correia et al. (2015)	fMRI	10	21	/Pa/ vs. Rest
Chiao et al. (2009)	fMRI	8	16	Pseudowords vs Rest
Seghier et al. (2008a)	fMRI	43	25	Pseudoword vs Rest
Rossell et al. (2001)	fMRI	8	8	Rest
Kiehl et al. (1999)	fMRI	6	19	Concrete vs baseline
Brown et al. (2021)	fMRI	23	5	Vocalization vs Fixation
Belyk et al. (2022)	fMRI	13	32	Imitation > Rest
Reading overt				
Fox et al. (1996)	PET	10	30	Solo vs. Rest, Activations, Controls
Tan et al. (2001)	fMRI	10	37	Regular Characters vs. Fixation
Fiez et al. (1999)	PET	11	15	Word Reading - Fixation
Jernigan et al. (1998)	PET	8	11	Word Identification > Fixation
Rumsey et al. (1997)	PET	14	14	Irregular Pronunciation - Fixation
Ingham et al. (2000)	PET	4	8	Overt Solo - Rest, Controls
De Nil et al. (2003)	PET	10	8	Oral Reading - Baseline, Controls
Tremblay and Gracco. (2006)	fMRI	12	4	Word Reading vs. Fixation
Wilson et al. (2009)	fMRI	5	8	High Frequency Regular Words vs. Rest, Normals
Kerr et al. (2004)	fMRI	14	22	Brain Activation During Read Task
Turkeltaub et al. (2002)	fMRI	32	28	Locations of Significant Maxima for fMRI Study
Dietz et al. (2005)	fMRI	16	4	All Conditions vs. Fixation
Azari et al. (2001)	PET	6	5	Religious, Recite vs. Rest: Religious Subjects
Riecker et al. (2000a)	fMRI	18	6	Overt Speech vs. Rest
Yarkoni et al. (2005)	fMRI	28	21	Word - Rest, fixation
Gonzalez Andino et al. (2005)	fMRI	20	21	Monosyllbic word
Seghier et al. (2008b)	fMRI	43	25	Read word aloud vs Fixation
Price et al. (1996)	PET	6	20	Real word vs Rest
Rumsey et al. (1997)	PET	14	14	Low frequency v.s Fixation
Ekert et al. (2021)	fMRI	59	8	Word Reading - Rest
Bitan et al. (2020)	fMRI	22	7	Word Reading vs. visual shape
Reading covert				
Mechelli et al. (2000)	fMRI	6	18	Words - Rest
Petersen et al. (1989)	PET	17	11	Passive Words, Visual - Fixation
Hagoort et al. (1999)	PET	11	7	Silent Words - Fixation
Beauregard et al. (1997)	PET	10	17	Concrete Words - Baseline
De Nil et al. (2003)	PET	10	6	Silent Reading - Baseline, Controls
Kuo et al. (2001)	fMRI	7	32	Reading - Fixation
Price et al. (1996)	PET	4	4	Reading words silently at 40 wpm - Rest
Cohen et al. (2003)	fMRI	9	11	Alphabetic Stimuli vs. Fixation

Table 2 (*continued*)

Category Included paper	Imaging method	N	Foci	Task and contrast
Petersen et al. (1989)	PET	7	6	Passive Words, Visual vs. Fixation
Meschyan and Hernandez. (2006)	fMRI	12	6	English vs. Rest
Liu et al. (2007)	fMRI	23	14	English Words > Fixation
Wang et al. (2006)	fMRI	12	6	Neutral Instructions > Rest, Adults > Children
Harrison et al. (2005)	fMRI	17	9	Covert reading word vs Fixation
Wang et al. (2013)	fMRI	21	11	Silent reading
Mechelli et al. (2000)	fMRI	6	10	Silent reading vs rest
Polk and Farah. (2002)	fMRI	8	9	Silent reading vs rest
Ozernov-Palchik et al. (2023)	fMRI	26	6	Covert reading; button press
Word Generation				
Fu et al. (2005)	fMRI	9	1	Difficult > Easy Letter Fluency, Normals
Braun et al. (1997)	PET	20	19	Relative Increases, Dysfluent Conditions, Controls
Vanlancker-Sidtis et al. (2003)	PET	9	13	Naming + Vocalization > Counting + Rest, Normals
Tranel et al. (2005)	PET	10	2	Tools, Non-Homonymous Nouns > Baseline
Kemeny et al. (2005)	fMRI	6	10	Sentence Construction vs. Syllable Generation, BOLD
Abrahams et al. (2003)	fMRI	18	2	Significant Correlation during Confrontation Naming, Task Performance
Petersen et al. (1989)	PET	7	14	Generate Verbs, Visual vs. Repeat Words, Visual
Desai et al. (2006)	fMRI	25	31	Generate Regular Verbs - Read Regular Present Tense Verbs
Petersen et al. (1988)	PET	17	8	Generate Words - Repeat Words, Visual
Saccuman et al. (2006)	fMRI	13	7	Non-Manipulable vs. Manipulable Items
Fu et al. (2005)	fMRI	11	39	Difficult Letter Fluency vs. Repetition
Shapiro et al. (2005)	PET	12	4	Morphological Processing (Production w/ Morphological Change) > Reference Task (No Morph. Change)
Haller et al. (2005)	fMRI	15	16	Sentence Generation - Word Reading
Klein et al. (1999)	PET	13	10	Verb Generation minus Word Repetition (English words)
Lurito et al. (2000)	fMRI	5	23	Generating - Repetition
Klein et al. (1995)	PET	12	11	L1 Synonym Generation - L1 Word Repeating
Frith et al. (1991)	PET	6	2	Verb Generation minus Word Repetition (English words)
Baker et al. (1997)	PET	10	10	Verbal Fluency - Repetition, Increases
Allen et al. (2006)	fMRI	10	6	Letter Fluency > Baseline, Sham Depletion
Martin et al. (1995)	PET	12	10	Action Word Generation - Object Naming
Müller et al. (1997)	PET	9	8	Generating Sentences - Sentence Repetition
Gauvin et al. (2021)	fMRI	20	4	Semantically related
Syntax discrimination				
Meyer et al. (2002)	fMRI	14	6	Syntactic Speech > Normal Speech
Vandenberghe et al. (2002)	PET	10	3	Increases Due to the Presence of Grammatical Structure
Luke et al. (2002)	fMRI	7	22	English Syntax - English Font
Heim et al. (2002a)	fMRI	12	1	GEN - NAME, Activations
Noppeney and Price. (2004)	fMRI	25	7	Reading sentence > viewing false font
Opitz and Friederici. (2007)	fMRI	24	10	Local Violation Sentences vs. Correct Sentences
Willms et al. (2011)	fMRI	16	7	Verbs > Nouns
Kroger et al. (2008)	fMRI	16	4	Level of Difficulty (Hard > Easy)

(*continued on next page*)

Table 2 (*continued*)

Category Included paper	Imaging method	N	Foci	Task and contrast
Herrmann et al. (2012)	fMRI	25	7	Univariate Analysis, grammaticality and perceptual markedness contrast
Caplan et al. (2000)	PET	11	3	Subject-Object, Center-Embedded Relative Clauses - Object-Subject, Right-Branching Relative Clauses
Grewe et al. (2005)	fMRI	16	7	on-pronominal objects contrast control sentences
Wartenburger et al. (2004)	fMRI	13	2	Main Effect of Grammaticality: Incorrect > Correct
Vandenberghe et al. (2002)	PET	10	1	Interaction Between Grammatical and Semantic Factor
Fedorenko et al. (2012)	fMRI	12	1	Syntactic information- lexical
Haller et al. (2007)	fMRI	16	10	Complex - Medium
Dogil et al. (2002)	fMRI	27	9	Complex sentence - baseline
Uddén et al. (2022)	fMRI	102	16	Sentence > word list

Notes: N: Number of participants; Foci: Number of foci

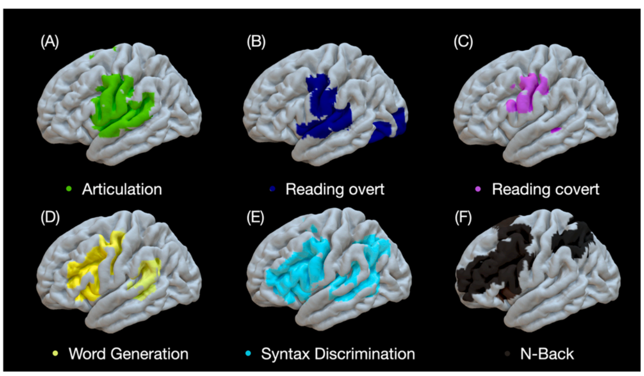

Fig. 1. Activation Likelihood Estimation (ALE) maps for six different tasks. These tasks include (A) articulation; (B) reading overt; (C) reading covert; (D) word generation; (E) syntax discrimination; (F) n-back. These maps are thresholded at a cluster-level family-wise error correction ($P < 0.05$) with a cluster-forming threshold of $P < 0.005$ using 5000 permutations. This means that the maps only show clusters of activation that are statistically significant, providing a robust overview of the brain regions involved in each task.

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 (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 pre-central 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 generation, syntax discrimination, and n-back tasks revealed co-activations in the left middle frontal gyrus, left superior frontal gyrus, and left insula (Fig. 2D and Table 5).

The four systems are merged and mapped onto the surface for visualization, shown in Fig. 2E. The systems proposed by Fedorenko and Thompson-Schill (2014) are shown in Fig. 2F.

3.3. MACM results

The MACM analysis was conducted to depict the patterns of co-activations between the identified 21 ROIs. The matrix values by columns represent output connections (the degree of co-activation in other regions when an ROI is activated), and by rows represent input connections (the degree of an ROI is co-activated when another region is activated). It is important to note that while we use terms like 'directionality' and 'causality', MACM does not provide direct temporal or causal information. Instead, these terms reflect patterns of co-activation that inform our understanding of the hierarchical organization within the language network. 'Bidirectional' connections indicate significant co-activation between two regions in both directions, while 'unidirectional' connections suggest significant co-activation in one direction only. These patterns allow us to infer the relative positioning of different components within the network hierarchy, rather than implying direct causal relationships. The matrix shown in Fig. 3A displays the statistical power of co-activated brain regions when a given region is reported across studies. The averaged results of Fig. 3A are also presented at the network level for better interpretation (Fig. 3B). For the high-level language system, it demonstrates significant output and input connections to the domain-general system (output/input $Z = 4.75/7.31$) only. For domai9n-general systems, it shows significant output connections to all three systems and input connections from the high-level language ($Z = 4.75$) and speech control systems ($Z = 5.47$), except from the motor and perception system ($Z = 0$). For the speech-control system, it has strong output connectivity to both the domain-general ($Z = 5.47$) and motor and perception system ($Z = 5.20$) while receiving input connectivity from the domain-general system only ($Z = 3.79$). The motor and perception system receives input connectivity from both domain-general ($Z = 3.24$) and speech-control systems ($Z = 5.20$). Fig. 4 illustrates the overall meta-analytic connectivity model with output and input directional based on Fig. 3B.

3.4. Corresponding cognitive function

To provide cognitive inference for the four systems identified by the meta-analytic approach in BrainMap, we utilized the Neurosynth meta-database to search for the cognition terms most likely involved in each system. We found that the acoustic term can be linked only to the motor and perception system, while the phonological, verbal, production, naming, and lexical terms are shared among the four systems (Fig. 5). The domain-general system shared non-verbal related terms, including working memory, demands, maintenance, letter with the speech-control

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 Temporal Gyrus	41	-51	-18	19	0.0382
	17,456	R	Precentral Gyrus	6	52	-5	19	0.0352
	6096	L	Medial Frontal Gyrus	6	-2	0.5	53	0.0311
	4856	R	Culmen	-[a]	26	-57	-22	0.0227
	3928	R	Lentiform Nucleus	-[a]	23	-4	5	0.0205
	3416	L	Thalamus	-[a]	-12	-17	4	0.0302
	3344	L	Culmen	-[a]	-19	-58	-23	0.0202
	3080	L	Lentiform Nucleus	-[a]	-20	-1	5	0.0192
	2112	R	Thalamus	-[a]	12	-15	4	0.0212
Reading Overt								
	14,865	R	Superior Temporal Gyrus	6	52	-20	6	0.0318
	6848	L	Superior Temporal Gyrus	41	-51	-23	6	0.0248
	6744	L	Precentral Gyrus	6	-49	-8	30	0.0484
	6336	L	Declive	37	-31	-57	-16	0.0201
	5616	R	Devlice	19	21	-61	-16	0.0222
	3336	L	Medial Frontal Gyrus	6	-1	1	51	0.0237
	3064	L	Inferior Occipital Gyrus	18	-26	-91	-5	0.0210
	1536	R	Inferior Occipital Gyrus	18	22	-87	-6	0.0227
Reading Covert								
	1856	L	Inferior Frontal Gyrus	9	-53	4	23	0.0164
	1608	L	Precentral Gyrus	4	-49	-12	41	0.0160
	1224	L	Fusiform Gyrus	37	-39	-40	-15	0.0175
Word Generation								
	12,192	L	Middle Frontal Gyrus	6	-44	17	16	0.0201
	4000	L	Cingulate Gyrus	22	-49	-34	2	0.0117
	1896	L	Superior Frontal Gyrus	6	-1	10	55	0.0192
Syntax Discrimination								
	28,640	L	Inferior Frontal Gyrus	6	-44	13	17	0.0528
	9040	L	Superior Temporal Gyrus	22	-49	-34	2	0.0363
	6648	L	Inferior Parietal Lobule	39	-36	-58	36	0.0382
	3600	L	Medial Frontal Gyrus	6	-1	3	49	0.0362
	2784	R	Insula	13	37	18	4	0.0338
	1936	R	Precentral Gyrus	6	44	3	31	0.0331
N-Back								
	35,624	R	Precuneus	7	1	-56	51	0.0792
	28,880	L	Middle Frontal Gyrus	6	-37	32	24	0.0561
	25,176	R	Medial Frontal Gyrus	6	12	15	50	0.0505
	11,088	R	Middle Frontal Gyrus	9	36	40	23	0.0601
	3496	L	Insula	13	-31	23	1	0.382

Notes: Side represent the location of left (L) or right(R) hemisphere. BA: Broadmann Area.
[a] there is no correspondimg Brodmann area.

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

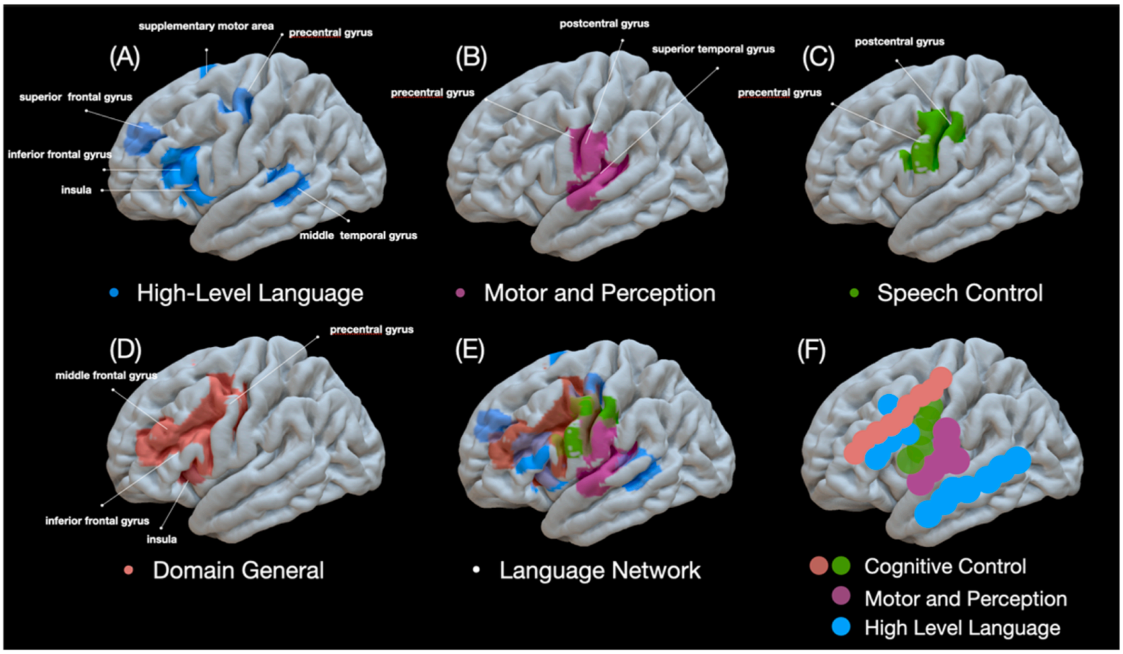

Fig. 2. The overview of four language-related region from meta-analysis. The contrast activation including (A) high-level language and (B) motor and perception. (A) High-Level language presents more activation for word generation and syntax discrimination > n-back. (B) Motor and perception shows greater 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 mm^3). (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 mm^3. 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 (mm^3)	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 mm^3. 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

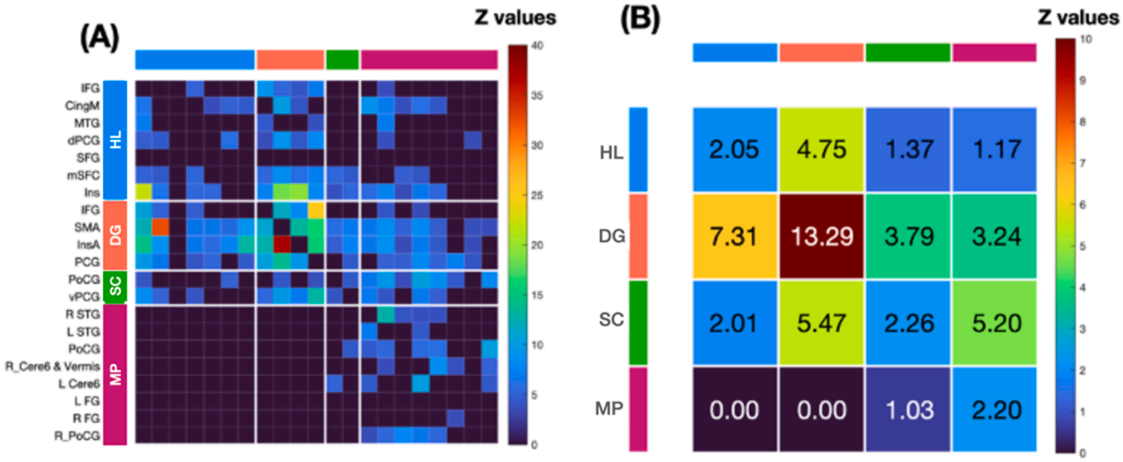

Fig. 3. Seed-to-whole brain meta-analytic connectivity modelling (MACM). (A) MACM connectivity matrix. ($P < 0.001$ corrected for multiple comparisons). (B) MACM connectivity matrix of the four domains with a threshold of z values > 3.48 (Gifuni et al., 2017). IFG, inferior frontal gyrus; MCG, middle 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.

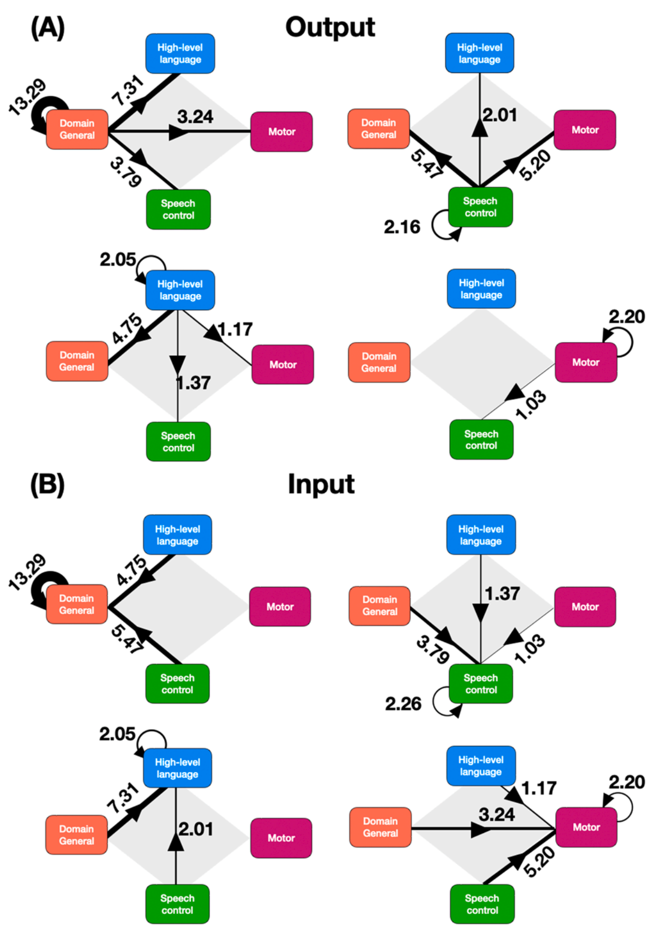

Fig. 4. Meta-Analytic Connectivity Modeling (MACM) Analysis. Fig. 4 illustrates the co-activations among the four systems using MACM. Output connections show co-activation in other regions when a specific region is activated, while input connections show co-activation in a specific region when other 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

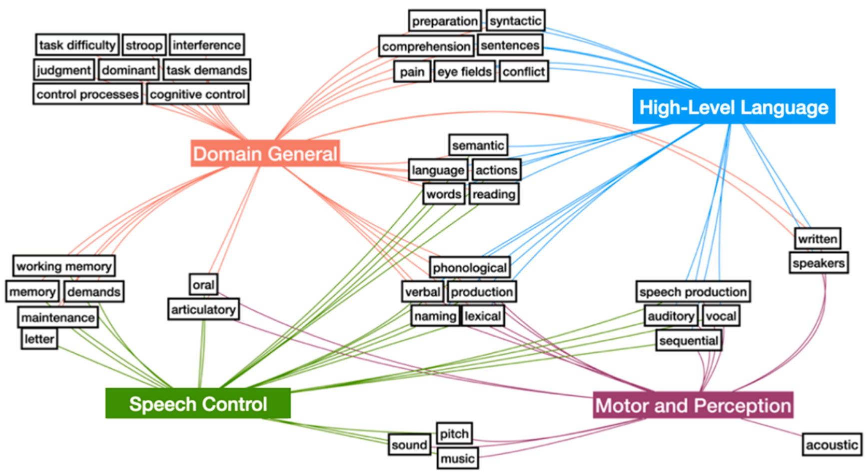

Fig. 5. Metadata characterization of functional preference in four system via Neurosynth. Word clouds were generated base on the correlation coefficient greater than 0.075 is preserved and assigned intersection between the system.

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 the brain.

To further clarify the hierarchy between the four language production systems discovered in the study, we conducted MACM to explore the possible directionality of connectivity between the defined systems. As expected, the motor perception system is only evoked when other systems are activated, suggesting that the motor perception primarily receives input from other systems and acts as the lowest level in language production. Moreover, the high-level language system was found to connect closely with the domain-general system and lacks a direct connection with the motor perception system. This aligns with prior research showing that direct cortical stimulation on BA44 and BA45 disrupted phonological and semantic skills without affecting articulatory motor (Makuuchi et al., 2009). Surprisingly, despite the anatomical adjacency of BA44 and vPCG, the high-level language system was not found to have directional connectivity with the speech control system. Taken together with previous evidence, our findings suggest that Broca's area is implicated in multifunctional roles within high-level language (Fedorenko et al., 2011b) and domain-general related cognitions (Duncan, 2010), but does not participate in speech output. Given the previous evidence and the current findings, we believe that considering the role of speech control system between comprehension-based (Friederici, 2011) and production-based (Kearney and Guenther, 2019) processes is key to understanding of mechanisms of successful verbal communication (Baldo et al., 2008; Buchsbaum et al., 2011; Hickok and Poeppel, 2007). In this case, our current findings may bridge the gap between the models proposed by Hickok and Poeppel (2007), Fedorenko and Thompson-Schill (2014), in terms of the transformation from abstract language processing (syntax, semantic) to concrete motor processing. In this study, we proposed a putative speech production network model, in which the high-level language system may be manipulated by the domain-general system in response to high-demanded language tasks, while the speech control system may act as a gateway between the domain-general and the speech motor perception system, both spatially and functionally.

We wish to acknowledge several limitations concerning the study's inferences and the proposed model for understanding language production. First, the ALE algorithm does not consider variables that may differ between studies, such as scanning or analysis parameters, potentially impacting the results. Secondly, we used coordinate-based meta-analysis instead of image-based meta-analysis. Coordinate-based meta-analysis relies on reported activation foci in journal papers, which may result in the loss of information due to the limited number of local maxima coordinates reported. While image-based meta-analysis based on whole-brain statistical images may provide a more comprehensive depiction of results, the resources for such meta-analysis remain scarce at present. Therefore, we encourage future task-based functional studies to share statistical result images to facilitate the conduct of large-scale meta-analyses (Salimi-Khorshidi et al., 2009). Third, to balance between task-specific precision and network-level generalizability, we utilized partially overlapping set of papers for the ALE and MACM analyses, which may have limited the overall generalizability of our findings. However, current design enables ALE to pinpoint language-specific ROIs based on task-specific activation patterns, while MACM explores these findings to connectivity patterns derived from co-activation across multiple language production tasks. As a complementary approach, our study identifies a distinct speech control system and empirically establishes its intermediate role bridging domain-general, high-level language, and motor-perception systems, which was not explicitly defined in prior frameworks (Kohn et al., 2014). Fourth, the BrainMap database is not a comprehensive meta-database and heavily relies on users to convert articles into corresponding formats and upload them to Brainmap. Therefore, the number of articles in different categories uploaded to Brainmap may be limited and potentially biased due to manual selection. As a result, the speech-related tasks may be insufficient to reflect the actual brain activation during human speech. Fifth, meta-analytic results reflect findings from task-based fMRI studies based on population averages and may not be generalizable to the individual level. Sixth, our study was limited to English-speaking participants, which may limit the generalizability of our findings to other languages. While this decision was made to ensure a homogeneous dataset and maximize statistical power, it is important for future studies to investigate potential language-specific differences in the neural architecture of language processing Our research employed a meta-analytic approach, aggregating results from numerous studies. Through conjunction and contrast analyses, we further explored the intersections and differences in the research. Although the sensitivity could not reach the level of individual analysis, the methods used in this paper still revealed some results worth exploring. Lastly, it is also worth noting that defining the pattern relationship between domain-general and speech control systems is difficult, and the proposed model (Fig. 6) relied solely on the connectivity strength calculated by MACM, which could change with the import of more articles.

To the best of our knowledge, this is the first study to map the four brain-network systems involved in the language production process using meta-analytic approaches and evaluate the possible hierarchical relationship between them. This study emphasizes the importance of the precentral gyrus in the production process because it is frequently coactivated with other systems. It is partially aligned with the model proposed by Friederici (2011) but suggests more strongly that the precentral gyrus plays a critical role in forward feedback in the production process (Guenther and Hickok, 2016). We propose that the language production process can be divided into two pathways: simple and complex. During simple pronunciation, the process can be completed solely by the speech control and the motor perception system. When the task demands sophisticated sentences or concept comprehension, the speech control system collaborates with the domain-general to reach out to the high-level language system and integrate information in both directions, which then transmits back to the speech control system and finally to the motor system for speech. Whether it is a simple or complex pathway, the speech control system acts as the center of intermediate

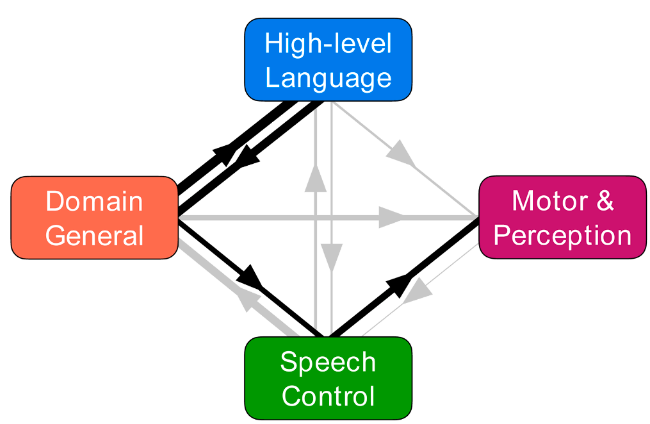

Fig. 6. A schematic framework of the multiple language system. This figure delineates the intricate interplay among four distinct systems, underscoring the robust bidirectional interaction between the domain-general and high-level language systems. It further highlights the propensity of the high-level language system to relay information to the motor region via the domain-general and language-selective pathways.

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.

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Data availability

Data will be made available on request.

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