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Review article

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# The language network as a natural kind within the broader landscape of the human brain

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## Abstract

Language behaviour is complex, but neuroscientific evidence disentangles it into distinct components supported by dedicated brain areas or networks. In this Review, we describe the 'core' language network, which includes left-hemisphere frontal and temporal areas, and show that it is strongly interconnected, independent of input and output modalities, causally important for language and language-selective. We discuss evidence that this language network plausibly stores language knowledge and supports core linguistic computations related to accessing words and constructions from memory and combining them to interpret (decode) or generate (encode) linguistic messages. We emphasize that the language network works closely with, but is distinct from, both lower-level — perceptual and motor — mechanisms and higher-level systems of knowledge and reasoning. The perceptual and motor mechanisms process linguistic signals, but, in contrast to the language network, are sensitive only to these signals' surface properties, not their meanings; the systems of knowledge and reasoning (such as the system that supports social reasoning) are sometimes engaged during language use but are not language-selective. This Review lays a foundation both for in-depth investigations of these different components of the language processing pipeline and for probing inter-component interactions.

## Sections



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## Introduction

Today, you may have reminded your daughter about her tennis practice, listened to your father complain about his neighbour, skimmed an article about local politics or written a report for work. None of these behaviours would be possible without language. How does our brain support this quintessentially human ability — language processing?

Language is a system of conventionalized symbols that a person can use to communicate specific, detailed meanings to others. To support this sophisticated communication system, our brain carries out complex, multicomponent operations that map between meanings and linguistic forms (words or word sequences) and between linguistic forms and the perceptual signals that instantiate those forms. During language comprehension, one needs to perceive linguistic signals (such as speech, sign or written text) and decode the intended meanings while integrating them with preceding linguistic context and non-linguistic knowledge sources. During language production, one needs to transform intended meanings into linguistic form and then generate corresponding physical output (speech, sign or written text). Many brain areas must act in concert to support these complex language processing behaviours. But do all these areas operate as an indivisible whole, or can this language processing pipeline be partitioned into distinct components ("nearly decomposable systems"[1])?

Different components of language (or linguistic) processing have been disentangled through an iterative process of theorizing and empirical testing (Box 1). This iterative process has yielded a detailed picture of the neural infrastructure of language, revealing that the brain's linguistic capacity is supported by a set of language-specific representations, which capture regularities at the levels of sounds, words and syntactic structure, along with a large set of form-meaning mappings for words and constructions[2,3]. These language-specific representations are used to decode linguistic messages during language comprehension and encode them during language production[2,3]. This core language system is distinct from modality-specific perceptual systems that deliver information to it during comprehension[4,5]; motor systems that receive information from it during production[6]; and cognitive systems of knowledge and reasoning that interact with it to make transformations between thoughts and linguistic forms and to achieve diverse goals during real-life language use[7–9].

The separation between either linguistic and perceptual processing or linguistic and cognitive processing is not a given. Indeed, one can imagine an architecture in which comprehension of auditory language (speech) fully takes place within the auditory cortex and processing of written language (text) fully takes place within the visual cortex. Or one can imagine an architecture in which language leverages the same neural resources as those required for thought, as in proposals arguing for a universal syntactic composition engine[10–12] (see ref. 13 for an alternative proposal). Part of the difficulty in discovering the dissociations we discuss in this Review may have had to do with methodological limitations of past work. Most early functional MRI (fMRI) work on language relied on a group-averaging approach, which assumes voxel-wise alignment across brains, leading to information loss and blurring of the activation patterns (Box 1). Combined with reliance on paradigms that conflate language with speech or with general cognitive effort, the group-averaging approach contributed to the lack of clarity on the relationship between language processing and perceptual, motor and cognitive processes in the brain. However, a gradual shift in cognitive neuroscience to individual-subject analyses[14–18], including in language research[19–25], has produced a set of robust and replicable findings about the language network and its relationship with other systems, suggesting that language processing carves out a specific set of regions in the human brain.

In this Review, we discuss brain areas that are specific to language — what we refer to as the language network — and position them in relation to perception, motor planning and cognition (Fig. 1). Drawing on evidence from brain imaging studies, intracranial recording and stimulation work, and investigations of patients with developmental and acquired speech, language and cognitive disorders, we show that the language network constitutes a natural kind — an ontologically meaningful grouping of brain areas on the basis of their response properties and functional cohesion. For brain imaging, we primarily draw on fMRI data from studies that have relied on the individual-subject functional localization approach[14,19] (Box 1), which was essential in clarifying the distinctions discussed. We first introduce the language network and summarize its key properties. Then, we discuss the internal structure and computations of the language network. Next, we overview the perceptual and motor brain areas that subserve comprehension and production but are functionally distinct from the language network: we show how, unlike the language areas, these areas are not sensitive to the meaning of linguistic messages, only to the surface properties of linguistic stimuli. We then examine several networks that support human thought (knowledge and reasoning abilities) and show that, although they interact with the language network during real-life language use, they are distinct from it in that they are not language-selective. Last, we summarize the contributions of this body of work, highlight some open questions and make suggestions for addressing these questions in future research.

## The language network as a natural kind

Every typical adult human brain contains a set of areas that are specialized for language (Fig. 2). Below, we describe the core functional properties of the language areas and show that they form an integrated network.

### Anatomy and inter-connectivity

Despite substantial inter-individual variability in the anatomy-to-function mapping (Fig. 2b and Box 1), the language network occupies a well-defined position in the brain (Fig. 2a). This network consists of lateral frontal areas (located within the inferior and middle frontal gyri) and lateral temporal areas (located within the superior and middle temporal gyri, stretching from the temporal pole to the posterior extent of the temporal lobe). These areas are lateralized to the left hemisphere in most individuals, as evidenced by stronger and more spatially extensive responses to language in the left hemisphere and by a higher likelihood of aphasia following left-hemisphere damage[26–28]. The reason for the left-hemisphere language dominance remains debated[29–31], but left-hemispheric lateralization does not appear to be critical for language function. First, in some individuals with no known neurological or genetic conditions, frontal and temporal language areas may not show a hemispheric bias or may show right-hemispheric lateralization, without any effect on linguistic abilities[32,33]. Second, in the presence of early left-hemisphere damage (for example, due to early-childhood stroke), a language network can develop in the right hemisphere, again with no discernable behavioural consequences[34–36]. That said, in many developmental disorders (such as autism, developmental language disorder and epilepsy) language responses have been reported to be more bilateral[37–39], and at least in some studies, more bilateral responses have been linked to worse behavioural outcomes[40].

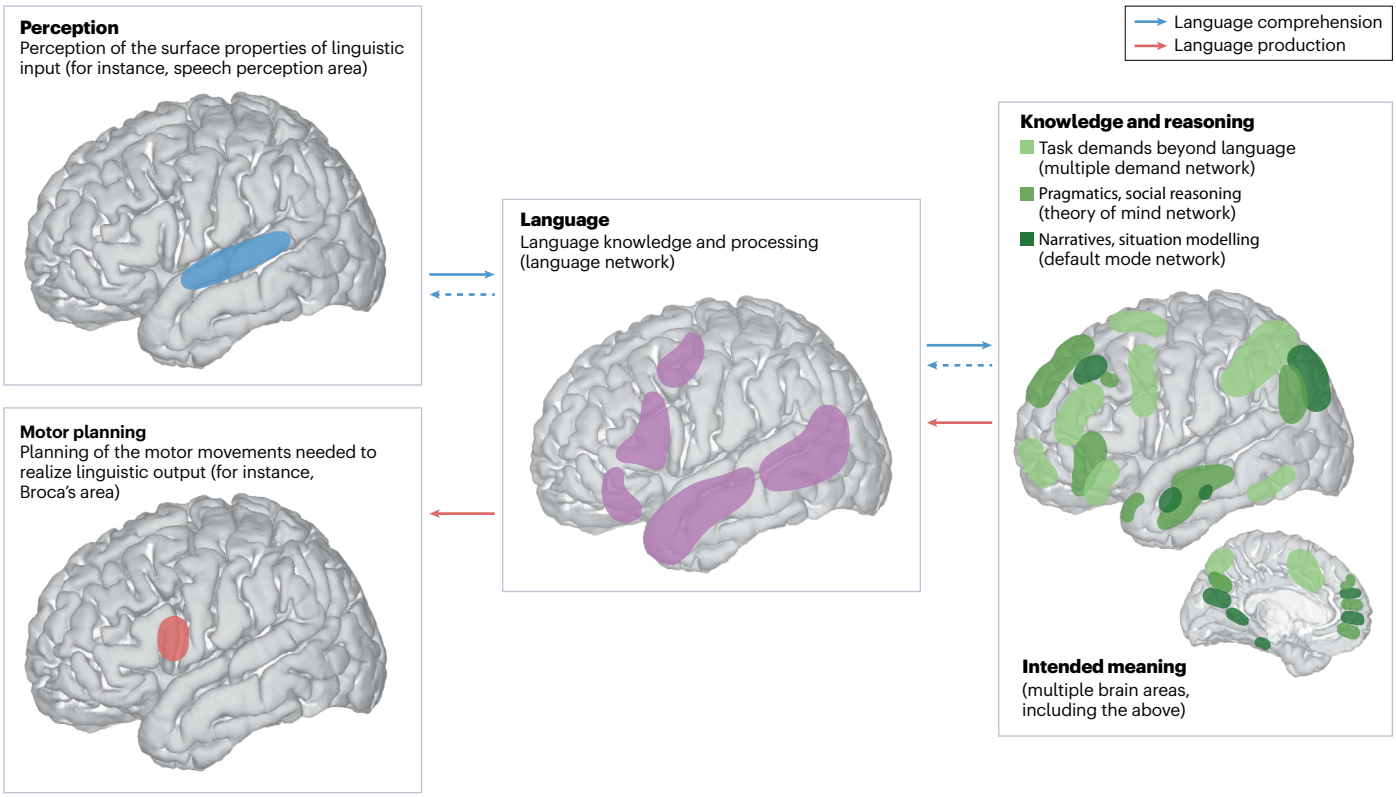



**Fig. 1 | Brain systems that support language comprehension and language production.** Both language comprehension (blue arrows) and language production (red arrows) require the core language system (purple) to decode and encode linguistic messages, respectively (see 'The language network as a natural kind' and 'The internal structure and core computations of the language network'), but also require lower-level perceptual and motor mechanisms (blue and red, respectively; see 'The language network and language-relevant perceptual and premotor areas') and higher-level systems of knowledge and reasoning (green) (note that we do not imply that no other brain areas or networks contribute to thought processes — we simply focus on three well-characterized networks that must interact with the language network during real-life use; see 'The cognitive networks the language network interacts with to support real-life language use'). For comprehension, the bottom-up processing of linguistic input (solid arrows) is complemented by top-down influences (dashed arrows) of both general knowledge and reasoning on linguistic interpretation[319–322] (Box 2), and linguistic knowledge on perceptual processes[249–251]. All brain areas schematically represent an average anatomical location (see Supplementary methods for details); functional areas in individual brains are smaller than these schematic representations and vary in their precise locations.

In addition to the lateral frontal and temporal areas, the language network includes other cortical areas such as the homotopic areas in the non-language-dominant hemisphere[41,42] (Fig. 2a,b), cortical-midline areas[23] and an area on the ventral temporal surface[5,43]; subcortical areas[44]; and cerebellar areas[45,46]. The contributions to language processing of these different components of what is sometimes referred to as the 'extended language network' remain an active area of research. In this Review, we focus on the 'core' frontal and temporal areas in the language-dominant hemisphere.

The language network can be identified in individual participants in a few minutes of fMRI scanning by contrasting brain responses during the processing of a language stimulus versus the processing of a stimulus that is similar to language in its surface properties but lacks linguistic meaning and structure. Common localizers (Box 1 and Fig. 4c) use a contrast between reading or listening to sentences and reading or listening to non-word lists, or between listening to speech in one's native language and listening to speech played backwards or speech in an unfamiliar language[19,47–50]. Although variable across individuals (Fig. 2b and Box 1), the topography of the language-responsive areas and their properties (for example, the magnitude of response to language or the degree of left-hemispheric lateralization) are relatively stable within individuals over time[51] (Fig. 2c) (but see ref. 52 for evidence that this does not hold for studies that do not use localizers).

Furthermore, the language network is strongly interconnected. Several white-matter tracts connect different parts of the language network[53,54], although the precise contributions of the different tracts remain debated[55]. The network is also strongly functionally connected, as evidenced by a high degree of correlated activity among the language areas during so-called naturalistic cognition paradigms[23,56,57]. This strong functional connectivity suggests that the different areas work together in the service of a common goal. In fact, the language network can be identified on the basis of functional connectivity alone[23], further establishing its existence as a natural kind and not a product of a single methodological approach, such as functional localization (Box 1).

Note that although throughout this Review we talk about functional brain areas as discrete entities with sharp borders, our arguments do not critically require this property and are compatible with gradual

## Box 1

# Beyond coarse anatomy: the importance of functional localization

The question of what constitutes meaningful units of analysis in the brain has long been controversial[14,350]. Two main alternatives include anatomical definitions (brain area X is an area that falls in a particular location in the brain, typically described in terms of macroanatomy such as sulci and gyri) and functional definitions (brain area X is an area that performs some perceptual, motor or cognitive function: for example, the fusiform face area is an area that supports face perception[351] or the visual middle temporal area is an area that processes visual motion[352]). In many parts of the brain, the relationship between anatomy and function is complex, which makes it difficult to predict function from an anatomical location alone[353]. Consider the images of the language network in individual participants shown in Fig. 2b: even with the naked eye, it is easy to appreciate the inter-individual variability in the precise anatomical locations and sizes and/or shapes of these functional areas (see refs. 19,23,49,51 for quantitative evidence). Yet, for many years, both patient and neuroimaging studies on the neural basis of speech and language have used anatomical definitions. Terms such as Broca's area and Wernicke's area have been extensively used, but they were defined anatomically, not functionally, and these definitions have varied substantially across researchers[220], leading to massive confusion and occasional nihilism about the very idea of localization of function.

A key problem for anatomical definitions is the functional heterogeneity of the association cortex[354]. For example, language areas lie adjacent to a few distinct functional areas, including lower-level speech perception and articulation areas and areas that belong to non-language cognitive networks. As a result, any macroanatomical area (for instance, some portion of the inferior frontal gyrus (IFG) or of the superior temporal gyrus (STG)) will inevitably encompass multiple functionally distinct areas. The combination of inter-individual topographic variability and functional heterogeneity creates a massive problem for analyses that average brains voxel-wise in a common space, as much past speech and language research has done. Because any given voxel in a common space often corresponds to different functional areas across individuals[131], such analyses lead to blurring of neighbouring areas and information loss[14,15].

Functional localization provides a solution[14,19,351] (see ref. 355 for an alternative approach). This approach relies on extensively validated paradigms called 'localizers' (see Fig. 4c for examples) that target a particular perceptual, motor or cognitive process. The localizer contrasts are typically motivated by work in experimental psychology and patient investigations. Localizer paradigms afford greater confidence that the 'same' brain area is referred to across individuals, studies, laboratories and species, and — through their consistent use — enable meaningful accumulation of knowledge. Brain areas and networks identified by well-validated localizers correspond closely to areas and networks that can be identified bottom-up from large amounts of resting-state data by clustering voxel time courses[23,356]. This correspondence suggests that localizers are simply an efficient way to identify the relevant area(s), and in doing so, they respect the brain's intrinsic organization rather than imposing structure where there is none. Finally, although functional localization originated in functional MRI (fMRI), it has been successfully ported to intracranial human recordings, magnetoencephalography and animal physiology[155,252,357–359].

Perhaps the most common functional localizer for the language network relies on a contrast between reading or listening to sentences (for example, 'nobody could have predicted the earthquake') versus pronounceable non-word sequences (for example, 'u bizby acworrily mape las pome'; Fig. 4c)[19]. However, an important feature of an effective localizer is that it is generalizable. Indeed, the sentences > non-words localizer successfully generalizes to diverse other contrasts between a language stimulus and a perceptually matched condition, including auditorily presented sentences or passages versus muffled and/or acoustically degraded sentences or passages[48,50], and forward speech versus reversed speech[47] (including using audiovisual stimuli[70]). The fact that the specific localizer paradigm for the language network does not matter is essential to showing the validity of the functional localization approach in language neuroscience, and such robust paradigms show a strong correspondence with subdivisions that can be identified from task-free functional correlation analyses[23,356].

changes between nearby functional areas (see 'Open questions and a way forward' for a discussion).

### Responsiveness to different kinds of language

As elaborated below, the language areas engage during both comprehension and production; are input and output modality-independent; respond during different tasks; and are similar across languages. Furthermore, these areas are sensitive to linguistic regularities at different information scales, from sequences of phonemes to words to sentences.

First, the language network is engaged during both comprehension and production (see Supplementary Fig. 1). A number of studies have revealed strong overlap in both frontal and temporal areas during comprehension versus generation of linguistic content[58–60]. These results overturn the classic model of the neurobiology of language that separates production and comprehension[61–63] (but see 'The language network and language-relevant perceptual and premotor areas' for evidence of segregation at the level of perceptual and motor processes). Second, the language areas are modality-independent: they respond to diverse kinds of input, including spoken, written and signed language[19,64–67] (Fig. 2d), and they respond during generation of diverse kinds of output, including speaking and typing[60] (see Supplementary Fig. 1). Third, the language network responds to language in different task contexts, whether individuals are passively comprehending (including when processing rich naturalistic stimuli, such as stories, dialogues and movies), trying to remember words when reading or listening to sentences, making judgements about words or sentences, or answering comprehension questions[24,68–70]. Fourth, the

language network is similar in its topography and properties across diverse languages both across speakers[50] and within bilingual or multilingual individuals[71–73]. Last, the language network is sensitive to linguistic regularities at different scales, from sub-lexical structure (phonology and morphology) to word forms and meanings (lexical semantics), to phrase-level combinatorial structure (syntax and compositional semantics). This sensitivity is evidenced by the language network's engagement by diverse paradigms — including those that use single, unconnected words (word reading or listening, picture naming, semantic judgements, verbal fluency or verb generation[60,74]) and sentences (sentence reading or listening, sentence judgements or sentence–picture matching[65,75]) — its sensitivity to linguistic manipulations at these different scales[19,76] (see 'The internal structure and core computations of the language network'), and the ability of researchers to decode and encode[77] diverse linguistic features (phonological, syntactic and semantic) using the language network's activity[78–82].

Together, these properties suggest that the language network stores abstract (modality-independent) linguistic knowledge and carries out core linguistic computations that are necessary for decoding and encoding linguistic messages across tasks and languages.

### Causal role in language ability

The left-hemisphere frontal and temporal brain areas, which house the language network, are causally important for language. Damage to these areas in adulthood leads to aphasia — deficits in language comprehension and production[26,83–87]. The literature on aphasia is extensive and complex. This complexity stems, in part, from the fact that brain damage does not typically respect functional subdivisions and often affects multiple nearby distinct areas. Moreover, the precise locations of functional areas vary across individuals and are not predictable from macroanatomy (as discussed in Box 1). Because individuals with aphasia will not have typically undergone systematic functional mapping prior to their brain injury, it is often difficult to determine which functional areas are affected by the lesion[88]. Nevertheless, several brain–behaviour associations have emerged robustly (some of which will be discussed in 'The language network and language-relevant perceptual and premotor areas').

With respect to the language network proper, circumscribed damage is typically associated with relatively quick recovery[83,89,90]. Extensive damage that affects multiple network components and the underlying white-matter tracts is typically required for long-lasting linguistic deficits[90]. Quick recovery from circumscribed damage suggests that the language network is characterized by some degree of redundancy, although its posterior temporal component may be the most critical and irreplaceable, given that damage to it is associated with longer-lasting and more severe deficits[83,90].

### Selectivity for language versus non-linguistic inputs and tasks

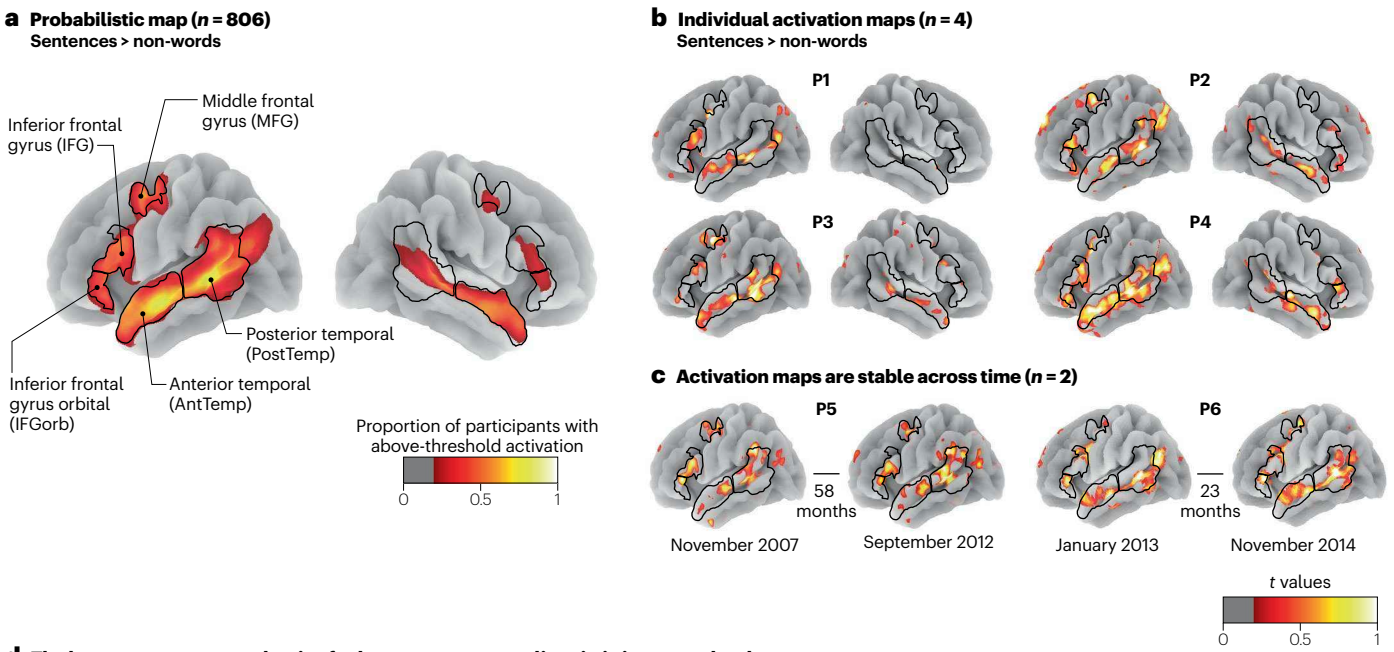
The language areas are highly selective for language processing relative to diverse non-linguistic inputs and tasks[91] (Fig. 2d). Language has been argued to share machinery with numerous cognitive functions and domains, including the processing of hierarchically structured inputs[10,12], executive functions[92–94], conceptual thought[95–97] and action observation[98,99]. However, these claims have not found empirical support. When the language areas are identified functionally in individual participants (Box 1), they show remarkable selectivity for language (Fig. 2d; see Supplementary Fig. 1). In particular, the language areas are not engaged when participants listen to music — a rich, hierarchically structured stimulus[91,100–102] — and show little or no response when participants perform demanding cognitive tasks, including solving arithmetic problems[22,91,103,104] and logic puzzles[105,106], understanding computer code[107,108] and carrying out working memory and cognitive control tasks[24,50,91,109,110]. Language areas are also not recruited for semantic tasks on pictorial inputs[60,111] (but see refs. 112,113) and show little response when individuals process socially relevant information, including faces, bodies and hands[101,114,115]; when they observe others' actions[114], including communicative signals such as eye gaze and speech-accompanying gestures[114,116]; or when they reason about others' mental states — what is often referred to as mind-reading or having a theory of mind[101,117,118]. Finally, language areas show only a weak response when participants perceive[19,50,119,120] or articulate[60] meaningless non-words or syllable sequences (the existence of these weakly positive responses can be explained by the surface similarity of these stimuli to well-formed language; see 'The internal structure and core computations of the language network').

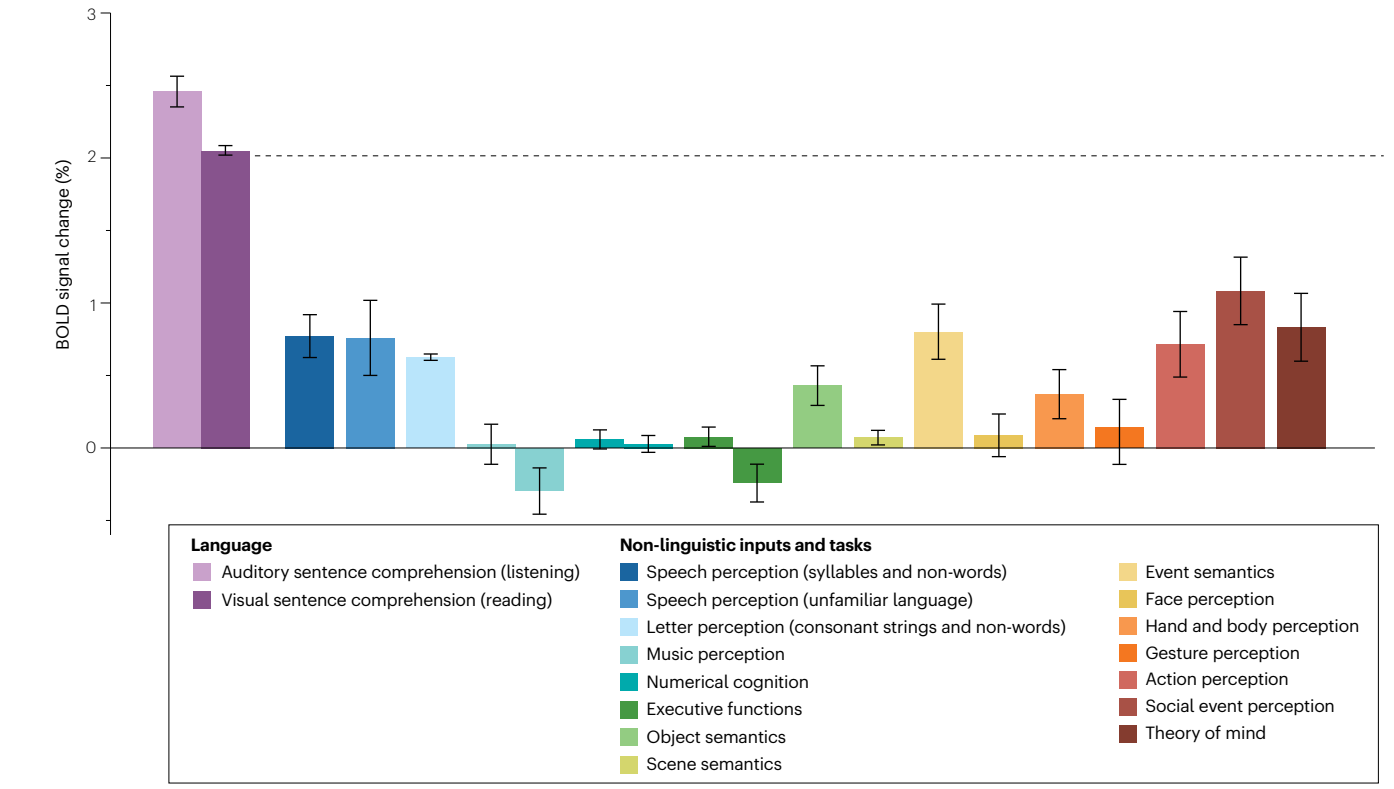
This extensive neuroimaging evidence that the language network shows selectivity for language versus non-linguistic inputs and tasks is complemented by behavioural evidence from aphasia. If brain damage is primarily restricted to the language areas, individuals with aphasia lose their linguistic abilities but retain their non-linguistic abilities, including music perception[102], mathematics[121,122], general reasoning[123,124], conceptual semantics[111] and social skills, including theory of mind[123,125–128]. This preservation of non-linguistic abilities even extends to cases in which the relevant task elicits some response in the language areas in healthy adults. For example, a meaning-judgement task on pictures engages the language network to some degree (albeit less than linguistic inputs; Fig. 2d), but patients with severe aphasia are not impaired on this task[112]. This pattern suggests that a weakly positive response to some non-linguistic inputs or tasks in the language areas may be epiphenomenal (that is, not indicative of the critical role of the language areas in the relevant ability). It is also worth noting that although both linguistic and non-linguistic abilities may be affected in some cases of brain damage[129,130], this is neither surprising nor informative given the proximity between the language system and other cognitive systems[23,131,132]; cases showing dissociations between linguistic and non-linguistic abilities are much more informative.

**Summary.** The constellation of properties of the language-responsive areas that we have delineated in this section justify the term 'the language network'. The word 'language' indicates that the core function of these brain areas is language processing: these areas respond to language in all its manifestations, are causally important for language function and are selective for language (see Box 2 for caveats). The word 'network' conveys that this distributed set of brain areas form an interconnected system that is distinct from other areas of the brain. Identifying stable systems within the brain with a unique functional profile is a core goal of cognitive neuroscience: to partition the brain into natural subdivisions (Box 2). Another core goal is to understand how each subdivision contributes to perception, action and cognition. Next, we summarize progress in the latter effort — to understand how the language network supports language processing.

## The internal structure and core computations of the language network

In this section, we dive into the contributions of the language network to language processing. We focus on two key properties of this network: its




sensitivity to linguistic structure at multiple information scales, and the functional similarity of its different areas.

### Sensitivity to regularities at the sub-lexical, word, and phrase and sentence level, but not discourse level

Human languages are characterized by structure (regular patterns or 'regularities') at different levels, from how sounds and word parts go together (phonology and morphology) to what meanings words carry (lexical semantics), how words combine to create phrases and sentences (syntax and compositional semantics), and how sentences go together to create coherent narratives and conversations (discourse). The human brain could, in principle, process these different kinds of regularity in separate specialized areas (see refs. 133–138 for examples where such distinctions have been advocated). On the other extreme,

**Fig. 2 | The topography of the language network, its variability across individuals, its stability within individuals over time and its selectivity for language over non-linguistic inputs and tasks. a**, A probabilistic activation overlap map created from 806 individual maps (obtained with functional MRI (fMRI)) for a language 'localizer' task (Box 1) based on a contrast of reading or listening to sentences and reading or listening to perceptually similar but incomprehensible stimuli (such as a non-word list)[49]. The activations are restricted to the frontal and temporal areas. **b**, Sample activation maps for the localizer contrast in four participants (see Supplementary methods). As can be seen from these maps, the broad topography (left-lateralized frontal and temporal activation) is similar across individuals, but the precise locations, shapes and sizes of the language areas vary across individuals, which highlights the importance of individual-level functional localization (Box 1; for quantitative evidence of inter-individual variability, see refs. 19,23,51). **c**, Activation maps for two individuals each scanned twice across the span of ~5 years (P5) and ~2 years (P6)[51] (see Supplementary methods). In contrast to the inter-individual variability illustrated in panel **b**, the language network is extremely stable within individuals over time (for quantitative evidence, see ref. 51). Black outlines in panels **a**–**c** denote 'parcels', which are derived from a probabilistic overlap map and mark the areas within which the majority of individuals show responses to language; these parcels are used to constrain the selection of functional regions of interest (fROIs) in individual participants (see Supplementary methods). **d**, Responses, as measured with fMRI, in the language network during language processing and diverse non-linguistic inputs and tasks. The language network is strongly selective for language processing over diverse non-linguistic inputs and tasks: the response during language processing is at least twice as high as during any non-linguistic input or task. Language network responses are averaged across the five core left-hemisphere areas; language fROIs are defined in individual participants for all experiments; and independent data subsets are used for defining the fROIs and estimating their responses, to avoid circularity (see Supplementary methods). Error bars represent s.e.m. by participants (see Supplementary methods for details and Supplementary Fig. 1 for data from a wider range of non-linguistic conditions). Dashed horizontal line is drawn from the reading-based language localizer, for which we have more data, to facilitate the comparisons with non-linguistic conditions. Note that the functional profiles of the knowledge and reasoning networks differ sharply from this profile (and from each other; see 'The cognitive networks the language network interacts with to support real-life language use'). For example, the multiple demand network shows little to no response during the sentence comprehension conditions and instead shows robust responses during many demanding tasks (see ref. 131 for a side-by-side comparison), and the theory of mind network shows little to no response during the sentence comprehension conditions and instead shows a strong response during social reasoning tasks (see refs. 101,118 for direct comparisons).

the brain could use the same area to process them all. The reality is closer to the second possibility.

Much evidence suggests that linguistic patterns at different levels are processed within the language network. In particular, the language network is sensitive to phonotactic 'well-formedness' of letter or sound strings[76] (Fig. 3a,b) and to morphological structure[139]. It also supports the retrieval of individual word meanings, as indicated by a stronger response to real words than non-words[19,119] (Fig. 3a,b) and by responses during tasks that require semantic processing of words (such as meaning relatedness judgement tasks[74,104]). Furthermore, the language network supports combinatorial syntactic and semantic processes (cognitive processes required for combining words into phrases and sentences), as indicated by a stronger response to sentences than word lists[19,140,141] (Fig. 3a,b), modulation of neural responses by the difficulty of sentence construction — including the costs associated with predicting upcoming words[142–144] and integrating incoming words into an evolving representation of sentence structure in memory[75,145–147] — and sensitivity to many other syntactic and semantic manipulations[148–150].

That so-called 'jabberwocky' sentences (made up of non-words; for example, 'The flumpy blork was clooding in the meaves') elicit a stronger response than non-word lists[19,141] (Fig. 3a,b) further suggests that the language network is sensitive to abstract syntactic patterns. Importantly, however, lexical-semantic processes (related to accessing word meanings from memory) and combinatorial processes (related to combining words into phrases and sentences) are strongly integrated in every area of the language network during both comprehension[19,47,147] and production[60] (Fig. 3a,b), contrary to proposals that syntactic processing is spatially separable from lexical-semantic processing and other aspects of language[133,138,151–153]. Even at a finer spatial scale, as probed with multivariate pattern analyses[154] or intracranial recordings[155,156], every neural population within the language network that supports combinatorial processing also processes individual word meanings. This evidence aligns with the idea that natural language syntax is highly lexicalized, such that the rules for how words combine depend strongly on the particular words — rather than broad categories such as nouns (object-denoting and entity-denoting words) and verbs (action-denoting and state-denoting words)[2,157,158].

In contrast to regularities at and below the sentence level, computations related to building discourse structure are not supported by the language areas (see Box 2 for a discussion): the language network responds as strongly to lists of unconnected sentences as to connected passages[159–162] (Fig. 3a,b). Instead, other brain networks support these computations (see 'The cognitive networks the language network interacts with to support real-life language use').

## Functional differences among the language areas?

**Past claims about dissociations within the language network.** Many claims have been made about dissociations within the language network on the basis of functional brain imaging studies and reviews or meta-analyses thereof[136,163–167]; voxel-based morphometry and voxel–lesion symptom mapping studies of patients with stroke aphasia[84,87,168] or primary progressive aphasia[169,170]; and transcranial magnetic stimulation[171,172] or intracranial stimulation[173–176] studies. These dissociation claims have sometimes been based on paradigms in which the experimental conditions of interest — a combination of stimuli (such as sentences on a screen) and tasks (such as passive reading of them) — are not matched for difficulty and/or where critical control conditions are missing, which complicates interpretation. Some claims have further contradicted one another (for example, different researchers have argued for a different language area being the main syntactic hub; see ref. 148 for discussion). Most importantly for our purposes, much prior work has not functionally identified the language areas, which makes these dissociation claims challenging to evaluate with respect to the proposal outlined in this Review. In particular, it is impossible to determine whether any dissociation claimed is between two language areas or between a language area and a nearby functionally distinct area, such as a lower-level perceptual or premotor area (see 'The language network and language-relevant perceptual and premotor areas') or a higher-level cognitive area (see 'The cognitive networks the language network interacts with to support real-life language use').

## Box 2

# The language network versus language: ontological kinds at different levels

In this Review, we describe the language network — a physical component of the brain — and its relationship to language — a function of the mind. Mapping between neuroscience and cognitive science in such a way is not always straightforward[360]: one needs to postulate and rigorously evaluate the linking functions between the brain and the mind, which includes identifying the right units of analysis that can be linked. On the neuroscience side, much progress in identifying the right units has been made thanks to functional localization approaches (Box 1) and data-driven parcellations of individual-specific functional connectivity maps[23,299,361]. On the cognitive side, the relevant concepts come from folk psychology ('language' or 'reasoning') and disciplines, such as linguistics and cognitive science, that break these broad folk-psychological concepts into distinct sub-components ('syntax' and 'pragmatics' for language, or 'induction' and 'deduction' for reasoning), often on theoretical grounds. Such a priori cognitive concepts typically do not neatly map onto the brain, requiring iterative refinement of the cognitive ontology so that it aligns best with the neural subdivisions discovered in neuroscience[362].

As we argue throughout the Review, there exists a remarkable degree of alignment between the concept of language derived from folk psychology and/or linguistics and the set of functions performed by the language network. However, this alignment is imperfect; for instance, discourse processing is an essential component of language as a cognitive function[363], yet the language network does not support it (see 'The internal structure and core computations of the language network'). Thus, 'language' in 'the language network' is an approximation, a convenient shorthand, for the network's function rather than a precise description. Furthermore, other ontological distinctions from linguistics, such as syntax versus semantics, do not map onto dissociable brain components at all. Thus, much caution is needed when attempting to assign cognitive or linguistic labels to brain areas: our cognitive ontologies may not align 1:1 with the neural architecture.

Some have argued that the mapping endeavour should be abandoned altogether in favour of a holistic interactionist study of the brain[364] and/or an 'inside out' approach to neuroscience, with bottom-up discoveries driving the process of clustering brain computations rather than assigning labels from the top down[365,366]. Although bottom-up label-free approaches are doubtlessly valuable for making progress in neuroscience, our Review is testament that top-down approaches also provide value and that cognitive labels such as 'language' are a rich source of useful initial hypotheses for what a brain area or network might do.

In addition to these past claims about functional dissociations between language areas, some have argued for dissociations among different aspects of language without specifying the particular brain areas implicated, typically based on behavioural dissociations in individuals with brain damage (see also ref. 177 for a review of investigations of individual differences in linguistic abilities). For example, some have argued for the separability of noun versus verb processing[178,179] or for the separability of syntax from other aspects of language ('agrammatism'[180,181]). However, many claims about dissociations within language per se — in contrast to dissociations that could be explained by a combination of a linguistic impairment and an impairment in the lower-level perceptual or motor processing or higher-level cognitive processing — have been questioned empirically and/or conceptually (for example, see refs. 182–184 for evidence against the idea that agrammatism is associated with a selective loss of syntactic ability; see ref. 185 for a review).

**Similar functional profiles for the different language network areas.** The evidence from the functional localization approach in fMRI has so far revealed highly similar functional profiles among the language areas, in contrast to clear dissociations between language areas and perceptual or premotor areas (see 'The language network and language-relevant perceptual and premotor areas'). All language areas are sensitive to sub-lexical regularities, word meanings and combinatorial linguistic structure (Fig. 3a,b), support prediction and integration during syntactic structure building[75,142–144,147,186] and are similarly modulated by diverse linguistic manipulations[148–150]. These similarities hold even at the grain of preferences for particular linguistic stimuli; for example, the relative magnitudes of response to specific sentences are highly similar across the different language areas, with all areas showing maximal responses to sentences that are somewhat difficult to process[187] (Fig. 3c).

However, one brain area that was originally included as part of the language network[19] — the language-responsive area in the angular gyrus — has been found over the past decade to consistently pattern differently from the rest of the network. Although, similar to other language areas, this area responds more to sentences than control conditions, such as non-word lists, it is less strongly functionally connected with other language areas[56,104,118], is less selective for language, showing a strong response to non-linguistic meaningful stimuli[112,118,188], and is not sensitive to syntactic complexity[75,141,143,147,189]. Thus, we no longer consider this area to be a part of the language network.

**Making meaningful progress in understanding the internal architecture of the language network.** More work is needed to understand the internal organization and information flow within the language network. To make meaningful progress, it would be helpful to agree on the standard of evidence for functional dissociations. Minimally, for fMRI investigations, the following two criteria have to be met to argue that two language areas differ functionally: the language areas should be identified functionally in individual participants using a previously validated approach (note that this criterion rules out the utility of group-averaging studies or meta-analyses of activation peaks), and a reliable area-by-condition interaction statistic should be reported (specifically, it is not sufficient to show that language area L1 is sensitive to manipulation M and language area L2 is less or not sensitive to

manipulation M; it is critical to also show that the two areas reliably differ in their sensitivity to M)[190]. Furthermore, if reporting a single dissociation (as in the preceding example), it is important to account for the overall level of neural response and the level of responsiveness to language stimuli in the relevant language areas. In our example, area L2 may have an overall weaker neural signal, which would lead to lower responsiveness to M (but may not reflect a true functional difference from L1). In general, as with patient studies[191], double dissociations are more powerful: showing that area L1 is more sensitive to manipulation M1 than manipulation M2, and area L2 is more sensitive to manipulation M2 than M1. In addition to these criteria, to minimize the chances of spurious findings, and in line with the field's increasing emphasis on robustness and replicability[192], the result should also be replicated with a new group of participants and, ideally, generalized to a different paradigm that targets the same cognitive process(es) (for example, if areas L1 and L2 dissociate in their sensitivity to syntactic complexity in a controlled paradigm, they should also show a dissociation during naturalistic comprehension). Similar criteria can be formulated for other approaches, including patient investigations and intracranial recording and stimulation studies.

Intracranial human recording approaches, which continue to gain popularity, perhaps combined with the use of neural network language models[187,193–196], may lead to substantial advances in our understanding of the organization of the language network in the coming years. Indeed, intracranial recordings have already helped uncover functional heterogeneity within the network that does not correspond to regional boundaries. Regev, Casto et al., in a non-peer-reviewed preprint[197], reported evidence for neural populations with distinct 'temporal receptive windows'[198], displaying sensitivity to different-length contexts ranging from one word to multi-word spans (see also refs. 199–201). These neural populations were distributed across the language network, which suggests that all language areas have direct access to linguistic representations at multiple scales, including single-word processing and combinatorial syntactic and semantic processing, as discussed earlier in this section. Importantly, this functional heterogeneity does not undermine the very idea that the language network is a 'thing'; although different cells and cell populations within the network are likely to perform distinct computations or represent different information, they share something deep about their functionality — they jointly contribute to some aspect of language processing.

**Summary.** To summarize, many distinctions within the language network that have been advocated in the past have not withstood empirical and statistical scrutiny, or can be explained as dissociations between a language area and a nearby functionally distinct area. Moreover, aspects of language that are often studied by different subfields of linguistics (such as phonology, morphology or syntax; but see refs. 3,202,203 for usage-based approaches, which do not draw sharp boundaries between linguistic structure at different levels) are all processed by the same set of brain areas comprising the language network, although some heterogeneity among interleaved neural populations has already been uncovered and more distinctions are likely to be found in future work.

## The language network and language-relevant perceptual and premotor areas

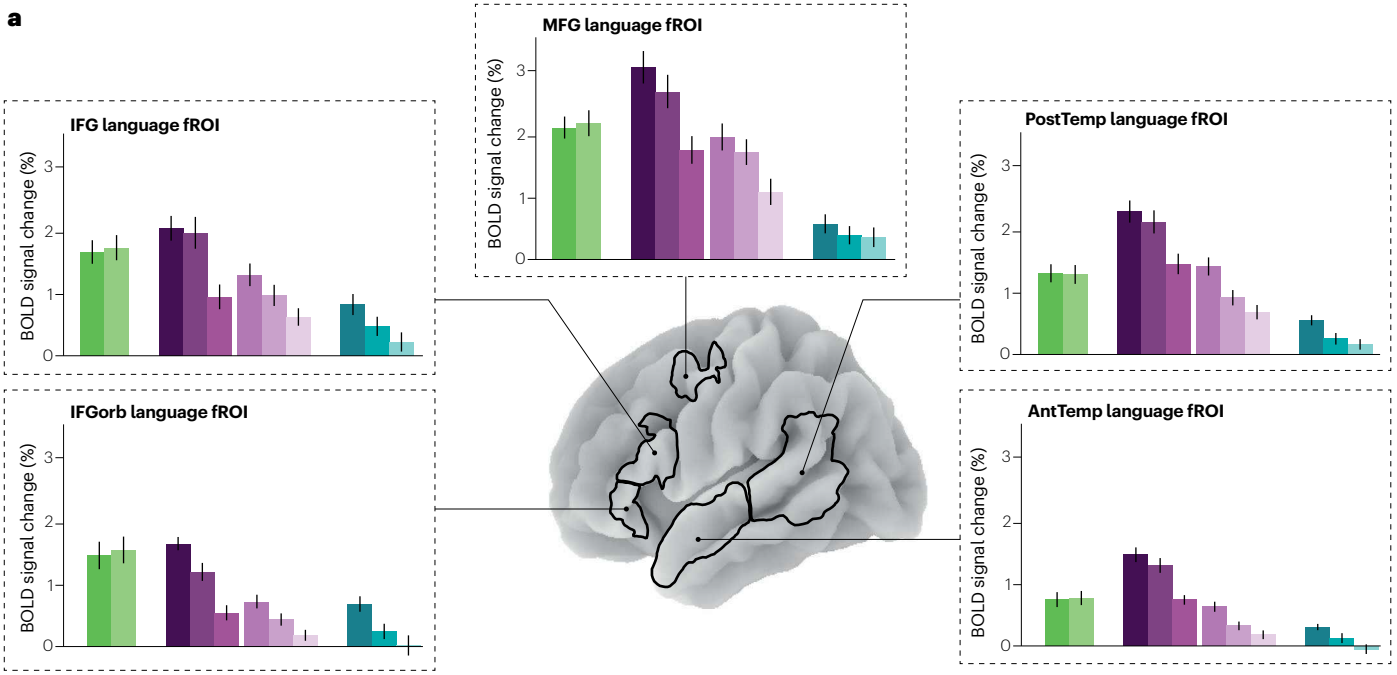
As noted above, the language network is input and output modality-independent (Fig. 2d; see Supplementary Fig. 1). How can it handle such diverse inputs (for example, speech, text and sign) and generate such diverse outputs? The answer lies in the plethora of brain areas that support language-relevant perceptual and motor processes. These areas are distinct from the language network as well as from general-purpose sensory and motor areas, such as the primary auditory or primary motor cortex. Below, we highlight the key functional difference between the language areas and specialized perceptual and premotor areas, and discuss evidence for this difference with respect to both spoken and written language.

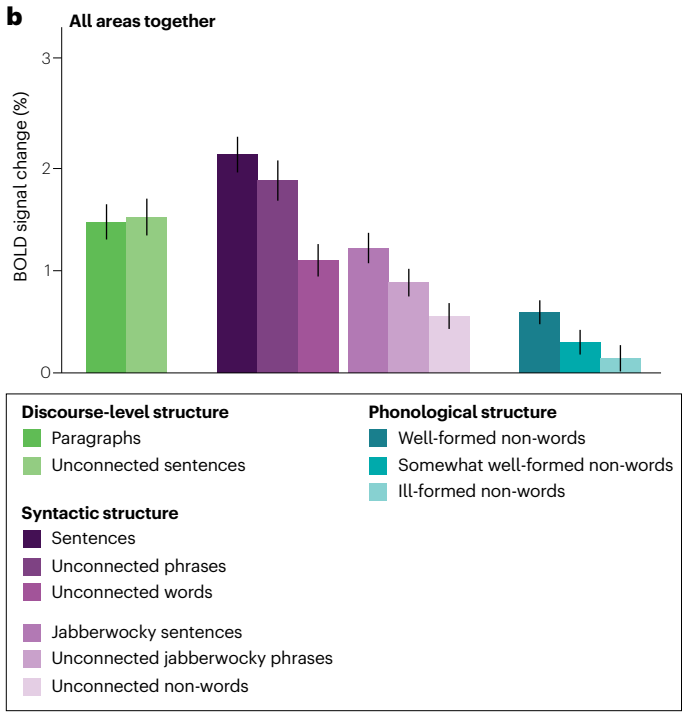
A body of work has demonstrated the existence of brain areas that are selective for speech perception, speech articulation and reading (visual processing of scripts). A key feature that distinguishes these areas from the language network areas is their insensitivity to meaning. In contrast to the language areas, which are robustly sensitive to the meaning of linguistic signals, specialized perceptual and premotor areas are not (Fig. 4). Consider a non-word such as 'blork': although it is not associated with meaning in our lexicon, one can discern the speech sounds upon hearing it, repeat it out loud and read or write it, if one is literate. Thus, the perceptual and premotor areas can still perform their computations given that they exclusively deal with the surface properties of linguistic stimuli, such as the sounds of speech or the visual shapes of the letters. For example, the speech perception area responds as strongly to non-word lists or speech in an unfamiliar language as it does to sentences in a familiar language[204,205]; this pattern of similar responses to meaningful versus meaningless linguistic stimuli also holds for the premotor articulation area (E.F., A. Wolna, J. Szewczyk, M. Diaz, A. Domagalik, M. Szwed, Z. Wodniecka, unpublished work) and the reading area[5,206,207]. (Note that although some have reported sensitivity to lexical and semantic effects within the superior temporal gyrus[208–211], it is impossible to determine — without functional localization — whether these effects arise within the speech perception area or the nearby language area (Fig. 4 and Box 1).) The insensitivity of these areas to the meaning of linguistic stimuli rules out their contribution to higher-level language processes, such as lexical access and syntactic structure building.

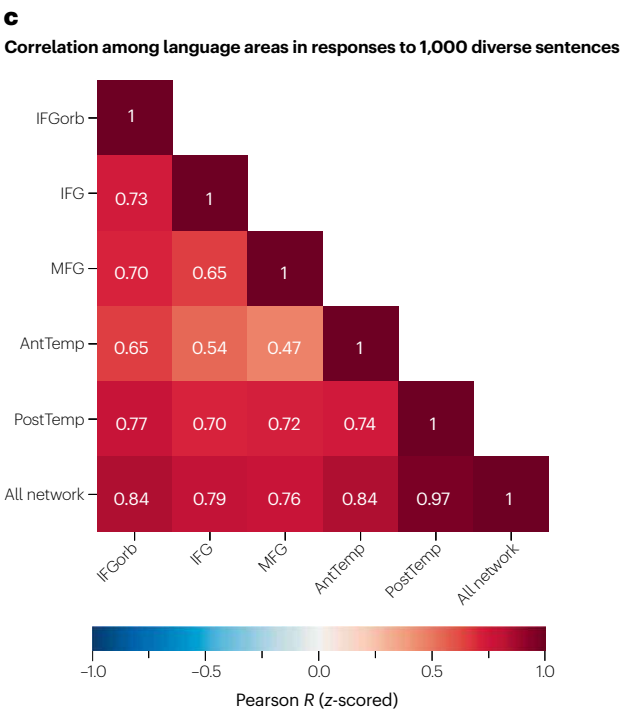
### Speech

**Speech perception.** An area in the superior temporal gyrus and superior temporal sulcus bilaterally responds robustly to speech[4,212,213]. Although debated at some point[214], Norman-Haignere et al.[204] established that this area is selective for speech over diverse natural sound categories (see also refs. 205,215,216). This speech selectivity cannot be reduced to lower-level acoustic features; such features explain less than half of the variance in the speech perception area's response to sounds[204]. As such, this area must be selective for higher-level spectro-temporal structure — variations across the frequency (spectral) and time (temporal) domains in the speech signal — that creates the percept of speech, and may correspond to the area that Wernicke discovered in patients with selective auditory comprehension deficits[63].

Although the computations that the speech perception area performs are a matter of ongoing research, some findings provide important hints. First, this area is sensitive to speech-specific temporal structure, as evidenced by reduced responses to temporally scrambled speech[4,204], and its temporal receptive window is approximately 500 ms[4] — a timescale that falls between syllables and words, in contrast to the longer receptive window of the language areas (a timescale that extends to multi-word sequences), as discussed above. Second, neural populations in the superior temporal gyrus, which encompasses the speech perception area, plausibly support the processing of




phonemes and syllables: some cells and neural populations show selectivity for particular phonetic features such as the place and manner of articulation[213,217], or reflect categorical perception of consonants[213] or the mapping between the formants and vowel categories[218]. In tandem, the evidence suggests that the speech perception area is selective for speech sounds relative to other auditory inputs, tuned to spectro-temporal properties of speech, and supports the early stages of speech processing before word forms are linked to meanings.

**Speech articulation.** Broca[219] described a patient with selective difficulties in articulation. The patient could utter only a single syllable ("tan"[219]), but could make non-speech sounds and oral-motor movements and exhibited no other linguistic or cognitive deficits. A post-mortem autopsy revealed a lesion in the posterior portion of the patient's left inferior frontal gyrus (IFG). The lesion site has since been known as 'Broca's area', although anatomical rather than functional definitions of this area have dominated the literature[220] (Box 1), which has

**Fig. 3 | Sensitivity of the language network to linguistic structure at multiple information scales, and functional similarity of its different areas.** **a**,**b**, Responses in the five left-hemisphere language areas (panel **a**) and in the left-hemisphere language network overall (panel **b**) to linguistic manipulations at three information scales: discourse structure[162], syntactic structure[147] and phonological structure[76]. The language areas all show a similar response profile (despite slight apparent differences, no region by condition interactions come out as reliable, even in well-powered studies[190]). They show a lack of sensitivity to discourse structure, as evidenced by a similarly strong response to unconnected sentences as to connected paragraphs; in other words, the costs associated with inter-sentence connections are not processed by the language areas (see 'The cognitive networks the language network interacts with to support real-life language use' for a discussion of sensitivity to discourse structure in theory of mind and default mode network areas). By contrast, the language areas show strong sensitivity to syntactic structure and to phonotactic well-formedness, with stronger responses to more linguistically well-formed stimuli. For syntactic manipulations, effects of structure are present in both stimuli consisting of real words and stimuli in which words are replaced with non-words (so-called 'jabberwocky' stimuli), although the response to the latter is overall weaker, which shows that lexical information strongly modulates responses in the language network (see also refs. 19,47). In the brain template, black outlines denote 'parcels' (as in Fig. 2a,b), which are derived from a probabilistic overlap map and mark the areas within which the majority of individuals show responses to language; these parcels are used to constrain the selection of functional regions of interest (fROIs) in individual participants (see Supplementary methods), and functional areas in individual brains are a small fraction of these parcels and vary in their precise locations within the parcel (see Fig. 2b,c for sample individual areas). **c**, Correlations among the five language areas with respect to their responses to 1,000 diverse sentences[187] (also shown are correlations between each of the five language regions and the language network as a whole, in the bottom row, which is less critical to the current point). All correlations are high (between 0.47 and 0.77; average 0.667), which suggests that even at a fine-grained level of individual linguistic stimuli (such as sentences), the language areas have similar preferences. AntTemp, anterior temporal; IFG, inferior frontal gyrus; IFGorb, inferior frontal gyrus orbital; MFG, middle frontal gyrus; PostTemp, posterior temporal. Panel **c** adapted from ref. 187, Springer Nature Ltd.

led to much confusion given the functional heterogeneity of the left inferior frontal cortex[131].

Broca's discovery has stood the test of time, with many subsequent investigations confirming the existence of an area in the inferior frontal cortex that supports articulation[6,221–224]. However, the field did go through a period when the role of Broca's area in articulation was questioned. Dronkers[225] performed a lesion overlap analysis for a set of patients who had experienced a stroke in the left middle cerebral artery and exhibited articulatory deficits ('apraxia of speech'). The only shared area of damage in these patients was the superior precentral gyrus of the insula (SPGI), leading to a claim that the SPGI, not Broca's area, is responsible for articulation. However, as Hillis et al.[221] pointed out, Dronkers did not examine the probability that a lesion in the SPGI causes articulatory deficits, which is important given the generally high vulnerability of the anterior insula to damage caused by middle cerebral artery stroke. Hillis et al. examined patients with and without damage in the left insula (as a result of a middle cerebral artery stroke) and did not find an association between insular (including SPGI) damage and articulatory deficits; instead, their analysis revealed a consistent association between damage to the posterior left IFG (Broca's area) and articulatory deficits (see also ref. 226). Moreover, Fedorenko et al.[227] did not find support for the claim that the SPGI is selective for articulation: using fMRI, they showed that the SPGI responds strongly to non-speech oral-motor movements and shows little to no response to articulation, in contrast to Broca's area, which responded strongly to articulation and showed sensitivity to articulatory complexity.

Of course, Broca's area is not the only brain region that enables speech articulation. Brain imaging studies have found that Broca's area, functionally defined (Fig. 4c and Box 1), works closely with several other brain areas as part of the 'articulation network'[6,223]. One such area is the ventral sensorimotor cortex (vSMC). (Although in Fig. 4 we talk about primary motor areas, the somatosensory cortex has long been shown to work closely with the adjacent motor areas for the relevant effectors during movement production[228–230].) As measured with fMRI, Broca's area and the vSMC both respond during the production of speech sounds and show sensitivity to articulatory complexity[223,231], but their contributions to articulation differ. First, they are active during different stages of speech production: Broca's area is active during the preparation of speech motor plans, whereas the vSMC is active during their execution[222]. In line with the somatotopic organization of the vSMC[232], neural populations therein show selectivity for particular articulators (lips, tongue, vocal cords), and contain information about articulator states (such as whether the lips are pursed or the tongue's position)[233]. Second, Long et al.[224] showed that interfering with the activity of these two brain areas leads to different effects on speech articulation: interfering with Broca's area leads to slower speech (apraxia of speech-like symptoms[219,234]), whereas interfering with the vSMC leads to slurring (dysarthria of speech-like symptoms[235]). Last, Broca's area, but not the vSMC, shows some selectivity for speech production relative to the production of non-speech oral-motor movements[223], which explains the existence of selective articulatory deficits in patients with damage to this brain region[219,221,226]. In tandem, the evidence suggests that Broca's area is a critical, most speech articulation-selective node of the articulation network: it prepares speech motor plans and sends them to the vSMC, which implements articulatory movements (but also supports non-speech movements by the lips, tongue and vocal cords; Fig. 4c).

## Reading and writing

Approximately 5,000 years ago, human societies began to develop writing systems. Currently, more than half of the world's ~7,000 languages have written forms[236]. How do our brains process written language — a culturally recent invention?

**Reading.** Dejerine[237] described a patient with a selective deficit in recognizing letters and written words. This patient could recognize other visual objects, could perceive and copy letter shapes, and exhibited no other linguistic or cognitive deficits (even their writing was intact). A post-mortem autopsy revealed a lesion on the ventral surface of the left temporal lobe. More than a century later, brain imaging investigations identified an area in the left ventral visual cortex that appears to support reading ability[238]. This area is known as the visual word-form area (VWFA). When properly defined (for example, by a contrast between words or non-words and line drawings of objects compared with coarser contrasts such as words > checkerboards; Fig. 4c), this area responds similarly strongly to strings of letters and real words[206,207]. Thus, similar to the speech perception area, which processes the auditory form of words (or non-words), the VWFA processes their visual form.

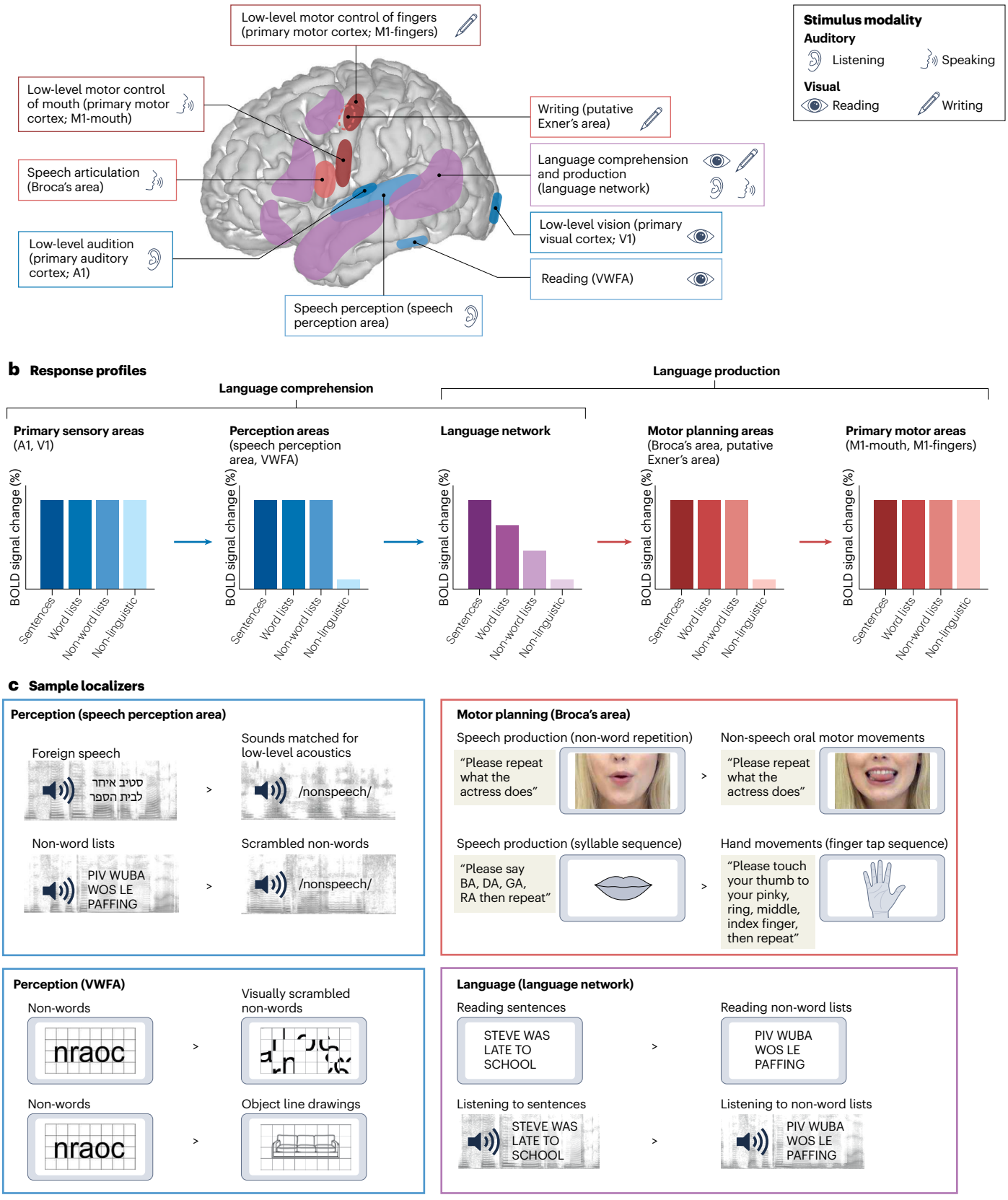

a Brain areas that respond to lingusitic stimuli
Low-level motor control of fingers (primary motor cortex; M1-fingers)
Low-level motor control of mouth (primary motor cortex; M1-mouth)
Speech articulation (Broca's area)
Low-level audition (primary auditory cortex; A1)
Writing (putative Exner's area)
Language comprehension and production (language network)
Low-level vision (primary visual cortex; V1)
Reading (VWFA)
Speech perception (speech perception area)
Stimulus modality
Auditory
Listening
Speaking
Visual
Reading
Writing
b Response profiles
Language comprehension
Language production
Primary sensory areas (A1, V1)
Perception areas (speech perception area, VWFA)
Language network
Motor planning areas (Broca's area, putative Exner's area)
Primary motor areas (M1-mouth, M1-fingers)
BOLD signal change (%)
Sentences
Word lists
Non-word lists
Non-linguistic
c Sample localizers
Perception (speech perception area)
Foreign speech
סטיב איחר לבית הספר
Sounds matched for low-level acoustics
/nonspeech/
Non-word lists
PIV WUBA WOS LE PAFFING
Scrambled non-words
/nonspeech/
Motor planning (Broca's area)
Speech production (non-word repetition)
"Please repeat what the actress does"
Non-speech oral motor movements
"Please repeat what the actress does"
Speech production (syllable sequence)
"Please say BA, DA, GA, RA then repeat"
Hand movements (finger tap sequence)
"Please touch your thumb to your pinky, ring, middle, index finger, then repeat"
Perception (VWFA)
Non-words
nraoc
Visually scrambled non-words
Non-words
nraoc
Object line drawings
Language (language network)
Reading sentences
STEVE WAS LATE TO SCHOOL
Reading non-word lists
PIV WUBA WOS LE PAFFING
Listening to sentences
STEVE WAS LATE TO SCHOOL
Listening to non-word lists
PIV WUBA WOS LE PAFFING

**Fig. 4 | Sensitivity to meaning in the language network, but not in specialized perceptual and premotor areas. a**, Primary sensory (dark blue) and primary motor (dark red) areas, the specialized perceptual areas (blue), which include the speech perception area and the visual word-form area (VWFA), premotor areas (red), which include Broca's area and the putative Exner's area, and the language areas (purple) respond to linguistic stimuli in visual and/or auditory modalities. **b**, The language network (identified with a language network localizer; as in the purple box in panel **c**) is strongly selective for language (showing little or no response to non-linguistic inputs and tasks) and sensitive to the meaning of linguistic messages (with stronger responses to sentences, which convey compositional meanings; weaker responses to word lists, which only convey word-level meanings; and weaker still responses to meaningless non-word lists). This pattern holds for both language comprehension (listening and reading) and production (speaking and writing). The perception areas — the speech perception area (listening) and the VWFA (reading) (identified with localizers as in the blue boxes in panel **c**) — and the motor planning areas — Broca's area (speaking; identified with a localizer as in the red box in panel **c**) and the putative Exner's area (writing) — are also strongly selective for language relative to non-linguistic stimuli. However, in contrast to the language network, these areas are not sensitive to linguistic meaning (showing similar response profiles to sentences, word lists and non-word lists), only to the surface properties of linguistic stimuli. These specialized perceptual and premotor areas have, in turn, distinct profiles from primary sensory and motor areas, which are not selective for linguistic inputs. (It is worth noting that the speech perception area may correspond to Wernicke's area[63] as originally defined (an area in the superior temporal cortex that stores 'sound images' of words; cf. anatomical definitions that have dominated the field[220]), but this relationship deserves a more extensive discussion, which is beyond the scope of this Review.) **c**, Two sample localizers for the speech perception area (listening to meaningless (to the participant) speech sounds versus acoustically matched control conditions), for the VWFA (viewing meaningless letter strings versus visually scrambled letter strings or object line drawings), for Broca's area (producing meaningless syllable sequences versus non-speech oral-motor movements or hand movements; note that the latter contrast would also activate the sensorimotor cortical areas that control the mouth) and the language network (listening to or reading sentences versus perceptually similar conditions). All brain areas schematically represent average anatomical location; functional areas in individual brains are smaller than these schematic representations, vary in their precise locations and show no or minimal overlap with one another (Box 1). All profiles are schematic but based on data from published studies (speech perception area: refs. 4,204,205; VWFA: refs. 5,206,207; Broca's area: ref. 223; see Supplementary methods).

Similar to the speech perception area, the VWFA is strongly selective: it responds more to letter strings in a familiar script than to other visual stimuli[5,206,207,239]. This area serves as a prime example of experience-driven specialization: it develops as individuals learn to read[240] and it responds only to scripts that individuals are familiar with (for example, it shows a low response to Hebrew letters in individuals unfamiliar with the Hebrew alphabet[206]). Furthermore, in line with evidence from individuals with reading deficits, interfering with the VWFA's activity leads to a temporary inability to identify letters or read words[241]. In tandem, the evidence suggests that the VWFA is a critical, visual word-form selective area: it is tuned to visual properties of familiar scripts and supports the early stages of reading before word forms are linked to meanings.

**Writing.** The neural basis of motor planning and execution during written language production has received relatively limited attention (but see ref. 242). As expected, execution of hand-motor movements recruits the finger and hand areas of the sensorimotor cortex[243,244]. However, whether Broca's area plays a role during written (or signed) language production, in addition to speech articulation, is currently not known. Broca's area may be output modality-independent and have a role in creating motor plans regardless of whether they are eventually implemented by the lips, tongue and vocal cords, or by the fingers and hands. Some evidence seems to support this possibility[245,246]. It is also possible that Broca's area is selective for planning speech motor movements, and a distinct area supports planning motor movements during writing (and perhaps signing). Such an area was proposed by Exner[247,248], but the evidence remains scarce[243]. Individual subject-level investigations may help to further illuminate the motor planning and execution stages of written (and signed) language production.

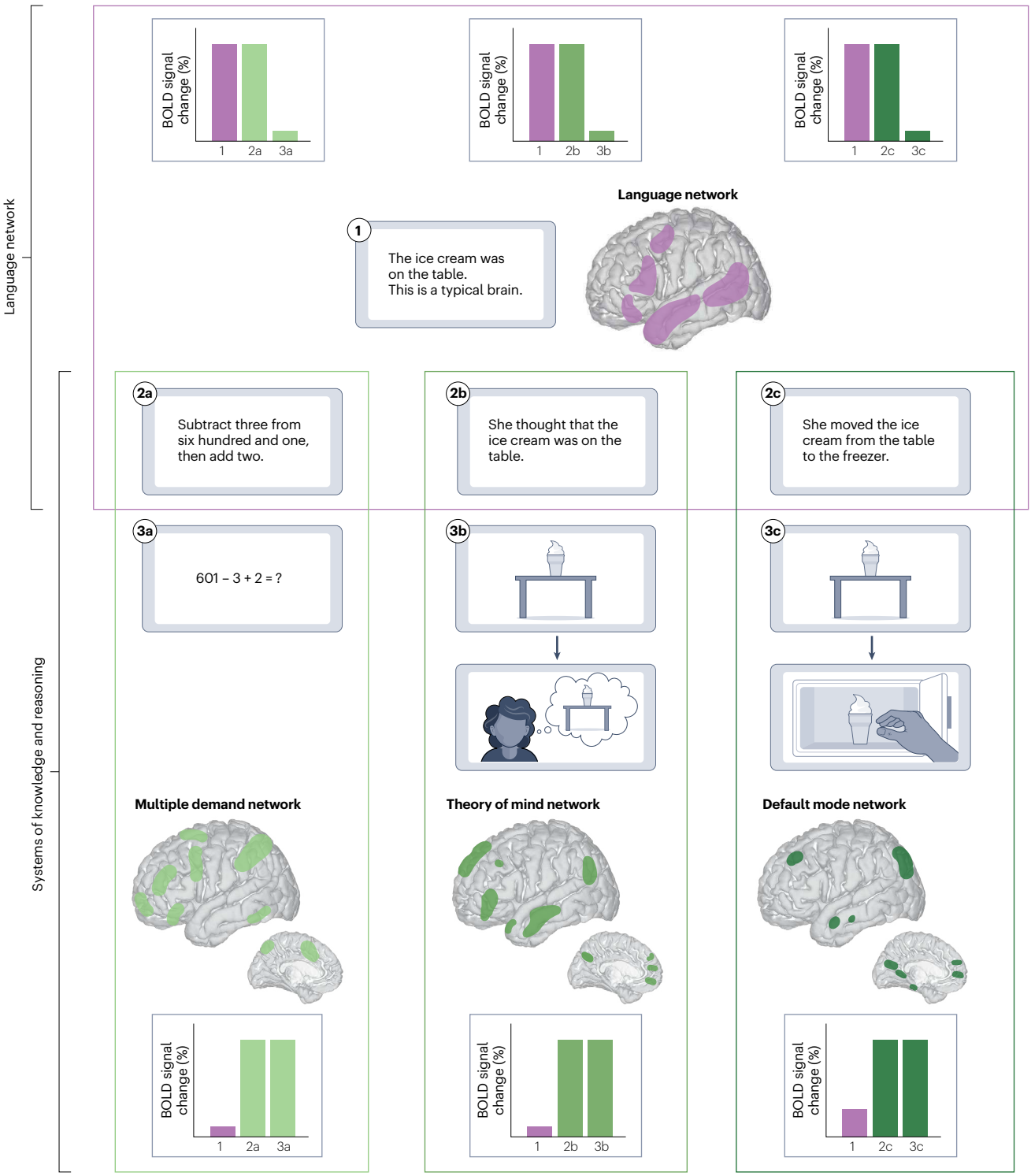
**Summary.** In summary, the language network (Figs. 2,3) is distinct from both perceptual and motor mechanisms (Fig. 4). During comprehension (Fig. 1), linguistic information flows from general-purpose sensory systems (most commonly, primary auditory and visual cortical areas) to specialized perceptual systems (such as the speech perception area or the VWFA) before reaching the language areas. Of course, linguistic context (processed in the language network) affects these perceptual processes[249–251]. During production (Fig. 1), the language network formulates linguistic messages (by converting conceptual representations into word sequences), and then — for spoken production — passes them to Broca's area, which prepares motor-articulatory plans and sends them to primary motor areas for execution. The passing of information from the language areas to Broca's area may proceed via the speech perception area (which may be needed to convert words into sound sequences) or a subset thereof that specifically implements the auditory to sensorimotor transformation[137,252]. The systems that support motor planning and execution for written and signed language production deserve more attention.

## The cognitive networks the language network interacts with to support real-life language use

The language network is neither the starting point during production nor the end point during comprehension (Fig. 1). During production, it receives input from the systems that support our ability to think and encodes them into a word sequence. During comprehension, the language network decodes the input it receives from specialized perceptual areas and passes it to other cognitive systems, which can use this new information to update existing knowledge structures and to reason about and act in the world.

Tight integration between language and the rest of the mind is critical for efficient language use in real-world situations. Language is a tool that allows humans to acquire knowledge, share new ideas, build relationships, and make and follow requests (see ref. 253 for a recent discussion). These behaviours necessarily require fast and continuous interaction between language processing and other cognitive capacities, such as executive functions, social cognition and general world knowledge. Moreover, empirically, some cognitive processes that may seem to be essential parts of language — such as building discourse-level structure by connecting information across sentences — draw on cortical areas that lie outside the language network and support computations that are not specific to language (Fig. 5 and Box 2).

Below, we discuss three neural systems that work with the language network to support real-life language use. A key feature that




distinguishes these systems from the core language areas is their lack of selectivity for language (Fig. 5). In contrast to the language network (Fig. 2d), they respond to cognitive demands or to particular semantic content regardless of whether the information is delivered through language or other representational means.

## Multiple demand network: task demands beyond comprehension and production

**Network properties.** The multiple demand network comprises bilateral frontal and parietal, medial prefrontal and posterolateral inferior temporal domain-general areas that are active during

**Fig. 5 | Selectivity for language in the language network, but not in systems of knowledge and reasoning.** The language network responds to diverse linguistic content but is strongly selective for language over diverse non-linguistic input and tasks, including mathematics[91,103] and meaningful pictorial or video inputs[112,118]. This selectivity of the language system (purple) is reflected by strong responses to random unconnected sentences (1) and semantically diverse sentences (2a, 2b, 2c) but not to mathematical expressions (3a) or meaningful pictures or videos (3b, 3c). By contrast, systems of knowledge and reasoning respond to content irrespective of whether this content is delivered verbally or in another format, so they are not selective for language. For example, the multiple demand network (light green) responds to mathematical statements presented as sentences (2a) or as mathematical expressions (3a)[22], but not to sentences that do not have the right kind of content and that are not accompanied by a task (1)[68]. The theory of mind network (mid-green) responds to stimuli that invoke thoughts about mental states (knowledge, beliefs, desires) presented verbally (2b) or as pictures or videos (3b)[69,279,281], but not to sentences that lack mental state content (1). The default mode network (dark green) responds to connected narratives, verbal (2c) and pictorial (3c)[306,307], but not to unconnected sentences (1). All brain areas schematically represent average anatomical location; functional areas in individual brains are smaller than these schematic representations, vary in their precise locations and show no or minimal overlap with one another (Box 1). All profiles are schematic but based on data from published studies (see Supplementary methods).

diverse cognitively challenging tasks, with stronger responses during more difficult conditions or tasks[7,254–259] (Fig. 5). The hard > easy response signature holds across tasks that differ in the representation format (spatial versus verbal working memory tasks) and the nature of the task (mathematical problems, logic puzzles, novel task learning)[254,256,258,259]. Activity in the multiple demand network has been linked to constructs such as working memory, cognitive control and attention — all critical ingredients of goal-directed behaviours. Individual differences in the activity in this network have been linked to differences in fluid intelligence[260] and damage to this network is associated with a reduction in executive abilities and fluid intelligence[261–264].

**Dissociation from the language network.** The multiple demand network and the language network are robustly dissociated, as evidenced by neuroimaging studies, both task-based and naturalistic[23,56,57,109,132,256,265], and studies of individuals with brain damage[266,267]. This dissociation holds even when examining responses to linguistic difficulty: in particular, linguistic difficulty manipulations tax the language network and elicit little or no response in the multiple demand network[24,68,143,147,268] (see ref. 13 for a review).

**Contributions to language.** First, the multiple demand network is recruited in the presence of task demands beyond language comprehension or self-generated language production, such as answering a question, deciding whether a word was present in a sentence or naming a picture on demand[60,68]. Second, it is required for processing certain types of content, such as mathematical or logic statements[22,103,105–107]. As noted in its properties above, in stark contrast to the language network, the multiple demand areas process these types of content regardless of the format in which it arrives (for example, the expression '601 − 3 + 2 =' versus the sentence 'Subtract three from six hundred and one, then add two'; Fig. 5). Last, the multiple demand network is engaged in some cases of effortful language comprehension, such as when processing acoustically degraded, temporally compressed or accented speech[65,269,270]; when listening to speech in a foreign language in which one has limited proficiency[73]; or when reading at fast presentation rates[65]. Some have also argued that parts of the multiple demand network can support language processing following damage to the language network[271–275]. However, this claim remains controversial; a few studies and meta-analyses have failed to find evidence of the multiple demand network's engagement during language processing in individuals with aphasia[276–278] (see also ref. 276 for alternative explanations of the putative evidence for the multiple demand network's engagement).

### Theory of mind network: pragmatics and social reasoning

**Network properties.** The theory of mind network comprises, most prominently, brain areas in the bilateral temporo-parietal junction and along the cortical midline that are engaged when one is thinking about one's own or others' mental states[8,279–281]. This engagement generalizes across the mental state's content, format (linguistic versus pictorial or video) and evidence source[8,279,281–284] (see ref. 285 for a review). By adulthood, these areas, especially the component that resides in the right-hemispheric temporo-parietal junction, become exquisitely selective for theory of mind relative to processing diverse other kinds of socially relevant information: they do not respond to social stimuli (such as faces, voices or biological motion[101]), to descriptions of another person's physical attributes, bodily sensations or broadly social attributes[280,281,286], or to general executive demands[284].

**Dissociation from the language network.** The theory of mind network is anatomically and functionally distinct from the language network. These networks show different response patterns in diverse experimental paradigms[101,117,118] and they track different information when processing rich naturalistic stimuli[69]. They also dissociate in their patterns of inter-area correlations during naturalistic cognition[23,57,132]. Last, even severe damage to language processing mechanisms can leave social reasoning unimpaired[124,126,127,287,288].

**Contributions to language.** First, the theory of mind network is engaged during some aspects of non-literal language comprehension, including phenomena such as sarcasm, indirect speech and conversational implicature, where understanding the meaning of an utterance requires inferring the beliefs, desires and intentions of the speaker[289–292] (see ref. 293 for a review; see ref. 294 for a meta-analysis). Second, this network — along with the default mode network, as discussed below — supports the processing of discourse-level structure: relationships between clauses in narratives[162,295]. Third, it is more strongly engaged during the processing of conversations compared with monologues[70], presumably because of the greater demands on representing different perspectives. Last, the theory of mind network supports the processing of semantic content related to mental states in both texts and movies[69,280,281,295].

### The default mode network: narratives and situation modelling

**Network properties.** The default mode network owes its name to the fact that it is more active at rest (the 'default' state) than during externally oriented demanding tasks[296]. This network comprises, most prominently, bilateral areas in the medial prefrontal and medial parietal cortex, around the temporo-parietal junction and in the temporal pole. Although the default mode network's topography

## Glossary

### Aphasia
Impairments in understanding and/or producing language as a result of brain damage (such as stroke or neural degeneration).

### Apraxia of speech
Impairments in producing sounds, syllables and words because of neurological problems with speech motor planning; speech of individuals with apraxia contains sound distortions, groping for sounds and errors in stress or rhythm, but they do not have difficulties making non-speech oral-motor movements.

### Causally important
For a particular function, if interfering with a neural unit's (such as a cell or a brain area) activity or structural integrity leads to observable impairment of that function.

### Compositional semantics
The system of relationships between phrases and sentences and meanings; a key principle of compositional semantics in natural language is that the meaning of a multi-word sequence (for example, a phrase) is determined by the meanings of the composite words and the syntactic rules that were used to combine those words.

### Constructions
Learned pairings between a linguistic form and meaning; importantly, constructions encompass not only single morphemes and words but also multi-word sequences, which can correspond to complex meanings.

### Contrast
A pair of conditions that differ in a critical (stimulus-related or task-related) feature of interest; localizers use a particular contrast to localize a brain area or areas that support some perceptual, motor or cognitive function.

### Discourse
The system of relationships among clauses and sentences in multi-sentence sequences, including narratives and conversations.

### Double dissociations
Complementary cases of selective deficits in two perceptual, motor or cognitive functions (for example, if in one individual, language is impaired but general reasoning is preserved, but in another individual language is preserved but reasoning is impaired); or selective relationships between two brain areas and two perceptual, motor or cognitive functions where brain area A supports function F1 but not function F2, and brain area B supports function F2 but not F1 (for example, damage to the language areas leads to difficulties in understanding and producing language but leaves abilities supported by the multiple demand network, such as executive abilities and formal reasoning abilities, unimpaired; by contrast, damage to the multiple demand network areas leads to difficulties with executive control and reasoning but leaves linguistic functions unimpaired).

### Dysarthria of speech
Impairments in producing sounds, syllables and words because of weakening or improper coordination of the muscles of the articulatory organs (caused by brain or nerve damage); speech of individuals with dysarthria sounds slurred or mumbling and they also have difficulties in making non-speech oral-motor movements.

### Functional connectivity
Correlation in activity patterns between different brain areas, often measured during naturalistic cognition paradigms.

### Functional localization
An analytic approach that aggregates brain data from multiple participants while taking into account inter-individual differences in the precise locations of functional areas. This approach uses a localizer to find areas of interest within individual participants' brains and then measures the response in these areas to some condition(s) of interest; group-level statistical comparisons are performed on the measures extracted from the individually identified areas, which circumvents the need to average brains.

### Group-averaging
An analytic approach that aggregates brain data from multiple participants by averaging individual brain images projected into a common coordinate space; because functional areas vary in their precise locations across individuals, this approach leads to blurring and can generate misleading results.

### Homotopic areas
Each brain area exists in two copies — one in each hemisphere; an area in one hemisphere that is the corresponding area in the other hemisphere (for example, the areas homotopic to the language areas are areas in the right hemisphere that correspond to the left-hemisphere language areas).

### Language processing pipeline
A set of perceptual, motor and cognitive processes that jointly enable language comprehension or language production: in comprehension, the pipeline encompasses perceptual processing of linguistic inputs, mapping linguistic forms to meanings and integrating these meanings with preceding linguistic context and non-linguistic knowledge sources; in production, the pipeline encompasses the transformation of intended meanings into linguistic form, and planning and generating the physical output.

### Lexical semantics
The system of relationships between word forms and word meanings.

### Linguistic regularities
Structure, or regular patterns, in linguistic sequences; regular patterns characterize all levels of language, from sounds to words, to sentences, to connected discourses.

### Meanings
The meanings of words and phrases (for example, the word 'dog' has meaning to an English speaker, whereas the word 'chien' ('dog' in French) or a non-word 'xog' does not have meaning to an English speaker, under typical circumstances); or a collection of associative, abstract and generalizable knowledge associated with a given cue, either linguistic or non-linguistic (for example, the word 'dog', a picture of a dog and the sound of a dog's barking are all associated with a similar meaning, although different cues or contexts may make some aspects of the meaning more or less salient).

### Modality-independent
If a brain area responds to stimuli across different input or output modalities (for example, spoken language, written language or signed language).

### Morphology
The system of relationships among 'morphemes', which are the smallest meaning-bearing units in a language; morphemes can be complete words, such as 'cat', but also word parts, such as '-ful' and 'anti-'.

### Naturalistic cognition paradigms
Paradigms that do not rely on controlled, experimenter-crafted conditions and contrasts but, instead, present rich naturalistic stimuli (such as movies or narratives) or feature open-ended designs, such as a resting state (task-free, stimulus-free periods during the study).

### Phonology
The system of relationships among speech sounds in a language; the rules that govern the possible combinations and orderings of sounds are called phonotactics.

## Glossary (continued)

**Single dissociation**
A selective deficit in a perceptual, motor or cognitive function (for example, aphasia is a selective deficit in understanding or producing language); or a selective relationship between some brain area and a perceptual, motor or cognitive function (for example, brain damage to the language areas leads to aphasia but leaves other cognitive processes unimpaired).

**Surface properties of linguistic stimuli**
Properties that are tied to the form of a linguistic stimulus; the form is determined by the input or output modality (for example, for speech they have to do with the speech sounds, and for written language they have to do with the visual shapes of letters).

**Syntax**
The system of constraints on how words can combine into phrases and sentences to create complex meanings.

**Tasks**
What participants are asked to do during an experiment (for example, passive reading or answering comprehension questions).

**Theory of mind**
The ability to understand and take into account another individual's mental state.

resembles that of the theory of mind network and some have argued that the two networks are overlapping or the same[297,298], evidence from individual-subject approaches (Box 1) shows that these two networks are functionally distinct although their component regions are located in close proximity[23,115,132,299,300]. The exact role of the default mode network in cognition is debated, with different studies linking it to episodic projection[9,132,300], self-directed processing[301,302], internal scene construction[303] or spatial information processing (based on one non-peer-reviewed preprint[115]). The key property of the default mode network that concerns us here is its sensitivity to long-range temporal contexts. In contrast to the language network's receptive window of a few words, the default mode network's receptive window is on the scale of minutes, which allows it to connect information across multiple sentences or events[159,161,198,304]. The default mode network's activity reflects high-level differences in people's information processing (for instance, whether the person watching a movie knows the ending[305]), and encodes specific event schemas, such as going to a restaurant or boarding a plane[306]. Thus, the default mode network appears to track abstract, input-invariant, global situational context.

**Dissociation from the language network.** Similar to the multiple demand and theory of mind networks, the default mode network is not language-selective: it tracks long-range information for both linguistic and non-linguistic inputs[306,307]. Furthermore, the default mode network encodes information in an input-invariant way, such that patterns of response to a particular event schema (such as going to a restaurant) are as similar between a story and a movie as between two stories[306]. Thus, the informational content of the default mode network is abstract. Last, the default mode network clearly dissociates from the language network in its response profile[132,265], functional correlation patterns[23,132] and how brain damage or stimulation in relevant areas affects behaviour[308,309].

**Contributions to language.** The default mode network's long temporal receptive window allows it to track not only sentence-level but also discourse-level linguistic structure. Indeed, this network is recruited for coherent texts more than for disconnected sentences[295,310,311] and can integrate information over multiple sentences[159,161,193,199,201]. Thus, the task of constructing a coherent overall representation of a narrative or a dialogue requires not only the language network but also the non-language-specific default mode network areas. (If the hypothesis about the bias of the default mode network towards spatial information is correct[115], then this network may also be important for interpreting linguistic meanings that deal with spatial layouts.)

**Summary.** Thus, real-life language use involves joint recruitment of the language network and brain networks that are required for other cognitive functions. We discussed three higher-order networks whose role in language processing is best understood (Fig. 5). Other systems, including the emotion-processing centres, visual object recognition areas and areas that support social perception, almost certainly come into play as well in different language-use scenarios. Understanding how the different networks interact and share information remains a challenge for future research.

## Open questions and a way forward

How does neuroscience contribute to our understanding of language and its relationship with the rest of the human mind? Perhaps most importantly, it enables us to build an empirically validated cognitive ontology[312,313] of basic processes that contribute to language comprehension and production (Fig. 1 and Box 2). Some of the distinctions that we have discussed here have been previously postulated on theoretical grounds; some have further been supported by evidence from behavioural experiments, including in patients with brain damage. However, fMRI as a tool is unparalleled for uncovering the structure of the mind: its non-invasive nature, relatively high spatial precision and whole-brain coverage, when combined with careful experimentation, can reveal which cognitive processes share machinery and which are supported by distinct resources[314]. The functional localization approach (Box 1) has proven a powerful way to accumulate knowledge and has helped paint a rich and detailed picture of the ventral visual stream[314] and higher-level cognitive systems, such as the theory of mind network[285] and, now, language processing (Fig. 1).

What is next in cognitive neuroscience of language? We outline some directions below.

### The problem of meaning

A core distinction between the language network and adjacent perceptual and premotor areas is that the language network is sensitive to meaningful linguistic content. Does this sensitivity imply that the language network is sensitive to any meaningful (semantic) content, whether it is verbal or non-verbal? We argue that this is not the case: meaningful non-verbal inputs (such as pictures or videos) activate the language areas weakly or not at all[60,107,111–113,188] (Fig. 2d; see Supplementary Fig. 1), and individuals with damaged language areas retain the ability to understand the world around them[111,112,124,125]. Thus, the language network responds to meaningful language, not to meaning in general.

Furthermore, the kinds of meaning that the language network responds to can be superficial and not make sense with respect to one's

world knowledge. For example, the language areas respond strongly to well-formed but incoherent sentences, such as "Colourless green ideas sleep furiously"[315]. At the same time, naturalistic language understanding engages a broad set of brain areas beyond the language network[20,159]. Thus, we speculate that language understanding includes two distinct meaning-making components: the language network extracts the lexical forms (words) from linguistic inputs, accesses their meanings and combines them using syntactic and compositional semantic rules; and this resulting representation is integrated with information from other brain regions to enable deep, context-sensitive and actionable language understanding.

How does the language network pass information to downstream brain systems? What is the format of this information and what computations are used to integrate linguistic information with other inputs and the brain's internal states? These questions remain wide open. Some have argued that semantic information is broadly distributed across the brain[20]; others that certain regions act as amodal semantic 'hubs'[316]; and yet others that linguistic meaning is fundamentally grounded in sensorimotor representations[317]. In this Review, we do not commit to a particular theory of meaning, although we recognize that the account of language as a system of computations that transform form to meaning should ultimately specify what the end point of those transformations looks like.

Finally, our account of language comprehension as information transfer from perception areas to the language network and then to higher-order cognitive networks (Fig. 1) will eventually need to account for the vast body of psycholinguistic work that shows that non-linguistic sources of knowledge can affect language processing early on[318–323]. The blurred lines between linguistic and non-linguistic modulators of language processing have sometimes led to scepticism regarding the separability of language from the rest of cognition[324,325] (Box 2). However, we believe that this tension can eventually be resolved through a better understanding of the top-down influences of higher-order cognitive networks on the language network and of the ways in which some of these effects may be explained by language network internal processes without requiring sophisticated cognitive processing (after all, distributional linguistic information, which is presumably stored within the language network, contains a wealth of knowledge about the world[326–328]).

### Sharp edges versus functional gradients

We have discussed a few functional distinctions, including those between the language areas and perceptual and premotor areas (Fig. 4), and between the language areas and areas that belong to other cognitive networks (Fig. 5). Although we have schematically drawn these various areas as 'blobs' with sharp edges, none of our arguments hinge on this property of the functional regions. Future studies should use high spatial resolution tools to test the nature of the boundaries between nearby areas. For example, one could test whether there is a gradual functional change between the speech perception area and the nearby temporal language area, with some cells that fall between the speech and the language area showing mixed selectivity. Importantly, the existence of such gradients would not detract from the fact that the peaks in this functional landscape are robustly functionally different, which makes them interesting as objects of investigation (see ref. 314 for a discussion).

### A mechanistic understanding of language processing

One set of questions concerns the separable individual components of language comprehension and production (Fig. 1). A rich characterization of the functional profiles of these different components, including their selectivity for particular kinds of inputs or tasks, critically constrains the computations they are likely to support, but more work is needed to actually decipher the nature of those computations. Doing so will likely require synergistic use of diverse research tools, including the emergent ones such as intracranial human recordings, which continue to increase in their sophistication[217,329], and artificial neural network models, which accurately capture neural responses in diverse perceptual, motor and cognitive domains[330,331], including speech and language[187,193–196,332] (see ref. 333 for a review).

Another set of questions concern the interaction of different components with each other during complex behaviours. For example, how do representations get transformed and/or compressed as they are passed from the speech perception area to the language network and then to higher-order cognitive systems? Or how do non-linguistic information sources affect language processing, as has long been shown to be the case[318–323]? Such questions require high-density temporally resolved recordings in multiple brain areas simultaneously – methods that are not currently available, even in animal neuroscience. Building multicomponent artificial neural networks – for example, networks that combine a language component and a component for world knowledge or some aspect of reasoning (see ref. 334 for a discussion in one preprint article yet to undergo peer review) – may help get some traction on these questions.

### Language in development and evolution

Differentiating the language network from other components of language processing is likely to accelerate progress in our understanding of language development. Developmental research has already provided ample evidence for dissociation between language, speech perception and articulation, and higher-level cognition. For instance, the ability to discriminate phonemes and languages develops long before language comprehension[335,336], babbling precedes word production[337,338] and higher-order cognitive abilities (such as executive control and theory of mind) develop later than linguistic abilities and take time to mature[339,340]. Tracing the emergence of the earliest speech perception and articulation brain mechanisms, and understanding their role in language acquisition and in the development of the language network, as well as the integration of the language network with other brain areas over developmental time, remain critical areas of future work. Disentangling different components supporting language behaviour is also critical for studies of language evolution. In cross-species comparative research, distinct homologies must be established for the perceptual, motor and higher-level (meaning-sensitive) components of animal and human communication systems.

### Language as a tool to augment thought

Last, differentiating the language network from the systems of knowledge and reasoning is likely to help us to understand the role of language in human cognition. As reviewed, several higher-level cognitive systems (implemented in the multiple demand, theory of mind and default mode networks) that support different aspects of thought are important for many aspects of language use but are, critically, not language-selective. As a result, some individuals with even severe aphasia can nevertheless retain the ability to reason, plan and understand the world[341]. That said, under certain conditions, language might play a supportive role for certain cognitive functions. For example, the availability of linguistic labels can help people to perform working memory tasks[342], numerical tasks[343] and concept-learning tasks[344–346], although

a mechanistic understanding of how the language network helps during these tasks is currently lacking. For instance, Benn, Ivanova et al.[111] showed that an object categorization task that was previously argued to rely on language resources[3,47] did not actually recruit the language network. Exploring whether, when and why the language network might be involved in non-linguistic behaviours provides a critical test for theories that place language at the core of complex thought[95–97,348,349].

In conclusion, the language network constitutes a natural kind, distinct from both language-relevant perceptual and motor mechanisms and from cognitive systems that support real-life language use. These distinctions provide a critical foundation for both in-depth investigations of each individual component of language processing ("divide and conquer"[14]) and for probing inter-component interactions, paving the path forward for the twenty-first-century neuroscience of language.

## Data availability

The data used to generate the activation maps in Fig. 2a,b were released as part of Lipkin et al.[49] and are available for download at https://figshare.com/articles/dataset/LanADataset/20425209. The data used to generate Fig. 2c were released as a supplement to Mahowald and Fedorenko[51] and are available at: https://doi.org/10.6084/m9.figshare.22183564. The data used to generate the bar graphs in Figs. 2d and 3a,b come from published and pre-printed papers but, for convenience and ease of figure reproducibility, have been consolidated and placed on a dedicated Open Science Framework (OSF) page: https://osf.io/4tdcx/ (see Supplementary methods for details).

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## Author contributions

The authors contributed equally to all aspects of the article.

## Competing interests

The authors declare no competing interests.

## Additional information

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