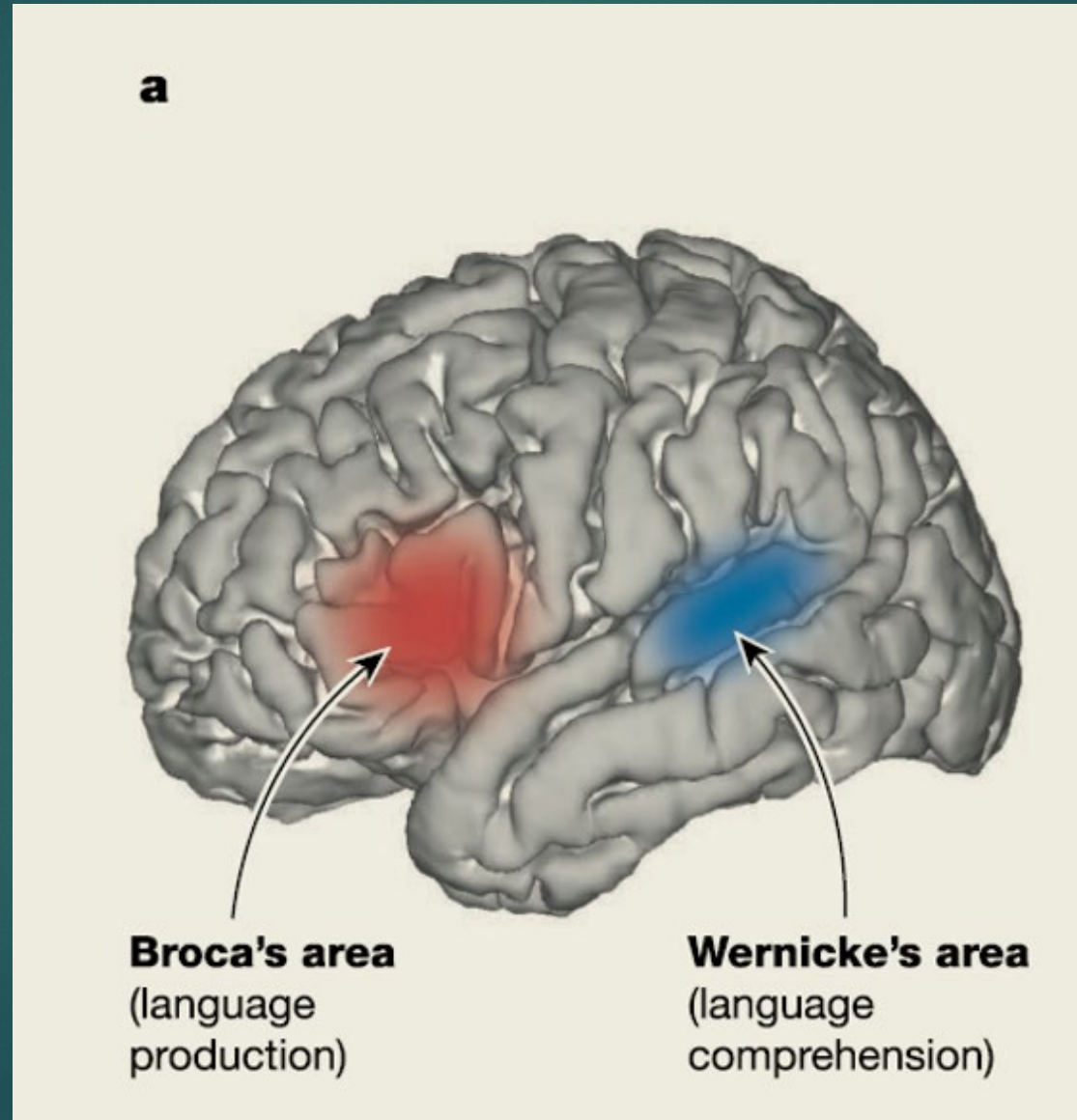


Evolution of Language  
February 2025  
by  
Charles J Vella, PhD

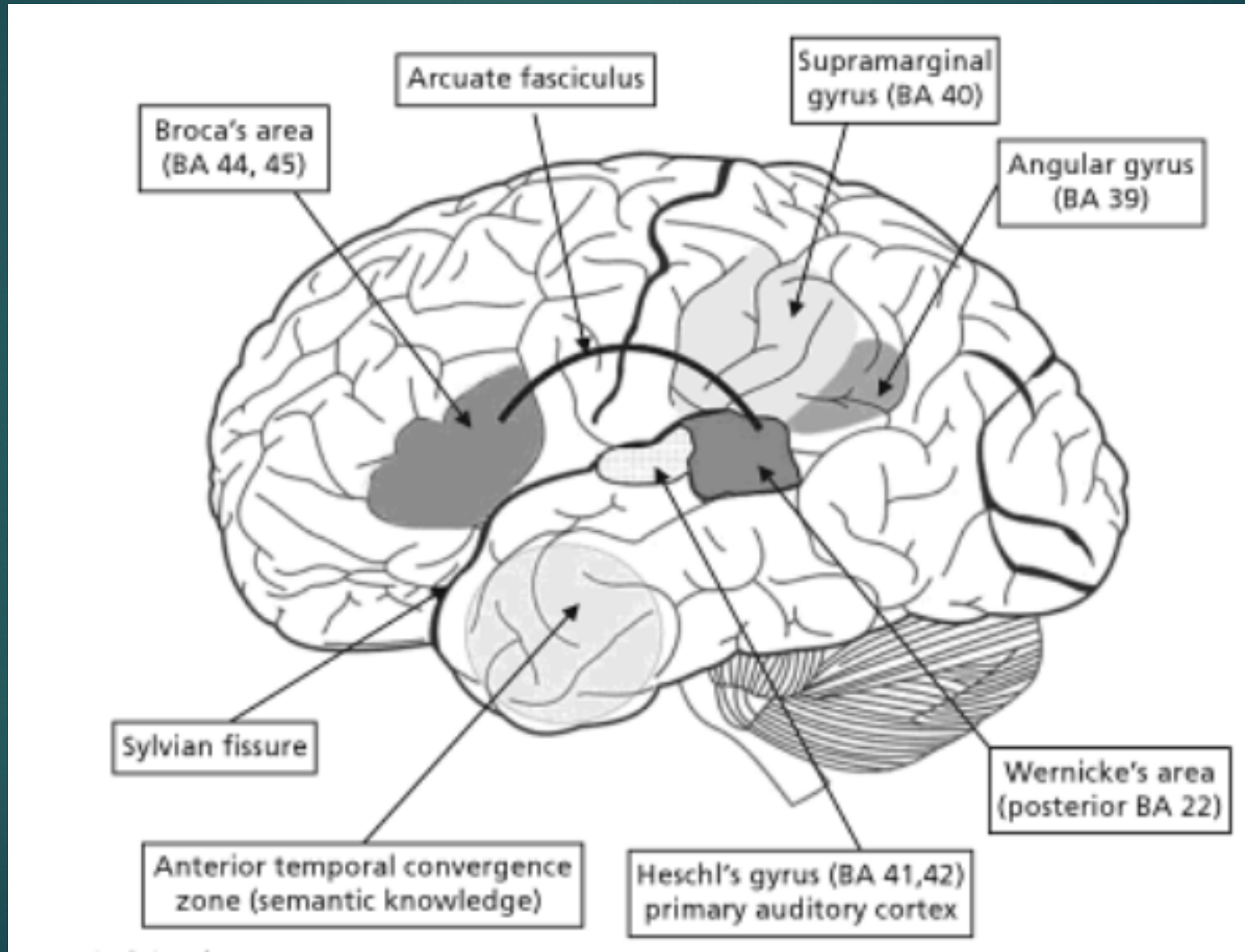
# Dynamic networks model

- ▶ Brain isn't just functionally modular, with highly localized processors. While certain regions are specialized to process certain types of information and are active during certain tasks, they are all part of distributed functional networks.
- ▶ The Central Nervous System is an integrated, wide, dynamic network made up of cortical functional epicenters connected by both short-local and large-scale white matter fibers.
- ▶ Brain function results from parallel streams of information dynamically modulated within an interactive, multimodal, and widely distributed circuit.

# The classic model of the neurobiology of language,



# Multiple Language Areas



Tractography:  
Tracing of  
white matter  
fibers

Arcuate  
fasciculus =  
classically  
highway  
between  
Broca's and  
Wernicke's




19th century



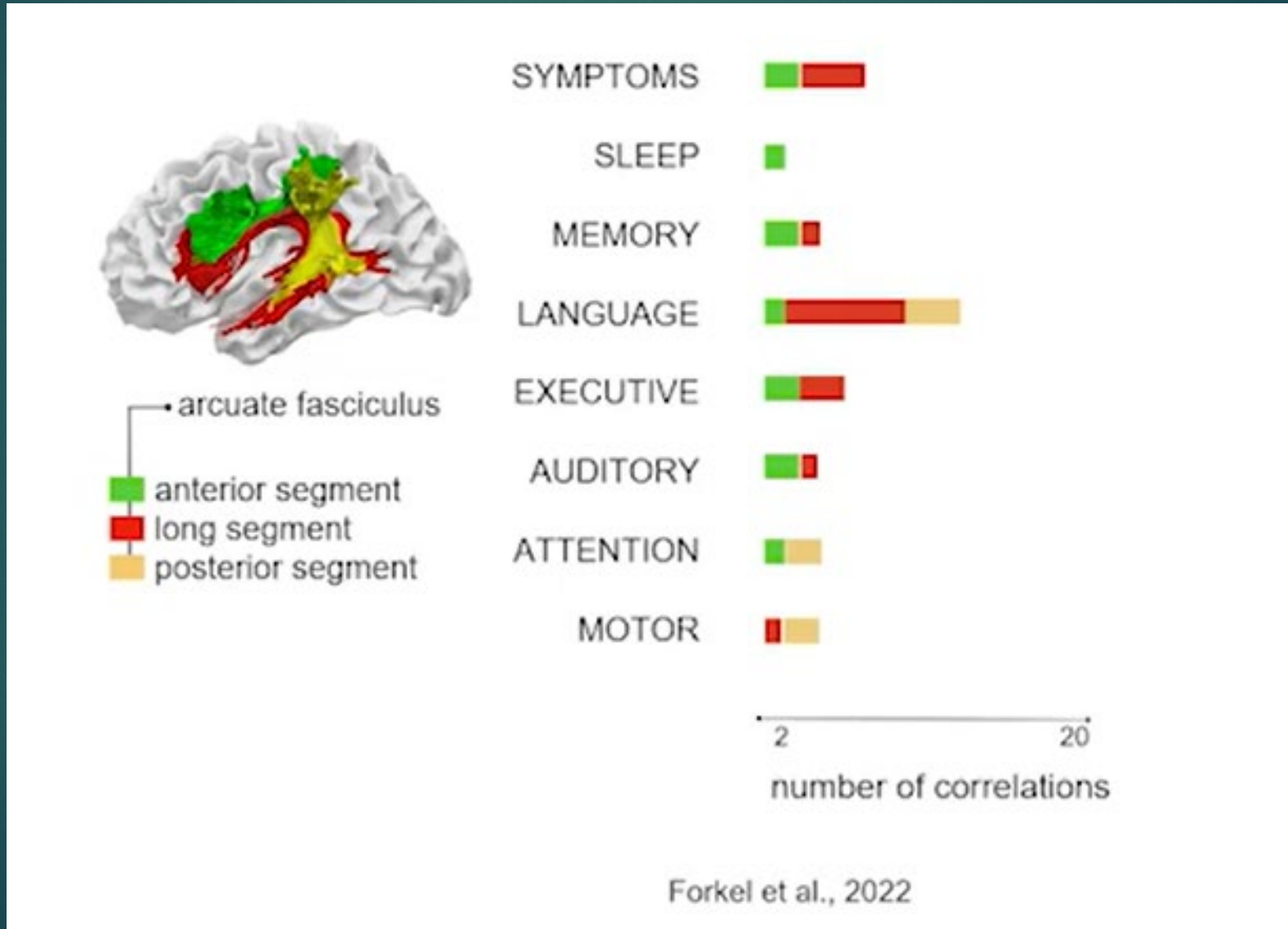
Arcuate fasciculus

## Early 2000s

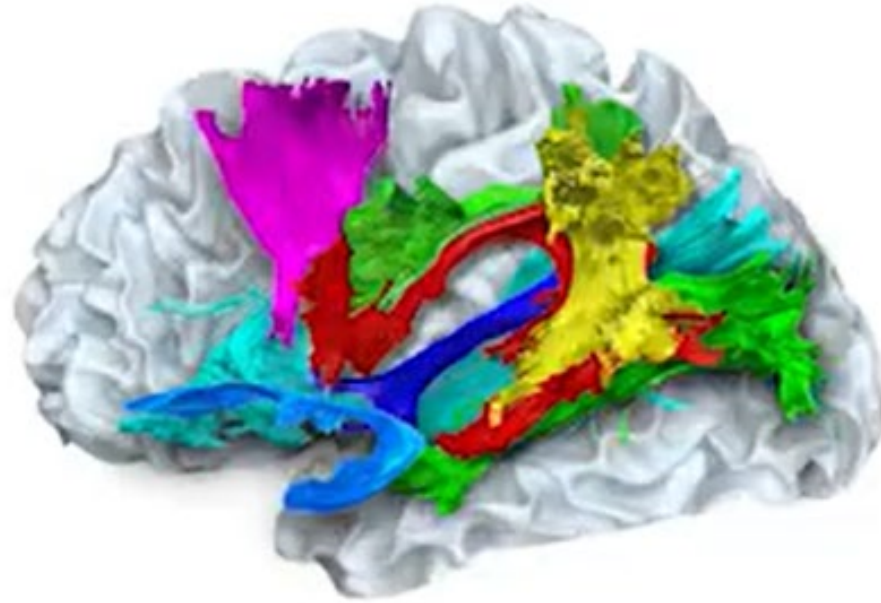


-  Anterior segment
-  Long segment
-  Posterior segment

# Arcuate fasciculus: multiple functions – dynamically recruited based on what brain needs: ‘one tract-one function’ does not hold



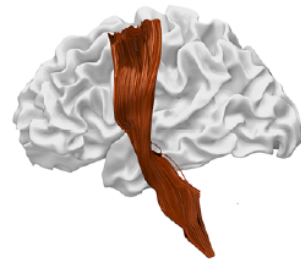
## 21st century



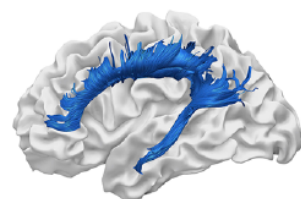
-  Frontal Aslant Tract
-  Uncinate fasciculus
-  Temporal longitudinal fasciculus (TLF)
-  Inferior fronto-occipital fasciculus (iFOF)
-  Inferior longitudinal fasciculus (ILF)



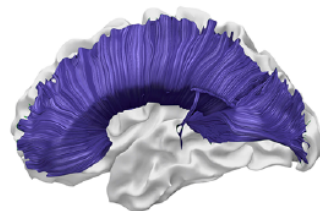
# Multiple functions for each major white matter system



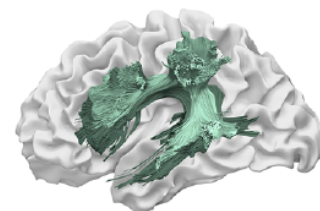
corticospinal tract



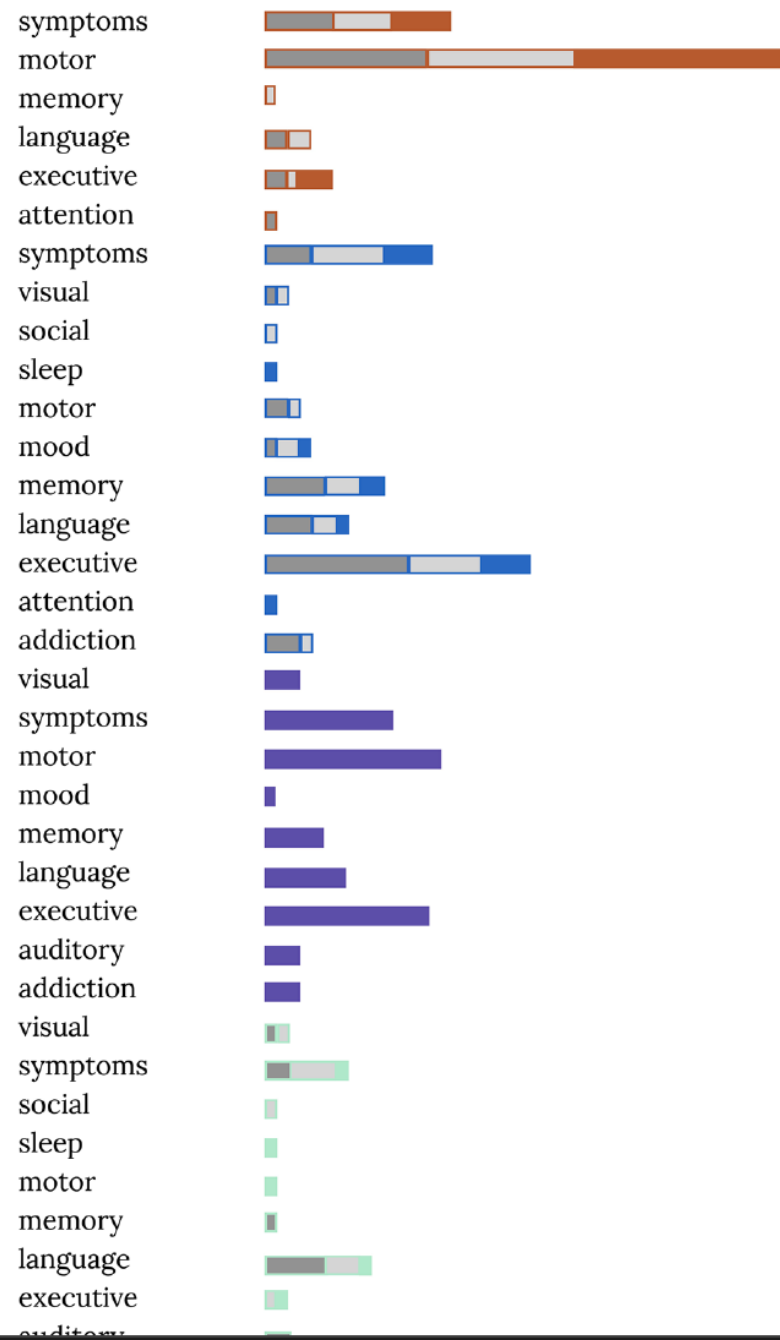
cingulum

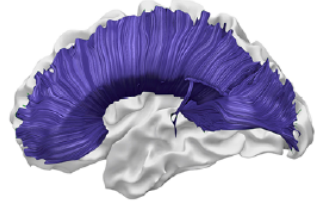


corpus callosum

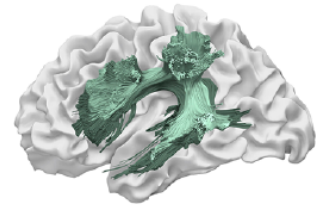


arcuate fasciculus

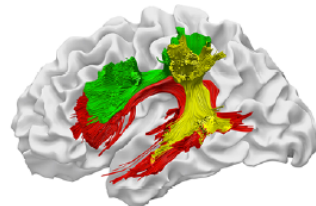




corpus callosum

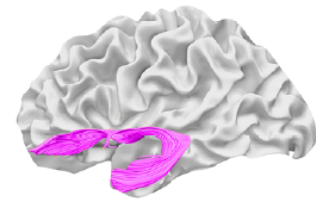


arcuate fasciculus

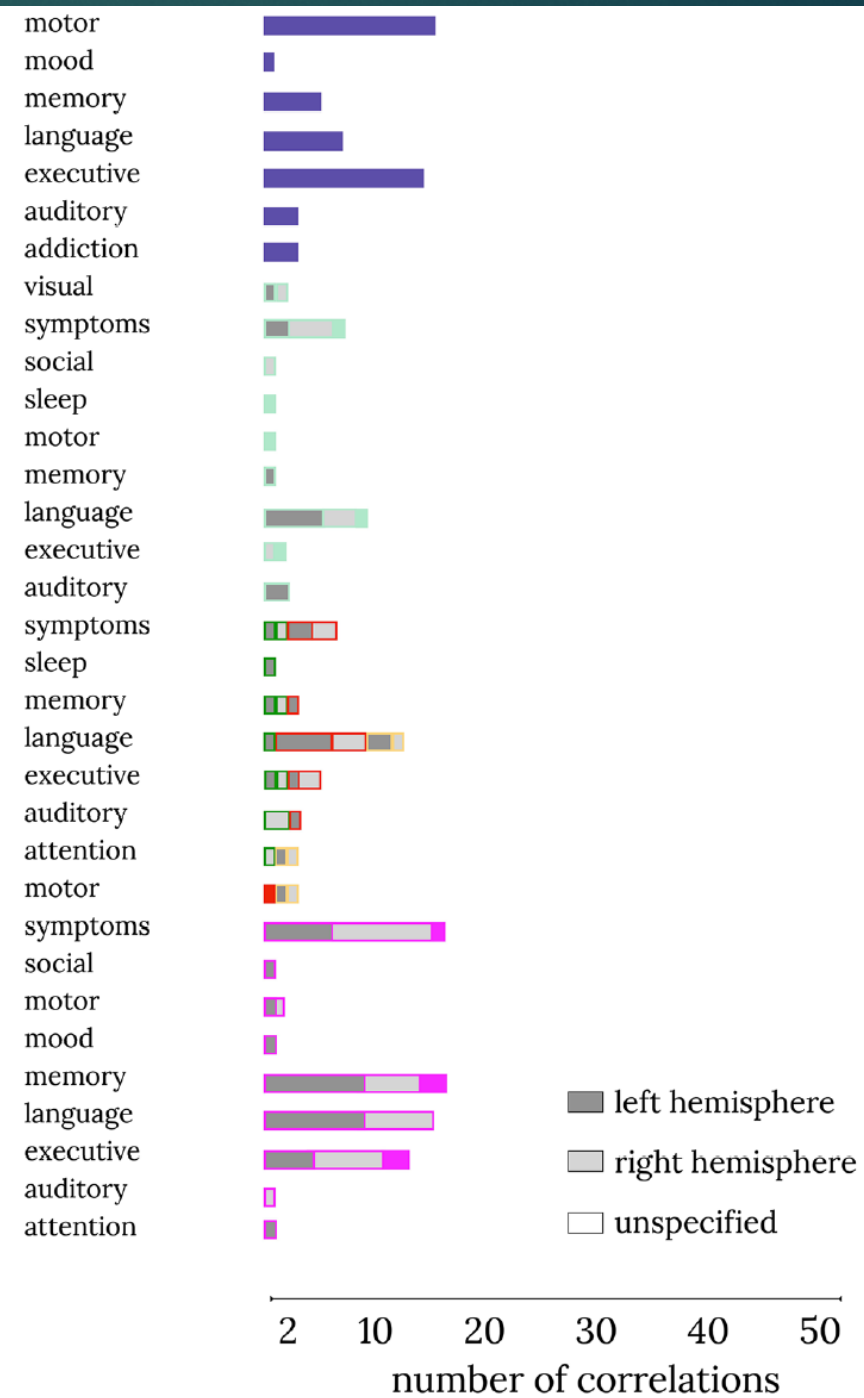


arcuate fasciculus

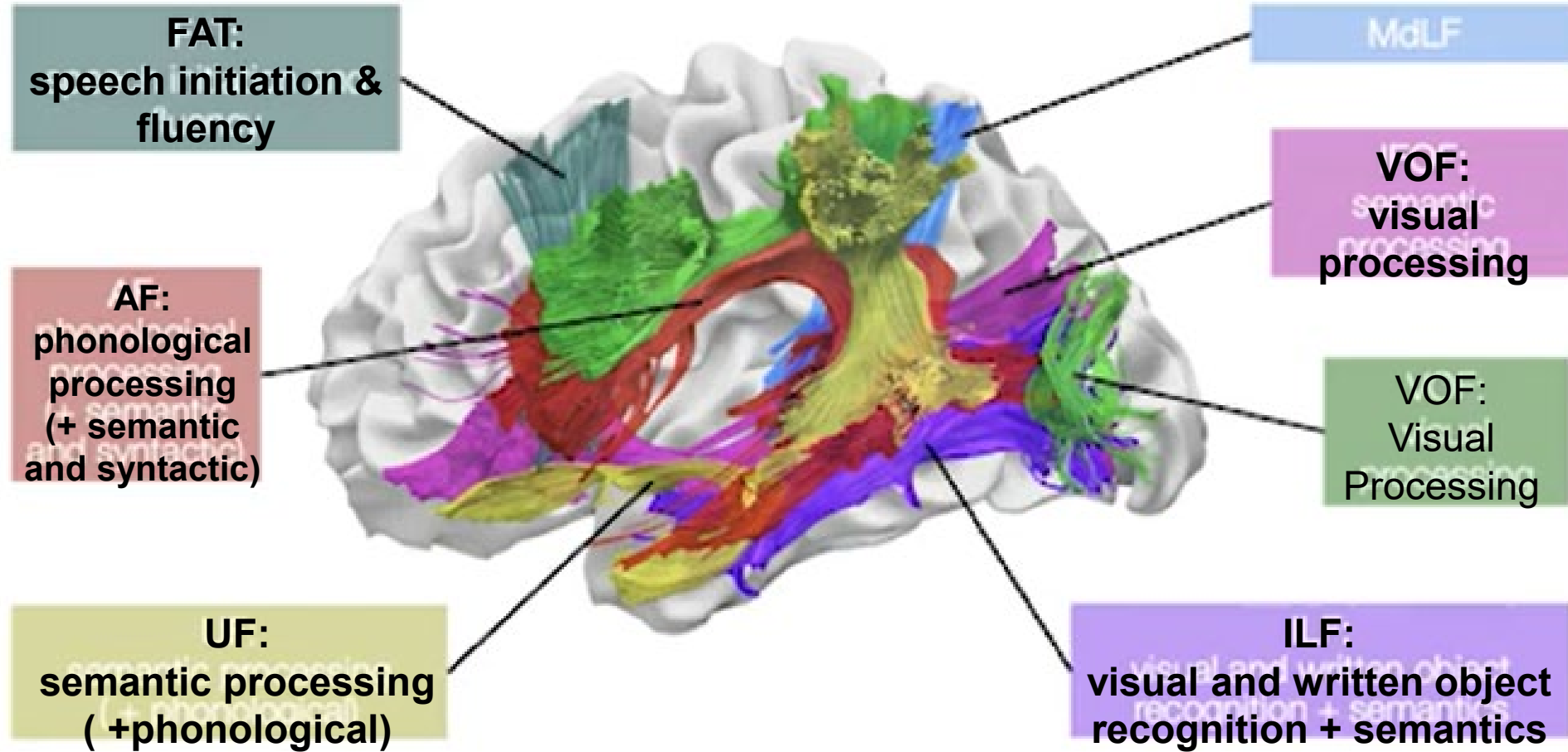
- anterior segment
- long segment
- posterior segment



uncinate fasciculus



# nTMS Speech and Language Mapping



Lots of variability: lower ancient subcortical structures less variable, lateral more variable, experientially based

## Inter-individual variability



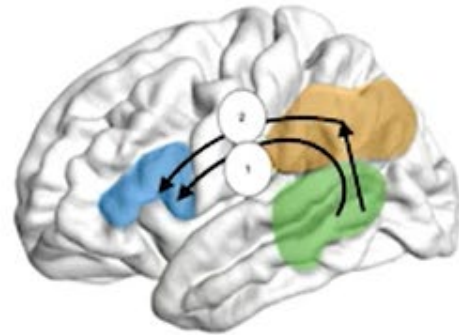
# Like an orchestra, no one language system; but a dynamic variety of areas that work when needed

## Emerging Properties of the connected brain



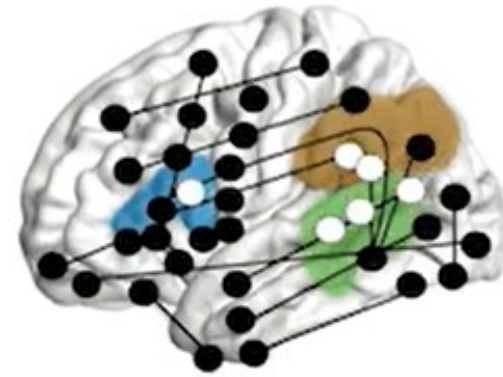
**Modular model**

- "Broca's area"
- "Geschwind's area"
- "Wernicke's area"



**Hierarchical model**

- ① Direct processing route
- ② Indirect processing route



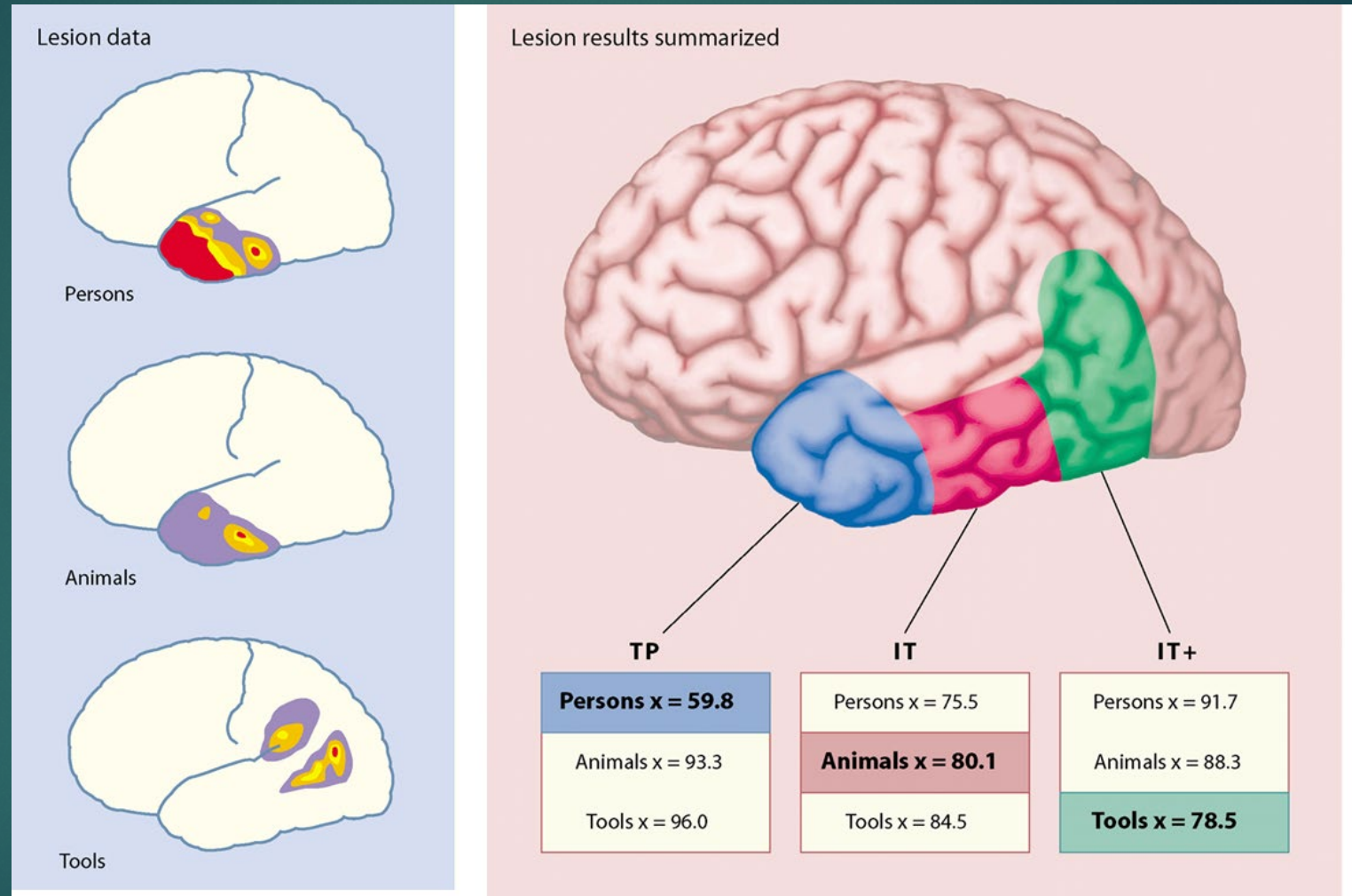
**Integrative model**

- Inactive
- Active



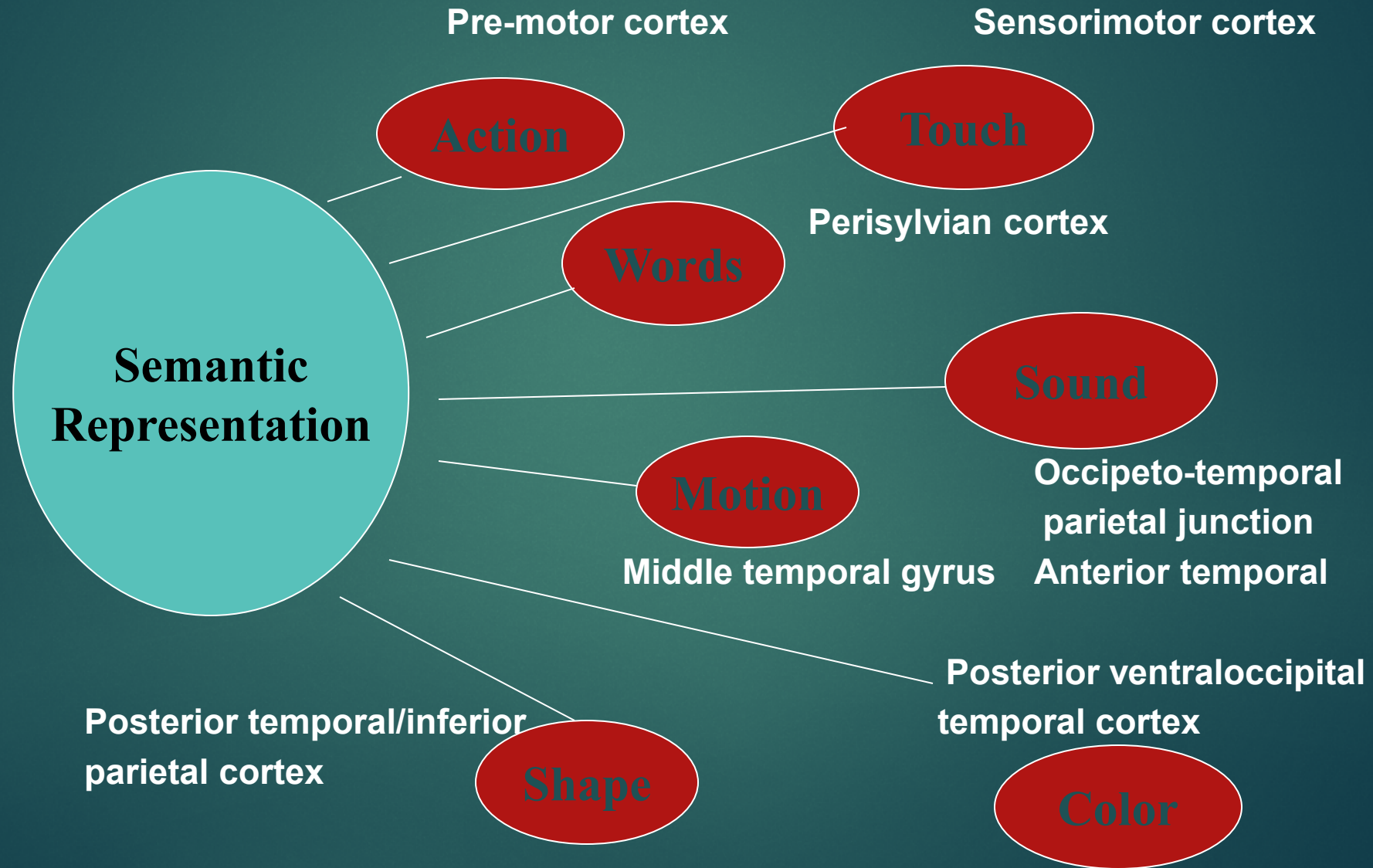
Thiebaut de Schotten & Forkel, 2022

# Semantic Knowledge: Location of people, animals and tools: lesion based



Location of brain lesions that are correlated with selective deficits in naming persons, animals or tools (Damasio et al., 1996).

# Locations of Semantic Memory



# Naming Errors: Ubiquitous; no correlation with memory decline

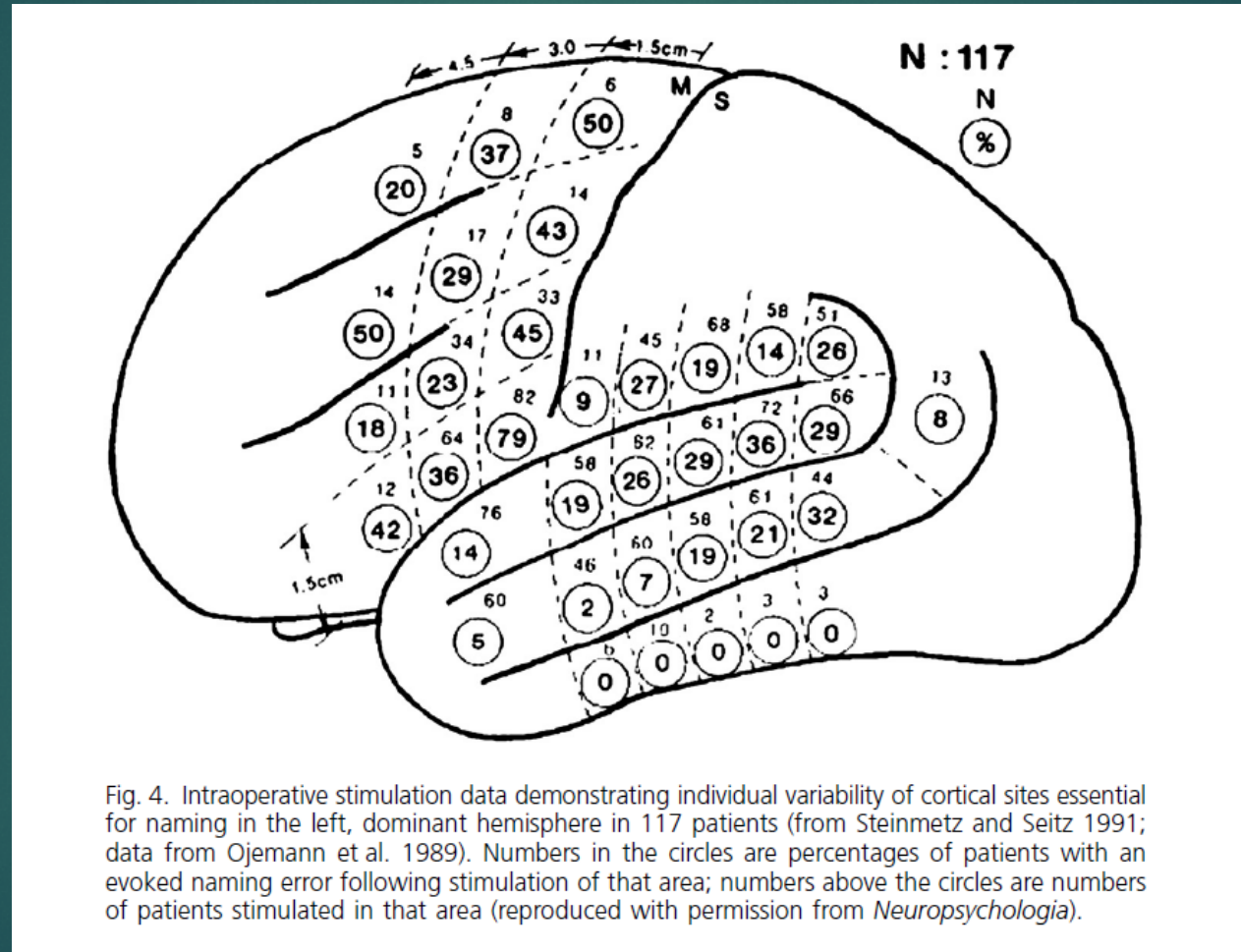
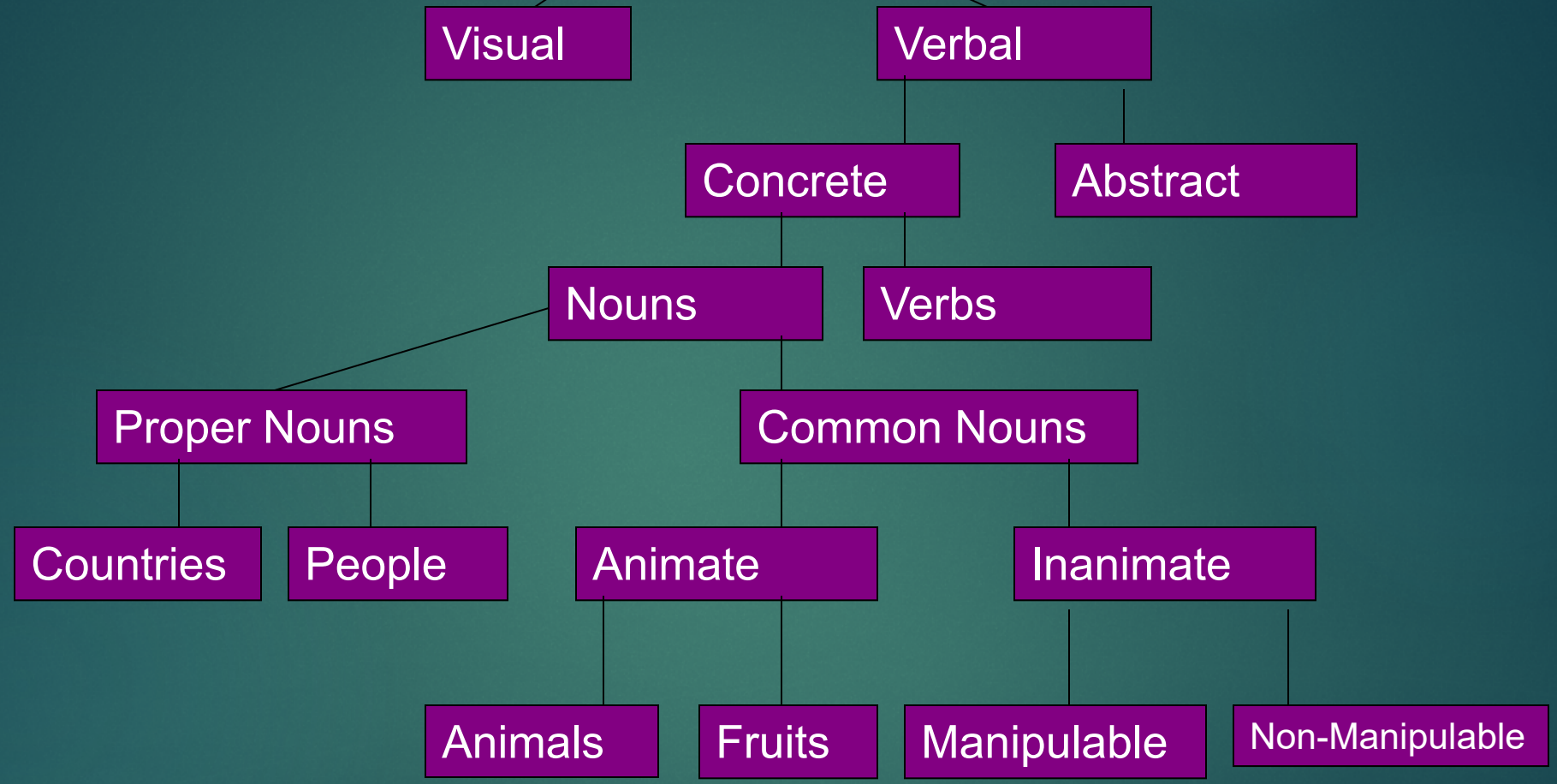


Fig. 4. Intraoperative stimulation data demonstrating individual variability of cortical sites essential for naming in the left, dominant hemisphere in 117 patients (from Steinmetz and Seitz 1991; data from Ojemann et al. 1989). Numbers in the circles are percentages of patients with an evoked naming error following stimulation of that area; numbers above the circles are numbers of patients stimulated in that area (reproduced with permission from *Neuropsychologia*).

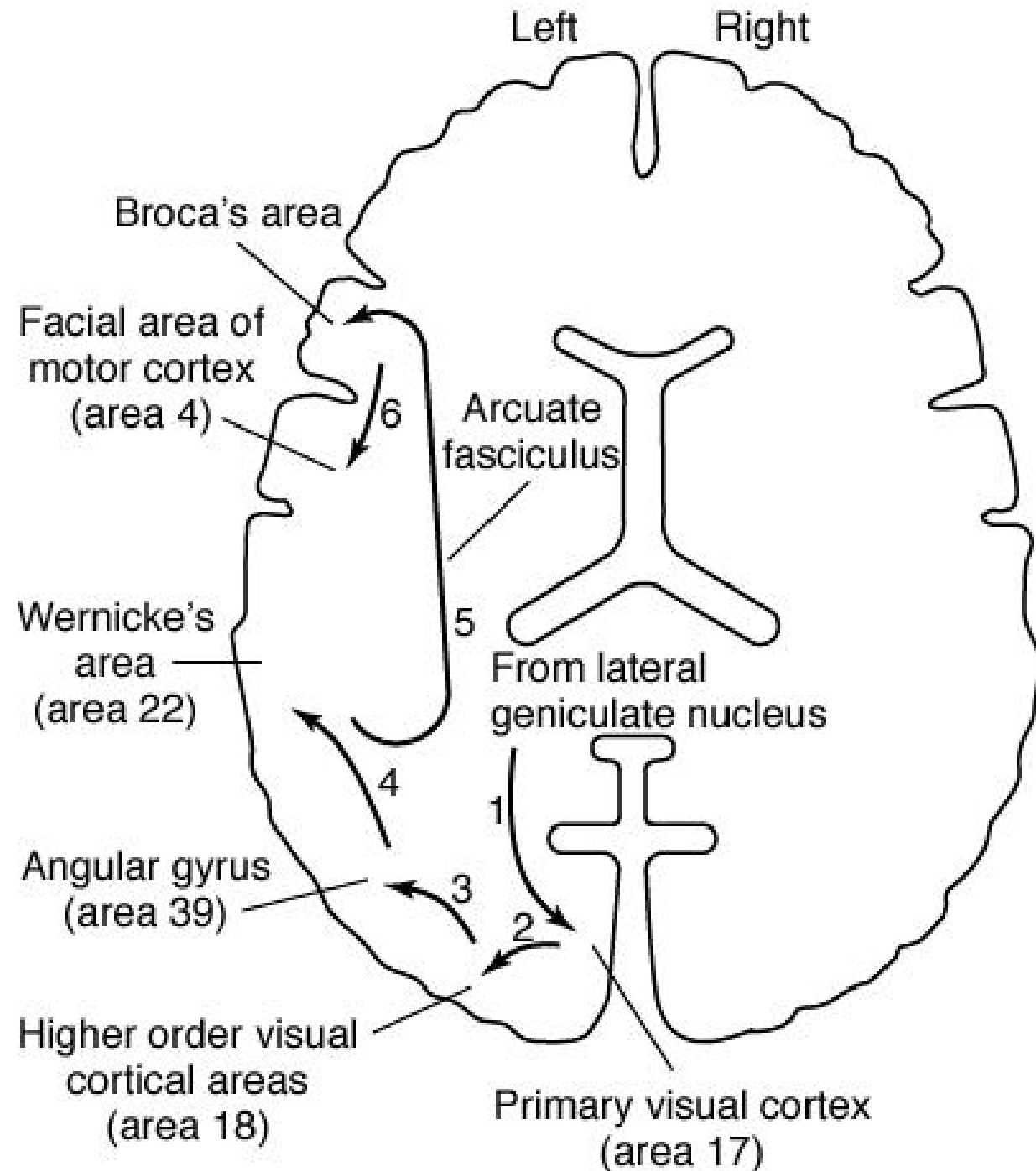


# Topography of Semantic Knowledge: How Brain Stores Information from Lesions/-strokes

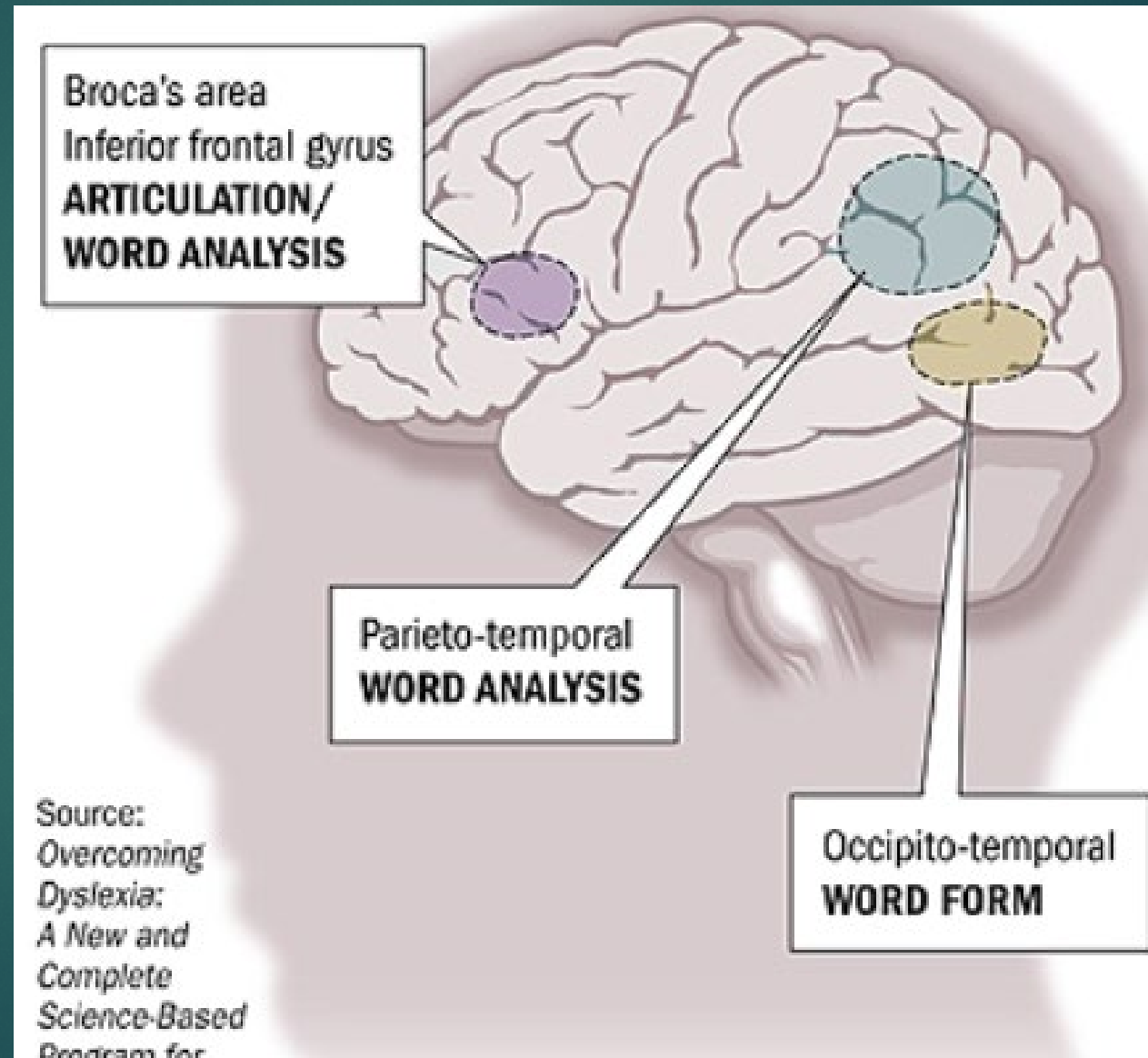


Other Known Categories: indoor / outdoor, vegetables, how to cook them

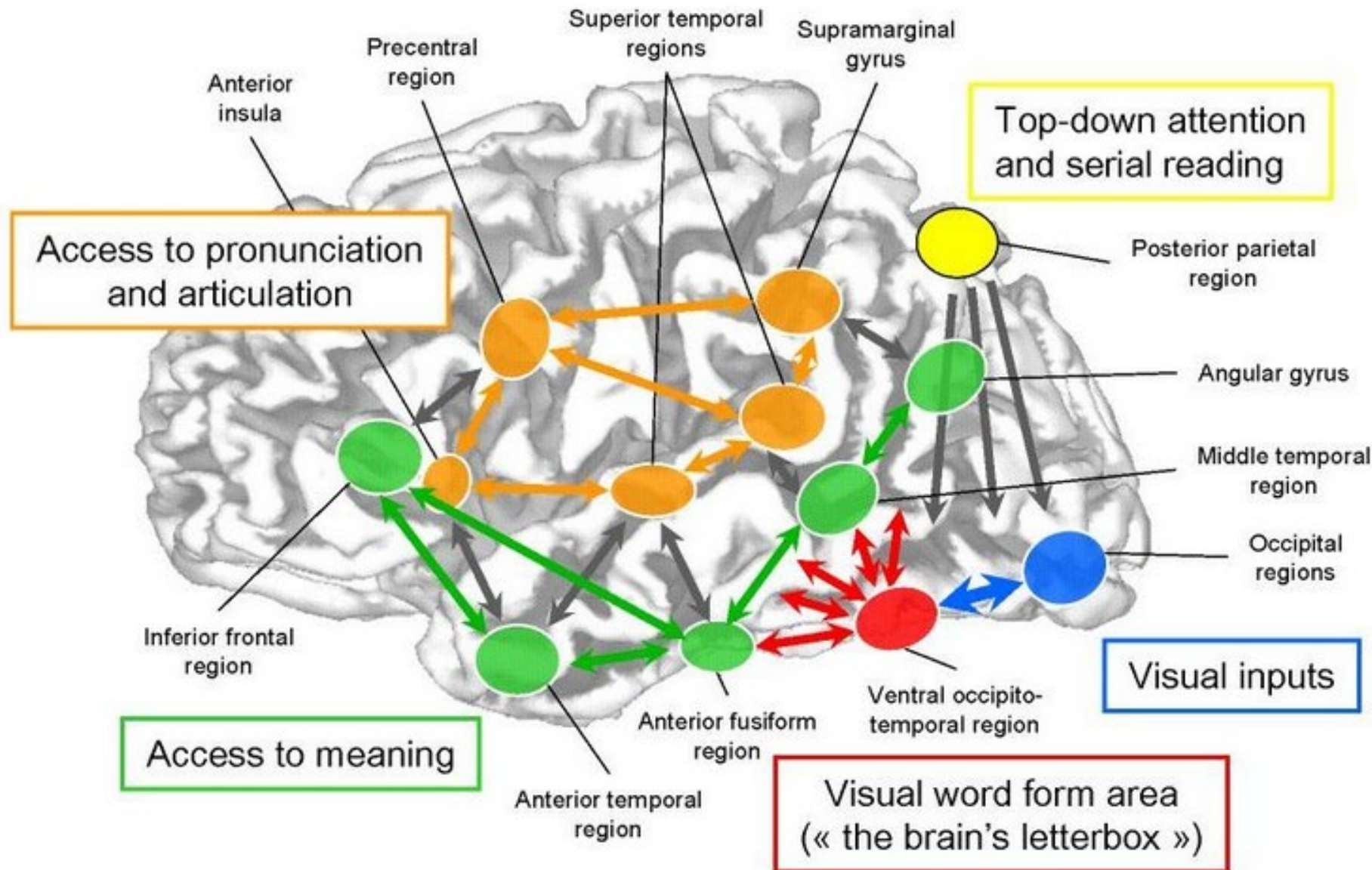
Speaking a  
seen word  
requires  
6 areas



# Reading System: 3 basic areas



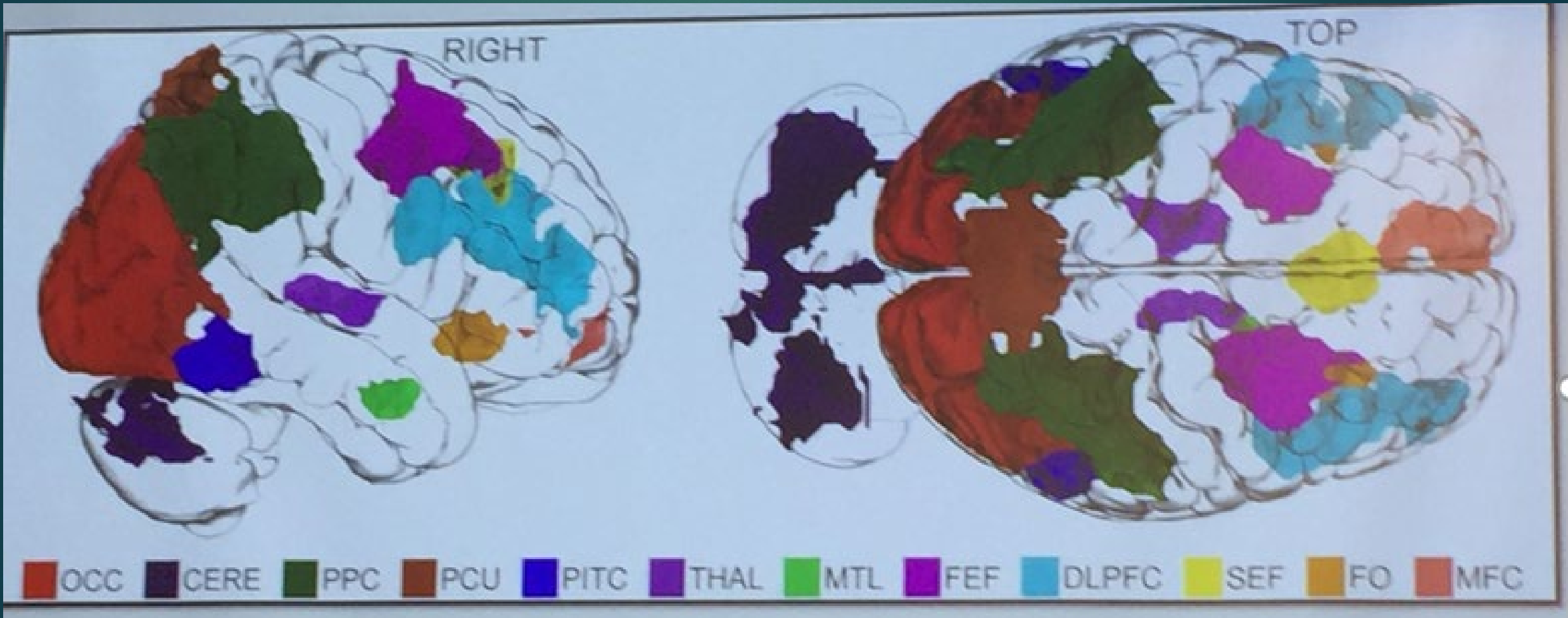
## A modern vision of the cortical networks for reading



Reading in brain = only 6000 years old

Reading = exaptation of existing systems

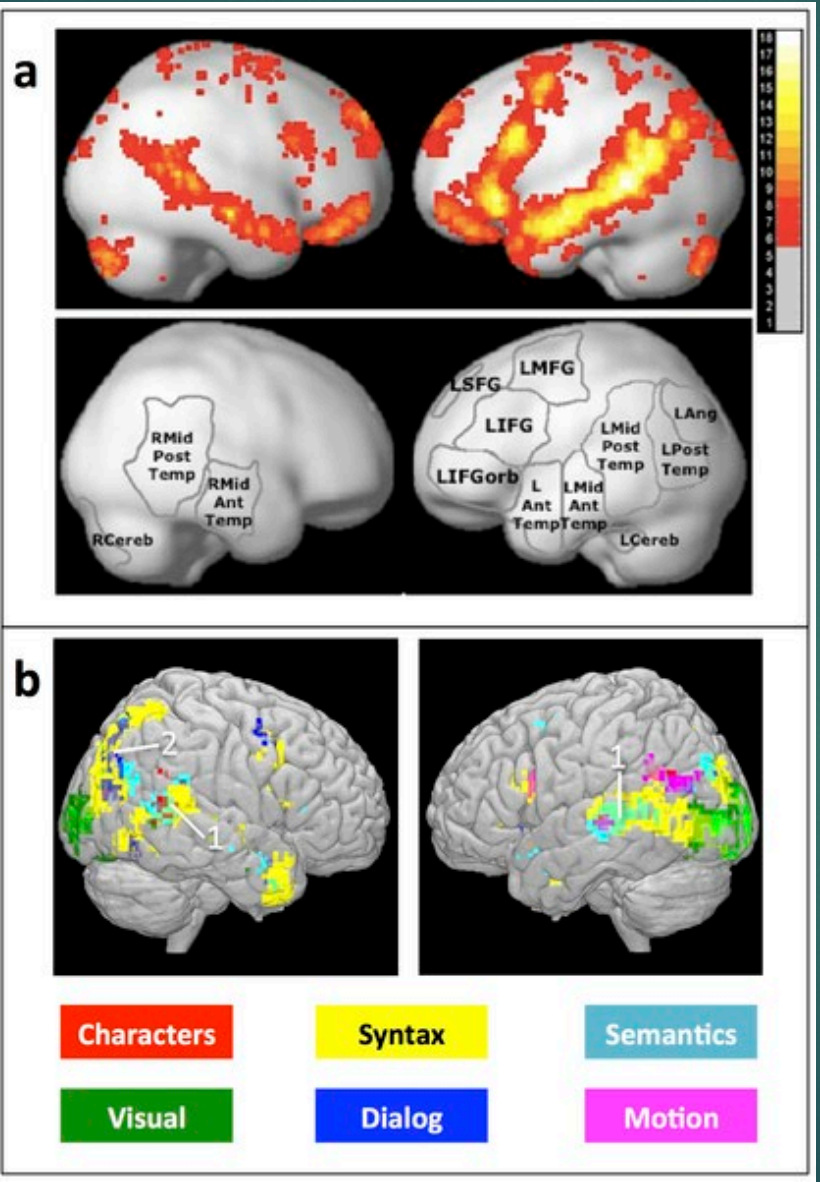
# Reading activates more brain areas than any other activity



# Reading Harry Potter: sentence reading activates all brain areas

- ▶ **Statistical model is able to classify which of two novel passages of the story is being read** with an accuracy of 74% based on neural activity while reading.
- ▶ **Brain areas involved:**
  - ▶ Angular Gyrus: lexical semantics (bilateral); physical motions of story characters
  - ▶ Fusiform Gyrus
  - ▶ Inferior frontal: high level word integration (right); semantics of individual words (left); Physical motions of story characters; dialog among story characters (right)
  - ▶ Inferior temporal
  - ▶ Middle temporal: semantics of individual words (bilateral), identities of different story characters
  - ▶ Superior temporal: sentence length (L), syntax (R); semantics of individual words (R); Physical motions of story characters; identities of different story characters , protagonist's perspective (right)
  - ▶ Temporal pole: high level word integration (bilateral)
  - ▶ Occipital: word length (left Visual Word Form Area)
  - ▶ Precentral Gyrus
  - ▶ Precuneus
  - ▶ Temporal Parietal Junction: sentence length/syntax (left & esp. right); dialog among story characters (right)
  - ▶ Supplementary Motor Gyrus

**Reading Harry Potter:** Map of the patterns of representation: regions involved in sentence processing: which information process they represent.



# Decoding Brains – Jack Gallant, UCB

- ▶ J. L. Gallant, UCB (<http://gallantlab.org/>): Predictive models of brain activity are the gold standard of computational neuroscience
- ▶ Using EEG, fMRI for voxel analysis & statistical analysis: how each element of the visual system encodes information
- ▶ Models can be inverted in order to decode brain activity, providing a direct way to do "brain reading", and to build brain-machine interfaces (BMI) and neural prosthetics.
- ▶ Lab has been able to make videos of what people see, what people are semantically thinking about



# Meaning in the brain

- ▶ In the brain, language pops up everywhere.
- ▶ All across the wrinkly expanse of the brain's outer layer, a **constellation** of different regions handle the meaning of language
- ▶ **Gallant lab:** new detailed map hints that humans comprehend language in a way that's much more complicated — and involves many more brain areas — than scientists previously thought

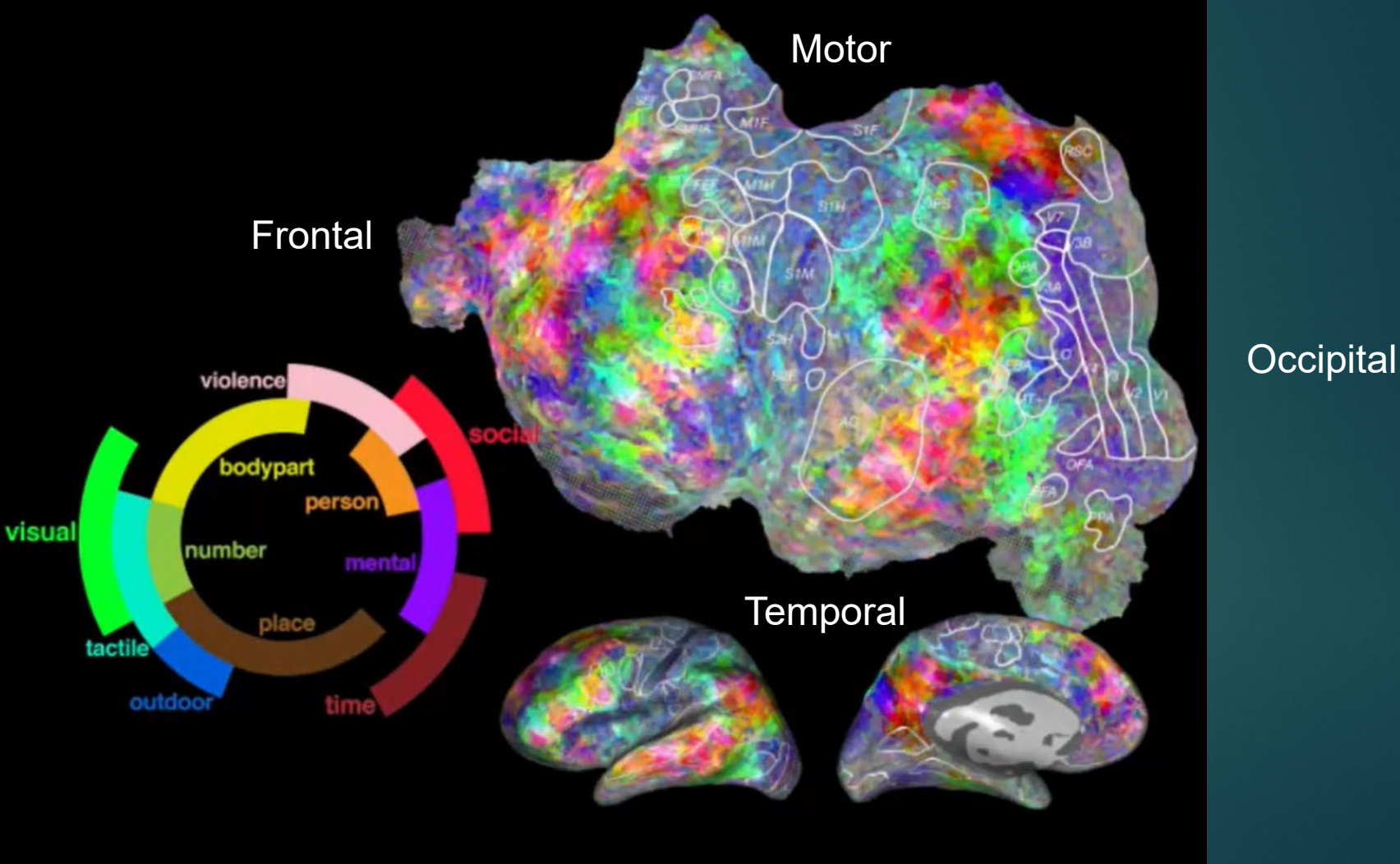
# Meaning

- ▶ Gallant mapped the activity of some 60,000 to 80,000 pea-sized regions across cerebral cortex, as people lay in a functional MRI machine and listened to stories from *The Moth Radio Hour*. Used real life, complicated stories
- ▶ Used a computer program to decipher the meaning of every 1- to 2-second snippet of the stories and then cataloged where 985 concepts showed up in the brain.

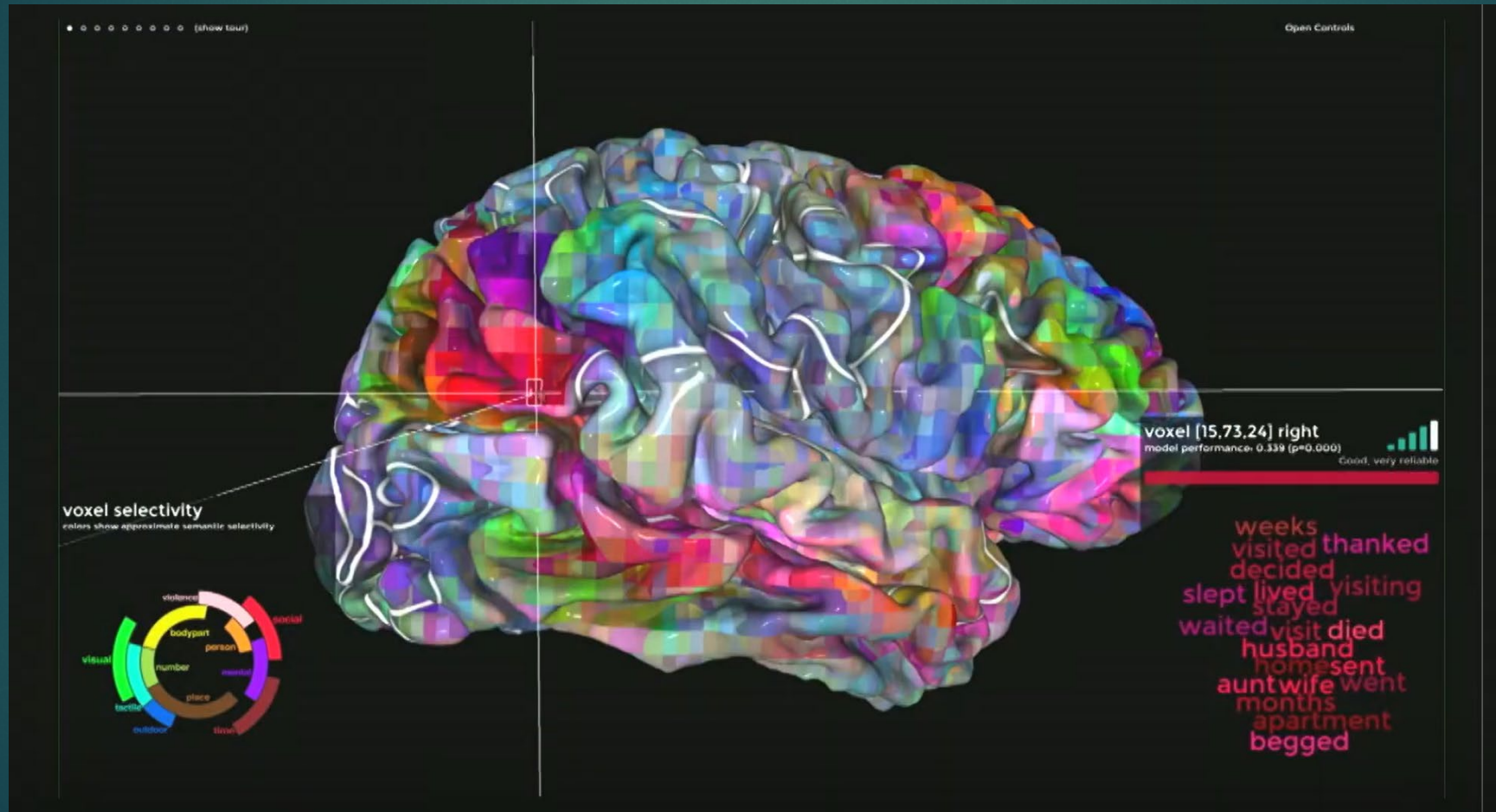
## Meaning 2

- ▶ Often, the same word appeared in different locations, depending on meaning association. Most areas within the semantic system represent information about specific semantic domains, or groups of related concepts. Each semantic concept is represented in multiple semantic areas, and each semantic area represents multiple semantic concepts.
- ▶ The brain maps of the **seven American participants** in the study looked remarkably similar – **same locations for similar words**

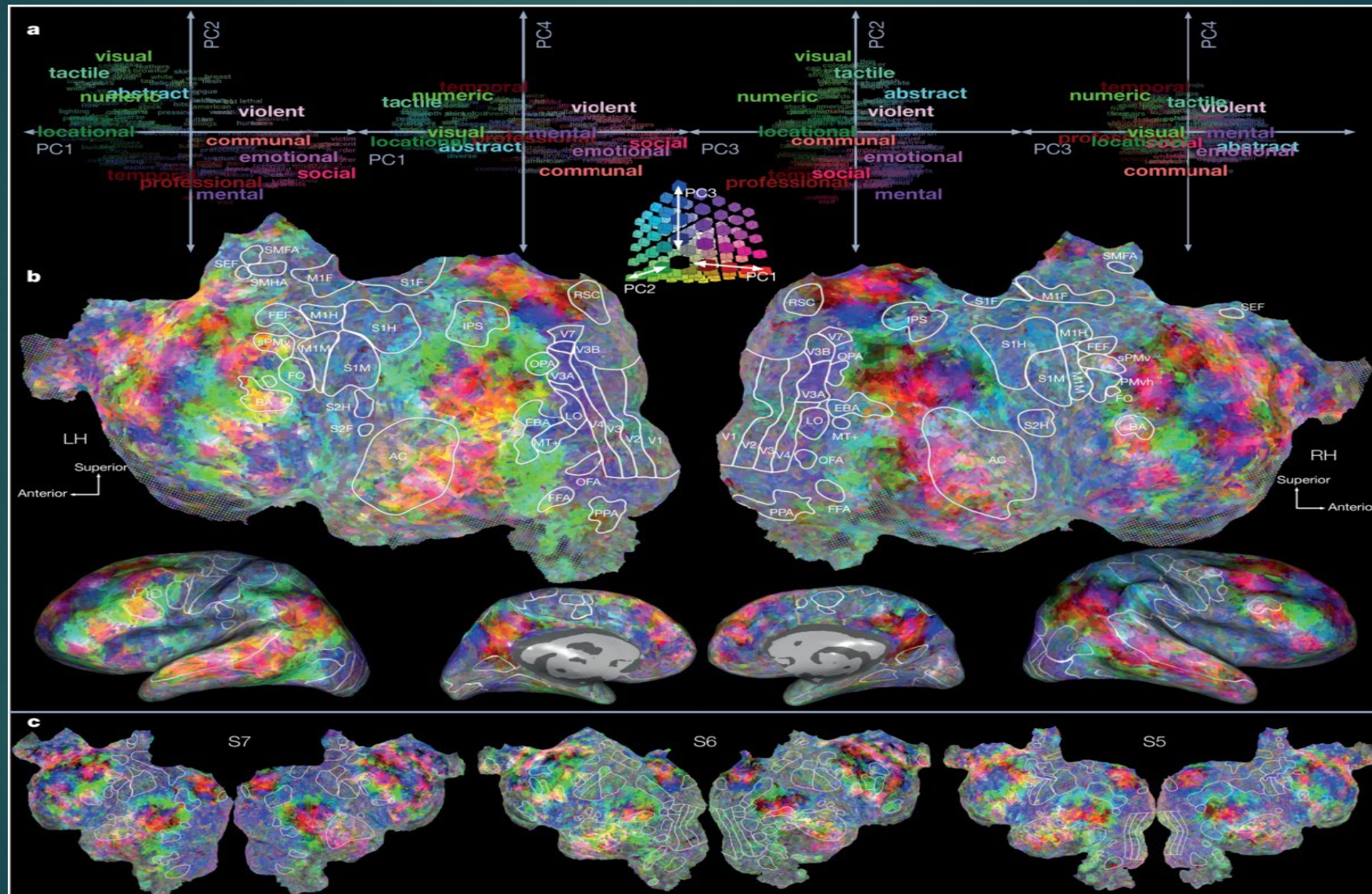
Can map with fMRI: Left hemisphere; colors = kind of semantic info (red=social; green=visual; purple=ideas (justice); maps 10,000 semantic types)

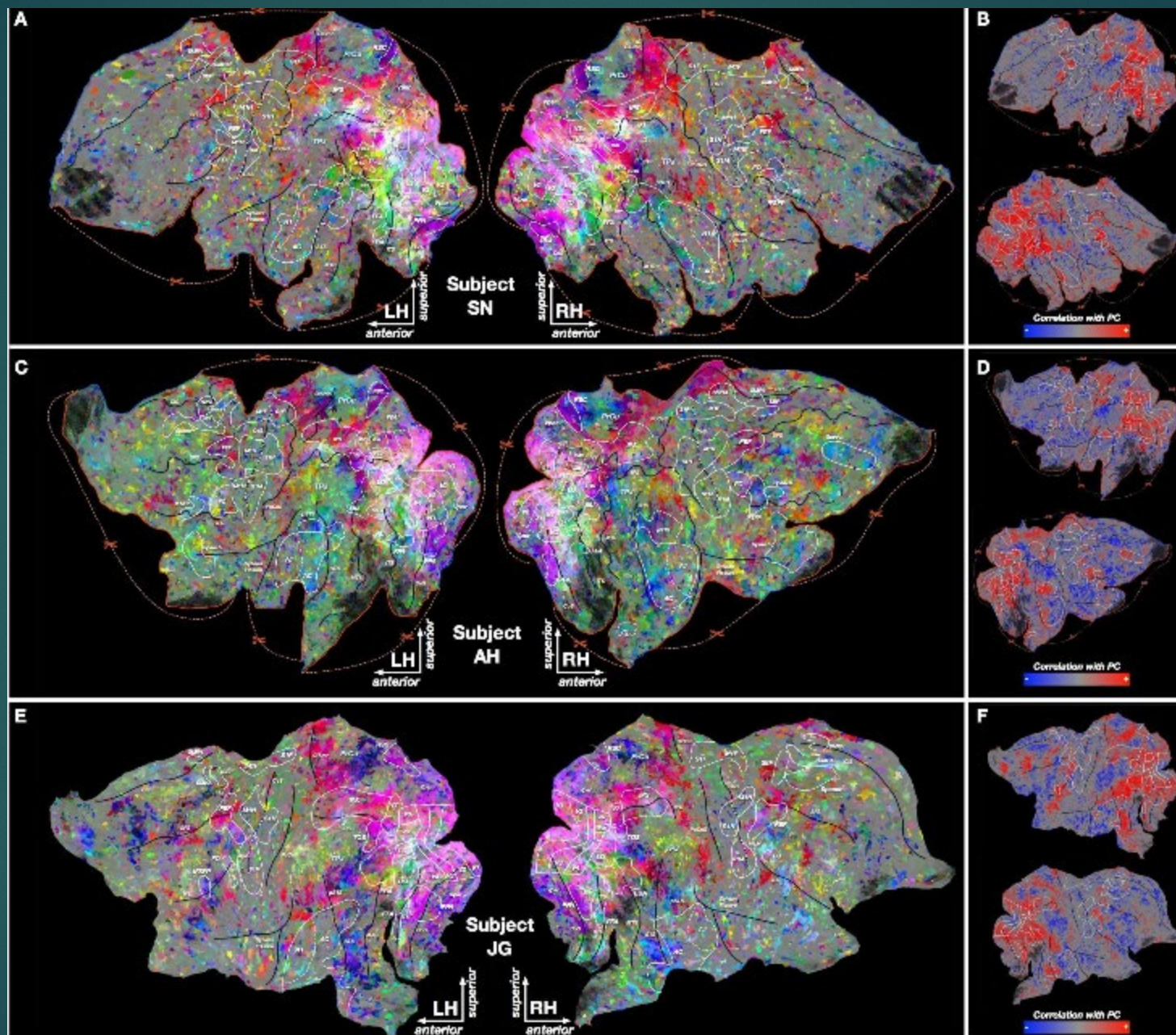


Website brain viewer: touch area, i.e. red = social – gives you concepts: father, marriage, wife, etc.; green = quantity - wgts, money, dates, time



# Principal components of voxel-wise semantic models



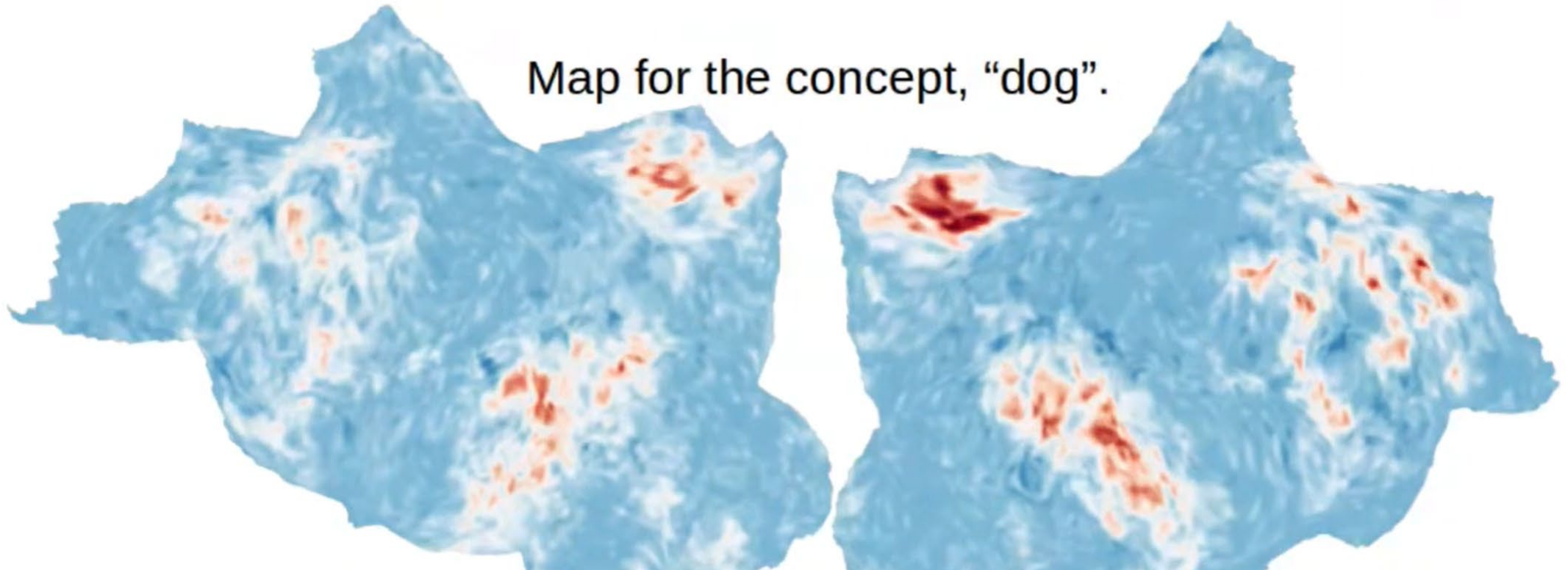


Cortical maps of semantic representation

## Dog activation: bark, fur, etc.; csness binds this together

Each concept is represented at multiple locations in this network and each location represents a family of related concepts

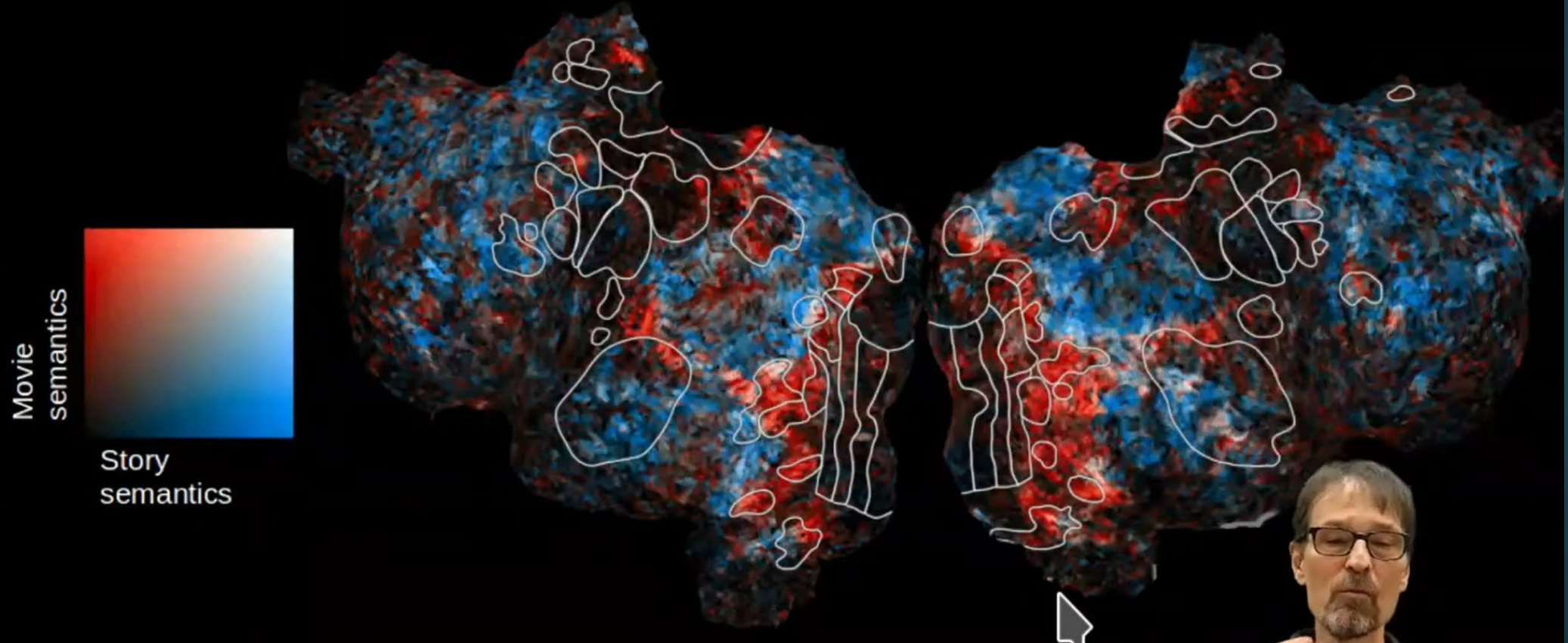
Map for the concept, "dog".





Modal concepts = sensory, red; blue = amodal, concepts; modal feeds amodal

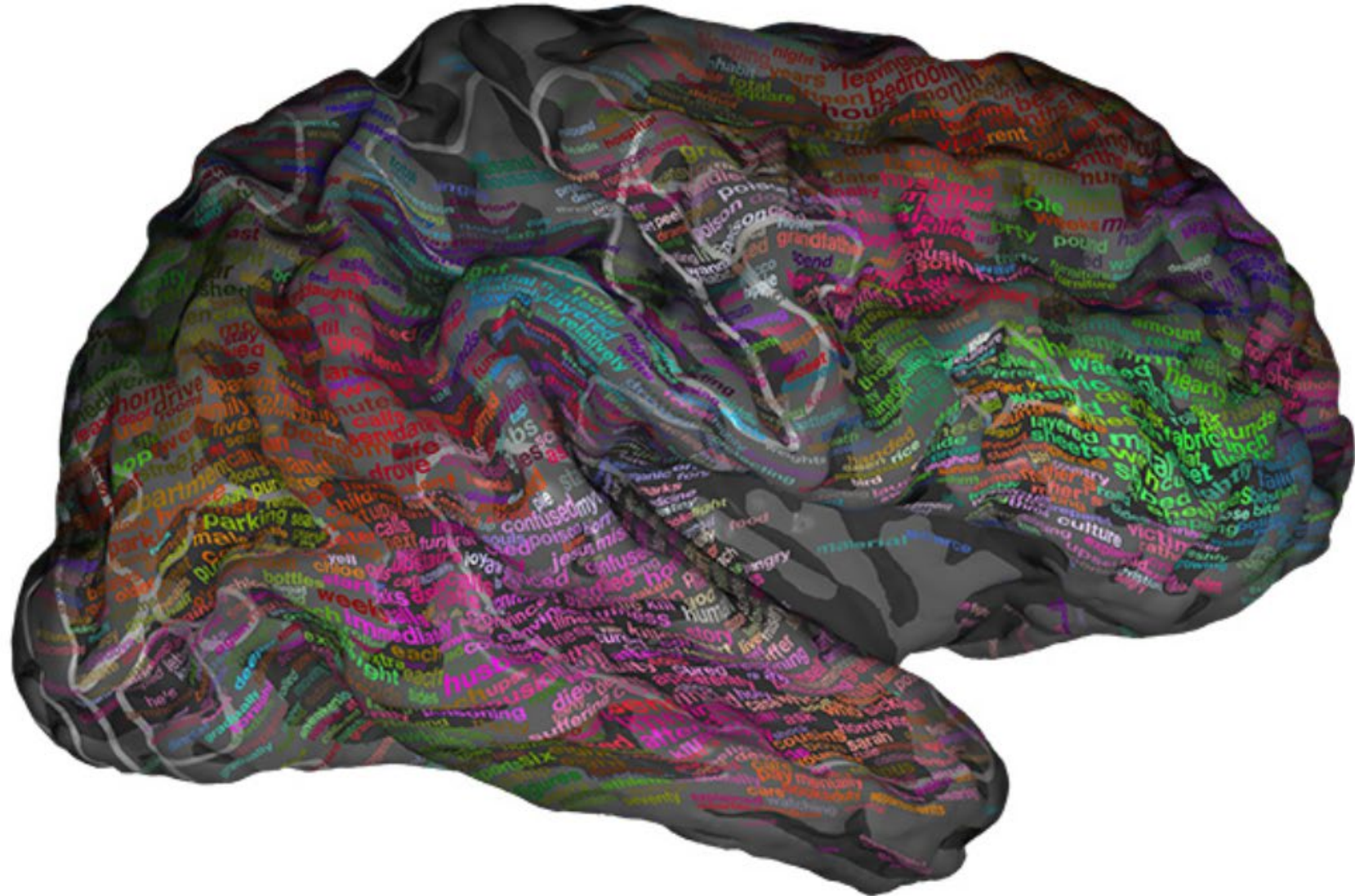
The visual system contains a modal conceptual network that represents the contents of the visual world



# Image of a kiss: social area activations



# Meaning in the Brain: Listening to narrative stories – areas activated by meaning



# Meaning in both hemispheres

- ▶ One striking aspect of our atlas is that the distribution of semantically selective areas is relatively symmetrical across the two cerebral hemispheres.
- ▶ This finding is inconsistent with human lesion studies that support the idea that semantic representation is lateralized to the left hemisphere. Suggests that right hemisphere areas may respond more strongly to narrative stimuli than to the words and short phrases used in most studies.
- ▶ Thought decoder: Possibility of decoding the words in a person's thoughts.

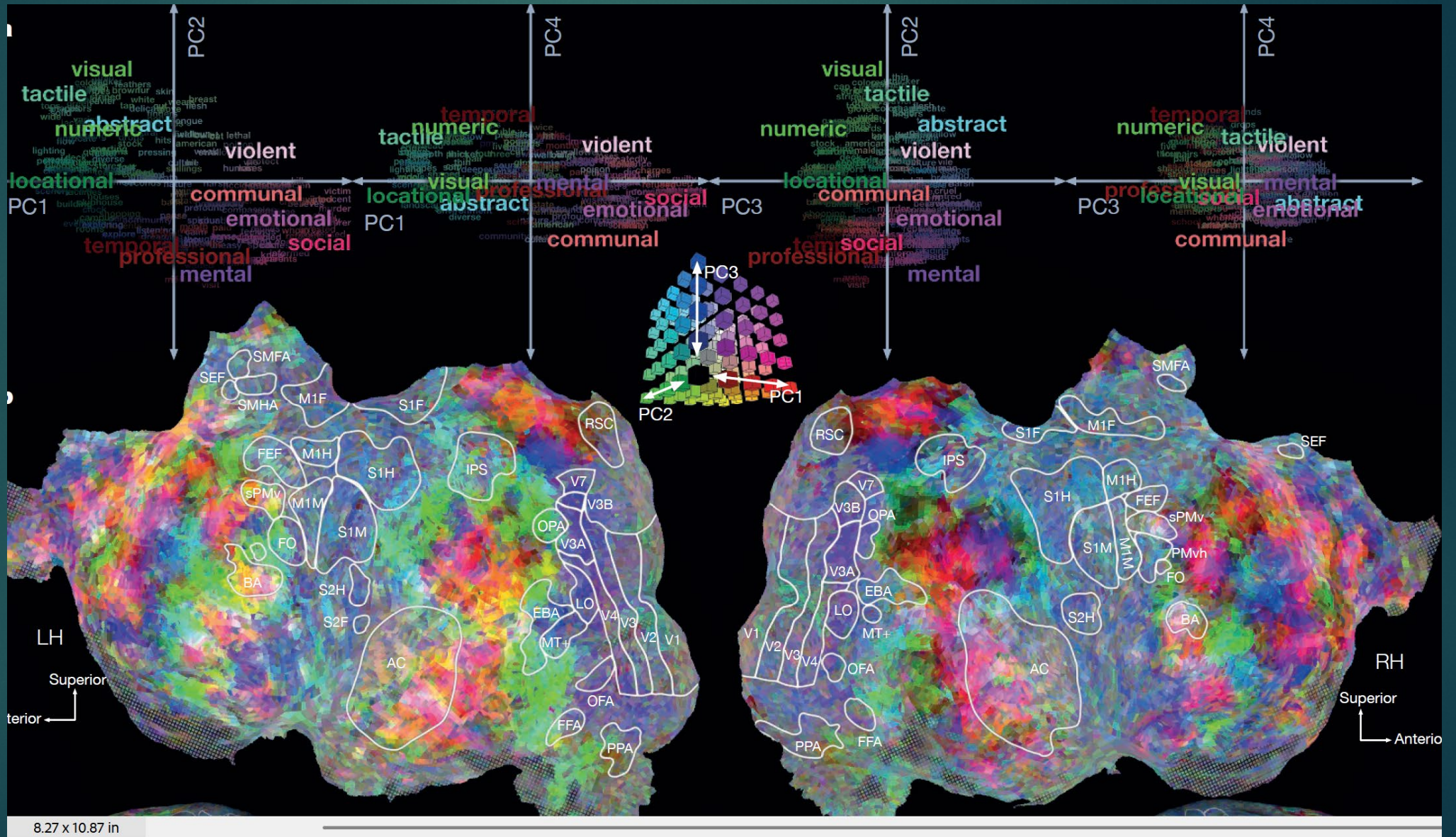
# Physics in the brain

- ▶ **Thinking about physics** prompts common brain-activation patterns (rhythm processing and sentence structure processing)
- ▶ Study: **30 physics concepts in fMRI** - machine learning could identify which of 2 types of physics concepts individual was thinking
- ▶ **All participants used same brain areas for same concepts**; same brain regions repurposed for specific types of concepts
- ▶ Brain responses for scientific concepts of “frequency” or “wavelength” occurred in regions that active “periodicity” region which handles watching dancers, music listening, hearing rhythmic patterns
- ▶ **Brain responses for mathematical equations trigger areas that process sentences**

# Concepts are in both hemispheres

- ▶ One striking aspect of our atlas is that the distribution of semantically selective areas is relatively symmetrical across the two cerebral hemispheres. This finding is inconsistent with human lesion studies that support the idea that semantic representation is lateralized to the left hemisphere.
- ▶ Another interesting aspect of these results is that the organization of semantically selective brain areas seems to be highly consistent across individuals. This might suggest that innate anatomical connectivity or cortical cytoarchitecture constrains the organization of high-level semantic representations. It is also possible that this is owing to common life experiences of the subjects, all of whom were raised and educated in Western industrial societies.

# Jack Gallant, USB: possible general-purpose language decoder



# Not domain-specificity, but a distributed brain system

- ▶ A strong argument against domain-specificity and in favor of a distributed representation of knowledge in the brain lies in the inherent flexibility and adaptability of human cognition, suggesting that knowledge is not neatly compartmentalized into separate modules but rather interwoven across various brain regions.
- ▶ Supported by evidence from neuroimaging studies showing complex patterns of brain activation across diverse cognitive tasks, indicating a distributed network involved in processing information rather than dedicated localized modules for specific domains.



# Distributed brain system

## Key points against domain-specificity/functional specificity:

- ▶ **Neural plasticity and learning:** The brain continuously adapts to new experiences and situations, readily modifying neural connections to incorporate new knowledge, which is difficult to explain with a strictly domain-specific model where modules are pre-wired for specific functions
- ▶ **Overlap in brain activation:** Neuroimaging studies consistently demonstrate that many brain regions are activated across different cognitive domains, suggesting that a single area can contribute to various functions depending on the task demands rather than being dedicated to a single domain.
- ▶ **Emergent properties:** Complex cognitive abilities may arise from interactions between multiple brain regions, rather than being solely attributed to a single, specialized module.

## Arguments for distributed representation:

- ▶ **Difficulty in defining domain boundaries:** Distinguishing clear boundaries between cognitive domains can be challenging, as many real-world tasks require integration of information across different areas of knowledge.
- ▶ **Semantic networks:** Concepts are represented as interconnected nodes in a vast network, where related concepts are closely linked, enabling efficient retrieval and transfer of knowledge across domains.
- ▶ **Embodied cognition:** Knowledge is grounded in our bodily experiences and interactions with the environment, leading to a distributed representation that integrates sensory, motor, and conceptual information.
- ▶ **Experience-dependent development:** The brain dynamically restructures itself based on individual experiences, shaping the pattern of distributed representations across neural networks.

## Example evidence:

### •Face perception:

While specific areas in the brain may show a preference for processing faces, research suggests that face recognition also involves a distributed network that integrates information from other sensory modalities and conceptual knowledge.

### •Language processing:

Understanding language requires not only dedicated language areas but also engagement of regions related to semantics, context, and prior knowledge, highlighting the distributed nature of language comprehension.

### •Conclusion:

The growing body of evidence points towards a distributed model of knowledge representation in the brain, where information is integrated across multiple brain regions, allowing for flexibility, adaptability, and seamless transfer across cognitive domains, rather than being confined to discrete, domain-specific modules.

# Neuroplasticity: Experience changes our brains: London Taxi Drivers

If you lived in London, and wanted to grow your hippocampus, which driving job would you choose?



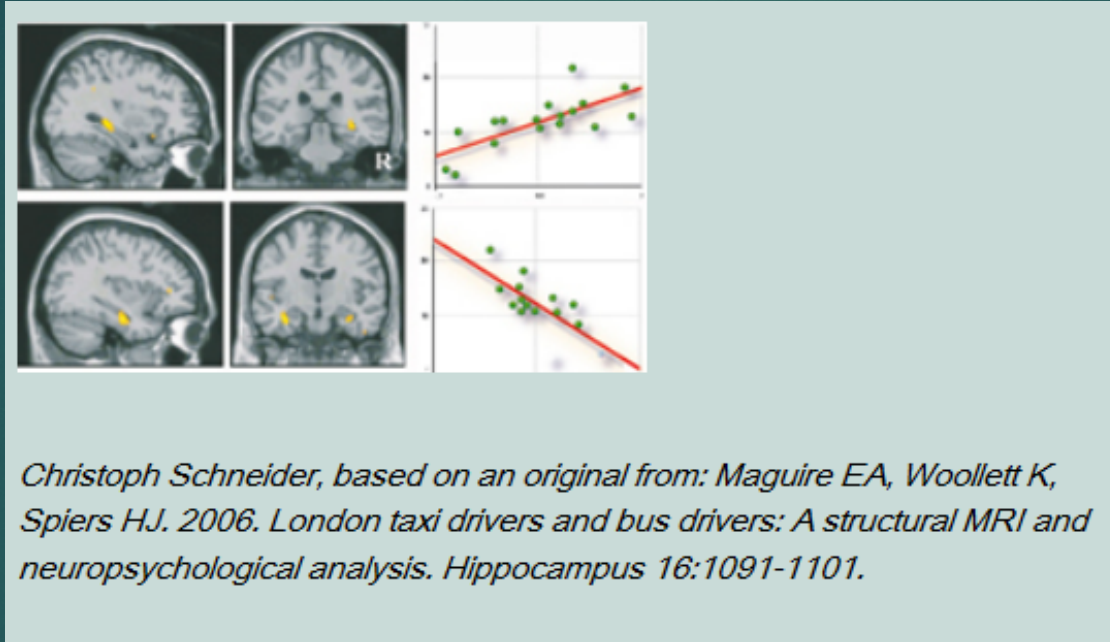
3 year Knowledge exam: 3 of 10 pass

25,000 streets

1400 landmarks

**Study of London Taxi cab drivers** (vs. bus drivers): To earn their licenses, cab drivers in training spend three to four years driving around the city on mopeds, memorizing a labyrinth of 25,000 streets within a 10-kilometer radius of Charing Cross train station, as well as thousands of tourist attractions and hot spots. "The Knowledge" exams that only about 30 percent of hopefuls pass.

# Larger Right Posterior Hippocampus in London Taxi Drivers: 7% larger , but otherwise normal memory

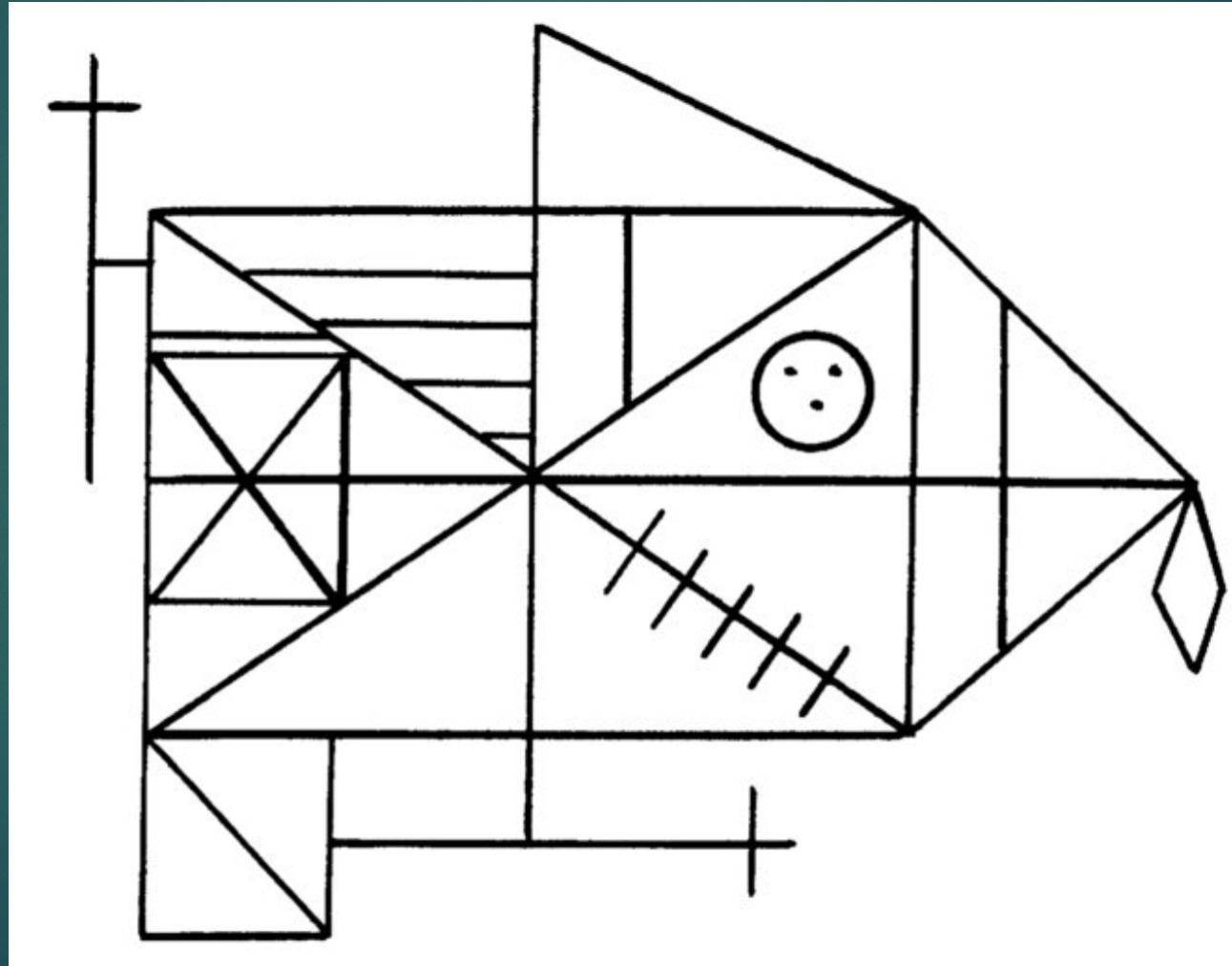


Enlarged the posterior hippocampus at the expense of the anterior

London taxi drivers who earned their licenses performed far better than those who failed—even though they had performed equally four years earlier. And MRIs showed that the successful trainees' hippocampi had grown over time.

The successful trainees did not perform better on all tests of memory, however.  
Licensed taxi drivers did worse than non-taxi drivers on the Rey-Osterrieth Complex Figure Test.

# Rey-Osterrieth Complex Figure Test.



### \*\*\* CJV review of Evelina Fedorenko's MIT lab research

- ▶ Evelina Fedorenko's MIT lab: Language and thought in the human brain
- ▶ I review 45 studies of her MIT lab on our current understanding of how the brain processes language. Using fMRI imaging analysis.
- ▶ Her lab has proven that much of our understanding of the brain's language processing is unlike what we previously understood.

# Thought ≠ Language

- ▶ \*\* A major conclusion is that language is independent of thinking processes: these are two separate, independent processes.
- ▶ Damage can effect one and not the other or vice versa.
- ▶ Concludes that there are no specific language hubs (language is processed throughout the system);
- ▶ \*\* Language is totally a left hemisphere phenomena



\*\*\* Language is primarily a tool for communication rather than thought -- Evelina Fedorenko, et al., 2023

- ▶ What is language for? Researchers make the case that it's a tool for communication, not for thought.
- ▶ \*\* Recent evidence from neuroscience to argue that in modern humans, language is a tool for communication, contrary to a prominent view that we use language for thinking.

# Language vs Cognition

## ▶ Evidence that:

- ▶ brain network that supports linguistic ability in humans.
- ▶ review evidence for a double dissociation between language and thought, and discuss several properties of language that suggest that it is optimized for communication.

## ▶ Language does not appear to be a prerequisite for complex thought, including symbolic thought.

## ▶ Instead, language is a powerful tool for the transmission of cultural knowledge; It plausibly co-evolved with our thinking and reasoning capacities, and only reflects, rather than gives rise to, the signature sophistication of human cognition.

# Historical perspectives

- ▶ Two broad hypotheses have dominated this discussion:

- ▶ One proposal is that language primarily serves a communicative function—it enables us to share knowledge, thoughts, and feelings with one another.
- ▶ Another proposal is that language mediates thinking and cognition.

# Language in thinking

- ▶ The specific hypotheses about the role of language in thinking have ranged from
  - ▶ strong claims that language is necessary for all forms of (at least propositional) thought to
  - ▶ weaker claims that language may only be critical for, or can facilitate, certain aspects of thinking and reasoning,
  - ▶ and claims that language helps scaffold certain kinds of learning during development but may no longer be needed in mature brains.

# Communication

- ▶ An ability to accurately transmit information would plausibly facilitate cooperative behaviors such as hunting, scavenging and long-distance travel, and enable passing of knowledge and skills to offspring (cultural transmission).
- ▶ An improved reasoning capacity would plausibly enable more sophisticated planning and decision making, creation of better tools and better problem-solving abilities.

# Evidence for purpose of language

- ▶ The primary evidence about the lives of early hominins comes from sparse archaeological records. Brains do not fossilize, and even if they did, only coarse information about brain function could be gleaned from brain size, shape and anatomy.
- ▶ Certain traits may evolve for one reason but subsequently serve a different function owing to changes in the species' ecology: a phenomenon known as exaptation. A brain region can be coopted for another purpose.
- ▶ As a result of these challenges, we do not aspire to make strong claims about the evolutionary origins of language.

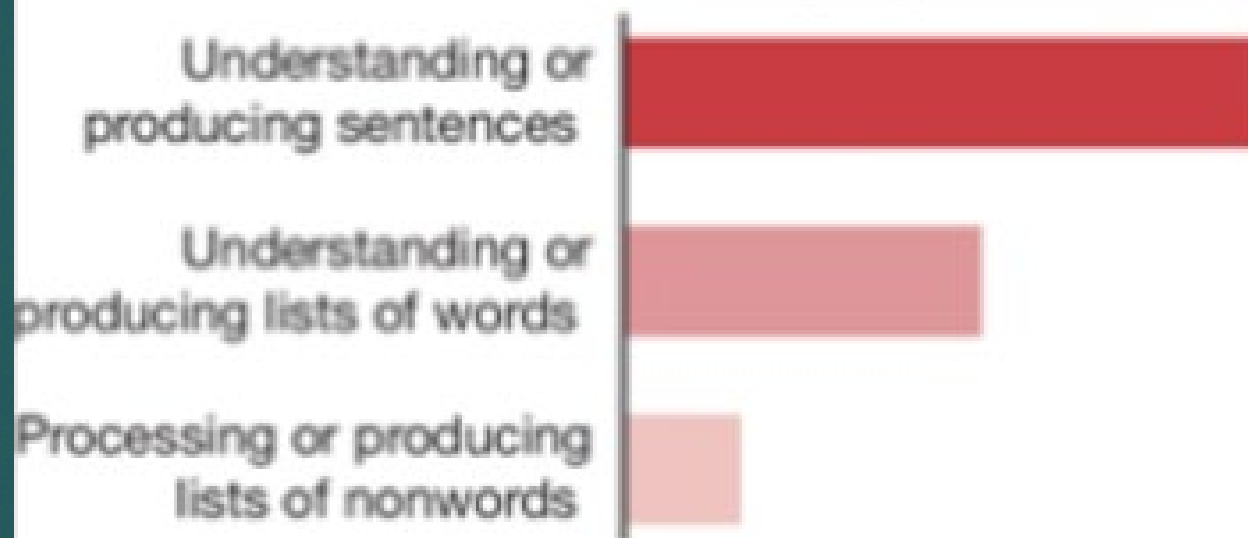
# The language network in the human brain

- ▶ There is at present no unequivocal empirical support for any form of thinking requiring linguistic representations (words or syntactic structures).
- ▶ Language production and language understanding are supported by an interconnected set of brain areas in the left hemisphere, often referred to as the 'language network'

## a Sample language networks in individual brains



### Responses in the language areas





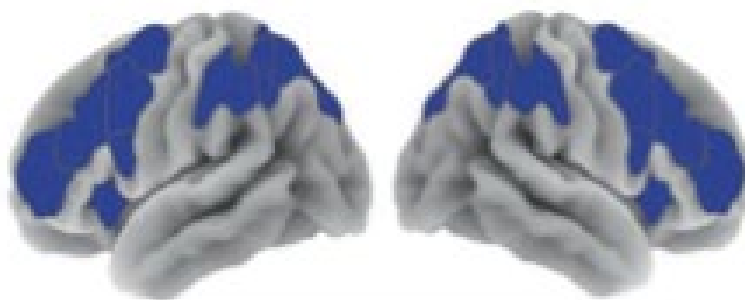
**b** Language network



**Supported functions:**  
Language comprehension  
Language production

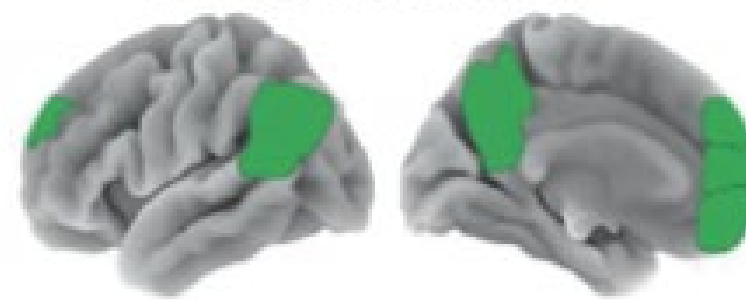
Some networks that support thinking and reasoning

Multiple demand network



**Supported functions:**  
Executive functions  
Novel problem solving  
Mathematics  
Some forms of reasoning  
Computer code comprehension

Theory of mind network



**Supported functions:**  
Social reasoning  
Mentalizing



# Language is not necessary or sufficient for thought

- ▶ If language mediates some forms of thought, then those forms of thought should not be possible in the absence of language because they should critically depend on linguistic representations (the 'necessity of language for thought' argument).
- ▶ Moreover, the presence of language (or an intact linguistic ability) should be associated with the capacity for those forms of thought (the 'sufficiency of language for thought' argument).

# Language is unnecessary for thought

- ▶ \*\*\* Language is not necessary for any tested forms of thought
- ▶ \*\*\* If linguistic ability mediates our ability to engage in certain forms of thought, then linguistic impairments should be associated with concomitant difficulties in those aspects of thinking and reasoning.

# Severe linguistic deficits with normal thought

- ▶ The evidence is unequivocal—there are many cases of individuals with severe linguistic impairments, affecting both lexical and syntactic abilities, who nevertheless exhibit intact abilities to engage in many forms of thought—
  - ▶ they can solve mathematical problems,
  - ▶ perform executive planning and follow non-verbal instructions,
  - ▶ engage in diverse forms of reasoning,
  - ▶ including formal logical reasoning,
  - ▶ causal reasoning about the world and scientific reasoning,
  - ▶ to understand what another person believes or thinks and

# Normal thought in language deficits

- ▶ perform pragmatic inference,
  - ▶ to navigate in the world,
  - ▶ and to make semantic judgements about objects and events.
- 
- ▶ This body of evidence challenges both general claims about the importance of language for thought, and a number of specific proposals about the critical role of language in particular kinds of thinking, including mathematical reasoning, cross-domain information integration, and categorization.

# Severe aphasia, normal thought

- ▶ \*\* Despite losing their linguistic ability, some individuals with severe aphasia are able to perform all tested forms of thinking and reasoning, as evidenced by their intact performance on diverse cognitive tasks.
- ▶ They simply cannot map those thoughts onto linguistic expressions, either in language production (they cannot convey their thoughts to others through language) or in understanding (they cannot extract meaning from others' words and sentences).

# Classic Language Model: Broca's and Wernicke's areas

- ▶ Many textbooks continue to use the classic model of the neural basis of language.
- ▶ This model consists of two cortical areas—Broca's area in the inferior frontal cortex and Wernicke's area in the posterior superior temporal cortex—which are argued to support language production and comprehension, respectively, and which are connected by a dorsal fiber bundle called the arcuate fasciculus.

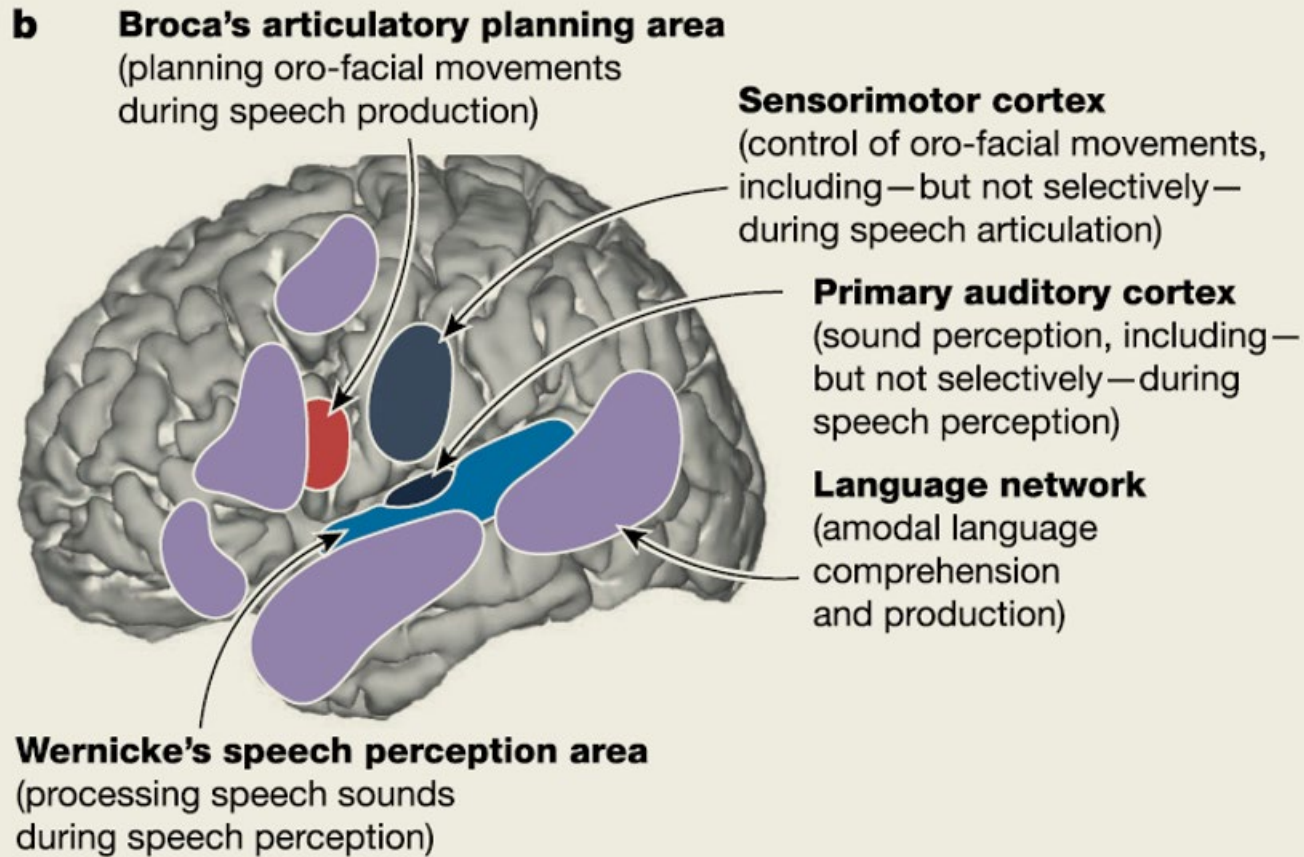
# Difference in anatomical vs functional brain analysis

- ▶ We believe that much of the confusion about Broca's and Wernicke's areas has resulted from frequent conflation of speech (spoken language) and language (the abstract system of form-to-meaning mappings) in experimental designs and scientific discourse, and predominant reliance in human cognitive neuroscience on anatomical rather than functional definitions of brain areas.



# Frontal Asiant Tract (FAT)

- ▶ FAT = white matter tract connecting the supplementary motor complex and lateral superior frontal gyrus to the inferior frontal gyrus.
- ▶
- ▶ FAT was shown to have multiple roles: in speech and language functions (verbal fluency, initiation and inhibition of speech, sentence production, and lexical decision), working memory, visual–motor activities, orofacial movements, social community tasks, attention, and music processing.
- ▶ **Associated with neurological disorders**, such as primary progressive aphasia, post-stroke aphasia, stuttering, Foix–Chavany–Marie syndrome (speech & feeding muscle paralysis), social communication deficit in autism spectrum disorders, and attention–deficit hyperactivity disorder



A model based on the current knowledge of neurobiology of language:

Broca's (articulatory planning) area (red) and Wernicke's (speech perception) area (blue), and a set of frontal and temporal areas that jointly support high-level language comprehension and production (purple).

Also primary auditory cortex, which provides input to Wernicke's (speech perception) area, and sensorimotor cortex, to which Broca's (articulatory planning) area provides input.

# Newer nomenclature

- ▶ \*\*Adding function into these areas' names (for example, 'Broca's articulatory planning area' and 'Wernicke's speech perception area') and using validated 'localizer' paradigms to separate these areas from nearby functionally distinct areas is likely to lead to progress and alleviate confusion.
- ▶ \*\*Absent from the classic model are the 'higher-level language areas', which store abstract linguistic knowledge and support comprehension and production.

# Classic vs Higher-level language network

- ▶ There is a straightforward explanation for the absence of these areas from the early proposals of the neurobiology of language.
- ▶ The early evidence about brain–behavior relationships came from reports of selective deficits following brain damage. Because Broca's and Wernicke's areas are relatively circumscribed and specialized for particular functions, their damage is more likely to lead to deficits.
- ▶ \*\* By contrast, the higher-level language network is distributed across extensive portions of the left temporal and frontal cortex, with different language regions exhibiting similar functional profiles

# High level language network

- ▶ No individual part of the high-level language network may be critically needed for linguistic function.
- ▶ Circumscribed lesions to the language network do not lead to severe or long-lasting deficits.

# FMRI study of language network: silent during thought

- ▶ \*\*\* All regions of the language network are largely 'silent' during all tested forms of thought:
  - ▶ including mathematical reasoning, formal logical reasoning, performing demanding executive function tasks such as working memory or cognitive control tasks, understanding computer code, thinking about others' mental states, and making semantic judgments about objects or events.

# Multi-domain cognitive areas = thought

- ▶ Multi-domain areas: These cognitive tasks engage other brain areas that are non-overlapping with the language network, although they sometimes lie in close proximity to the language areas.
- ▶ **It remains possible** that future work will uncover some thinking tasks that will engage language areas and that will prove challenging for patients with aphasia, but no such tasks have been found so far.

# Children have multi-domain processors

- ▶ \*\* First, recent evidence suggests that the dissociation between the language network and systems that support thinking and reasoning is already present in young children,
- ▶ And second, some children growing up with no access to language can nevertheless reason in complex ways



# Children with no language

- ▶ In particular, some deaf children who are born to hearing parents grow up with little or no exposure to language, sometimes for years, because they cannot hear speech and their parents or caregivers do not know sign language.
- ▶ Lack of access to language has harmful consequences for many aspects of cognition, which is to be expected given that language provides a critical source of information for learning about the world.

# Language & thought are separate brain functions

- ▶ \*\* Nevertheless, individuals who experience language deprivation unquestionably exhibit a capacity for complex cognitive function:
- ▶ They can still learn to do mathematics, to engage in relational reasoning, to build causal chains, and to acquire rich and sophisticated knowledge of the world.
- ▶ Thus, it appears that in typical development, language and reasoning develop in parallel

# Intact language does not imply intact thought

- ▶ \*\* Finally, it is worth mentioning that pre-verbal infants and many animal species—including non-human primates, corvids, elephants and cephalopods—exhibit impressive inferential and problem-solving abilities, apparently without language.
- ▶ This evidence suggests that all the types of thought tested to date are possible without language.
- ▶ Contrary to the view that language mediates thinking, an intact language system does not appear to entail intact reasoning abilities.

# Intact language with impaired cognition

- ▶ **\*\* Evidence from both developmental and acquired brain disorders suggests that intellectual impairments can be present even when linguistic abilities are largely intact.**
- ▶ **For example, several genetic disorders are characterized by varying degrees of intellectual disability (Down syndrome and Williams syndrome, among others), yet their linguistic abilities of people with these disorders appear to be close to typical.**
- ▶ **Even if subtle linguistic deficits are observed, the foundational capacities for processing word meanings and linguistic structure building hypotheses—are intact. Some neuropsychiatric disorders, such as schizophrenia, affect the ability to think and reason, but again spare language.**

# Intact language, deficit in thinking

- ▶ Finally, many individuals with acquired brain damage exhibit difficulties in reasoning and problem solving but appear to have full command of their linguistic abilities.
- ▶ In other words, having an intact language system does not bring with it 'for free' an ability to think: thinking capacities can be impaired in the presence of intact language.

# Language is for talking to others

- ▶ Language appears to not be necessary for any forms of thought tested so far, and that language is not sufficient for thought.
- ▶ **\*\*** Many features of natural languages appear to be optimized for efficient information transfer, we have argued for communication being the primary function of language.

# Association Cortex Networks

- ▶ Evidence from human brain evolution instead suggests parallel increases in the sophistication of multiple cognitive systems.
- ▶ Relative to the brains of other animals, including non-human primates, the association cortex—which houses mental processes above and beyond perception and motor control—has expanded substantially and disproportionately in the human brain.
- ▶ The association cortex spans frontal, temporal and parietal lobes and, in humans, comprises multiple large-scale networks—ensembles of brain areas that jointly support some aspect of cognition.
- ▶ The language network is just one of these networks

# Frontal-parietal network: Multiple Demand

- ▶ \*\* Other networks: The frontal-parietal network referred to as the 'multiple demand' network,
  - ▶ supports diverse goal-directed behaviors, including novel problem solving, and
  - ▶ damage of this network leads to impairments in fluid intelligence.
- ▶ Mathematical and logical reasoning and the processing of computer code also draw on the multiple demand network.



# Other Networks

## ▶ \*\*Other such networks:

- ▶ 'theory of mind' network, which supports social reasoning, including mentalizing or thinking about others' thoughts
- ▶ 'default' network, whose functions remain debated, with some linking its regions to episodic projection into the past or future and spatial cognition and reasoning. (Network disconnected in psilocybin trips)

▶ At least some of the networks have homologues in non-human animal brains.

# Network expansion – simultaneous?

- ▶ Whether this expansion proceeded in a truly parallel fashion, or whether the emergence or expansion of one network critically drove the expansion of other networks is not known, but the parallel development possibility is perhaps more plausible given that diverse cognitive abilities probably increased the probability of survival.
  - ▶ including social sophistication (being able to model the minds of others), the ability to infer causal structures in the world, flexible problem solving and planning for the future, and better communicative ability.

# Language features

- ▶ But large studies have suggested that languages have been optimized to transfer information clearly and efficiently.
- ▶ Frequently used words are shorter, making languages easier to learn and speeding the flow of information.
- ▶ Rules of grammar put words close to each other so that their combined meaning is easier to understand.

# ChatGPT and LLMs: good at language, maybe not thinking

- ▶ Separating thought and language could help explain why artificial intelligence systems like ChatGPT are so good at some tasks and so bad at others. ChatGPT may produce language answers, but may not “think”
- ▶ Computer scientists train these programs on vast amounts of text, uncovering rules about how words are connected.
- ▶ \*\* These programs are starting to mimic the language network in the human brain — but falling short on reasoning.

# Conclusions on Language and Thought

- ▶ **\*\* Evidence from aphasia research suggests that**
  - ▶ all tested forms of thought are possible in the absence of language, and
  - ▶ fMRI evidence suggests that engaging in diverse forms of thinking and reasoning does not recruit the language network.
  
- ▶ **\*\* Moreover, intact linguistic abilities do not entail intact thinking abilities.**

# Conclusions

- ▶ \*\* Together, this evidence suggests that language is unlikely to be a critical substrate for any form of thought.
- ▶ \*\* Although access to words, syntactic structures or non-linguistic symbols can facilitate performance on certain cognitive tasks, language is dissociated from thinking and reasoning.
- ▶ Diverse properties of human languages render them easy to produce, easy to learn and understand, concise and efficient for use, and robust to noise.

# Language = knowledge transmission

- ▶ **\*\* Language serves a primarily communicative function and reflects, rather than gives rise to, the signature sophistication of human cognition.**
- ▶ Instead of providing the key substrate for thinking and reasoning, language likely transformed our species by enabling cross-generational transmission of acquired knowledge.
- ▶ **\*\* Language = massively useful tool for knowledge transmission.**

### \*\*\* Broad domain-generalty in focal regions of frontal and parietal cortex

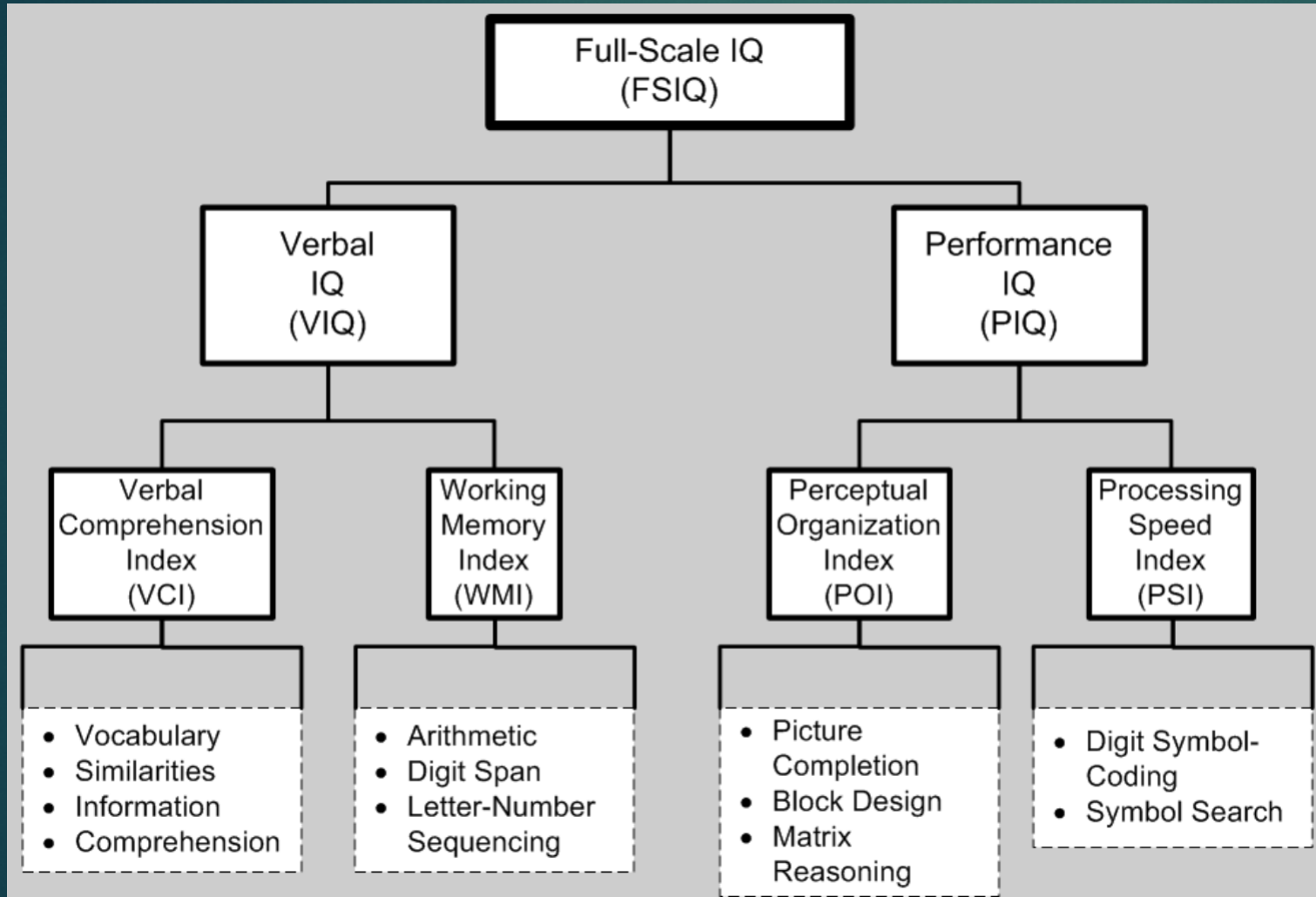
- ▶ One of the oldest debates in cognitive neuroscience concerns the degree of functional specialization present in the human brain.
- ▶ There several highly specialized brain components dedicated to particular mental functions, like face recognition or motion perception.
- ▶ However, our cognitive versatility suggests the additional existence of more general-purpose machinery.
- ▶ Thus, human cognition arises from hardware that includes not only specialized components, but also very general-purpose ones that plausibly enable us to solve novel problems.



### \*\*\* The domain-generality of the Multiple Demand network

- ▶ The association cortex contains a bilateral network of frontal and parietal areas that are highly domain-general.
- ▶ \*\* These MD areas are engaged during diverse goal-directed behaviors and have been linked to **general fluid intelligence**, which encompasses executive functions (working memory, cognitive control, and attention), domain-general reasoning abilities, skill acquisition, and novel problem solving. Some domains, like numerical cognition, logical reasoning, and the processing of computer code also recruit this network.
- ▶ Multiple Demand brain areas possess domain-generality

# Wechsler Adult Intelligence Scale



CJV: WAIS IQ test:  
Verbal vs Performance IQ;

Verbal = language related measures = vocabulary, general knowledge, comprehension, and similarities; these tasks rely heavily on accumulated knowledge and past learning  
**Performance IQ = Fluid IQ** = ability to solve novel problems, esp. non-verbal ones.

# WAIS Block Design subtest



# WAIS Visual Puzzle

“Which 3 of these pieces go together to make this puzzle?”



1

2

3



4

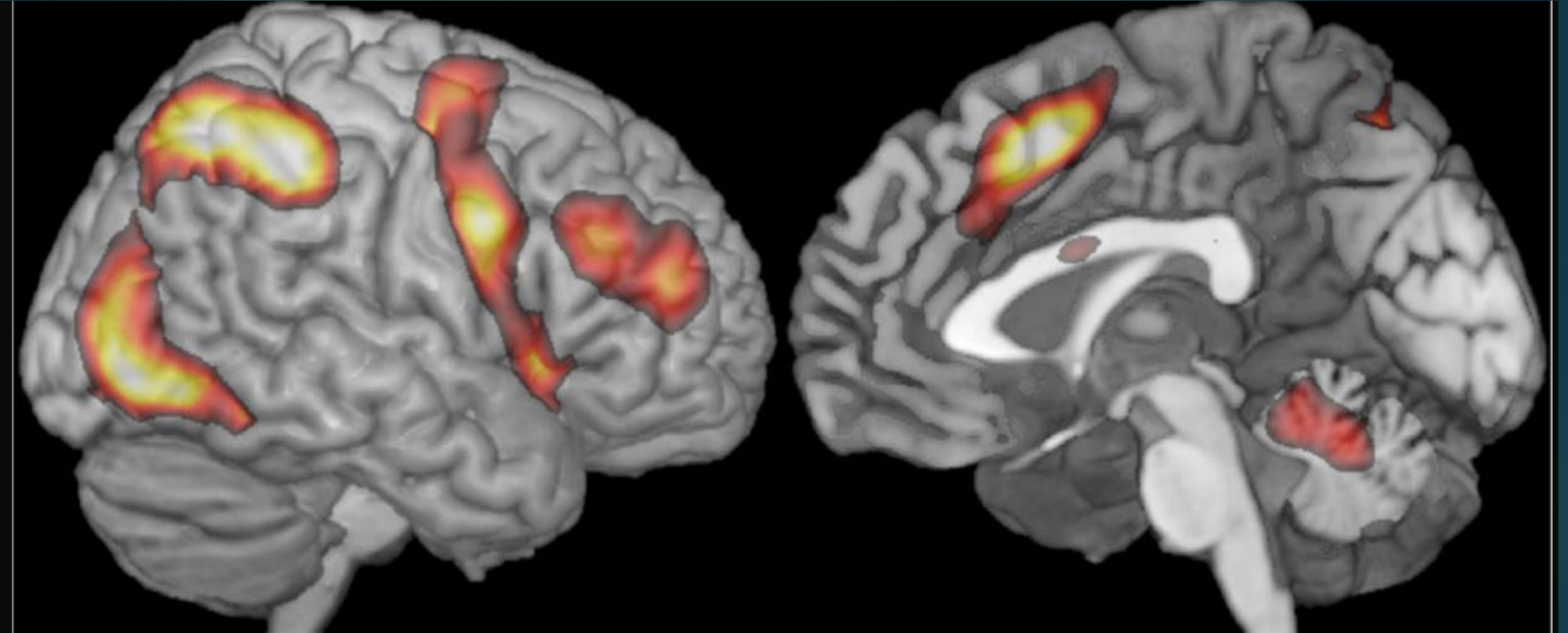
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6

# Multi-domain brain regions: frontal-parietal areas

- ▶ \*\* A number of frontal and parietal regions are thought to be domain- and process-general: that is, active during a wide variety of demanding cognitive tasks.
- ▶ Thus, in addition to domain-specific brain regions (i.e. vision) tailored to solve particular problems of longstanding importance to our species, the human brain also contains a set of functionally general regions that plausibly endow us with the cognitive flexibility necessary to solve novel problems.
- ▶ Brain regions throughout the MD system respond across a wide range of demanding cognitive tasks.

A group-level representation of the Multiple Domain activity based on average activity in left and right hemispheres



# Both general and specific functional brain regions

- ▶ Provide strong evidence for the functional generality of a set of regions in the frontal and parietal lobes that are broadly engaged in a wide range of tasks, from mental arithmetic, to holding information in working memory, to filtering and suppressing task-irrelevant information.
- ▶ \*\* Activity in the fronto-parietal multiple-demand network is robustly associated with individual differences in working memory and fluid intelligence

# MD regions associated with WM & fluid intelligence

- ▶ \*\* Numerous brain lesion and fMRI studies have linked individual differences in executive abilities and fluid intelligence to brain regions of the fronto-parietal “multiple-demand” (MD) network.
- ▶ \*\* Found that stronger activity in MD regions was robustly associated with more accurate and faster responses on a spatial working memory task, as well as, fluid intelligence.



# MD regions and intelligence

- ▶ Demonstrate that a core component of individual differences variance in executive abilities and fluid intelligence is selectively and robustly positively associated with the level of activity in the MD network
- ▶ \*\* MD regions—engaged by executive function tasks—are the best predictors of individual differences in general intelligence; associated with frontal and parietal MD brain regions.

\*\*\* Fluid intelligence is supported by the multiple-demand system not the language system

- ▶ Damage to the Multiple Demand network is associated with deficits in fluid intelligence.
- ▶ For example, the amount of damage to frontal or parietal, but not temporal, cortices predicts fluid intelligence deficit. However, frontal and parietal lobes are structurally and functionally heterogeneous. They contain domain-general regions that respond across diverse tasks, but also specialized regions that respond selectively during language processing.
- ▶ \*\* MD-weighted, but not language-weighted, lesion volumes predicted fluid intelligence deficit (with the opposite pattern observed for verbal fluency), indicating that fluid intelligence is specifically tied to the MD system, and undermining claims that language is at the core of complex thought.

# Missing a temporal lobe

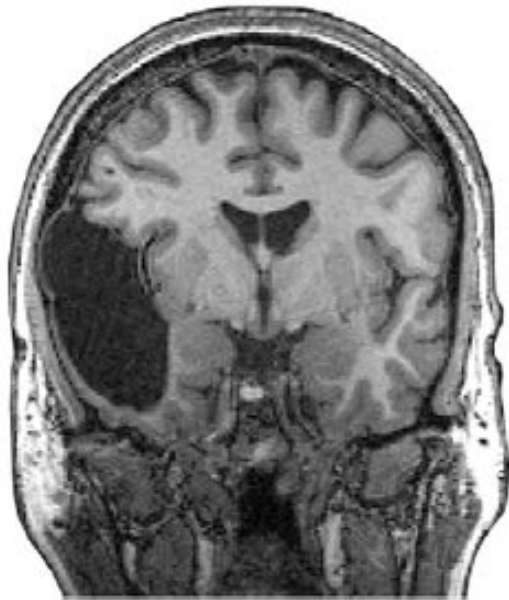
- ▶ \*\* A unique family: one sibling missing their left temporal lobe from infancy, another missing the right temporal lobe from infancy, and a third anatomically neurotypical. None of the siblings manifested behavioral deficits.
- ▶ \*\* Our findings suggest that the functional organization of the auditory cortex in the intact hemispheres is preserved in the affected siblings despite lacking the other temporal lobe from infancy.

# Temporal lobe absence: what happens to language?

A

**POI 1**

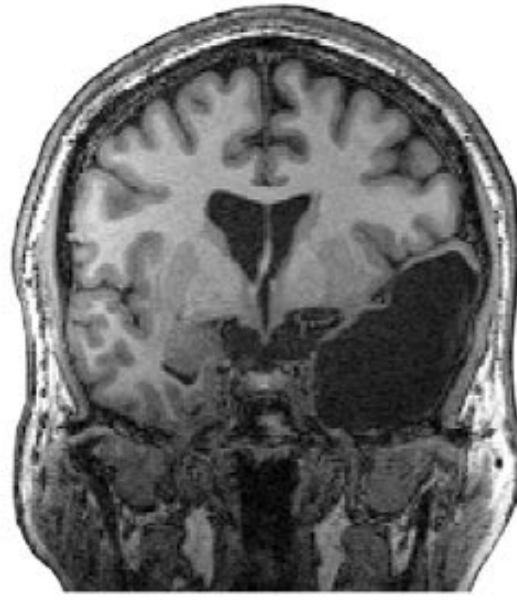
**Left** temp lobe missing



B

**POI 2**

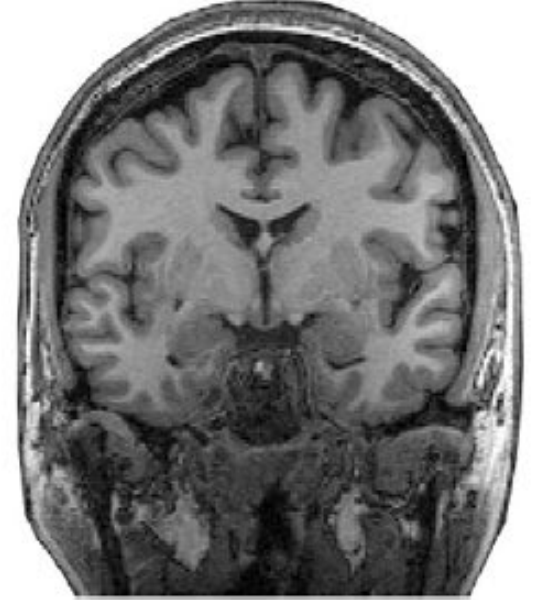
**Right** temp lobe missing



C

**POI 3**

Neurotypical



\*\*\* Preserved functional organization of auditory cortex in two individuals missing one temporal lobe from infancy

- ▶ These papers investigate the functional architecture in individuals with atypical brains, such as individuals with early strokes, large cysts, or hydrocephalus. Here are the papers that have come out of this project so far.
- ▶ Auditory cortex (AC) organization (normally housed in left temporal lobe) tested in participants with only one temporal lobe
- ▶ Features of auditory components, including speech and music, are normal
- ▶ AC organization is robust to whether it is bilateral or present in one hemisphere

# Absence of temporal lobe

- ▶ \*\* All siblings manifested typical-like auditory responses in their intact hemispheres. These results suggest that the development of the auditory cortex in each hemisphere does not depend on the existence of the other hemisphere, highlighting the redundancy and equipotentiality of the bilateral auditory system.
- ▶ \*\* The siblings that lacked one temporal lobe manifested intact auditory, linguistic, and general cognitive abilities.

## \*\* Language processing in the occipital cortex of congenitally blind adults

- ▶ Language processing in congenitally blind individuals
- ▶ \*\* Congenitally blind individuals have typical-like language areas in the left frontal and temporal cortex, but additionally have a region in the occipital cortex that also supports language comprehension.

# Congenitally blind also use occipital cortex for language

- ▶ \*\* Congenitally blind individuals also activate the visual cortex in some verbal tasks. We provide evidence that this visual cortex activity in fact reflects language processing.
- ▶ \*\* We find that in congenitally blind individuals, the left visual cortex behaves similarly to classic language regions. We conclude that brain regions that are thought to have evolved for vision can take on language processing as a result of early experience.



### \*\*\* Neuronal recordings of language

- ▶ Humans possess an exceptional ability to extract nuanced meaning through language.
- ▶ To start addressing these questions, the scientists used a **novel technology that allowed them to simultaneously record the activities of up to a hundred neurons from the brain while people listened to sentences** (such as, "the child bent down to smell the rose") **and short stories** (for example, about the life and times of Elvis Presley).

# Neuron linguistic specificity

- ▶ Using this new technique, the investigators discovered how neurons in the brain map words to particular meanings and how they distinguish certain meanings from others.
- ▶ For example, we found that while certain neurons preferentially activated when people heard words such as 'ran' or 'jumped,' which reflect actions, other neurons preferentially activated when hearing words that have emotional connotations, such as 'happy' or 'sad,'”
- ▶ To comprehend language, though, it is not enough to only understand the meaning of words, but also to accurately follow their meanings within sentences.

# Neurons

- ▶ Found that certain neurons in the brain are able to reliably distinguish between such words, and they continuously anticipate the most likely meaning of the words based on the sentence contexts in which they are heard. Which is what LLMs do.
- ▶ **\*\*That is, based on the activities of the neurons, the team could determine the general ideas and concepts experienced by an individual as they were being comprehended during speech.**

# \*\*\* Semantic encoding during language comprehension at single-cell resolution -- Mohsen Jamali, et al., 2024 – MIT lab

- ▶ Here we recorded from single cells in the left language-dominant prefrontal cortex as participants listened to semantically diverse sentences and naturalistic stories.
- ▶ \*\* Fine-scale cortical representation of semantic information by individual neurons. Neurons response selectively to specific word meanings and reliably distinguished words from nonwords.
- ▶ Moreover, rather than responding to the words as fixed memory representations, their activities were highly dynamic, reflecting the words' meanings based on their specific sentence contexts and independent of their phonetic form.

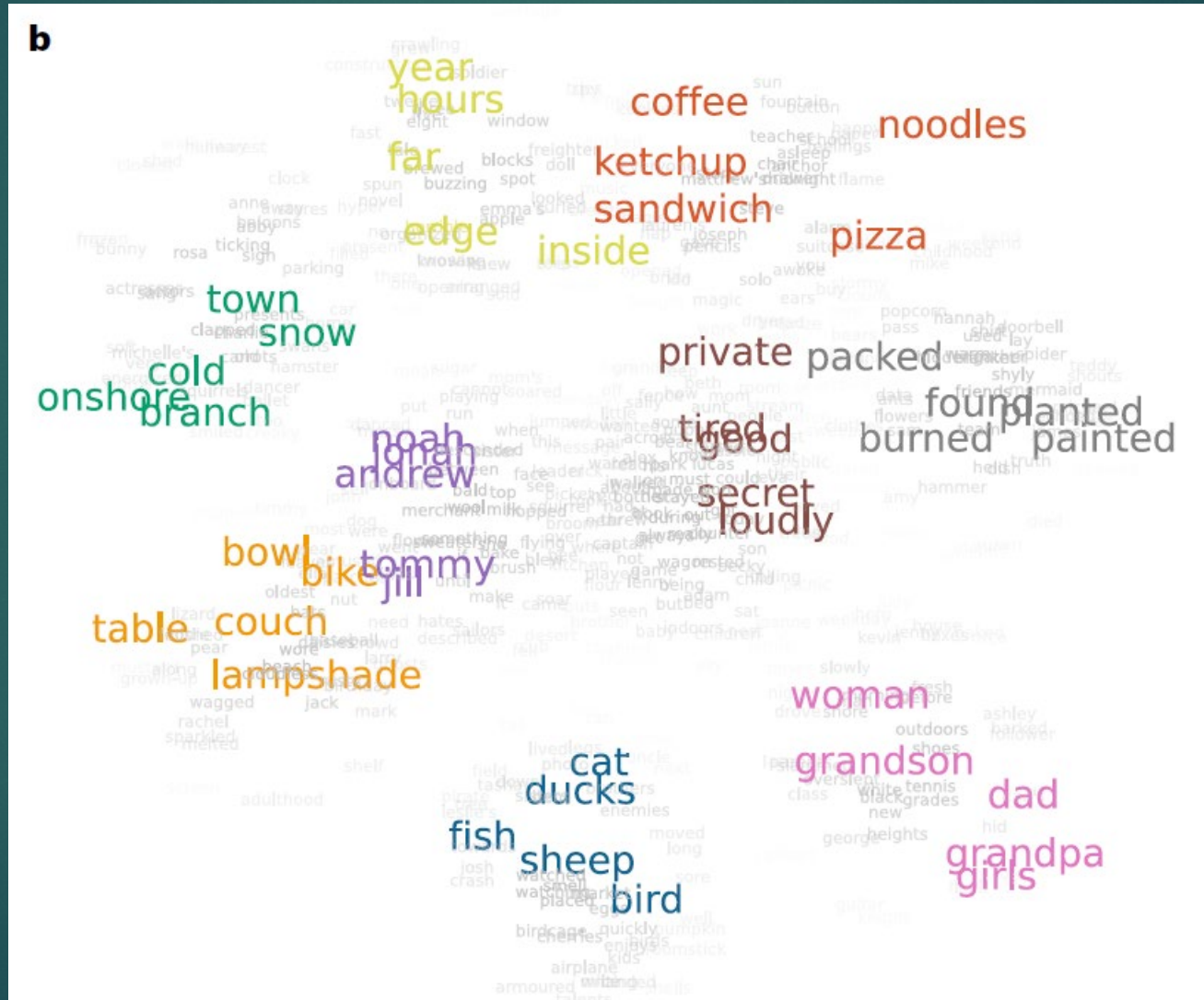
# Language at the single neuron level

- ▶ Recruited ten people about to undergo surgery for epilepsy, each of whom had had electrodes implanted in their brains to determine the source of their seizures.
- ▶ The electrodes allowed the researchers to **record activity from around 300 neurons in each person's prefrontal cortex.**
- ▶ As participants listened to multiple short sentences containing a total of around 450 words, the scientists recorded which neurons fired and when.
- ▶ Around two or three distinct neurons lit up for each word, although the team recorded only the activity of a tiny fraction of the prefrontal cortex's billions of neurons.

# Words trigger specific neurons

- ▶ The words that the same set of neurons responded to fell into similar categories, such as actions, or words associated with people.
- ▶ The team also found that words that the brain might associate with one another, such as 'duck' and 'egg', triggered some of the same neurons.
- ▶ Other groups of neurons responded to words associated with more-abstract concepts: relational words such as 'above' and 'behind', for instance.

# Organization of semantic representations



# Prefrontal meaning detection

- ▶ \*\* The categories that the brain assigns to words were similar between participants suggesting human brains all group meanings in the same way.
- ▶ \*\* The prefrontal cortex neurons didn't distinguish words by their sounds, only their meanings.
- ▶ When a person heard the word 'son' in a sentence, for instance, words associated with family members lit up. But those neurons didn't respond to 'Sun' in a sentence, despite these words having an identical sound.
- ▶ Neurons could determine not only the neurons that corresponded to words and their categories, but also the order in which they were spoken.



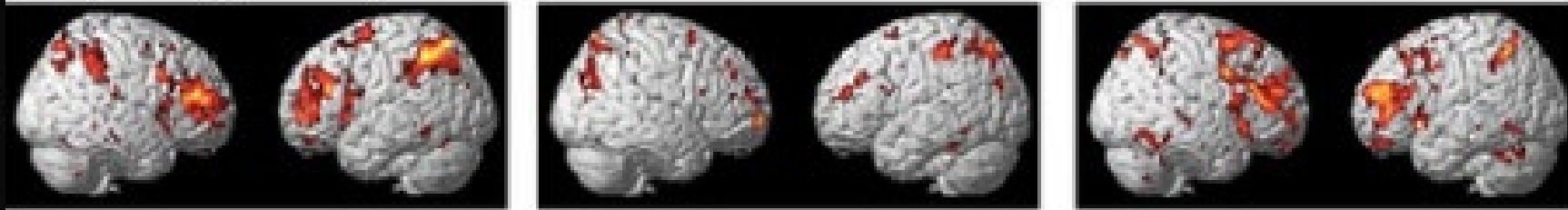
# \*\*\* Functional specificity for high-level linguistic processing in the human brain

- ▶ \*\* The neuropsychological literature, features striking dissociations between deficits in linguistic and nonlinguistic abilities,
- ▶ vs. the neuroimaging literature, which has argued for overlap between activations for linguistic and nonlinguistic processes, including arithmetic, domain general abilities like cognitive control, and music.
- ▶ Here, we use functional MRI to define classic language regions functionally in each subject individually and then examine the response of these regions to the nonlinguistic functions most commonly argued to engage these regions: arithmetic, working memory, cognitive control, and music.

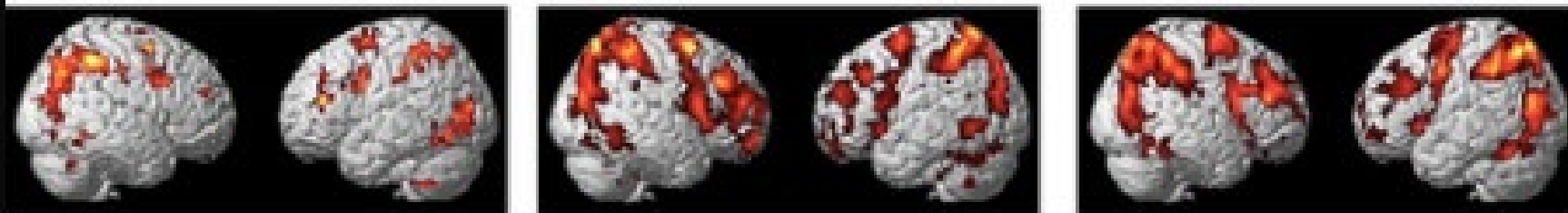
# Language areas do not respond to non-language functions

- ▶ \*\* We find little or no response in language regions to these nonlinguistic functions.
- ▶ These data support a clear distinction between language and other cognitive processes, resolving the prior conflict between the neuropsychological and neuroimaging literatures.

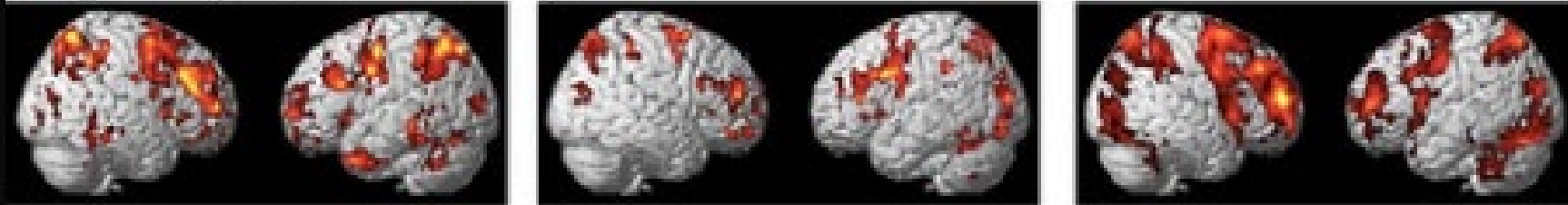
### Expt 1 (Math)



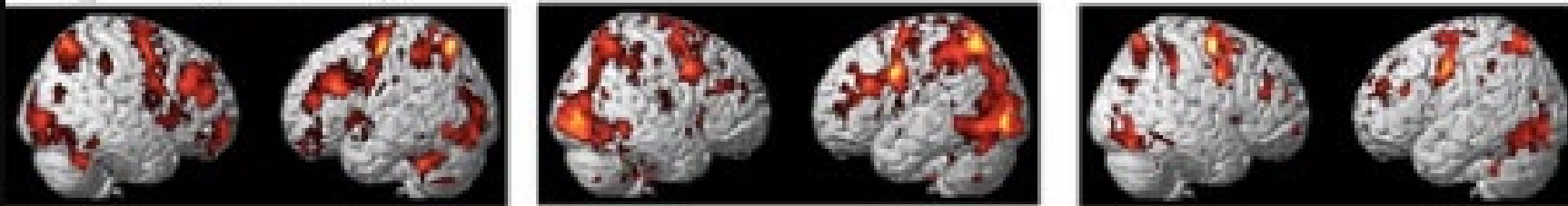
### Expt 2 (Spatial WM)



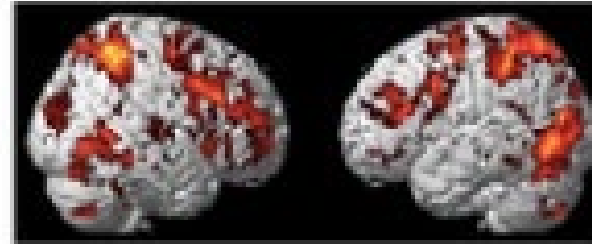
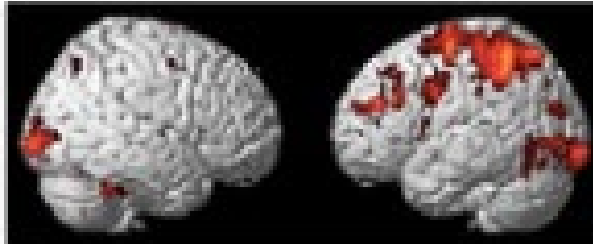
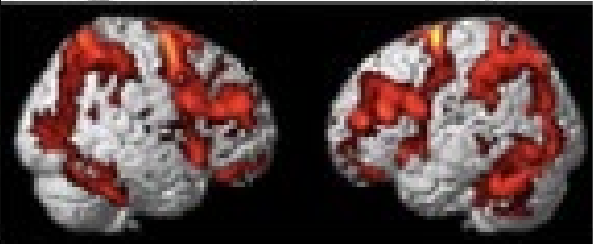
### Expt 3 (Verbal WM)



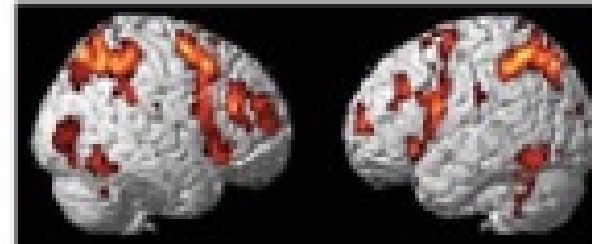
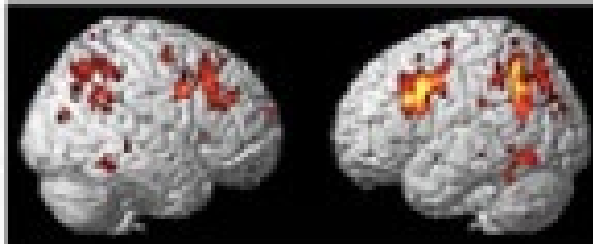
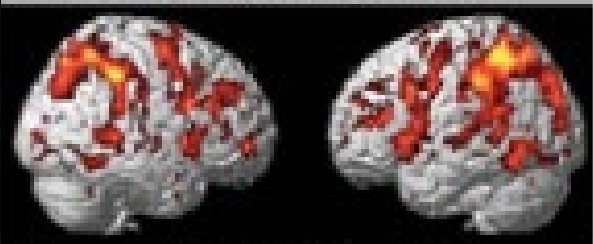
### Expt 4 (MSIT)



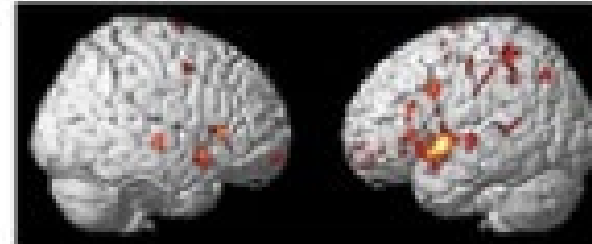
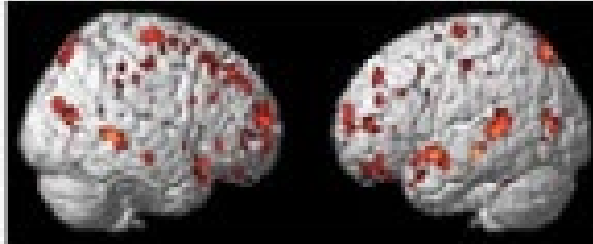
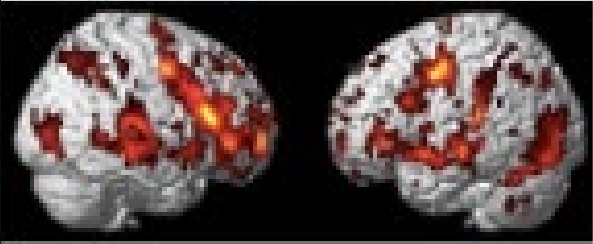
### Expt 5 (vMSIT)



### Expt 6 (Stroop)



### Expt 7 (Music)



# Stroop test: read color of word, not the word – how fast?

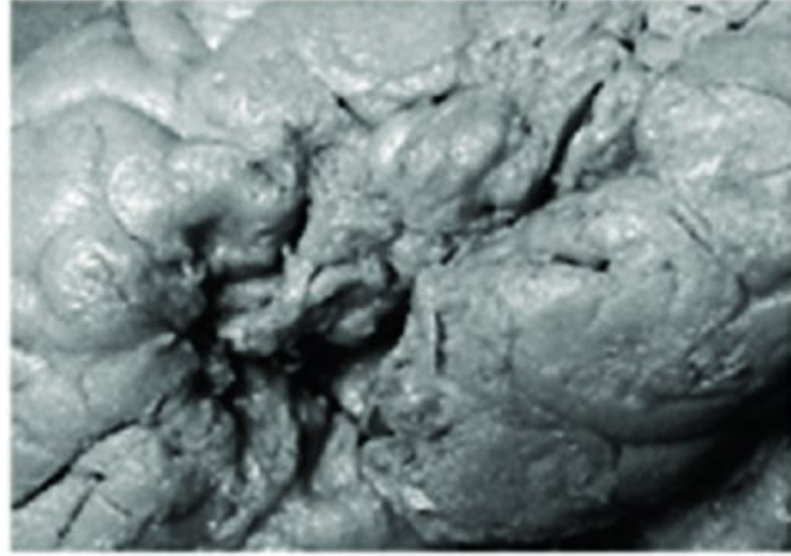
blue	red	brown	green	purple	blue	purple
purple	brown	green	blue	red	green	blue
purple	red	blue	purple	brown	brown	green
brown	purple	purple	green	blue	blue	blue
purple	red	red	brown	blue	red	purple
purple	blue	brown	purple	green	green	blue
green	purple	purple	red	green	purple	red
blue	brown	brown	red	brown	brown	green
purple	blue	brown	brown	green	green	purple
brown	brown	red	blue	blue	blue	purple

# Broca's famous aphasia case: Brain of "Tan"

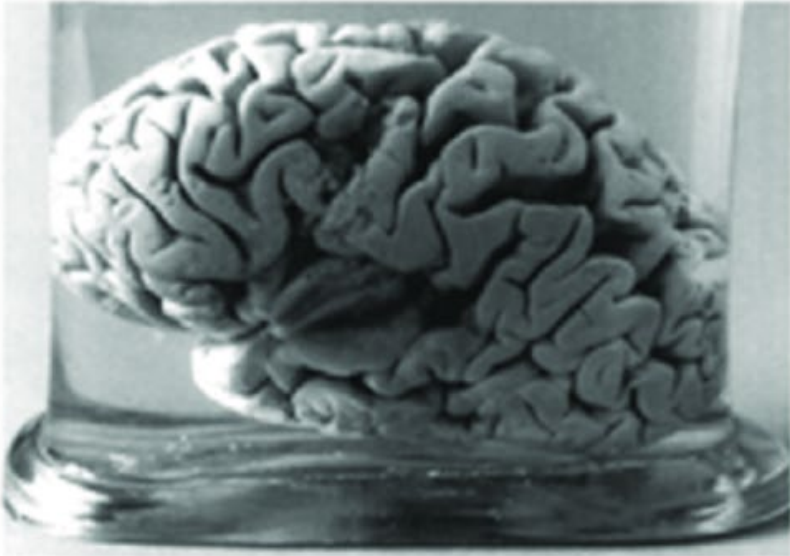
A



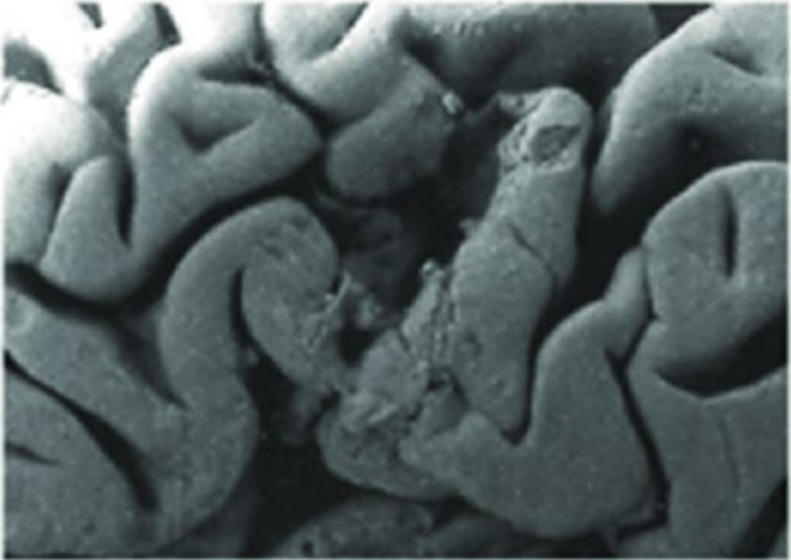
B



C



D



## \*\*\* Language-Selective and Domain-General Regions Lie Side by Side within Broca's Area

- ▶ In 1861, Paul Broca stood up before the Anthropological Society of Paris and announced that the left frontal lobe was the seat of speech. Ever since, Broca's eponymous brain region has served as a primary battleground for one of the central debates in the science of the mind and brain:
- ▶ \*\* Is human cognition produced by highly specialized brain regions, each conducting a specific mental process, or instead by more general-purpose brain mechanisms, each broadly engaged in a wide range of cognitive tasks?

## Broca's area: 2 tasks

- ▶ For Broca's area, the debate focuses on specialization for language versus domain-general functions
- ▶ \*\* Here, using single-subject fMRI, we find that both ideas are right: Broca's area contains two sets of subregions lying side by side, one quite specifically engaged in language processing, surrounded by another that is broadly engaged across a wide variety of tasks and content domains.



# Broca's area

- ▶ Broca's area contains both language-selective and domain-general subregions
  - ▶ • "Broca's aphasia" plausibly results from damage to both sets of subregions
  - ▶ • Human cognition is produced by both specialized and general-purpose brain regions
  - ▶ Helps resolve the longstanding debate about whether Broca's area is language-specific or domain-general: our data show that it is both, in different subregions

\*\*\* The language network and the Multiple Demand (MD) network are robustly dissociated

- ▶ \*\* The Multiple Demand (MD) network has been linked to general fluid intelligence, which encompasses executive functions (working memory, cognitive control, and attention), domain-general reasoning abilities, skill acquisition, and novel problem solving.
- ▶ Many have argued over the years that language is what made us smart, and that language mediates complex thought and reasoning.

• Is the language network dissociable from the multiple-demand and default mode networks?

- Data-driven support for a triple language/multiple-demand/default mode dissociation.

# Complex cognitive processes

- ▶ Complex cognitive processes, including language, rely on multiple mental operations that are carried out by several large-scale functional networks in the frontal, temporal, and parietal association cortices of the human brain.
- ▶ The central division of cognitive labor is between two fronto-parietal bilateral networks:
  - ▶ (a) the multiple demand (MD) network, which supports executive processes, such as working memory and cognitive control, and is engaged by diverse task domains, including language, especially when comprehension gets difficult; and
  - ▶ (b) the default mode network (DMN), which supports introspective processes, such as mind wandering, and is active when we are not engaged in processing external stimuli.

# Language network

- ▶ These two networks are strongly dissociated in both their functional profiles and their patterns of activity fluctuations during naturalistic cognition.
- ▶ Study focuses on the functional relationship between these two networks and a third network:
  - ▶ (c) the fronto-temporal left-lateralized “core” language network, which is selectively recruited by linguistic processing.
- ▶ Is the language network distinct and dissociated from both the MD network and the DMN, or is it synchronized and integrated with one or both of them? Recent work has provided evidence for a dissociation between the language network and the MD network.

## 3 dissociated networks

- ▶ \*\* Thus, using our novel method, we replicate the language/MD network dissociation discovered previously with other approaches, and also show that the language network is robustly dissociated from the DMN, overall suggesting that these three networks contribute to high-level cognition in different ways and, perhaps, support distinct computations.

# There is a Language-specific Working Memory

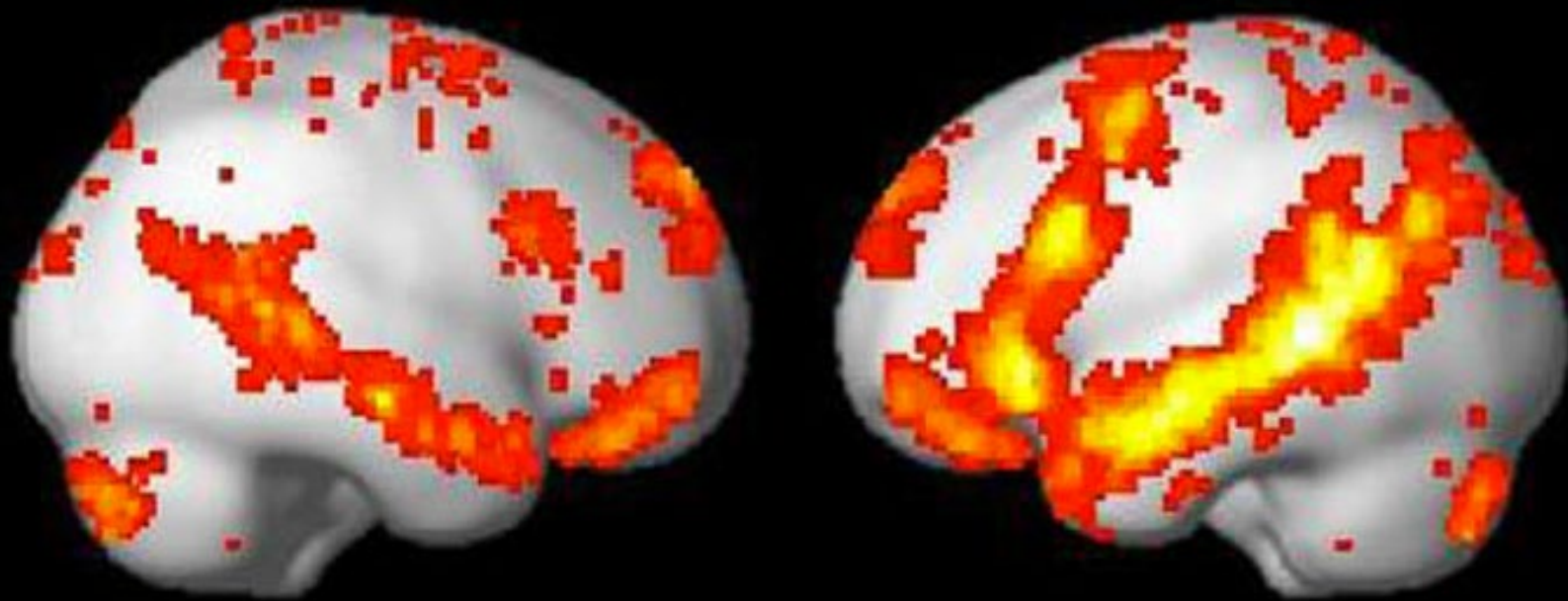
- ▶ Results show robust surprisal-independent effects of memory demand in the language network and no effect of memory demand in the multiple-demand network.
- ▶ \*\* Our findings thus support the view that language comprehension involves computationally demanding word-by-word structure building operations in working memory.

## 2 types of working memory

- ▶ \*\* Further, these memory operations appear to be primarily conducted by the same neural resources that store linguistic knowledge, with no evidence of involvement of brain regions known to support working memory across domains.
- ▶ \*\* Supports the existence of a distributed but domain-specific working memory resource that plays a core role in language comprehension, with no evidence of recruitment of domain-general working memory resources housed within the multiple-demand network.

\*\*\* The role of domain-general cognitive control in language comprehension -- Evelina Fedorenko

## The language system





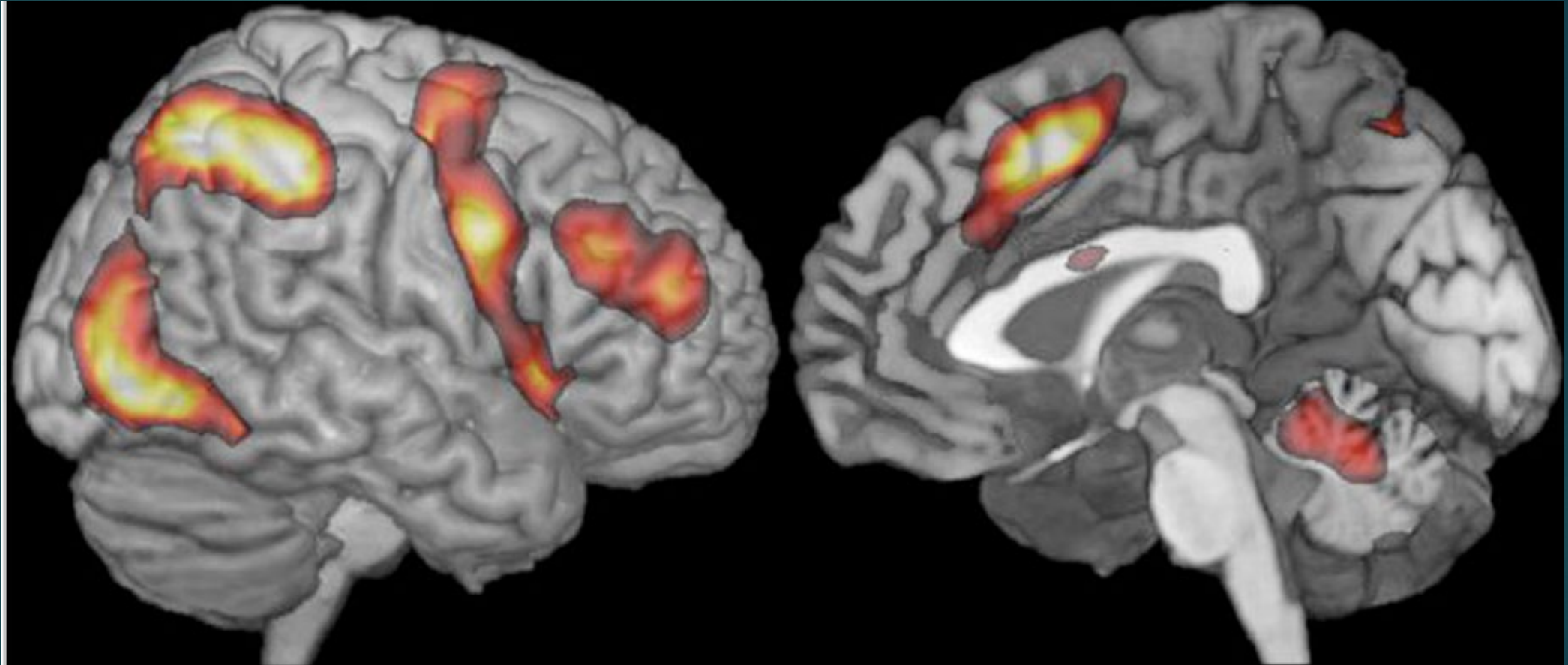
# If you ask Google AI: Does right hemisphere have language functions?

- ▶ Yes, while the left hemisphere is primarily responsible for language functions, the right hemisphere also plays a significant role in language processing, particularly in understanding the emotional tone of speech (prosody), interpreting figurative language like sarcasm and metaphors, and comprehending the overall context of a conversation; essentially, the social and emotional aspects of language.
- ▶ Key points about the right hemisphere's role in language:
  - **Prosody:** The right hemisphere is crucial for interpreting the **emotional tone and inflection in speech (prosody)**.
  - **Figurative language:** Understanding **sarcasm, metaphors, and other non-literal language** relies heavily on the right hemisphere.

# Right hemisphere

- **Discourse comprehension:** The right hemisphere contributes to understanding the overall meaning and context of a conversation.
- **Social communication:** Interpreting social cues and nuances in language is facilitated by the right hemisphere.
- Also hemineglect (unilateral neglect) and anosognosia (inability to see dysfunction)
- MIT lab disagrees!!

# Multiple-demand network



\*\*\* The language network is selective for language relative to social perception

- ▶ Language is typically used in social settings.
- ▶ Does language share machinery with our abilities to process other socially-relevant information, like facial expressions or body language? It doesn't appear so.
- ▶ This paper shows that language-responsive brain areas do not respond during the observation of dynamic faces, hands, or bodies.

# Language areas unreactive to action observation/imitation

- ▶ All language regions, including those in “Broca’s area” showed little or no response during action observation/imitation.
- 1) High-level language regions are highly selective for language processing
- ▶ To conclude, action observation and action imitation do not recruit the left-lateralized high-level language processing network

\*\*\* Language-responsive brain areas do not respond during the observation of communicative actions (co-speech gestures)

- ▶ Speech-accompanying gestures are not processed by the language-processing mechanisms
- ▶ Whenever speech was present, language regions responded robustly and equally to videos with gestures or grooming movements.
- ▶ In contrast, language regions responded weakly when silent videos with gestures or grooming movements were processed.
- ▶ Contra prior claims, language-processing regions do not respond to co-speech gestures in the absence of speech.

\*\*\* The language network is selective for language relative to social cognition (Theory of Mind)

- ▶ Does language share machinery with mechanisms that support reasoning about others' minds?
- ▶ These papers show that the language network robustly dissociates from the Theory of Mind network, although the Paunov et al. (2019, *J Neurophys*) paper also shows that the two networks show some degree of functional correlation

# Language and ToM

- ▶ Do not find evidence that the core language areas are engaged in ToM reasoning
- ▶ These results argue against cognitive and neural overlap between language processing and ToM.
- ▶ In exploratory analyses, we find responses to social processing in the “periphery” of the language network—right-hemisphere homotopes of core language areas and areas in bilateral angular gyri—but these responses are not selectively ToM-related and may reflect general visual semantic processing.



## ToM has a separate network from language

- ▶ Thus, the language network shows neither a general response to ToM nor selectivity for ToM relative to other kinds of social processing.
- ▶ Identified a ToM-selective “default network B” and show that this network is spatially distinct from the language network in individual brains.

# RH language?

- ▶ A common theme in this literature associates RH homotopes (mirrors) of language areas with the social, pragmatic, nonliteral, and/or affective aspects of speech processing and/or language comprehension
- ▶ 2 recent studies argued that the primary function of these areas may be social rather than linguistic.

# ToM and language are separate

- ▶ If the language network is not involved in making inferences about others' thoughts, how then do these inferences enter into language processing in order to inform rapid incremental sentence comprehension?
- ▶ This occurs via rapid feedback from the ToM network. Language and ToM networks show reliable functional correlations with each other over time
- ▶ We find no evidence of mentalizing in the core LH language network using a nonverbal ToM task, and we further find no selectivity for mentalizing over other kinds of social cognition.

\*\*\* The language network is selective for language relative to computer code comprehension

- ▶ Understanding computer code draws on the Multiple Demand network, and not the language network.
- ▶ We find that both the Multiple Demand and Language systems encode **specific code properties** and uniquely align with machine learned representations of code.
- ▶ These findings suggest at least **two distinct neural mechanisms mediating computer program comprehension and evaluation.**

\*\*\* The language network is selective for language relative to the processing of non-linguistic meaning

- ▶ A lot of what we know about the world we learn from language. We can also understand complex meanings from non-linguistic inputs, like a picture, a video, or a sequence of sounds.
- ▶ This paper shows that the language network shows some response to visual semantics (understanding pictures of events), although the response is
  - ▶ i) much lower than the response to sentences, and apparently,
  - ▶ ii) **not functionally critical for visual semantic processing** given that individuals without a functioning language system have no difficulties with visual event semantics.

### \*\*\* Language network is not engaged during semantic object categorization

- ▶ Individuals with severe aphasia are not impaired in object categorization.
- ▶ The relationship between language and thought is the subject of long-standing debate. One claim states that language facilitates categorization of objects based on a certain feature (e.g. color) through the use of category labels that reduce interference from other, irrelevant features.

# MD network does categorization of objects

- ▶ fMRI results revealed little activity in language-responsive brain regions during categorization of objects; instead, categorization recruited the domain-general multiple-demand network.
- ▶ Overall, our study shows that categorizing items is not a language-dependent task in the adult brain.
- ▶ Instead, this task relies on the domain-general multiple demand system, which supports diverse goal-directed behaviors.

\*\*\* The language network is selective for language relative to music processing

- ▶ Language areas show little/no response when participants listen to music.
- ▶ Study: music processing does not engage the language network; furthermore, individuals with severe aphasia are still able to process music structure.



### \*\*\* The human language system, including its inferior frontal component in “Broca’s area” does not support music perception

- ▶ Using a robust individual-subject fMRI approach, we examined the responses of language brain regions to music stimuli, and probed the musical abilities of individuals with severe aphasia.
- ▶ Across 4 experiments, we obtained a clear answer: music perception does not engage the language system, and judgments about music structure are possible even in the presence of severe damage to the language network.
- ▶ Thus, the mechanisms that process structure in language do not appear to process music, including music syntax.
- ▶ \*\* We further found that the ability to make well-formed judgments about the tonal structure of music was preserved in patients with severe aphasia who cannot make grammaticality judgments for sentences.

# Semantics and syntax do not have separate hubs



▶ Contrary to prior claims, we find distributed sensitivity to both syntax and semantics throughout a broad frontotemporal brain network.

▶ \*\* There is an integrated network for language in the human brain within which internal specialization is primarily a matter of degree rather than kind, in contrast with influential proposals that advocate distinct specialization of different brain areas for different types of linguistic functions.

# No one area of syntax

- ▶ Growing evidence that linguistic representations and computations over a range of levels of description (phonological, lexical, syntactic, and combinatorial semantic) are largely distributed across the language network - no separate hubs
- ▶ Our results show that the burden of lexical semantic, syntactic, and combinatorial-semantic processing is distributed across diverse cortical areas, and that no single area or set of areas constitutes the syntax hub

### \*\*\* All language regions respond more strongly during production

- ▶ Finally, contra some proposals, we find no evidence of brain regions—within or outside the language network—that selectively support phrase-structure building in production relative to comprehension.
- ▶ \*\* Instead, all language regions respond more strongly during production than comprehension, suggesting that production incurs a greater cost for the language network.
- ▶ \*\* Together, these results align with the idea that language comprehension and production draw on the same knowledge representations, which are stored in a distributed manner within the language-selective network and are used to both interpret and generate linguistic utterances

# Language comprehension = core operation of language

## ▶ In summary, it appears that syntactic processing

- ▶ (a) is not focally carried out in a particular brain region within the language network, but is distributed across the left lateral frontal and temporal areas; and
- ▶ (b) is supported by the very same brain regions that support the processing of word meanings and semantic composition.

## ▶ \*\* We would further argue that semantic composition, not syntactic structure building is primary in language comprehension and is the core operation driving the language-selective areas

### \*\*\* The cross-linguistic universality of the language-processing mechanisms

- ▶ Approximately 7,000 languages are spoken and signed across the world,
- ▶ \*\* This paper demonstrates that the language network is similar across native speakers of 45 different languages.
- ▶ This includes left-lateralization, strong functional integration among its brain regions and functional selectivity for language processing.

### \*\*\* The Small and Efficient Language Network of Polyglots and Hyper-polyglots

- ▶ The language network of polyglots is smaller in size and works less during the processing of native language compared to non-polyglots.
- ▶ Is there something special about the minds and brains of such polyglots?
- ▶ \*\* Polyglots ( $n = 17$ , including nine “hyper-polyglots” with proficiency in 10–55 languages) used fewer neural resources to process language: Their activations were smaller in both magnitude and extent..

# Polyglots have more efficient language processing

- ▶ The groups were also similar in their activation of two other brain networks—the multiple demand network and the default mode network.
- ▶ We hypothesize that the activation reduction in the language network is experientially driven, such that the acquisition and use of multiple languages makes language processing generally more efficient.
- ▶ \*\* At the same time, our finding of decreased activity within the language network in polyglots stands in sharp contrast to the pattern of increased activity reported previously in bilinguals



### \*\*\* Pragmatics

- ▶ Understanding language entails much more than simply decoding the literal meaning of each sentence: our interpretation of each utterance is powerfully shaped by our knowledge of the intent of the speaker, the linguistic and social context of the utterance, and our general world knowledge.
- ▶ This ability to exploit speaker intent and background knowledge to go beyond the literal meaning of the sentence is called “pragmatics”.
- ▶ Pragmatic reasoning is most critically needed during conversational exchanges.

\*\*\* The language network and the Theory of Mind network are dissociated but show some degree of information sharing

- ▶ \*\* The language network robustly dissociates from the Theory of Mind network, but the two networks show some degree of functional correlation (which may be taken to suggest frequent interactions and information sharing).

# No evidence of theory of mind reasoning in the human language network

- ▶ \*\* Language comprehension and the ability to infer others' thoughts (theory of mind [ToM]) are interrelated during development and language use.
- ▶ Study: reveals that all core language regions respond more strongly when participants read vignettes about false beliefs compared to the control vignettes.
- ▶ \*\* However, we show that these differences are largely due to linguistic confounds, and no such effects appear in a nonverbal ToM task.

\*\*\* Frontal language areas do not emerge in the absence of temporal language areas:  
A case study of an individual born without a left temporal lobe

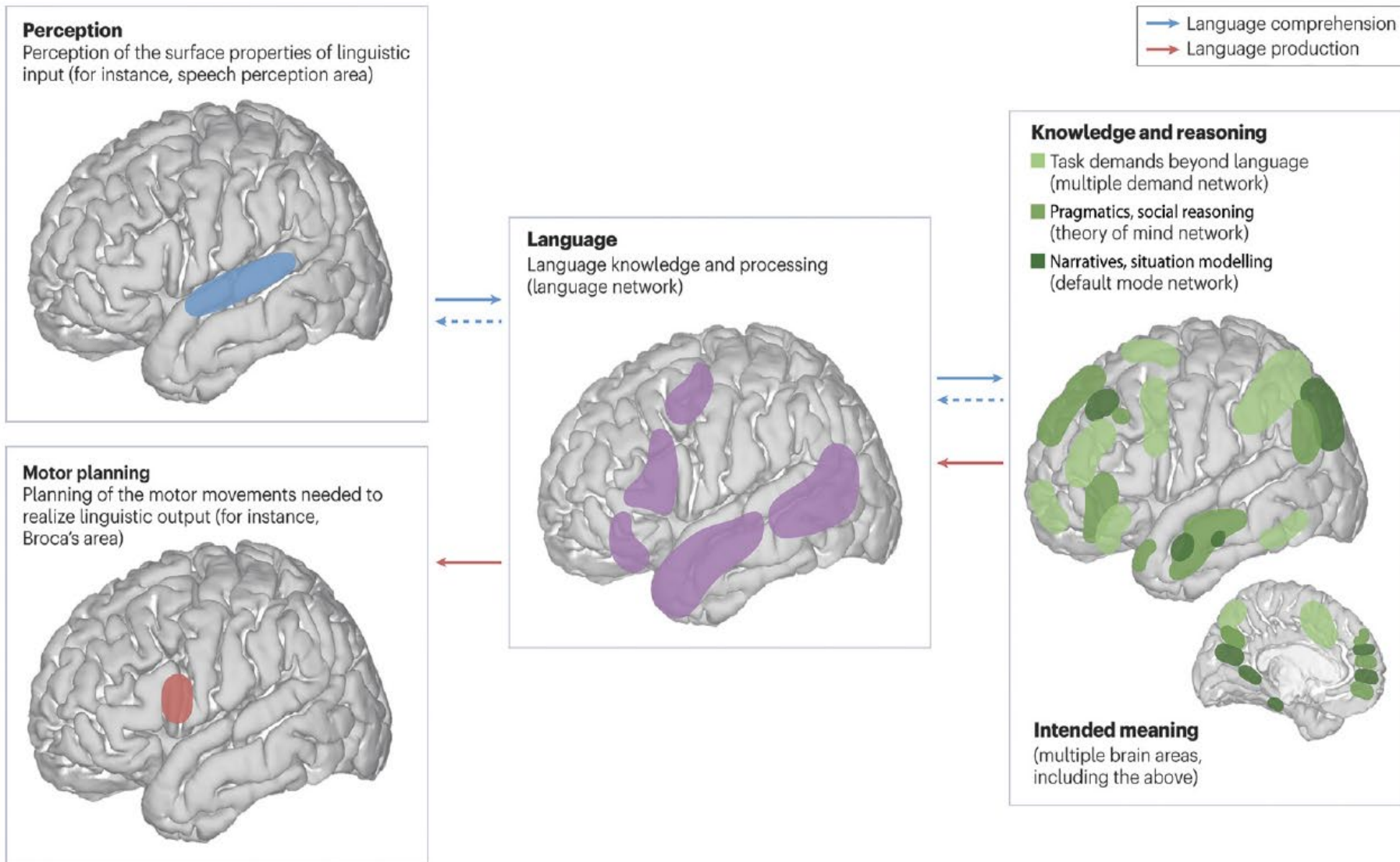
- No response to language was detected in the left frontal lobe of an individual (EG) born without her left temporal lobe.
- The findings suggest that temporal language areas are necessary for the emergence of frontal language areas.
- Normal Language processing relies on a left-lateralized fronto-temporal brain network. How this network emerges ontogenetically remains debated.

# Temporal language area required for frontal language area

- ▶ **\*\* Find that—as expected for early left-hemisphere damage—EG has a fully functional language network in her right hemisphere and intact linguistic abilities.**
- ▶ **\*\* However, we detect no response to language in EG's left frontal lobe. Another network—the multiple demand network—is robustly present in frontal lobes bilaterally, suggesting that EG's left frontal cortex can support non-linguistic cognition.**
- ▶ **\*\* The existence of temporal language areas therefore appears to be a prerequisite for the emergence of the frontal language areas.**

# \*\*\* Can ChatGPT help researchers understand how the human brain handles language? M. Mitchell Waldrop, 2024

- ▶ **Large language models** are surprisingly good at mimicking our speech and writing. Now they're **serving as an electronic lab rat for language**, offering insights into the mysteries of one of humankind's most important abilities.
- ▶ These computer simulations of language were working in ways that were strikingly similar to the left-hemisphere language regions of our brains, using the same computational principles
- ▶ **But the AI–brain alignment doesn't seem to encompass many cognitive skills other than language.**



According to advanced fMRI techniques, the left-hemisphere language network serves as a data switchyard for language comprehension and production. Reprinted with permission from ref. 4.

# Brain is about prediction

- ▶ \*\* Many researchers have come to believe that prediction plays a critical role almost everywhere in the brain.
- ▶ Known as the predictive brain hypothesis, it's the notion that the brain “processes information by constantly comparing what is actually coming in with what it is expecting to come in. The brain then uses the inevitable surprises as opportunities to improve its predictions for next time.
- ▶ When you consciously follow a conversation or a story, the evidence suggests that your subconscious brain is constantly using everything it knows about the current context, and the world in general, to update its guess for what will be said next. That's exactly what the transformer-based AI language models are trained to do.



# \*\*\* From Action to Cognition: Neural Reuse, Network Theory and the Emergence of Higher Cognitive Functions -- Radek Ptak, et al., 2021

- ▶ Neural reuse theories generally take a developmental approach and model the brain as a dynamic system composed of highly flexible neural networks. They often argue against domain-specificity and for a distributed, embodied representation of knowledge.
- ▶ The term neural reuse describes the capacity of the brain to adapt to changing demands by reutilizing some of its structures or resources in a new context.
- ▶ Neural reuse is thus a fundamentally adaptive feature of the brain. Its result will not be just a modification of the existent behavioral (or cognitive) repertoire, but the emergence of an entirely new capacity. Neural reuse ultimately results in a structural reorganization of brain circuits, but also in a new arrangement of computational operations.

## Local or Distributed: Two Views of the Structure-Function Relationship

- ▶ While early observations by Broca , Wernicke or Gerstmann and others suggested a high degree of specialization of distinct brain areas for language, visual perception, arithmetic or even recognition of body parts, later authors emphasized the difficulty to find the precise location of representations in specialized parts of the brain.
- ▶ Thus, after reviewing results from other studies and himself performing lesion studies on various parts of the rat brain, **K. Lashley concluded that brain function depended on volume, not the precise location of the removed cortex.**
- ▶ There are indications that **the subordinate parts are all equally capable of performing the functions of the whole'.**

# Equipotentiality, Degeneracy, Neural reuse

- ▶ Based on his data, he proposed the concept of equipotentiality, which reflects the capacity of the intact cortex to take over any function from an injured brain region.
- ▶ Edelman's concept of degeneracy: the variable relationship between function and structure. When applied to brain function, degeneracy reflects the capacity of structurally dissimilar brain areas to carry out similar functions under some conditions, but different functions under other conditions. As we will see, this is a fundamental premise of neural reuse theories.

# Evolutionary concept

- ▶ The concept of neural reuse assumptions:
- ▶ **Evolutionary perspective:** neural changes are triggered by a need for adaptation to changing environments.
- ▶ Neural reuse is a form of **exaptation**, that is, the **adaptation** of a specific trait to serve a new function while also maintaining its original function
- ▶ Reuse is expressed during development and maturation and is therefore dependent on neural and cognitive plasticity.
- ▶ Domain-specific representations are **not genetically predetermined**, but **emerge through changing interactions with the environment**

# Brain's simulation ability: mirror neurons

- ▶ The same cognitive processes are involved when we perform a particular behavior, or just imagine performing this behavior. For example, imagining the grasping of an object activates the same neural structures, motor processes and cognitive representations as actually grasping the object.
- ▶ Both in motor cognition and in the understanding of other people's actions, intentions, emotions or, more generally, internal states.
- ▶ Several authors have designated mirror neurons (specialized cells of the premotor cortex, which are active when a person performs an action or merely observes someone else performing the action) as the neural basis for simulation. Basis of empathy.

## Example of exaptation

- ▶ The acquisition of reading gradually encroached upon the face sensitive areas in the left hemisphere. Thus, in agreement with neuronal recycling theory, a culturally acquired ability (reading) reshapes cortical maps by competing with a genetically transmitted ability (face processing).

# Fusiform gyrus: face recognition and reading ability

- ▶ The ability to recognize faces depends on functional development of face-selective regions in the fusiform gyrus, esp. in right hemisphere. The introduction of reading alters the function of this region in left hemisphere.
- ▶ They substantiate the neuronal recycling model, according this architecture is at once prespecified for visual recognition and yet sufficiently flexible to acquire new culturally defined categories.

# Exaptation

- ▶ Brain areas are activated by a variety of different tasks, and that language (presumably a recent acquisition in human history) activates more distributed and scattered brain regions than perception or attention.
- ▶ In sum, neural reuse theories distinguish themselves by emphasizing the interaction between inherited characteristics of brain circuits and environmental (or cultural) pressures requiring a new cognitive function to be accommodated within existing structures.
- ▶ Most of them assume some form of exaptation, that is, the reutilization of a phylogenetically old trait or structure in a different context. They argue against a localist view of brain function, and some of them put into perspective the assumption that cognitive architectures are universal.



# Functional Networks Provide the Necessary Conditions for Neural Reuse

- ▶ 1. The brain is organized into large-scale, highly interactive networks, whereby there are many more short-range (local) than long-range white matter connections. This architecture maximizes efficiency while minimizing energy consumption.
- ▶ 2. Networks consist of nodes and connections, whereby some 'hubs' are of greater importance than others and some connections are stronger than others.

# Networks

- ▶ 3. **A network structure appears at rest or during activity.** The high degree of energy consumption during 'rest' indicates that a large quantity of information processing is intrinsic and occurs without external stimulation.
- ▶ 4. **Focal lesions have local as well as distant effects on network function.** Distant effects modify intrahemispheric networks or cross-hemispheric connections and may manifest in increased or decreased activity of distant brain regions.

# Flexibility in Networks

- ▶ Developmental studies indicate that motor and sensory networks appear earlier during brain maturation than networks associated with functions such as working memory, attention or cognitive flexibility.
- ▶ The level of functional specialization of these 'higher-order' networks is much less fixed, and different network configurations may be associated with distinct functions.
- ▶ Thus, networks may 'borrow' sub-components for particular tasks and may contribute to what is not necessarily their primary function. This conclusion applies particularly to higher cognitive functions,

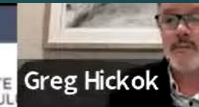
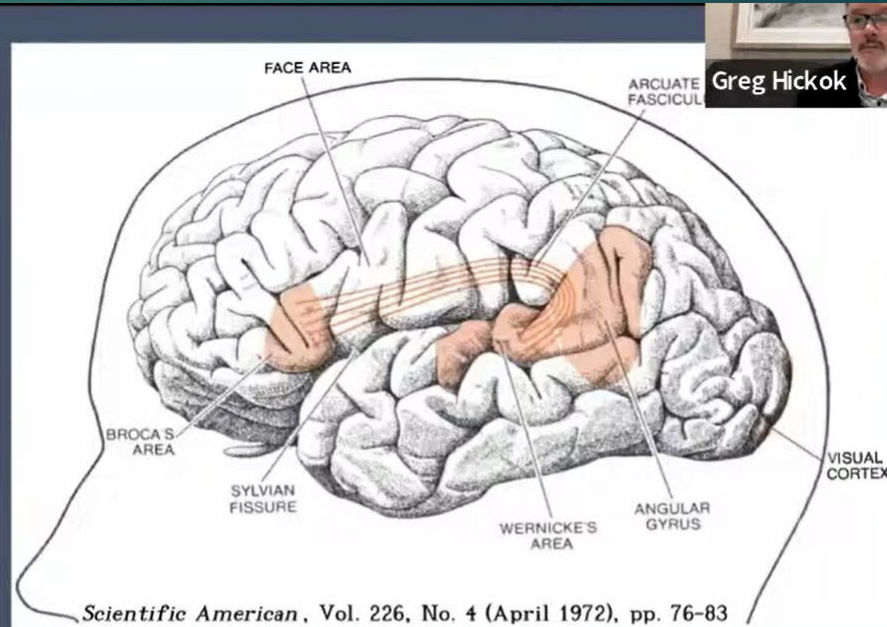
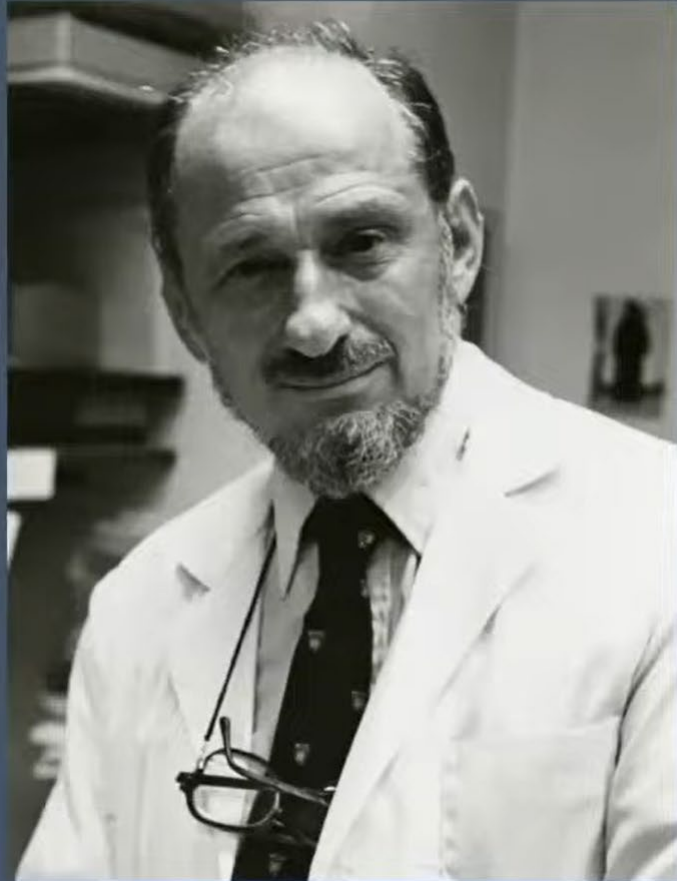
# Lesion studies

- ▶ In sum, brain networks are characterized by a high degree of functional diversity, which provides a building stone for a highly interactive brain and neural reuse.
- ▶ Is this conclusion incompatible with the main assumption of lesion studies, namely that if a lesion produces a deficit in function X, then the damaged area must somehow be necessary for that function?
- ▶ **We do not think so.** First, the **major contribution of lesion studies** has been the precise analysis of cognitive architecture through the **identification of functional sub-components**, not the identification of specialized brain areas. These studies deal with **functional associations and dissociations**, and these—not the anatomo-functional relationships—constitute the building blocks for theoretical reasoning in cognitive neuropsychology

# Examples of reuse

- ▶ There is also evidence that spatial representations in the parietal cortex have been reused for number cognition, or that a part of the spatial reorienting system is involved in social perspective taking.
- ▶ Yet another example of neural reuse is the interaction between emotion and action control, as emotional stimuli may affect motor cortex excitability.
- ▶ Finally, some studies indicate that the human episodic memory system emerged from a spatial orienting system within the medial temporal lobes.

# Norman Geschwind



**PRIMARY LANGUAGE AREAS** of the human brain are thought to be located in the left hemisphere, because only rarely does damage to the right hemisphere cause language disorders. Broca's area, which is adjacent to the region of the motor cortex that controls the movement of the muscles of the lips, the jaw, the tongue, the soft palate and the vocal cords, apparently incorporates programs for the coordination of these muscles in speech. Damage to Broca's area results in slow and labored speech, but comprehension of

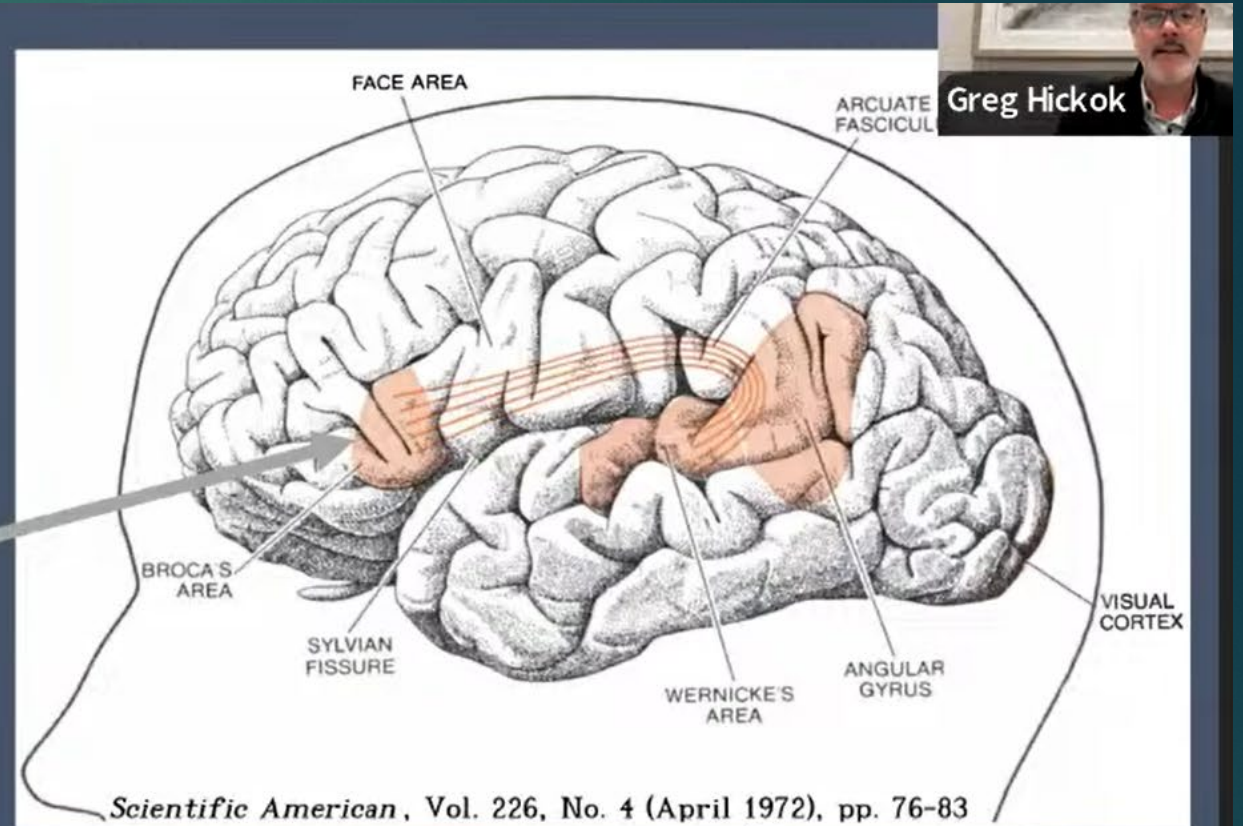
# Broca's: not speech coordination

But now we know better

First: hierarchical motor control

Broca's area:

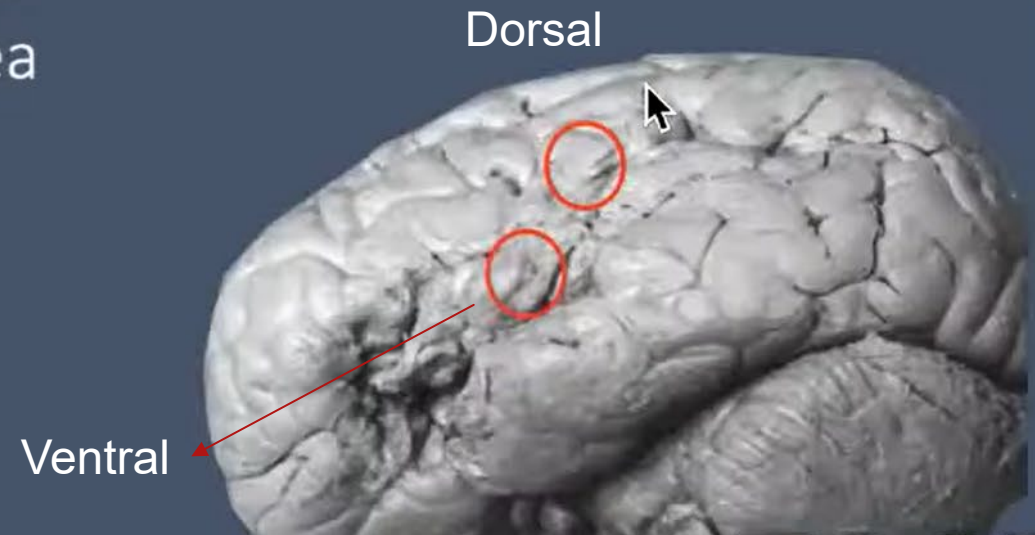
- Cognitive control
- Lexical selection
- Syntax
- Sequencing



# Where is the faculty of articulate speech?

There seem to be two

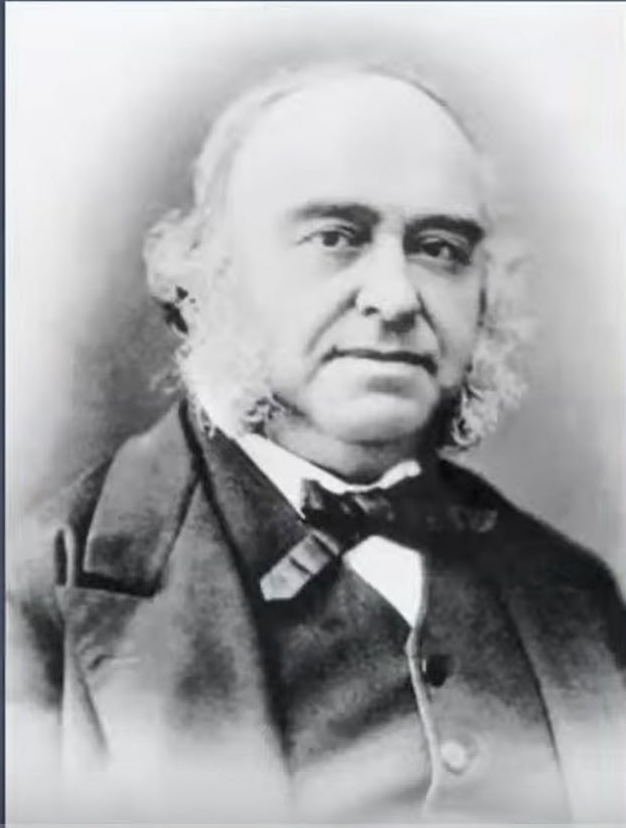
- Both on the precentral gyrus
- One posterior to Broca's area
- One more dorsal



Central to speech arrest is not Broca's, but precentral ventral area; anomia ("This is...") does hit Broca's



# \*\*\* Greg Hickok: Dorsal and Ventral language streams



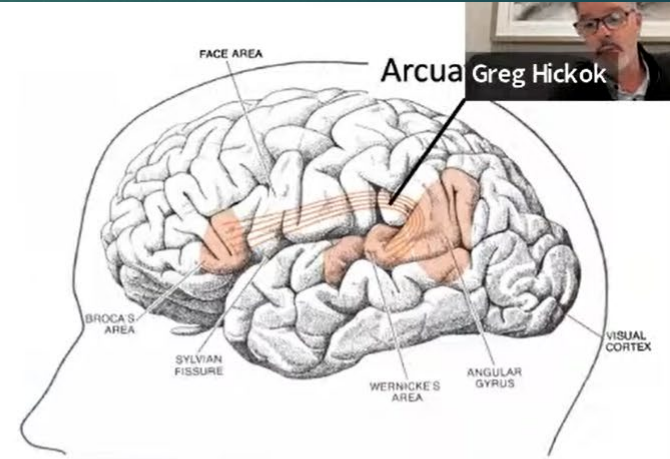
In the beginning there was Broca's area

*"the faculty that coordinates the proper movement of articulated language"*

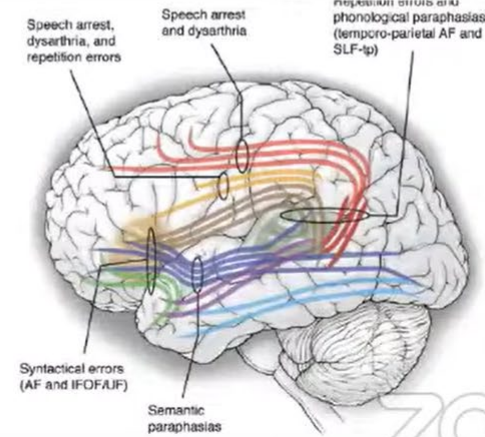
—Broca (1861)

# The connectome of speech repetition

Classic view:



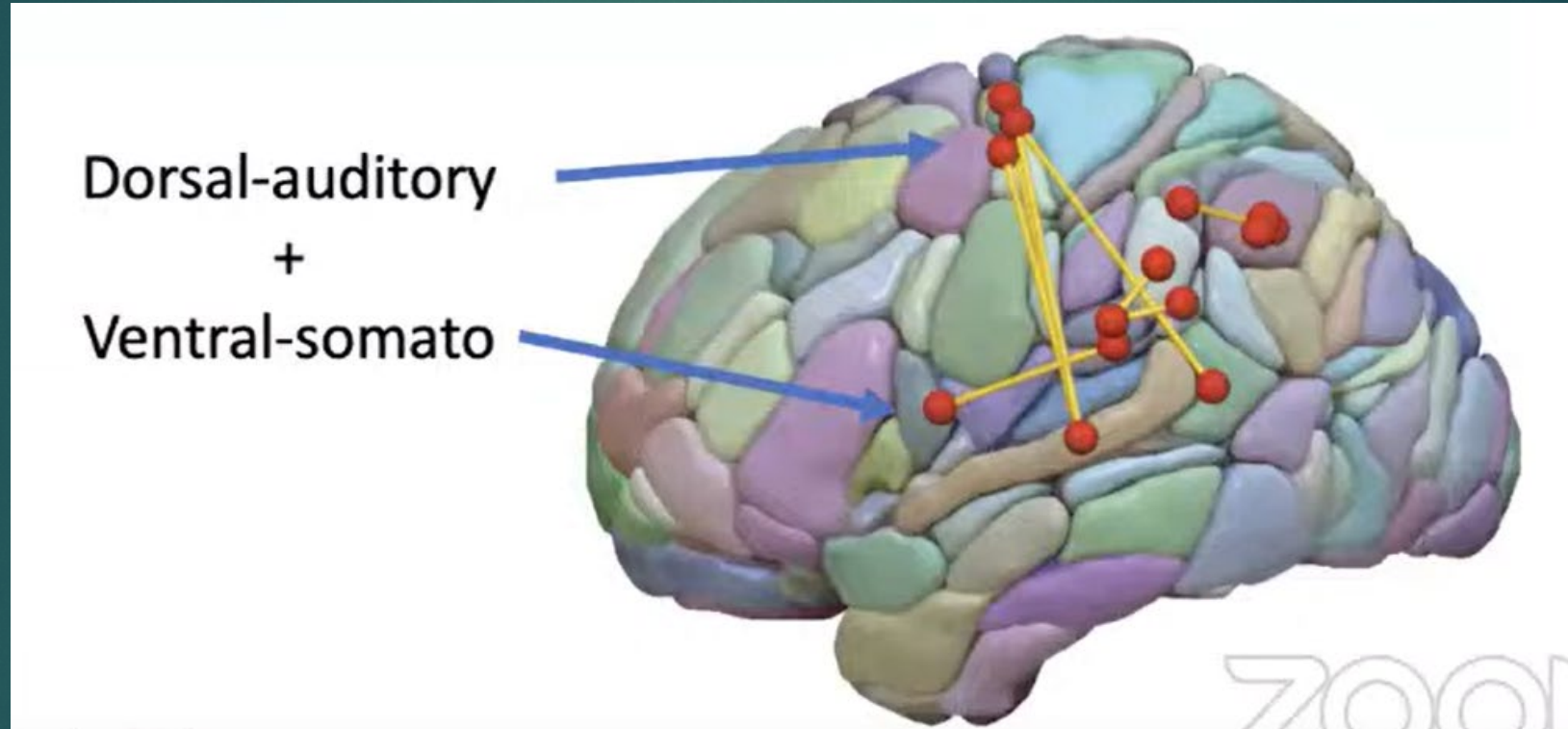
It's more complicated:



Chiang et al. (2015) *J. Neurosurgery*, 122:250-261



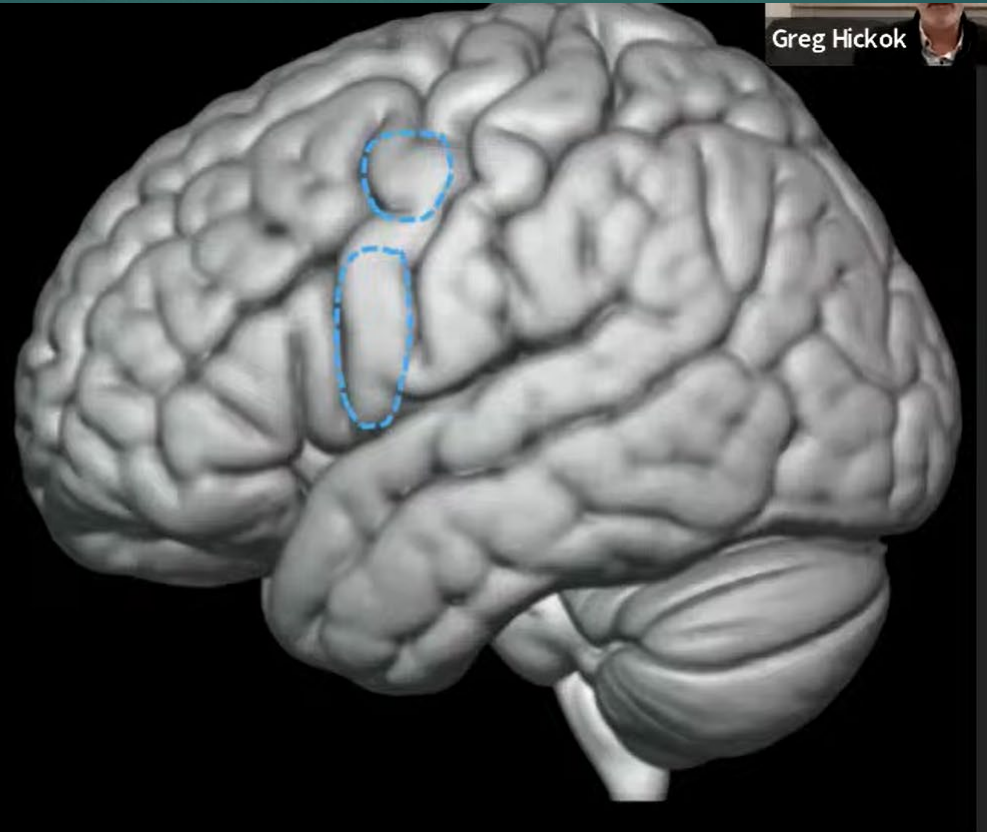
# Stroke induced aphasia: repetition deficit



# Two motor speech areas: neither are Broca's

## Interim Summary

- *Two motor speech areas*
- *Neither are Broca's area*



The dorsal (but not ventral) precentral speech area:

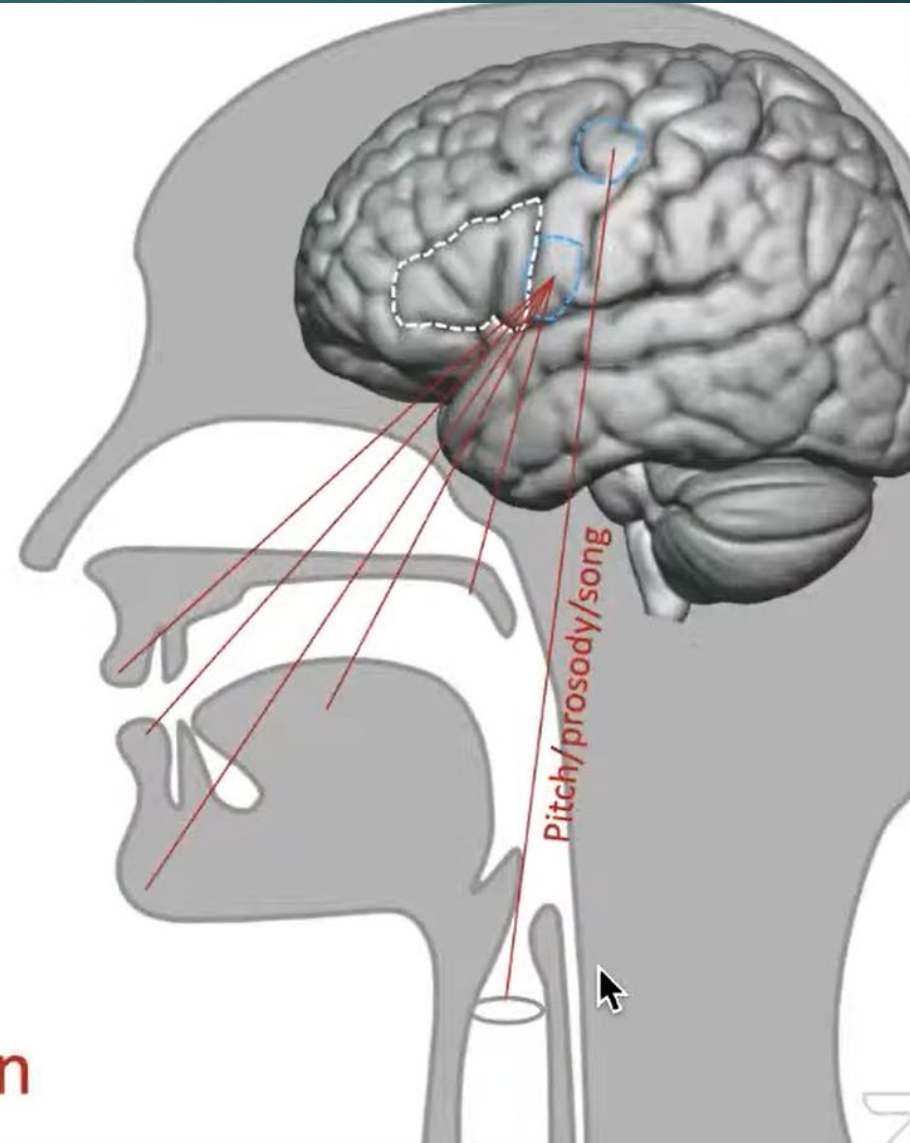
- . Is involved in controlling **voice pitch** during speaking & singing
- . Codes pitch-related acoustic features during speech listening

= **auditory pitch**

# Theory Update

New Theory:

Dual Speech Coordination

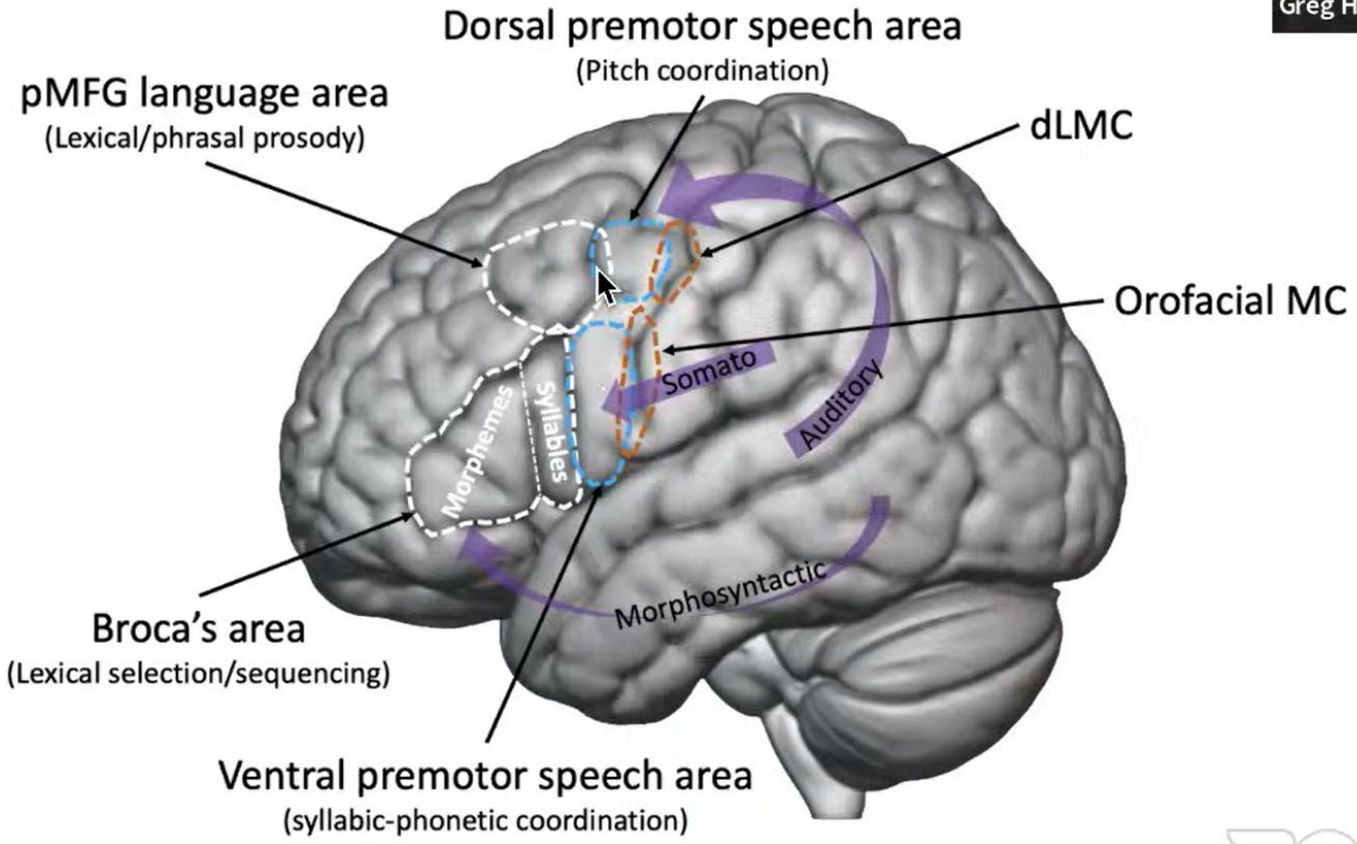


New:  
**Dorsal** =  
pitch  
**Ventral** =  
supralary-  
ngeal  
parts

Not  
Broca's



Greg Hickok



**Dorsal: larynx control**  
– pitch coordination;  
auditory input

**Ventral: syllabic-  
phonetic coordination;**  
somato-sensory input

## Why Two Systems?

- ▶ It makes sense evolutionarily
- ▶ Pitch control requires pitch-related auditory input
- ▶ The non-human primate ventral system controls orofacial gestures but doesn't get the right kind of auditory input. What motor-related system does get the right kind of input? A more dorsal orienting/attention system.
- ▶ Pitch related to environmental orientation
- ▶ The **dPCSA** evolved from a premotor orienting system, initially in support of song. Sandwiched between eye fields.
- ▶ The **vPCSA** evolved later from orofacial control circuits. Earlier lip-smacking control in primates

# dPMSA before vPMSA

▶ In What Order did they Evolve?

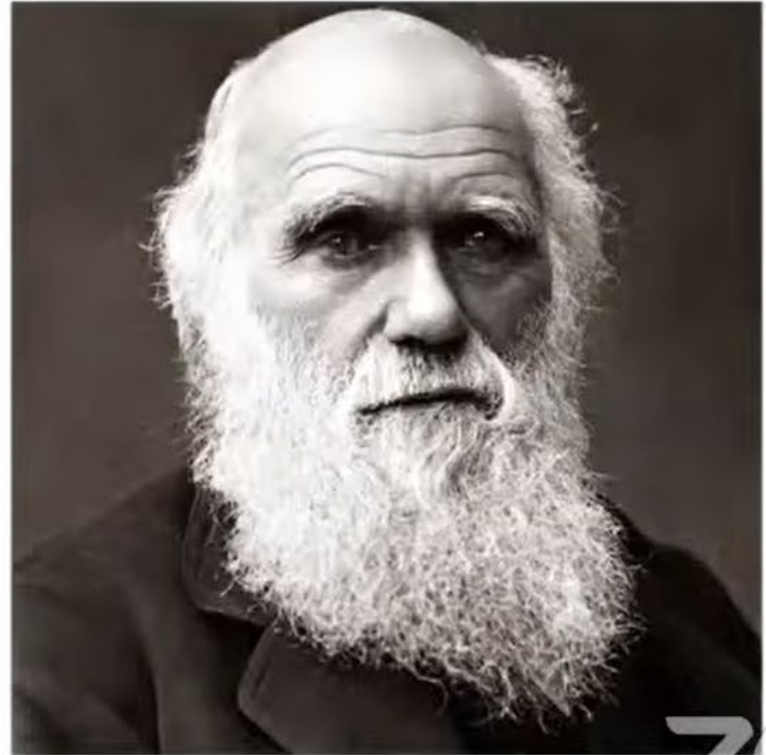
▶ Hypothesis:

- ▶ Ventral orofacial control of mastication, oral grasping, & lip-smacking
- ▶ Dorsal laryngeal coordination (dLMC, dPMSA)
- ▶ Ventral phonetic coordination (vPMSA)



# Pitch related control system

Maybe Darwin was right about song  
as a first early step toward the  
evolution of language



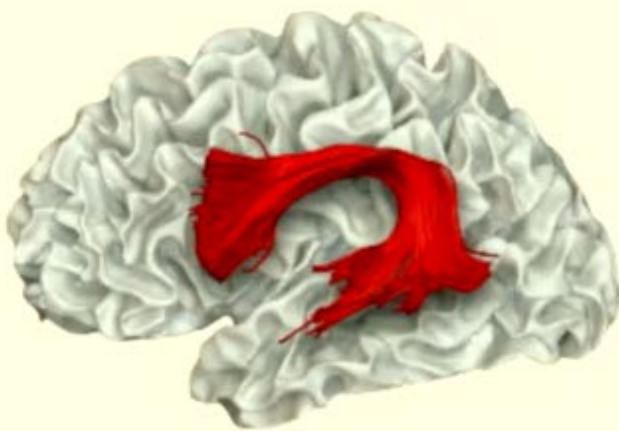
# Dual stream processing systems: Dorsal and Ventral

- ▶ **Auditory**: When listening to speech, ventral controls comprehension; dorsal controls reproduction of speech



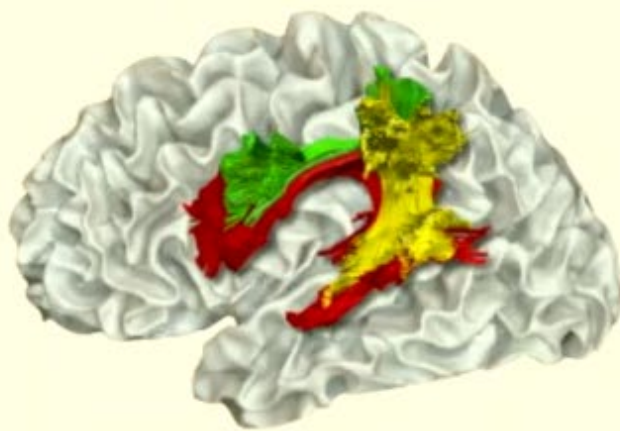
## Language connectome: then and now

19th century



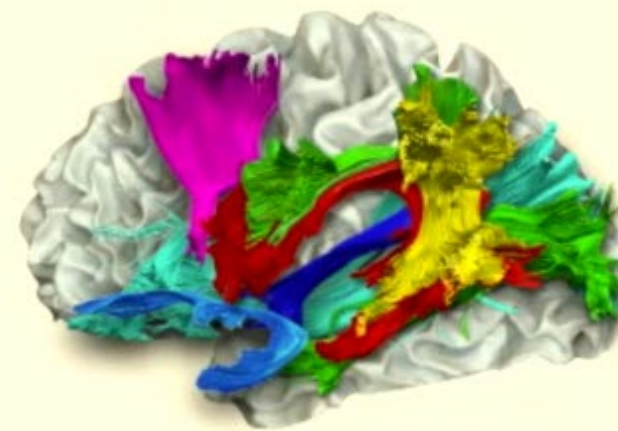
Arcuate fasciculus

Early 2000s



- Anterior segment
- Long segment
- Posterior segment

21st century



- Frontal Aslant Tract
- Uncinate fasciculus
- Temporal longitudinal fasciculus (TLF)
- Inferior fronto-occipital fasciculus (iFOF)
- Inferior longitudinal fasciculus (ILF)