The extended language network: Language-selective brain areas whose contributions to language remain to be discovered

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INTRODUCTION

Neuroimaging evidence converges in showing that language processing engages a **left fronto-temporal network** in the brain and the right homotopic areas [1, 2]

However, other **cortical, sub-cortical, and cerebellar** brain areas have been identified in studies on language processing [3-5]

- Language is studied using diverse tasks and paradigms
- Some of them might not effectively isolate language from task-related processes [6]

The **language localizer task** is an extensively validated paradigm which allows for the identification of the language network in individual brains, using a broad and robust contrast [7]

Research question

Are there any brain regions, beyond the fronto-temporal network, that reliably and selectively respond to language?

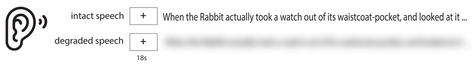
METHODS: design

722 participants, multiple fMRI experiments

n=706: reading language task



n=86: auditory language task



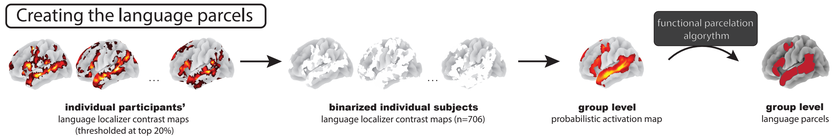
n=422: spatial working memory task



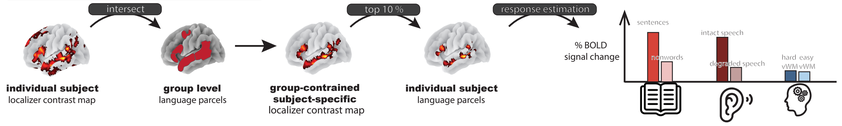
METHODS: analytical approach

Group-constrained subject-specific (GSS) approach [7]

Creating the language parcels



Creating the language parcels



MEET THE AUTHORS!



Aaron Wright

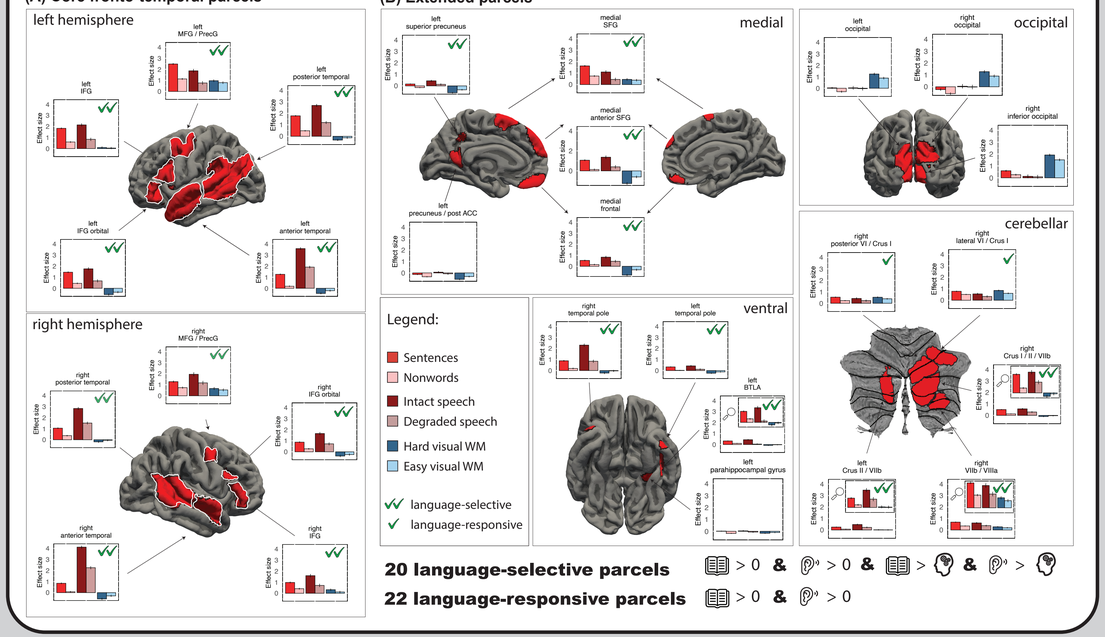
1st-year post-bacc in the BCS Research Scholars Program and an RA in EvLab. Interested in language and bilingualism

Agata Wolna

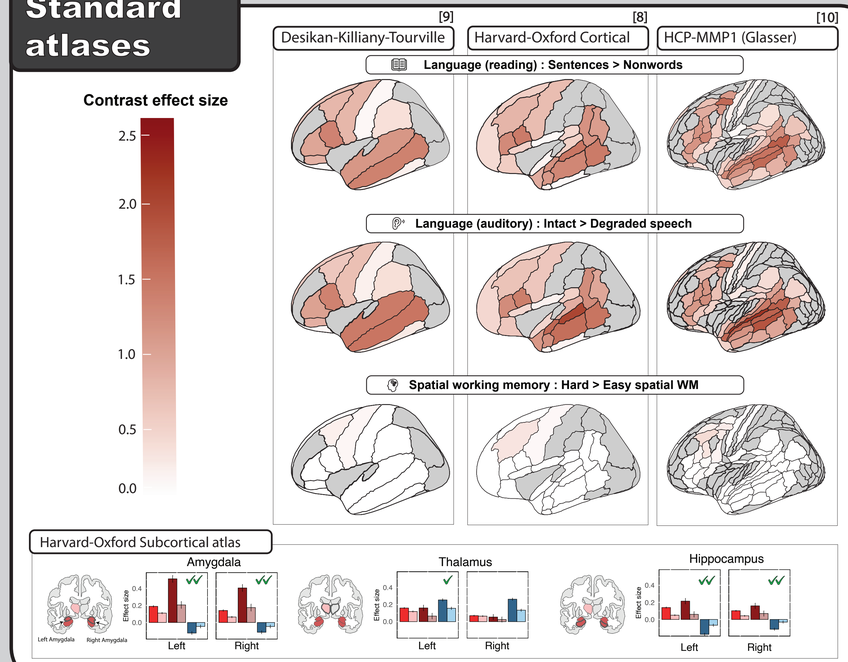


Post-doc in EvLab. Interested in brain organization of language and its relationship to speech perception and articulation

RESULTS: GSS language parcels



Standard atlases



SUMMARY

1. The functionally-defined GSS language parcels and anatomical atlases provide converging results: **language selectively engages: core lateral fronto-temporal regions**
2. We also find language-selective responses in: **left medial frontal, ventral temporal, and cerebellar regions**

   as well as subcortically in: **bilateral amygdalae and hippocampi**
3. There are additional language regions that respond to language, **although not selectively! left thalamus, right cerebellum**

   These regions may also be important to understand language in the brain!

   ? **mixed selectivity** → **integrating information across cortical networks**
4. Although widely distributed, at the individual level the language system takes up <1.5% of the brain ... which equals the size of a large strawberry

References: [1] Lipkin, B., Tuckute, G., Affourtit, J., Small, H., Mineroff, Z., Kean, H., ... & Fedorenko, E. (2022). LanA (Language Atlas): A probabilistic atlas for the language network based on fMRI data from> 800 individuals. BioRxiv, 2022-03. [2] Price, C. J. (2010). The anatomy of language: a review of 100 fMRI studies published in 2009. Annals of the new York Academy of Sciences, 1191(1), 62-88. [3] Turker, S., Kuhnke, P., Eickhoff, S. B., Caspers, S., & Hartwigsen, G. (2023). Cortical, subcortical, and cerebellar contributions to language processing: A meta-analytic review of 403 neuroimaging experiments. Psychological Bulletin. [4] LeBel, A., & D'Mello, A. M. (2023). A seat at the (language) table: Incorporating the cerebellum into frameworks for language processing. Current Opinion in Behavioral Sciences, 53, 101310. [5] Booth, J. R., Wood, L., Lu, D., Houk, J. C., & Bitan, T. (2007). The role of the basal ganglia and cerebellum in language processing. Brain research, 1133, 136-144. [6] Fedorenko, E., Ivanova, A. A., & Regev, T. I. (2024). The language network as a natural kind within the broader landscape of the human brain. Nature Reviews Neuroscience, 1-24. [7] Fedorenko, E., Hsieh, P. J., Nieto-Castañón, A., Whitfield-Gabrieli, S., & Kanwisher, N. (2010). New method for fMRI investigations of language: defining ROIs functionally in individual subjects. Journal of neurophysiology, 104(2), 1177-1194.[8] Desikan, R. S., Ségonne, F., Fischl, B., Quinn, B. T., Dickerson, B. C., Blacker, D., ... & Killiany, R. J. (2006). An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. Neuroimage, 31(3), 968-980. [9] Klein, A., & Tourville, J. (2012). 101 labeled brain images and a consistent human cortical labeling protocol. Frontiers in neuroscience, 6, 171. [10] Glasser, M. F., Coalson, T. S., Robinson, E. C., Hacker, C. D., Harwell, J., Yacoub, E., ... & Van Essen, D. C. (2016). A multi-modal parcellation of human cerebral cortex. Nature, 536(7615), 171-178.

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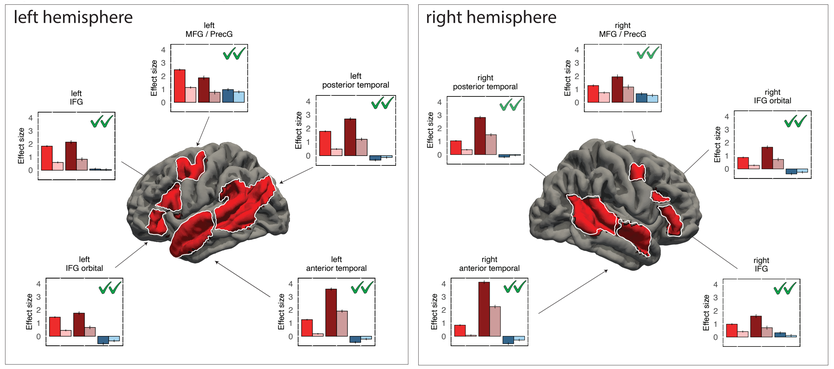
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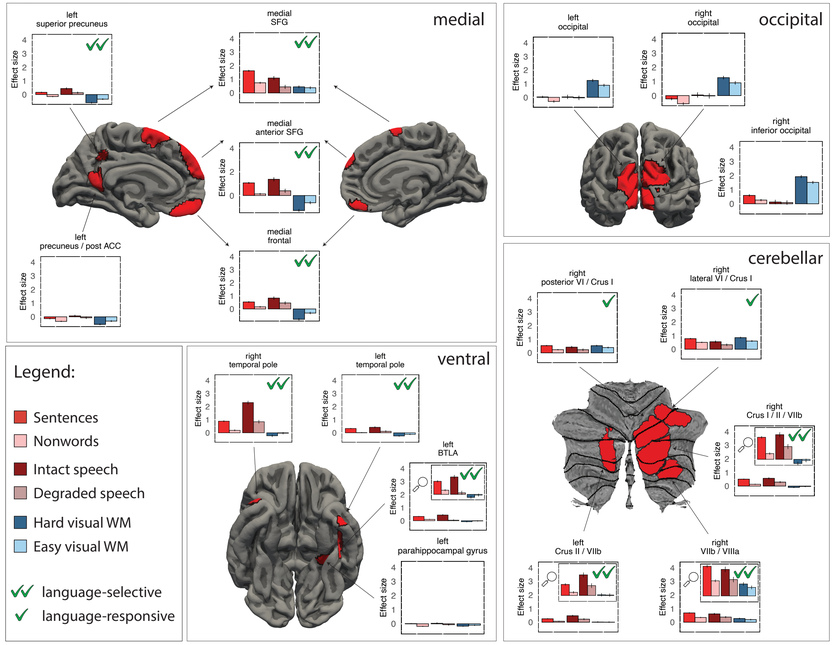
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RESULTS: GSS language parcels

(A) Core fronto-temporal parcels



(B) Extended parcels



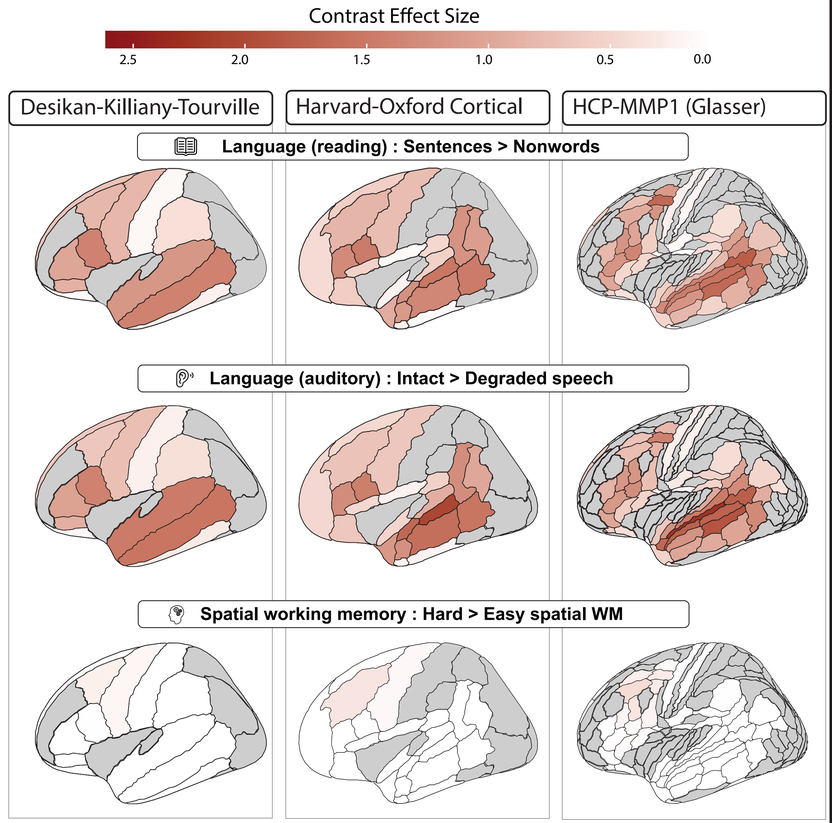
Legend:

- Sentences
- Nonwords
- Intact speech
- Degraded speech
- Hard visual WM
- Easy visual WM

✓✓ language-selective

✓ language-responsive

RESULTS: standard cortical atlases



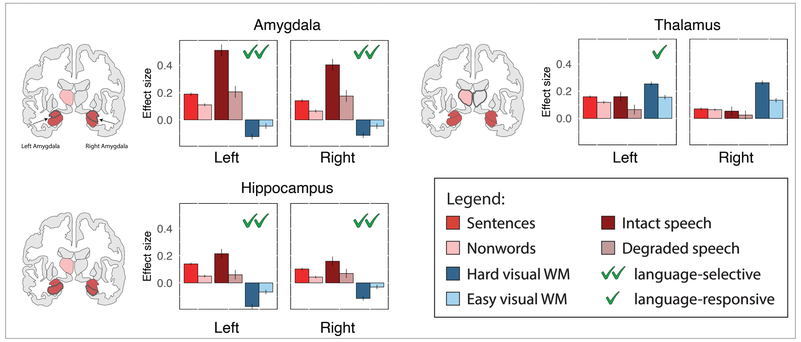
Coarse, anatomy-based parcellations are not well-suited to study language: language processing in the brain **does not "obey" anatomical boundaries**

Function-based parcellations, like GSS and some standard parcellations (including Glasser but also atlases based on functional connectivity, e.g., Shain et al., 2025), **provide a better window to study language in the brain**

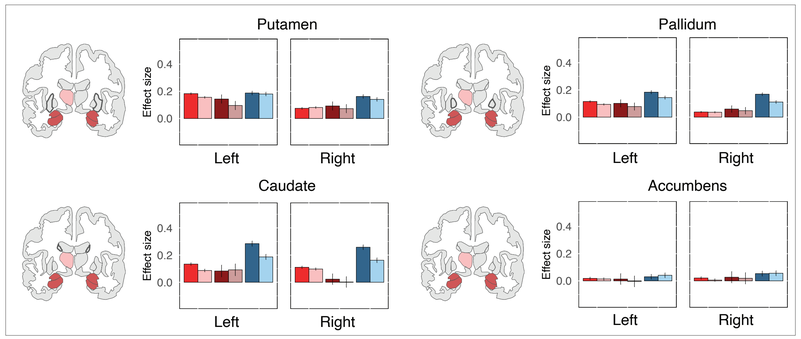
! Regardless of the group-level parcellation used, **language responses** should always be studied using **subject-specific, functionally localized regions!**

RESULTS: subcortical responses

(A) Subcortical structures that contain language-selective or language-responsive fROIs



(B) Subcortical structures that do not contain language-selective or language-responsive fROIs



Challanging previous claims, we find **no responsiveness to langauge** (amodal response to both reading and auditory language processing) in **basal ganglia and occipital cortex**

? In previous reports, language processing might be conflated with domain-general task, and attentional demands

! Not all language paradigms are well-suited to identify language-selective brain regions!

References: [1] Lipkin, B., Tuckute, G., Affourtit, J., Small, H., Mineroff, Z., Kean, H., ... & Fedorenko, E. (2022). LanA (Language Atlas): A probabilistic atlas for the language network based on fMRI data from> 800 individuals. BioRxiv, 2022-03. [2] Price, C. J. (2010). The anatomy of language: a review of 100 fMRI studies published in 2009. Annals of the new York Academy of Sciences, 1191(1), 62-88. [3] Turker, S., Kuhnke, P., Eickhoff, S. B., Caspers, S., & Hartwigsen, G. (2023). Cortical, subcortical, and cerebellar contributions to language processing: A meta-analytic review of 403 neuroimaging experiments. Psychological Bulletin. [4] LeBel, A., & D'Mello, A. M. (2023). A seat at the (language) table: incorporating the cerebellum into frameworks for language processing. Current Opinion in Behavioral Sciences, 53, 101310. [5] Booth, J. R., Wood, L., Lu, D., Houk, J. C., & Bitan, T. (2007). The role of the basal ganglia and cerebellum in language processing. Brain research, 1133, 136-144. [6] Fedorenko, E., Ivanova, A. A., & Regev, T. I. (2024). The language network as a natural kind within the broader landscape of the human brain. Nature Reviews Neuroscience, 1-24. [7] Fedorenko, E., Hsieh, P. J., Nieto-Castañón, A., Whitfield-Gabrieli, S., & Kanwisher, N. (2010). New method for fMRI investigations of language: defining ROIs functionally in individual subjects. Journal of neurophysiology, 104(2), 1177-1194.[8] Desikan, R. S., Ségonne, F., Fischl, B., Quinn, B. T., Dickerson, B. C., Blacker, D., ... & Killiany, R. J. (2006). An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. Neuroimage, 31(3), 968-980. [9] Klein, A., & Tourville, J. (2012). 101 labeled brain images and a consistent human cortical labeling protocol. Frontiers in neuroscience, 6, 171. [10] Glasser, M. F., Coalson, T. S., Robinson, E. C., Hacker, C. D., Harwell, J., Yacoub, E., ... & Van Essen, D. C. (2016). A multi-modal parcellation of human cerebral cortex. Nature, 536(7615), 171-178.