Evidence for selective and modality-dependent functional connectivity and cross-modal activation between auditory and visual word form areas: A possible substrate to learn a visual lexicon?

Lillian Chang, Suneel Banerjee, Philip Cho, Vishnu Pendri, Plamen Nikolov, Srikanth Damera, Xiong Jiang, Josef Rauschecker, Maximilian Riesenhuber
Georgetown University Medical Center — Department of Neuroscience

Objective

- The visual word form area (VWFA) in the occipitotemporal cortex has been shown to contain lexical representations for written words[1-3].
- An area in the anterior temporal lobe has been argued to be the auditory analogue of the VWFA, with lexical representations for auditory words—a so-called auditory word form area (AWFA)[4, 5].
- While it is unclear how the VWFA develops such representations, one possibility is that the VWFA receives a top-down 'teaching signal' from auditory lexical representations via the AWFA.

Testing for a Direct Coupling Between the AWFA and VWFA

- The ventral "what" streams for reading (Fig 1A) and auditory speech processing (Fig 1B) contain lexica for written words (VWFA) and spoken words (AWFA).
- We hypothesize that the VWFA incorporates information from auditory words via direct coupling between the VWFA and AWFA.
- To test our hypothesis, we determined cross-modal selectivity and functional connectivity between individually-localized VWFA, AWFA, and other areas associated with written and auditory speech processing.
- To precisely test for direct coupling between the AWFA and VWFA, we then re-analyzed data from a larger database (Mother of all Unification Studies; MOUS[7]) by calculating MEG signal coherence between these regions.

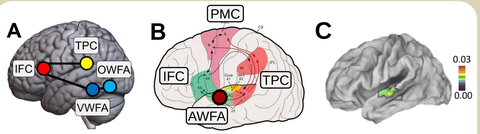
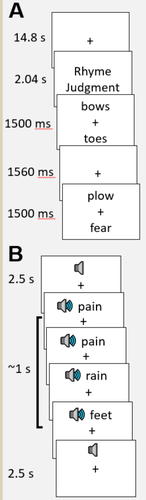


Fig 1A. Regions in the ventral "what" and dorsal "how" reading pathways. **B.** Model of auditory speech processing from Rauschecker & Scott (2009)[6] with the AWFA included (dark red circle). AWFA location based on **C.** DeWitt & Rauschecker (2012)[4].

Written and Auditory Word Selectivity in Individually-Localized ROIs

Experimental Design



Subjects: 28 right-handed English speakers (12 females). Ages 18-34.

Written word localizer (Fig 2A)

- Task: Participants were instructed to perform one of 4 tasks in the block.
  - Rhyme Judgment
  - Syllable Judgment
  - Identity Judgment
  - Random Pattern Judgment

Auditory word localizer (Fig 2B)

- Task: Participants performed an auditory oddball task. They responded with a button-press if any of the 4 stimuli in a short block was a repeat.
- Stimulus conditions:
  - Real Word (RW)
  - Pseudoword (PW)
  - Scrambled Word

Acquisition parameters

- 3T Siemens Prisma-fit scanner with a 64-channel head coil.
- Written word localizer: TR = 2.04s, TE = 35ms
- Auditory word localizer: TR = 9s, TE = 35ms

Fig 2. Experimental paradigms

Variability in Individual-subject ROI Locations

Regions-of-interest (ROIs) were defined through contrast masking done at the first-level analyses (SPM12).

Contrasts

- VWFA, OWFA (Fig 3B): Main contrast of Written Word Processing (Rhyme Judgment, Syllable Judgment, and Identity Judgment combined) vs. Fixation (p<0.005, uncorrected) masked by the contrast of Written Word Processing vs. Random Pattern (p<0.05, uncorrected).
- TPC_W, IFC_W (Fig 3B): Main contrast of Rhyme Judgment vs. Fixation (p<0.005, uncorrected) masked by the contrast of Rhyme Judgment vs. Identity Judgment (p<0.05, uncorrected).
- VWFA, OWFA, TPC_W, and IFC_W contrasts based on Glezer et al. (2016)[8].
- AWFA, PMC, TPC_A, IFC_A (Fig 3C): Auditory Word Processing (RW and PW combined) versus Silence (p<0.005, uncorrected) masked by the contrast of Auditory Word Processing versus Scrambled Words (p<0.05, uncorrected).

ROI sizes: Thresholds were adjusted to obtain clusters that were between 10 and 50 voxels.

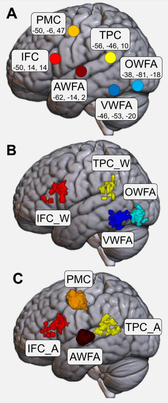


Fig 3A. Reference locations to create individual-subject ROIs using the **B.** written word and **C.** auditory word localizers. VWFA: visual word form area, OWFA: occipital word form area, TPC: temporal parietal cortex, IFC: inferior frontal cortex, AWFA: auditory word form area, PMC: premotor cortex.

Cross-modal Selectivity for Written and Auditory Words

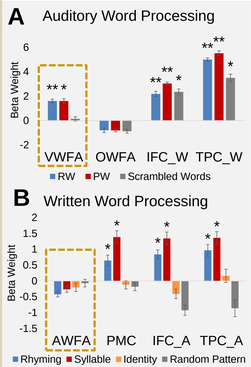


Fig 4. Activation profiles. Beta weights extracted using CoSMoMVPA. One sample t-tests. *p<0.05, **p<0.0001.

- VWFA is selective for auditory words (Fig 4A; p<0.0001), but written words does not activate the AWFA (Fig 4B).
- VWFA is the only orthographic ROI selective for auditory words; no activation in OWFA (Fig 4A).

Functional Connectivity Differs for Written and Auditory Word Processing

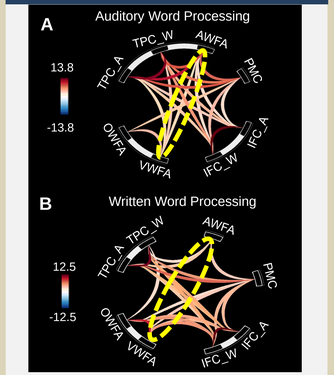


Fig 5. ROI-to-ROI stimulus-driven functional connectivity using CONN 21.a for **A.** auditory word processing (RW, PW combined) and **B.** written word processing (rhyme, syllable, identity combined). Connection threshold: p-uncorrected<0.05, two-sided. Cluster threshold: ROI-level p-FDR <0.05. Color bar corresponds to T values.

- Significant connectivity between the AWFA and VWFA only for auditory word processing (Fig 5A; T(25)=3.24, p-FDR= 0.006) but not during written word processing (Fig 5B).

Exploring the Dynamical Interactions Using the MOUS MEG Dataset[7]

Experimental Design

Subjects: 90 right-handed Dutch speakers (47 females). Ages 18-33.

Auditory MEG

- Stimuli: 120 spoken sentences in Dutch, and 120 of their scrambled spoken word list counterparts.
- Task: Stimuli were presented in a total of 24 blocks, alternating between sentence blocks (containing 5 sentences) and word list blocks (containing 5 word lists). To check for compliance, 20% of the trials were followed by a 'Yes'/'No' question about the content of the previous sentence/word list.

Acquisition parameters: 275-channel axial gradiometer system (CTF).

Preprocessing:

- Butterworth filter for high- (0.2 Hz) and low- (30 Hz) pass filtering.
- Manually removed trials with eye movements and other artifacts.
- MEG data were epoched into windows -0.5s pre-stimulus and 0.9s post-stimulus.

Calculating word onsets: Word onsets of stimuli (first word in a sentence or a scrambled word list) were identified using AlignTool[8, 9].

MEG Analyses

Beamforming: After obtaining the sensor averages, we used LCMV beamforming on 8196 dipole locations. Cortical surfaces surface-registered to template mesh.

ROIs: Center coordinates were obtained for the VWFA, AWFA, IFC, and TPC by thresholding second-level activation maps for word frequency for the written and auditory fMRI scans. Dipole locations within 10 mm of center.

Coherence: At 14 Hz, coherence between ROIs was calculated at 0.5 ms intervals from -0.2s to 0.5s around the stimulus. Time window was determined by 1/f.

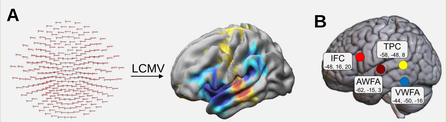


Fig 6A. Sensor layout and time-courses (left), and snapshot of source-reconstructed dynamics following LCMV beamforming (right) **B.** ROI locations for MEG analyses.

MEG Coherence Supports Direct Coupling Between the AWFA and VWFA

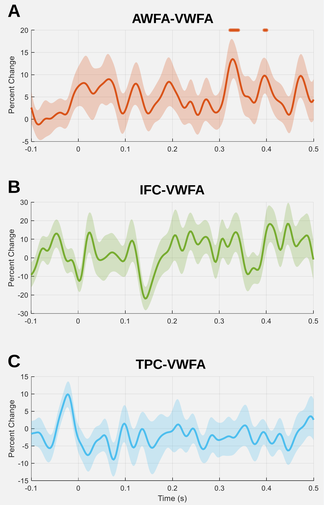


Figure 7. MEG coherence analyses computed at 14 Hz between the **A.** AWFA and VWFA **B.** IFC and VWFA **C.** TPC and VWFA. Coherence is plotted as percent signal change from average baseline coherence. Shaded area represents the standard error of the mean. Significance is marked where time windows reach p<0.01.

- Significant coherence found between the AWFA and VWFA starting around 300 ms (p<0.01).
- In contrast, we find no evidence for interactions between the VWFA and IFC or VWFA and TPC, supporting our hypothesis that VWFA responses to auditory words were due to a direct coupling of AWFA and VWFA, in line with anatomical data[11].

Conclusions

- The VWFA shows cross-modal selectivity and functional connectivity with the AWFA during auditory word processing but not visual word processing.
- Coherence analyses of the MOUS MEG dataset identifies significant coherence between the VWFA and AWFA starting 300 ms after auditory word onset. In contrast, no evidence was found for coherence between the VWFA and IFG and TPC.
- Our fMRI activation, functional connectivity, and MEG analyses thus support a model in which the AWFA provides a teaching signal to develop the written word lexicon in the VWFA.

Acknowledgements

- Research supported by the National Science Foundation (BCS-1756313).
- MEG data obtained from MOUS dataset
- Dr. Ian DeWitt for the auditory scrambling code used in the localizer.

References

1. Glezer, L. S., Jiang, X., & Riesenhuber, M. (2009). Evidence for highly selective neuronal tuning to whole words in the "visual word form area". *Neuron, 62*(2), 199-204.
2. Kronbichler, M., Hutzler, F., Wimmer, H., Mair, A., Staffen, W., & Ladurner, G. (2004). The visual word form area and the frequency with which words are encountered: evidence from a parametric fMRI study. *Neuroimage, 21*(3), 946-953.
3. Lochy, A., Jacques, C., Maillard, L., Colnat-Coulbois, S., Rossion, B., & Jonas, J. (2018). Selective visual representation of letters and words in the left ventral occipito-temporal cortex with intracerebral recordings. *Proceedings of the National Academy of Sciences, 115*(32), E7595-E7604.
4. DeWitt, I., & Rauschecker, J. P. (2013). Wernicke's area revisited: parallel streams and word processing. *Brain and language, 127*(2), 181-191.
5. Damera, S. R., Mattei, J., Glezer, L., Cox, P., Jiang, X., Rauschecker, J., & Riesenhuber, M. A Lexicon in the Anterior Auditory Ventral Stream: Preliminary evidence from an fMRI-RA study [abstract]. In: Eleventh Annual Meeting of the Society for the Neurobiology of Language; 2019 Aug 20-22; Helsinki, Finland. Abstract E66.
6. Rauschecker, J. P., & Scott, S. K. (2009). Maps and streams in the auditory cortex: nonhuman primates illuminate human speech processing. *Nature neuroscience, 12*(6), 718-724.
7. Schoffelen, J. M., Oostenveld, R., Lam, N. H., Uddén, J., Hultén, A., & Hagoort, P. (2019). A 204-subject multimodal neuroimaging dataset to study language processing. *Scientific data, 6*(1), 1-13.
8. Glezer, L. S., Eden, G., Jiang, X., Luetje, M., Napoliello, E., Kim, J., & Riesenhuber, M. (2016). Uncovering phonological and orthographic selectivity across the reading network using fMRI-RA. *Neuroimage, 138*, 248-256.
9. Schillingmann, L., Wrede, B., & Belke, E. (2017). AlignTool (Version 0c2855a) [Computer software]. Retrieved from https://ruhr-uni-bochum.sciebo.de/s/CcV7nfx44kg3i30.
10. Belke, E., Keite, V., & Schillingmann, L. (2017). AlignTool Documentation (Version 0c2855a). Retrieved from https://www.linguistics.rub.de/~belke/aligntool.shtml.
11. Bouhali, F., de Schotten, M. T., Pinel, P., Poupon, C., Mangin, J. F., Dehaene, S., & Cohen, L. (2014). Anatomical connections of the visual word form area. *Journal of Neuroscience, 34*(46), 15402-15414.

PosterPosters.com
Your Research Poster, Printed For Less