The language network is selective and distinct from other cognition in both function and connectivity in early childhood

Hiersche, K.J.[1, 2]*, Schettini, E.[1,2], Li, J.[1, 2], Saygin, Z.M.[1, 2]*

1. Department of Psychology, The Ohio State University, Columbus, OH, USA, 43215

2. Center for Cognitive and Behavioral Brain Imaging, The Ohio State University, Columbus, OH, USA, 43215

*Correspondence to: hiersche.1@osu.edu and saygin.3@osu.edu

Abstract

Is language distinct from other cognition? Does the neural machinery for language emerge from general-purpose neural mechanisms early in development, becoming tuned for language only after years of experience and maturation? In adults, language is supported by a frontotemporal network that is functionally and connectionally dissociated from adjacent domain-general cortex supporting other, more general cognitive functions. We scanned young children (2-9 years of age) on an auditory language localizer, spatial working memory localizer (engaging the domain-general multiple demand (MD) network), and a resting state scan. Subject-specific functional regions of interest (fROIs) defined with the language task showed consistent selectivity to auditory sentences in key left hemisphere regions, and were not engaged for spatial working memory, showing similar domain-specificity as reported in adults; and despite known prolonged development of frontal cortices, the left inferior frontal cortex ("Broca's area") showed some of the most robust specificity for linguistic content. Thus, despite immature language skills, young children already have left-lateralized brain regions dedicated to linguistic content. Children also showed higher within-network (language-language) connectivity than between-network connectivity (language-to-MD fROIs defined with the working memory task), in both hemispheres, but with higher within-network connectivity on the left. Language-selectivity increased with age (replicated in a subset of children scanned longitudinally) while specificity of language connectivity did not change with age (again replicated longitudinally), suggesting that connectivity is more static than, and may perhaps earmark, functional specificity. By age 2, the language network is specialized for linguistic processing (domain-specific) function, is distinct from adjacent cortex, and is not engaged in other higher-order cognitive processing.

Introduction

Language is a uniquely human cognitive skill. Remarkably, children develop language skills naturally through exposure, without explicit training or formal education in the first few years of life (Lenneberg, 1967; Sharp & Hillenbrand, 2008). But when does the adult-like language network emerge in the brain and, is it already selective for linguistic content in children as young as 2 years of age? In adults, distinct frontal and temporal regions support high-level language (Fedorenko et al., 2010, 2011; Vigneau et al., 2006). This amodal language network robustly and reliably responds to the semantic and syntactic properties of language (Fedorenko et al., 2010), is left-lateralized (Ojemann, 1991), and consistent across languages (Malik-Moraleda et al., 2021). Using individualized functional regions of interest (fROIs), Fedorenko and colleagues (2010) also showed that this language network is specialized for linguistic processing (domain-specific) and is not engaged in other higher-order cognitive processing like performing arithmetic, cognitive control, or working memory (Fedorenko et al., 2012). Instead, adjacent regions engage in these domain-general processes (Multiple Demand (MD) network) (Duncan, 2010; Fedorenko 2012). The language network is distinct from this domain-general network in both neural responses (Fedorenko et al., 2012) and connectivity (Blank et al., 2014). These previous results suggest that the domain of language is indeed distinct from other cognition, or at least draws on different neural mechanisms, in adults. Is the language network already specialized for linguistic content in early childhood and distinct from adjacent domain-general cortex in both function and connectivity? Or does this specialized language network emerge from domain-general cortex later in development?

A review of language network development suggests that children show activation in traditional perisylvian language regions with increasing activation in the left hemisphere (LH) with age (Weiss-Croft & Baldeweg, 2015). Similarly, a recent meta-analysis reported language activation in the left inferior frontal, bilateral superior temporal, and middle temporal gyri (Enge et al., 2020) in samples of older children. Some have argued that while temporal language

regions emerge in early childhood (ages 5-6) (Weiss et al., 2018), the frontal regions are slower to develop their specificity to linguistic content, emerging only after 7-8 years of age (Wang et al., 2021). Others have seen frontal language network activation in children as young as 4 years old (Olulade et al,. 2021). However, longitudinal work reports increasing language activation in both frontal (Szaflarski et al., 2006) and temporal (Szaflarski et al., 2012) regions during development, and there is evidence of increasing functional connectivity (FC) within the language network with age and language ability (Xiao, Brauer, et al., 2016; Xiao, Friederici, et al., 2016). One limitation of prior work is that task performance, particularly in expressive language studies, may confound results due to age-related effects on performance (Weiss-Croft & Baldeweg, 2015). Second, the precise location of these language regions can vary across subjects (Amunts et al., 1999; Juch et al., 2005; Tomaiuolo et al., 1999), and it is likely that group level analyses in previous literature blurred the boundaries of language and non-language cortex. A recent exception is Olulade and colleagues (2020) (Olulade et al., 2020) who used individual activation maps, finding bilateral language activation in superior temporal cortices, with laterality increasing with age. Finally, it is possible that the previously reported age-related increases in linguistic activation may in fact reflect gains in nonlinguistic processes (e.g. domain-general executive function). To date, no prior work has yet disentangled linguistic and nonlinguistic activation on a single-subject basis in children. This is important for understanding the neural mechanisms that underlie linguistic processing, because it is plausible that general purpose neural machinery bootstraps the development of this uniquely human cognitive skill.

If the language network does in fact emerge from domain-general cortex, we would expect that language regions would show little selectivity to linguistic content, would also engage in other cognition such as working memory (engaging the MD network), and that selectivity to linguistic content would increase with age (both cross-sectionally and across time within an individual) while MD task engagement would decrease. However, if the language

network is functionally specific in early childhood, we would expect significant selectivity to linguistic content and no responsiveness to the MD localizer task.

Here we investigate the development of the high-level language network and its differentiation from domain general cortex in a young group of children ages 2-9 years old. We leverage individual subject data on two separate fMRI tasks, use single-subject fROIs defined in native anatomy, to account for variability in the precise location of these regions (Fedorenko et al., 2010, 2013), and directly compare linguistic and nonlinguistic activation in the same subjects. We also examine the within- and between-network resting-state connectivity of the language vs. MD fROIs. We assess any age-related changes in linguistic selectivity and connectivity both cross-sectionally and longitudinally in a subset of participants.

Results

Is the language network already selective for high-level linguistic content in children as young as 2 years of age? Is it specific for language or is it initially part of domain-general cortex in early childhood? We explored selectivity and specificity in both function and connectivity using individual-subject activation to two separate tasks as well as cross-sectional and longitudinal analysis.

Is the high-level language network already selective for linguistic content in young children?

First, we wanted to ensure that our language fROIs were not confounded with adjacent speech areas that respond to higher order properties of human-produced speech sounds (but which are not tuned for high-level linguistic properties like semantics and syntax). We defined speech fROIs per subject using the contrast of Nonsense > Texturized speech. We found that these fROIs were indeed selective for speech (10%: LH: $t(33)=6.7$, Bonferroni-Holm $p=1.1 \times 10^{-7}$; RH: $t(33)=3.4$, Bonferroni-Holm $p=9.2 \times 10^{-4}$, one-sample t-tests), were not selective for language (i.e. activation for Sentences were no different than activation for Nonsense (10%: LH: $p=0.063$; RH: $p=0.063$, paired-samples t-tests), and the LH speech region was not significantly more selective than the right ($p=0.054$, paired-samples t-tests). These results also serve as a

sanity check because speech regions have been previously identified even in infants (Dehaene-Lambertz et al., 2002). Further, by first defining these speech fROIs, we were able to remove any overlap with temporal language fROIs (below).

Next, we addressed our main question and asked whether the language network is selective for high-level language in children 2-9 years of age. We defined language fROIs in two ways to keep with prior literature: using Sentences > Texturized speech, which controls for low-level auditory features in sentences, and Sentences > Nonsense sentences which presumably defines a more specific language region by additionally controlling for the rhythm and prosody of speech. For fROIs defined using Sentences > Texturized speech, we found significant selectivity for all LH fROIs, all surviving Bonferroni-Holm multiple comparison correction. Results were largely consistent regardless of the threshold used (5%,10%, 20%; see **Table 1** for 10% threshold, additional in **Supplemental Table 1**). In the right hemisphere (RH), only the superior temporal gyrus consistently showed significant selectivity to language.

Using the more specific contrast of Sentences > Nonsense sentences yielded similar results, with consistent selectivity at all thresholds (see **Table 1** for 10% threshold, additional in **Supplemental Table 1**). The LH showed significant selectivity in all fROIs, with most surviving multiple comparison correction, and consistent with the Sentences > Texturized contrast, across thresholds only the superior temporal fROI showed consistent, significant selectivity to language in the RH (**Figure 1**).

Is the selectivity of the language network associated with age?

The only language fROI to show a consistent, positive relationship with age, regardless of contrast or threshold, was the LH posterior temporal region, (Sentences > Texturized all $r>0.3$ and all $p<0.05$, Sentences > Nonsense all $r>0.48$ and all $p<0.01$, surviving multiple comparison correction). The Sentences > Texturized contrast showed a positive relationship between age in LH superior temporal, inferior frontal, and middle frontal fROIs (all $r>0.3$ and all $p<0.05$), with the middle frontal region surviving multiple comparison (see **Supplemental Table 2**).

fROI	Language Selectivity: Sentences > Texturized		MD Selectivity: Hard > Easy		Language vs. MD	
LH	*t*-stat (SD)	P-value	*t*-stat (SD)	P-value	*t*-stat (SD)	P-value
Posterior Temporal	3.82 (0.45)	2.8×10^{-4}**	-1.04 (0.90)	0.85	2.73 (0.98)	0.011*
Superior Temporal	7.76 (0.30)	3.0×10^{-9}**	-0.29 (0.90)	0.62	2.88 (0.84)	0.0075**
Angular Gyrus	2.03 (0.42)	0.025**	0.74 (0.89)	0.23	0.36 (1.03)	0.72
Inferior Frontal	2.62 (0.50)	0.0065**	-1.20 (0.72)	0.88	2.42 (0.92)	0.022**
Middle Frontal	2.18 (0.43)	0.018**	0.49 (0.72)	0.32	0.78 (0.95)	0.44
Orbital Inferior Frontal	2.93 (0.55)	0.0030**	-0.27 (0.79)	0.61	1.83 (1.00)	0.078
RH	*t*-stat (SD)	P-value	*t*-stat (SD)	P-value	*t*-stat (SD)	P-value
Posterior Temporal	2.17 (0.40)	0.018*	0.53 (0.75)	0.30	0.40 (0.90)	0.69
Superior Temporal	4.67 (0.34)	2.4×10^{-5}**	-0.49 (0.88)	0.69	2.10 (0.92)	0.045*
Angular Gyrus	1.30 (0.45)	0.082	2.67 (0.70)	0.0063**	-1.36 (0.90)	0.18
Inferior Frontal	0.78 (0.44)	0.22	-0.19 (0.77)	0.57	0.49 (0.90)	0.63
Middle Frontal	0.15 (0.48)	0.44	-0.58 (0.75)	0.72	0.59 (0.93)	0.56
Orbital Inferior Frontal	1.85 (0.41)	0.037*	-1.37 (0.74)	0.91	1.89 (0.88)	0.069
	Language Selectivity: Sentences > Nonsense		**MD Selectivity: Hard > Easy**		**Language vs. MD**	
LH	*t*-stat (SD)	P-value	*t*-stat (SD)	P-value	*t*-stat (SD)	P-value
Posterior Temporal	3.78 (0.34)	3.1×10^{-4}**	-0.80 (0.89)	0.78	2.19 (0.94)	0.037*
Superior Temporal	4.22 (0.43)	8.9×10^{-5}**	-1.26 (0.89)	0.89	2.71 (1.03)	0.011*
Angular Gyrus	2.02 (0.46)	0.026*	0.37 (0.86)	0.36	0.50 (1.04)	0.62
Inferior Frontal	2.16 (0.45)	0.019*	0.74 (0.81)	0.23	0.68 (0.82)	0.50
Middle Frontal	2.03 (0.45)	0.025*	0.75 (0.78)	0.23	0.48 (0.99)	0.64
Orbital Inferior Frontal	2.62 (0.45)	0.0067**	-1.90 (0.80)	0.97	2.88 (0.97)	0.0075**
RH	*t*-stat (SD)	P-value	*t*-stat (SD)	P-value	*t*-stat (SD)	P-value
Posterior Temporal	1.45 (0.31)	0.078	0.62 (0.80)	0.27	0.18 (0.81)	0.86
Superior Temporal	2.28 (0.44)	0.015*	-0.52 (0.86)	0.70	1.67 (0.99)	0.11
Angular Gyrus	-0.21 (0.45)	0.58	2.97 (0.68)	0.0030**	-2.91 (0.70)	0.0071**
Inferior Frontal	1.70 (0.39)	0.049*	0.39 (0.80)	0.35	0.60 (0.76)	0.55
Middle Frontal	1.58 (0.43)	0.062	0.06 (0.86)	0.48	0.65 (0.92)	0.52
Orbital Inferior Frontal	1.37 (0.45)	0.089	0.02 (0.75)	0.49	0.85 (0.85)	0.40

Table 1. Selectivity of the language fROIs (defined with top 10% of activation) during a language localizer task and multiple demand task. One-tailed t-tests were conducted to determine if selectivity index to language or MD was significantly greater than zero. Two-tailed t-tests were conducted to determine if language and MD selectivity were

significantly different; t-values, standard deviation and p-values are reported. Asterisks indicate level of significance (* $p < 0.05$; ** Bonferroni-Holm corrected $p < 0.05$). LH: left hemisphere, RH: right hemisphere

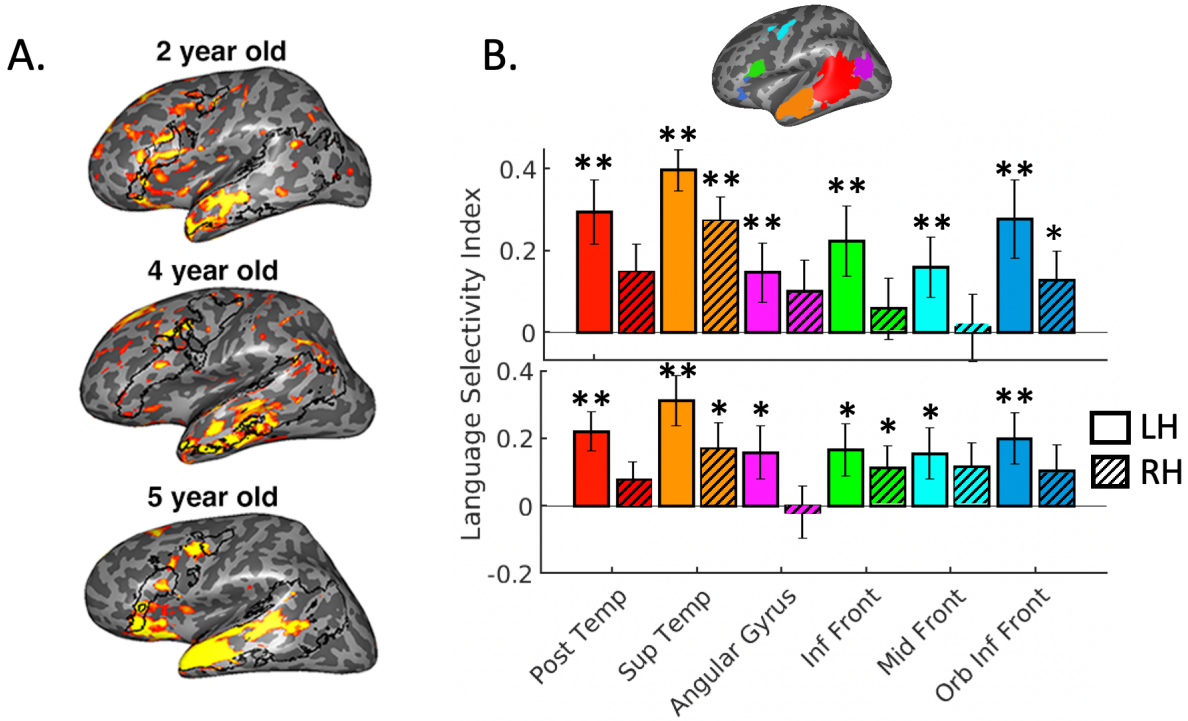

Figure 1: Mean selectivity of the high-level frontotemporal language network. A. Activation to Sentences > Nonsense for example subjects (thresholded at $P_{uncorrected} < 0.01$). B. Mean selectivity in the LH (opaque) and RH (crosshatch) language fROIs during the language localizer task. fROIs were defined using the top 10% of responding voxels within larger parcels for Meaningful Sentences > Texturized Speech (top) and Meaningful Sentences > Nonsense Sentences (bottom). One-tailed t-tests were conducted to test if selectivity index to language was significantly greater than zero. Asterisks indicate level of significance (* $p < 0.05$; ** Bonferroni-Holm $p < 0.05$, corrected for 6 comparisons per hemisphere). Error bars denote standard error. LH: left hemisphere, RH: right hemisphere

Is the high-level language network specific for linguistic content and differentiated from domain-general cortex?

Next, we asked whether the language network is *specific* for high-level language in children. We used the same fROIs as above and extracted PSCs from an independent run of the language task and also from the separate MD task. Across almost all fROIs, language selectivity was higher than selectivity to the MD task (**Figure 2**). The LH language fROIs, whether defined using Sentences > Nonsense or Sentences > Texturized, did not show effort-related activation (i.e. higher Hard vs. Easy activation in the spatial working memory task, see **Table 1** for 10% threshold, additional in **Supplemental Table 3**). Consistently, across thresholds and for either language contrast, the right angular gyrus was the only language fROI that showed Hard vs. Easy selectivity significantly greater than zero. Most LH fROIs responded significantly more to language than MD (all uncorrected $p<0.05$, see **Table 1** for 10% threshold, additional in **Supplemental Table 4**). These results suggest specificity for linguistic content in the language network in young children, and just like in adults, nonlinguistic abilities, like holding content in working memory, are supported by a separate cortical network.

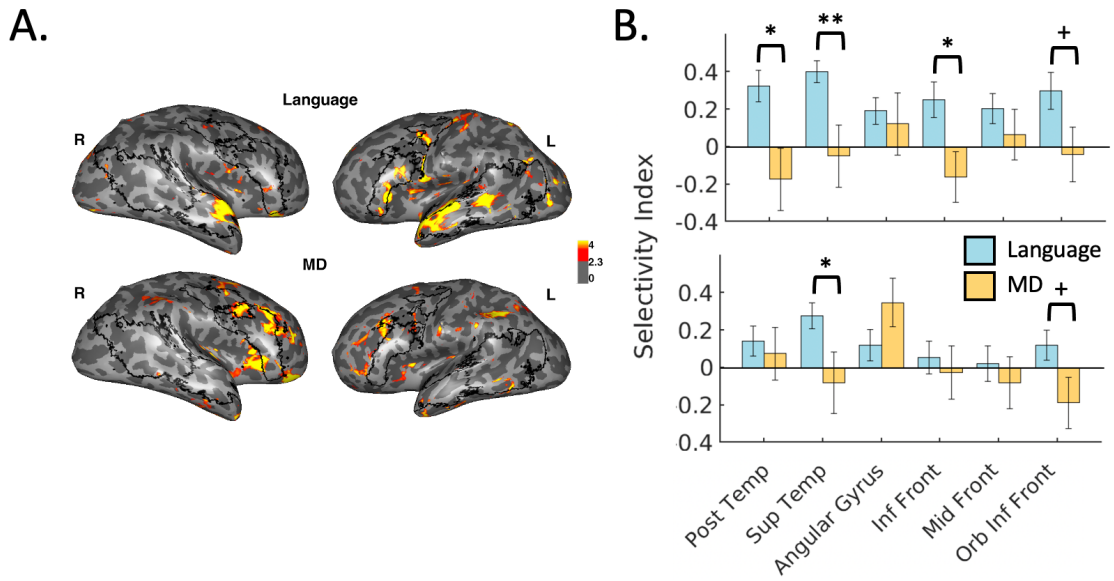

Figure 2: A. Language (top) and MD (bottom) significant activation for an example subject (threshold at $P_{uncorrected} < 0.001$). B. Mean selectivity in LH (top) and RH (bottom) language fROIs (Sentences > Texturized) for language (blue) and spatial working memory/MD (yellow). Two-tailed, paired samples t-tests were conducted to test if the selectivity index was significantly different between language and MD. Asterisks indicate level of significance (+ $p < 0.08$; * $p < 0.05$; ** Bonferroni-Holm $p < 0.05$, corrected for 6 comparisons per hemisphere). Error bars denote standard error.

Is the high-level language network differentiated from domain-general cortex in connectivity?

Next, we defined MD fROIs in each subject using the same procedure as for language fROIs (see Methods) and examined the connectivity of subject-defined language fROIs and MD fROIs (see **Figure 4a**) during rest, to see if the language network is preferentially connected to itself. Because the two language contrasts yield similar results, we use the Sentences > Texturized contrast for the rest of the analyses (here and below). Two-tailed, one-sample *t*-tests were conducted to assess if within-network connectivity of the language network was significantly greater than zero. Both the LH and RH language network show significant within-

network connectivity (LH: t(31)=14.0, p=6.4 x 10^{-15}; RH: t(31)=9.9, p=4.2 x 10^{-11}). Paired-samples *t*-tests revealed that the within-network connectivity of the LH was significantly higher than the right (t(31)=2.8, p=8.2 x 10^{-3}). Additionally, frontal language fROIs were significantly connected with temporal language fROIs by hemisphere, (LH: t(31)=9.2, p=4.6 x 10^{-11}; RH: t(31)=8.7, p=8.6 x 10^{-10}).

While the language network showed significant connectivity with MD network (LH: t(31)=8.4, p=1.6 x 10^{-9}, RH: t(31)= 8.6, p=1.0 x 10^{-9}), the within-network connectivity of the language network was significantly higher than between-network connectivity (i.e. language to MD connectivity): within vs between-network LH: t(31)=4.2, p=2.3 x 10^{-4}; RH: t(31)=2.7, p=0.012 (see **Figure 4b**). Further, temporal language fROIs were more connected with the frontal language fROIs than with the frontal MD fROIs (within vs between frontal to temporal LH: t(31)=4.3, p=1.6 x 10^{-4}; RH: t(31)=4.8, p=3.6 x 10^{-5}). All results held after Bonferroni-Holm multiple comparisons correction (see **Figure 4b**).

Within-network language connectivity showed no relationship with age in this cross-sectional sample (**Supplemental Table 5**). Additionally, there was no relationship with age and the difference in within- vs. between-network connectivity of language and MD regions.

Is the differentiation of the language network from the MD network reflected within individuals over time?

A subset of our participants were scanned at more than one timepoint, approximately a year apart, and completed both tasks and resting-state scan at all timepoints (N=13). In these participants, we found that the LH language network shows selectivity to language in almost all fROIs (as was shown for the cross-sectional sample, see **Supplemental Table 6**) and also does not show MD task engagement (all p>0.05; see **Supplemental Table 6**). The change in language selectivity across timepoints was significant for the LH superior temporal (t(13)=2.31, p=0.031), inferior frontal (t(13)=2.28, p=0.042), and orbital inferior frontal (t(13)=2.44, p=0.039) fROIs. The RH language fROIs showed no change in selectivity over time. There were no

significant changes in selectivity to the MD task except for the LH inferior frontal fROI (t(12)=-2.07, p=0.0078) which decreased in selectivity, but this fROI showed no significant selectivity at either timepoint (TP1: t(12)=0.82, p=0.22, TP2: t(12)=-1.13, p=0.86). Overall, these data replicate the cross-sectional results.

Longitudinal resting-state data also show a similar pattern as the cross-sectional analyses: the within-network connectivity of LH language fROIs was significantly higher than between-network connectivity of language-MD fROIs for both timepoints (TP1: t(13)=2.6, p=0.021; TP2: t(13)=2.7, p=0.019), but interestingly not for the right (TP1: t(13)=-0.46, p=0.66; TP2: t(13)=1.2, p=0.23), which was significant in the cross-sectional analysis. Similarly, at both timepoints, the temporal language regions are more connected to language frontal regions than MD frontal regions in the LH (TP1: t(13)=3.3, p=6.1 x 10^{-3}; TP2: t(13)=2.4, p=0.031), but not right (TP1: t(13)=1.2, p=0.26; TP2: t(13)=1.8, p=0.091). Looking at the difference in connectivity over time, we observed a marginal increase in within-network language FC by hemisphere between timepoints (LH: t(13)=2.2, p=0.04, RH: t(13)=2.2, p=0.048), not surviving multiple-comparison correction, and no increases in between-network connectivity of language and MD (LH: t(13)=1.8, p=0.09; RH: t(13)=1.4, p=0.19). We also found no changes across time in connectivity between temporal to frontal language fROIs (LH: t(13)=1.7, p=0.11; RH: t(13)=1.6, p=0.14) and no changes in temporal language connectivity to frontal MD fROIs (LH: t(12)=-0.35, p=0.73; RH: t(12)=0.40, p=0.70). (See **Figure 4c**).

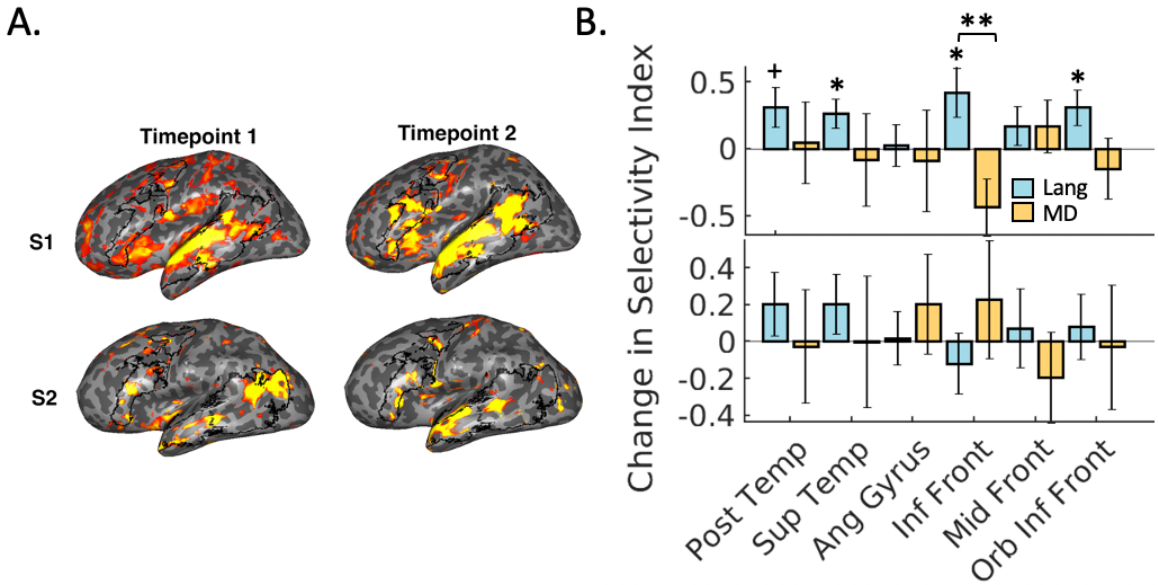

Figure 3. Changes in language fROI selectivity to language and MD tasks over two longitudinal visits. A. LH response to language (Sentences > Texturized Speech) during timepoint 1 (LH) and timepoint 2 (RH) for two additional example subjects ($P_{uncorrected}$ < 0.001). B. Changes in selectivity to language and MD in the language fROIs in the LH (top) and RH (bottom). One-tailed t-tests were conducted to test if change in selectivity index to language or MD was significantly greater than zero. Two-tailed, paired-samples t-tests were conducted to assess whether longitudinal changes were different between tasks. Asterisks indicate level of significance (+ p < 0.06; * p < .05; ** Bonferroni-Holm p < .05, corrected for 6 comparisons per hemisphere). Error bars denote standard error.

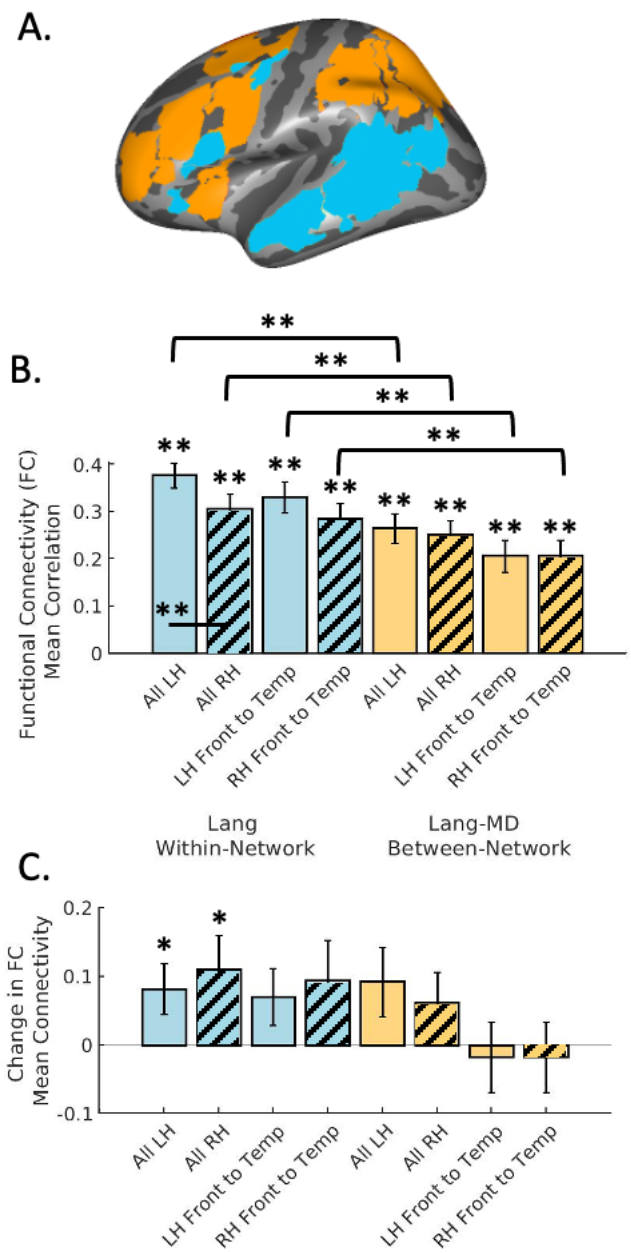

Figure 4: Within- and between-network FC of the language and MD fROIs. A: Six bilateral language (blue) and 10 bilateral MD (yellow) parcels, used to define fROIs. B: The cross-sectional FC results. C: Change in FC for longitudinal in LH (opaque) and RH (crosshatch). One-sample, two-tailed t-tests were used to established if FC or change in FC was significantly greater than zero. Repeated-measures t-tests were used to compare FC across within- and

between-network connectivity. Asterisks indicate level of significance (* p < 0 .05; ** Bonferroni-Holm p < .05), Error bars denote standard error.

Discussion

Understanding the development of the language network and its specificity in function and connectivity will help us better understand the neural mechanisms that underlie uniquely human cognition. Here we examined the selectivity of language fROIs to high-level language and their specificity by comparing responses to another cognitive task in a cross-sectional and longitudinal sample of children. Additionally, we assessed the within- and between-network connectivity of the language and MD networks.

We used subject-specific fROIs to account for individual variability in the precise location of the language network across individuals. We also included two different ways to define fROIs to keep with previous literature (which used control conditions ranging from rest, to auditory tones, to foreign language, and reversed speech (Enge et al., 2020)). We demonstrated linguistic selectivity using the contrast of meaningful Sentences > Texturized speech, as well as with a more strigent control condition of meaningful Sentences > Nonsense sentences, and find largely similar results between the two, across three different thresholds for defining the fROIs (i.e. the top 5%, 10 and 20% of voxels within larger parcels). We observed consistent activation in both temporal and frontal regions, even in our youngest subjects. This supports research that has shown frontal language network activation (Olulade et al., 2020). The use of individually-defined fROIs not only lets us account for individual-variability, it also ensures we are only looking at language-senstive regions for each participant.

Our analyses show that these language-specific regions are not domain-general as they do not show any responsiveness to the MD task. If language development is part of general skill-learning (as has been suggested by (Chater & Christiansen, 2018; McCauley, 2020)), as

opposed to a domain-specific function, we may expect the language regions to be responsive to a spatial working memory task that localizes the MD network. However, our results mirror work in adults showing that language and MD regions exist side by side in Broca's area, and yet are functionally distinct (Fedorenko et al., 2012). While no previous study empirically investigated the neural dissociation of linguistic vs. non-linguistic content in children, numerous papers have proposed that the development of language is related to the development of cognitive flexibility (a domain-general cognitive ability that activates the domain-general, MD network; Duncan, 2010). For example, it is possible that learning language faciliates changes in cognitive flexibility and vice versa. One review examined the relationship between cognitive flexibility, inner speech, and language in children and young adults, finding that while inner-speech and language are not required for cognitive flexibility, it can enhance performance on a variety of cognitive flexibility tasks (Cragg & Nation, 2010). We do not rule out this possibility and suggest that perhaps this interaction between cognitive flexibility and language is supported by the significant connectivity between language and MD fROIs in our sample; but this connectivity was dwarfed by within-network language connectivity, suggesting that the language network is indeed distinct with specificity for linguistic content and largely independent of other adjacent cognitive networks.

We observed higher within- vs. between-network connectivity in the LH than in the RH in both cross-sectional and longitudinal data, as well as largely left-lateralized selectivity and specificity for language. These results mimic what previous studies show in adults, with language typically left-lateralized (Fedorenko et al., 2010) and with significantly higher left than right within-network FC (Blank et al., 2014). Despite this clear laterality, we also observed bilateral superior temporal selectivity, which aligns with prior work showing bilateral language activation in this region in children (Enge et al., 2020). While we show these results in children as young as two years old, it would be of interest for future studies to longitudinally explore when this laterality of language emerges.

Additionally, we see that that linguistic selectivity increased with age in the LH temporal and frontal regions, which was mirrored within-subjects longitudinally. Prior studies examining expressive language did not report increases in language activation with age in the inferior or middle frontal regions after accounting for task difficulty (Weiss-Croft & Baldeweg, 2015), but saw decreases in the left angular gyrus and orbital inferior frontal gyrus; these discrepancies may perhaps be due to the use of group-level activation maps introducing confounds by including adjacent non-language cortex in the analyses. We observed increasing selectivity in left inferior frontal regions both cross-sectionally and within individuals which supports prior work on receptive language (Berl et al., 2012, Szaflarski et al., 2006). Indeed, so-called Broca's area (or in our case, the language- selective portion of Broca's area which is an anatomical area) was where we observed some of the most prominent language activations *and* the greatest increases in language selectivity across time. We observed no significant change in LH language fROI selectivity to the MD task across time longitudinally within the same subject, suggesting that the domain-specific language cortex emerges independently from domain-general cortex. Together, these data suggest that both frontal and temporal regions of the language network are largely developed in children as young as two, but that the selectivity of these regions increases over time independently from domain-general processes and instead may reflect gains in linguistic skills including grammar, vocabulary, comprehension (e.g. (Abrahams et al., 2003; Ardila, 2011, 2012). There were no reliable increases in within- vs. between-network FC cross-sectionally and longitudinally, which suggests that specificity of connections are more static than neural specificity, at least for the domain of language. This supports previous work testing the connectivity-fingerprints hypothesis, where connectivity precedes and perhaps drives the functional organization and specificity of cortex (Hannagan et al., 2015; Li et al., 2020; Saygin et al., 2016; Yu et al., 2020).

Here, we examine the distinction between the domain-specific language network and domain-general MD network and find that they are distinct in their funciton and connectivity in

young children. However, we do not examine the development of the MD network itself, focusing only on the responsiveness of language fROIs to a task that evokes the MD network in adults. Other work has demonstrated robust MD network activation to this task in young children and that this activation increases with increasing task performance, independently of age (Schettini et al., 2022). It would be interesting for future work to explore the age-dependent changes in the linguistic network with respect to increasing performance on executive function tasks and related MD network activation, as well as to explore connectivity and cross-talk between these two networks across age. Further, the age-related increases in selectivity we observe are likely due to gains in linguistic ability, which future work can explore with bigger cohorts. And while the current longitudinal set of subjects is much smaller than the cross-sectional, the alignment of the two sets of results increases confidence in our inferences. Future work should continue to examine the relationship between the selectivity and connectivity of the language network with performance on behavioral measures of language ability, preferably in longitudinal samples (Marek et al., 2022).

In conclusion, these results show that functionally defined, subject-specific language fROIs are specialized for language and are distinct from adjacent domain-general cortex in both their selectivity and connectivity. Specialization of function increases with age, perhaps to support ongoing gains in linguistic ability. Comparing linguistic and nonlinguistic function within the same subjects across time in early development is essential for understanding the neural mechanisms that underlie uniqely human cognition.

Methods

Participants

Data were collected from 43 children. Of the 43 children, 34 children completed structural imaging and two runs of the language localizer task during at least one timepoint (19 female, 22 right-handed, mean age=6.13 years, age min and max = 2.97-9.07 years) and were used in the cross-sectional analysis. A subset of this group completed the multiple demand

(MD) localizer (N=29, mean age=6.51 years). Of the 43 children, 32 completed resting state scans and at least one run of the language and MD localizers and were therefore included in the resting state analysis. For children who completed all scans at multiple timepoints, the earliest timepoint was prioritized for cross-sectional analysis.

18 children returned for at least one subsequent, yearly timepoint and 14 of those children (8 female, timepoint 1 (TP1): mean age=5.98 years, age min and max = 3.95-7.9 years; timepoint 2 (TP2): mean age =7.48 years, age min and max = 4.74-9.07 years, mean time between appointments=1.50 years) completed two runs of the language localizer at their latest timepoint, as well as at least one run of the language localizer at an earlier timepoint and were therefore included in the longitudinal analysis. All but one of these children completed at least one run of the MD task at each timepoint, as well as a resting state and structural imaging and were included in the MD longitudinal analysis.

This study was approved by the institutional review boards at The Ohio State University. Parents gave written consent and children gave verbal assent to participate.

Data acquisition and Preprocessing

Anatomical: Images were acquired on a Siemens Prisma 3T scanner with a 32-channel phase array receiver head coil. Foam padding was used for head stabilization and increased comfort throughout all scanning. A whole-head, high resolution T1-weighted magnetization-prepared rapid acquisition with gradient echo (MPRAGE) scan was acquired (repetition time (TR) = 2300 ms, echo time (TE) = 2.9ms, voxel resolution = 1.00 mm^3). Data were analyzed with Freesurfer v.6.0.0, FsFast, FSL, and custom Matlab (version R2020a) code. A semi-automated processing stream (recon-all from Freesurfer) was used for structural MRI data processing. Major preprocessing steps include intensity correction, skull strip, surface co-registration, spatial smoothing, white matter and subcortical segmentation, and cortical parcellation. Cortical gray matter masks were created in native anatomy for each subject.

Functional Localizers: A series of functional localizers were completed by each child. A language localizer task (Fedorenko et al., 2010) was used to functionally locate the regions of the brain responsive to the lexical and structural properties of language. Participants listened to blocks of meaningful sentences, nonsense sentences (controlling for prosody but constructed from phonemically intact nonsense words), and texturized speech (controlling for low-level auditory features). Each run consisted of 4 blocks of each condition and three 14 second fixation blocks. Each block contained three trials (6 seconds each); each trial ended with a visual queue to press a button.

Additionally, a spatial working memory task (Fedorenko et al., 2013) with blocked easy and hard conditions (task difficulty adjusted by age) were used to functionally define brain regions associated with the domain-general MD network, which is distinct from the language network (Blank et al., 2014; Fedorenko et al., 2012). In each trial, participants viewed a grid of six boxes. For the easy condition, 2 of these blocks would flash blue, then the child would see two grids with some blue boxes highlighted in each and had to indicate, using a button press, which grid (the one on the left or right) was the correct pattern matching the first presentation. The number of boxes that must be remembered was increased for the more difficult condition. Each child completed at least one run of this task outside of the scanner, to ensure they understood the task.

Functional images for the language localizer were acquired with the echo-planar imaging (EPI) sequence: TR=1000ms, TE=28ms, 244 TRs, voxel resolution = 2x2x3 mm. The same TR and TE were used in the spatial working memory task (344 TRs). Functional data was preprocessed with motion correction (aligning all timepoints to the first timepoint in the scan, all time points with >1mm total vector motion between consecutive timepoints were included as a nuisance regressor), distortion correction, and bbregister (Greve & Fischl, 2008) was used to register functional data to the subject's anatomical space, and then data was resampled to $1x1x1mm^3$. All data were analyzed in each individual's native anatomy.

Resting: Resting-state fMRI data were also acquired 34 participants, using multiband (MB) 4x accelerated echo-planar imaging (TE/TR=28/1000ms, voxel size=2x2x3 mm). The resting-state scan lasted approximately 5 minutes and consisted of 290 volumes for a single run. Freesurfer's FS-Fast preprocessing (https://surfer.nmr.mgh.harvard.edu/fswiki/FsFastAnlysisBySteps) was used to complete motion correction and smooth gray matter (3 FWHM kernel). Additional preprocessing included linear interpolation for spikes over 0.5 mm and a bandpass filer at 0.009-0.08 Hz. All functional connectivity (FC) analyses were performed in native functional space.

Statistical Analysis

Task fMRI Analysis: Preprocessed data were entered into a volume-based, first-level general linear model (GLM) analysis. Data were detrended, smoothed (language localizer: 5mm FWHM kernel, MD localizer: 4mm FWHM kernel), with a regressor entered for each condition of interest (language localizer: meaningful sentences, nonsense sentences, texturized speech; MD localizer: hard and easy conditions), as well as six motion parameters as nuisance regressors. Timepoints with motion exceeded 1mm framewise displacement (total motion between two consecutive timepoints) were included as an additional nuisance regressor. A block design with a standard boxcar function convolved with the canonical hemodynamic response function (standard gamma function (d=2.25 and t=1.25)) was used. Relevant contrasts (language localizer: Sentences > Nonsense, Sentences > Texturized, and Nonsense > Texturized; spatial working memory localizer: Hard > Easy) were included in the level 1 processing. The resulting beta estimates and contrast maps were used for further analyses. Across both localizers, any run that exceeded the threshold of more than 25% of timepoints with greater than 1mm total vector motion between subsequent timepoints were excluded from the analysis.

Defining subject-specific functional regions of interest

Twelve frontotemporal language network (six in each hemisphere) and two speech (one in each hemisphere) subject-specific fROIs were created using the group-constrained subject-

specific approach (Fedorenko et al., 2010). Language fROIs were defined using two separate contrasts, Sentences > Nonsense and Sentences > Texturized speech, and speech fROIs were defined using Nonsense>Texturized contrast. We used parcels as spatially constrained search spaces for defining individual subject fROIs. These parcels (Fedorenko et al., 2010; https://evlab.mit.edu/funcloc/) contain the regions typically activated by high-level language (for language parcels) and speech (for speech parcels) and were defined based on previous studies in adults. Upon visual inspection, the frontal parcels did not fully capture some children's hotspots of frontal language activation (see supplemental methods). The frontal parcels were therefore dilated by 3 (with Freesurfer's mri_binarize command), which also helped make the frontal parcels more comparable in size to the temporal parcels. These parcels were all registered to each participant's native anatomy using CVS registration (Zöllei et al., 2010). Participant-specific fMRI contrasts maps from one run of the GLM analysis were masked to only include gray matter voxels, and we took the intersection of these contrast maps with the parcels to identify fROIs for each individual subject. We defined fROIs as the top 5%, 10%, and 20% of voxels that fell within each parcel/search space (for language fROIs we used contrast of Sentences > Nonsense and also Sentences > Texturized, for speech fROIs we used the contrast of Nonsense > Texturized). Speech fROIs were distinct from the Sentences > Texturized defined language fROIs. Any overlapping voxels between speech fROIs and language fROIs were assigned based on the contrast to which the voxel responded more strongly. The beta estimates from an independent run of the language localizer task were then used to extract the percent signal change (PSC) for each condition (Sentences, Nonsense, Texturized; Easy, and Hard) within the subject-specific fROIs. Each subject completed two runs of the language task in a single timepoint, therefore one run was used to define fROIs and the other run was used to extract the PSC, then this was repeated using opposite run orders and PSC results were averaged together for each participant. For the spatial working memory task, we used the fROIs as defined from the independent language task and extracted PSCs for the

Hard and Easy conditions (averaged across runs for children who completed more than one run).

For the 14 longitudinal subjects, the latest timepoint subject-specific fROIs were registered to each subject's earlier timepoint anatomical space using Freesurfer's CVS registration (Zöllei et al., 2010), and PSCs to each condition of interest was extracted from the earlier timepoint's beta estimates from the first-level GLM.

Selectivity

To quantify an individual's selectivity to language, speech, or MD within each fROI, we calculated a selectivity index by subtracting the PSC to the condition of interest with the control condition and dividing by the sum of all conditions.

$$(1)\ \text{Speech Selectivity} = \frac{PSC_{Nonsense} - PSC_{Texturized}}{PSC_{Sentences} + PSC_{Nonsense} + PSC_{Texturized}}$$

$$(2)\ \text{Language Selectivity (Sentences > Texturized)} = \frac{PSC_{Sentences} - PSC_{Texturized}}{PSC_{Sentences} + PSC_{Nonsense} + PSC_{Texturized}}$$

$$(3)\ \text{Language Selectivity (Sentences > Nonsense)} = \frac{PSC_{Sentences} - PSC_{Nonsense}}{PSC_{Sentences} + PSC_{Nonsense} + PSC_{Texturized}}$$

$$(4)\ \text{Multiple Demand Selectivity} = \frac{PSC_{Hard} - PSC_{Easy}}{PSC_{Hard} + PSC_{Easy}}$$

A one-sample, one-tailed t-test was used to determine if an fROI was significantly selectivity to its preferred category (selectivity index significantly greater than zero) with Bonferroni-Holm (Holm, 1979) multiple comparison by hemisphere. For longitudinal comparisons, the difference between selectivity and timepoint 1 and timepoint 2 was calculated for both language and MD within each language fROI, respectively. One-sample, two-tailed t-tests were used to determine if the change in selectivity over time was significantly greater than zero and paired, two-tailed t-tests were used to determine if the change in language selectivity was significantly different from the change in MD selectivity.

Selectivity and age:

Pearson correlations were used to examine the relationship between selectivity index and age in the cross-sectional sample. Bonferroni-Holm correction, for 6 fROIs per hemisphere, were applied.

Within- and Between-network Connectivity

For 34 unique children, the mean time course was extracted from six bilateral language fROIs (as defined above with the Sentences > Nonsense 10% threshold) and 10 bilateral MD fROIs (as defined above with the Hard > Easy 10% threshold) registered to the subject-specific resting state data. Functional connectivity (FC) was calculated using Pearson's correlations between each pair of fROIs. To generate normally distributed values, each FC value was Fisher z-transformed. Paired *t*-tests were used to determine significance of the mean connectivity between language fROIs (grouped by hemisphere and by lobe, Bonferroni-Holm correction by task with 6 comparisons each) and also to compare within-network (language to language and MD to MD) vs. between-network (language to MD, Bonferroni-Holm correction for 4 comparisons) connectivity. Pearson's correlations were used to assess the relationship between FC and age.

For the 14 longitudinal subjects, the latest timepoint subject-specific language and MD fROIs were registered to each subject's earlier timepoint resting state data using Freesurfer's CVS registration (Zöllei et al., 2010). The mean time course was extracted, and FC was calculated. Changes in FC were assessed similarly to changes in selectivity; one-sample *t*-tests were used to determine if the difference in FC between timepoints was significantly than zero for both within- and between-network FC (Bonferroni-Holm correction for 6 comparisons).

Author Contributions

K.H.: conceptualization, formal analysis, methodology, writing-original draft & editing; E.S. and J.L.: conceptualization, formal analysis; Z.M.S conceptualization, supervision, writing-review & editing.

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Competing Interests

The authors declare no competing financial interests.

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