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# Lifespan differences in background functional connectivity of core cognitive large-scale brain networks

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ABSTRACT

Large-scale brain networks undergo functional reorganization over the course of the lifespan, with concurrent implications for cognition. Characterizing network connectivity during a task may provide complementary insight into cognitive development and aging, to that provided by resting-state. We assessed network background connectivity, which refers to connectivity that remains after task effects have been regressed out, during a visual memory-encoding task in a lifespan sample. More specifically we assessed the within- and between-network background connectivity of the default mode, salience, and frontoparietal networks. Within-network background connectivity of salience and frontoparietal networks differed between age groups, with late-life adults showing lower connectivity. We did not find an effect of age group in default mode network background connectivity, contrary to previous findings using resting-state. However, default mode between-network background connectivity with salience and frontoparietal networks was greater in mid-life and late-life adults than in younger age groups. Overall, our findings in a lifespan sample are in line with previous observations of age-related network de-differentiation. However, the lack of age effect in default mode network background connectivity suggests that background connectivity indeed represents a complementary measure to resting-state connectivity, providing a differential glance of network connectivity during a particular state.

## 1. Introduction

Across both development and aging, large-scale brain networks undergo functional reorganization with accompanying implications for cognition. The lifespan trajectories of higher cognitive networks appear to differ from those of primary sensory networks, in that the higher-level networks integrate later in development and are vulnerable to earlier decline in aging. Three such networks have been proposed to be especially integral to cognition (Bressler and Menon, 2010): the default mode network (DMN) facilitates internal processing; the frontoparietal network (FPN) is critical to external, goal-driven attention; and the salience network (SN) modulates the DMN and FPN as needed based on situational context.

Higher cognition relies on the functional organization of these networks, both in terms of how a network node interacts with other nodes within a network (within-network connectivity), as well as how nodes of a given network interact with nodes of a different network (between-network connectivity). These networks have predominantly been investigated using resting-state functional magnetic resonance imaging (fMRI), in which functional neuroimaging data is collected in the absence of an external task. The most studied of these networks in terms of lifespan differences is the DMN. Strength of functional connectivity among nodes of the DMN increases from childhood through adolescence and into adulthood (Fair et al., 2008), particularly along the anterior/posterior axis (Supekar et al., 2010). Conversely, DMN within-network connectivity decreases during aging (Andrews-Hanna et al., 2007; Damoiseaux et al., 2008), as does within-network connectivity of the SN (Onoda et al., 2012) and the FPN (Campbell et al., 2012; Geerligs et al., 2015a). Functional reorganization also occurs at the level of interactions between networks, with cognitive networks becoming more functionally segregated during development (Gu et al., 2015). In older adults, between-network functional connectivity is increased relative to younger adults (Chan et al., 2014), resulting in reduced network segregation (Geerligs et al., 2015a; Song et al., 2014). Overall, within- and between-network resting-state connectivity, and more broadly network segregation, are altered in development and aging.

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Beyond examining resting-state functional connectivity, i.e. in the absence of external stimulation, intrinsic networks are also connected during task performance (Smith et al., 2009). The analysis of background connectivity, by regressing out the effects of task stimuli, allows for examination of functional connectivity while the participant is performing a task, without being inherently tied to regional co-activation to stimuli. Some work comparing younger and older adults using this technique suggests differential age group patterns between resting-state and background connectivity. Geerligs et al. (2015b) found that general trend of decreasing within-network connectivity in higher cognitive networks with age was especially pronounced during a movie task, while Grady et al. (2016) found differences between younger and older adults in DMN within-network resting-state connectivity but not in background connectivity. The age group differences identified in resting-state connectivity may therefore be state-dependent, and only provide a partial view of age-related differences in network connectivity. Characterizing age group differences in background connectivity can provide complementary insight into network functional reorganization across the lifespan and its association with cognition.

Our objective is to characterize age-related patterns of within- and between-network connectivity strength in the default mode, salience, and frontoparietal networks in the context of a visual memory-encoding task, across age groups ranging from childhood to late-life adulthood. Based on previous work examining lifespan age group differences in resting-state connectivity (e.g. Geerligs et al., 2015a), we hypothesize there will be an effect of age on within-network connectivity strength in all three networks, with older adults showing reduced connectivity in all three networks relative to young adults, and children showing reduced DMN connectivity relative to young adults. We further hypothesize that there will be an effect of age on between-network connectivity strength, with older adults and children showing increased between-network connectivity relative to young adults. Finally, given the importance of the DMN to episodic memory encoding (Daselaar et al., 2004; Lustig et al., 2003), we hypothesize that within-DMN background connectivity will be associated with memory performance during a post-encoding recognition task.

## 2. Methods

### 2.1. Participants

We recruited 162 healthy participants from the Metro Detroit community, from a younger sample with age range 8–25 years (n = 101, age 15.13 ± 4.97 years (mean ± standard deviation), 51 females) and an older sample with age range 45–85 years (n = 61; age 67.89 ± 8.38 years; 53 females). Data from a subset of the younger sample have previously been included in Tang et al. (2018), while data from a subset of the older sample have previously been included in Hayes et al. (2017). Detailed methods for data collection in each sample have been described in those articles; summaries of shared and distinct procedures for each group are provided below. All participants were right-handed (as assessed using the Edinburgh Handedness Inventory (Oldfield, 1971)), with no history of psychiatric or neurological disorders, and were free of MRI contraindications. Participants in the older sample had scores ≥ 25 on the Mini-Mental State Examination (Folstein et al., 1975), which is considered within the cognitively normal range (Tombaugh and McIntyre, 1992). Furthermore, all older participants performed in the cognitively normal range as determined by either clinical assessment or performance on Wechsler Memory Scale IV indices of no less than 1.5 standard deviations below the normative mean (Drozdick et al., 2018). Older participants were additionally screened for current use of psychotropic medications, uncontrolled medical conditions, brain injury and radiation or chemotherapy for cancer treatment, which served as additional exclusion criteria. All participants ages 18 and older provided informed consent, while for participants younger than 18 parental consent was obtained and participants provided written or oral assent. Studies were approved by the Wayne State University IRB.

Data for two participants in the older sample were excluded as incomplete due to interrupted data collection. We excluded an additional 44 participants for neuroimaging data quality concerns such as excessive motion (see Table 1). Following these exclusions, a total of 116 datasets were included (see Table 2 for demographics).

To examine the effect of age we binned participants into five age groups in our analyses. Three age groups were defined in the younger sample: children (8–12 years), adolescents (13−17), and young adults (18−25); two age groups were defined in the older sample: mid-life adult (45−64), and late-life adult (65−85). Participant demographics across groups are presented in Table 2. Gender distribution significantly differed across age groups, $\chi^2(4) = 9.97$, $p = 0.041$, as the late-life adult sample had a larger proportion of female participants than the children. We assessed participant IQ in the younger sample using the Kaufman Brief Intelligence Test version 2 (Kaufman and Kaufman, 2014; scores were not available for one child and one adolescent) and in the older sample using the Wechsler Abbreviated Scale of Intelligence II (Wechsler, 2011). Group analysis showed that IQ significantly differed across age groups, $F(4109) = 5.03$, $p = 0.001$, as the late-life adults had lower IQ scores than the children and young adults. Mid-life adults also had lower IQ scores than the young adults. Gender was therefore included as a covariate in all regression models. IQ was included as a covariate in regression models with memory performance as the dependent variable. Mean framewise displacement and percent of outlier volumes were included as covariates in regression models with background connectivity as the dependent variable.

### 2.2. Subsequent memory task

A detailed description of the paradigm can be found in prior work (Pruitt et al., 2021). Briefly, participants were presented with indoor and outdoor visual scenes from a stimulus set used in prior studies (Chai et al., 2010, 2014; Ofen et al., 2007). They were instructed to memorize the scenes while making an indoor/outdoor judgment for each scene for preforming a subsequent recognition test. Participants then completed a postscan recognition test outside of the scanner, approximately 30 min after encoding, during which they were asked to indicate if each scene presented was “old” or “new” and if they were “sure” or “not sure” of this decision.

### 2.3. Behavioral analysis

Recognition responses were classified based on accuracy with respect to the encoding phase (correctly identifying scenes studied during encoding as old and foils as new) and confidence rating (high or low). Trials in which studied scenes were subsequently recognized with high confidence were labeled high-confidence hit trials (Hit-HC), whereas trials in which scenes were subsequently recognized with low confidence were labeled low-confidence hit trials (Hit-LC). Trials in which studied scenes were later classified as ‘new’ were labeled as miss trials (Miss) regardless of the confidence rating. Incorrect recognition of

**Table 1**
Participant exclusion criteria by age group.

| Exclusion Criteria | Children | Adolescents | Young Adults | Mid-life | Late-life |
|---|---|---|---|---|---|
| Recruited | 38 | 31 | 32 | 25 | 36 |
| Outlier volumes > 20% | 2 | 0 | 0 | 2 | 4 |
| Motion spike > 1 voxel | 17 | 2 | 2 | 3 | 11 |
| Encoding interrupted | 0 | 0 | 0 | 2 | 0 |
| Grey matter atrophy (mask dropout) | 0 | 0 | 0 | 0 | 1 |
| Included | 19 | 29 | 30 | 18 | 20 |

**Table 2**
Participant demographics by age group. Gender distribution and IQ differ across age groups, with late-life adults having a higher proportion of women than children, and lower IQ than children and young adults. Note: Mid-life and late-life adults completed a different IQ test (Wechsler Abbreviated Scale of Intelligence-II) than children, adolescents, and young adults (Kaufman Brief Intelligence Test-II). Age group differences in IQ may therefore reflect, in part, differences between the tests rather than true differences in IQ between age groups.

| Participant characteristics | Children | Adolescents | Young Adults | Mid-life | Late-life | Test-statistic | p |
|---|---|---|---|---|---|---|---|
| Sample Size | 19 | 29 | 30 | 18 | 20 | | |
| Age | 9.84 ± 1.46 | 15.21 ± 1.32 | 21.10 ± 2.14 | 59.89 ± 5.13 | 72.5 ± 5.44 | | |
| Gender (F/M) | 9/10 | 16/13 | 16/14 | 12/6 | 18/2 | 9.970† | 0.041 |
| IQ | 109.14 ± 13.92 | 105.18 ± 14.21 | 110.63 ± 12.04 | 98.78 ± 12.43 | 97.05 ± 11.71 | 5.027†† | 0.001 |
| % outlier volumes | 5.33 ± 3.88 | 4.28 ± 2.92 | 3.61 ± 2.19 | 8.47 ± 6.05 | 8.52 ± 5.47 | 7.370†† | < 0.001 |
| Mean framewise displacement (mm) | 0.40 ± 0.27 | 0.19 ± 0.12 | 0.17 ± 0.10 | 0.24 ± 0.16 | 0.30 ± 0.20 | 9.364†† | < 0.001 |
| † chi-squared | | | | | | | |
| †† F | | | | | | | |

foil items as old with high confidence was labeled 'high-confidence false alarm'. The proportion of high-confidence hit trials (out of the total number encoding trials) and the proportion of high confidence false alarm trials (out of the total number of foils) were used in calculation of recognition accuracy. Thus, recognition accuracy (*pR-HC*) was calculated by subtracting the proportion of high-confidence false alarms from the proportion of high-confidence hits (i.e., Hit-HC - FA-HC) as has been done in prior studies using this paradigm (Chai et al., 2014, 2010; Ofen et al., 2007). Low-confidence responses were not included in the calculation of recognition accuracy as such responses are less likely to indicate reliable discriminability between remembered items and foils (Park et al., 2013).

### 2.4. MRI data acquisition

Participants completed their scan session at the Wayne State University MR Research Facility at Harper University Hospital (Detroit, MI), on a 3-T Siemens Magnetom Verio scanner using a 32-channel Head Matrix coil. T1-weighted whole-brain anatomy images were acquired using a magnetization-prepared rapid gradient-echo sequence. Younger sample (ages 8–25): 192 sagittal slices, repetition time (TR) = 2200 ms, echo time (TE) = 4.26 ms, flip angle (FA) = 9°, field of view (FOV) = 256 mm, 192 × 256 voxels, and voxel size = 1 mm × 0.5 mm × 1 mm. Older sample (ages 45–85): 176 slices, TR = 1680 ms, TE = 3.51 ms, FA = 9°, FOV = 256 mm, voxel size = 0.7 mm × 0.7 mm × 1.3 mm).

Functional images were acquired using a T2 * -weighted gradient-echo sequence (Younger sample: 30 slices parallel to the AC–PC plane, TR = 2000 ms, TE = 30 ms, FA = 90°, voxel size = 3.1 mm × 3.1 mm × 4 mm; older sample: 37 slices parallel to the AC-PC plane, TR = 2200 ms, TE = 30 ms, FA = 80°, FOV = 220 mm, voxel size = 2.8 mm × 2.8 mm × 2.8 mm). In the younger sample, the encoding task was completed in three consecutive functional runs of 118 volumes each. In the older sample, the task was completed in one functional run of 276 volumes.

### 2.5. Imaging analysis

*Preprocessing*: We used FSL_motion_outliers (FSLv5.0.8, FMRIB's Software Library, https://fsl.fmrib.ox.ac.uk/fsl/; Jenkinson et al., 2012) to determine the maximum volume-to-volume framewise displacement for each run. Thirty-five participants with a maximum framewise displacement greater than the voxel width (3.1 mm in younger sample, 2.75 mm in older sample) were excluded from analysis to limit contamination of group results by motion spike-induced signal artifacts.

Functional imaging data were then processed with the SPM12 package (v6906; Wellcome Department of Imaging Neuroscience, London, UK; https://www.fil.ion.ucl.ac.uk/spm/software/spm12/) running on MATLAB (R2016b). Images were motion-corrected, normalized to the Montreal Neurological Institute (MNI) template, and smoothed with an 8 mm full-width half-maximum Gaussian kernel. Additionally, we screened functional images using Artifact Detection Tools (ART) (http://www.nitrc.org/projects/artifact_detect/) to identify outlier volumes in pre-processed data. Specifically, an outlier volume was identified if (1) the global mean intensity of the volume was more than 3 SD from the mean volume intensity of the run, or (2) volume-to-volume difference of a composite motion parameter exceeded 0.5 mm. Eight participants for whom > 20 % of their volumes were identified as outliers were excluded from analysis. Outlier volumes were later "censored" in individual-level models using spike regression as part of our denoising approach (Satterthwaite et al., 2013), to mitigate the impact of in-scanner head motion spikes on subsequent analyses.

*Regions of interest (ROIs):* Nodes of the three networks were defined using the network atlas in the CONN toolbox (www.nitrc.org/projects/conn, RRID:SCR_009550; Whitfield-Gabrieli and Nieto-Castanon, 2012). These ROIs were derived from an ICA decomposition of the Human Connectome Project (n = 497 dataset). We included all regions of interest that were available for each network. The default mode network included four regions of interest: medial PFC (mPFC), posterior cingulate cortex (PCC), and left and right angular gyrus (lAG, rAG). The salience network included seven regions of interest: anterior cingulate cortex (ACC), left and right anterior insula (laINS, raINS), left and right supramarginal gyrus (lSMG, rSMG), and left and right inferior frontal cortex (lIFC, rIFC). The frontoparietal network included four regions of interest: left and right dorsolateral prefrontal cortex (lPFC, rPFC) and left and right posterior parietal cortex (lPar, rPar).

*Individual-level models*: Network connectivity strength values were calculated using CONN toolbox. For participants in the younger sample, who completed three task runs, the two runs with the lowest average framewise displacement were included in the individual-level models (as done in Pruitt et al., 2021). We made this choice, rather than using the first two runs, to reduce the group differences in motion. This approach brings the average framewise displacement of the children (the highest motion age group) in line with the other age groups.

For each participant, average timeseries were extracted across all voxels within each ROI. Effects of nuisance covariates were regressed out of the timeseries ("denoising"): these included average BOLD signal extracted from subject-level white matter mask, average BOLD signal extracted from subject-level cerebrospinal fluid mask, 6 motion parameters (3 translation and 3 rotation), outliers (1 per outlier, as identified by ART), and a regressor modeling the onset times of task stimuli. Each encoding event was modeled as a block with the duration of the visual stimulus (3 or 3.4 s) and convolved with a canonical model of the hemodynamic response function. This task regressor was included to remove specific task effects and account for correlation between ROI timeseries that may arise from co-activation to the stimuli. Following removal of the task effects, correlation among the residual timeseries are thought to reflect background functional connectivity; that is, connectivity in response to the general demands of the task rather than in response to the stimuli themselves (Al-Aidroos et al., 2012; Norman-Haignere et al., 2012). A high-pass filter was applied to remove frequencies below 0.008 Hz.

Pairwise correlations were Fisher-transformed to Z-values. Within-network connectivity strength was calculated as the average pairwise

connectivity among nodes within a network. For example, a participant's within-DMN value would be the average of the pairwise mPFC-PCC, mPFC-lAG, mPFC- rAG, PCC-lAG, PCC-rAG, and lAG-rAG connectivity. between-network connectivity strength was calculated as the average pairwise connectivity between all nodes of the respective networks.

*Group analyses:* Group analyses were computed using SPSS (v25, IBM). We calculated effects of age group on network connectivity strength using univariate general linear models with gender, mean framewise displacement, and percent of outlier volumes as covariates. Given that participants had different numbers of outlier volumes censored in their individual-level models, percent of outlier volumes was included in group-level models to account for the differential loss of temporal degrees of freedom in each participant's individual-level model. We also investigated the overall predictive ability of the network connectivity strength values for recognition performance using separate univariate general linear models that also included gender, age group and IQ.

## 3. Results

In meeting our study objective, we characterized age-related patterns of within- and between-network background connectivity during a visual memory-encoding task, for five age groups across the lifespan. Post hoc pairwise comparisons were corrected for multiple comparisons using the Bonferroni approach.

### 3.1. Within-network background connectivity

#### 3.1.1. Default mode network

We did not find a significant effect of age group on within-network DMN connectivity strength, $F(4107) = 1.630$, $p = 0.172$, partial $\eta^2_P = 0.057$ (Fig. 1a), controlling for gender, mean framewise displacement, and percent of outlier volumes.

#### 3.1.2. Salience network

We found a significant effect of age group on within-network SN connectivity strength, $F(4107) = 13.792$, $p < 0.001$, partial $\eta^2_P = 0.340$ (Fig. 1b), controlling for gender, mean framewise displacement, and percent of outlier volumes. Post hoc pairwise comparisons of estimated marginal means revealed mid-life and late-life adults demonstrated attenuated within-salience network connectivity relative to children, adolescents, and young adults.

#### 3.1.3. Frontoparietal network

We found a significant effect of age group on within-network FPN connectivity strength, $F(4107) = 4.358$, $p = 0.003$, partial $\eta^2_P = 0.140$ (Fig. 1c), controlling for gender, mean framewise displacement, and percent of outlier volumes. Post hoc pairwise comparisons of estimated marginal means revealed late-life adults demonstrated attenuated within-frontoparietal network connectivity relative to children and young adults.

### 3.2. Between-network background connectivity

*DMN-SN:* We found a significant effect of age group on DMN-SN between-network connectivity strength, $F(4107) = 20.604$, $p < 0.001$, $\eta^2_P = 0.435$ (Fig. 2a), controlling for gender, mean framewise displacement, and percent of outlier volumes. Post hoc pairwise comparisons of estimated marginal means revealed mid-life and late-life adults demonstrated more positively correlated DMN-SN between-network connectivity relative to the children, adolescents and young adults.

*FPN-SN:* We found a significant effect of age group on FPN-SN between-network connectivity strength, $F(4107) = 3.354$, $p = 0.013$, $\eta^2_P = 0.111$ (Fig. 2b), controlling for gender, mean framewise displacement, and percent of outlier volumes. Post hoc pairwise comparisons of estimated marginal means revealed mid-life adults demonstrated more positively correlated FPN-SN between-network connectivity relative to the children and young adults.

*DMN-FPN:* We found a significant effect of age group on DMN-FPN between-network connectivity strength, $F(4107) = 8.270$, $p < 0.001$, $\eta^2_P = 0.236$ (Fig. 2c), controlling for gender, mean framewise displacement, and percent of outlier volumes. Post hoc pairwise comparisons of estimated marginal means revealed mid-life and late-life adults demonstrated more positively correlated DMN-FPN between-network connectivity relative to the adolescents and young adults. Furthermore, mid-life adults demonstrated more positively correlated DMN-FPN between-network connectivity relative to children.

### 3.3. Exploratory approaches to examining effect of age on network background connectivity

We further investigated the question of age-effect in background connectivity using two exploratory approaches. First, we tested a two-group comparison, comparing background network connectivity in the younger sample (ages 8–25) and older sample (ages 45–85), rather than using five age-groups. Second, we ran separate within-group analyses for the younger and older samples which used age as a continuous variable. The results of these analyses are in line with the findings using five age-groups, and can be found in Supplementary Materials.

### 3.4. Network background connectivity associations with recognition accuracy

None of the six connectivity measures associated with recognition accuracy after controlling for age group, gender, and IQ (all $p$-values $> 0.25$, $\eta^2_P < 0.012$).

## 4. Discussion

In a sample which included participants ranging from children to older adults, we examined background functional connectivity within and between three large-scale cognitive brain networks – the default mode network (DMN), salience network (SN) and frontoparietal network (FPN) – in the context of a visual encoding task. In our sample there was a significant effect of age-group on within-network connectivity values in the SN and FPN, but not the DMN. In addition, there was a significant effect of age-group on between-network connectivity values for DMN-SN and DMN-FPN. So, DMN connectivity with other cognitive brain networks is significantly greater in the older compared to the younger groups, in line with previous observations of reduced network segregation in aging (Chan et al., 2014; Geerligs et al., 2015a; Song et al., 2014), even though within-DMN connectivity during memory encoding may be maintained during older adulthood. We did not find any association between network connectivity measures and memory performance. In the context of previous work, the pattern of within-DMN connectivity across age groups during memory encoding highlights that background connectivity represents a complementary measure to resting-state connectivity, as each shows different age-related patterns and provides a glimpse of network connectivity during a particular state.

The age-related differences in frontoparietal and salience within-network background connectivity are in line with lifespan patterns of connectivity in these networks more generally, including during resting-state (Geerligs et al., 2015a; Onoda et al., 2012), with late-life adults showing lower connectivity than younger groups. Contrary to our hypothesis, we did not observe age-related differences in default mode within-network background connectivity. This finding stands in contrast to the resting-state literature, which robustly demonstrates relatively reduced within-DMN connectivity with greater age (Andrews-Hanna et al., 2007; Betzel et al., 2014; Tomasi and Volkow, 2012). However, our finding is in line with a previous investigation of task background

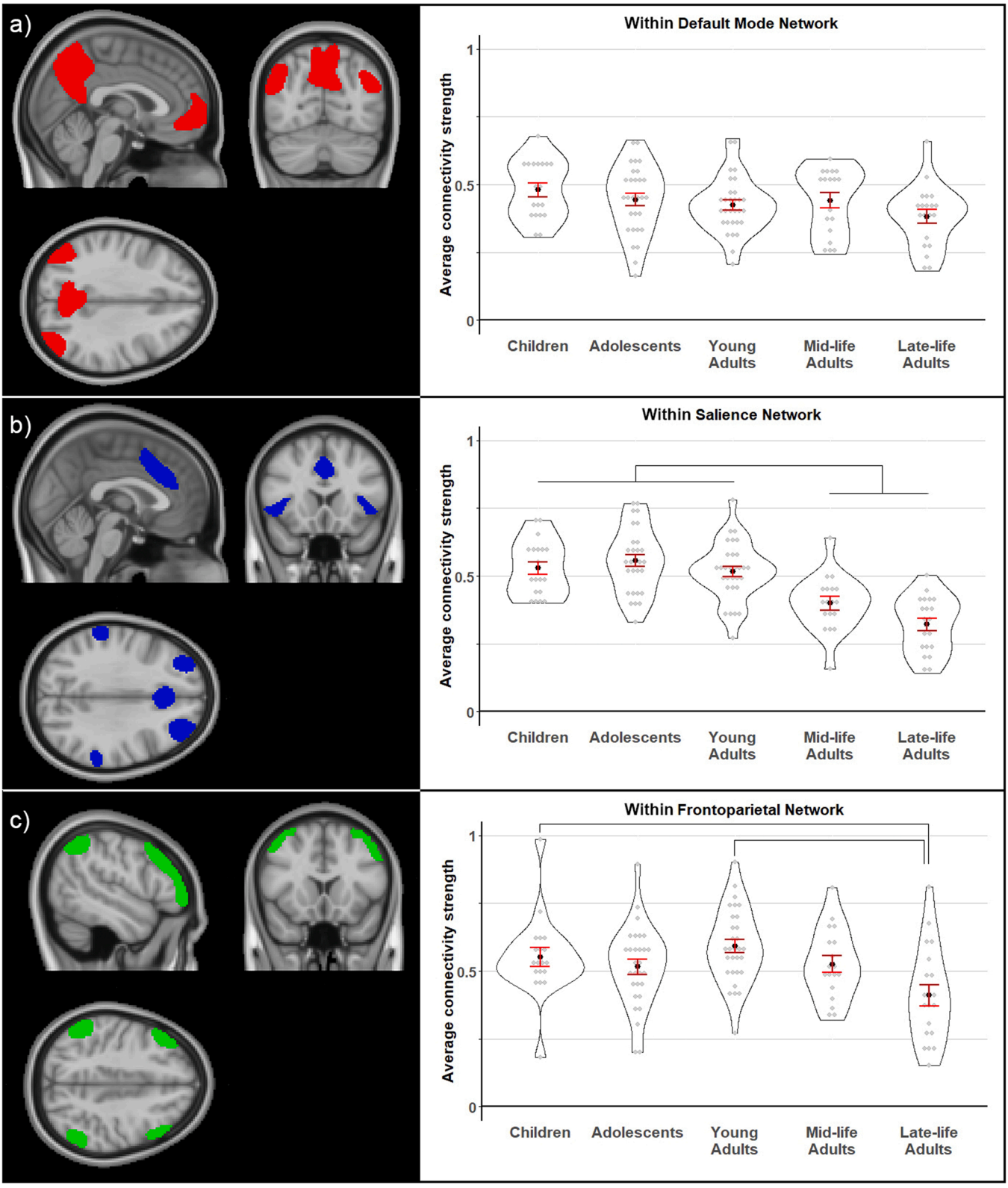


**Fig. 1.** Within-network Background Connectivity by Age Group. a) Default Mode Network. Left: Regions of interest for the DMN are displayed in red. Right: There was not a significant effect of age group on within-network DMN connectivity. b) Salience Network. Left: Regions of interest for the SN are displayed in blue. Right: There was a significant effect of age group on within-SN connectivity. Within-SN connectivity was significantly attenuated in mid-life and late-life adults compared to children, adolescents and young adults. c) Frontoparietal Network. Left: Regions of interest for the FPN are displayed in green. Right: There was a significant effect of age group on within-FPN connectivity. Within-FPN connectivity was significantly attenuated in late-life adults compared to children and young adults.

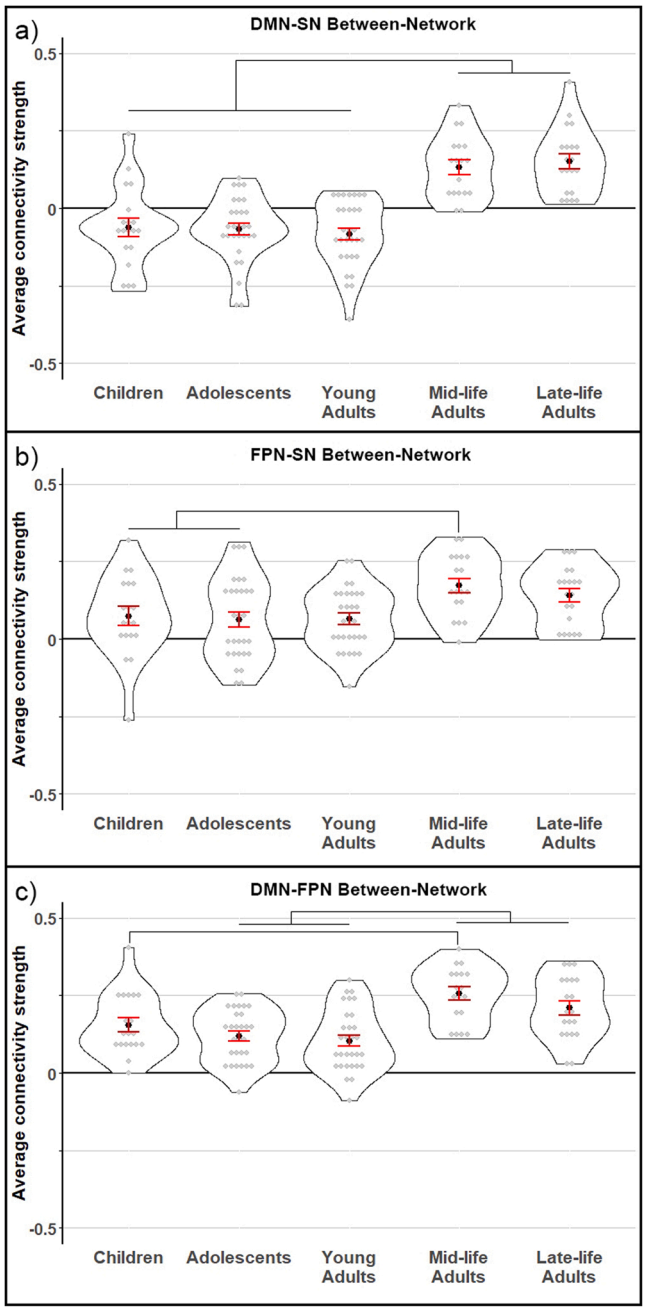


**Fig. 2.** Between-network Background Connectivity by Age Group. a) Default Mode and Salience Networks. There was a significant effect of age group on DMN-SN between-network connectivity. Mid-life and late-life adults showed more positive connectivity relative to children, adolescents, and young adults. b) Frontoparietal and Salience Networks: There was a significant effect of age group on FPN-SN between-network connectivity. Mid-life adults showed more positive connectivity relative to children and young adults. c) Default Mode and Frontoparietal Networks. There was a significant effect of age group on DMN-FPN between-network connectivity. Mid-life and late-life adults showed more positive connectivity relative to adolescents and young adults. Furthermore, mid-life adults showed more positive connectivity relative to children.

connectivity in aging (Grady et al., 2016), which likewise did not find a difference in within-DMN task background connectivity between a group of young adults and older adults, despite seeing such a difference for resting-state connectivity in the same sample. The authors suggest this may be related to previous observations of lower reductions in DMN activity in older compared to younger adults during active task performance. Another consideration is that the memory encoding task used in the current study uniquely engages regions in the DMN, which demonstrate a negative subsequent memory effect (see Pruitt et al., 2021). In contrast, regions of the FPN and SN show little overlap with positive or negative subsequent memory effects. Engagement of these regions by general task demands may prevent the lower DMN connectivity seen during resting-state in older adults. As SN and FPN are not similarly engaged by memory encoding task demands, this may be why these networks do show age-related differences in background connectivity. Our observation of greater between-network connectivity in older adults, specifically DMN-SN and DMN-FPN, is in line with age-related patterns of resting-state connectivity. Taken with the within-network findings, the higher between-network background connectivity in older adults suggests less "distinct" SN and FPN, reflective of an overall pattern of de-differentiation (Dennis and Cabeza, 2011; Park et al., 2004) in these networks.

We did not observe hypothesized group differences in background connectivity between children and young adults. These differences were expected based on previous evidence of increasing within-network (Fair et al., 2008) and decreasing between-network (Gu et al., 2015) resting-state functional connectivity across development, which together signify a more general trend of increased network segregation. In considering why we did not observe these developmental effects, one possibility is that there is a developmental effect in background connectivity that we were not able to detect with our approach. With this in mind, we tried an alternative approach: exploratory analyses conducted within the younger (age 8–25) and older (45–85) samples separately used age as a continuous variable rather than age groups. These analyses also did not find any statistically-significant associations of age and background connectivity across development (see Supplementary Materials). Whether age is modeled by group or continuously, it may be that any developmental effect in background connectivity is sufficiently subtle that we are not able to detect it with our sample size. Another possibility is that there truly is not a meaningful developmental effect of background connectivity within and between these networks. It is unclear why this may be the case but could potentially reflect that network organization which facilitates the meeting of task demands matures earlier in life than network organization measured using resting-state fMRI. Replication and further exploration will be valuable in better understanding this finding.

Recognition performance was not associated with within-DMN background connectivity during memory encoding, nor with any other measure of within- or between-network background connectivity. A plausible explanation for the lack of such association is that task-evoked responses that contain meaningful information related to subsequent memory outcomes are lost in task background connectivity, in which those task-evoked responses are regressed out. Although measures of task-evoked response are often associated with task performance, including in this sample and task (Pruitt et al., 2021), previous investigations into the association between task background connectivity and task performance provide mixed evidence for such a link. Grady et al. (2016) found that frontoparietal control (including regions from the FPN and SN) task background connectivity to other networks was not a predictor of task performance; performance association with DMN connectivity was not examined. In Duncan et al. (2014), task background functional connectivity between the hippocampal subfield CA1 and the ventral tegmental area was associated with delayed, but not immediate, memory retrieval performance. Our paradigm tested effects at the early stages of memory formation thus providing converging evidence that measures of background connectivity are not associated with early mnemonic processes, but may be associated with mnemonic processes that unfold over longer temporal scales.

There are limitations to the current study, which merit consideration when evaluating the presented findings. First, this work uses a cross-sectional approach to examine age-related patterns. A major goal of lifespan research is to evaluate how individuals change across the stages of life, and this goal requires a longitudinal approach. The current work,

therefore, is limited to characterizing differences between groups (higher, lower, or no difference in connectivity) rather than changes across time (increase, decrease, or maintenance of connectivity). Second, while our sample allows us to characterize age-related patterns of connectivity across several age groups, it does not include adults between the ages of 25–45. This limits our ability to determine at what point in adulthood we begin to see, for example, lower within-SN connectivity. Inclusion of this age group in future research will allow for greater specificity regarding when these observed differences begin to emerge. Third, resting-state fMRI data is available for only a small proportion of our sample, meaning that we are not able to directly compare background task connectivity and resting-state connectivity in our participants, which would provide further insight into changes in network connectivity during task that are not directly related to task stimuli, as well as how task/rest network modulation differs across the lifespan. This too is a valuable objective for future research. Fourth, we used different tests to measure IQ in our younger sample (Kaufman Brief Intelligence Scale-II) and older sample (Wechsler Abbreviated Scale of Intelligence-II). The observed age group differences in IQ may therefore reflect, in part, differences between the two tests rather than true differences in IQ. IQ was also included as a covariate in regression models with memory performance as the dependent variable, and so this potential bias in scores between participants must also be considered when interpreting these results. Despite these concerns, we felt the analyses examining associations with cognitive performance were stronger with a potentially-biased measure of IQ, than without controlling for these individual differences at all. Fifth, our regions of interest were selected based on a specific brain network parcellation, the network atlas in CONN toolbox, which is derived from an ICA analysis of the Human Connectome Project data. Intrinsic networks can be spatially defined in a variety of ways and different definitions may include or exclude particular regions. In interpreting any results which use a particular atlas or parcellation, it is important to consider that findings may differ if another parcellation were used. Sixth, while study procedures were largely harmonized between the younger and older samples, there are some differences that merit mention in both fMRI acquisition (repetition time; acquired voxel size) and task procedures (stimulus duration, wording of instructions). Despite these minor methodological differences, we observed expected age-effect patterns in task performance and neural task effects in expected regions (Pruitt et al., 2021). However, confidence in our current findings could be increased by replication in a lifespan sample with identical study protocols.

In conclusion, this work utilizes a unique lifespan sample to reveal age-related patterns of within- and between-DMN background connectivity during memory encoding. We demonstrate significant effects of age group within salience network and frontoparietal network connectivity, as well as connectivity between the three networks. In the context of previous work, our results suggest that background connectivity may be less predictive of task performance than task-evoked response. However, the similarity of within-DMN background connectivity across age groups, in contrast to previous resting-state findings, further emphasizes that measures of task connectivity provide additional insight into cognitive aging beyond that provided by resting-state. Furthermore, the lack of observed developmental effects in background connectivity, in contrast to previous resting-state findings of age-related network segregation, merits further investigation.

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*Declarations of interest*

None.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neures.2022.09.005.

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