

Exploring the late maturation of an intrinsic episodic memory network: A resting-state fMRI study

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ABSTRACT

Previous research suggests that episodic memory relies on functional neural networks, which are present even in the absence of an explicit task. The regions that integrate these networks and the developmental changes in intrinsic functional connectivity remain elusive. In the present study, we outlined an intrinsic episodic memory network (iEMN) based on a systematic selection of functional connectivity studies, and inspected network differences in resting-state fMRI between adolescents (13–17 years old) and adults (23–27 years old) from the publicly available NKI-Rockland Sample. Through a review of brain regions commonly associated with episodic memory networks, we identified a potential iEMN composed by 14 bilateral ROIs, distributed across temporal, frontal and parietal lobes. Within this network, we found an increase in resting-state connectivity from adolescents to adults between the right temporal pole and two regions in the right lateral prefrontal cortex. We argue that the coordination of these brain regions, connecting areas of semantic processing and areas of controlled retrieval, arises as an important feature towards the full maturation of the episodic memory system. The findings add to evidence suggesting that adolescence is a key period in memory development and highlights the role of intrinsic functional connectivity in such development.

1. Introduction

Episodic memory is a central ability that allows us to encode and retrieve information about specific past events embedded in their contextual details (e.g., the place, time, and the people or objects present; Tulving, 1985). It plays a critical role in autobiographical memory and the construction of the self (Conway and Rubin, 1993). Developmental work has shown that episodic memory matures until early adulthood, with the specific trajectories depending on the mnemonic processes (e.g., recollection vs. familiarity) or type of retrieval involved (e.g., recall or recognition; Brainerd et al., 2009). There is large agreement that familiarity (i.e., feeling that an event has happened before without the conscious retrieval of specific details) stabilizes in early childhood. In contrast, recollection (i.e., the ability to vividly and consciously retrieve an event along with its contextual details), improves throughout adolescence (e.g., Ghetti and Angelini, 2008; Ofen et al., 2007). The late development of recollection until adulthood has been mostly associated with the protracted development of cognitive control abilities, and the late maturation of the prefrontal cortex (PFC). For example, Andrade and Raposo (2021) showed that, relative to young

adults, adolescents' lower recognition memory performance was restricted to recollection of items semantically (rather than perceptually) encoded, and that this effect was predicted by individual differences in cognitive control abilities. Moreover, Ofen and colleagues (2007) found that PFC activation during memory formation increased with age (from 8 to 24 years old) and correlated with subsequent retrieval of specific details of the encoded scenes. The results suggest that age-dependent maturation of the PFC is critical for the formation and subsequent retrieval of detailed memories.

In addition to isolated brain regions, the cognitive neuroscience literature has been progressively evolving towards the study of global brain networks in order to understand cognitive functioning. Several studies have shown the importance of functional interactions between PFC and medial temporal lobe (MTL) for episodic memory functioning (Palacio and Cardenas, 2019; Simons and Spiers, 2003). Nonetheless, there is still no consensus regarding which regions reveal functional interactions associated with successful memory processing. Moreover, few studies have investigated the development of an episodic memory network during childhood and adolescence, by implementing appropriate functional network analyses (e.g., Ofen et al., 2012; Tang et al.,

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2018, 2020).

In the present study we examined age-related differences between adolescents and adults in a potential episodic memory network. This network was investigated using resting-state functional MRI, considering that there is growing evidence for intrinsic functional networks (i.e., without the performance of a task) that show high overlap with the respective cognitive functions and their development (Cole et al., 2014; Seeley et al., 2007; Stevens, 2016).

1.1. Episodic memory networks: task-based evidence

Functional connectivity methods have been widely used during performance of sensory, motor or cognitive tasks, such as language, emotion, reward processing or social cognition (i.e., *task-based* fMRI; Cole et al., 2014; Stevens, 2016). In the episodic memory field, extensive work has been devoted to investigate the set of regions associated with our ability to form, consolidate, and retrieve details about past events. The specific regions and networks reported vary depending on the memory stage (encoding vs. retrieval), the mnemonic processes involved (recollection vs. familiarity) and the tasks used (e.g., item recognition, associative memory, recall). Despite this variability, research has consistently described higher functional connectivity for remembered than forgotten events (Geib et al., 2017a; King et al., 2015; Schedlbauer et al., 2014).

In a systematic review of 53 studies with adults, Palacio and Cardenas (2019) have highlighted segregated memory networks for encoding and retrieval. In the PFC, the inferior frontal gyrus was more relevant during retrieval while the medial PFC played a role at encoding. The hippocampus and the dorsolateral PFC were instead part of both encoding and retrieval networks. Other studies have probed how depth of encoding modulates connectivity patterns, with deep or semantically elaborated encoding favoring PFC and inferior parietal cortex connectivity (Amlien et al., 2019; Schott et al., 2013). As for retrieval, the ability to remember specific details of an event (i.e., context vs. item memory) was associated with increased connectivity strength between medial temporal lobe (MTL) regions, inferior frontal gyrus and angular gyrus (Palacio and Cardenas, 2019). To inspect controlled retrieval, Paz-Alonso et al. (2013a) inspected a mnemonic control network whereas King et al. (2015) investigated a core recollection network. Both studies found increased connectivity associated with successful controlled retrieval between the hippocampus, middle temporal gyrus, posterior cingulate cortex and dorsolateral PFC. Finally, Ranganath and Ritchey (2012) have defined a memory retrieval network composed by two sub-systems, both linked on the hippocampus. The anterior temporal system, formed by subcortical regions, temporopolar cortex and lateral orbitofrontal cortex, was associated with familiarity judgments and semantic memory. The posterior medial system, composed mainly by parahippocampal cortex and parietal regions, was linked to recollection processes. This division, however, has been recently questioned, since Cooper and Ritchey (2019) found an increment in connectivity and integration between these two sub-systems, associated with higher precision and quantity of the episodic details retrieved.

Despite the substantial effort to identify how different regions cooperate during memory processing, the functional interactions between regions are still not well characterized. Multiple episodic memory networks have been identified and tested, but without a consensus on which regions compose a broad and consistent network.

1.2. Episodic memory networks: resting-state evidence

Functional connectivity has been increasingly investigated through *resting-state* fMRI (i.e., in the absence of an overt task or the presentation of external stimuli) which allows the identification of synchronized temporal patterns of spontaneous neuronal activity (typically below 0.1 Hz) between spatially distinct brain regions (Biswal et al., 1995; Cole et al., 2014; Damoiseaux et al., 2006). Several resting-state functional

networks have been identified and shown to be consistently replicable so far (Power et al., 2011; Uddin et al., 2019). Some of these have matched, with high correspondence and consistency, both task-based networks and univariate activation patterns during task performance (Cole et al., 2014; Ritchey et al., 2014; Smith et al., 2009). Strong correlation between resting-state networks and behavioral performance has also been observed (Lewis et al., 2009; Touroutoglou et al., 2015; van Duijvenvoorde et al., 2016), lending support to the view that the brain integrates a functional network architecture based on *intrinsic connectivity networks* (ICNs; Cole et al., 2014; Seeley et al., 2007; Seitzman et al., 2019; Stevens, 2016), which are present both during and in the absence of task demands.

Studies specifically exploring *intrinsic episodic memory networks* (iEMNs) have revealed that some resting-state networks show similar activation patterns to encoding (Ritchey et al., 2014) and retrieval processes (Andrews-Hanna et al., 2014; Vincent et al., 2006), corroborating that resting-state profiles are useful and informative when studying memory networks. Ritchey et al. (2014) found that regions that coupled together during resting-state were also part of the same network during an associative memory encoding task. Moreover, a positive correlation was observed between the full resting-state connectivity matrix and the matrix of the task activation analysis. Other studies have established links between resting-state and memory retrieval networks. Vincent et al. (2006) reported a resting-state network derived from seeds in the hippocampal formation which involved several regions in the parietal cortex. These regions overlapped with those showing greater activation in recognition memory tasks, particularly during successful recollection. Similarly, Andrews-Hanna et al. (2014) found positive functional correlations between regions activated during performance of a memory task and a medial temporal network identified during resting-state. Finally, Barredo et al. (2015) reported a reliable resting-state network along the ventral frontotemporal pathway, supporting interactions between ventrolateral PFC and MTL, similar to the task-based functional connectivity network of controlled retrieval. Other studies have described these iEMNs as posterior subnetworks of the default mode network (DMN; Ritchey and Cooper, 2020) or have highlighted interactions between the DMN and other intrinsic networks, such as the lateral frontoparietal control network (Fornito et al., 2012; Westphal et al., 2017; for a review see Palacio and Cardenas, 2019). These authors have argued that the potential involvement of the DMN in episodic memory advocates in favor of an on-going mnemonic processing during resting-state mode.

1.3. Development of episodic memory networks

From childhood to adulthood, the development of large-scale functional networks is generally characterized by decreasing functional connectivity between closer anatomical regions (short-range or local connections) and increasing functional connectivity between more distant regions (long-range or global connections; Dosenbach et al., 2010; Fair et al., 2007, 2009). Studies with children and adolescents have shown an age-related functional strengthening within areas of the DMN and within other intrinsic functional networks (Sherman et al., 2014; Stevens et al., 2009; Uddin et al., 2011). In their seminal work, Fair et al. (2007) investigated the development of resting-state functional connectivity associated with cognitive control in children (7–9 years old), adolescents (10–15 years old) and adults (20–31 years old). In addition to demonstrating the short/long-range dichotomy in connectivity development, the study reported a continuous strengthening of the frontoparietal control network with age. Thus, ICNs involving long-range connections seem to gain within-network strength along development.

Only a scarce number of studies using task-based fMRI have examined developmental changes in functional connectivity in the episodic memory domain. Testing participants aged 11–19 years old, and using two seeds in the MTL, Menon et al. (2005) found an age-related increase

in functional connectivity, coupling the left entorhinal cortex with the left dorsolateral PFC, during memory encoding. Along the same line, in Tang et al. (2020), a seed in the posterior hippocampus correlated positively with the inferior frontal gyrus with such coupling increasing from 8 to 25 year-olds. Previous work by Tang et al. (2018) have reported that functional connectivity between lateral PFC and both MTL and inferior parietal lobe increased with age during successful memory formation, while medial PFC and MTL connectivity decreased along age. Focusing on retrieval networks, Ofen et al. (2012) have revealed increases in connectivity between MTL and PFC associated with successful remembering from 8 to 21 years old. In another study with three age groups (8–9, 11–12 and 18–30 years old), Paz-Alonso et al. (2013b) found age-related increased connectivity associated with successful memory recognition of semantically related words. This result, observed in adults but not in the youngest group, demonstrated functional coupling between the hippocampus and the dorsolateral PFC as well as between the hippocampus and the posterior parietal cortex. Finally, Fynes-Clinton et al. (2019) investigated the development of the “common memory network” (Burianová et al., 2010), which contemplates episodic, autobiographical and semantic retrieval networks. Testing three age groups (10–12, 14–16 and 20–35 years old), the authors observed a wide neural pattern that correlated positively with age, including temporal and prefrontal areas, inferior parietal lobe, cingulate cortex and other subcortical structures. Of note, even though adolescents had similar behavioral performance to adults, their neural activity was analogous to the children’s pattern, which, according to the authors, suggests that maturation of a common memory network may only occur in late adolescence or early adulthood (Fynes-Clinton et al., 2019).

In sum, for episodic memory and other cognitive functions, the literature shows that functional integration and correlation strength between distant brain regions continue to develop until adulthood (Stevens, 2016; Stevens et al., 2009). Adolescence may thus emerge as a key developmental period to an efficient network integration, particularly between MTL and frontoparietal regions (Calabro et al., 2020; Ghetti and Fandakova, 2020).

1.4. Present study

Several behavioral and fMRI studies demonstrate that episodic memory develops throughout adolescence (Andrade and Raposo, 2021; Ghetti and Fandakova, 2020; Ofen et al., 2007; Sprondel et al., 2012). Moreover, as seen above, research supports the existence of iEMN(s), present even in the absence of task demands. The protracted maturation of such networks may underlie the late development of some mnemonic functions, including controlled retrieval and recollection. Yet, there is no consensus on which regions compose an iEMN, and developmental studies are scarce, particularly those focusing on adolescence.

In the present study, we outline an iEMN based on previous functional connectivity studies, and explore developmental differences in this network between adolescents (13–17 years old) and adults (23–27 years old). The age limits of adolescence have been much debated, but the most consensual period for human adolescence is between 13 and 17 years old (Cohen et al., 2016). As such, for congruency with prior work and for replicability purposes, this is the age interval that we have considered in the current study. In light of the developmental literature, we expected age-related connectivity increases between MTL (hippocampus and parahippocampal cortex) and both ventrolateral (Ofen et al., 2012; Tang et al., 2018, 2020) and dorsolateral PFC (Menon et al., 2005; Paz-Alonso et al., 2013b), as well as between inferior parietal lobe and lateral PFC (Fynes-Clinton et al., 2019; Tang et al., 2018). Since previous studies included participants ranging from childhood to adulthood, it is plausible that a comparison restricted to groups closer in age, notably adolescents and adults, will show a developmental trajectory in a subset of these regions only, while other regions may have already achieved full maturation by adolescence.

2. Methods

2.1. Participants

Participants were selected from the publicly available NKI-Rockland Sample (http://fcon_1000.projects.nitrc.org/indi/enhanced/index.html) of the Nathan Kline Institute (NKI; Nooner et al., 2012). This growing dataset comprises four studies, which integrate the International Neuroimaging Data-sharing Initiative (INDI; http://fcon_1000.projects.nitrc.org) and include participants across the lifespan (from 6 to 85 years old). Participant recruitment was performed in the Rockland County (New York, USA), an area with a population that parallels the one in the entire country of the USA in terms of ethnic and economic diversity (for more details, see Nooner et al., 2012). All participants were neurotypical subjects (for more details, see <https://clinicaltrials.gov/ct2/show/NCT03775941>). The studies were approved by the NKI Institutional Review Board, and all participants provided informed consent as well as the legal guardians of the minor participants (Nooner et al., 2012).

From the eight data releases available to date, we selected the neuroimaging raw data (i.e., nifti files) of the 58 adolescents aged 13–17 years old and the 61 adults aged 23–27 years old that integrate the database. Seven adolescents and one adult were excluded due to unavailability of the structural image, the resting-state image, or both. Another adolescent was excluded due to a poor-quality structural image, with part of the structural brain image missing. Thus, the final sample comprised 50 adolescents (24 female, 43 right-handed, $M_{age} = 14.9$ years, $SD_{age} = 1.3$, age range = 13–17 years) and 60 adults (31 female, 53 right-handed, $M_{age} = 24.8$ years, $SD_{age} = 1.5$, age range = 23–27 years).

2.2. Definition of the proposed iEMN

As reviewed above, there is a large variability across studies on the brain regions involved in a potential iEMN. Thus, to investigate the development of such a network, we first outlined its constituting ROIs based on a group of functional connectivity studies. The selection of these studies followed a set of predefined criteria, although it did not intend to be a systematic review. Articles were indexed in PubMed, and included fMRI-based functional connectivity (in resting state or during task performance) and its relation to episodic memory in healthy adolescents (13–17 years old) or young adults (18–35 years old). The protocol for searching the database included the use of various keywords, such as “fMRI”, “functional connectivity”, “resting state”, “episodic memory”, “adolescence”, “adults”. We used Boolean operators to exclude work that included neurodiverse samples (e.g., “autism”), as well as non-healthy populations (e.g., “epilepsy”). The articles were screened and included in the analysis only if they complied with the previous criteria. Articles that encompassed certain biases were excluded. Notably, we excluded studies that: (1) although referring to “networks”, implemented fMRI methods that do not allow analyzing functional connectivity (such as univariate fMRI; McDermott et al., 2017; Richter et al., 2016; Rugg and Vilberg, 2013); (2) restricted the analysis to the computation of functional connectivity between a subset of regions, as opposed to between individual regions and the rest of the brain, as our interest was to explore the whole brain (Menon et al., 2005; Paz-Alonso et al., 2013b; Touroutoglou et al., 2015; van Kesteren et al., 2010); (3) reported large brain modules or clusters instead of pinpointing well-defined ROIs (as is the case of community detection and independent component analyses, or analyses between global networks; Cooper and Ritchey, 2019; Fornito et al., 2012; Kim and Voss, 2019; Ritchey et al., 2014; Sneve et al., 2017; Westphal et al., 2017); (4) review papers, because most of them selected studies in a biased fashion, according to the theory or framework of interest (Gilmore et al., 2015; Ritchey and Cooper, 2020), the only exception being the inclusion of a systematic review that followed a pre-defined and unbiased protocol (i.e., Palacio

and Cardenas, 2019). Then, to delineate a consensual iEMN and with a more parsimonious number of ROIs, we identified the regions that are more commonly part of episodic memory networks by selecting the regions with greatest overlap across studies, i.e., common to six or more networks. This threshold was meant as a tradeoff between choosing too many regions (risking loss of specificity) and too few regions (with the risk of ending up with a poorly characterized network).

2.3. Functional connectivity analysis

We then tested developmental differences within this network during resting-state fMRI, by comparing adolescents and adults from the NKI-Rockland Sample. In order to quantify the changes in such network, ROI-to-ROI connectivity analysis and graph theory approaches have been very effective in defining the functional architecture of not only the adult brain (for a review, see Uddin et al., 2019) but also the developing brain (for reviews, see Grayson and Fair, 2017; Khundrakpam et al., 2016) and, more particularly, the adolescent brain (for a review, see Stevens, 2016). Moreover, this method allows both an a priori selection of the ROIs potentially comprising the iEMN, and an equal treatment of all the brain regions covered (without focusing, for example, on a single seed region).

2.3.1. Image acquisition

Participants were scanned using a 3 T Siemens Magnetom Tim Trio scanner. Resting-state images were acquired with a standard echoplanar imaging (EPI) sequence, with the following parameters: repetition time (TR) = 2500 ms; echo time (TE) = 30 ms; flip angle (FA) = 80°; field of view (FOV) = 216 × 216 mm; voxel size = 3.0 × 3.0 × 3.0 mm; number of slices = 38; interleaved slice acquisition; number of volumes = 120. Acquisition time (TA) was 5 min 5 s, a resting-state scan duration that has proven to produce reliable correlation estimates of network connectivity (Van Dijk et al., 2010) and that was already previously implemented with young developmental samples (that tend to show excessive motion in longer scan sessions; Jolles et al., 2011). Each structural 3D T1-weighted image was acquired with a magnetization-prepared rapid gradient echo (MPRAGE) sequence, with the following parameters: TR = 1900 ms; TE = 2.52 ms; FA = 9°; FOV = 250 × 250 mm; voxel size = 1.0 × 1.0 × 1.0 mm; number of slices = 176; TA = 4 min 18 s.

Participants received instructions to keep their eyes open and fixate on a cross displayed on a screen (Petrican et al., 2017), which is the most common resting-state condition (Palacio and Cardenas, 2019).

2.3.2. Image preprocessing and denoising

Using the Statistical Parametric Mapping software (SPM12; www.fil.ion.ucl.ac.uk), we first inspected all images and manually re-set the origin at the anterior commissure in all structural images. Preprocessing was performed using the CONN functional connectivity toolbox (version 20b; Whitfield-Gabrieli and Nieto-Castanon, 2012), implemented in Matlab (version R2020b; The Mathworks Inc., Massachusetts, USA). The first four volumes were removed to allow for the MR signal to reach equilibrium. We then applied CONN's default preprocessing pipeline, which resorts to SPM12. It comprised realignment of the functional volumes, slice-timing correction, normalization (to MNI-152 template with 2-mm isotropic voxels) and smoothing (with a 6-mm FWHM Gaussian kernel). We also performed segmentation of gray matter, white matter, and cerebrospinal fluid (CSF) in the structural volumes.

In resting-state functional connectivity, head motion has a stronger noising effect on data when compared to conventional BOLD fMRI. Moreover, it has been shown that motion increases local or short-range correlations and decreases long-range correlations, mimicking developmental differences previously found between children and adults (Satterthwaite et al., 2012; Van Dijk et al., 2012). We therefore applied an additional “scrubbing” (or censoring) process within this pipeline, which was performed by the Artifact Detection Tools software (ART;

www.nitrc.org/projects/artifact_detect). This process efficiently identifies to-be-removed outlier frames in the functional volumes associated with high head-motion artifacts. For this procedure, we selected the software's default/intermediate scrubbing settings (97th percentiles in normative sample), identifying time points marked with a framewise displacement greater than 0.9 mm or with a mean global BOLD signal change greater than 5 standard deviation units. No participants were excluded based on either motion or noise. A total of 217 frames (adolescents) and 103 frames (adults) were censored due to excessive motion. This represents an average of 4.34 and 1.72 frames for adolescents and adults, respectively. Twenty-five adolescents (out of 50) and 41 adults (out of 60) had no outlier frames and therefore did not require frame censoring. The preprocessing stage was then followed by a thorough denoising procedure, in order to definitely remove from the BOLD signal time-series both motion and physiological noise artifacts, increasing the validity and sensitivity of the following analyses (Whitfield-Gabrieli and Nieto-Castanon, 2012). Concerning the rigid body motion correction, CONN uses the data coming from both spatial realignment and scrubbing preprocessing stages. Regarding physiological noise correction, CONN implements at this stage the anatomical Component-based noise Correction method (aCompCor; Behzadi et al., 2007), which effectively identifies and estimates noise BOLD signals in white matter and CSF ROIs, mainly associated with cardiac rhythm and respiration. Briefly, the first step of the denoising procedure consisted on a nuisance regression, taking into account the following confounding factors: 12 realignment parameters (three of rotation, three of translation, and their corresponding first-order temporal derivatives); variable scrubbing parameters (ranging from zero to 29, depending on the participant); white matter mask plus CSF mask parameters (five parameters each, derived from a principal component analysis decomposition, as suggested by Behzadi et al., 2007); and two additional rest session-related parameters with low denoising impact (linked to potential initial transient/magnetization effects). All these covariates were linearly regressed out. In the final denoising steps, the residual BOLD time-series were temporal band-pass filtered (0.008 – 0.09 Hz) and linearly detrended (both default options in CONN).

2.3.3. Network node definition

During CONN's setup stage, we spatially parcellated the brain voxels into 116 discrete anatomical cortical and subcortical ROIs, according to the Automated Anatomical Labeling atlas (AAL; with 1-mm isotropic voxels; Tzourio-Mazoyer et al., 2002). This template parcellates both cortical and subcortical regions through the identification of cerebral gyri and sulci boundaries (Geib et al., 2017a).

These AAL ROIs represented the neural network nodes and, for each of these ROIs, we extracted an average time course of the corresponding voxels (the ROI time-series) prior to the smoothing preprocessing stage, to avoid losing spatial specificity. Then, we delineated the potential iEMN by restricting the whole AAL atlas to the brain regions identified as the most common within the episodic memory networks selected. Note that some brain regions correspond to more than one AAL node. Namely: the middle temporal pole was added as part of the middle temporal gyrus; the inferior frontal gyrus included the subregions pars opercularis, pars triangularis and pars orbitalis; the middle frontal gyrus also included its orbital part.

2.3.4. ROI-to-ROI connectivity and graph theory approaches

We looked for age-related connectivity differences using two approaches. Firstly, we performed ROI-to-ROI functional connectivity analyses. Each ROI time-series was correlated with each other, through pairwise bivariate Pearson correlations, resulting in a ROI-to-ROI correlation matrix for each participant, with the correlation coefficients representing the functional connectivity strength between each pair of nodes; Fisher z-transformations were applied to the correlation coefficients, in order to improve data normality and allow the application of the ensuing standard General Linear Models (GLM) analyses; these

analyses were performed in order to acquire population-level estimates and inferences. Using as input the participants' Fisher-transformed correlation matrices, we first tested if there were significant correlations arising within the network, both between age groups (applying the contrast adults > adolescents) and across age groups (i.e., including all participants together). The analyses' significance level was thresholded at $p < .05$, and false positive rate was controlled using false discovery rate (FDR)-corrected p -values (Benjamini and Hochberg, 1995). The

results are displayed in *connectome rings*, a way of representing ROI-to-ROI connectivity matrices in the CONN toolbox.

Secondly, we looked for graph theory metrics that could differ between adolescents and adults. For this purpose, we obtained adjacency matrices for each participant by thresholding the ROI-to-ROI correlation values with CONN's default threshold, i.e., choosing 0.15 as the network-level cost (or as the proportion of surviving correlations). Since there is no consensual thresholding strategy in the literature, we

Table 1
Main characteristics and results of 15 studies investigating episodic memory networks.

Study	Age group (N)	fMRI acquisition	Behavioral task	Connectivity method	Memory network	Brain regions integrating each network
Tang et al. (2020)	8–25 (96)	Task-based at encoding	Subsequent recognition of scenes	Seed-based	Memory formation network (<i>correlated with age</i>)	pHipp (seed) / IFG
Amlien et al. (2019)	18–38 (123)	Task-based at retrieval	Source recognition of objects (semantically encoded)	Graph theory	Semantic elaboration encoding network	r MFG / r IPL / left SFG
Fynes-Clinton et al. (2019)	10–12 (21); 14–16 (20); 20–35 (21)	Task-based at retrieval	Autobiographical + Semantic + Episodic two-alternative forced-choice	PLS	Common memory network (<i>correlated with age</i>)	bi IPL / bi MTG / bi IFG / CC / left AMG / bi THA / INS / STG / mFG
Palacio and Cardenas (2019); retrieval)	18–65 (mean 27)	Systematic review (resting-state + task-based at retrieval)	–	PPI; PLS; Seed-based; ICA; Graph theory; etc.	Episodic retrieval network	PCC / Hipp / PCU / PHC / mPFC / AG / dLPFC / IFG / MTG
Palacio and Cardenas (2019); encoding)	"	Systematic review (resting-state + task-based at encoding)	–	"	Episodic encoding network	Hipp / mPFC / IFG / dLPFC / PHC
Tang et al. (2018)	8–25 (75)	Task-based at encoding	Subsequent recognition of scenes	PPI	Memory formation network (<i>correlated with age</i>)	IFG / SFG / mPFC (seeds) / r PHG / r FusG / left SOG / left MOG / left cuneus / r IPL / r SMG
Geib et al. (2017a)	18–30 (17)	Task-based at retrieval	Recognition of words (with high confidence)	Graph theory	Episodic retrieval network	left Hipp / bi dSFG / left MFG / left CAU / bi SMG / left PCU / bi postcentral gyrus / r PreCG / r ITG / r MOG
Geib et al. (2017b)	18–30 (21)	Task-based at retrieval	Cued recall of scenes (only vivid memories)	Graph theory	Vivid episodic retrieval network	r Hipp / r IFG / left ACC / r MCC / r SMG / CAU / etc
Barredo et al. (2015)	mean 24 (18)	Task-based at retrieval (+ Resting-state for comparison)	Source recognition of words	Seed-based	Controlled retrieval network	avLPFC / aTC (MTG pole) / HPC / OFC (middle) / INS / a+pMTG
King et al. (2015)	19–29 (24+36+28)	Task-based at retrieval	Remember/know + Associative recognition + Source recognition	PPI	Core recollection network	left AG / mPFC / PCC / Hipp / left MTG (seeds) / dLPFC / dACC / extrastriate visual cortex (IOG)
Andrews-Hanna et al. (2014)	19–28 (33)	Resting-state	Remember/know of picture-word pairs	Seed-based	Episodic retrieval / recollection network	pIPL (seed) / LSOC / PCU / MFG / SFG / PCC / pITG / OFC (middle) / SMG
Schedlbauer et al. (2014)	20–28 (16)	Task-based at retrieval	Spatiotemporal recognition of scenes	Graph theory	Memory retrieval network	r Hipp / r PCU / left MFG
Schott et al. (2013)	18–38 (64)	Task-based at retrieval	Free recall of words (semantically encoded)	PPI	Semantic encoding network	left Hipp (seed) / IFG / MFG / SFG / IPC / PCC / mFG / PreCG / PHG / AMG / STG / MTG / PCU / THA / putamen
Paz-Alonso et al. (2013a)	8–9 (15); 11–12 (14); 18–30 (14)	Task-based at retrieval	Recall/suppress of word pairs	Seed-based	Mnemonic control network	bi Hipp (seeds) / MOG / PCU / SPG / MTG / PHG / FusG / PCC / MCC / THA / SFG / dLPFC
Ofen et al. (2012)	8–21 (69)	Task-based at retrieval	Recognition of scenes	PPI	Memory retrieval network (<i>correlated with age</i>)	bi PHG (seeds) / left IFG
Vincent et al. (2006)	18–35 (47) + 2 previous studies	Resting-state	Remember/know + Semantic elaborated recognition (from 2 previous studies)	Seed-based	Recollection / semantic retrieval network	bi Hipp (seeds) / vPCU / PCC / bi IPL / retrosplenial cortex

Note. N = number of participants; PPI = psychophysiological interaction method; ICA = independent component analysis method; PLS = partial least squares method; Brain regions: A = anterior; p = posterior; d = dorsal; v = ventral; r = right (left = left); bi = bilateral; m = medial; L = lateral; Hipp = hippocampus (includes hippocampal cortex/gyrus); PHC/PHG = parahippocampal cortex/gyrus; AMG = amygdala; THA = thalamus; CAU = caudate nucleus; INS = insular cortex; CC = cingulate cortex; ACC = anterior cingulate cortex; MCC = mid-cingulate cortex; PCC = posterior cingulate cortex; ITG = inferior temporal gyrus; MTG = middle temporal gyrus; STG = superior temporal gyrus; FusG = fusiform gyrus; PFC = prefrontal cortex; IFG = inferior frontal gyrus; vLPFC = ventrolateral prefrontal cortex; MFG = middle frontal gyrus; dLPFC = dorsolateral prefrontal cortex; SFG = superior frontal gyrus; OFC = orbitofrontal cortex; PreCG = precentral gyrus; PCU = precuneus; IPL = inferior parietal lobe; AG = angular gyrus; SMG = supramarginal gyrus; IOG = inferior occipital gyrus; MOG = middle occipital gyrus; SOG = superior occipital gyrus.

additionally explored other thresholds. Namely, we followed the recommendation of one of CONN's developers, Alfonso Nieto-Castanon, by choosing thresholds that maximize jointly local and global network efficiencies (see https://www.nitrc.org/forum/forum.php?thread_id=9338&forum_id=1144), leading to values of 0.09 for cost threshold, 0.5 for correlation coefficient threshold, and 1.4 for z-score threshold (the three optional thresholds in CONN). With age group as a between-subjects factor (adults > adolescents), we implemented these thresholds at a time to analyze the seven metrics available in CONN: *global and local efficiencies, betweenness centrality, cost, average path length, clustering coefficient, and degree*.

3. Results

3.1. Intrinsic episodic memory network

Table 1 summarizes the main characteristics and results of the 15 selected studies that investigated episodic memory networks following the set of predefined criteria. These studies are described according to age groups, type of fMRI acquisition (resting-state or task-based), behavioral memory task performed (short description), connectivity method implemented, label of the memory network found (and if it correlated with age), and a more detailed description of all the brain regions integrating each episodic memory network selected. It is noteworthy that, even though some networks have been given the same name or label in the literature (e.g., episodic retrieval network), they are constituted by different regions (as is the case of the retrieval network of Palacio and Cardenas, 2019, and the network of Geib et al., 2017a).

To outline a consensual iEMN, Table 2 identifies the brain regions that are more commonly part of episodic memory networks (i.e., regions that overlap across studies). The rows in Table 2 indicate all brain regions common to two or more networks (if a specific brain region was part of only one network, this region was labeled as "other brain region"). Then, the iEMN was delineated by choosing the ROIs common to six or more networks. The resulting network included the following 10 bilateral regions: hippocampus; parahippocampal gyrus; middle temporal gyrus; medial PFC; inferior frontal gyrus (including ventrolateral PFC); middle frontal gyrus (including dorsolateral PFC); superior frontal gyrus; precuneus; inferior parietal lobe; posterior cingulate cortex. Due to the fact some brain regions correspond to more than one AAL node, this resulted in the identification of 14 bilateral ROIs of the AAL brain atlas.

3.2. Connectivity differences between age groups

We conducted a univariate GLM analysis for the connections within the defined iEMN. As illustrated in Fig. 1, the connectivity pattern of this network was similar in adolescents and adults. Across the two age groups, several significant correlations emerged (210 positive correlations and 90 negative correlations, among the 28 ROIs).

Introducing age group as a between-subjects factor (adults > adolescents), we found age-related correlations between the right middle temporal pole (MNI coordinates of this ROI's center of mass [x, y, z] = [44, 15, -32]) and two ROIs in the PFC (see Fig. 2). The right middle temporal pole correlated positively with the right middle frontal cortex ([38, 33, 34] $t(108) = 3.78, p = .007$) and with the right middle orbitofrontal cortex ([33, 53, -11] $t(108) = 3.24, p = .043$), and more so for adults than adolescents. These increased correlations for adults were restricted to regions in the right hemisphere. No contralateral homologous pattern, reaching significance or near significance was found. No stronger correlations were found for adolescents relative to adults.

None of the seven graph theory metrics analyzed revealed significant differences between adolescents and adults for the selected iEMN. This is probably associated with the small number of connections showing an age-related increase, which hampers the quantification network metrics.

Table 2
Brain Regions Integrating Each One of the 16 Episodic Memory Networks.

Brain regions	Subcortical structures										Insular cortex				Cingulate cortex						Temporal lobe				Frontal lobe							Parietal lobe				Occipital lobe			Other																	
	Hipp				PHC		AMG		THA		CAU		ACC		MCC		PCC		MTG	ITG	STG	FusG	mPFC	IFG	MFG	SFG	PreCG	PCU	IPL	AG	SMG	MOG	SOG																							
	11	6	2	3	3	2	2	2	2	3	3	7	3	3	6	6	3	2	2	2	2	6	6	9	10	6	2	2	7	6	2	4	3	2																						
Tang et al. (2020)	X																																																							
Amlie et al. (2019)				X	X																																					X														
Fynes-Clinton et al. (2019)						X	X																																							X										
Palacio and Cardenas (2019); retrieval)						X	X																																							X										
Palacio and Cardenas (2019); encoding)						X	X																																								X									
Tang et al. (2018)						X	X														X																												X							
Geib et al. (2017a)						X	X																																											X						
Geib et al. (2017b)						X	X																																														X			
Barrero et al. (2015)						X	X																																													X				
King et al. (2015)						X	X																																																	X
Andrews-Hanna et al. (2014)						X	X																																																	X
Schedlbauer et al. (2014)						X	X																																															X		
Schott et al. (2013)						X	X																																														X			
Paz-Alonso et al. (2013a)						X	X																																														X			
Ofen et al. (2012)						X	X																																														X			
Vincent et al. (2006)						X	X																																														X			
Number of times present	11	6	2	3	2	2	3	3	3	7	3	3	3	6	6	3	2	2	2	2	2	6	9	10	6	2	2	7	6	2	4	3	2	3	2	4	4	3	2										X	< 2						

Note. The brain regions present in a high number of networks (i.e., > 5) and, thus, selected as part of the iEMN are represented in bold. Hipp = hippocampus (includes hippocampal cortex/gyrus); PHC = parahippocampal cortex/gyrus; AMG = amygdala; THA = thalamus; CAU = caudate nucleus; ACC = anterior cingulate cortex; MCC = mid-cingulate cortex; PCC = posterior cingulate cortex; ITG = inferior temporal gyrus; MTG = middle temporal gyrus; STG = superior temporal gyrus; FusG = fusiform gyrus; mPFC = medial prefrontal cortex; IFG = inferior frontal gyrus (includes ventrolateral prefrontal cortex); MFG = middle frontal gyrus (includes dorsolateral prefrontal cortex); SFG = superior frontal gyrus; PreCG = precentral gyrus; PCU = precuneus; IPL = inferior parietal lobe; AG = angular gyrus; SMG = supramarginal gyrus; MOG = middle occipital gyrus; SOG = superior occipital gyrus.

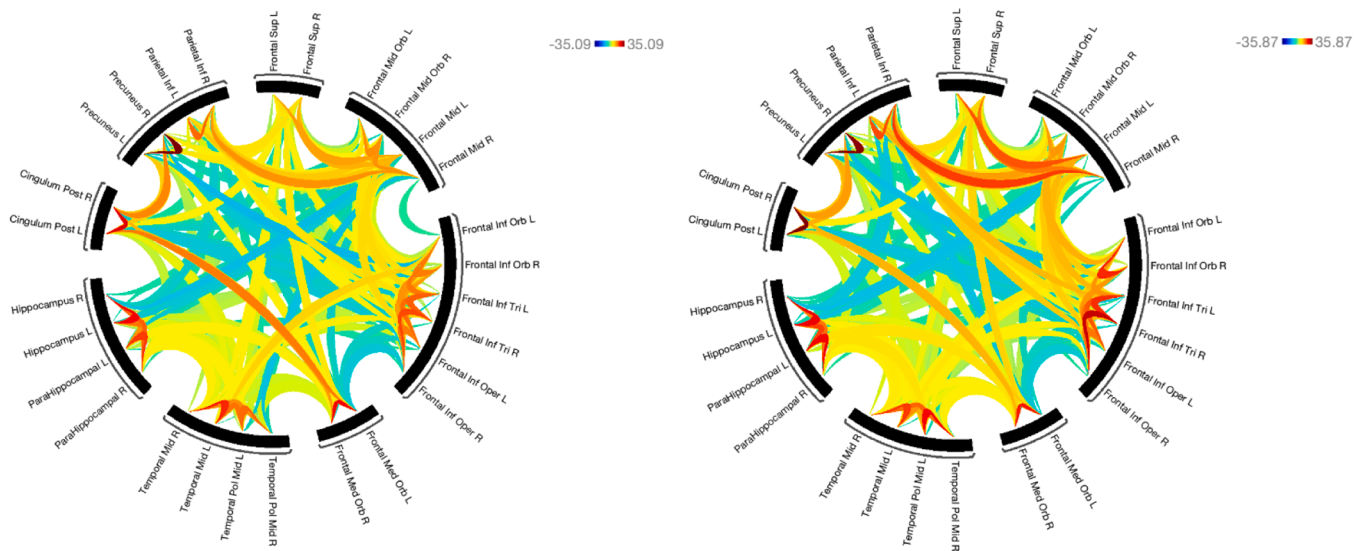


Fig. 1. Connectome Rings of Adolescents (Left) and Adults (Right) Representing the Connectivity Patterns of the Defined iEMN. Note. Positive correlations are represented in red and orange colors, and negative correlations are represented in blue and green colors; the darker the color, the higher the Fisher-transformed correlation value between two ROIs.

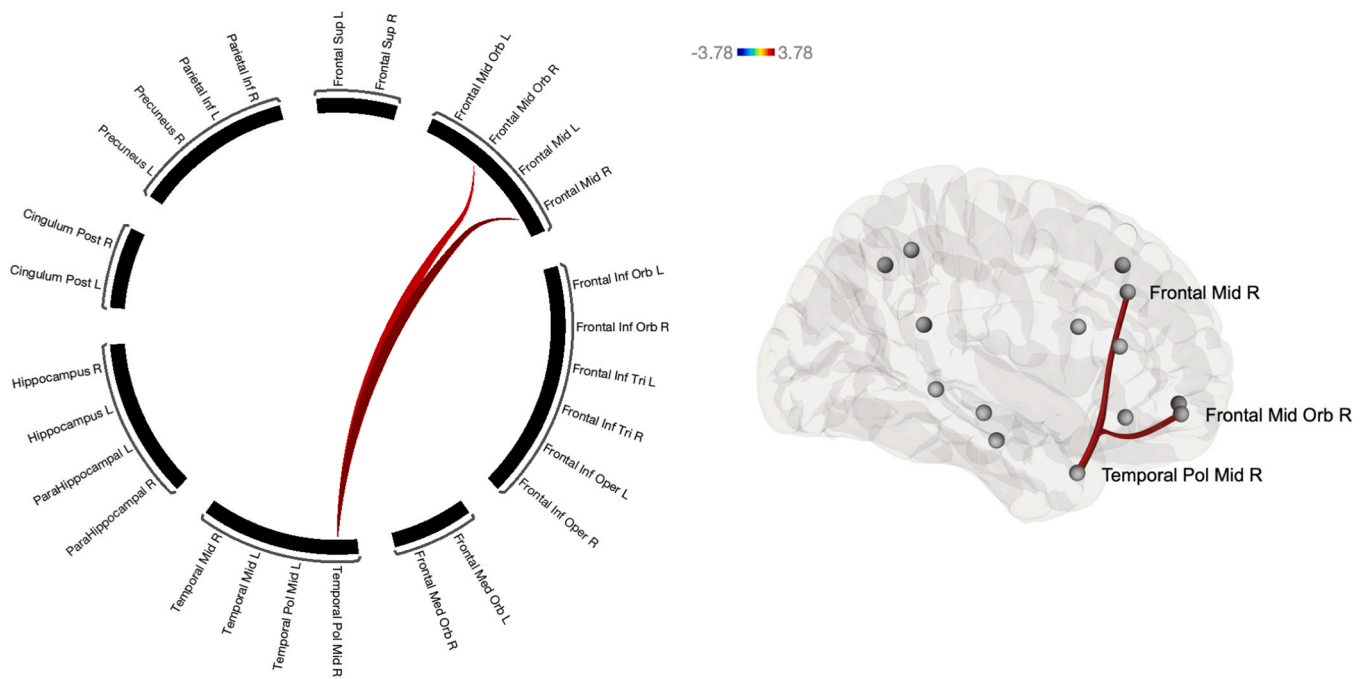


Fig. 2. Connectome Ring (Left) and Cortical Localization (Right; Sagittal View) of the Difference Between Adults and Adolescents, Representing the Age-related Connectivity Pattern of the Defined iEMN. Note. Age-related (adults > adolescents) positive correlations among ROIs are represented in red colors; the darker the color, the higher the Fisher-transformed correlation value between two ROIs.

4. Discussion

The purpose of this study was twofold. First, we aimed to identify the brain regions most commonly associated with the episodic memory networks in the literature. We selected 15 studies that propose episodic memory networks based on resting-state and task-based functional connectivity analyses. This resulted in the identification of 14 bilateral ROIs of the AAL brain atlas, distributed across temporal, frontal and parietal lobes. This systematization procedure allowed us to narrow the variability of networks previously found and to steer future investigations to a more concrete and literature-based iEMN. Importantly, this set of regions aligns well with regions typically found in fMRI

studies of episodic memory, being considered core memory sites (for reviews, see Ghetti and Fandakova, 2020; Mitchell and Johnson, 2009; Palacio and Cardenas, 2019; Ritchey and Cooper, 2020; Simons and Spiers, 2003). Second, we were mostly interested in exploring the late maturation of this potential iEMN, by inspecting age-related differences in resting-state imaging between adolescents and adults. To achieve this purpose, we took advantage of the NKI-Rockland Sample database, one of the most acknowledged open-source datasets (Horien et al., 2021).

4.1. Age-related connectivity between temporal pole and prefrontal cortex

Overall, the findings demonstrated high similarity amid the

connectivity patterns of the two age groups. Nevertheless, two age-related increases in connectivity emerged within the proposed episodic memory network. Specifically, the right temporal pole [Brodmann's area (BA) 38] showed a correlational increase with two regions in the PFC: the right dorsolateral PFC (BA 9/46) and the right rostralateral PFC (BA 10). These functional connections are consistent with the findings of previous studies that inspected episodic memory networks (see Table 1). Namely, in Barredo et al.'s study (2015), a control retrieval network integrated the anterior temporal cortex as well as the lateral orbitofrontal cortex, whereas King et al. (2015) and Paz-Alonso et al. (2013a) showed that the middle temporal gyrus and the dorsolateral PFC were part of recollection/mnemonic control networks. Interestingly, these networks have been associated with controlled retrieval abilities, which are known to have a protracted development until adulthood (Andrade and Raposo, 2021; Ofen et al., 2007; Sprondel et al., 2012). PFC recruitment during memory processing has long been associated with mnemonic strategies requiring cognitive control (Blumenfeld and Ranganath, 2007; Wagner, 2002), and the prolonged maturation of this region impacts the development of the episodic memory system (Ofen et al., 2007; Tang et al., 2018).

Within the PFC, the dorsolateral and the rostralateral/frontopolar portions have been implicated in mnemonic processes such as selection and manipulation of information, or context and post-retrieval monitoring (Dobbins et al., 2002; Hayama and Rugg, 2009). Other studies suggest that the dorsolateral PFC plays a key role in successful recollection, which requires high demands of information manipulation and organization, and usually involves establishing associations between items during encoding (Blumenfeld and Ranganath, 2007; Mitchell and Johnson, 2009; Simons and Spiers, 2003). Of note, the dorsolateral PFC undergoes a prolonged period of maturation which lasts into adulthood (Giedd, 2004), suggesting that maturation of this region may be critical to the full development of memory abilities.

Regarding the temporal lobe, we hypothesized that the medial temporal areas (namely, the hippocampus) could be key in the development of the defined iEMN. Notwithstanding, although the major role of the hippocampus in episodic memory processing (Eichenbaum et al., 2007), some literature has shown that this structure does not seem to be topologically central in resting-state networks (Geib et al., 2017b; Tomasi and Volkow, 2010). In contrast to our initial prediction, results showed a developmental increase in connectivity between the right PFC and the right temporal pole (rather than the medial temporal cortex). The anterior temporal lobe is critical in semantic memory and has been considered a semantic hub, responsible for the storage of semantic knowledge and structures across learning episodes (Lambon Ralph et al., 2017; Patterson et al., 2007). There is an ample consensus that episodic and semantic memory systems interact very closely, both in adulthood and along development (Renoult et al., 2019; Renoult and Rugg, 2020). Several studies have shown that attributing a cohesive meaning or semantic content to an episodic event improves memory strength, increasing the probability that the event is accurately remembered later on (Craik and Lockhart, 1972; Raposo et al., 2016; Staresina et al., 2009). Thus, we can speculate that the late maturation of the functional connectivity between the PFC and the temporal pole may underlie the prolonged development of controlled semantic abilities and the use of semantic elaboration strategies to promote episodic retrieval (Andrade and Raposo, 2021; Ghetti and Angelini, 2008).

4.2. Right-lateralized age-related differences

Compared to adults, children and adolescents tend to show reduced hemispheric lateralization of fMRI activations in various cognitive functions, such as attention, language and cognitive control (Booth et al., 2003; Szafarski et al., 2006). Indeed, lateralization increases with age (Hopf et al., 2013), with the networks linked to these cognitive functions showing high lateralization in adulthood (Corbetta and Shulman, 2002; Toga and Thompson, 2003). However, in memory studies,

the scenario is not straightforward, especially in what concerns the intervention of the PFC in episodic memory.

In the present study, age-related increases in the defined iEMN connectivity emerged in the right hemisphere only. In the literature, right and left dorsolateral and rostralateral PFC have been associated with different functions (Wagner, 2002). While regions on the left are recruited when retrieval involves remembering specific episodic details, right-lateralized activations reflect item memory or familiarity strength. On the other hand, more recently, the right dorsolateral PFC has been linked to controlled retrieval and the suppression of memories (Anderson and Hanslmayr, 2014; Paz-Alonso et al., 2013a). Thus, even though prior research corroborates the importance of the right lateral PFC in memory processing, further investigation is warranted to clarify the functional role of these regions and their connectivity patterns along development. Of interest, in complement to the functional data, previous observations at the structural level suggest a more prolonged decrease in gray matter density in the right than the left PFC (Gogtay et al., 2004). Since decreases in gray matter density correspond to a maturation process (for a review, see Lenroot and Giedd, 2006), this might help to explain the right-lateralized developmental results in the current study.

4.3. The uncinate fasciculus: connecting the "dots"?

Functional ICNs are often supported by structural connectivity, i.e., white matter tracks physically interconnecting brain regions (Greicius et al., 2009; Skudlarski et al., 2008; van den Heuvel et al., 2009). Several studies have reported that white matter tracts involved in memory functioning develop until adulthood (Lebel and Beaulieu, 2011; Lebel et al., 2012), with additional research showing significant correlations between the development of these tracts and the development of memory abilities (Mabbott et al., 2009; Wendelken et al., 2015). One such white matter pathway is the uncinate fasciculus (UF), which presents a protracted maturation certainly surpassing adolescence and extending until the age of 35, according to some studies (Lebel and Beaulieu, 2011; Lebel et al., 2012; for a review, see Olson et al., 2015). The UF is a long-range monosynaptic and bi-directional tract. It connects, at one end, anterior temporal lobe regions (such as the temporal pole; BA 38) and medial temporal areas (such as the perirhinal cortex, the anterior parahippocampal gyrus and the amygdala) and, at the other end, the lateral orbitofrontal cortex (BAs 10 and 11) and the pars orbitalis of the inferior frontal gyrus (BA 47; Olson et al., 2015).

Critically, in the present study we found age-related changes in the functional connectivity between the temporal pole (BA 38) and the rostralateral PFC (BA 10), with stronger connectivity in adults than

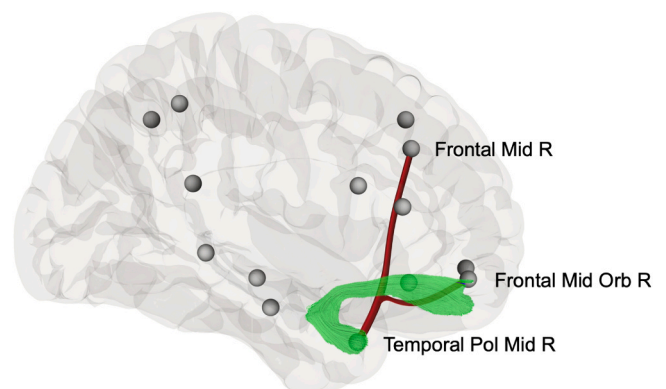


Fig. 3. Overlap Between the Right Uncinate Fasciculus' Tractography and the Age-related Connectivity Found for the iEMN Defined. Note. In red are the two potential iEMN connections that showed increases from adolescence to adulthood in our study; in green is the tractography of the right uncinate fasciculus (adapted from Yeh et al., 2018).

adolescents. This functional connectivity circuitry partially overlaps with the UF (see Fig. 3), suggesting that this structural pathway may underlie the functional connectivity observed. The UF connects regions responsible for the storage of semantic memories (temporal pole) and areas associated with control processes or semantic selection strategies (lateral PFC; Harvey et al., 2013). Earlier studies have reported positive correlations between the integrity of the UF (measured through fractional anisotropy or mean diffusivity) and increments in episodic memory performance (Alm et al., 2016; Mabbott et al., 2009; Wendelken et al., 2015). Namely, Alm et al. (2016) have revealed that this brain-behavior relationship stands out when competition in stimulus choice is required to accomplish successful retrieval. Additionally, Wendelken et al. (2015) have shown a significant correlation between UF integrity and mnemonic control along development. In short, our resting-state functional connectivity results are consistent with prior work on structural connectivity, providing complementary data about the developmental trajectory of an iEMN.

4.4. Limitations and future studies

We investigated a potential iEMN based on resting-state fMRI. Although resting state has been widely used and significant correlations between resting-state networks and behavioral performance have been reported, future studies should address this relationship more directly, by correlating the iEMN results with episodic memory performance. This would allow to more firmly support the link between the age-related connectivity differences observed and the late development of recollection abilities. Besides, as mentioned before, the relationship between the development of resting-state functional connectivity and the development of structural connectivity (measured, for example, through diffusion-weighted MRI) is also noteworthy to investigate. Both of these associations should be inspected in future studies, to corroborate the results of the present study, but also to shed light on the *triad* of brain function, brain structure, and behavioral performance, especially in the maturational period of adolescence.

A caveat of our approach concerns the heterogeneity across studies used to define the memory network. All were functional connectivity studies, but while some used resting-state, others were task-based. Some studies included developmental samples, whereas others comprised only adults. This may have biased the results, particularly if the regions comprising an iEMN change across development. Our selection approach and the fact that most existing studies are with adults may preclude the identification of regions more important earlier in development. Also, by restricting our samples to adolescents (13–17 years) and adults (23–27 years), there is an important age gap from 17 to 23 years that was not assessed. Hence, potential changes in the iEMN could not be captured at this age range, which constitutes a shortcoming as this period is associated with nonlinear and varying rates of maturation of several regions, including the PFC and hippocampus (e.g., Gogtay et al., 2004). Additionally, the definition of the iEMN implied a decision about the number of mentions required for the inclusion of a given region across the pool of selected studies. The chosen threshold (six) was meant to be a tradeoff between specificity and thoroughness, but we cannot rule out this choice as a potential source of bias. Another point related to the process of iEMN characterization is the predominance of task-based studies in the pool of studies selected to define the network, which was subsequently analyzed from a resting-state perspective. It has been known for a long time that resting-state networks include regions which are functionally relevant and are recruited by active tasks (van den Heuvel et al., 2009). Further studies are required to assess the amount of overlap between the iEMN and rest networks such as the Default Mode Network, the amount of mutual interaction and to which extent the functional connectivity within the iEMN is modulated by the execution of memory-related tasks.

Another potential limitation concerns the use of a cross-sectional design. Age-related results obtained with cross-sectional samples

comprise potential confounds associated with individual variability on other variables changing over time, besides age (Maxwell and Cole, 2007). Thus, it is important that future studies investigate the development of episodic memory during adolescence using longitudinal samples, in which the development of the variables of interest is more easily isolated from other variables changing over time.

5. Conclusion

In this study, we first conducted a literature review to systematize the most consensual brain regions integrating different episodic memory networks. Grounded on these findings and on evidence favoring the existence of ICNs, we outlined a potential iEMN including 14 bilateral ROIs. Based on previous work that demonstrates that episodic memory is not fully developed until adulthood, we then investigated if this network changed its connectivity pattern from adolescence to adulthood. We found age-related increases in connectivity between the right temporal pole (BA 38) and two regions in the right lateral PFC (BA 9/46 and BA 10). These changes may underpin the development of mnemonic control processes and semantic elaboration strategies and may be interpreted in the light of the uncinate fasciculus' late maturation.

CRediT authorship contribution statement

Alexandre Andrade: Writing – review & editing, Validation, Supervision, Software, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Ana Raposo:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Miguel Ângelo Andrade:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of Competing Interest

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Data availability

For the purpose of this study, the authors selected data from the publicly available NKI-Rockland Sample (http://fcon_1000.projects.nitrc.org/indi/enhanced/index.html) of the Nathan Kline Institute (NKI; Nooner et al., 2012).

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