Variation in brain aging: A review and perspective on the utility of individualized approaches to the study of functional networks in aging

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Abstract:
Healthy aging is associated with cognitive decline across multiple domains, including executive function, memory, and attention. These cognitive changes can often influence an individual's ability to function and quality of life. However, the degree to which individuals experience cognitive decline, as well as the trajectory of these changes, exhibits wide variability across people. These cognitive abilities are thought to depend on the coordinated activity of large-scale networks. Like behavioral effects, large variation can be seen in brain structure and function with aging, including in large-scale functional networks. However, tracking this variation requires methods that reliably measure individual brain networks and their changes over time. Here, we review the literature on age-related cognitive decline and on age-related differences in brain structure and function. We focus particularly on functional networks and the individual variation that exists in these measures. We propose that novel individual-centered fMRI approaches can shed new light on patterns of inter- and intra-individual variability in aging. These approaches may be instrumental in understanding the neural bases of cognitive decline.

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Highlights

- Age-related brain and cognitive changes are wide-spread and can impact a person's quality of life
- Cognitive and brain measures exhibit a wide range of variability across individuals
- The functions that decline with age arise from the interactions across brain regions and systems
- Variation in the brain's functional organization is revealed by the use of individualized methods
- Individualized approaches will improve the study of sources of variation in neurocognitive aging

1. Introduction

Aging, even in the absence of disease, is commonly accompanied by alterations to the brain's anatomy and physiology that can result in impairment of cognitive function (Deary et al., 2009; Fabiani, 2012). This cognitive decline can impact quality of life and life satisfaction (Abrahamson et al., 2012; St. John & Montgomery, 2010). Given the impending increase in the proportion of the population that will be at risk of experiencing age-related cognitive decline in the coming decades (Anderson et al., 2012), increasing our understanding of the mechanisms underlying these impairments is imperative.

A large body of research has been dedicated to the important question of the neural correlates of cognitive decline. These investigations have found age-related differences at every level of brain organization, from small-scale changes such as decreased numbers of synapses (Masliah et al., 1993) and altered neurotransmission (Bäckman et al., 2010), to large-scale decreases in grey and white matter volume (Raz et al., 2005; Resnick et al., 2003). Cognitive phenomena affected during aging, such as memory, attention and other executive functions, are particularly linked to the interactions between regions comprising large-scale functional networks (also called 'systems') (Mesulam, 1998). Thus, age-related changes to functional networks are likely to be central to changes in cognition.

Importantly, investigations of the neurobiological bases for cognitive decline can be hampered by the wide inter-individual variability that exists in

the onset and trajectory of brain aging, as seen in cognitive as well as structural and functional brain measurements (**Figure 1**). Thus, a central issue to the study of aging is to understand what neurobiological factors lead age-related changes in cognitive abilities to vary so widely, across individuals and across domains, and to use this knowledge to guide interventions.

However, accurately tracking individual differences, and differentiating them from other forms of noise, requires reliable individualized approaches for measuring brain networks and cognition. Individualized fMRI approaches have been developed to embrace inter-individual variability by mapping person-specific functional organization, rather than applying the same assumptions to every brain (Gratton & Braga, 2021). In this way, we are beginning to learn more about how individual differences in functional architecture relate to cognition and behavior. However, most current work has focused on investigating this relationship in young adults, with only few exceptions (Huang et al., 2021; Kantarovich et al., 2022; Mwilambwe-Tshilobo et al., 2023; Setton, Mwilambwe-Tshilobo, Girn, et al., 2022; Setton, Mwilambwe-Tshilobo, Sheldon, et al., 2022).

In this review, we discuss cognitive aging and concomitant changes in large-scale brain networks, with a focus on inter-individual variability in these measures. We also review issues that arise in studying individual differences using neuroimaging data due to age-related confounds that contaminate measures of functional networks. We close by emphasizing the potential of

using individualized approaches in the study of functional networks in aging and their relationship to cognitive decline.

2. Individual differences in cognition and brain aging

Older adults often exhibit a decrease in cognitive performance, with a large degree of variability in the onset, trajectory, and severity of deficits. Age-related changes in cognition include diminished working memory capacity (Park et al., 2002), decreased processing speed (Salthouse, 1996), reduction in cognitive flexibility (Grady & Garrett, 2014), and impaired episodic memory (D. B. Mitchell, 1989). Conversely, some cognitive processes, such as semantic and procedural memory, are preserved across the lifespan (D. B. Mitchell, 1989). Thus, while aging is associated with declines across multiple domains, not all cognitive functions are affected.

It is important to note, however, that while the aforementioned age-related changes have been repeatedly observed across the literature *on average*, there is also a considerable range of variability in both the onset and rate of this decline (Fabiani, 2012; Hedden & Gabrieli, 2004; See **Figure 1** for an example). In fact, beginning in midlife, greater age is associated with greater inter-individual (and intra-individual) variability in cognitive performance (Christensen, 2001; LaPlume et al., 2022). This age-related increase in variability has been reported in both cross-sectional (Christensen, 2001; LaPlume et al., 2022) and longitudinal (Christensen, 2001) studies. However, the extent of variability is dependent on the construct being measured. For example, processes with greater cognitive and motoric

demands result in higher age-related inter-individual variability when comparing older and young adults (Shammi et al., 1998). Furthermore, fluid intelligence, which involves processes related to reasoning and problem solving during novel experiences and is susceptible to age-related decline, has a higher level of heterogeneity than crystallized intelligence, which includes learned procedures and acquired knowledge and shows less decrease, if any, when comparing across age groups (Christensen et al., 1994). This evidence further demonstrates that not all cognitive functions are uniformly affected during aging.

In addition to its association with increasing age, variability is positively correlated with age-related decline. For instance, among a cross-sectional sample ages 18-90, the 60 to 90 age range, which is associated with a rapid decline in cognitive function, even in the absence of diagnosed disease, also demonstrates a steep increase in inter-individual variability (LaPlume et al., 2022), suggesting that, while some individuals deteriorate dramatically and begin showing signs of decline early on, others may be only slightly affected. Beyond normative aging, rapid deterioration has been associated with declines in specific cognitive functions within individuals with neurodegenerative dementias depending on the pathology (Elahi & Miller, 2017). On the other end of the spectrum are cognitive “SuperAgers”: 80+ year-old individuals whose performance on cognitive tasks of episodic memory is at least as good as individuals 20-30 years younger (Harrison et al., 2012; Rogalski et al., 2013). Thus, aging is associated with a wide range

of variability in the trajectories that individuals follow with respect to cognitive decline.

Age-related changes in brain function are also apparent in functional activations in response to cognitive tasks measured by the blood oxygen dependent level (BOLD) signal with functional Magnetic Resonance Imaging (fMRI). The literature has consistently found that, when comparing young and older adults, older adult brains show overactivation that manifests in a variety of patterns (Cabeza, 2002; Davis et al., 2008; S.-C. Li & Lindenberger, 1999). These patterns include the activation of bilateral regions, or contralateral recruitment (Cabeza, 2002), increased activation of frontal regions, or posterior-to-anterior shift (Grady et al., 1994), and more dispersed task-evoked activations that are less differentiated, or neural de-differentiation (S.-C. Li & Lindenberger, 1999). These age-related changes in brain activity, likely resulting from various causes, demonstrate how the effects of aging are far-reaching, extending beyond individual brain regions and affecting interactions across brain regions.

Functional changes in aging often coincide with changes to the brain's structure and anatomy. For example, cross-sectional literature has reported that aging is associated with loss of grey matter, including cortical thinning (Walhovd et al., 2011), decreased integrity of white matter (Gunning-Dixon et al., 2009), and dopamine receptor depletion (Bäckman et al., 2010). Longitudinal analysis has further elaborated on structural changes, finding that the reduction in grey matter disproportionately affects frontal regions,

hippocampus, caudate nucleus, and the cerebellum, while visual areas are mostly unaffected (Raz et al., 2005). However, unique patterns of atrophy emerge as functionally related brain regions exhibit correlated grey matter volume even in healthy older adults (Seeley et al., 2009). White matter fibers, which connect brain regions, are also affected with age, with greater differences seen in prefrontal and inferior parietal white matter (Raz et al., 2005). At the microstructural level, studies measuring diffusion tensor imaging (DTI) have found that fractional anisotropy, which reflects white matter integrity, decreases with age, while mean diffusivity, which indicates the presence of diffusion barriers, increases with age across white matter pathways (Abe et al., 2008; Lebel et al., 2012; Storsve et al., 2016). Structural connectivity is an important topic in aging and loss of that connectivity has been associated with decreased processing speed. In this review, we do not focus on structural connectivity, but rather emphasize functional connectivity, though we acknowledge the importance of studying both constructs in parallel. Importantly, several areas–including the lateral prefrontal cortex (**Figure 1**), the cerebellum, and prefrontal white matter–exhibit significant individual variation in shrinkage rates (Raz et al., 2010). While the mid-50s has been identified as a pivotal period for structural decline, individuals also greatly differ in the time of onset of structural deterioration (Raz et al., 2005; Yap et al., 2013).

Individual trajectories of age-related decline appear to depend on several variables, including not only lifespan factors related to the passage of time,

but also broad life-course factors related to experiences, genetics, and an individual's environment (Bender & Raz, 2012; Cutler, 2009; de Frias et al., 2014; Zanjani et al., 2013). Interactions between adverse and compensatory life-course factors and genetics can lead to a longitudinal enrichment or depletion of neural resources (Reuter-Lorenz & Park, 2014). Moreover, the wide range of individual differences in cognitive performance and decline may arise as a consequence of accumulated pathological factors (or their absence, as observed in SuperAging) as well as from the accumulation of plasticity in response to life experiences. Factors such as longer education, greater physical activity, and bilingualism have been proposed to promote the accumulation of neural resources in individuals that may mitigate the effects of decline caused by aging or disease (Cabeza et al., 2018). Additionally, there exists a longitudinal association between social participation and cognitive ability: older adults who engage in more social activities maintain a higher cognitive ability (Bourassa et al., 2017). Various mechanisms have been suggested to explain the enhanced episodic memory performance of SuperAgers, including greater brain volume (especially in the hippocampus and anterior cingulate), increased number of neurons and synapses, and the minimization of pathology compared to normative controls (de Godoy et al., 2021).

On the other extreme, a cross-sectional analysis of nutritional deficiencies (González-Gross et al., 2001) and a longitudinal study of persistent depressive symptoms (Paterniti et al., 2002) link these factors with a higher likelihood of

cognitive decline. Furthermore, changes in the vascular system are often associated with structural and cognitive decline; vascular abnormalities have a longitudinal association with an increase in white matter hyperintenisities (Raz et al., 2007) and cognitive dsyfunction (E. J. Van Dijk et al., 2008). Interestingly, a cross-sectional analysis by (Bowie et al., 2023) found declines in cerebral arterial elasticity temporally precedes an acceleration of white matter hyperintenisity development suggesting that declines in vascular support systems may initiate a cascade of declines in brain structure and function. It is worth noting that these factors are likely not acting independently from each other. For example, socioeconomic status has previously been correlated with physical exercise (Carroll et al., 2020) and access to healthy foods (Larson et al., 2009), as well as functional specialization of brain networks and anatomical integrity in the brain (Chan et al., 2018). The combination of and interactions between these compensatory and detrimental factors lead to a diversity of profiles in cognitive decline across individuals, who can exhibit different trajectories when tested at multiple times.

As summarized in this section, age-related changes in cognition vary widely among individuals due to several biological and environmental factors that influence the trajectory of brain aging. What is also clear from the brain aging literature is that aging is associated with changes in many different brain regions and their function, not simply isolated portions of the cortex. The interactions across these distributed regions, which are crucial to cognitive functions, can be examined by measuring functional brain networks. In the

next section, we discuss age-related changes to the large-scale functional networks of the brain.

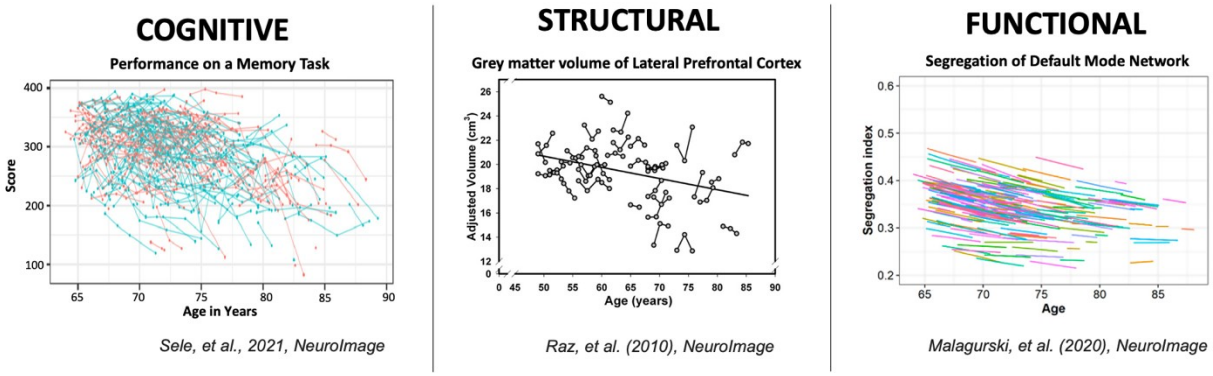

Figure 1 - Variation is observed across cognitive, structural, and functional measures in aging. The left panel shows variation in a memory battery across 1-5 timepoints collected across 7 years from a sample of 232 older adult participants (Sele et al., 2021). In this study, memory was measured using the Verbal Learning and Memory Test. The middle panel shows variation in the longitudinal trajectory of grey matter volume measured with structural MRI of the lateral prefrontal cortex (adjusted for intracranial volume) from 40 participants across 1-3 assessments each ~15 months apart (Raz et al., 2010). The right panel shows variation in the longitudinal change in functional network segregation of the Default Mode Network after linear mixed effects analysis for a sample of 232 across 1-5 timepoints collected within 7 years (Malagurski et al., 2020) (note that raw measures show even larger patterns of variability than those plotted here). In each case, a negative trend is seen with age, but with considerable variability in baseline and trajectory across participants.

3. Functional brain networks in aging

Functional brain networks can be measured using an fMRI technique called functional connectivity. This technique quantifies statistical associations in the patterns of activity between brain regions through methods like time-series correlations (Biswal et al., 1995) and independent component analysis (van de Ven et al., 2004). At its simplest, functional connectivity involves measuring the temporal correlation in the patterns of activity exhibited by pairs of regions. The technique operates on the assumption that functionally related regions will exhibit similar patterns of activity (Biswal et al., 1995). Conversely, if two regions are not functionally

related and belong to different systems, then their patterns of activity will not show high similarity. Large-scale functional “networks” or “systems” can be defined by extending these techniques across multiple regions of the brain (see K. R. A. Van Dijk et al., 2010 for a review).

Functional network mapping can be conducted using fMRI data collected while participants complete tasks or are in a resting state. During resting-state scans, individuals are placed inside an MRI scanner and instructed to stay awake, but let their minds wander without focusing on any specific thoughts. Resting-state paradigms provide several advantages to the study of brain networks. First, there is no specific task involved, which facilitates data collection of populations that may not have the cognitive resources necessary to perform particular tasks, such as older adults with dementia. Second, functional interactions between functionally related regions have been shown to be present at rest and show spatial correspondence with task-evoked activations (e.g. Biswal et al., 1995; Power et al., 2011; Smith et al., 2009; Yeo et al., 2011). Importantly, functional connectivity measured during the resting state is similar (although not identical) to that observed during tasks (M. W. Cole et al., 2014; Gratton et al., 2018; **Figure 4B**). Thus, resting-state functional connectivity allows us to map the functional organization of the brain without the need for a specific task to target a particular network.

Aging is associated with changes in the functional connectivity of the brain (Ferreira & Busatto, 2013). Cross-sectional research shows that, in

general, the strength of functional connectivity tends to decrease with age (Andrews-Hanna et al., 2007), with the most substantial decline occurring between the ages of 75-79[1] (Farràs-Permanyer et al., 2019). It is thought that these changes in functional connectivity are in part due to white matter loss and demyelination, which impair the exchange of information across regions (Andrews-Hanna et al., 2007; O'Sullivan et al., 2001). However, other alternative explanations may include the loss of coherent neuronal function in aging (Dennis & Thompson, 2014).

While functional connectivity has been observed to generally decrease, age-related effects appear to vary by network (Sala-Llonch et al., 2015). Within-network connectivity in primary sensory systems is often reported to show little differences across age groups (Geerligs et al., 2015; H.-Y. Zhang et al., 2014). Conversely, these networks show increased connectivity with other networks (King et al., 2018; Rodriguez-Sabate et al., 2019; Seidler et al., 2015), suggesting decreased functional specialization. Association networks appear to consistently exhibit decreased within-network connectivity with age, suggesting perhaps a greater vulnerability with aging. Studies on network changes in aging have converged on four networks that appear to be especially relevant to cognitive changes in aging: the default mode network (DMN), the cingulo-opercular network (CON), the

[1] Interestingly, in this study individuals aged 80 or older exhibit a general increase in functional connectivity, which is thought to reflect compensatory mechanisms (Farràs-Permanyer et al., 2019). Alternatively, this increased functional connectivity might reflect a bias towards the inclusion of only individuals with exceptional health in this age group, as others may be precluded from participating in research due to a higher risk of various dementias and cardiovascular disease.

frontoparietal network (FPN), and the dorsal attention network (DAN). Notably, these networks have been referred to by different names in the literature due to differences in nomenclature across groups (Uddin et al., 2023). Here, we discuss these four networks as defined by (Power et al., 2011), although alternative parcellations of the cerebral cortex exist (e.g. (Schaefer et al., 2018; Yeo et al., 2011). At least for the Power and Schaefer/Yeo networks, these tend to show a relatively similar network topography to those described by Power and colleagues (Kong et al., 2024), but at times single networks may be broken up into multiple sub-units (e.g. FP into FP-A, FP-B), reflecting a different resolution of network descriptions. In addition, network nomenclature can sometimes be in conflict (e.g., “cingulo-opercular” vs. “ventral attention” vs. “salience”). Finding a consensus across different network atlases is an ongoing effort, but for clarity in this review we focus only on one set of network definitions. The networks in their canonical form are shown in **Figure 2**.

One of the most studied of these is the default mode network (DMN; Ferreira & Busatto, 2013; Mevel et al., 2011; Sala-Llonch et al., 2015). This term is used to refer to a set of brain regions that tend to be active during rest conditions, including the medial prefrontal cortex, inferior parietal lobule, hippocampus, the posterior cingulate cortex and precuneus (Buckner & DiNicola, 2019). These regions are also among those that have been shown to exhibit longitudinal decreases in grey matter volume during the aging process (Raz et al., 2010). The DMN has been implicated in episodic

and prospective memory (Andrews-Hanna et al., 2010; Spreng & Grady, 2010), which are two functions that are often impaired in older adults (Grady & Craik, 2000). Cross-sectional research has shown that DMN functional connectivity decreases in aging, even in the absence of pathological conditions (Andrews-Hanna et al., 2007; Grady et al., 2016; Zonneveld et al., 2019), although this pattern appears exacerbated in Alzheimer's disease (see Mevel et al., 2011 for a review). In addition to within-network connectivity decreases, the interactions of the DMN with other networks are also impacted in aging (Rodriguez-Sabate et al., 2019; Spreng & Schacter, 2012; Spreng & Turner, 2019). These altered internetwork interactions have been hypothesized to have important implications for the cognitive changes that are typically observed in older adults (Spreng & Turner, 2019).

The cingulo-opercular network (CON) refers to a system which includes the dorsal anterior cingulate and anterior insula. The literature often treats the cingulo-opercular and salience networks as synonymous (see Uddin et al., 2023 on the issue of network nomenclature), despite evidence that two distinct networks exist in near proximity (the cingulo-opercular has a more dorsal position in the insula and more posterior position along the midline frontal lobe; Dosenbach et al., 2024; Seeley, 2019); given the terminological confusion, for the purposes of this review, we don't attempt to distinguish literature on these networks in aging. While the CON has received relatively less attention in aging research, studies on young adults have shed light on its crucial role in cognition (Dosenbach et al., 2008; Menon & Uddin, 2010).

The CON is thought to play a pivotal role in stable behavioral control (Dosenbach et al., 2007), and disruptions in its functional connectivity have been associated with age-related impairments in visual processing speed (Ruiz-Rizzo et al., 2019). Structural and functional changes within the CON, including gray matter reductions and weaker functional connectivity, have been documented in the context of aging and cognitive decline (Geerligs et al., 2015). Moreover, reduced functional connectivity in the Salience network has been implicated in neurodegenerative conditions such as frontotemporal dementia (Seeley et al., 2009; J. Zhou et al., 2010; see **Box 1**). Interestingly, studies on SuperAgers reveal greater structural integrity in the CON and DMN, as evidenced by increased cortical thickness (Sun et al., 2016). This suggests a potential link between the structural health of these networks and exceptional cognitive aging in some individuals.

The frontoparietal network (FPN), sometimes referred to as the executive control network (see Uddin et al., 2023 for terminology), comprises primary regions along the dorsolateral prefrontal cortex and the supramarginal gyrus of the parietal lobe (Marek & Dosenbach, 2018). This network has been linked to executive functions, especially moment-to-moment, or phasic, adaptation to those functions (Assem et al., 2020; Dosenbach et al., 2007), playing a crucial role in cognitive control mechanisms. Research on the FPN in aging has illuminated age-related differences within this network. Older adults, compared to their younger counterparts, exhibit reduced functional connectivity within this network

(Betzel et al., 2014; Campbell et al., 2012; Oschmann & Gawryluk, 2020). In a study by Campbell and colleagues, this reduction was correlated with greater distractibility on implicit memory tasks, shedding light on the impact of age-related changes on cognitive performance (Campbell et al., 2012).

The dorsal attention network (DAN) has key regions in the superior parietal lobule, in the posterior part of the superior frontal gyrus, and near the junction of the inferior temporal gyrus and the occipital lobe. This network is associated with top-down mechanisms in visuospatial attention (Corbetta & Shulman, 2002). As with the other networks related to executive function listed above, decreases in functional correlations have also been observed in the DAN with increasing age (Andrews-Hanna et al., 2007).

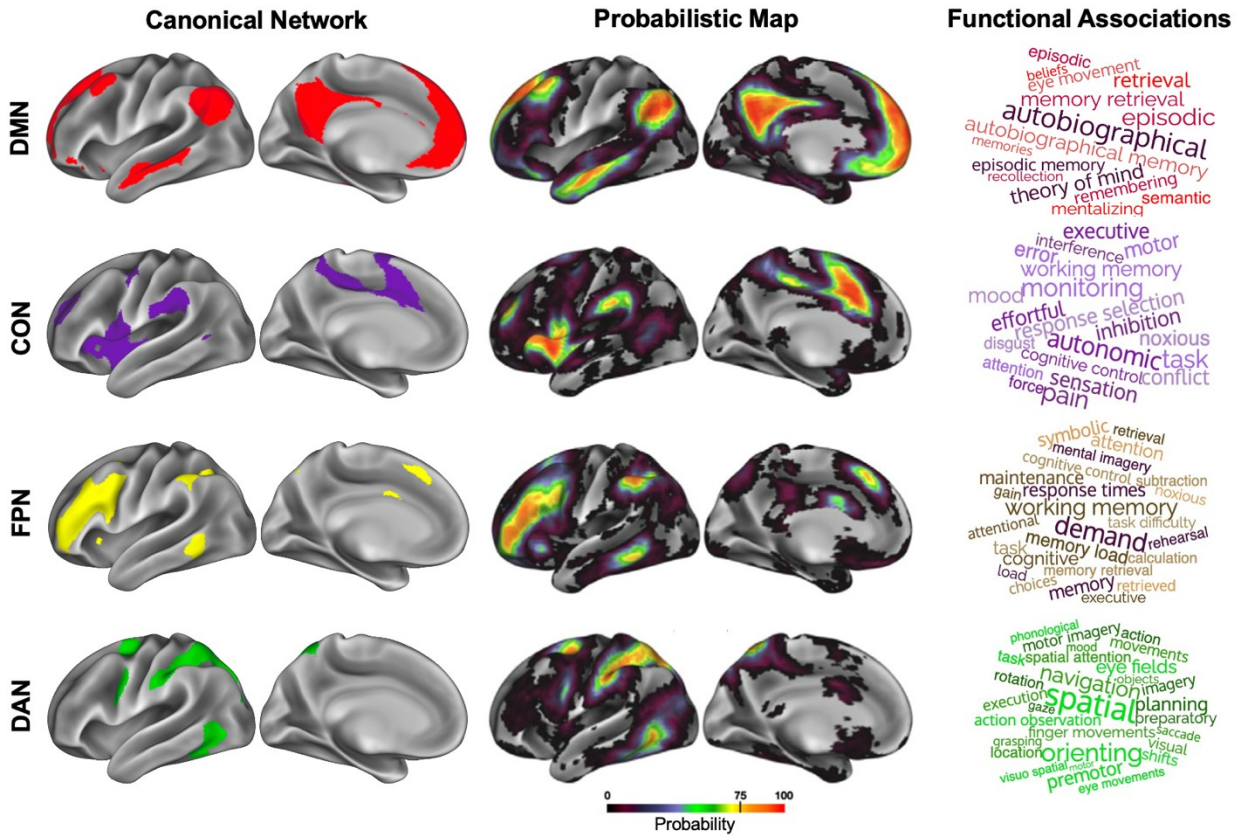

Figure 2 – Networks commonly described in the aging literature. This figure shows four networks which are commonly described in the aging literature as showing age-related differences: the Default Mode Network (DMN), Cingulo-opercular Network (CON), the Frontoparietal Network (FPN), and the Dorsal Attention Network (DAN). The left column, shows the networks in their canonical form based on the Power atlas (Power et al., 2011). The middle column shows a probabilistic map for each network, derived from individualized mapping, showing the probability of a brain region belonging to each of the networks (Dworetsky et al., 2021). The areas showing the highest probability of belonging to each network (in warm colors) closely correspond to the canonical network maps. However, each of the networks show a degree of individual variability, evidenced by the prominent areas with lower probabilities of belonging to that network. The right column shows the more commonly associated cognitive correlates for each network derived from a Neurosynth meta-analysis carried out by examining the functional associations to the three ROI's with the highest probability of belonging to each network (ROIs were derived from (Dworetsky et al., 2021)). Distinct cognitive correlates have been associated with each network, although each network also includes a fairly broad swath of functional terms, indicating that single networks likely participate in multiple different functions.

Box 1: Neurodegenerative Disorders and Functional Networks

Dysfunction of brain networks has also been implicated in multiple neurodegenerative disorders. In a seminal study, Seeley and colleagues compared atrophic patterns across healthy older adults and participants diagnosed with five different neurodegenerative disorders, including Alzheimer's disease, frontotemporal dementia, and semantic dementia (Seeley et al., 2009). They established a profile of atrophy for each group and observed that each syndrome exhibited distinct atrophic patterns that corresponded spatially with specific intrinsic connectivity networks. The authors used this evidence to theorize that neurodegenerative diseases target specific networks.

Since then, several studies have strengthened the evidence suggesting a link between specific networks and age-related disorders. For example, Alzheimer's disease appears to target the default mode network (Buckner et al., 2005; Greicius et al., 2004; Mevel et al., 2011; Z. Zhang et al., 2023; J. Zhou et al., 2010), while frontotemporal dementia shows a profile that overlaps substantially with the salience network (Rosen et al., 2002; J. Zhou et al., 2010). Parkinson's disease appears to selectively affect functional connectivity of cortical sensorimotor, thalamic, and cerebellar networks (Gratton et al., 2019). The network-selective effects across various neurodegenerative disorders points to a system-level vulnerability for neurodegeneration.

Individual differences also play a role in the progression of disorders. For example, in Alzheimer's disease, the manifestation and progression of the disease vary widely among individuals, both in its cognitive presentation (Stopford et al., 2008) as well as neurodegeneration (Das et al., 2021). For instance, the typical Alzheimer's-related amyloid and tau pathologies can lead to variations in network disruptions, such as those observed in the default mode network (DMN), hippocampal network, and salience network (Balthazar et al., 2014; Dautricourt et al., 2021; Wales & Leung, 2021).

Beyond Alzheimer's disease, the realm of neurodegenerative diseases offers a myriad of examples that underscore the diverse network alterations observed in aging individuals. For example, in Parkinson's disease, dopaminergic deficits predominantly affect the basal ganglia network, leading to motor symptoms (Blandini et al., 2000). However, some individuals may exhibit atypical network disruptions that contribute to non-motor symptoms (Saeed et al., 2020), further highlighting the significance of individual differences. Recognizing the extensive variability in brain network changes during aging is pivotal not only for a deeper understanding of neurodegenerative diseases but also for the development of personalized medicine approaches (Vogel et al., 2023). Tailoring interventions and therapies to an individual's specific network alterations can enhance treatment efficacy and improve patient outcomes.

While increasing evidence shows that networks play a role in the progression of disease in neurodegenerative dementias and disorders, the exact role has not yet been defined (see Vogel et al., 2023 for an excellent review of this topic). One hypothesis is that networks act as passive conduits for pathological proteins to be transported, possibly trans-synaptically. A different, but not mutually exclusive, hypothesis is that networks play an active role in the transmission of pathological processes: while the strength of connectivity between two given regions affects the rate with which pathological proteins are transmitted, the increase in the pathological proteins changes the rate of neurotransmission, thus actively

influencing the spread of disease. Determining the role of networks in age-related disorders will be crucial for understanding how individuals transition from healthy to pathological aging, and how treatments can be tailored to the individual. However, due to heterogeneity across individuals, accounting for individual differences in network organization will be an important step forward in that direction.

As alluded to in the paragraphs above, the interactions between these networks are also altered with aging (Hausman et al., 2022). These altered interactions may reflect impairments when switching between internalized and externalized cognition (Spreng et al., 2012). For example, work by Spreng and Schacter showed that young adults flexibly switch their co-activation patterns, with the FPN and DMN co-activated during autobiographical, and the FPN and DAN co-activated in visuospatial planning (Spreng & Schacter, 2012). However, in older adults there was reduced deactivation of DMN regions during the visuospatial planning task, which was interpreted by the authors as a diminished ability to suppress the network. In addition, coupling of the DMN and FPN was seen during both autobiographical and visuospatial planning tasks, suggesting increased functional connectivity of these two networks.

One useful way of characterizing changes across multiple networks at once and their interactions is by representing brain networks as graphs and leveraging tools from the field of graph theory (Sporns, 2018). In this context, brain regions are represented as nodes in a graph, and the functional connectivity between any pair of nodes is represented as an edge (**Figure 3B**). From this graph, metrics can be computed that quantify the topography of the network and how information can be transferred across it.

A number of graph metrics have been reported to differ with age (reviewed in Deery et al., 2023), including global efficiency (the average inverse shortest path length in the network, a measure of integration; Achard & Bullmore, 2007; J. S. X. Chong et al., 2019), local efficiency (like global efficiency but within node clusters; Bagarinao et al., 2019; Bassett & Bullmore, 2006; Cao et al., 2014), integration (rapid exchange of information across multiple distributed regions; Bagarinao et al., 2019; Escrichs et al., 2021), modularity (the degree to which a system divides into distinct clusters or modules of highly interconnected regions; Cao et al., 2014; Gallen et al., 2016), and segregation (the processing of specialized information within a group of highly interconnected brain regions; Chan et al., 2014; Malagurski et al., 2020). These findings suggest that the functional organization of the brain, at large, is affected by age.

The perhaps most consistent finding from this domain is that the segregation of the brain into distinct networks declines with age, both cross-sectionally (Betzel et al., 2014; Chan et al., 2014; **Figure 3**) and longitudinally (Malagurski et al., 2020; see right-most panel in **Figure 1**). That is, as we age, brain regions begin interacting with regions in different systems more while interacting less with regions within the same network, which can be measured with a segregation index. A lower segregation index reflects lower functional specialization of a network. This phenomenon of desegregation is hypothesized to be related to neural de-differentiation (Chan et al., 2014), as discussed in the previous section (see Koen & Rugg,

2019 on de-differentiation). Interestingly, higher-order cognitive networks are more affected by desegregation, while sensorimotor systems are relatively unaffected and demonstrate increased resistance to connectivity disruptions with age (Chan et al., 2014). The decreased segregation observed among older adults is a consistent finding in both resting state and during cognitive tasks (Chou et al., 2013). Relatedly, modularity, which describes the degree to which a network exhibits clustering of its nodes into distinct subnetworks, also decreases with age (Cao et al., 2014). In older adults, this decline in modularity is thought to reflect a reduction in the functional integrity of network modules (Gallen et al., 2016). Similarly, other graph metrics point to a decrease in the extent to which regions couple into tight knit groups (e.g., local efficiency) and an increase in longer-distance projections (e.g., global efficiency, integration; Bagarinao et al., 2019; Bassett & Bullmore, 2006; Chan et al., 2014).

While there are consistent patterns of network alterations associated with aging, individual differences play a significant role in determining the extent and nature of these alterations. Li and colleagues explored the impact of individual differences on functional brain connectivity in aging (R. Li et al., 2017). Their findings revealed that individual variability in functional connectivity was more pronounced in the frontal and parietal cortex, regions associated with higher-order cognitive functions, as well as in the cerebellum, a region often overlooked in aging research. Notably, these same regions exhibit higher individual differences in functional connectivity

in younger adults as well (Mueller et al., 2013). These areas with heightened inter-individual variability exhibited strong correlations with cognitive performance, highlighting their relevance to tasks related to memory, attention, and executive functions. Long-range and inter-network connections emerged as key factors influencing cognitive ability differences in older adults (R. Li et al., 2017), underscoring the importance of considering individual differences in the connectivity between brain networks to gain a deeper understanding of cognitive aging.

Moreover, recent studies have provided additional insights into the relationship between lifestyle factors and functional connectivity in aging individuals. Dorsman et al. (2020) reported that in a sample of older adults, within-subject increases in physical activity were associated with greater functional connectivity between frontal-parietal and subcortical networks. Similarly, aerobic fitness has also been linked to differences in functional connectivity in older adults (Voss et al., 2010). Individual differences in aerobic fitness were found to be particularly associated with variations in the DMN, as well as tests of executive function and spatial memory. These findings highlight the potential impact of exercise on functional brain networks in aging populations.

The evidence reviewed in this section summarizes the notable effects of aging on functional large-scale systems. These findings have shed light on the importance of studying brain networks to understand how cognitive functions co-decline with network integrity. This has prompted the creation of

multiple datasets with the aim of characterizing age-related changes to functional systems with large samples of deeply phenotyped individuals (e.g. NKI-enhanced dataset (Nooner et al., 2012) and HCP-Aging dataset (Bookheimer et al., 2019), the Cam-CAN dataset (Shafto et al., 2014), among others). These studies will be crucial for understanding how brain networks change at a population level and their relationship to other physiological and cognitive age-related changes. However, a significant limitation is that researchers often face a choice between large sample sizes and extensive data per individual. While large sample sizes allow us to detect population-level effects, they do not adequately capture individual variability in brain network organization and cognitive decline. In the following section, we explore this limitation and others in greater detail.

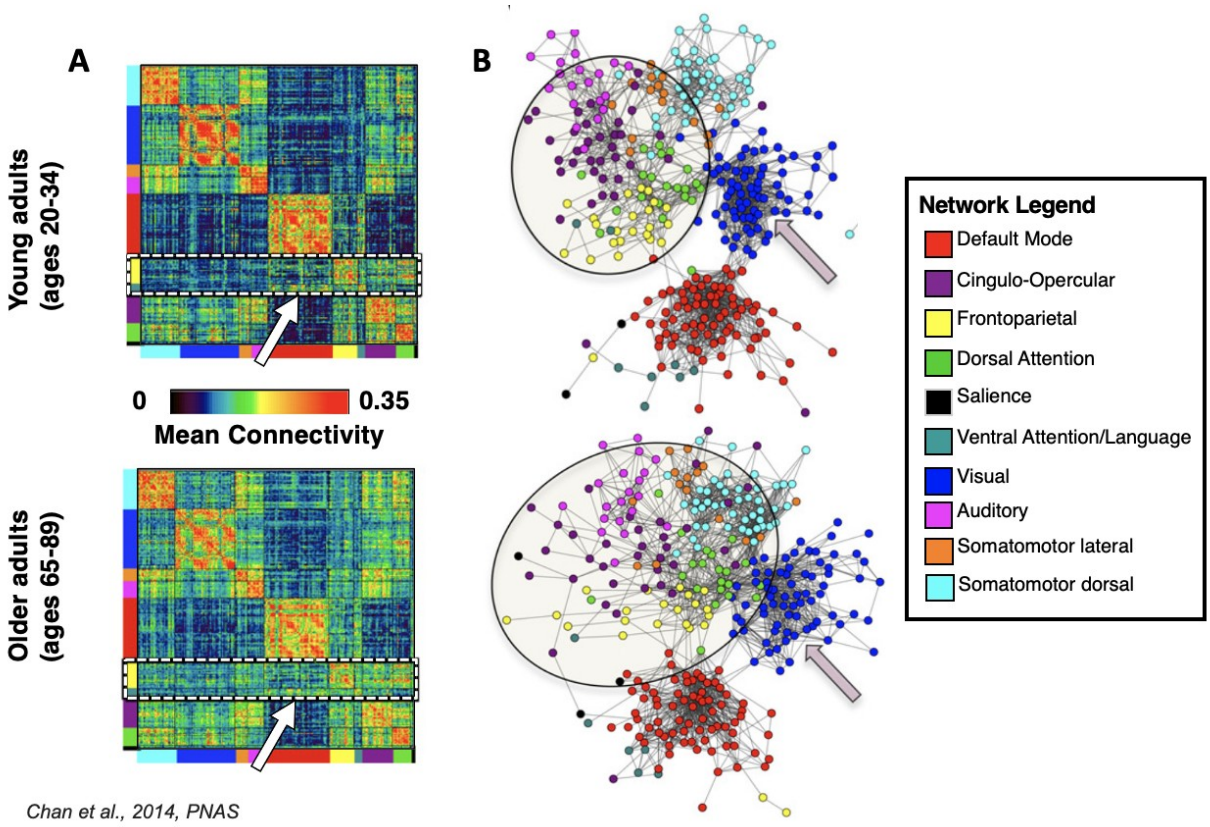

Figure 3- Functional networks in young and older adults. Networks are depicted here as functional connectivity matrices (left) and spring-embedded graphs (right) for young (top) and older (bottom) adults, adapted from (Chan et al., 2014). **A)** In functional connectivity matrices each row and column correspond to a node, and the color depicts the mean connectivity (z-scored), where cooler colors show lower connectivity, and warmer colors show higher connectivity (see color bar). The colors on axes correspond to the network label (see network legend). This visualization method allows us to see the typical structure where the connectivity within networks, shown on the on-diagonal blocks, is higher than the connectivity between networks shown on the off-diagonal blocks. Comparing the young adults (top) and older adults (bottom) visualization, we can appreciate that the colors appear less intense in older adults showing that within-network connectivity is decreasing, and between-network is increasing. **B)** In spring-embedded plots, each circle depicts a node, or brain region, and the lines signify an edge, or functional connectivity, between them. The color of each circle denotes the network label (see network legend). These plots show the relationships between nodes according to the spatial distance on the plot, where nodes that are more highly connected are more spatially proximal to each other. In these plots, we can see that nodes of the same color are highly interconnected and tend to cluster together, but there are connections across clusters of nodes as well. In comparing graphs from younger (top) and older adults (bottom), it is also apparent that there is decreased clustering of the nodes in older age. The arrow and circles emphasize noticeable examples of desegregation: the arrows point to the visual network, which shows some desegregation but looks relatively similar across the two age-groups, and the circles encapsulate two major cognitive control networks, the cingulo-opercular network (deep purple) and frontoparietal network (yellow), which have noticeably more distant nodes in older adults compared to younger adults.

4. Difficulties of studying individual differences in brain networks and aging

While substantial research points to variability in cognitive and neural trajectories associated with aging, studying individual differences in brain networks and their relationship with aging poses inherent challenges. For example, empirical and methodological choices such as scan length, preprocessing strategies, and parcellation choice can influence functional connectivity measures. In this section we expand on issues that in our view represent a significant hinderance to the study of aging networks, and particularly the study of individual differences in this domain. We discuss the importance of data quantity, denoising strategies, and parcellation choice given systematic differences across age groups and the great deal of heterogeneity that exists in aging brains.

4.1Scan time and data quantities

Research conducted thus far has uncovered many age-related changes to the brain's functional connectome, with less segregated, less modular systems, and less efficient transfer of information in older adults (see Deery et al., 2023 for a review). These age-related differences in functional networks have been correlated with cognitive measurements, and in many cases were found to be related to decreasing cognitive performance. However, an important consideration when interpreting existing evidence is that many previous studies have relied on limited resting-state functional connectivity data from each individual, typically ranging from 5 to 10 minutes. With this quantity of data, individualized functional connectivity

measures have low reliability (Birn et al., 2013; Gordon et al., 2017; Noble et al., 2017). Thus, more data than is typically collected is needed to achieve reliable measures of functional connectivity.

Reliability is typically calculated from z-scored functional connectivity matrices within an individual by using intraclass correlation or related measures (Birn et al., 2013; Noble et al., 2017), though it can also be calculated from the consistency of spatial brain-wide connectivity maps (Gordon et al., 2017). Gordon and colleagues specifically addressed this question of reliability at the individual level using both connectivity matrices and spatial connectivity maps in a small group of highly sampled younger adults, with 10 functional MRI sessions each (Gordon et al., 2017). Using a test-retest reliability analysis, where both connectivity matrices and spatial maps calculated from a large volume of data are compared to connectivity calculated using increasing amounts of data using correlation, they determined that with approximately 30-45 minutes of high-quality (low-motion) data, individualized measures of cortical functional connectivity could achieve very high reliability ($r>.9$). The amount of data necessary to achieve such levels of reliability notably differs with signal quality, such that some regions (e.g., cortex) achieve high reliability more quickly than regions with lower SNR (e.g., basal ganglia, thalamus, cerebellum). For example, Marek et al. (2018) found that 90 minutes of data are necessary to achieve reliable cerebellar functional connectivity, and Greene et al. (2020) found that for subcortical measures, 100 minutes of data were necessary to

achieve r>0.7 reliability. Importantly, these estimates of data quantities needed to achieve high reliability are based on single-echo MRI sequences. Recent evidence discussed in section 5 suggests that these data quantities are reduced when multi-echo fMRI sequences are employed (Lynch et al., 2021), facilitating the process of acquiring reliable measures at the individual level.

In addition to functional connectivity, measures of network properties, like modularity and global efficiency, (Gordon et al., 2017), and segregation (Han et al., 2024), also need similar amounts of data to achieve high reliability. Notably, for these measures, the magnitude of the metric changes rapidly at small quantities of data and only stabilizes at around 30 minutes. Of crucial importance, the apparent noise in these measures with small data quantities does not appear to be random, but instead a systematic bias is introduced. For example, with smaller quantities of data, modularity values will be systematically lower than those with greater amounts of data, and the value increases more rapidly at smaller amounts of data, making it such that differences in modularity could be inflated by even slight differences in data quantity (**Figure 4A**). This suggests that with the typical amounts of data that are collected for most studies, not only are the metrics biased, but they may also differ systematically based on the amount of data that is used to calculate them.

Motion is another factor that indirectly contributes to systematic differences in data quantities. While most studies collect the same amount of

data per person, a frequent strategy to mitigate the effects of motion on functional connectivity data is to identify high-motion frames and remove them. However, due to the higher degrees of motion in older adults relative to young adults (Gratton, Dworetsky, et al., 2020; Saccà et al., 2021), this will also lead to systematic differences in the amount of data that are included in an analysis when high-motion frames are removed, which may be interpreted as age-related. Thus, as a strategy to prevent bias due to differing amounts of data, it may be beneficial for researchers to match the amount of data when comparing across individuals and across groups.

4.2 Non-neuronal sources of variability

Measures of functional connectivity are influenced by various sources of non-neuronal activity, such as head motion and respiratory artifacts, with older adults exhibiting pronounced susceptibility (Gratton, Dworetsky, et al., 2020; Saccà et al., 2021). Head motion is perhaps the best studied artifact, and is a confounding factor that is particularly important to address since even submillimeter movements can bias functional connectivity data in distance-specific ways, such that long-range connections are particularly affected (Power et al., 2012; Satterthwaite et al., 2012).

The effects of motion on functional connectivity measures are exacerbated by the fact that they differ systematically across populations, with developmental (Satterthwaite et al., 2012), older adult (Madan, 2018; Saccà et al., 2021; Savalia et al., 2017), and clinical (Dosenbach et al., 2017; Pardoe et al., 2016) populations exhibiting higher levels of motion than

neurotypical younger adults. Importantly, this systematic difference in motion levels, if not properly addressed, can lead to robust, but inaccurate findings. For example, previously multiple studies found that neurodevelopment in youth is associated with increasing long-range connections and decreased local connectivity (Dosenbach et al., 2010; Fair et al., 2007, 2008, 2009). However, it has been shown that much of the original age-related effects on functional connectivity were inflated by motion (Satterthwaite et al., 2013). Importantly, and relevant to the literature on aging, Satterthwaite and colleagues also discovered that, while motion-related noise inflated age-related differences in functional connectivity, it also obfuscated differences in functional segregation, which were enhanced by controlling for head movement. These findings underscore the importance of addressing head motion to obtain accurate and reliable functional connectivity measures.

In addition to head motion, a potential non-neuronal signal that can bias functional connectivity estimates is respiration (Birn, 2012). Respiratory signals can influence resting-state data in several ways. First, changes in respiration – especially deep breaths – cause changes to the partial pressure of carbon dioxide (pCO2; a measure of CO2 in the blood), which in turn dramatically affects the BOLD signal (Bright et al., 2009; Kastrup et al., 1998; Poulin et al., 1996; Power et al., 2020). Secondly, respiration causes enlargement of the chest cavity, which leads to dynamic disturbances in the magnetic field (Fair et al., 2020; Gratton, Dworetsky, et al., 2020; Power et

al., 2020). The disturbances in the magnetic field can appear as high-frequency “motion” in functional alignment metrics, thereby acting as a confound when motion denoising strategies are applied to functional connectivity data. Both respiration-related effects are exacerbated in older adults, who may have more difficulty breathing in prone positions (leading to more changes in respiration; Gratton et al., 2020). Thus, in order to measure true differences in functional connectivity, it is important to attenuate potential confounding factors related to individual differences in breathing rate, as well as systematic differences across groups as a function of age and physical health.

Given that there is a systematic difference in the head motion and breathing rate between younger and older adults, and that these parameters bias functional connectivity, addressing their effects is crucial to disentangle true aging-related effects on functional connectivity. However, this may be particularly crucial in individual differences research given that participants differ from one another in the degrees of motion that they exhibit and the frequency of respiration, depending on factors such as cardiovascular health (Gratton, Dworetsky, et al., 2020). For example, in a study by Siegel et al. (2017), the links between head motion during fMRI data collection (measured via frame-to-frame signal variance) and behavioral, demographic, and physiological measures were examined in the Human Connectome Project (HCP). They found that a number of these measures correlated with head motion in the MRI scanner, including brain volume, BMI, measures of tobacco

use, fluid intelligence and other cognitive abilities, and with psychiatric scales such as the DSM Antisocial Behavior (Siegel et al., 2017). Because of this dependency, not accounting for motion led to inflated functional connectivity-behavior relationships.

Understanding age-related differences in fMRI signal is further complicated given the reliance of the BOLD signal on vascular physiology. The neurovascular coupling that leads to a measurable increase in blood flow after neural activity may be affected by age and, subsequently, may not be equivalent across older and younger adults (Turner et al., 2023; see Zimmerman et al., 2021 for a review). Age-related changes in the BOLD hemodynamic response have been found within the motor cortex (D'Esposito et al., 1999) and primary sensory regions (Buckner et al., 2000) with differences attributed to a reduced signal-to-noise ratio in older adults (D'Esposito et al., 1999). However, the strength and direction of age-related changes in BOLD signal is variable, with some regions showing no difference in BOLD neurovascular coupling across the lifespan (Abdelkarim et al., 2019).

A number of strategies have been developed to address these non-neuronal biases on fMRI functional connectivity. For example, motion and respiratory denoising can be employed through additional pre-processing steps. Ciric et al. (2017) compared many strategies for denoising functional connectivity data, and showed that a combination of motion censoring and global signal regression (along with related techniques) was able to dramatically reduce both inflation and distance-dependent artifacts

associated with motion. These strategies were also able to address the brain-behavior confounds observed in Siegel et al. (2017). Mitigating for vasculature-related confounds can be a challenging endeavor, and often involves collecting additional types of data, such as arterial spin labeling (ASL), or breath-hold tasks to measure the CO2 reactivity of blood vessels (see Tsvetanov et al., 2020) for a description of multiple strategies). However, it is important to note the dependency of neural activity of the vasculature of the brain, often forming a highly integrated system where, when vascular physiology breaks down, so does neural physiology (see Zimmerman et al., 2021 for a review). Thus, separating vascular from neural activity may not always be feasible nor desired. Nonetheless, when possible, capturing information about vascular integrity may be useful for disentangling age-related effects that are caused by vasculature changes from qualitative differences in the way that the brain processes information as we age.

4.3Heterogeneity in structural and functional brain organization

Challenges in the study of aging of functional networks can also arise due to heterogeneity in the structural and functional organization of the brain. A common step in the preprocessing of neuroimaging data is to align individual brains to a brain template or ‘atlas’ (typically MNI or Talaraich) using automated structural registration based on macro-anatomical features. Difficulties in this step, as emphasized by Buckner et al. (2004), stem from

significant variability in head size and brain anatomy among the older adult population. Unlike younger adults, older adults often exhibit significant brain atrophy, which can further complicate the anatomical registration process, potentially leading to greater registration errors in brains with greater atrophy. One potential solution is to use a template based on merging data from young and old adults, rather than using a template based on younger adults alone (Buckner et al., 2004). Buckner et al. (2004) showed that in addition to this method performing well, it *minimally* biased the registration from patients of dementia who showed substantial atrophy compared to alternative methods.

Heterogeneity in the functional organization of the brain can also cause challenges when mapping the boundaries across distinct brain regions across multiple individuals. Much prior work has relied on a-priori parcellations[1], or delineations between brain regions that are assigned to different functional networks, with network assignment usually based on (young-adult) group average representations of brain networks. These parcellations are then used to extract a signal of interest in a given dataset. For example, the a-priori Gordon parcellation (Gordon et al., 2016) can be used to extract the average signal for a specific network (e.g. DMN) within each participant in a study. These measures can then be used to calculate different metrics or properties

[1] Here, we refer to specifically functional parcellations, but note that parcellations that are based on structural features are also commonly used

of the individual parcels or networks, and to draw conclusions about their relationship to cognition and behavior.

However, given the substantial changes to the brain's functional organization that occur with aging, such as network desegregation, the application of parcellations based on young adults may introduce a systematic difference in the fit of published parcellations to different age groups. In particular, functional connectivity may appear aberrant in older adults relative to young adults for multiple reasons, including: (1) networks break down, as it is typically interpreted, or (2) networks vary systematically in older adults, not fitting the group average template based on young adult data and contaminating functional connectivity measures. Bryce et al. (2021) showed that parcellation choice matters in developmental samples (particularly in within-network connectivity), and Han et al. (2018) suggests this may be the case in older adults as well. Namely, the spatial correspondence of brain parcellations derived from young adults decreases with increasing age, suggesting a systematic change in the underlying functional architecture. Thus, brain parcellations tend to be more accurate when a group parcellation that has been derived from individuals from similar ages is applied. That same study found that the variance of these measurements increased with age, suggesting a systematic difference in inter-individual variability across groups (Han et al., 2018). This, compounded with the increased inter-individual variability in rs-FC in older adults, suggests that using parcellations from young adults on older brains

may yield incorrect (or at least heterogeneous) measurements of functional connectivity. This evidence, along with the findings reviewed throughout this section, underscore the importance of considering how heterogeneity impacts methodological choices when interpreting results in aging research.

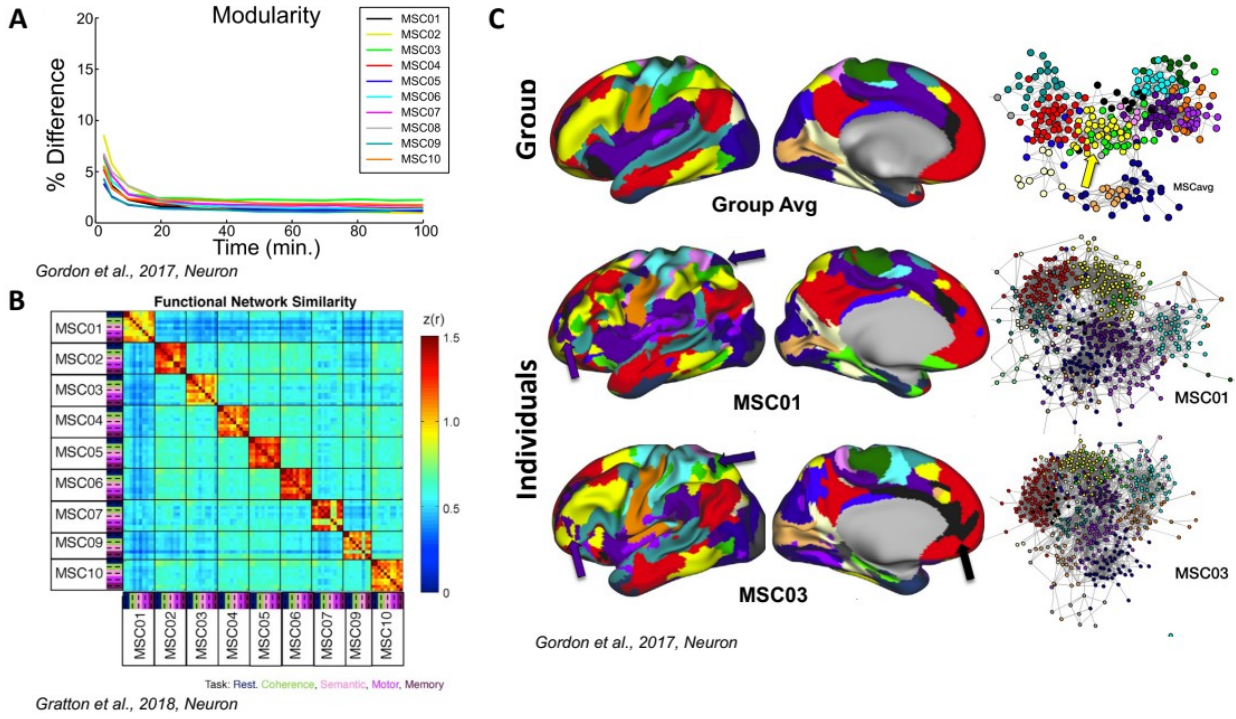

Figure 4 - Precision measures of resting-state functional connectivity in a cohort of highly sampled individuals from the Midnight Scan Club (MSC). A) Analyses of test-retest consistency of modularity measurements show that the value of the modularity index changes very rapidly at small quantities of data, but stabilizes at >20 minutes of high-quality data (Gordon et al., 2017). In this plot, each line depicts one individual; the y-axis plots the difference between the modularity metric in a sub-sample of data (amount indicated on the x-axis) and modularity measured from a very large pool of held out data from that individual. **B**) Comparisons of the resting-state functional connectivity maps across individuals and across tasks show that individuals exhibit similar patterns of rs-FC across sessions and tasks (indicated by the warm colors in the on-diagonal blocks) and show substantially lower similarities to other individuals (indicated by the cool colors on the off-diagonal blocks) (Gratton et al., 2018). Each row and column correspond to a session and task group by participant. Thus, functional connectivity is largely consistent within a person over time and task states, but distinct across people. **C**) Mapping individual-specific networks on the brain shows that individual maps exhibit localized regions that are not present in the group average representation of functional networks (Gordon et al., 2017). These brain visualizations show the spatial organization of brain networks for the group average (top) and for two individuals (bottom). The arrows point to regions of networks that are present in the individual maps, but not in the group average. Next to the brain visualizations, we show the spring-embedded plots. Again, these graphs

show some broad consistency across individuals, but also exhibit idiosyncrasies in their organization.

5. Individualized approaches and potential for the study of aging

As reviewed, cognitive and neural metrics change with age, but to variable degrees across individuals. However, heterogeneity across various sources of noise (e.g. head motion and respiration), as well as in structural and functional organization of the brain can contaminate observations, while systematic differences in these factors can bias results of comparisons across age groups. In this section, we discuss the utility of individualized approaches to not only mitigate the effects of heterogeneity, but also exploit it to expand our understanding of the brain bases of age-related cognitive changes.

5.1 Precision fMRI

An important limitation of fMRI is that it has intrinsically low signal-to-noise ratio. In order to increase the signal in fMRI data, a common approach is to average data across subjects. This approach has the advantage of increasing the signal of interest and reducing sampling variability, but it obfuscates idiosyncratic information. An alternative way to improve signal to noise, that also preserves individual-specific features in the data, is to collect extended amounts of data from each individual. This paradigm, which we call *precision fMRI* (and others have called ‘dense sampling’ or ‘deep imaging’), entails collecting over 1 hour of resting-state fMRI data from each participant, typically across multiple sessions, in combination with stringent denoising to address motion and physiological artifacts. This approach was

pioneered by Russ Poldrack and colleagues in the MyConnectome study, where a single individual completed 84 sessions over more than a year, accumulating around 14 hours of resting-state fMRI data(Poldrack, 2021; Poldrack et al., 2015). Using these extended data quantities, Laumann and colleagues characterized the individual's brain functional organization and compared it to a group average (Laumann et al., 2015). A striking observation was that, while the spatial organization of the individual-specific network map resembled that of the group average, the individual exhibited idiosyncratic topological features. Since then, multiple datasets with extended acquisition have been collected. For example, the Midnight Scan Club study collected about five hours of resting-state fMRI data from ten individuals across ten sessions (Gordon et al., 2017), while a study by Braga and Buckner collected over two hours from four individuals across 24 sessions (Braga & Buckner, 2017). For additional examples and characteristics of precision fMRI studies, the reader is referred to (Gratton, Kraus, et al., 2020) (see Table 1 in that work). By collecting extended amounts of data and using state-of-the-art motion filtering techniques, precision fMRI has proven to produce highly reliable measures of individualized rs-FC across multiple individuals (Gordon et al., 2017).

Importantly, these precision measures have been shown to be stable across sessions as well as task states (Gratton et al., 2018; **Figure 4B**), suggesting that individualized rs-FC measures are able to measure trait characteristics of functional brain networks. To date, however, the stability of

precision fMRI measurements has only been studied in young-to-middle-aged adults. Some evidence suggests the decreased stability of network measures in older adults (Iordan et al., 2018), suggesting higher temporal variability of functional connectivity in aging. Thus, the stability of precision measures in older adults will be important to establish the feasibility of their use as biomarkers. However, the high degrees of stability observed in younger adults using extended amounts of data are encouraging that the same will hold true for older adults. Precision fMRI approaches will be crucial to determine this. Additionally, the combination of extended amounts of data and appropriate denoising techniques will be important as to determine to what degree decreased stability in older adults may be due to neural and non-neural (e.g. increased motion) sources of variability.

Precision fMRI has been used to map the organization of networks at the individual level, not only in the cortex (Gordon et al., 2017; **Figure 4C**), but also in the subcortex (Greene et al., 2020) and the cerebellum (Marek et al., 2018). The ability to reliably map the functional organization of regions in the brain that are difficult to image due to the low signal-to-noise ratio opens the door to answer many important questions. For example, in recent years the importance of the cerebellum in cognition (Janacsek et al., 2022), in neurocognitive aging (Arleo et al., 2023; Bernard, 2022), and in disorders like Alzheimer's disease (Gellersen et al., 2021; Schmahmann, 2016) has begun to be elucidated. However, this structure is frequently ignored due to its low signal-to-noise ratio and physiological confounds, among other factors

(Priovoulos & Bazin, 2023). The utilization of precision fMRI methodology overcomes some of these difficulties, thus allowing the opportunity to characterize functional changes that occur in the cerebellum (where structural changes are prominent) during healthy and pathological aging.

Most importantly to our topic of variability in aging, precision approaches represent an advancement in our ability to measure individual differences in functional brain networks (see arrows in **Figure 4C**). Studying the profiles of network variability in older adults will be important to elucidate the sources that drive increased variability in cognitive decline—knowledge that is imperative for the development of predictive models and targeted treatments. For example, a longitudinal precision fMRI study would allow us to map the trajectory of functional organization at the local and global level and how these trajectories relate to participant characteristics. Such a study design combined with multimodal imaging approaches, for example ASL sequences, could be a powerful approach to address questions on the causal relationship between degradation of cerebro-vasculature and brain reorganization. Precision fMRI combined with reliable behavioral measures can allow researchers to disentangle brain changes that may indicate beneficial, compensatory mechanisms versus changes to the organization of the brain that contribute to a decline in cognitive functions.

However, a hurdle in applying these methodologies to any population, but particularly one which systematically displays higher degrees of motion such as older adults, is the large quantities of data that are needed in order

to obtain reliable individualized measurements. Obtaining these amounts of data represents a financial and time constraint for researchers, and a considerable time commitment from research participants. Furthermore, it prompts an important concern that the need for longer scanning periods may result in biased samples, since some participants may not be able to complete these more extensive data collection procedures. Indeed, a bias already exists in most fMRI studies of aging, as only individuals who are healthy enough to evade MRI contraindications (and the frequently included exclusion criteria for other pre-existing neural and psychiatric conditions) and who have the ability to attend laboratory visits are able to participate in this research. Longer scan times may result in further exclusion of individuals who may be uncomfortable with or unable to lay for prolonged periods of time in an MRI scanner.

This is an important concern that will need to be addressed in future precision fMRI research in aging in particular. In our laboratory, we have previously successfully collected such quantities from healthy older participants (NIA pilot sub-project of P30AG13854: Precision mapping of brain networks in older adults, and NIMH R01MH118370-S1: Individual differences across the lifespan), as well as patients of Parkinson's Disease (R01NS124738: Precision Mapping Functional Connectivity in Parkinson's Disease) utilizing various strategies to mitigate some of these issues. First, we used a multi-session approach, where participants were invited to five MRI sessions that were approximately one hour long each. Rather than

collecting multiple hours of MRI data in one day, participants were only in the scanner for about one hour a day, making this design more tolerable and thus reducing discomfort. Increased rates of attrition may be a risk of multi-session designs, although it should be noted that attrition was minimal in our experience. In our most recent aging precision fMRI study (with 3 behavioral and 5 MRI sessions), we were able to collect data from 75 participants (ages 62-75), with >90% retention after the first MRI session. In addition to breaking the study up into multiple sessions, each session was comprised of multiple 5-minute long resting-state runs with on-line motion monitoring software (Dosenbach et al., 2017). The multiple short runs allowed us to give participants breaks from keeping their eyes open and to communicate with the participant in-between runs to ensure their comfort, while the on-line motion monitoring system allowed us to provide them with feedback in-between runs to keep motion to a minimum. By using these strategies in a pilot study (NIA pilot grant P30AG13854: Precision mapping of brain networks in older adults), we were able to collect at least 40 minutes of resting-state data per session from eight older adults (ages 65-75) with a high percentage of the data (87% on average) retained after motion filtering. Thus, the collection of extended amounts of data can be feasible in older adults.

In addition to the usage of strategies to ameliorate the burden of long scanning sessions on older adults, new sequences continue to be developed and tested that promise to alleviate this concern. Multi-echo sequences have been used to obtain reliable individual-specific functional connectivity

measures with smaller amounts of data (Lynch et al., 2020). In multi-echo fMRI, multiple images are collected per volume, which allows for improved contrast, reduced susceptibility artifact, and an increased ability to model non-neuronal noise (Lynch et al., 2021). These advantages over single-echo sequences result in increased test-retest reliability with shorter scan times. The utilization of multi-echo sequences could facilitate the collection of highly reliable individualized datasets and may be especially fruitful for populations for which acquiring large amounts of data is particularly difficult, such as older adult and clinical populations. We are hopeful that with the development of these new techniques, the potential for bias and burden on research participants will be ameliorated.

5.2 Individualized parcellations:

Group average representations of the brain's functional organization have yielded important insights for the study of brain-behavior relationships. However, there is substantial variability in the size, location, and properties of functional networks across individuals (Braga & Buckner, 2017; Finn et al., 2015; Gordon et al., 2017; Marek et al., 2018; Mueller et al., 2013; Seitzman et al., 2019). Thus, examining the functional architecture of the brain at the individual level may be crucial to elucidate the links between networks and behavior. As we enter a new era of personalized neuroscience, approaches have been developed to mitigate some of the sources of bias and noise that have prevented us from acquiring reliable individual-specific brain measures

using traditional methods. These approaches aim to create robust and reliable representations of brain organization at the individual-level.

One area of focus is to map boundaries of cortical regions, or parcellations, that are specific to each person. At least two different approaches exist to accomplish this: a prior-based approach and a data-driven approach. Prior-based models rely on group-average brain parcellations, but allow for variability across individuals in the size, shape and exact location of parcels. This approach has several benefits, including that it requires less data, and simplifies comparisons across individuals (e.g. by constraining the number of brain regions, or parcels, such that each person has the same number). Importantly, individual-specific network topography representations acquired using prior-based approaches have been shown to increase the predictive accuracy of network measures on behavioral and cognitive factors (Kong et al., 2019). In contrast to prior-based models, data-driven approaches are agnostic to the group-average parcellation of the brain and only rely on the individual's data to delineate the boundaries between functionally meaningful units (Gordon et al., 2016; Wig et al., 2014). While these approaches require substantially more data to obtain a reliable map of the individual's functional organization and often result in solutions with differing number of cortical areas per individual (complicating cross-subject comparisons), they are not constrained by group-based priors, and thus are more sensitive to individual differences.

It is important to establish the validity of individualized representations of spatial topography. There are several lines of evidence that have been used to show that individualized network maps reflect meaningful deviations in functional organization. First, individualized network maps have been shown to match on to individualized task responses better than group defined maps (Salvo et al., 2021). For example, (Gordon et al., 2017) showed this correspondence for the motor and context networks, while (DiNicola et al., 2020) showed this for the DMN-A and DMN-B networks, (Braga et al., 2020) for the language network, and (Du et al., 2024) showed correspondence across a range of task contrasts. Additionally, (Tavor et al., 2016) has also demonstrated that individualized network maps can be used to predict individual task activations across a range of contrasts in the Human Connectome Project. Second, individual network maps can be compared with non-fMRI based measures, such as fine-scale anatomical features. In (Gordon et al., 2017), the authors were able to demonstrate that individualized network maps better aligned with shifts in myelin content across regions of the temporo-parietal cortex. Third, individual network approaches have been shown to outperform group-average network definitions in predicting behavioral measures outside of the scanner, across a range of cognitive, personality, and emotion measures (Kong et al., 2019, 2021). Thus, a number of validation approaches have suggested that individualized network methods outperform standard group approaches in identifying functional neuroanatomic units in the human brain.

The application of these approaches may be especially important to the study of how cortical organization changes as a function of increasing age. As described in previous sections, humans generally exhibit a large degree of variability in brain measurements to begin with, and this may be exacerbated by variable patterns of atrophy stemming from heterogenous life trajectories and other factors that influence the course of brain aging. This assumption is supported by observations of higher individual variability in rs-FC (Ma et al., 2021) and increased variance in rs-FC patterns within parcellations in older cohorts (Han et al., 2018), which may be linked to higher spatial variability. High spatial variability can create issues by giving rise to heterogenous and inaccurate measures of rs-FC in older adults when a group average parcellation with a poor fit is applied to an individual. Moreover, higher spatial heterogeneity may also mean that, by averaging together data from across older participants, we are obtaining a representation that is not accurately depicting an individual brain.

This spatial variability can be addressed with the use of individualized parcellations, underscoring the importance of using such methods to study aging. Individualized parcellations have been shown to produce more homogenous measures of functional connectivity (Gordon et al., 2016). Similarly, (Han et al., 2018) showed that using a group parcellation that is appropriate for the age group also produces more homogenous measures, although variance was still higher for older adults compared to young adults. This suggests, not only that there may be systematic differences in spatial

organization across young and older adults (thus using a group average parcellation of young adults is not appropriate for aging studies), but also that individual specific parcellations may produce more accurate measures of the connections across brain regions. Using more precise measures of functional connectivity in older adults can help us identify whether age-related effects are due to true qualitative changes in brain networks, or to increased spatial variability, which would introduce noise into our measures. Moreover, given recent evidence suggesting that individual differences in spatial topography of functional networks can predict several cognitive and personality measures with higher accuracy (Kong et al., 2019), applying individualized parcellation approaches may be a fruitful avenue to study how age-related changes to the organization of the brain are related to declining cognitive functions.

5.2 Insights from individualized approaches

While the development of individualized approaches is relatively recent, their utility is becoming increasingly apparent as we begin gaining insights about the brain through their application. For example, Gratton and colleagues used a precision fMRI dataset and individualized network mapping to examine the factors that drive functional connectivity patterns in individuals, and found that individualized networks are driven largely by group and individual-specific factors, and to a much lesser extent by day-to-day and task-related variation (Gratton et al., 2018). In the cerebellum, Marek and colleagues found that there is a greater degree of inter-individual

variability compared to the cortex (Marek et al., 2018). Interestingly, there is a 2.3x over-representation of the frontoparietal network in this structure. That is, compared to the proportion of cortical surface area dedicated to this network, the proportion of cerebellar surface area is 2.3 times larger on average. The frontoparietal system is highly important for cognitive control and cognition in general (Marek & Dosenbach, 2018), and it is affected during the aging process (Campbell et al., 2012). Despite this, little is known about how the representation of this network is affected in the cerebellum in older adults. In the subcortex, Greene and colleagues used precision fMRI to disentangle the overlapping functional connectivity of multiple networks in single regions (Greene et al., 2020). This overlap could in theory be due to two different reasons. It could be due to 1) true connectivity and integration across multiple networks, or 2) to artifact arising from averaging together data from multiple individuals with heterogenous patterns of functional connectivity. They found that, in the basal ganglia and thalamus, there are true “integration zones” where connectivity is high with multiple networks, and these integration zones occur with predictable combinations of networks. Furthermore, evidence continues to emerge suggesting that some large-scale networks can be further parcellated into multiple sub-networks that are linked to separate, if related, tasks (Braga & Buckner, 2017; DiNicola et al., 2020; Gratton et al., 2022). Importantly, the increased resolution that individualized approaches gives us is necessary to observe these subnetworks, as these subnetworks are often spatially interdigitated with

one another, and inter-individual heterogeneity can blur these closely juxtaposed regions. Thus, individualized approaches allow us to map the functional organization of the brain with increased reliability, stability, and detail than ever before.

With elucidating the individual-specific organization of functional networks comes the ability to identify regions with idiosyncratic functional connectivity, that have large deviation between an individual and a group average (Seitzman et al., 2019). These regions, which we have called “network variants,” are identified by comparing the functional connectivity brain maps of each individual with that of the group average using spatial correlation. The resulting spatial correlation maps are then thresholded to the lowest similarity values to show the regions where each individual is most different from the group (see **Figure 5**). These network variant regions have been found in every individual that has been studied so far. Importantly, they appear in consistent locations across sessions, are more typically associated with higher-order cognitive networks, show activation related to the network assigned to it based on the individual’s data (Seitzman et al., 2019), and they appear consistently across rest and task states (Kraus et al., 2021), suggesting these are trait-like features unique to the individual rather than artefactual deviations from the average. Interestingly, network variants are not always simple shifts in the borders of functional networks that you would observe if one network encroached on another but can appear also in isolated locations that are more distant from

the network. These types of deviations have been previously referred to as “ectopic intrusions”, and may be more tightly linked to environmental, as opposed to genetic, influences (Dworetsky et al., 2024). Crucially for the study of brain-behavior relationships, network variant regions have been shown to be related to behavior. In their work to characterize network variants, Seitzman, Gratton, and colleagues found that the network profile of variants correlated with measures of life satisfaction and history of drug abuse (Seitzman et al., 2019). Network variants have also been shown to relate to handedness (Perez et al., 2022), and ongoing work is dedicated to examining their relationship with higher-order cognitive functions. Notably, this work has largely focused on examining individualized networks in young adults, and not in older adults.

So far, only a small amount of literature has leveraged individualized approaches to the study of aging populations. In these works, individualized parcellations and multi-echo sequences were used to obtain personalized measures of brain network organization with higher signal-to-noise ratios, reliability, and sensitivity to individual differences relative to traditional methods. These studies have found patterns of global network de-differentiation, as well as topographically discrete, network-specific patterns of de-differentiation (Setton, Mwilambwe-Tshilobo, Girn, et al., 2022), replicating previous results, but using person-specific parcellation schemes that can capture individual variation in cortical organization with higher precision (M. Chong et al., 2017). Individualized approaches have also shown

associations between functional connectivity and measures of loneliness and empathy (Mwilambwe-Tshilobo et al., 2023), autobiographical memory (Setton, Mwilambwe-Tshilobo, Sheldon, et al., 2022), and with individual differences in moral decision making (Huang et al., 2021). Interestingly, within- and between-network connectivity have also been associated with brain health, defined via white matter lesion load (Kantarovich et al., 2022). While these studies do not directly compare brain behavior correlations using individualized parcellations compared to group-based parcellations in older adults, the correlation values reported tend to be higher (typically within the range of r=0.2 and r=0.5) than most studies that measure the relationship between rs-FC and various domains of behavior. Similar findings support the higher sensitivity of individualized parcellations for brain-behavior predictions in young adults (Kong et al., 2019, 2021) and clinical cohorts (Brennan et al., 2019; D. Wang et al., 2020). In patients of obsessive-compulsive disorder (Brennan et al., 2019) and psychotic illnesses (D. Wang et al., 2020), individualized parcellation schemes significantly predicted a variety of symptoms, while typical group-level parcellations performed at chance. Similarly, (Gordon et al., 2018) found that highly-reliable measures (derived from higher data quantities) are necessary to obtain functional connectivity measures that are sensitive for prediction of symptoms related to traumatic brain injuries in veterans. Beyond brain-behavior correlations, it has also been shown that individualized parcellations regions of interest (ROIs) perform better than atlas ROIs when assessing annual percentage

change in tau using PET (Leuzy et al., 2023). The evidence presented here suggests that using reliable measures of rs-FC combined with individualized approaches to mapping the organization of brain networks may be necessary to obtain the sensitivity required to produce biomarkers with clinical utility.

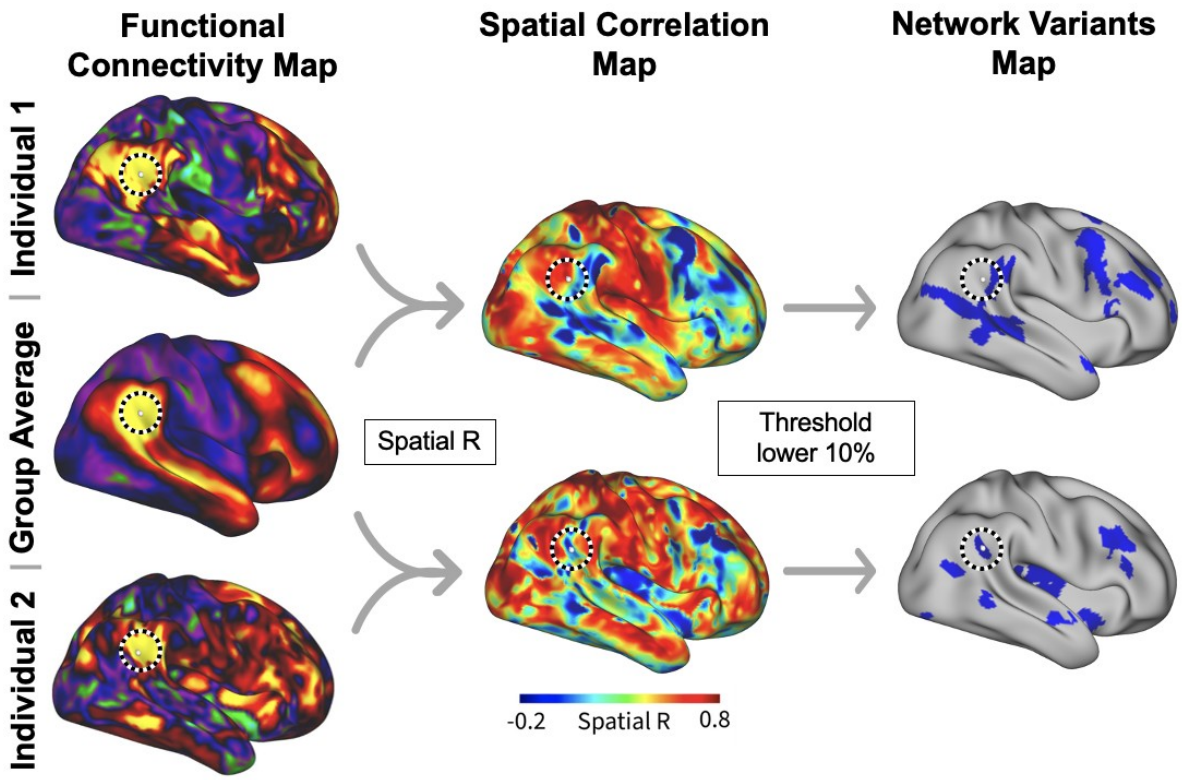

Figure 5 – Network variants are regions of low similarity between functional connectivity maps of a group average and a single individual. *Regions of idiosyncratic functional connectivity (FC) patterns, or network variants, are identified by comparing the whole-brain connectivity patterns between a group average and a single individual using spatial correlation. For each vertex, the FC map for the group and the individual are compared, thus resulting in a spatial correlation map which contains a similarity value per vertex. This spatial correlation map is then thresholded to the lowest 10% of correlations to obtain the regions that are most dissimilar between the individual and the group. These resulting regions are what we call network variants. Upon their identification, these regions are typically assigned to the networks with which their connectivity patterns overlap the most. (Seitzman et al., 2019) found that the task-evoked activation within variant regions corresponds to the network to which they are assigned based on connectivity patterns, rather than the network to which their anatomical location is typically associated with, suggesting that they represent true individual differences in functional organization.*

6 Open questions and future directions:

As we have discussed throughout this review, the promise of embracing individualized approaches in the study of neurocognitive aging has become increasingly evident. As our understanding of the complex interplay between genetics, lifestyle, and environmental factors in aging-related cognitive decline deepens, it is crucial that future research aimed at investigating the neural substrates of cognitive decline prioritizes obtaining reliable brain network measures that have high predictive validity over cognitive measures. By moving beyond the conventional one-size-fits-all group average approach, the field can unlock the rich tapestry of individual differences in neurocognitive trajectories of age-related changes to brain networks.

In addition to increasing our understanding of how changes to the brain throughout the lifespan affect cognition, the use of individualized approaches to the study of brain networks may have important therapeutic implications. One example is aiding in the design of targeted neurostimulation-based therapies tailored to the unique functional neuroanatomy of an individual. A number of groups have argued that these tailored approaches, where precision imaging is used to identify optimal target sites in each individual, may be more effective than a standard “one-site-fits-all” approach (see (Cash & Zalesky, 2024) for an interesting review). Such benefits are beginning to be observed in treatments for Parkinson’s disease (e.g. (Q. Wang et al., 2021) using person-specific structural connectivity) and depression (e.g. Lynch et al., 2022; Siddiqi et al., 2021) and being tested in clinical trials (E. J.

Cole et al., 2022). Beyond pathological conditions, an increasing number of studies have observed the benefit of using personalized targets (relative to a standard target) to deliver neuromodulation that improves cognitive performance (e.g. Cash et al., 2021, 2022; Dengler et al., 2024), suggesting such therapies may in the future be used to ameliorate cognitive decline. Another important application for individualized approaches could be the improvement of diagnostic techniques for neurocognitive disorders. Identification of network-based biomarkers for age-related pathologies would provide objective and non-invasive diagnostic criteria. Furthermore, it may allow us to identify such deviations from a normative trajectory early enough to apply preventative therapies. The potential for this application of precision fMRI is supported by the observation that individualized network approaches outperform group average methods in predicting cognitive, personality, and emotional variables (Kong et al., 2019) and benefit from added scan time for each individual (Ooi et al., 2024). In these ways, and potentially more, individualized methods to studying brain networks could be crucial for preventing and treating age-related disorders.

Some important questions remain, however. As discussed previously, precision fMRI techniques have been validated in younger adults, providing a benchmark for the amount of data needed to obtain highly reliable representations of resting-state functional connectivity, metrics of network properties, individualized network topography, as well as how much is needed to reliably map idiosyncratic regions of functional connectivity.

However, these benchmarks have yet to be established for older adults. As we move towards applying these novel methodologies to the study of aging, it will be important to determine how much data we need to obtain reliable measures in this age demographic, as well as how stable these measures are across days and longer delays.

On the question of network correlates of individual differences in cognition and behavior, our group considers the investigation of network variants particularly promising. These regions which show highly dissimilar patterns of functional connectivity between an individual and the group average exhibit characteristics that suggest a relationship with behavior and, in particular, with higher-order cognitive function (Seitzman et al., 2019). Network variants are currently unexplored in older adults. Given previous findings of their relationship with behavior, these variant regions could clue us in on how the organization of functional networks changes as we age on a more topographically discrete level, and potentially lead to the development of biomarkers for cognitive decline across various domains.

Beyond individual differences in cortical networks, the need to examine the role of the subcortex, particularly the cerebellum, in cognition has become increasingly apparent (Janacsek et al., 2022; Koziol et al., 2014). There is mounting evidence suggesting the importance of the cerebellum in cognitive aging (Arleo et al., 2023; Bernard, 2022). For example, there is some evidence linking the cerebellum to age-related differences in processing speed (Arleo et al., 2023; Eckert, 2010; Gao et al., 2020)—a

strong predictor of cognitive decline (Salthouse & Ferrer-Caja, 2003). Due to this evidence, it has been suggested that cerebello-cortical connectivity plays a mechanistic role in mediating processing speed, which results in age-related changes in speed of processing when cerebellar atrophy occurs in older age (Arleo et al., 2023). However, the specific networks involved are less clear. Elucidating the identities of these networks may be difficult due to increased inter-individual variability in the spatial topography of the cerebellum (Marek et al., 2018). Hence, individualized approaches may facilitate the exploration of this often overlooked region to examine topographic individual differences in cerebellar organization in older adults, which could uncover important factors contributing to decline across multiple cognitive domains.

While we consider that applying individualized approaches to the study of brain networks will prove to be a powerful tool to elucidate the brain changes that may lead to individual differences in cognitive deficits, we also believe that correlating these unique patterns of changes to functional organization with different trajectories will warrant the use of similar deep phenotyping approaches to reliably characterize an individual's cognitive ability (for a similar idea applied to the study of psychopathology see Kraus et al., 2023). Furthermore, the utilization of highly reliable functional connectivity and behavioral/cognitive measurements could be especially fruitful when combined with longitudinal approaches to track how changes in cognitive measures follow changes to the organization of functional

networks. Future directions should focus on harnessing these methods to identify biomarkers of cognitive decline in healthy and pathological aging, and to tailor interventions and assessments specifically to an individual's unique profile. This paradigm shift will not only enhance our capacity to predict and prevent cognitive decline but also lay the foundation for a more precise and effective personalized medicine approach to neurocognitive aging, ultimately promoting healthy aging and well-being for individuals as they traverse the later stages of life.

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Citation Diversity Statement:
Recent work in several fields of science has identified a bias in citation practices such that papers from women and other minority scholars are under-cited relative to the number of such papers in the field (Bertolero et al., 2020; Caplar et al., 2017; Chatterjee & Werner, 2021; Dion et al., 2018; Dworkin et al., 2020; Fulvio et al., 2021; Maliniak et al., 2013; S. M. Mitchell et al., 2013; X. Wang et al., 2021). Here we sought to proactively consider choosing references that reflect the diversity of the field in thought, form of contribution, gender, race, ethnicity, and other factors. First, we obtained the predicted gender of the first and last author of each reference by using databases that store the probability of a first name being carried by a woman (Dworkin et al., 2020; D. Zhou et al., 2020). By this measure and excluding self-citations to the first and last authors of our current paper), our references contain 13.33% woman(first)/woman(last), 7.31% man/woman, 27.36% woman/man, and 51.99% man/man. This method is limited in that a) names, pronouns, and social media profiles used to construct the databases may not, in every case, be indicative of gender identity and b) it cannot account for intersex, non-binary, or transgender people. Second, we obtained predicted racial/ethnic category of the first and last author of each reference by databases that store the probability of a first and last name being carried by an author of color (Ambekar et al., 2009; Chintalapati et al., 2023). By this measure (and excluding self-citations), our references contain 11.62% author of color (first)/author of color(last), 15.61% white author/author of color, 20.08% author of color/white author, and 52.69% white author/white author. This method is limited in that a) names and Florida Voter

Data to make the predictions may not be indicative of racial/ethnic identity, and b) it cannot account for Indigenous and mixed-race authors, or those who may face differential biases due to the ambiguous racialization or ethnicization of their names. We look forward to future work that could help us to better understand how to support equitable practices in science.

References:

Abdelkarim, D., Zhao, Y., Turner, M. P., Sivakolundu, D. K., Lu, H., & Rypma, B. (2019). A neural-vascular complex of age-related changes in the human brain: Anatomy, physiology, and implications for neurocognitive aging. *Neuroscience & Biobehavioral Reviews*, *107*, 927–944. https://doi.org/10.1016/j.neubiorev.2019.09.005

Abe, O., Yamasue, H., Aoki, S., Suga, M., Yamada, H., Kasai, K., Masutani, Y., Kato, N., Kato, N., & Ohtomo, K. (2008). Aging in the CNS: Comparison of gray/white matter volume and diffusion tensor data. *Neurobiology of Aging*, *29*(1), 102–116. https://doi.org/10.1016/j.neurobiolaging.2006.09.003

Abrahamson, K., Clark, D., Perkins, A., & Arling, G. (2012). Does Cognitive Impairment Influence Quality of Life Among Nursing Home Residents? *The Gerontologist*, *52*(5), 632–640. https://doi.org/10.1093/geront/gnr137

Achard, S., & Bullmore, E. (2007). Efficiency and Cost of Economical Brain Functional Networks. *PLOS Computational Biology*, *3*(2), e17. https://doi.org/10.1371/journal.pcbi.0030017

Ambekar, A., Ward, C., Mohammed, J., Male, S., & Skiena, S. (2009). Name-ethnicity classification from open sources. *Proceedings of the 15th ACM*

SIGKDD International Conference on Knowledge Discovery and Data Mining - KDD '09, 49. https://doi.org/10.1145/1557019.1557032

Anderson, L. A., Goodman, R. A., Holtzman, D., Posner, S. F., & Northridge, M. E. (2012). Aging in the United States: Opportunities and Challenges for Public Health. *American Journal of Public Health*, *102*(3), 393–395. https://doi.org/10.2105/AJPH.2011.300617

Andrews-Hanna, J. R., Reidler, J. S., Sepulcre, J., Poulin, R., & Buckner, R. L. (2010). Functional-Anatomic Fractionation of the Brain's Default Network. *Neuron*, *65*(4), 550–562. https://doi.org/10.1016/j.neuron.2010.02.005

Andrews-Hanna, J. R., Snyder, A. Z., Vincent, J. L., Lustig, C., Head, D., Raichle, M. E., & Buckner, R. L. (2007). Disruption of Large-Scale Brain Systems in Advanced Aging. *Neuron*, *56*(5), 924–935. https://doi.org/10.1016/j.neuron.2007.10.038

Arleo, A., Bareš, M., Bernard, J. A., Bogoian, H. R., Bruchhage, M. M. K., Bryant, P., Carlson, E. S., Chan, C. C. H., Chen, L.-K., Chung, C.-P., Dotson, V. M., Filip, P., Guell, X., Habas, C., Jacobs, H. I. L., Kakei, S., Lee, T. M. C., Leggio, M., Misiura, M., … Manto, M. (2023). Consensus Paper: Cerebellum and Ageing. *The Cerebellum*. https://doi.org/10.1007/s12311-023-01577-7

Assem, M., Blank, I. A., Mineroff, Z., Ademoğlu, A., & Fedorenko, E. (2020). Activity in the fronto-parietal multiple-demand network is robustly associated with individual differences in working memory and fluid

intelligence. *Cortex*, *131*, 1–16. https://doi.org/10.1016/j.cortex.2020.06.013

Bäckman, L., Lindenberger, U., Li, S.-C., & Nyberg, L. (2010). Linking cognitive aging to alterations in dopamine neurotransmitter functioning: Recent data and future avenues. *Neuroscience & Biobehavioral Reviews*, *34*(5), 670–677. https://doi.org/10.1016/j.neubiorev.2009.12.008

Bagarinao, E., Watanabe, H., Maesawa, S., Mori, D., Hara, K., Kawabata, K., Yoneyama, N., Ohdake, R., Imai, K., Masuda, M., Yokoi, T., Ogura, A., Taoka, T., Koyama, S., Tanabe, H. C., Katsuno, M., Wakabayashi, T., Kuzuya, M., Ozaki, N., … Sobue, G. (2019). Reorganization of brain networks and its association with general cognitive performance over the adult lifespan. *Scientific Reports*, *9*(1), Article 1. https://doi.org/10.1038/s41598-019-47922-x

Balthazar, M. L. F., Pereira, F. R. S., Lopes, T. M., Da Silva, E. L., Coan, A. C., Campos, B. M., Duncan, N. W., Stella, F., Northoff, G., Damasceno, B. P., & Cendes, F. (2014). Neuropsychiatric symptoms in Alzheimer’s disease are related to functional connectivity alterations in the salience network. *Human Brain Mapping*, *35*(4), 1237–1246. https://doi.org/10.1002/hbm.22248

Bassett, D. S., & Bullmore, E. T. (2006). Small-World Brain Networks. *The Neuroscientist*. https://doi.org/10.1177/1073858406293182

Bender, A. R., & Raz, N. (2012). Age-related differences in memory and executive functions in healthy APOE ε4 carriers: The contribution of individual differences in prefrontal volumes and systolic blood pressure. *Neuropsychologia*, *50*(5), 704–714. https://doi.org/10.1016/j.neuropsychologia.2011.12.025

Bernard, J. A. (2022). Don’t forget the little brain: A framework for incorporating the cerebellum into the understanding of cognitive aging. *Neuroscience & Biobehavioral Reviews*, *137*, 104639. https://doi.org/10.1016/j.neubiorev.2022.104639

Bertolero, M. A., Dworkin, J. D., David, S. U., Lloreda, C. L., Srivastava, P., Stiso, J., Zhou, D., Dzirasa, K., Fair, D. A., Kaczkurkin, A. N., Marlin, B. J., Shohamy, D., Uddin, L. Q., Zurn, P., & Bassett, D. S. (2020). *Racial and ethnic imbalance in neuroscience reference lists and intersections with gender* (p. 2020.10.12.336230). bioRxiv. https://doi.org/10.1101/2020.10.12.336230

Betzel, R. F., Byrge, L., He, Y., Goñi, J., Zuo, X.-N., & Sporns, O. (2014). Changes in structural and functional connectivity among resting-state networks across the human lifespan. *NeuroImage*, *102*, 345–357. https://doi.org/10.1016/j.neuroimage.2014.07.067

Birn, R. M. (2012). The role of physiological noise in resting-state functional connectivity. *NeuroImage*, *62*(2), 864–870. https://doi.org/10.1016/j.neuroimage.2012.01.016

Birn, R. M., Molloy, E. K., Patriat, R., Parker, T., Meier, T. B., Kirk, G. R., Nair, V. A., Meyerand, M. E., & Prabhakaran, V. (2013). The effect of scan length on the reliability of resting-state fMRI connectivity estimates. *NeuroImage*, *83*, 550–558. https://doi.org/10.1016/j.neuroimage.2013.05.099

Biswal, B., Zerrin Yetkin, F., Haughton, V. M., & Hyde, J. S. (1995). Functional connectivity in the motor cortex of resting human brain using echo-planar mri. *Magnetic Resonance in Medicine*, *34*(4), 537–541. https://doi.org/10.1002/mrm.1910340409

Blandini, F., Nappi, G., Tassorelli, C., & Martignoni, E. (2000). Functional changes of the basal ganglia circuitry in Parkinson's disease. *Progress in Neurobiology*, *62*(1), 63–88. https://doi.org/10.1016/S0301-0082(99)00067-2

Bookheimer, S. Y., Salat, D. H., Terpstra, M., Ances, B. M., Barch, D. M., Buckner, R. L., Burgess, G. C., Curtiss, S. W., Diaz-Santos, M., Elam, J. S., Fischl, B., Greve, D. N., Hagy, H. A., Harms, M. P., Hatch, O. M., Hedden, T., Hodge, C., Japardi, K. C., Kuhn, T. P., … Yacoub, E. (2019). The Lifespan Human Connectome Project in Aging: An overview. *NeuroImage*, *185*, 335–348. https://doi.org/10.1016/j.neuroimage.2018.10.009

Bourassa, K. J., Memel, M., Woolverton, C., & Sbarra, D. A. (2017). Social participation predicts cognitive functioning in aging adults over time: Comparisons with physical health, depression, and physical activity.

Aging & Mental Health, *21*(2), 133–146. https://doi.org/10.1080/13607863.2015.1081152

Bowie, D. C., Low, K. A., Rubenstein, S. L., Islam, S. S., Zimmerman, B., Sutton, B. P., Gratton, G., & Fabiani, M. (2023). *Neurovascular Mechanisms of Cognitive Aging: Arteriosclerosis Precipitates Demyelination and Cognitive Decline* (p. 2023.09.06.556562). bioRxiv. https://doi.org/10.1101/2023.09.06.556562

Braga, R. M., & Buckner, R. L. (2017). Parallel Interdigitated Distributed Networks within the Individual Estimated by Intrinsic Functional Connectivity. *Neuron*, *95*(2), 457-471.e5. https://doi.org/10.1016/j.neuron.2017.06.038

Braga, R. M., DiNicola, L. M., Becker, H. C., & Buckner, R. L. (2020). Situating the left-lateralized language network in the broader organization of multiple specialized large-scale distributed networks. *Journal of Neurophysiology*, *124*(5), 1415–1448. https://doi.org/10.1152/jn.00753.2019

Brennan, B. P., Wang, D., Li, M., Perriello, C., Ren, J., Elias, J. A., Van Kirk, N. P., Krompinger, J. W., Pope, H. G., Haber, S. N., Rauch, S. L., Baker, J. T., & Liu, H. (2019). Use of an Individual-Level Approach to Identify Cortical Connectivity Biomarkers in Obsessive-Compulsive Disorder. *Biological Psychiatry. Cognitive Neuroscience and Neuroimaging*, *4*(1), 27–38. https://doi.org/10.1016/j.bpsc.2018.07.014

Bright, M. G., Bulte, D. P., Jezzard, P., & Duyn, J. H. (2009). Characterization of regional heterogeneity in cerebrovascular reactivity dynamics using novel hypocapnia task and BOLD fMRI. *NeuroImage*, *48*(1), 166–175. https://doi.org/10.1016/j.neuroimage.2009.05.026

Bryce, N. V., Flournoy, J. C., Guassi Moreira, J. F., Rosen, M. L., Sambook, K. A., Mair, P., & McLaughlin, K. A. (2021). Brain parcellation selection: An overlooked decision point with meaningful effects on individual differences in resting-state functional connectivity. *NeuroImage*, *243*, 118487. https://doi.org/10.1016/j.neuroimage.2021.118487

Buckner, R. L., & DiNicola, L. M. (2019). The brain's default network: Updated anatomy, physiology and evolving insights. *Nature Reviews Neuroscience*, *20*(10), 593–608. https://doi.org/10.1038/s41583-019-0212-7

Buckner, R. L., Head, D., Parker, J., Fotenos, A. F., Marcus, D., Morris, J. C., & Snyder, A. Z. (2004). A unified approach for morphometric and functional data analysis in young, old, and demented adults using automated atlas-based head size normalization: Reliability and validation against manual measurement of total intracranial volume. *NeuroImage*, *23*(2), 724–738. https://doi.org/10.1016/j.neuroimage.2004.06.018

Buckner, R. L., Snyder, A. Z., Sanders, A. L., Raichle, M. E., & Morris, J. C. (2000). Functional Brain Imaging of Young, Nondemented, and

Demented Older Adults. *Journal of Cognitive Neuroscience*, *12*(Supplement 2), 24–34. https://doi.org/10.1162/089892900564046

Buckner, R. L., Snyder, A. Z., Shannon, B. J., LaRossa, G., Sachs, R., Fotenos, A. F., Sheline, Y. I., Klunk, W. E., Mathis, C. A., Morris, J. C., & Mintun, M. A. (2005). Molecular, Structural, and Functional Characterization of Alzheimer's Disease: Evidence for a Relationship between Default Activity, Amyloid, and Memory. *Journal of Neuroscience*, *25*(34), 7709–7717. https://doi.org/10.1523/JNEUROSCI.2177-05.2005

Cabeza, R. (2002). *Hemispheric Asymmetry Reduction in Older Adults: The HAROLD Model*. 16. https://doi.org/10.1037/0882-7974.17.1.85

Cabeza, R., Albert, M., Belleville, S., Craik, F. I. M., Duarte, A., Grady, C. L., Lindenberger, U., Nyberg, L., Park, D. C., Reuter-Lorenz, P. A., Rugg, M. D., Steffener, J., & Rajah, M. N. (2018). Maintenance, reserve and compensation: The cognitive neuroscience of healthy ageing. *Nature Reviews Neuroscience*, *19*(11), 701–710. https://doi.org/10.1038/s41583-018-0068-2

Campbell, K. L., Grady, C. L., Ng, C., & Hasher, L. (2012). Age differences in the frontoparietal cognitive control network: Implications for distractibility. *Neuropsychologia*, *50*(9), 2212–2223. https://doi.org/10.1016/j.neuropsychologia.2012.05.025

Cao, M., Wang, J.-H., Dai, Z.-J., Cao, X.-Y., Jiang, L.-L., Fan, F.-M., Song, X.-W., Xia, M.-R., Shu, N., Dong, Q., Milham, M. P., Castellanos, F. X., Zuo, X.-N., & He, Y. (2014). Topological organization of the human brain

functional connectome across the lifespan. *Developmental Cognitive Neuroscience*, *7*, 76–93. https://doi.org/10.1016/j.dcn.2013.11.004

Caplar, N., Tacchella, S., & Birrer, S. (2017). Quantitative evaluation of gender bias in astronomical publications from citation counts. *Nature Astronomy*, *1*(6), Article 6. https://doi.org/10.1038/s41550-017-0141

Carroll, S. J., Dale, M. J., Niyonsenga, T., Taylor, A. W., & Daniel, M. (2020). Associations between area socioeconomic status, individual mental health, physical activity, diet and change in cardiometabolic risk amongst a cohort of Australian adults: A longitudinal path analysis. *PLOS ONE*, *15*(5), e0233793. https://doi.org/10.1371/journal.pone.0233793

Cash, R. F. H., Cocchi, L., Lv, J., Fitzgerald, P. B., & Zalesky, A. (2021). Functional Magnetic Resonance Imaging–Guided Personalization of Transcranial Magnetic Stimulation Treatment for Depression. *JAMA Psychiatry*, *78*(3), 337–339. https://doi.org/10.1001/jamapsychiatry.2020.3794

Cash, R. F. H., Hendrikse, J., Fernando, K. B., Thompson, S., Suo, C., Fornito, A., Yücel, M., Rogasch, N. C., Zalesky, A., & Coxon, J. P. (2022). Personalized brain stimulation of memory networks. *Brain Stimulation*, *15*(5), 1300–1304. https://doi.org/10.1016/j.brs.2022.09.004

Cash, R. F. H., & Zalesky, A. (2024). *Personalized and Circuit-Based Transcranial Magnetic Stimulation: Evidence, Controversies, and Opportunities*.

https://www.biologicalpsychiatryjournal.com/article/S0006-3223(23)01742-0/fulltext

Chan, M. Y., Na, J., Agres, P. F., Savalia, N. K., Park, D. C., & Wig, G. S. (2018). Socioeconomic status moderates age-related differences in the brain's functional network organization and anatomy across the adult lifespan. *Proceedings of the National Academy of Sciences*, *115*(22), E5144–E5153. https://doi.org/10.1073/pnas.1714021115

Chan, M. Y., Park, D. C., Savalia, N. K., Petersen, S. E., & Wig, G. S. (2014). Decreased segregation of brain systems across the healthy adult lifespan. *Proceedings of the National Academy of Sciences*, *111*(46). https://doi.org/10.1073/pnas.1415122111

Chatterjee, P., & Werner, R. M. (2021). Gender Disparity in Citations in High-Impact Journal Articles. *JAMA Network Open*, *4*(7), e2114509. https://doi.org/10.1001/jamanetworkopen.2021.14509

Chintalapati, R., Laohaprapanon, S., & Sood, G. (2023). *Predicting Race and Ethnicity From the Sequence of Characters in a Name* (arXiv:1805.02109). arXiv. https://doi.org/10.48550/arXiv.1805.02109

Chong, J. S. X., Ng, K. K., Tandi, J., Wang, C., Poh, J.-H., Lo, J. C., Chee, M. W. L., & Zhou, J. H. (2019). Longitudinal Changes in the Cerebral Cortex Functional Organization of Healthy Elderly. *Journal of Neuroscience*, *39*(28), 5534–5550. https://doi.org/10.1523/JNEUROSCI.1451-18.2019

Chong, M., Bhushan, C., Joshi, A. A., Choi, S., Haldar, J. P., Shattuck, D. W., Spreng, R. N., & Leahy, R. M. (2017). Individual parcellation of resting

fMRI with a group functional connectivity prior. *NeuroImage*, *156*, 87–100. https://doi.org/10.1016/j.neuroimage.2017.04.054

Chou, Y., Chen, N., & Madden, D. J. (2013). Functional brain connectivity and cognition: Effects of adult age and task demands. *Neurobiology of Aging*, *34*(8), 1925–1934. https://doi.org/10.1016/j.neurobiolaging.2013.02.012

Christensen, H. (2001). What Cognitive Changes can be Expected with Normal Ageing? *Australian & New Zealand Journal of Psychiatry*, *35*(6), 768–775. https://doi.org/10.1046/j.1440-1614.2001.00966.x

Christensen, H., Mackinnon, A., Jorm, A. F., Henderson, A. S., Scott, L. R., & Korten, A. E. (1994). Age differences and interindividual variation in cognition in community-dwelling elderly. *Psychology and Aging*, *9*(3), 381–390. https://doi.org/10.1037/0882-7974.9.3.381

Ciric, R., Wolf, D. H., Power, J. D., Roalf, D. R., Baum, G. L., Ruparel, K., Shinohara, R. T., Elliott, M. A., Eickhoff, S. B., Davatzikos, C., Gur, R. C., Gur, R. E., Bassett, D. S., & Satterthwaite, T. D. (2017). Benchmarking of participant-level confound regression strategies for the control of motion artifact in studies of functional connectivity. *NeuroImage*, *154*, 174–187. https://doi.org/10.1016/j.neuroimage.2017.03.020

Cole, E. J., Phillips, A. L., Bentzley, B. S., Stimpson, K. H., Nejad, R., Barmak, F., Veerapal, C., Khan, N., Cherian, K., Felber, E., Brown, R., Choi, E., King, S., Pankow, H., Bishop, J. H., Azeez, A., Coetzee, J., Rapier, R., Odenwald, N., … Williams, N. R. (2022). Stanford Neuromodulation

Therapy (SNT): A Double-Blind Randomized Controlled Trial. *American Journal of Psychiatry*, *179*(2), 132–141. https://doi.org/10.1176/appi.ajp.2021.20101429

Cole, M. W., Bassett, D. S., Power, J. D., Braver, T. S., & Petersen, S. E. (2014). Intrinsic and Task-Evoked Network Architectures of the Human Brain. *Neuron*, *83*(1), 238–251. https://doi.org/10.1016/j.neuron.2014.05.014

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*(3), 201–215. https://doi.org/10.1038/nrn755

Cutler, S. J. (2009). Aging and Genetics: The Future is Here. *The Gerontologist*, *49*(2), 283–285. https://doi.org/10.1093/geront/gnp017

Das, S. R., Lyu, X., Duong, M. T., Xie, L., McCollum, L., de Flores, R., DiCalogero, M., Irwin, D. J., Dickerson, B. C., Nasrallah, I. M., Yushkevich, P. A., Wolk, D. A., & Initiative, A. D. N. (2021). Tau-Atrophy Variability Reveals Phenotypic Heterogeneity in Alzheimer's Disease. *Annals of Neurology*, *90*(5), 751–762. https://doi.org/10.1002/ana.26233

Dautricourt, S., de Flores, R., Landeau, B., Poisnel, G., Vanhoutte, M., Delcroix, N., Eustache, F., Vivien, D., de la Sayette, V., & Chételat, G. (2021). Longitudinal Changes in Hippocampal Network Connectivity in Alzheimer's Disease. *Annals of Neurology*, *90*(3), 391–406. https://doi.org/10.1002/ana.26168

Davis, S. W., Dennis, N. A., Daselaar, S. M., Fleck, M. S., & Cabeza, R. (2008). Que PASA? The Posterior-Anterior Shift in Aging. *Cerebral Cortex*, *18*(5), 1201–1209. https://doi.org/10.1093/cercor/bhm155

de Frias, C. M., Schaie, K. W., & Willis, S. L. (2014). Hypertension moderates the effect of APOE on 21-year cognitive trajectories. *Psychology and Aging*, *29*(2), 431–439. https://doi.org/10.1037/a0036828

de Godoy, L. L., Alves, C. A. P. F., Saavedra, J. S. M., Studart-Neto, A., Nitrini, R., da Costa Leite, C., & Bisdas, S. (2021). Understanding brain resilience in superagers: A systematic review. *Neuroradiology*, *63*(5), 663–683. https://doi.org/10.1007/s00234-020-02562-1

Deary, I. J., Corley, J., Gow, A. J., Harris, S. E., Houlihan, L. M., Marioni, R. E., Penke, L., Rafnsson, S. B., & Starr, J. M. (2009). Age-associated cognitive decline. *British Medical Bulletin*, *92*(1), 135–152. https://doi.org/10.1093/bmb/ldp033

Deery, H. A., Di Paolo, R., Moran, C., Egan, G. F., & Jamadar, S. D. (2023). The older adult brain is less modular, more integrated, and less efficient at rest: A systematic review of large-scale resting-state functional brain networks in aging. *Psychophysiology*, *60*(1), e14159. https://doi.org/10.1111/psyp.14159

Dengler, J., Deck, B. L., Stoll, H., Fernandez-Nunez, G., Kelkar, A. S., Rich, R. R., Erickson, B. A., Erani, F., Faseyitan, O., Hamilton, R. H., & Medaglia, J. D. (2024). Enhancing cognitive control with transcranial magnetic

stimulation in subject-specific frontoparietal networks. *Cortex*, *172*, 141–158. https://doi.org/10.1016/j.cortex.2023.11.020

Dennis, E. L., & Thompson, P. M. (2014). Functional Brain Connectivity Using fMRI in Aging and Alzheimer's Disease. *Neuropsychology Review*, *24*(1), 49–62. https://doi.org/10.1007/s11065-014-9249-6

D'Esposito, M., Zarahn, E., Aguirre, G. K., & Rypma, B. (1999). The Effect of Normal Aging on the Coupling of Neural Activity to the Bold Hemodynamic Response. *NeuroImage*, *10*(1), 6–14. https://doi.org/10.1006/nimg.1999.0444

DiNicola, L. M., Braga, R. M., & Buckner, R. L. (2020). Parallel distributed networks dissociate episodic and social functions within the individual. *Journal of Neurophysiology*, *123*(3), 1144–1179. https://doi.org/10.1152/jn.00529.2019

Dion, M. L., Sumner, J. L., & Mitchell, S. M. (2018). Gendered Citation Patterns across Political Science and Social Science Methodology Fields. *Political Analysis*, *26*(3), 312–327. https://doi.org/10.1017/pan.2018.12

Dorsman, K. A., Weiner-Light, S., Staffaroni, A. M., Brown, J. A., Wolf, A., Cobigo, Y., Walters, S., Kramer, J. H., & Casaletto, K. B. (2020). Get Moving! Increases in Physical Activity Are Associated With Increasing Functional Connectivity Trajectories in Typically Aging Adults. *Frontiers in Aging Neuroscience*, *12*. https://www.frontiersin.org/articles/10.3389/fnagi.2020.00104

Dosenbach, N. U. F., Fair, D. A., Cohen, A. L., Schlaggar, B. L., & Petersen, S. E. (2008). A dual-networks architecture of top-down control. *Trends in Cognitive Sciences*, *12*(3), 99–105. https://doi.org/10.1016/j.tics.2008.01.001

Dosenbach, N. U. F., Fair, D. A., Miezin, F. M., Cohen, A. L., Wenger, K. K., Dosenbach, R. A. T., Fox, M. D., Snyder, A. Z., Vincent, J. L., Raichle, M. E., Schlaggar, B. L., & Petersen, S. E. (2007). Distinct brain networks for adaptive and stable task control in humans. *Proceedings of the National Academy of Sciences*, *104*(26), 11073–11078. https://doi.org/10.1073/pnas.0704320104

Dosenbach, N. U. F., Koller, J. M., Earl, E. A., Miranda-Dominguez, O., Klein, R. L., Van, A. N., Snyder, A. Z., Nagel, B. J., Nigg, J. T., Nguyen, A. L., Wesevich, V., Greene, D. J., & Fair, D. A. (2017). Real-time motion analytics during brain MRI improve data quality and reduce costs. *NeuroImage*, *161*, 80–93. https://doi.org/10.1016/j.neuroimage.2017.08.025

Dosenbach, N. U. F., Nardos, B., Cohen, A. L., Fair, D. A., Power, J. D., Church, J. A., Nelson, S. M., Wig, G. S., Vogel, A. C., Lessov-Schlaggar, C. N., Barnes, K. A., Dubis, J. W., Feczko, E., Coalson, R. S., Pruett, J. R., Barch, D. M., Petersen, S. E., & Schlaggar, B. L. (2010). Prediction of Individual Brain Maturity Using fMRI. *Science*, *329*(5997), 1358–1361. https://doi.org/10.1126/science.1194144

Dosenbach, N. U. F., Raichle, M., & Gordon, E. M. (2024). *The brain's cingulo-opercular action-mode network* [Preprint]. PsyArXiv. https://doi.org/10.31234/osf.io/2vt79

Du, J., DiNicola, L. M., Angeli, P. A., Saadon-Grosman, N., Sun, W., Kaiser, S., Ladopoulou, J., Xue, A., Yeo, B. T. T., Eldaief, M. C., & Buckner, R. L. (2024). Organization of the human cerebral cortex estimated within individuals: Networks, global topography, and function. *Journal of Neurophysiology*, *131*(6), 1014–1082. https://doi.org/10.1152/jn.00308.2023

Dworetsky, A., Seitzman, B. A., Adeyemo, B., Neta, M., Coalson, R. S., Petersen, S. E., & Gratton, C. (2021). Probabilistic mapping of human functional brain networks identifies regions of high group consensus. *NeuroImage*, *237*, 118164. https://doi.org/10.1016/j.neuroimage.2021.118164

Dworetsky, A., Seitzman, B. A., Adeyemo, B., Nielsen, A. N., Hatoum, A. S., Smith, D. M., Nichols, T. E., Neta, M., Petersen, S. E., & Gratton, C. (2024). Two common and distinct forms of variation in human functional brain networks. *Nature Neuroscience*, *27*(6), 1187–1198. https://doi.org/10.1038/s41593-024-01618-2

Dworkin, J. D., Linn, K. A., Teich, E. G., Zurn, P., Shinohara, R. T., & Bassett, D. S. (2020). The extent and drivers of gender imbalance in neuroscience reference lists. *Nature Neuroscience*, *23*(8), 918–926. https://doi.org/10.1038/s41593-020-0658-y

Eckert. (2010). Age-related changes in processing speed: Unique contributions of cerebellar and prefrontal cortex. *Frontiers in Human Neuroscience*. https://doi.org/10.3389/neuro.09.010.2010

Elahi, F. M., & Miller, B. L. (2017). A clinicopathological approach to the diagnosis of dementia. *Nature Reviews Neurology*, *13*(8), Article 8. https://doi.org/10.1038/nrneurol.2017.96

Escrichs, A., Biarnes, C., Garre-Olmo, J., Fernández-Real, J. M., Ramos, R., Pamplona, R., Brugada, R., Serena, J., Ramió-Torrentà, L., Coll-De-Tuero, G., Gallart, L., Barretina, J., Vilanova, J. C., Mayneris-Perxachs, J., Essig, M., Figley, C. R., Pedraza, S., Puig, J., & Deco, G. (2021). Whole-Brain Dynamics in Aging: Disruptions in Functional Connectivity and the Role of the Rich Club. *Cerebral Cortex*, *31*(5), 2466–2481. https://doi.org/10.1093/cercor/bhaa367

Fabiani, M. (2012). It was the best of times, it was the worst of times: A psychophysiologist’s view of cognitive aging: A psychophysiologist’s view of cognitive aging. *Psychophysiology*, *49*(3), 283–304. https://doi.org/10.1111/j.1469-8986.2011.01331.x

Fair, D. A., Cohen, A. L., Dosenbach, N. U. F., Church, J. A., Miezin, F. M., Barch, D. M., Raichle, M. E., Petersen, S. E., & Schlaggar, B. L. (2008). The maturing architecture of the brain’s default network. *Proceedings of the National Academy of Sciences*, *105*(10), 4028–4032. https://doi.org/10.1073/pnas.0800376105

Fair, D. A., Cohen, A. L., Power, J. D., Dosenbach, N. U. F., Church, J. A., Miezin, F. M., Schlaggar, B. L., & Petersen, S. E. (2009). Functional Brain Networks Develop from a “Local to Distributed” Organization. *PLOS Computational Biology*, *5*(5), e1000381. https://doi.org/10.1371/journal.pcbi.1000381

Fair, D. A., Dosenbach, N. U. F., Church, J. A., Cohen, A. L., Brahmbhatt, S., Miezin, F. M., Barch, D. M., Raichle, M. E., Petersen, S. E., & Schlaggar, B. L. (2007). Development of distinct control networks through segregation and integration. *Proceedings of the National Academy of Sciences*, *104*(33), 13507–13512. https://doi.org/10.1073/pnas.0705843104

Fair, D. A., Miranda-Dominguez, O., Snyder, A. Z., Perrone, A., Earl, E. A., Van, A. N., Koller, J. M., Feczko, E., Tisdall, M. D., van der Kouwe, A., Klein, R. L., Mirro, A. E., Hampton, J. M., Adeyemo, B., Laumann, T. O., Gratton, C., Greene, D. J., Schlaggar, B. L., Hagler, D. J., … Dosenbach, N. U. F. (2020). Correction of respiratory artifacts in MRI head motion estimates. *NeuroImage*, *208*, 116400. https://doi.org/10.1016/j.neuroimage.2019.116400

Farràs-Permanyer, L., Mancho-Fora, N., Montalà-Flaquer, M., Bartrés-Faz, D., Vaqué-Alcázar, L., Peró-Cebollero, M., & Guàrdia-Olmos, J. (2019). Age-related changes in resting-state functional connectivity in older adults. *Neural Regeneration Research*, *14*(9), 1544–1555. https://doi.org/10.4103/1673-5374.255976

Ferreira, L. K., & Busatto, G. F. (2013). Resting-state functional connectivity in normal brain aging. *Neuroscience & Biobehavioral Reviews*, *37*(3), 384–400. https://doi.org/10.1016/j.neubiorev.2013.01.017

Finn, E. S., Shen, X., Scheinost, D., Rosenberg, M. D., Huang, J., Chun, M. M., Papademetris, X., & Constable, R. T. (2015). Functional connectome fingerprinting: Identifying individuals using patterns of brain connectivity. *Nature Neuroscience*, *18*(11), 1664–1671. https://doi.org/10.1038/nn.4135

Fulvio, J. M., Akinnola, I., & Postle, B. R. (2021). Gender (Im)balance in Citation Practices in Cognitive Neuroscience. *Journal of Cognitive Neuroscience*, *33*(1), 3–7. https://doi.org/10.1162/jocn_a_01643

Gallen, C. L., Turner, G. R., Adnan, A., & D'Esposito, M. (2016). Reconfiguration of brain network architecture to support executive control in aging. *Neurobiology of Aging*, *44*, 42–52. https://doi.org/10.1016/j.neurobiolaging.2016.04.003

Gao, M., Wong, C. H. Y., Huang, H., Shao, R., Huang, R., Chan, C. C. H., & Lee, T. M. C. (2020). Connectome-based models can predict processing speed in older adults. *NeuroImage*, *223*, 117290. https://doi.org/10.1016/j.neuroimage.2020.117290

Geerligs, L., Renken, R. J., Saliasi, E., Maurits, N. M., & Lorist, M. M. (2015). A Brain-Wide Study of Age-Related Changes in Functional Connectivity. *Cerebral Cortex*, *25*(7), 1987–1999. https://doi.org/10.1093/cercor/bhu012

Gellersen, H. M., Guell, X., & Sami, S. (2021). Differential vulnerability of the cerebellum in healthy ageing and Alzheimer's disease. *NeuroImage: Clinical*, *30*, 102605. https://doi.org/10.1016/j.nicl.2021.102605

González-Gross, M., Marcos, A., & Pietrzik, K. (2001). Nutrition and cognitive impairment in the elderly. *British Journal of Nutrition*, *86*(3), 313–321. https://doi.org/10.1079/BJN2001388

Gordon, E. M., Laumann, T. O., Adeyemo, B., Huckins, J. F., Kelley, W. M., & Petersen, S. E. (2016). Generation and Evaluation of a Cortical Area Parcellation from Resting-State Correlations. *Cerebral Cortex*, *26*(1), 288–303. https://doi.org/10.1093/cercor/bhu239

Gordon, E. M., Laumann, T. O., Gilmore, A. W., Newbold, D. J., Greene, D. J., Berg, J. J., Ortega, M., Hoyt-Drazen, C., Gratton, C., Sun, H., Hampton, J. M., Coalson, R. S., Nguyen, A. L., McDermott, K. B., Shimony, J. S., Snyder, A. Z., Schlaggar, B. L., Petersen, S. E., Nelson, S. M., & Dosenbach, N. U. F. (2017). Precision Functional Mapping of Individual Human Brains. *Neuron*, *95*(4), 791-807.e7. https://doi.org/10.1016/j.neuron.2017.07.011

Gordon, E. M., Scheibel, R. S., Zambrano-Vazquez, L., Jia-Richards, M., May, G. J., Meyer, E. C., & Nelson, S. M. (2018). High-Fidelity Measures of Whole-Brain Functional Connectivity and White Matter Integrity Mediate Relationships between Traumatic Brain Injury and Post-Traumatic Stress Disorder Symptoms. *Journal of Neurotrauma*, *35*(5), 767–779. https://doi.org/10.1089/neu.2017.5428

Grady, C., & Craik, F. I. (2000). Changes in memory processing with age. *Current Opinion in Neurobiology*, *10*(2), 224–231. https://doi.org/10.1016/S0959-4388(00)00073-8

Grady, C., & Garrett, D. D. (2014). Understanding variability in the BOLD signal and why it matters for aging. *Brain Imaging and Behavior*, *8*(2), 274–283. https://doi.org/10.1007/s11682-013-9253-0

Grady, C., Maisog, J., Horwitz, B., Ungerleider, L., Mentis, M., Salerno, J., Pietrini, P., Wagner, E., & Haxby, J. (1994). Age-related changes in cortical blood flow activation during visual processing of faces and location. *The Journal of Neuroscience*, *14*(3), 1450–1462. https://doi.org/10.1523/JNEUROSCI.14-03-01450.1994

Grady, C., Sarraf, S., Saverino, C., & Campbell, K. (2016). Age differences in the functional interactions among the default, frontoparietal control, and dorsal attention networks. *Neurobiology of Aging*, *41*, 159–172. https://doi.org/10.1016/j.neurobiolaging.2016.02.020

Gratton, C., & Braga, R. M. (2021). Editorial overview: Deep imaging of the individual brain: past, practice, and promise. *Current Opinion in Behavioral Sciences*, *40*, iii–vi. https://doi.org/10.1016/j.cobeha.2021.06.011

Gratton, C., Dworetsky, A., Adeyemo, B., Seitzman, B. A., Smith, D. M., Petersen, S. E., & Neta, M. (2022). *The cingulo-opercular network is composed of two distinct sub-systems*. https://doi.org/10.1101/2022.09.16.508254

Gratton, C., Dworetsky, A., Coalson, R. S., Adeyemo, B., Laumann, T. O., Wig, G. S., Kong, T. S., Gratton, G., Fabiani, M., Barch, D. M., Tranel, D., Miranda-Dominguez, O., Fair, D. A., Dosenbach, N. U. F., Snyder, A. Z., Perlmutter, J. S., Petersen, S. E., & Campbell, M. C. (2020). Removal of high frequency contamination from motion estimates in single-band fMRI saves data without biasing functional connectivity. *NeuroImage*, *217*, 116866. https://doi.org/10.1016/j.neuroimage.2020.116866

Gratton, C., Koller, J. M., Shannon, W., Greene, D. J., Maiti, B., Snyder, A. Z., Petersen, S. E., Perlmutter, J. S., & Campbell, M. C. (2019). Emergent Functional Network Effects in Parkinson Disease. *Cerebral Cortex*, *29*(6), 2509–2523. https://doi.org/10.1093/cercor/bhy121

Gratton, C., Kraus, B. T., Greene, D. J., Gordon, E. M., Laumann, T. O., Nelson, S. M., Dosenbach, N. U. F., & Petersen, S. E. (2020). Defining Individual-Specific Functional Neuroanatomy for Precision Psychiatry. *Biological Psychiatry*, *88*(1), 28–39. https://doi.org/10.1016/j.biopsych.2019.10.026

Gratton, C., Laumann, T. O., Nielsen, A. N., Greene, D. J., Gordon, E. M., Gilmore, A. W., Nelson, S. M., Coalson, R. S., Snyder, A. Z., Schlaggar, B. L., Dosenbach, N. U. F., & Petersen, S. E. (2018). Functional Brain Networks Are Dominated by Stable Group and Individual Factors, Not Cognitive or Daily Variation. *Neuron*, *98*(2), 439-452.e5. https://doi.org/10.1016/j.neuron.2018.03.035

Greene, D. J., Marek, S., Gordon, E. M., Siegel, J. S., Gratton, C., Laumann, T. O., Gilmore, A. W., Berg, J. J., Nguyen, A. L., Dierker, D., Van, A. N., Ortega, M., Newbold, D. J., Hampton, J. M., Nielsen, A. N., McDermott, K. B., Roland, J. L., Norris, S. A., Nelson, S. M., … Dosenbach, N. U. F. (2020). Integrative and Network-Specific Connectivity of the Basal Ganglia and Thalamus Defined in Individuals. *Neuron*, *105*(4), 742-758.e6. https://doi.org/10.1016/j.neuron.2019.11.012

Greicius, M. D., Srivastava, G., Reiss, A. L., & Menon, V. (2004). Default-mode network activity distinguishes Alzheimer's disease from healthy aging: Evidence from functional MRI. *Proceedings of the National Academy of Sciences*, *101*(13), 4637–4642. https://doi.org/10.1073/pnas.0308627101

Gunning-Dixon, F. M., Brickman, A. M., Cheng, J. C., & Alexopoulos, G. S. (2009). Aging of cerebral white matter: A review of MRI findings. *International Journal of Geriatric Psychiatry*, *24*(2), 109–117. https://doi.org/10.1002/gps.2087

Han, L., Chan, M. Y., Agres, P. F., Winter-Nelson, E., Zhang, Z., & Wig, G. S. (2024). Measures of resting-state brain network segregation and integration vary in relation to data quantity: Implications for within and between subject comparisons of functional brain network organization. *Cerebral Cortex*, *34*(2), bhad506. https://doi.org/10.1093/cercor/bhad506

Han, L., Savalia, N. K., Chan, M. Y., Agres, P. F., Nair, A. S., & Wig, G. S. (2018). Functional Parcellation of the Cerebral Cortex Across the Human Adult Lifespan. *Cerebral Cortex*, *28*(12), 4403–4423. https://doi.org/10.1093/cercor/bhy218

Harrison, T. M., Weintraub, S., Mesulam, M.-M., & Rogalski, E. (2012). Superior Memory and Higher Cortical Volumes in Unusually Successful Cognitive Aging. *Journal of the International Neuropsychological Society : JINS*, *18*(6), 1081–1085. https://doi.org/10.1017/S1355617712000847

Hausman, H. K., Hardcastle, C., Albizu, A., Kraft, J. N., Evangelista, N. D., Boutzoukas, E. M., Langer, K., O'Shea, A., Van Etten, E. J., Bharadwaj, P. K., Song, H., Smith, S. G., Porges, E., DeKosky, S. T., Hishaw, G. A., Wu, S., Marsiske, M., Cohen, R., Alexander, G. E., & Woods, A. J. (2022). Cingulo-opercular and frontoparietal control network connectivity and executive functioning in older adults. *GeroScience*, *44*(2), 847–866. https://doi.org/10.1007/s11357-021-00503-1

Hedden, T., & Gabrieli, J. D. E. (2004). Insights into the ageing mind: A view from cognitive neuroscience. *Nature Reviews Neuroscience*, *5*(2), 87–96. https://doi.org/10.1038/nrn1323

Huang, S., Faul, L., Sevinc, G., Mwilambwe-Tshilobo, L., Setton, R., Lockrow, A. W., Ebner, N. C., Turner, G. R., Spreng, R. N., & De Brigard, F. (2021). Age differences in intuitive moral decision-making: Associations with

inter-network neural connectivity. *Psychology and Aging*, *36*(8), 902–916. https://doi.org/10.1037/pag0000633

Iordan, A. D., Cooke, K. A., Moored, K. D., Katz, B., Buschkuehl, M., Jaeggi, S. M., Jonides, J., Peltier, S. J., Polk, T. A., & Reuter-Lorenz, P. A. (2018). Aging and Network Properties: Stability Over Time and Links with Learning during Working Memory Training. *Frontiers in Aging Neuroscience*, *9*, 419. https://doi.org/10.3389/fnagi.2017.00419

Janacsek, K., Evans, T. M., Kiss, M., Shah, L., Blumenfeld, H., & Ullman, M. T. (2022). Subcortical Cognition: The Fruit Below the Rind. *Annual Review of Neuroscience*, *45*(1), null. https://doi.org/10.1146/annurev-neuro-110920-013544

Kantarovich, K., Mwilambwe-Tshilobo, L., Fernández-Cabello, S., Setton, R., Baracchini, G., Lockrow, A. W., Spreng, R. N., & Turner, G. R. (2022). White matter lesion load is associated with lower within- and greater between- network connectivity across older age. *Neurobiology of Aging*, *112*, 170–180. https://doi.org/10.1016/j.neurobiolaging.2022.01.005

Kastrup, A., Li, T.-Q., Takahashi, A., Glover, G. H., & Moseley, M. E. (1998). Functional Magnetic Resonance Imaging of Regional Cerebral Blood Oxygenation Changes During Breath Holding. *Stroke*, *29*(12), 2641–2645. https://doi.org/10.1161/01.STR.29.12.2641

King, B. R., van Ruitenbeek, P., Leunissen, I., Cuypers, K., Heise, K.-F., Santos Monteiro, T., Hermans, L., Levin, O., Albouy, G., Mantini, D., & Swinnen,

S. P. (2018). Age-Related Declines in Motor Performance are Associated With Decreased Segregation of Large-Scale Resting State Brain Networks. *Cerebral Cortex*, *28*(12), 4390–4402. https://doi.org/10.1093/cercor/bhx297

Koen, J. D., & Rugg, M. D. (2019). Neural Dedifferentiation in the Aging Brain. *Trends in Cognitive Sciences*, *23*(7), 547–559. https://doi.org/10.1016/j.tics.2019.04.012

Kong, R., Li, J., Orban, C., Sabuncu, M. R., Liu, H., Schaefer, A., Sun, N., Zuo, X.-N., Holmes, A. J., Eickhoff, S. B., & Yeo, B. T. T. (2019). Spatial Topography of Individual-Specific Cortical Networks Predicts Human Cognition, Personality, and Emotion. *Cerebral Cortex*, *29*(6), 2533–2551. https://doi.org/10.1093/cercor/bhy123

Kong, R., Spreng, R. N., Xue, A., Betzel, R. F., Cohen, J. R., Damoiseaux, J. S., Brigard, F. D., Eickhoff, S. B., Fornito, A., Gratton, C., Gordon, E. M., Holmes, A. J., Laird, A. R., Larson-Prior, L., Nickerson, L. D., Pinho, A. L., Razi, A., Sadaghiani, S., Shine, J. M., … Uddin, L. Q. (2024). *A network correspondence toolbox for quantitative evaluation of novel neuroimaging results*. https://doi.org/10.1101/2024.06.17.599426

Kong, R., Yang, Q., Gordon, E., Xue, A., Yan, X., Orban, C., Zuo, X.-N., Spreng, N., Ge, T., Holmes, A., Eickhoff, S., & Yeo, B. T. T. (2021). Individual-Specific Areal-Level Parcellations Improve Functional Connectivity Prediction of Behavior. *Cerebral Cortex*, *31*(10), 4477–4500. https://doi.org/10.1093/cercor/bhab101

Koziol, L. F., Budding, D., Andreasen, N., D’Arrigo, S., Bulgheroni, S., Imamizu, H., Ito, M., Manto, M., Marvel, C., Parker, K., Pezzulo, G., Ramnani, N., Riva, D., Schmahmann, J., Vandervert, L., & Yamazaki, T. (2014). Consensus Paper: The Cerebellum’s Role in Movement and Cognition. *The Cerebellum*, *13*(1), 151–177. https://doi.org/10.1007/s12311-013-0511-x

Kraus, B., Perez, D., Ladwig, Z., Seitzman, B. A., Dworetsky, A., Petersen, S. E., & Gratton, C. (2021). Network variants are similar between task and rest states. *NeuroImage*, *229*, 117743. https://doi.org/10.1016/j.neuroimage.2021.117743

Kraus, B., Zinbarg, R., Braga, R. M., Nusslock, R., Mittal, V. A., & Gratton, C. (2023). Insights from personalized models of brain and behavior for identifying biomarkers in psychiatry. *Neuroscience and Biobehavioral Reviews*, *152*, 105259. https://doi.org/10.1016/j.neubiorev.2023.105259

LaPlume, A. A., Anderson, N. D., McKetton, L., Levine, B., & Troyer, A. K. (2022). When I’m 64: Age-Related Variability in Over 40,000 Online Cognitive Test Takers. *The Journals of Gerontology: Series B*, *77*(1), 104–117. https://doi.org/10.1093/geronb/gbab143

Larson, N. I., Story, M. T., & Nelson, M. C. (2009). Neighborhood Environments: Disparities in Access to Healthy Foods in the U.S. *American Journal of Preventive Medicine*, *36*(1), 74-81.e10. https://doi.org/10.1016/j.amepre.2008.09.025

Laumann, T. O., Gordon, E. M., Adeyemo, B., Snyder, A. Z., Joo, S. J., Chen, M.-Y., Gilmore, A. W., McDermott, K. B., Nelson, S. M., Dosenbach, N. U. F., Schlaggar, B. L., Mumford, J. A., Poldrack, R. A., & Petersen, S. E. (2015). Functional System and Areal Organization of a Highly Sampled Individual Human Brain. *Neuron*, *87*(3), 657–670. https://doi.org/10.1016/j.neuron.2015.06.037

Lebel, C., Gee, M., Camicioli, R., Wieler, M., Martin, W., & Beaulieu, C. (2012). Diffusion tensor imaging of white matter tract evolution over the lifespan. *NeuroImage*, *60*(1), 340–352. https://doi.org/10.1016/j.neuroimage.2011.11.094

Leuzy, A., Binette, A. P., Vogel, J. W., Klein, G., Borroni, E., Tonietto, M., Strandberg, O., Mattsson-Carlgren, N., Palmqvist, S., Pontecorvo, M. J., Iaccarino, L., Stomrud, E., Ossenkoppele, R., Smith, R., Hansson, O., & Alzheimer's Disease Neuroimaging Initiative. (2023). Comparison of Group-Level and Individualized Brain Regions for Measuring Change in Longitudinal Tau Positron Emission Tomography in Alzheimer Disease. *JAMA Neurology*, *80*(6), 614–623. https://doi.org/10.1001/jamaneurol.2023.1067

Li, R., Yin, S., Zhu, X., Ren, W., Yu, J., Wang, P., Zheng, Z., Niu, Y.-N., Huang, X., & Li, J. (2017). Linking Inter-Individual Variability in Functional Brain Connectivity to Cognitive Ability in Elderly Individuals. *Frontiers in Aging Neuroscience*, *9*, 385. https://doi.org/10.3389/fnagi.2017.00385

Li, S.-C., & Lindenberger, U. (1999). Cross-level unification: A computational exploration of the link between deterioration of neurotransmitter systems and dedifferentiation of cognitive abilities in old age. In *Cognitive Science of Memory* (pp. 103–146). Hogrefe & Huber.

Lynch, C. J., Elbau, I. G., Ng, T. H., Wolk, D., Zhu, S., Ayaz, A., Power, J. D., Zebley, B., Gunning, F. M., & Liston, C. (2022). Automated optimization of TMS coil placement for personalized functional network engagement. *Neuron*, *110*(20), 3263-3277.e4. https://doi.org/10.1016/j.neuron.2022.08.012

Lynch, C. J., Elbau, I., & Liston, C. (2021). Improving precision functional mapping routines with multi-echo fMRI. *Current Opinion in Behavioral Sciences*, *40*, 113–119. https://doi.org/10.1016/j.cobeha.2021.03.017

Lynch, C. J., Power, J. D., Scult, M. A., Dubin, M., Gunning, F. M., & Liston, C. (2020). Rapid Precision Functional Mapping of Individuals Using Multi-Echo fMRI. *Cell Reports*, *33*(12), 108540. https://doi.org/10.1016/j.celrep.2020.108540

Ma, L., Tian, L., Hu, T., Jiang, T., & Zuo, N. (2021). Development of Individual Variability in Brain Functional Connectivity and Capability across the Adult Lifespan. *Cerebral Cortex*, *31*(8), 3925–3938. https://doi.org/10.1093/cercor/bhab059

Madan, C. R. (2018). Age differences in head motion and estimates of cortical morphology. *PeerJ*, *6*, e5176. https://doi.org/10.7717/peerj.5176

Malagurski, B., Liem, F., Oschwald, J., Mérillat, S., & Jäncke, L. (2020). Functional dedifferentiation of associative resting state networks in older adults – A longitudinal study. *NeuroImage*, *214*, 116680. https://doi.org/10.1016/j.neuroimage.2020.116680

Maliniak, D., Powers, R., & Walter, B. F. (2013). The Gender Citation Gap in International Relations. *International Organization*, *67*(4), 889–922. https://doi.org/10.1017/S0020818313000209

Marek, S., & Dosenbach, N. U. F. (2018). The frontoparietal network: Function, electrophysiology, and importance of individual precision mapping. *Dialogues in Clinical Neuroscience*, *20*(2), 133–140. https://doi.org/10.31887/DCNS.2018.20.2/smarek

Marek, S., Siegel, J. S., Gordon, E. M., Raut, R. V., Gratton, C., Newbold, D. J., Ortega, M., Laumann, T. O., Adeyemo, B., Miller, D. B., Zheng, A., Lopez, K. C., Berg, J. J., Coalson, R. S., Nguyen, A. L., Dierker, D., Van, A. N., Hoyt, C. R., McDermott, K. B., … Dosenbach, N. U. F. (2018). Spatial and Temporal Organization of the Individual Human Cerebellum. *Neuron*, *100*(4), 977-993.e7. https://doi.org/10.1016/j.neuron.2018.10.010

Masliah, E., Mallory, M., Hansen, L., DeTeresa, R., & Terry, R. D. (1993). Quantitative synaptic alterations in the human neocortex during normal aging. *Neurology*, *43*(1 Part 1), 192–192. https://doi.org/10.1212/WNL.43.1_Part_1.192

Menon, V., & Uddin, L. Q. (2010). Saliency, switching, attention and control: A network model of insula function. *Brain Structure and Function*, *214*(5), 655–667. https://doi.org/10.1007/s00429-010-0262-0

Mesulam, M. M. (1998). From sensation to cognition. *Brain*, *121*(6), 1013–1052. https://doi.org/10.1093/brain/121.6.1013

Mevel, K., Chételat, G., Eustache, F., & Desgranges, B. (2011). The Default Mode Network in Healthy Aging and Alzheimer's Disease. *International Journal of Alzheimer's Disease*, *2011*, e535816. https://doi.org/10.4061/2011/535816

Mitchell, D. B. (1989). How many memory systems? Evidence from aging. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *15*(1), 31–49. https://doi.org/10.1037/0278-7393.15.1.31

Mitchell, S. M., Lange, S., & Brus, H. (2013). Gendered Citation Patterns in International Relations Journals1. *International Studies Perspectives*, *14*(4), 485–492. https://doi.org/10.1111/insp.12026

Mueller, S., Wang, D., Fox, M. D., Yeo, B. T. T., Sepulcre, J., Sabuncu, M. R., Shafee, R., Lu, J., & Liu, H. (2013). Individual Variability in Functional Connectivity Architecture of the Human Brain. *Neuron*, *77*(3), 586–595. https://doi.org/10.1016/j.neuron.2012.12.028

Mwilambwe-Tshilobo, L., Setton, R., Bzdok, D., Turner, G. R., & Spreng, R. N. (2023). Age differences in functional brain networks associated with loneliness and empathy. *Network Neuroscience*, *7*(2), 496–521. https://doi.org/10.1162/netn_a_00293

Noble, S., Spann, M. N., Tokoglu, F., Shen, X., Constable, R. T., & Scheinost, D. (2017). Influences on the Test–Retest Reliability of Functional Connectivity MRI and its Relationship with Behavioral Utility. *Cerebral Cortex*, *27*(11), 5415–5429. https://doi.org/10.1093/cercor/bhx230

Nooner, K. B., Colcombe, S. J., Tobe, R. H., Mennes, M., Benedict, M. M., Moreno, A. L., Panek, L. J., Brown, S., Zavitz, S. T., Li, Q., Sikka, S., Gutman, D., Bangaru, S., Schlachter, R. T., Kamiel, S. M., Anwar, A. R., Hinz, C. M., Kaplan, M. S., Rachlin, A. B., … Milham, M. P. (2012). The NKI-Rockland Sample: A Model for Accelerating the Pace of Discovery Science in Psychiatry. *Frontiers in Neuroscience*, *6*. https://doi.org/10.3389/fnins.2012.00152

Ooi, L. Q. R., Orban, C., Nichols, T. E., Zhang, S., Tan, T. W. K., Kong, R., Marek, S., Dosenbach, N. U. F., Laumann, T., Gordon, E. M., Zhou, J. H., Bzdok, D., Eickhoff, S. B., Holmes, A. J., & Yeo, B. T. T. (2024). MRI economics: Balancing sample size and scan duration in brain wide association studies. *bioRxiv*, 2024.02.16.580448. https://doi.org/10.1101/2024.02.16.580448

Oschmann, M., & Gawryluk, J. R. (2020). A Longitudinal Study of Changes in Resting-State Functional Magnetic Resonance Imaging Functional Connectivity Networks During Healthy Aging. *Brain Connectivity*, *10*(7), 377–384. https://doi.org/10.1089/brain.2019.0724

O’Sullivan, M., Jones, D. K., Summers, P. E., Morris, R. G., Williams, S. C. R., & Markus, H. S. (2001). Evidence for cortical “disconnection” as a

mechanism of age-related cognitive decline. *Neurology*, *57*(4), 632–638. https://doi.org/10.1212/WNL.57.4.632

Pardoe, H. R., Kucharsky Hiess, R., & Kuzniecky, R. (2016). Motion and morphometry in clinical and nonclinical populations. *NeuroImage*, *135*, 177–185. https://doi.org/10.1016/j.neuroimage.2016.05.005

Park, D. C., Lautenschlager, G., Hedden, T., Davidson, N. S., Smith, A. D., & Smith, P. K. (2002). Models of visuospatial and verbal memory across the adult life span. *Psychology and Aging*, *17*(2), 299–320. https://doi.org/10.1037/0882-7974.17.2.299

Paterniti, S., Verdier-Taillefer, M.-H., Dufouil, C., & Alpérovitch, A. (2002). Depressive symptoms and cognitive decline in elderly people: Longitudinal study. *The British Journal of Psychiatry*, *181*(5), 406–410. https://doi.org/10.1192/bjp.181.5.406

Perez, D. C., Dworetsky, A., Braga, R. M., Beeman, M., & Gratton, C. (2022). Hemispheric Asymmetries of Individual Differences in Functional Connectivity. *bioRxiv*.

Poldrack, R. A. (2021). Diving into the deep end: A personal reflection on the MyConnectome study. *Current Opinion in Behavioral Sciences*, *40*, 1–4. https://doi.org/10.1016/j.cobeha.2020.10.008

Poldrack, R. A., Laumann, T. O., Koyejo, O., Gregory, B., Hover, A., Chen, M.-Y., Gorgolewski, K. J., Luci, J., Joo, S. J., Boyd, R. L., Hunicke-Smith, S., Simpson, Z. B., Caven, T., Sochat, V., Shine, J. M., Gordon, E., Snyder, A. Z., Adeyemo, B., Petersen, S. E., … Mumford, J. A. (2015). Long-term

neural and physiological phenotyping of a single human. *Nature Communications*, *6*(1), 8885. https://doi.org/10.1038/ncomms9885

Poulin, M. J., Liang, P. J., & Robbins, P. A. (1996). Dynamics of the cerebral blood flow response to step changes in end-tidal PCO2 and PO2 in humans. *Journal of Applied Physiology*, *81*(3), 1084–1095. https://doi.org/10.1152/jappl.1996.81.3.1084

Power, J. D., Barnes, K. A., Snyder, A. Z., Schlaggar, B. L., & Petersen, S. E. (2012). Spurious but systematic correlations in functional connectivity MRI networks arise from subject motion. *NeuroImage*, *59*(3), 2142–2154. https://doi.org/10.1016/j.neuroimage.2011.10.018

Power, J. D., Cohen, A. L., Nelson, S. M., Wig, G. S., Barnes, K. A., Church, J. A., Vogel, A. C., Laumann, T. O., Miezin, F. M., Schlaggar, B. L., & Petersen, S. E. (2011). Functional Network Organization of the Human Brain. *Neuron*, *72*(4), 665–678. https://doi.org/10.1016/j.neuron.2011.09.006

Power, J. D., Lynch, C. J., Dubin, M. J., Silver, B. M., Martin, A., & Jones, R. M. (2020). Characteristics of respiratory measures in young adults scanned at rest, including systematic changes and “missed” deep breaths. *NeuroImage*, *204*, 116234. https://doi.org/10.1016/j.neuroimage.2019.116234

Priovoulos, N., & Bazin, P.-L. (2023). Methods for cerebellar imaging analysis. *Current Opinion in Behavioral Sciences*, *54*, 101328. https://doi.org/10.1016/j.cobeha.2023.101328

Raz, N., Ghisletta, P., Rodrigue, K. M., Kennedy, K. M., & Lindenberger, U. (2010). Trajectories of brain aging in middle-aged and older adults: Regional and individual differences. *NeuroImage*, *51*(2), 501–511. https://doi.org/10.1016/j.neuroimage.2010.03.020

Raz, N., Lindenberger, U., Rodrigue, K. M., Kennedy, K. M., Head, D., Williamson, A., Dahle, C., Gerstorf, D., & Acker, J. D. (2005). Regional Brain Changes in Aging Healthy Adults: General Trends, Individual Differences and Modifiers. *Cerebral Cortex*, *15*(11), 1676–1689. https://doi.org/10.1093/cercor/bhi044

Raz, N., Rodrigue, K. M., Kennedy, K. M., & Acker, J. D. (2007). Vascular health and longitudinal changes in brain and cognition in middle-aged and older adults. *Neuropsychology*, *21*(2), 149–157. https://doi.org/10.1037/0894-4105.21.2.149

Resnick, S. M., Pham, D. L., Kraut, M. A., Zonderman, A. B., & Davatzikos, C. (2003). Longitudinal Magnetic Resonance Imaging Studies of Older Adults: A Shrinking Brain. *Journal of Neuroscience*, *23*(8), 3295–3301. https://doi.org/10.1523/JNEUROSCI.23-08-03295.2003

Reuter-Lorenz, P. A., & Park, D. C. (2014). How Does it STAC Up? Revisiting the Scaffolding Theory of Aging and Cognition. *Neuropsychology Review*, *24*(3), 355–370. https://doi.org/10.1007/s11065-014-9270-9

Rodriguez-Sabate, C., Morales, I., Sanchez, A., & Rodriguez, M. (2019). The functional interaction of the brain default network with motor networks

is modified by aging. *Behavioural Brain Research*, *372*, 112048. https://doi.org/10.1016/j.bbr.2019.112048

Rogalski, E. J., Gefen, T., Shi, J., Samimi, M., Bigio, E., Weintraub, S., Geula, C., & Mesulam, M.-M. (2013). Youthful Memory Capacity in Old Brains: Anatomic and Genetic Clues from the Northwestern SuperAging Project. *Journal of Cognitive Neuroscience*, *25*(1), 29–36. https://doi.org/10.1162/jocn_a_00300

Rosen, H. J., Gorno–Tempini, M. L., Goldman, W. P., Perry, R. J., Schuff, N., Weiner, M., Feiwell, R., Kramer, J. H., & Miller, B. L. (2002). Patterns of brain atrophy in frontotemporal dementia and semantic dementia. *Neurology*, *58*(2), 198–208. https://doi.org/10.1212/WNL.58.2.198

Ruiz-Rizzo, A. L., Sorg, C., Napiórkowski, N., Neitzel, J., Menegaux, A., Müller, H. J., Vangkilde, S., & Finke, K. (2019). Decreased cingulo-opercular network functional connectivity mediates the impact of aging on visual processing speed. *Neurobiology of Aging*, *73*, 50–60. https://doi.org/10.1016/j.neurobiolaging.2018.09.014

Saccà, V., Sarica, A., Quattrone, A., Rocca, F., Quattrone, A., & Novellino, F. (2021). Aging effect on head motion: A Machine Learning study on resting state fMRI data. *Journal of Neuroscience Methods*, *352*, 109084. https://doi.org/10.1016/j.jneumeth.2021.109084

Saeed, U., Lang, A. E., & Masellis, M. (2020). Neuroimaging Advances in Parkinson’s Disease and Atypical Parkinsonian Syndromes. *Frontiers in*

Neurology, *11*. https://www.frontiersin.org/articles/10.3389/fneur.2020.572976

Sala-Llonch, R., BartrÃ©s-Faz, D., & JunquÃ©, C. (2015). Reorganization of brain networks in aging: A review of functional connectivity studies. *Frontiers in Psychology*, *6*. https://doi.org/10.3389/fpsyg.2015.00663

Salthouse, T. A. (1996). *The Processing-Speed Theory of Adult Age Differences in Cognition*. 26.

Salthouse, T. A., & Ferrer-Caja, E. (2003). What needs to be explained to account for age-related effects on multiple cognitive variables? *Psychology and Aging*, *18*(1), 91–110. https://doi.org/10.1037/0882-7974.18.1.91

Salvo, J. J., Holubecki, A. M., & Braga, R. M. (2021). Correspondence between functional connectivity and task-related activity patterns within the individual. *Current Opinion in Behavioral Sciences*, *40*, 178–188. https://doi.org/10.1016/j.cobeha.2021.05.003

Satterthwaite, T. D., Wolf, D. H., Loughead, J., Ruparel, K., Elliott, M. A., Hakonarson, H., Gur, R. C., & Gur, R. E. (2012). Impact of in-scanner head motion on multiple measures of functional connectivity: Relevance for studies of neurodevelopment in youth. *NeuroImage*, *60*(1), 623–632. https://doi.org/10.1016/j.neuroimage.2011.12.063

Satterthwaite, T. D., Wolf, D. H., Ruparel, K., Erus, G., Elliott, M. A., Eickhoff, S. B., Gennatas, E. D., Jackson, C., Prabhakaran, K., Smith, A., Hakonarson, H., Verma, R., Davatzikos, C., Gur, R. E., & Gur, R. C.

(2013). Heterogeneous impact of motion on fundamental patterns of developmental changes in functional connectivity during youth. *NeuroImage*, *83*, 45–57. https://doi.org/10.1016/j.neuroimage.2013.06.045

Savalia, N. K., Agres, P. F., Chan, M. Y., Feczko, E. J., Kennedy, K. M., & Wig, G. S. (2017). Motion-related artifacts in structural brain images revealed with independent estimates of in-scanner head motion. *Human Brain Mapping*, *38*(1), 472–492. https://doi.org/10.1002/hbm.23397

Schaefer, A., Kong, R., Gordon, E. M., Laumann, T. O., Zuo, X.-N., Holmes, A. J., Eickhoff, S. B., & Yeo, B. T. T. (2018). Local-Global Parcellation of the Human Cerebral Cortex from Intrinsic Functional Connectivity MRI. *Cerebral Cortex (New York, N.Y.: 1991)*, *28*(9), 3095–3114. https://doi.org/10.1093/cercor/bhx179

Schmahmann, J. D. (2016). Cerebellum in Alzheimer's disease and frontotemporal dementia: Not a silent bystander. *Brain*, *139*(5), 1314–1318. https://doi.org/10.1093/brain/aww064

Seeley, W. W. (2019). The Salience Network: A Neural System for Perceiving and Responding to Homeostatic Demands. *The Journal of Neuroscience*, *39*(50), 9878–9882. https://doi.org/10.1523/JNEUROSCI.1138-17.2019

Seeley, W. W., Crawford, R. K., Zhou, J., Miller, B. L., & Greicius, M. D. (2009). Neurodegenerative Diseases Target Large-Scale Human Brain

Networks. *Neuron*, *62*(1), 42–52. https://doi.org/10.1016/j.neuron.2009.03.024

Seidler, R., Erdeniz, B., Koppelmans, V., Hirsiger, S., Mérillat, S., & Jäncke, L. (2015). Associations between age, motor function, and resting state sensorimotor network connectivity in healthy older adults. *NeuroImage*, *108*, 47–59. https://doi.org/10.1016/j.neuroimage.2014.12.023

Seitzman, B. A., Gratton, C., Laumann, T. O., Gordon, E. M., Adeyemo, B., Dworetsky, A., Kraus, B. T., Gilmore, A. W., Berg, J. J., Ortega, M., Nguyen, A., Greene, D. J., McDermott, K. B., Nelson, S. M., Lessov-Schlaggar, C. N., Schlaggar, B. L., Dosenbach, N. U. F., & Petersen, S. E. (2019). Trait-like variants in human functional brain networks. *Proceedings of the National Academy of Sciences*, *116*(45), 22851–22861. https://doi.org/10.1073/pnas.1902932116

Sele, S., Liem, F., Mérillat, S., & Jäncke, L. (2021). Age-related decline in the brain: A longitudinal study on inter-individual variability of cortical thickness, area, volume, and cognition. *NeuroImage*, *240*, 118370. https://doi.org/10.1016/j.neuroimage.2021.118370

Setton, R., Mwilambwe-Tshilobo, L., Girn, M., Lockrow, A. W., Baracchini, G., Hughes, C., Lowe, A. J., Cassidy, B. N., Li, J., Luh, W.-M., Bzdok, D., Leahy, R. M., Ge, T., Margulies, D. S., Misic, B., Bernhardt, B. C., Stevens, W. D., De Brigard, F., Kundu, P., … Spreng, R. N. (2022). Age

differences in the functional architecture of the human brain. *Cerebral Cortex*, *33*(1), 114–134. https://doi.org/10.1093/cercor/bhac056

Setton, R., Mwilambwe-Tshilobo, L., Sheldon, S., Turner, G. R., & Spreng, R. N. (2022). Hippocampus and temporal pole functional connectivity is associated with age and individual differences in autobiographical memory. *Proceedings of the National Academy of Sciences*, *119*(41), e2203039119. https://doi.org/10.1073/pnas.2203039119

Shafto, M. A., Tyler, L. K., Dixon, M., Taylor, J. R., Rowe, J. B., Cusack, R., Calder, A. J., Marslen-Wilson, W. D., Duncan, J., Dalgleish, T., Henson, R. N., Brayne, C., & Matthews, F. E. (2014). The Cambridge Centre for Ageing and Neuroscience (Cam-CAN) study protocol: A cross-sectional, lifespan, multidisciplinary examination of healthy cognitive ageing. *BMC Neurology*, *14*(1), 204. https://doi.org/10.1186/s12883-014-0204-1

Shammi, P., Bosman, E., & Stuss, D. T. (1998). Aging and Variability in Performance. *Aging, Neuropsychology, and Cognition*, *5*(1), 1–13. https://doi.org/10.1076/anec.5.1.1.23

Siddiqi, S. H., Weigand, A., Pascual-Leone, A., & Fox, M. D. (2021). Identification of Personalized Transcranial Magnetic Stimulation Targets Based on Subgenual Cingulate Connectivity: An Independent Replication. *Biological Psychiatry*, *90*(10), e55–e56. https://doi.org/10.1016/j.biopsych.2021.02.015

Siegel, J. S., Mitra, A., Laumann, T. O., Seitzman, B. A., Raichle, M., Corbetta, M., & Snyder, A. Z. (2017). Data Quality Influences Observed Links

Between Functional Connectivity and Behavior. *Cerebral Cortex*, *27*(9), 4492–4502. https://doi.org/10.1093/cercor/bhw253

Smith, S. M., Fox, P. T., Miller, K. L., Glahn, D. C., Fox, P. M., Mackay, C. E., Filippini, N., Watkins, K. E., Toro, R., Laird, A. R., & Beckmann, C. F. (2009). Correspondence of the brain's functional architecture during activation and rest. *Proceedings of the National Academy of Sciences*, *106*(31), 13040–13045. https://doi.org/10.1073/pnas.0905267106

Sporns, O. (2018). Graph theory methods: Applications in brain networks. *Dialogues in Clinical Neuroscience*, *20*(2), 111–121. https://doi.org/10.31887/DCNS.2018.20.2/osporns

Spreng, R. N., & Grady, C. L. (2010). Patterns of Brain Activity Supporting Autobiographical Memory, Prospection, and Theory of Mind, and Their Relationship to the Default Mode Network. *Journal of Cognitive Neuroscience*, *22*(6), 1112–1123. https://doi.org/10.1162/jocn.2009.21282

Spreng, R. N., & Schacter, D. L. (2012). Default Network Modulation and Large-Scale Network Interactivity in Healthy Young and Old Adults. *Cerebral Cortex*, *22*(11), 2610–2621. https://doi.org/10.1093/cercor/bhr339

Spreng, R. N., Sepulcre, J., Turner, G. R., Stevens, W. D., & Schacter, D. L. (2012). *Intrinsic Architecture Underlying the Relations among the Default, Dorsal Attention, and Frontoparietal Control Networks of the Human Brain*. *25*(1), 13. https://doi.org/10.1162/jocn_a_00281

Spreng, R. N., & Turner, G. R. (2019). The Shifting Architecture of Cognition and Brain Function in Older Adulthood. *Perspectives on Psychological Science*, *14*(4), 523–542. https://doi.org/10.1177/1745691619827511

St. John, P. D., & Montgomery, P. R. (2010). Cognitive impairment and life satisfaction in older adults. *International Journal of Geriatric Psychiatry*, *25*(8), 814–821. https://doi.org/10.1002/gps.2422

Stopford, C. L., Snowden, J. S., Thompson, J. C., & Neary, D. (2008). Variability in cognitive presentation of Alzheimer's disease. *Cortex*, *44*(2), 185–195. https://doi.org/10.1016/j.cortex.2005.11.002

Storsve, A. B., Fjell, A. M., Yendiki, A., & Walhovd, K. B. (2016). Longitudinal Changes in White Matter Tract Integrity across the Adult Lifespan and Its Relation to Cortical Thinning. *PLOS ONE*, *11*(6), e0156770. https://doi.org/10.1371/journal.pone.0156770

Sun, F. W., Stepanovic, M. R., Andreano, J., Barrett, L. F., Touroutoglou, A., & Dickerson, B. C. (2016). Youthful Brains in Older Adults: Preserved Neuroanatomy in the Default Mode and Salience Networks Contributes to Youthful Memory in Superaging. *Journal of Neuroscience*, *36*(37), 9659–9668. https://doi.org/10.1523/JNEUROSCI.1492-16.2016

Tavor, I., Jones, O. P., Mars, R. B., Smith, S. M., Behrens, T. E., & Jbabdi, S. (2016). Task-free MRI predicts individual differences in brain activity during task performance. *Science*, *352*(6282), 216–220. https://doi.org/10.1126/science.aad8127

Tsvetanov, K. A., Henson, R. N. A., & Rowe, J. B. (2020). Separating vascular and neuronal effects of age on fMRI BOLD signals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1815), 20190631. https://doi.org/10.1098/rstb.2019.0631

Turner, M. P., Zhao, Y., Abdelkarim, D., Liu, P., Spence, J. S., Hutchison, J. L., Sivakolundu, D. K., Thomas, B. P., Hubbard, N. A., Xu, C., Taneja, K., Lu, H., & Rypma, B. (2023). Altered linear coupling between stimulus-evoked blood flow and oxygen metabolism in the aging human brain. *Cerebral Cortex*, *33*(1), 135–151. https://doi.org/10.1093/cercor/bhac057

Uddin, L. Q., Betzel, R. F., Cohen, J. R., Damoiseaux, J. S., De Brigard, F., Eickhoff, S. B., Fornito, A., Gratton, C., Gordon, E. M., Laird, A. R., Larson-Prior, L., McIntosh, A. R., Nickerson, L. D., Pessoa, L., Pinho, A. L., Poldrack, R. A., Razi, A., Sadaghiani, S., Shine, J. M., … Spreng, R. N. (2023). Controversies and progress on standardization of large-scale brain network nomenclature. *Network Neuroscience*, *7*(3), 864–905. https://doi.org/10.1162/netn_a_00323

van de Ven, V. G., Formisano, E., Prvulovic, D., Roeder, C. H., & Linden, D. E. J. (2004). Functional connectivity as revealed by spatial independent component analysis of fMRI measurements during rest. *Human Brain Mapping*, *22*(3), 165–178. https://doi.org/10.1002/hbm.20022

Van Dijk, E. J., Prins, N. D., Vrooman, H. A., Hofman, A., Koudstaal, P. J., & Breteler, M. M. B. (2008). Progression of Cerebral Small Vessel Disease

in Relation to Risk Factors and Cognitive Consequences: Rotterdam Scan Study. *Stroke*, *39*(10), 2712–2719. https://doi.org/10.1161/STROKEAHA.107.513176

Van Dijk, K. R. A., Hedden, T., Venkataraman, A., Evans, K. C., Lazar, S. W., & Buckner, R. L. (2010). Intrinsic Functional Connectivity As a Tool For Human Connectomics: Theory, Properties, and Optimization. *Journal of Neurophysiology*, *103*(1), 297–321. https://doi.org/10.1152/jn.00783.2009

Vogel, J. W., Corriveau-Lecavalier, N., Franzmeier, N., Pereira, J. B., Brown, J. A., Maass, A., Botha, H., Seeley, W. W., Bassett, D. S., Jones, D. T., & Ewers, M. (2023). Connectome-based modelling of neurodegenerative diseases: Towards precision medicine and mechanistic insight. *Nature Reviews Neuroscience*, 1–20. https://doi.org/10.1038/s41583-023-00731-8

Voss, M. W., Erickson, K. I., Prakash, R. S., Chaddock, L., Malkowski, E., Alves, H., Kim, J. S., Morris, K. S., White, S. M., Wójcicki, T. R., Hu, L., Szabo, A., Klamm, E., McAuley, E., & Kramer, A. F. (2010). Functional connectivity: A source of variance in the association between cardiorespiratory fitness and cognition? *Neuropsychologia*, *48*(5), 1394–1406. https://doi.org/10.1016/j.neuropsychologia.2010.01.005

Wales, R. M., & Leung, H.-C. (2021). The Effects of Amyloid and Tau on Functional Network Connectivity in Older Populations. *Brain Connectivity*, *11*(8), 599–612. https://doi.org/10.1089/brain.2020.0902

Walhovd, K. B., Westlye, L. T., Amlien, I., Espeseth, T., Reinvang, I., Raz, N., Agartz, I., Salat, D. H., Greve, D. N., Fischl, B., Dale, A. M., & Fjell, A. M. (2011). Consistent neuroanatomical age-related volume differences across multiple samples. *Neurobiology of Aging*, *32*(5), 916–932. https://doi.org/10.1016/j.neurobiolaging.2009.05.013

Wang, D., Li, M., Wang, M., Schoeppe, F., Ren, J., Chen, H., Öngür, D., Brady, R. O., Baker, J. T., & Liu, H. (2020). Individual-specific functional connectivity markers track dimensional and categorical features of psychotic illness. *Molecular Psychiatry*, *25*(9), Article 9. https://doi.org/10.1038/s41380-018-0276-1

Wang, Q., Akram, H., Muthuraman, M., Gonzalez-Escamilla, G., Sheth, S. A., Oxenford, S., Yeh, F.-C., Groppa, S., Vanegas-Arroyave, N., Zrinzo, L., Li, N., Kühn, A., & Horn, A. (2021). Normative vs. Patient-specific brain connectivity in deep brain stimulation. *NeuroImage*, *224*, 117307. https://doi.org/10.1016/j.neuroimage.2020.117307

Wang, X., Dworkin, J. D., Zhou, D., Stiso, J., Falk, E. B., Bassett, D. S., Zurn, P., & Lydon-Staley, D. M. (2021). Gendered citation practices in the field of communication. *Annals of the International Communication Association*, *45*(2), 134–153. https://doi.org/10.1080/23808985.2021.1960180

Wig, G. S., Laumann, T. O., Cohen, A. L., Power, J. D., Nelson, S. M., Glasser, M. F., Miezin, F. M., Snyder, A. Z., Schlaggar, B. L., & Petersen, S. E. (2014). Parcellating an Individual Subject’s Cortical and Subcortical

Brain Structures Using Snowball Sampling of Resting-State Correlations. *Cerebral Cortex*, *24*(8), 2036–2054. https://doi.org/10.1093/cercor/bht056

Yap, Q. J., Teh, I., Fusar-Poli, P., Sum, M. Y., Kuswanto, C., & Sim, K. (2013). Tracking cerebral white matter changes across the lifespan: Insights from diffusion tensor imaging studies. *Journal of Neural Transmission*, *120*(9), 1369–1395. https://doi.org/10.1007/s00702-013-0971-7

Yeo, B. T. T., Krienen, F. M., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., Roffman, J. L., Smoller, J. W., Zöllei, L., Polimeni, J. R., Fischl, B., Liu, H., & Buckner, R. L. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *Journal of Neurophysiology*, *106*(3), 1125–1165. https://doi.org/10.1152/jn.00338.2011

Zanjani, F., Downer, B. G., Kruger, T. M., Willis, S. L., & Schaie, K. W. (2013). Alcohol effects on cognitive change in middle-aged and older adults. *Aging & Mental Health*, *17*(1), 12–23. https://doi.org/10.1080/13607863.2012.717254

Zhang, H.-Y., Chen, W.-X., Jiao, Y., Xu, Y., Zhang, X.-R., & Wu, J.-T. (2014). Selective Vulnerability Related to Aging in Large-Scale Resting Brain Networks. *PLOS ONE*, *9*(10), e108807. https://doi.org/10.1371/journal.pone.0108807

Zhang, Z., Chan, M. Y., Han, L., Carreno, C. A., Winter-Nelson, E., Wig, G. S., & for the Alzheimer’s Disease Neuroimaging Initiative (ADNI). (2023).

Dissociable Effects of Alzheimer's Disease-Related Cognitive Dysfunction and Aging on Functional Brain Network Segregation. *The Journal of Neuroscience*, *43*(46), 7879–7892. https://doi.org/10.1523/JNEUROSCI.0579-23.2023

Zhou, D., Cornblath, E., Stiso, J., Teich, E., Dworkin, J., Blevins, A., & Bassett, D. S. (2020). Gender diversity statement and code notebook v1. 0. 2020. *URL Https://Doi. Org/10.5281/Zenodo*, *3672110*. https://doi.org/10.5281/zenodo.4104748

Zhou, J., Greicius, M. D., Gennatas, E. D., Growdon, M. E., Jang, J. Y., Rabinovici, G. D., Kramer, J. H., Weiner, M., Miller, B. L., & Seeley, W. W. (2010). Divergent network connectivity changes in behavioural variant frontotemporal dementia and Alzheimer's disease. *Brain*, *133*(5), 1352–1367. https://doi.org/10.1093/brain/awq075

Zimmerman, B., Rypma, B., Gratton, G., & Fabiani, M. (2021). Age-related changes in cerebrovascular health and their effects on neural function and cognition: A comprehensive review. *Psychophysiology*, *58*(7), e13796. https://doi.org/10.1111/psyp.13796

Zonneveld, H. I., Pruim, R. HR., Bos, D., Vrooman, H. A., Muetzel, R. L., Hofman, A., Rombouts, S. ARB., van der Lugt, A., Niessen, W. J., Ikram, M. A., & Vernooij, M. W. (2019). Patterns of functional connectivity in an aging population: The Rotterdam Study. *NeuroImage*, *189*, 432–444. https://doi.org/10.1016/j.neuroimage.2019.01.041