A Neurocognitive Shift in Midlife: Linking Cognitive Flexibility and Functional-Metabolic Adaptation with the SENECA model

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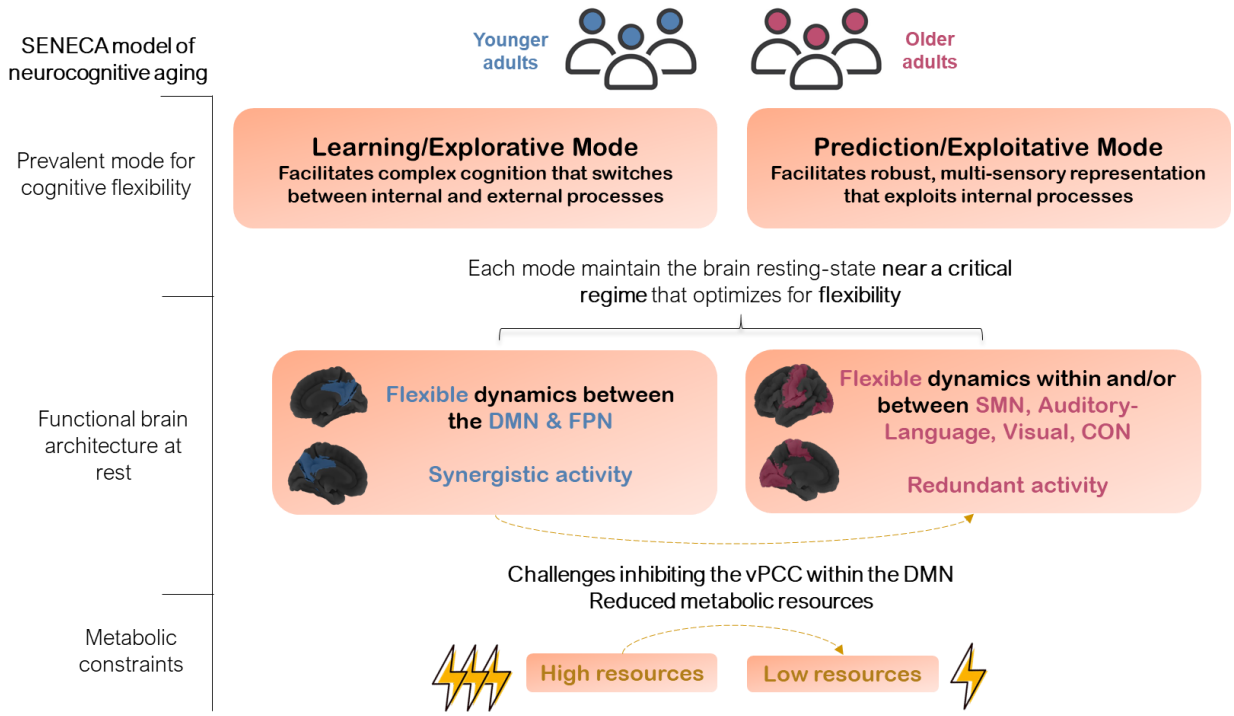
Graphical abstract



Abstract (184 words)

Cognitive flexibility in the human brain engages dynamic interactions between the Default Mode Network (DMN) and the Fronto-Parietal Network (FPN), a functional architecture that is metabolically demanding and thus potentially susceptible to age-related decline. How the aging brain reorganizes its functional architecture to sustain cognitive flexibility under metabolic constraints remains an open question. In this study, we modeled resting-state functional flexibility across the adult lifespan (ages 18–88) using structural balance theory. Our findings align with the predictions of the SENECA model (*Synergistic, Economical, Nonlinear, Emergent, Cognitive Aging*), revealing a midlife neurocognitive transition: (i) from a metabolically costly, flexible DMN-FPN architecture, toward (ii) a more redundant configuration dominated by low-cost, sensory-driven interactions. The medio-parietal DMN and the Cingulo-Opercular Network (CON) are crucial to this transition, contributing to maintain global brain activity near a critical dynamic regime in older adulthood that optimizes for cognitive flexibility in face of declining metabolic resources. These findings advance a theoretical and methodological framework for understanding neurocognitive flexibility in aging and underscore the importance of multimodal fMRI-PET studies in midlife. They also open promising avenues for translational applications in neuropathology.

Keywords: cognitive flexibility, cognitive aging, resting-state fMRI, metabolism, SENECA model

1. Introduction

A core idea in network neuroscience is that resting-state brain activity is organized to support rich functional dynamics at a minimal wiring cost – a phenomenon known as the *wiring economy* (Achard & Bullmore, 2007; Bullmore & Sporns, 2012; Shine & Poldrack, 2018; Takagi, 2021). Such economical dynamics position the brain in a near-critical regime – notably in the Default Mode Network (DMN) (Deco et al., 2011; Deco & Jirsa, 2012) – that enables rapid exploration and switching between different perceptual, motor, and cognitive cross-system configurations (Cocchi et al., 2017; Hancock et al., 2022; O'Byrne & Jerbi, 2022), and therefore facilitates a flexible functional and cognitive repertoire – i.e., neurocognitive flexibility (Q. Chen et al., 2025; Deco et al., 2013; Ionescu, 2017; R. Wang et al., 2021).

An emerging body of research suggests that such neurocognitive flexibility is regulated by high-level cognitive systems that involve self- and goal-oriented processes (Kupis et al., 2021; Nieberlein et al., 2024; Xia et al., 2022, 2024). Self-oriented processes typically engage the Default Mode Network (DMN) (Menon, 2023; Raichle, 2015); whereas goal-oriented processes primarily engage the Fronto-Parietal Network (FPN), known for its role in cognitive control (Camilleri et al., 2018). Therefore, the interplay between the DMN and FPN lends the control resources necessary for switching between externally-directed – when the DMN is deactivated – and internally-directed streams of cognition – when the DMN is activated. To be clear, external cognition is supported by *anticorrelated* DMN-FPN interactions – a competitive dynamic that suppresses goal-irrelevant thoughts (via DMN deactivation) to facilitate goal-directed attentional processes (via FPN activation) (Buckner & DiNicola, 2019; Finc et al., 2020; Raichle, 2015). In comparison, internal cognition, used for semantic memory, creative thinking (Adnan et al., 2019; Chen et al., 2025), or mental time travel (Chen et al., 2022), typically involves *correlated* activity DMN-FPN interactions – a cooperative dynamic that facilitates spontaneous, yet controlled cognition (Spreng et al., 2014).

This flexible switch between cooperative and competitive DMN-FPN dynamics gives rise to complex cognitive functions that draw on substantial neural flexibility (Cocchi et al., 2013; Luo et al., 2024; Paquola et al., 2025; Smallwood et al., 2021). One example of such cognitive function is semantic control – the ability to selectively access and manipulate learned semantic knowledge (Reilly et al., 2023). Many studies suggest that semantic control is particularly vulnerable to disruptions in neurocognitive flexibility as it engages regions adjacent to both the DMN and FPN (Branzi & Lambon Ralph, 2023; Chiou et al., 2018, 2023; Wang et al., 2024). More broadly, this suggests that complex cognitive functions that heavily rely on semantic control processes, such as langage, offer a valuable framework linking cognitive flexibility to real-word behavior (Benítez-Burraco & Ivanova, 2024), recapitulating the information flow between DMN-semantic and FPN-control systems beyond the traditional left-lateralized language network (Aliko et al., 2023; Dudschig, 2022; Forkel & Hagoort, 2024; Hasson et al., 2018; Hsieh et al., 2024; Krieger-Redwood et al., 2025; Roger, Rodrigues De Almeida, et al., 2022; X. Wang et al., 2020).

As the global population ages (United Nations, 2023), understanding the cognitive relevance of disruption in this DMN-FPN architecture becomes increasingly important. This could guide the development of interventions to sustain cognitive flexibility (Politakis et al., 2022; Uddin, 2021), and *in extenso*, prevent word retrieval and generation challenges in the older population (Alhanai et al., 2017; Baciu & Roger, 2024; Martínez-Ferreiro, 2024).

At a cognitive level, the accumulation of life experiences and knowledge about the world expands the semantic store (Cutler et al., 2025; Gollan & Goldrick, 2019). This is often reflected by preserved or even enhanced vocabulary and langage comprehension (Diaz et al., 2016; Harada et al., 2013; Hartshorne & Germine, 2015; Park & Reuter-Lorenz, 2009). In parallel, older adults show difficulties in inhibitory control processes, therefore reducing their ability to inhibit learned semantic associations that not relevant to the goal (Badre & Wagner, 2007;

Benítez-Burraco & Ivanova, 2023; Hoffman & MacPherson, 2022; Loaiza, 2024; S. Martin et al., 2022; Salthouse, 2019; Shafto & Tyler, 2014; Verhaegen & Poncelet, 2013).

At a brain level, influential models such as the DECHA (*Default-Executive Coupling Hypothesis in Aging*; Spreng & Turner, 2019) suggests that this reduced inhibition reduces the ability to inhibit the DMN at rest, thus disrupting competitive DMN-FPN interactions that uphold externally-directed processes crucial to semantic control (Guichet, Banjac, et al., 2024).

In this study, we argue that further insights on neurocognitive aging can be gained by considering metabolic constraints on this architecture (Camandola & Mattson, 2017; Palombit et al., 2022; Pellerin, 2025; Raz & Daugherty, 2018; Volpi et al., 2024; Wan et al., 2024). Metabolism is particularly relevant in the context of neurocognitive aging as the DMN accounts for up to 80% of the brain's energy consumption at rest (Luo et al., 2024; Shulman et al., 2004; Thomas Yeo et al., 2011; Zang et al., 2004) and shows the strongest coupling between neural activity and energy use of any large-scale network (Shokri-Kojori et al., 2019). Task-related DMN deactivation has also been linked to an increased metabolic response, suggesting that competitive DMN-FPN interactions represents a metabolically expensive mechanism for cognitive flexibility (Leonards et al., 2023; Stiernman et al., 2021). Previous fMRI-PET studies also suggest that GABAergic inhibition of the DMN is a high-cost mechanism, particularly regarding the posterior medial (pm) DMN, which is sensitive to the FPN control demands (Godbersen et al., 2023; Hahn et al., 2024). In sum, these studies suggests that competitive DMN-FPN dynamics are vulnerable to age-related decline in metabolism (Deery et al., 2024; Diniz & Crestani, 2023; Stranahan & Mattson, 2012). Therefore, we argue that comprehensive neurocognitive models should be explicit about how the brain reorganizes this DMN-FPN architecture when metabolic resources decline in older adults, and further explain its impact on cognitive flexibility.

In this regard, the SENECA model *(Synergistic, Economical, Nonlinear, Emergent, Cognitive Aging)* was recently introduced based on resting-state fMRI evidence (Guichet, Banjac, et al., 2024). While initially developed to explain age-related differences in lexical production, the model has the potential to encompass the broader domain of cognitive flexibility (Ionescu, 2017; Xia et al., 2024).

The present study

In the context of cognitive flexibility, the SENECA model makes three predictions that we propose to evaluate in this study.

- (**Prediction 1**) In face of declining metabolic resources, older adults maintain a *global wiring economy* to support flexible dynamics across brain systems, reflecting a form of whole-brain functional homeostasis. Thus, we expected no changes in flexibility at the whole-brain level.
- (**Prediction 2**) To maintain such homeostasis, the brain architecture may undergo spatially distributed changes that downregulates metabolically expensive mechanisms. Specifically, we anticipate a prevalence of flexible DMN-FPN dynamics in younger adulthood, particularly in the pmDMN, before the adoption of a brain architecture with lower metabolic demands around midlife. This new architecture may translate to increase flexibility in lower-level networks in older adulthood (Guichet, Banjac, et al., 2024), emphasizing the SMN for sensorimotor integration and the Cingulo-Opercular Network (CON) for cognitive control instead of the FPN (Sestieri et al., 2014; Wallis et al., 2015).
- (**Prediction 3**) The posterior cingulate cortex (PCC) is a hub linking the DMN and FPN (Fan et al., 2019; Goelman et al., 2024), crucial for semantic control (Krieger-Redwood et al., 2016) and highly-dependent on metabolic activity (Basten et al., 2015; Utevsky

et al., 2014). Because its dorsal (dPCC) and ventral (vPCC) components are differently integrated within the DMN (Godbersen et al., 2023), we expect that the dorsal PCC (dPCC), being more connected to FPN control, will become more rigid with age, while the ventral PCC (vPCC), tied to self-oriented representations, may increase its flexibility within the DMN (Leech et al., 2011; Leech & Sharp, 2014).

To operationalize the concept of neural flexibility, we analyzed resting-state functional connectomes from healthy adults aged 18-88 (Cam-CAN et al., 2014) using *structural balance theory* – a promising graph-theoretical approach (Saberi et al., 2024). This approach proposes to examine flexibility as the interaction between cooperative/correlated and competitive/anti-correlated dynamics (Cocchi et al., 2013; Fox et al., 2005; Luppi, Sanz Perl, et al., 2024; Sporns & Betzel, 2016). Their interaction can be classified into two motifs (Figure 1):

- **Rigid motifs**: Rigid configurations with minimal tension between regions (even number of anti-correlated connections).

- **Flexible motifs**: Flexible configurations that support dynamic reconfigurations between regions (odd number of anti-correlated connections).

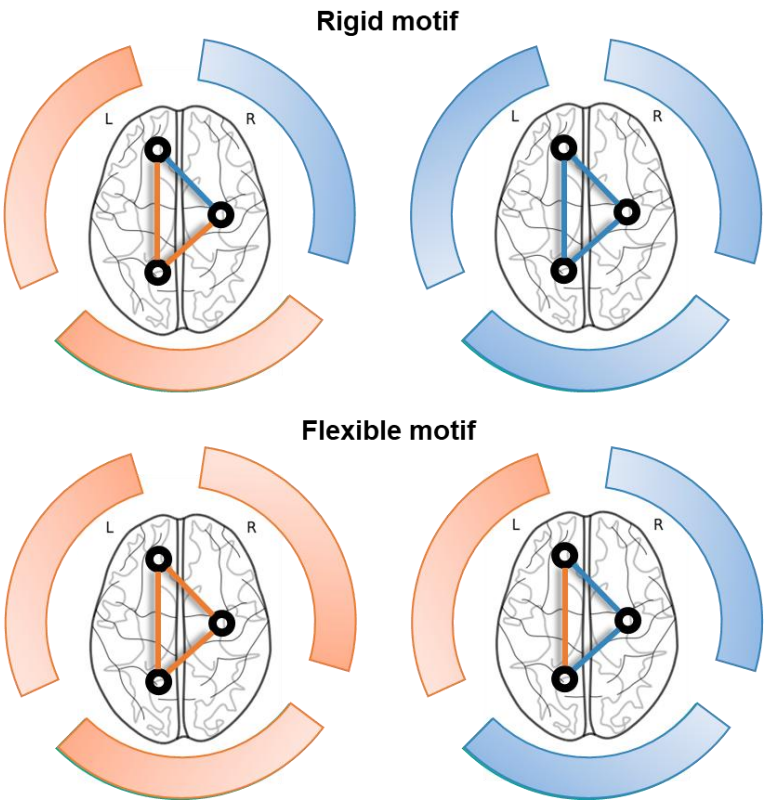


Figure 1. Neural flexibility framework. Based on the framework described in Saberi et al. (2024). Orange and Blue represents correlated and anti-correlated patterns of functional connectivity respectively.

2. Results

2.1. Prediction 1: Whole-brain level

A Bayesian practical equivalence test indicated that the ROPE (Region of Practical Equivalence) fully covered the 89% HDI of posterior samples [-1e-4; 1e-4], suggesting no change in whole-brain flexibility at rest throughout the adult lifespan (see Method). In comparison, the ratio of flexibility between versus within networks declined beyond midlife (F = 76.42, p < .001, edf = 1.93, signed partial R^2 = - .19). Collectively, this suggests that distributed changes in flexibility within and between networks contribute to maintain homeostasis at the whole-brain level (see Figure 2).

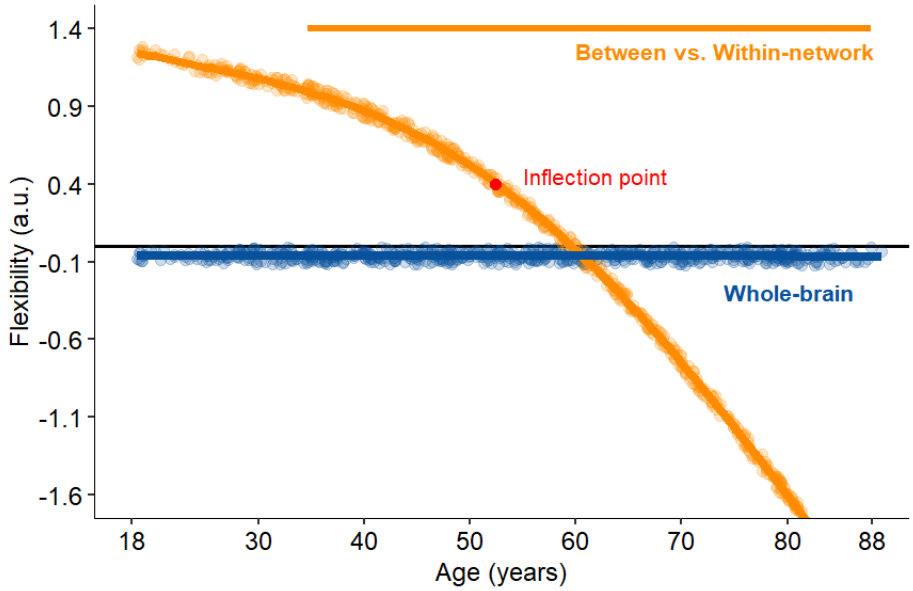


Figure 2. Whole-brain analysis

Bayesian equivalence test found no strong evidence of whole-brain changes in flexibility across the lifespan. The blue trajectory plots the mean expectation of posterior predictive distribution.

In comparison, Between vs. Within-network flexibility begins to decline around age 45 and accelerates in midlife. The orange trajectory plots the fitted values of a Generalized Additive Model (GAM). The bar on top represents the window of significant age-related changes and was determined by computing the 1st derivative of the fitted GAM smooth function. The inflection point in red is the age with the highest significant 2nd derivative.

2.2. Prediction 2: Network level

We decomposed whole-brain flexibility (i) within networks, and (ii) between networks (Figure 3). Model statistics reported in Table 1 in Supplementary Materials. Overall, results suggest

that most age-related changes in flexibility occur around midlife, with an inflection point around age 52.

Between networks. Between networks, only DMN-FPN had a substantial decline in flexibility beyond midlife (see upper right panel on Figure 3); whereas flexibility across lower-level networks exhibited important increases, especially considering Auditory-SMN and SMN-Visual couplings (see bottom panels on Figure 3).

Within networks. Age-related changes in within-network flexibility also occurred within lower-level networks with a similar inflection point in midlife, especially within the SMN, Auditory, Language and Visual 2 networks (see upper left panel on Figure 3).

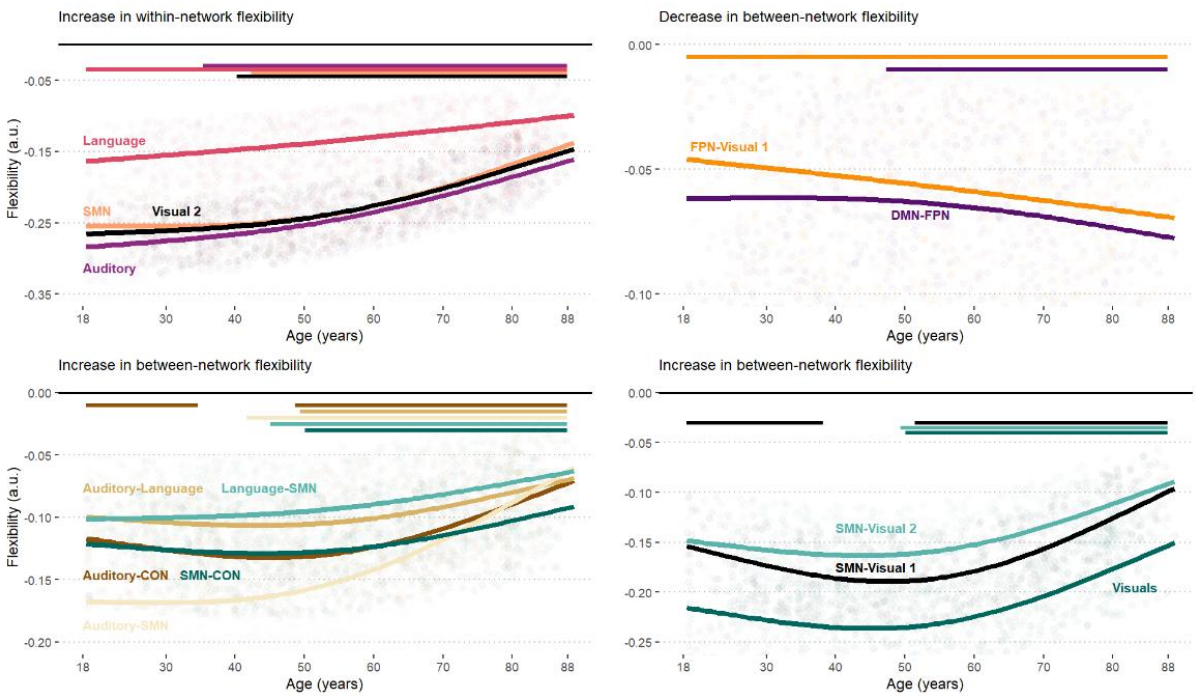


Figure 3. Age-related within and between-network flexibility

The trajectories plots the predicted values of Generalized Additive Models (GAM). Bars on top represent the window of significant age-related changes and were determined by computing the 1st derivative of the fitted GAM smooth function. We only illustrate the top significant trajectories.

2.3. Prediction 2 & 3: Regional flexibility in DMN-FPN & within DMN

DMN-FPN. Figure 4A shows that the decline in DMN-FPN flexibility is primarily driven by posterior cingulate regions, especially bilateral areas 7m and the bilateral parieto-occipital sulci (POS2). Overall, regions with stronger contributions were more posterior ($r_{(76)}$ = .52 [.34;.67] 95% CI, p < .001), superior ($r_{(76)}$ = .32 [.11;.51] 95% CI , p < .001), and medial ($r_{(76)}$ = .32 [.1;.5] 95% CI , p < .001).

Within the DMN. Figure 4B shows heterogeneity of the PCC activity within the DMN, but only in the left hemisphere. The left dPCC showed substantial decline until midlife, indicating more rigidity, at which point the left vPCC showed great flexibility.

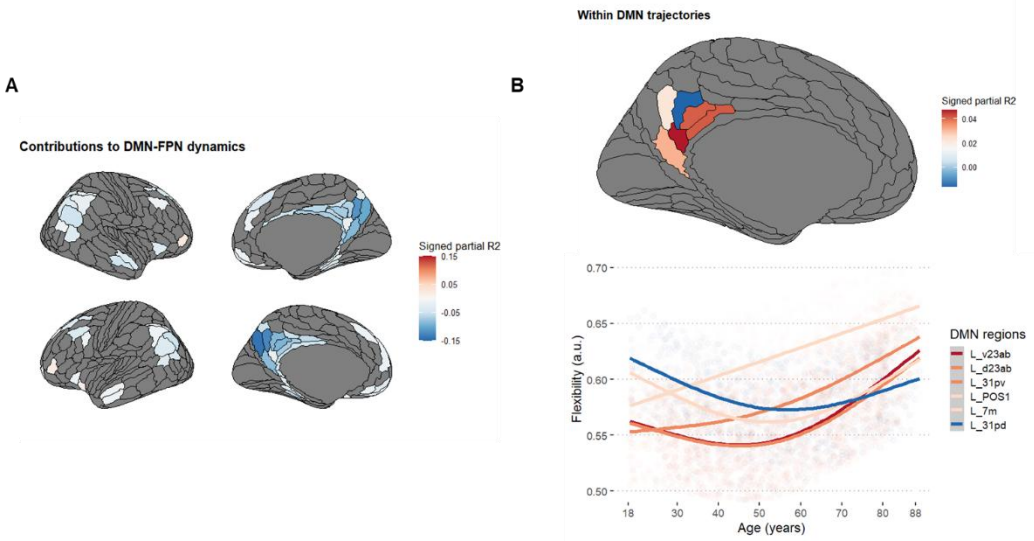


Figure 4. Regions contributing to changes in (A) DMN-FPN and (B) within DMN flexibility. Brain illustrations made with ggseg R-package (Mowinckel & Vidal-Piñeiro, 2020).

2.4. Complementary analysis: Regional flexibility at the whole-brain level

We evaluated the contribution of each region to flexible versus rigid motifs using a novel metric, ***Region Flexibility***. In line with our previous results, Figure 5 illustrates that most changes have an inflection point in midlife, with more flexibility in sensorimotor, auditory and visual cortices; and more rigidity in mostly posterior DMN and FPN areas. A thousand spin

tests preserving spatial autocorrelation revealed that these changes were strongly and significantly correlated to changes along the sensory-transmodal (G1) (r_s = .49, p_{spin} < .001).

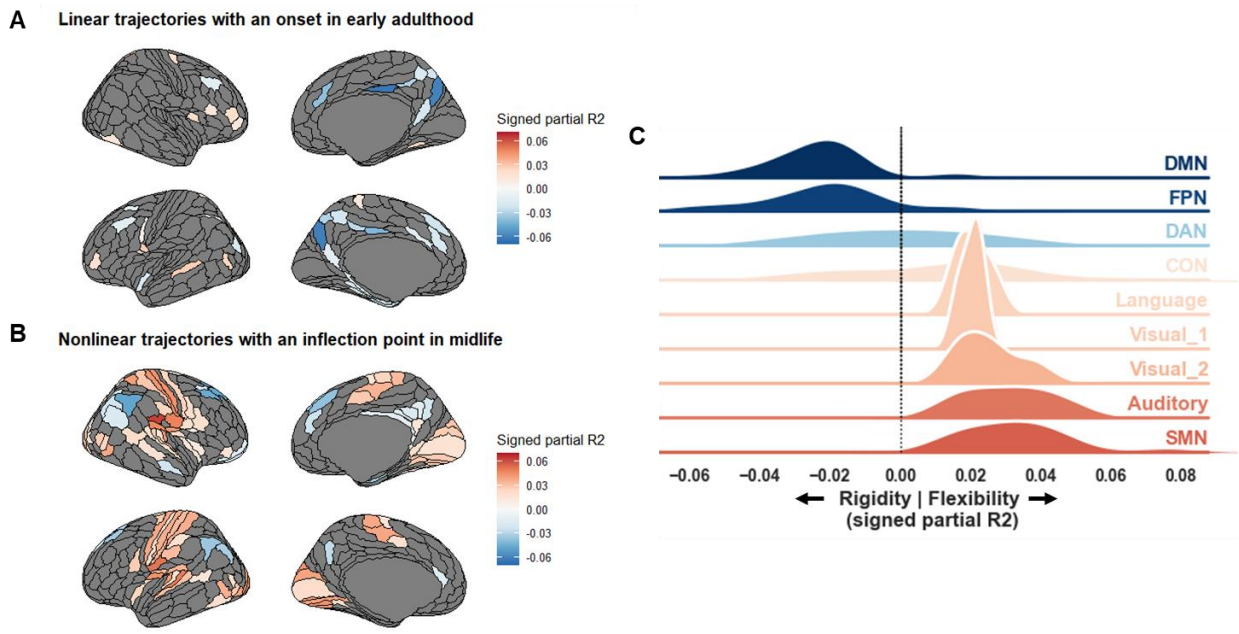


Figure 5. Age-related changes in Region Flexibility. (A & B) Results from GAM models. Red indicates an increase in flexibility, and Blue in rigidity. Brain illustrations made with ggseg R-package (Mowinckel & Vidal-Piñeiro, 2020). **(C)** Resting-state network description of panel A & B. The age-related trajectory for each region is available at: https://github.com/LPNC-LANG/SENECA_network_flexibility.

2.4. Robustness analysis

These findings remain valid when thresholding connectivity matrices using null models that preserve spatial and temporal autocorrelation (Shinn et al., 2023). When applying the more stringent correlation screening approach (Lbath et al., 2024), whole-brain and network-level results result also held. However, robustness could not be assessed at the region level using this approach as there was not enough significant connections to conduct reliable analyses (see Supplementary materials).

3. Discussion

To adapt to varying cognitive demands, resting-state dynamics are thought to reside in a critical regime that supports flexible reconfigurations of cognitive, perceptual, and motor systems (Thiebaut de Schotten & Forkel, 2022; Wang et al., 2021). In this study, we investigated how metabolic resources constrain the resting-state dynamics to optimize for neurocognitive flexibility throughout life. Specifically, we tested the predictions of the SENECA model (Guichet, Banjac, et al., 2024) using cross-sectional resting-state fMRI data from 628 healthy adults aged 18-88 and applied a novel graph-theoretical framework (Saberi et al., 2024).

Our findings support the model's predictions: (1) Changes in flexibility occur locally but not globally, suggesting that spatially distributed changes may contribute to preserve whole-brain homeostasis across the lifespan. (2) These local changes delineates two neurocognitive mode: a high-level DMN-FPN architecture that is more prevalent in younger adulthood, and a sensory-driven architecture that is more prevalent in older adulthood. (3) A similar shift was observed within the posterior medial (pm) DMN, reaffirming the unique role of the DMN in regulating cross-systems interactions.

Taken together, our results suggest that healthy neurocognitive aging is a dynamic phenomenon that implies substantial modifications to optimize for cognitive flexibility given available metabolic resources – marking midlife as a cognitive, functional, and "metabolic cliff" (Huo et al., 2020; Mattson, 2025; Shichkova et al., 2025). This challenges the narrative of a spatially-uniform, and linear neurocognitive decline across the lifespan. Below, we discuss our main findings before integrating our resulting within the SENECA model and highlighting perspectives for future works.

Maintenance of a whole-brain equilibrium across the lifespan

Our main finding is that the resting-state remains in a near-critical regime throughout life that sits in-between rigidity and flexibility (see Figure 1) (Cocchi et al., 2013; Luppi, Sanz Perl, et al., 2024). This regime appears to be sustained differently with age, through spatially distributed adjustments around midlife. Specifically, we noted (i) reduced flexibility between higher-level networks, and (ii) heightened flexibility within and between lower-level networks.

Such finding aligns with the idea of "local cost-efficiency trade-offs" for maintaining global functional homeostasis (Ramchandran et al., 2019), likely reflecting how the aging brain adapts its wiring economy mechanisms to meet for the decline in metabolic resources (Deery et al., 2024). Computational modeling further supports this interpretation, indicating that changes in brain energy induces local connectivity changes based on ongoing cognitive processing, while brain functional activity remains stable globally (Ashourvan et al., 2017; Beim Graben et al., 2019; Volpi et al., 2024). In sum, our study adds to compelling evidence that the brain energy supplying functional activity is heterogeneously distributed at rest (Aiello et al., 2015; Kleinridders et al., 2018; Riedl et al., 2014), in line with functional networks engaging distinct metabolic pathways (Shokri-Kojori et al., 2019).

A synergistic, DMN-FPN architecture in younger adults

With age, the DMN and FPN showed a reduced ability to flexible modulate their between-network connectivity, confirming reports of more rigid DMN-FPN connectivity in older adulthood (e.g., Spreng & Turner, 2019). This gain in rigidity could be further interpreted as a loss of synergistic communication between transmodal areas (Luppi et al., 2022; Margulies et al., 2016), as previously noted in older adulthood (Gatica et al., 2021, 2022), and could highlight difficulties sustaining the high metabolic demands of long-range competitive dynamics (Li et al., 2023; Luppi, Sanz Perl, et al., 2024).

Previous studies suggest that transmodal cortices draw from substantial glucose metabolism compared to lower-level networks (see the section *Additional metabolic considerations*; Luppi, Rosas, et al., 2024). Their important metabolic activity can be traced back to their relative independence from underlying structural constraints (for a review, see Fotiadis et al., 2024), facilitating "top-down projections that tend to jump synaptic levels" (Paquola et al., 2019). While this promotes denser interconnectivity across spatially distributed areas, and thus great flexibility, this comes at the cost of greater energy constraints that makes these networks vulnerable to aging (Diniz & Crestani, 2023; Takagi, 2021; Tomasi et al., 2013).

At the region level, complementary results clarified that age-related decline in DMN-FPN flexibility is driven by posterior medial regions in the PCC. This is consistent with our third hypothesis, highlighting the PCC as a key hub for cognitive flexibility in healthy younger adults, perhaps owing to its unique cortical morphology within the brain (Willbrand et al., 2022). Relatedly, age-related decline could reflect difficulties stimulating GABAergic inhibitory processes linked to the DMN glucose metabolism (Bi et al., 2020; Fortel et al., 2023; Xie et al., 2025), in turn affecting competitive DMN-FPN dynamics.

A redundant, sensory-driven architecture in older adults

Compared to the DMN and FPN, lower-level networks (SMN, auditory, visual, language) showed both increased within- and between-network flexibility beyond midlife. Particularly, observed increases in auditory-SMN, auditory-language, language-SMN, and SMN-visual flexibility could reflect the key role of the SMN in modulating the integration of auditory and visual stimuli in older adulthood.

This could represent the establishment of a sensory-driven processing strategy in older adulthood that demands less metabolic resources. Specifically, we propose to interpret our results as evidence for the processing of similar information within distinct sensory systems,

facilitating a multi-sensory representation. In this context, this strategy may stand as a more redundant approach for supporting cognitive flexibility, favoring robustness over precise neural code (Johnston et al., 2020; Johnston & Freedman, 2023).

This interpretation further agrees with a large body of work showing that the use of multiple sensory channels represents a compensatory strategy to overcome uni-sensory deficits during aging (De Dieuleveult et al., 2017; Hirst et al., 2019; Laurienti et al., 2006). Moreover, previous resting-state MEG teamwork (Guichet, Harquel, et al., 2024) also identified a similar sensory-driven mechanism thought to depend on alpha-band oscillatory activity, potentially compensating for inhibitory control deficits (Jensen & Mazaheri, 2010; Klimesch, 2012; Klimesch et al., 2007; Zioga et al., 2024). These considerations are in line with growing evidence supporting the facilitating role of multi-sensory integration, and particularly the importance of the sensorimotor system in neurocognition (Ferré et al., 2020; Goelman et al., 2024; Roger, Banjac, et al., 2022; Zapparoli et al., 2022).

The DMN and CON drive the midlife shift in dynamics

So far, our discussion gathered evidence showing that younger adults rely on a metabolically expensive, DMN-FPN synergistic mode, while older adults rely on a metabolically inexpensive, sensory-driven architecture with more redundancies for supporting cognitive flexibility. Additional results reveal that (i) posterior cingulate cortex (PCC) dynamics within the DMN, and (ii) between-network dynamics between lower-level networks and the cingulo-opercular network (CON) play a key role in this transition.

Regarding the DMN, dPCC connectivity showed more rigidity beyond midlife while the ventral portion was more engaged (see Figure 4). This contributes to challenge the traditional view of a cohesive task-negative DMN network (Chiou et al., 2020; Kernbach et al., 2018; Williams et al., 2022), and instead aligns with studies highlighting the crucial role of the DMN in cognitive

transitions between internal and external contexts (Crittenden et al., 2015; Kurtin et al., 2023; Paquola et al., 2025; Smith et al., 2018; Zhou et al., 2025). Specifically, our results suggest that medio-parietal DMN activity could support a young-like and older-like mode of cognitive flexibility, in line with prior conceptualizations of a "learning-to-prediction" (Brown et al., 2022), "exploration-to-exploitation" shift in midlife (Hills et al., 2015; Spreng & Turner, 2021; Wyatt et al., 2024).

In younger adults, greater flexibility of the dorsal medio-parietal circuitry may modulate the PMN subnetwork of the DMN (Parietal Memory Network), providing support for updating semantic representations with recent experiences (Zheng et al., 2021) – that is geared towards a *learning or explorative mode*. In comparison, in older adults, enhanced flexibility of ventral medio-parietal circuitry may facilitate the integration of self-related processes by modulating the CAN subnetwork of the DMN (Contextual Association Network) (Braga et al., 2019; Braga & Buckner, 2017), likely playing a key role for generating predictions based on a lifetime of learned associations between objects and associated contexts – that is geared towards a *prediction or exploitative mode.* This could help instantiate "situation models" in older adulthood – a form of embodied memory representation less prone to working memory deficits and generally well-preserved with age (Baltes & Lindenberger, 1997; Kintsch & Van Dijk, 1978; Lindenberger & Baltes, 1994; Lindenberger & Mayr, 2014; A. Martin, 2016; Wright, 2016).

Regarding the CON, increased between-network flexibility with the Auditory and SMN networks confirms its crucial role in age-related controlled cognition (Cao & Cannon, 2021; Crittenden et al., 2016; Hausman et al., 2022; Saberi et al., 2024). From a metabolic perspective, the CON may operate as a lower-cost, bottom-up system for attentional regulation, lending processing resources to goal-relevant networks in a more efficient manner than global FPN coordination (Cocuzza et al., 2020). From a cognitive perspective, one potential interpretation

is that it facilitates somatosensory feedback for preparing and evaluating action outcomes a preferential recruitment through its action-oriented subnetwork in older adulthood (D'Andrea et al., 2023; Dosenbach et al., 2024) and establishes a more embodied form of cognition via tight connectivity to the somato-cognitive action network (SCAN) (Gordon et al., 2023).

SENECA: A Neuroenergetic model of healthy cognitive aging

Overall, our study establishes novel links between cognitive flexibility, resting-state functional brain dynamics, and metabolic resource constraints. The proposed SENECA model posits that age-related declines in metabolic resources may drive shifts in neurocognitive strategies that balances the cost of cross-systems interactions between control-, self-, and action-oriented aspects of cognition (Buckner & DiNicola, 2019; Dosenbach et al., 2025; Gordon et al., 2020; Williams et al., 2022). Below, we propose a hypothetical scenario (see also the Graphical Abstract).

When metabolic resources are high in younger adulthood, the DMN can flexibly engage or disengage the dPCC to regulate cross-region coordination with the FPN. Cooperative DMN-FPN dynamics may provide the attentional resources for integrating novel internal experiences while competitive DMN-FPN dynamics may inhibit task-irrelevant interferences when more top-down control is required to discern between complex semantic relationships (Krieger-Redwood et al., 2019) and provide feedback control (Luppi, Sanz Perl, et al., 2024). This may correspond to a **synergistic mode** as a dynamic interaction between the DMN and FPN is needed to support cognitive flexibility.

Beyond midlife, as metabolic resources decline, inhibiting DMN activity becomes more difficult, thus leading to less competitive DMN-FPN dynamics. To support cognitive flexibility, the older adult brain may engage a different strategy that runs with less metabolic demands. This strategy may correspond to a **redundant mode** where similar information is processed in

distinct lower-level networks to facilitate a more robust multi-sensory mechanism. At the cognitive level, this could provide sufficient flexibility for comparing multi-sensory inputs against stored multimodal representations in the vPCC, exploiting memory-guided processes to generate enacted predictions to boost "working memory capacity limits" (Bar, 2007; Bubic, 2010; Chan et al., 2021; Yang et al., 2024).

Additional metabolic considerations

Most age-related changes occurred between lower-level, unimodal or higher-level, transmodal cortices. Such dissociation could be attributed to the higher costs for sustaining dynamic neural activity between sensory and transmodal areas, further highlighting this gradient as a cost-effective principle for cognitive flexibility (Ceballos et al., 2025; Margulies et al., 2016; Sydnor et al., 2021). From a metabolic perspective, this gradient aligns with the brain-wide distribution of oxygen metabolism (Camandola & Mattson, 2017; Vaishnavi et al., 2010), preferably promoting synaptic formation and growth in transmodal cortices (Goyal et al., 2014). Further studies showed that this oxygen mechanism persists across the lifespan (Goyal et al., 2017; Goyal & Raichle, 2013; Marder & Goaillard, 2006) but at significantly lower rates beyond early adulthood (Goyal et al., 2017; Takada et al., 1992). Thus, oxygen metabolism does not appear to explain the observed in neurocognitive mode as it remains the primary source of energy for sustaining brain activity (Dienel, 2019).

Recently, Luppi, Rosas, Noonan, et al. (2024) suggested that, as the metabolic demands in transmodal cortices exceeds the capacity of oxygen delivery by the vascular system, a mechanism known as nonoxidative glycolysis (i.e., that do not require oxygen) supplies the additional energy needed for synergistic cognitive processes. In comparison, lower-level networks show better management of energy supplied by oxygen (Fletcher et al., 2021). Thus, the shift in neurocognitive mode could reflect a lower reliance of such nonoxidative metabolic

activity. Further studies support this interpretation. For example, BOLD-fMRI responses – largely driven by regional cerebral blood flow (rCBF) – shows tight covariation with glucose metabolism during functional activity in comparison to oxygen metabolism (Dienel, 2012; Magistretti & Allaman, 2015; Paulson et al., 2010). Research also revealed that lower rCBF and glucose hypometabolism is a key element of older adults' decline in cognitive flexibility (Deery et al., 2024; Juttukonda et al., 2021; Tarumi & Zhang, 2018), especially in midlife (Huo et al., 2020; Thambisetty et al., 2013). However, further multimodal imaging approaches are needed to validate these claims (Sala et al., 2023; Voigt et al., 2023).

Limitations & Perspectives

The proposed model assumes that age-related declines in metabolic resources induces a different cognitive strategy. However, since metabolic activity cannot be directly manipulated in a provoked independent variable, the causal direction remains uncertain. It is equally plausible that shifts in cognitive activities, for instance based on heuristics – such as an increased reliance on a fast, intuitive (System 1) compared to slow, deliberative (System 2) processing in older adulthood (Kahneman, 2012), or a tendency toward cognitive closure over openness to experience – may themselves shape the neural architecture over time and, as a consequence, influence metabolic flexibility (Mattson, 2025).

Relatedly, numerous studies demonstrate that lifestyle factors – such as education, socioeconomic status, and physical activity – mediate the relationship between openness and enhanced cognitive functioning in older adulthood (Ihle et al., 2016, 2019; Montoliu et al., 2023; Stolz et al., 2023), with downstream effects on cognitive flexibility (Chung et al., 2012) and language performances (Iso-Markku et al., 2024; Khalili et al., 2024; Perez et al., 2025; Rahman et al., 2023). Another study also suggests that exercise and dietary factors could regulate the brain's metabolic efficiency through neurotrophic factor signaling, giving rise to

the concept of a "metabolic reserve" that complements cognitive reserve aspects (Stranahan & Mattson, 2012). In sum, future research is needed to disentangle how metabolic constraints shape cognitive preferences, or in turn, how enduring cognitive lifestyles actively sculpt brain metabolism and functional organization across the lifespan.

Additionally, we caution that the BOLD-fMRI response does not exclusively reflect glucose metabolism (Volpi et al., 2024). Regional CBF and lactate production also correlate with functional activity (Boumezbeur et al., 2010; Magistretti & Allaman, 2015) and independently vary across the lifespan (Ross et al., 2010; Shichkova et al., 2024). Thus, additional metabolic and vascular mechanisms, unaccounted for in our model, could also play a role in our results (Shichkova et al., 2025). Multimodal datasets could offer a more comprehensive assessment of metabolic alterations related to neurocognitive aging while mitigating vascular confounds, for example targeting age-related changes in glutamate and GABA concentrations using functional MR spectroscopy (Stanley & Raz, 2018).

Conclusion

The interplay between cognitive flexibility, functional brain dynamics, and metabolic constraints across the lifespan remains poorly understood. In this study, we investigated the flexibility of resting-state fMRI activity in a population-based sample of healthy adults aged 18-88. Our results reaffirm previous reports of a midlife shift in neurocognitive processing: (i) younger adults tend to rely on a metabolically costly, DMN-FPN strategy to flexibly adapt to internal and external task demands, whereas (ii) older adults increasingly engage a more energy-efficient, sensory-driven circuitry that supports multi-sensory integration strategy and exploits a lifetime of learned semantic associations. This shift may contribute to preserve whole-brain resting-state activity near a critical regime throughout life that optimizes for neurocognitive flexibility despite declining metabolic resources. Notably, the medio-parietal DMN and the CON may play key roles in orchestrating this shift.

Taken together, our study offers a novel theoretical and empirical perspective on healthy neurocognitive aging, opening avenues for extending the proposed SENECA model to neuropathology.

4. Material and Methods

4.1. Participants

Our dataset included 628 healthy adults (age range: 18-88; 310 males, 318 females) from the Cambridge Center for Ageing and Neuroscience Project (http://www.mrc-cbu.cam.ac.uk/: Cam-CAN et al., 2014). Details on participant recruitment are provided in Taylor et al. (2017).

4.2. MR acquisition and preprocessing

MR acquisition. As the data was sourced from Cam-CAN et al. (2014), we refer the reader to the latter reference for MR acquisition details. Data were preprocessed using the *fMRIPrep* software (https://fmriprep.org/en/stable/: Esteban et al., 2019). T1-weighted images underwent skull stripping, tissue segmentation, and spatial normalization. Resting-state fMRI data underwent motion correction, slice timing correction, susceptibility distortion correction, co-registration, and spatial normalization.

Functional connectomes. Denoised timeseries were aggregated using the 360-region HCP-MMP 1.0 atlas (Glasser et al., 2016).We used custom scripts to co-register the atlas to subject-space with ANTs (https://github.com/ANTsX/ANTsPy) and applied a confound removal strategy via Nilearn (https://nilearn.github.io/). Confounds included high-pass filtering, the full 24 motion parameters, and the full 8 white matter and CSF parameters as recommended in Wang et al. (2024). No global signal regression was performed as it introduces artefactual negative connections (Chai et al., 2012; Murphy & Fox, 2017; Saberi et al., 2022). We performed full scrubbing with a framewise displacement threshold set to 0.5 mm and the standardized DVARs to 1.5. In the event that all segments were removed with full scrubbing, the scrubbing parameter was decremented. Mean framewise displacement was also extracted and used as a covariate in subsequent statistical models. Spatial smoothing and standardization was applied to the signal using a 6mm full-width-at-half-maximum (FWHM) kernel. Finally,

functional connectomes were obtained by computing the Pearson correlation between time series.

4.3. Network flexibility modeling

Computations were performed in Python (version 3.9.12).

4.3.1. Whole-brain level

In line with Saberi et al. (2024), we define the flexibility of signed and fully-weighted and signed graph in Equation 1:

$$(1) \qquad Flexibility\ (F) \ = \ -\frac{1}{\binom{R}{3}} \sum_{i<j<k} \varphi(F_{ijk})$$

$$\text{with } \varphi(F_{ijk}) \ = \ sign(F_{ijk}) \cdot \left|F_{ijk}\right|^{1/3}$$

With $F_{ijk} \ = \ W_{ij}W_{ik}W_{jk}$ representing the product of the pairwise Pearson correlations (W) in the motif defined by regions i, j, and k. Each W can be positive or negative, thereby representing correlated or anti-correlated function activity. The value of each motif defined by $\varphi(F_{ijk})$ can be positive, indicating a prevalence of rigid motifs, or negative, indicating a prevalence of flexible motifs. The final flexibility metric (F) is obtained by taking the average of all motifs and applying the negative sign in front of the equation. This negative sign enables a more intuitive interpretation whereby higher values index greater flexibility in the system. Thus, the higher the F value, the greater the flexibility. Conversely, the lower the F value, the greater the rigidity.

4.3.2. Resting-state network level

We further examined the flexibility *within* networks and *between* networks. Within networks, we examined all motifs made up of regions from a single network N (see Equation 2a).

Let N_α represent a single network, and let I_α be the set of indices for regions in network N_α.

$$(2a) \qquad F_{\alpha} = -\frac{1}{\binom{|I_{\alpha}|}{3}}\left(\sum_{\substack{i,j,k\in I_{\alpha}\\ i<j<k}} \varphi(F_{ijk})\right)$$

Between networks, we examined motifs made up of at least one region from each network N (see Equation 2b). This allowed us to examine the motifs that resume the joint connectivity between pairs of networks.

Let N_{α} and N_{β} represent two networks, and let I_{α} and I_{β} be the sets of indices for regions in networks N_{α} and N_{β} respectively.

$$(2b) \qquad F_{\alpha\beta} = -\frac{1}{T}\left(\sum_{\substack{i\in I_{\alpha},j,k\in I_{\beta}\\ i<j<k}} \varphi(F_{ijk}) + \sum_{\substack{i\in I_{\beta},j,k\in I_{\alpha}\\ i<j<k}} \varphi(F_{ijk})\right)$$

With T = $\binom{|I_{\alpha}|}{1} \cdot \binom{|I_{\beta}|}{2} + \binom{|I_{\beta}|}{1} \cdot \binom{|I_{\alpha}|}{2}$ representing the two ways to select motifs spanning both networks: (i) a motif made of one region from N_{α} and two regions from N_{β}; and (b) a motif made of one region from N_{β} and two regions from N_{α}.

Between-Within network. We quantified the tendency of a network to exhibit more flexibility between versus within networks. We begin by making all values positive to avoid inconsistencies (Equation 3a). Then, we compute the average flexibility of all between and within components (Equation 3b & 3c) and their normalized ratio (Equation 3d).

Let F_{within} be the set of all within-network flexibility values, $F_{between}$ that of all between-network values, and F_{all} their union.

$$(3a) \qquad \widetilde{F_{all}} = F_{all} + |min(F_{all})| + \varepsilon \quad if \quad min(F_{all}) < 0$$

$$(3b) \qquad F_{average_between} = \frac{1}{|F_{between}|}\sum_{\alpha<\beta} \widetilde{F_{between,N_{\alpha\beta}}}$$

$$(3c) \qquad F_{average_within} = \frac{1}{|F_{within}|}\sum_{\alpha} \widetilde{F_{within,N_{\alpha}}}$$

$$\textbf{(3d)} \qquad \textbf{Between vs. Within Energy} = \frac{\mathbf{1}}{|\boldsymbol{N}|} \cdot \frac{\boldsymbol{F_{average_between}}}{\boldsymbol{F_{average_within}}}$$

with |N| the number of unique networks

4.3.3. Novel graph energy metric

We propose one novel metric at the region level called the ***Region Flexibility***. It quantifies the contribution of a region to flexible versus rigid motifs in the network (see Equation 4c). We first define the signed contribution of a region *r* as follows:

$$\text{(4a)} \qquad \frac{1}{T_r \cdot \mathrm{I}} \cdot \sum_{\substack{r \in \{i,j,k\} \\ i<j<k}} \varphi\left(F_{ijk}\right) \cdot \mathrm{I}$$

With $T_r = \binom{R-1}{2}$ representing the number of motifs to which a region *r* contributes. I is an indicator function observing whether the motif is strictly negative or positive. Then, we defined the ***Region Flexibility*** as:

$$\text{(4b)} \qquad \frac{\frac{1}{T_r^{(-)}} |Flexible_r|}{\frac{1}{T_r^{(+)}} Rigid_r} \quad \text{with} \quad \begin{matrix} Flexible_{r,} T_r^{(-)} \; when \; F_{ijk} < 0 \\ Rigid_r, T_r^{(+)} \; when \; F_{ijk} > 0 \end{matrix}$$

This simplifies to:

$$\textbf{(4c)} \qquad \boldsymbol{Region\ Energy} = \frac{|\boldsymbol{Flexible_r}|}{\boldsymbol{Rigid_r}} \cdot \frac{\boldsymbol{T_r^{(+)}}}{\boldsymbol{T_r^{(-)}}}$$

4.4. Statistical analysis

Statistical analyses were carried out in R (version 4.3.2). All models included sex, handedness, total intracranial volume, and mean framewise displacement as covariates.

Hypothesis 1. We computed the whole-brain network flexibility (see Equation 1) for each individual and built a Bayesian linear regression model with age as a predictor with the *brms* package (version 2.22.0; Bürkner, 2017). Using the *bayestestR* package (version 0.13.2; Makowski et al., 2019), we conducted a practical equivalence test (Kruschke, 2018) with a 89%

HDI (Highest Density Interval) to test whether energy consumption remains stable across the lifespan. The ROPE (Region of Practical Equivalence) limits were defined automatically using the *rope_range()* function. We also computing the global between versus within-network flexibility (see Equation 3) and built a generalized additive model (GAM) with age as a smooth predictor (parameters: *k = 3, method = REML*).

Hypothesis 2. We computed the flexibility within and between networks (see Equation 2) for 9 of the 12 networks mapped by Ji et al. (2019). We did not consider the lesser known networks (i.e., ventro-multimodal, posterior-multimodal, and orbito-affective). Then, we followed the same GAM procedure to examine the age effect on each network or pair of network. Significance thresholds were adjusted at the False Discovery Rate (FDR) across models that examined similar neural elements (that is either within-network or between-network).

Region-level hypothesis. We computed the proposed ***Region Flexibility*** (see Equation 4) for DMN and FPN regions with respect to DMN-FPN motifs. Similarly, we computed the flexibility of posterior-medial (pm) DMN regions considering DMN motifs. pmDMN regions were taken from the Posterior Cingulate division of the HCP-MMP1.0 atlas (Glasser et al., 2016). Then, we followed the same GAM procedure to examine the age effect as described previously.

4.5. Null models

We sought to replicate our analyses using thresholded matrices to minimize the number of functional connections caused by noise. We determined the statistical significance of each correlation coefficient following two approaches. In the first approach, we generated surrogates by randomizing timeseries, thereby preserving spatial and temporal autocorrelation as these measures are very sensitive to age in our dataset (Shinn et al., 2023). In the second approach,

we determined an absolute threshold (± 0.27) through the correlation screening method, with the goal of limiting false-positives due to intra-regional correlation (Lbath et al., 2024).

We added the subject-specific density as a covariate to preclude the effect of different network sizes between individuals (Rubinov & Sporns, 2010; Stumme et al., 2022; van den Heuvel et al., 2017). Indeed, the elimination of non-significant edges may distort graph theoretical measures due to differences in the number of remaining edges, and generally lead to more random network characterization in network in older adults due to overall low FC.

Data and code availability

Code is made publicly available at:
https://github.com/LPNC-LANG/SENECA_network_flexibility

Supplementary information

Supplementary materials

CRediT author statement

Conceptualization: CG; Methodology, Formal Analysis & Data Curation: CG; Writing – Original Draft: CG, MB; Writing – Review & Editing: CG, MB, MM, SA; Funding Acquisition: MB, MM, SA; Supervision: MB, MM.

Declaration of interests

The authors declare no competing interests.

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