Neurobiology of Aging 45 (2016) 149–160

Contents lists available at ScienceDirect

Neurobiology of Aging

journal homepage: www.elsevier.com/locate/neuaging

Attenuated anticorrelation between the default and dorsal attention networks with aging: evidence from task and rest

R. Nathan Spreng [a,b,*,1], W. Dale Stevens [c,**,1], Joseph D. Viviano [c], Daniel L. Schacter [d]

[a] Laboratory of Brain and Cognition, Department of Human Development, Cornell University, Ithaca, NY, USA
[b] Human Neuroscience Institute, Cornell University, Ithaca, NY, USA
[c] Cognition and Aging Neuroscience Laboratory, Department of Psychology, York University, Toronto, Ontario, Canada
[d] Department of Psychology, Harvard University, Cambridge, MA, USA

ARTICLE INFO

Article history:
Received 3 January 2013
Received in revised form 21 May 2016
Accepted 25 May 2016
Available online 3 June 2016

Keywords:
Default network
Dorsal attention network
Anticorrelation
Aging
fMRI
Resting-state functional connectivity
Medial temporal lobe

ABSTRACT

Anticorrelation between the default and dorsal attention networks is a central feature of human functional brain organization. Hallmarks of aging include impaired default network modulation and declining medial temporal lobe (MTL) function. However, it remains unclear if this anticorrelation is preserved into older adulthood during task performance, or how this is related to the intrinsic architecture of the brain. We hypothesized that older adults would show reduced within- and increased between-network functional connectivity (FC) across the default and dorsal attention networks. To test this hypothesis, we examined the effects of aging on task-related and intrinsic FC using functional magnetic resonance imaging during an autobiographical planning task known to engage the default network and during rest, respectively, with young (n = 72) and older (n = 79) participants. The task-related FC analysis revealed reduced anticorrelation with aging. At rest, there was a robust double dissociation, with older adults showing a pattern of reduced within-network FC, but increased between-network FC, across both networks, relative to young adults. Moreover, older adults showed reduced intrinsic resting-state FC of the MTL with both networks suggesting a fractionation of the MTL memory system in healthy aging. These findings demonstrate age-related dedifferentiation among these competitive large-scale networks during both task and rest, consistent with the idea that age-related changes are associated with a breakdown in the intrinsic functional architecture within and among large-scale brain networks.

1. Introduction

Anticorrelation between large-scale brain networks is a central feature of human functional brain organization (e.g., Fox et al., 2005; Fransson, 2005; Golland et al., 2008). Anticorrelation is observed as positive within-network functional connectivity (FC) concomitant with negative between-network FC of the dorsal attention and default networks (Fox et al., 2005). The dorsal attention network is composed of the frontal eye fields (FEF), the ventral frontal region precentral ventral (PrCv), middle temporal motion complex (MT+), inferior parietal sulcus (IPS), superior parietal lobule (SPL), and dorsolateral prefrontal cortex (DLPFC). Regions of the default network include medial prefrontal cortex (MPFC), posterior cingulate cortex (PCC), superior and inferior frontal gyrus, lateral temporal lobes, inferior parietal lobule (IPL), and the medial temporal lobes (MTLs; Fox et al., 2005), although there is evidence that the MTL may have a unique functional relationship with the default network (Eldaief et al., 2011; Ward et al., 2014) and comprises subregions that have dissociable patterns of FC (Kahn et al., 2008). The dorsal attention and default networks are inversely engaged during externally and internally directed cognition, respectively (Spreng et al., 2010a), and this reciprocal pattern of activity may serve as a critical neural substrate for flexibly allocating attentional resources and is important for healthy cognitive function (Whitfield-Gabrieli and Ford, 2012). Magnitude of anticorrelation is associated with externally directed task performance in young adults (e.g., Hampson et al., 2010).

Numerous age-related changes are apparent in brain activation during externally oriented attention (Spreng et al., 2010b), which reliably engages the dorsal attention network in the young (Gusnard et al., 2001; Spreng et al., 2010a). In addition, reductions

* Corresponding author at: Laboratory of Brain and Cognition, Department of Human Development, Cornell University, Martha Van Rensselaer Hall, Room G62C, Ithaca, NY 14853, USA. Tel.: 607-255-4396; fax: 607-255-9856.
** Corresponding author at: Department of Psychology, Sherman Health Science Research Centre, York University, 281 Ian Macdonald Blvd., Toronto, ON M3J 1P3, Canada. Tel.: 416-736-2100 x44662; fax: 416-736-5814.
E-mail addresses: nathan.spreng@gmail.com (R.N. Spreng), stevensd@yorku.ca (W.D. Stevens).
[1] Equal contribution.

0197-4580/$ – see front matter © 2016 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.neurobiolaging.2016.05.020

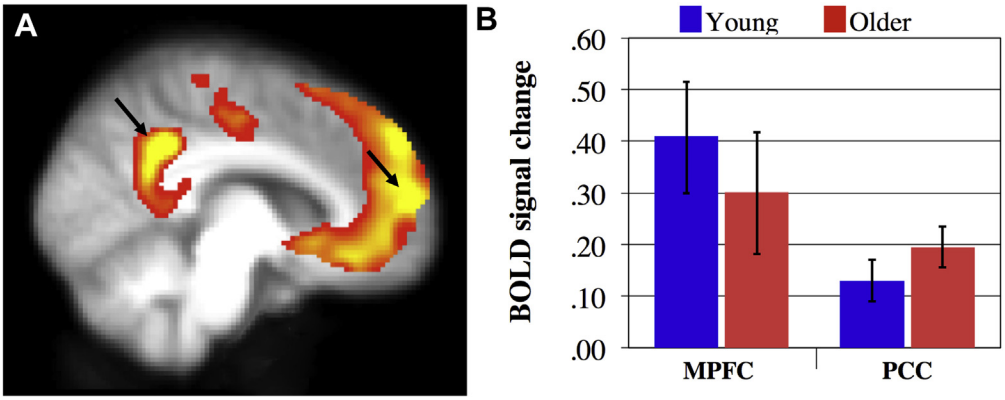

Fig. 1. Autobiographical planning task activation. (A) Young and older adults robustly engaged the default network during autobiographical planning, relative to visuospatial planning (see Spreng and Schacter, 2012). (B) MPFC and PCC (see arrows) activity was significantly elevated relative to fixation baseline in both young (t_{MPFC} (17) = 3.89, $p < 0.001$; t_{PCC} (17) = 3.26, $p < 0.005$) and older adults (t_{MPFC} (16) = 2.56, $p < 0.05$; t_{PCC} (17) = 3.80, $p < 0.001$). No differences were observed in the magnitude of MPFC or PCC activation between groups (t_{MPFC} (33) = 0.69, *ns*; t_{PCC} (34) = 1.00, *ns*). Differences between groups in the connectivity profile thus cannot be attributed to differences in task-related brain activity. Abbreviations: MPFC, medial prefrontal cortex; PCC, posterior cingulate cortex.

in task-related default network suppression and altered FC have been observed with advancing age (Andrews-Hanna et al., 2007; Damoiseaux et al., 2008; Grady et al., 2010; Hafkemeijer et al., 2012; Sala-Llonch et al., 2012; Sambataro et al., 2010; Stevens et al., 2008; Turner and Spreng, 2015). These findings complement whole-brain resting-state FC (RSFC) observations of a dedifferentiation of network connectivity with age, with increases in RSFC between large-scale brain systems in older adults (Betzel et al., 2014; Chan et al., 2014; Geerligs et al., 2015; Grady et al., 2016; Meunier et al., 2009; Onoda and Yamaguchi, 2013). It is unclear, however, if the robust pattern of anticorrelated activity between the default and dorsal attention networks is preserved into older adulthood.

Chan et al. (2014) observed increased correlations between default and dorsal attention networks as one feature of a larger pattern of reduced network segregation in older adulthood (see also, Grady et al., 2016). However age-related changes in anticorrelation between networks were not investigated in this study. Reduced anticorrelations between default and dorsal attention networks have been reported in older adults (Betzel et al., 2014; Wu et al., 2011). However, the use of mean global signal regression (GSR) in these studies may have altered the interregional correlation differences between groups (Murphy et al., 2009; Saad et al., 2012) complicating the interpretation of negative correlation values (Gotts et al., 2013). More recently, preprocessing procedures that do not rely on GSR have revealed that the antagonism between medial and lateral prefrontal cortex is attenuated in older adults (Keller et al., 2015), but age-related changes in anticorrelation between the dorsal attention and default networks more broadly have not been reported.

Consistent with the critical role of the MTL in episodic memory (Squire et al., 2004) and the marked deficits in episodic memory in age-related dementia, several studies have demonstrated reduced RSFC of the MTL in particular with other default network regions in individuals with mild cognitive impairment (Das et al., 2013, 2015; Jin et al., 2012), and Alzheimer's disease (for review see Hafkemeijer et al., 2012; Mevel et al., 2011), including patients in prodromal stages (Sperling et al., 2010; Wang et al., 2006). Episodic memory also shows declines in typical healthy aging (Grady, 2012), and there is evidence for MTL-cortical reductions in FC at rest with advancing age (Salami et al., 2014). An earlier study, however, found that while some subsystems of the default network showed differential patterns of RSFC between young and older adults, the MTL subsystem in particular, did not show any age-related differences (Campbell et al., 2013). Therefore, the extent to which FC of the MTL is altered in aging and potentially related to decline in memory remains unclear.

Spreng and Schacter (2012) assessed patterns of large-scale network activity in young and older adults during performance of an autobiographical planning task that engages the default network and a visuospatial planning task (the Tower of London) that engages the dorsal attention network (Spreng et al., 2010a), consistent with the anticorrelated domains of internalized and externalized cognition. Older adults robustly engaged the default network during the autobiographical planning task, not different in magnitude than their younger counterparts (Spreng and Schacter, 2012, see also Fig. 1). Unlike young adults, older adults had reduced suppression of the default network during visuospatial planning (Spreng and Schacter, 2012; Turner and Spreng, 2015). Thus, autobiographical planning provides a unique opportunity to examine FC patterns in older adults, and potential age-related changes in anticorrelation during a task known to engage the default network, without the confound of age-related differences in task-based activation patterns. In the present study, we examine (1) the impact of age on task-related MPFC connectivity during autobiographical planning using a multivariate FC analysis and (2) patterns of RSFC in young and older adults, leveraging a preprocessing strategy that does not involve GSR. Together these analyses provide the first evidence that aging is associated with reduced anticorrelation between the default and dorsal attention networks during task and rest and decreased intrinsic FC of the MTL across both networks.

2. Methods

2.1. Participants

All participants were healthy, with normal or corrected-to-normal visual acuity, and no history of psychiatric, neurologic, or other medical illness that could compromise cognitive functions. All participants gave written informed consent in accordance with the Harvard Institutional Review Board or the Human Subjects Research Committee at Massachusetts General Hospital.

2.1.1. Experiment 1

Task functional magnetic resonance imaging (fMRI) data were collected from 18 young adults (mean age = 22.8 ± 2.4 years; range = 19–27; 9 women) and 18 older adults (mean age = 71.4 ± 4.0 years; range = 63–78; 9 women) previously reported