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Dynamic range of frontoparietal functional modulation is associated with working memory capacity limitations in older adults

Jonathan G. Hakun[a,*], Nathan F. Johnson[b]

[a] Department of Psychology, The Pennsylvania State University, State College, PA 16801, USA
[b] Department of Rehabilitation Sciences, Division of Physical Therapy, University of Kentucky, Lexington, KY 40536, USA

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ABSTRACT

Older adults tend to over-activate regions throughout frontoparietal cortices and exhibit a reduced range of functional modulation during WM task performance compared to younger adults. While recent evidence suggests that reduced functional modulation is associated with poorer task performance, it remains unclear whether reduced range of modulation is indicative of general WM capacity-limitations. In the current study, we examined whether the range of functional modulation observed over multiple levels of WM task difficulty (N-Back) predicts in-scanner task performance and out-of-scanner psychometric estimates of WM capacity. Within our sample (60–77 years of age), age was negatively associated with frontoparietal modulation range. Individuals with greater modulation range exhibited more accurate N-Back performance. In addition, despite a lack of significant relationships between N-Back and complex span task performance, range of frontoparietal modulation during the N-Back significantly predicted domain-general estimates of WM capacity. Consistent with previous cross-sectional findings, older individuals with less modulation range exhibited greater activation at the lowest level of task difficulty but less activation at the highest levels of task difficulty. Our results are largely consistent with existing theories of neurocognitive aging (e.g. CRUNCH) but focus attention on dynamic range of functional modulation as a novel marker of WM capacity-limitations in older adults.

1. Introduction

Human aging is associated with declines in working memory (WM) and alterations in brain function (Bopp & Verhaeghen, 2005; Braver & West, 2008; Cabeza & Dennis, 2012; Drag & Bieliauskas, 2010; Grady, 2012; Lustig, Hasher, & Zacks, 2007; Park & Hedden, 2001; Reuter-Lorenz & Park, 2010). During WM task performance older adults tend to exhibit similar spatial patterns of activation to younger adults, but show altered patterns of activation modulation including increased response magnitude at low levels of task difficulty ("over-activation") and a more rapid approach of asymptotic activation levels as task difficulty increases (Cappell, Gmeindl, & Reuter-Lorenz, 2010; Mattay et al., 2006; Nagel et al., 2011; Schneider-Garces et al., 2010). While these modulatory patterns have advanced neurocognitive compensation theory (e.g. the compensation-related utilization of neural circuits hypothesis; CRUNCH; Reuter-Lorenz & Cappell, 2008), recent evidence suggests that altered modulation patterns, such as a reduced modulatory range, may track closely with individual and age psychometric differences in WM function (Schneider-Garces et al., 2010).

WM processing is associated with activation of regions throughout frontoparietal cortices (e.g., bilateral dorsal and ventral prefrontal cortices, anterior cingulate cortex, superior and lateral parietal cortices; Nee et al., 2013; Owen, McMillan, Laird, & Bullmore, 2005; Rottschy et al., 2012; Wager & Smith, 2003). Regions throughout this network tend to exhibit an orderly parametric response to experimental manipulations of task difficulty including manipulation of set-size (# of items to be maintained in WM) and judgment difficulty (# of items to search through in continuous performance WM tasks; Owen et al., 2005; Rottschy et al., 2012). In addition, asymptotic levels of activation have been observed across various neuroimaging modalities (e.g., EEG, fMRI) at set-sizes that match behavioral estimates of WM span (# of items a participant is estimated to be able to maintain in WM; Linden et al., 2003; McCollough, Machizawa, & Vogel, 2007; Song & Jiang, 2006; Todd & Marois, 2004, 2005; Vogel & Machizawa, 2004; Xu & Chun, 2006).

Age-associated reductions in frontoparietal functional modulation range have been observed in studies of WM function involving span tasks (e.g. memory search task; Cappell et al., 2010; Schneider-Garces et al., 2010) and continuous performance task paradigms (e.g. N-Back task; Kaup, Drummond, & Eyler, 2014; Mattay et al., 2006; Nagel et al.,

* Corresponding author at: Department of Psychology, The Pennsylvania State University, University Park, PA 16802-3104, USA.
E-mail address: jgh5196@psu.edu (J.G. Hakun).

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2011). It remains unclear whether declines in modulation range are due to general capacity limitations or distinct task-related impairments, as few studies have linked in-scanner modulation range with out-of-scanner psychometric measures. It is also unknown whether functional modulation range, like other neurocognitive functional markers such as over-activation (Cabeza, Anderson, Locantore, & McIntosh, 2002; Colcombe, Kramer, Erickson, & Scalf, 2005; Dolcos, Rice, & Cabeza, 2002), differentiates between high and low performing older adults. Based on recent evidence from meta-analyses showing that WM paradigms such as the N-Back and span tasks involve an overlapping, core frontoparietal network (Rottschy et al., 2012), we hypothesized that frontoparietal modulation range may reflect individual differences in WM capacity (WMC) limitations among older adults.

WM is the stage in information processing theories of human cognition associated with short-term representation of active memory traces (Baddeley, 2003). WM is capacity-limited and generally limited to only a few units/chunks of information (Cowan, 2005, 2010; Luck & Vogel, 2013; Miller, 1956; Turner & Engle, 1986). However, considerable individual differences exist in the amount of information that can be actively maintained in WM, particularly under conditions of distraction (Conway, Kane, & Engle, 2003; Kane & Engle, 2003). While short-term representation in WM is supported by separable storage units (e.g. visual vs verbal buffers; Baddeley & Hitch, 1974), individual differences in WMC are thought to emerge primarily through differences in domain-general abilities associated with actively maintaining, updating, and retrieving memory traces (Alvarez & Cavanagh, 2004; Barrouillet, Bernardin, & Camos, 2004; Bays, Catalao, & Husain, 2009; Cowan, 1999, 2005; Engle, 2002; Kane & Engle, 2003; Luck & Vogel, 2013; Oberauer, Lewandowsky, Farrell, Jarrold, & Greaves, 2012; Unsworth, Fukuda, Awh, & Vogel, 2014). Such a domain-general component of WM has been corroborated by functional imaging evidence showing overlapping activation patterns across verbal and visual WM task conditions in the core frontoparietal network associated with span and N-back task performance (Rottschy et al., 2012). Domain-general declines in WM processing have been the focus of several theories of cognitive aging (Braver & West, 2008; Hasher & Zacks, 1988; Lustig et al., 2007) and may help explain declines across multiple domains of cognition (Braver & West, 2008; Kennedy, Partridge, & Raz, 2008; Lustig et al., 2007; Park & Hedden, 2001; Park et al., 1996; Salthouse, 1990).

In the current study, we investigated domain-general WM function by examining composite estimates of frontoparietal functional modulation range and WMC through performance of visual and verbal versions of N-Back (in-scanner) and complex span tasks (out-of-scanner). Critically, previous research shows that performance on N-Back and span tasks is largely uncorrelated (sharing only a much as 2–5% variance; Kane, Conway, Miura, & Colflesh, 2007; Redick & Lindsey, 2013; Roberts & Gibson, 2002). However, latent estimates of performance on N-Back and complex span tasks covering multiple stimulus modalities were shown to be highly correlated in a previous study (Schmiedek, Hildebrandt, Lövdén, Lindenberger, & Wilhelm, 2009). Here we sought to determine whether functional modulation range in the core frontoparietal WM network, similarly, serves as an indicator of domain-general WMC in older adults.

Fifty-three participants between the ages of 60–77 years old participated in an fMRI scanning session where they performed visual and verbal N-Back task conditions and a separate cognitive assessment session where they completed visual and verbal complex span tasks (Operation Span and Symmetry Span). We first examined individual differences in functional modulation across levels of the N-Back task by fitting a parametric contrast to functional activation across all four levels of both task conditions (visual and verbal). After determining which regions scaled parametrically with increases in task demand we examined whether modulation range was associated with individual differences in conditional activation, performance during the N-Back task, and individual differences in psychometric WMC.

2. Methods

2.1. Participants

A total of 53 right-handed healthy older adults participated in the study (24M/29F; age range = 60–77, mean age = 66.62, age SD = 4.15). Written informed consent was obtained from each participant under an approved University of Kentucky Institutional Review Board protocol. Participants were recruited from the community and were financially compensated. Exclusionary criteria for the study included the following: color blindness, major head injury, stroke, neurological or psychiatric disorder, high blood pressure, diabetes, heart disease, the use of psychotropic drugs, and or the presence of metal fragments and/or metallic implants contraindicated for MRI. Two participants were excluded from analyses involving N-Back task performance due to missing data (< 70% of trials were recorded during 2-Back and 3-Back conditions).

2.2. Materials and procedure

2.2.1. N-Back task

Participants completed a 4-level N-Back task (Compare, 1-Back, 2-Back, 3-Back) that included verbal (letters) and visual (faces) task conditions. During the Compare task condition participants judged whether two stimuli presented side-by-side (either two letters or two faces) were the same or different. During the 1-Back condition, participants were asked to judge whether the item on the current trial matches the item presented one item back in history. Similarly, the 2-Back and 3-Back conditions involved the same procedure as the 1-Back but varied with respect to how far back in the trial history (2- or 3-Back) comparisons were made (Fig. 1). Responses were made using MRI compatible response button-boxes (one in each hand). Participants were asked to press the left button for “same” judgments and press the right button for “different” judgments. Participants were asked to respond as quickly and accurately as possible.

Task blocks were 40 s in duration (15 trials per block), and fixation periods were 17.5 s in duration. There were two runs. Each run began and ended with a fixation period (+ symbol presented centrally) and contained a total of 8 task blocks and 9 fixation periods. Each run contained two blocks of each N-Back level (including one block of each stimulus type). Each task block began with an instruction screen containing the task condition (e.g. “Compare”, “1-Back”) presented centrally for 2500 ms. Following the instruction screen, stimuli were presented centrally for 2000 ms each, separated by 500 ms of fixation. Eight upper-case letters were included (B, F, K, H, M, Q, R, Y) in the

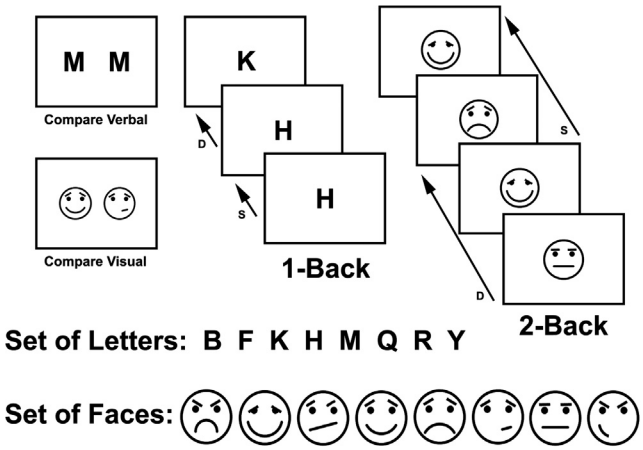

Fig. 1. N-Back task design. (TOP) Example verbal and visual stimulus displays for the Compare, 1-Back, and 2-Back task conditions. 3-Back condition is not displayed. (BOTTOM) Complete set of letter and face stimuli. S = “same”, D = Different”.

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