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Shared neural recruitment across working memory and motor control tasks as a function of task difficulty and age

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ABSTRACT
Past research suggests that working memory (WM) and motor control may engage similar cognitive and neural mechanisms in older adults, particularly when task difficulty increases. However, much of this evidence arises from comparisons across behavioral and imaging studies that test only one of the foregoing functional domains. The current study used fMRI within the same group of older adults to investigate whether WM and motor control recruit common mechanisms, and whether recruitment increased with task demand and age. A conjunction analysis across WM and motor tasks revealed engagement of several frontoparietal regions as a function of increasing task demand. A separate conjunction analysis which included age as a predictor showed comparable regions exhibit increased recruitment with both increasing task demand and age. Results suggest that the recruitment of common frontoparietal regions across WM and motor tasks in response to task difficulty is maintained across the older adult lifespan.

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Working memory; force; fMRI; aging; motor control

Introduction

The interdependence between working memory and motor control tasks emerged from a number of studies that note a decline in performance when the two tasks are performed concurrently. For example, when recalling complex information in working memory alongside a sensorimotor adaptation task, performance on the motor task becomes impaired (Li, Lindenberger, & Sikström, 2001; Lindenberger, Marsiske, & Baltes, 2000; Yogev-Seligmann, Hausdorff, & Giladi, 2008). Such a decrease in dual task performance is taken as evidence of an underlying link between working memory and motor control (Beilock, Bertenthal, Mccoy, & Carr, 2004; Lövdén, Schaefer, Pohlmeyer, & Lindenberger, 2008; Wulf & Prinz, 2001). The connection between these domains is further supported by neuroimaging studies showing that working memory and motor control are mediated by similar regions within the frontoparietal network (Faw, 2003; Ikkai & Curtis, 2011; Liao, Kronemer, Yau, Desmond, & Marvel, 2014; Marvel & Desmond, 2010, 2012; Marvel, Morgan, & Kronemer, 2019; Miller & Cohen, 2001). Specifically, neuroimaging studies of

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Supplemental data for this article can be accessed here.

verbal working memory have linked articulation with neural activity in the left inferior frontal gyrus, left premotor cortex, supplementary motor cortex, and phonological storage to activity in left inferior parietal cortex (Chen & Desmond, 2005; Fiez & Raichle, 1997; Jonides et al., 1998; Smith & Jonides, 1998). Research also finds that damage to, or temporary disruption of (e.g., transcranial magnetic stimulation), motor regions (Liao et al., 2014) negatively impacts working memory performance (Malouin, Belleville, Richards, Desrosiers, & Doyon, 2004; Ravizza et al., 2006; Ziemus et al., 2007). These findings emphasize the aforementioned interdependence between the domains of motor control and working memory.

Behavioral studies suggest that the interdependence between the working memory and motor systems persists, and may even increase, throughout the lifespan. For example, previous work demonstrates that while notwithstanding neurotypical age-related decreases in cognitive (Hasher & Zacks, 1988) and motor functioning (Mattay et al., 2002), age-related cognitive decline is the main cause for the deterioration of motor performance (Krampe, 2002; Li & Lindenberger, 2002). Additionally, a substantial body of research reports that the effects of age are exacerbated when motor and cognitive tasks are performed concurrently (Brauer, Woollacott, & Shumway-Cook, 2001; Kray & Lindenberger, 2000; Li & Lindenberger, 2002; Lövdén et al., 2008). For example, when simultaneously performing a working memory task and a motor task, such as walking and postural control, the dual-task cost is greater for older adults compared to younger adults (Doumas, Rapp, & Krampe, 2009; Lövdén et al., 2008). This suggests that age-related impairment in such dual-task performance arises from higher levels of task difficulty that may impede motor performance through a cross-domain resource competition (Kray & Lindenberger, 2000; Schaefer & Schumacher, 2011; Woollacott & Shumway-Cook, 2002).

Neuroimaging findings also suggest that older adults exhibit greater frontal recruitment compared to their younger counterparts in both motor (Heuninckx, 2005; Heuninckx, Wenderoth, & Swinnen, 2010; Mattay et al., 2002; Noble, Eng, Kokotilo, & Boyd, 2011; Ward, Brown, Thompson, & Frackowiak, 2003; see Ward, 2006 for a review) and working memory tasks (Cappell, Gmeindl, & Reuter-Lorenz, 2010; Reuter-Lorenz et al., 2000). In particular, age-related increases in neural activity have been observed in frontoparietal regions, including the anterior insula, frontal operculum, superior temporal gyrus, pre-supplemental motor area, dorsal premotor area, left rostral cingulate cortex, left superior frontal gyrus, and middle frontal gyrus during a hand-foot motor coordination task performed at low and high levels of task difficulty (Heuninckx, 2005). Importantly, it has been suggested that this upregulation of frontoparietal regions in working memory and motor skill tasks may occur as a function of increased task demand (Faw, 2003; Marvel & Desmond, 2010; Voelcker-Rehage, Stronge, & Alberts, 2006). These results suggest that the effect of age on working memory and motor skills performance are exacerbated by increases in cognitive task demands. Supporting evidence for this relationship comes from research involving individuals with Autism Spectrum Disorder (ASD) and Attention Deficit Hyperactivity Disorder (ADHD) who, like older adults, are characterized by working memory deficits. Specifically, research from Neely and colleagues reports that when individuals with ASD (Neely et al., 2019) and ADHD (Neely et al., 2016) are asked to maintain force output without visual feedback, the rate of decay of force output is related to deficits in executive function in both patient groups. These studies suggest that deficits in memory guided force output may be related to deficits in working memory abilities. Importantly, however, an explicit behavioral test of working memory, such as the n-back task, was not included in these studies. Thus, one of the goals of the current work was to extend previous work in motor control by examining neural recruitment associated with a visually guided grip force task and a measure of working memory (e.g., n-back task), within the same group of participants.

Although the foregoing research demonstrates a probable link between working memory and motor skills, few studies have examined whether such behaviors are functionally coupled across domains in aging and whether task difficulty and age affect this coupling. Furthermore, while age effects are typically examined by comparing younger and older cohorts, it is unclear whether they persist as a function of increasing age within an older cohort. The current study had three main objectives: (1) Determine whether the neural substrates of working memory and motor control share common neural resources in an older adult sample; (2) Examine whether the recruitment of common neural mechanisms is affected when difficulty across both tasks increases; and (3) Investigate whether these overlapping neural regions are alerted with increasing age. To accomplish these aims we employed an n-back working memory task and a visually guided grip force task. Both tasks were chosen as they allow for examination of their respective constructs (working memory and motor control) in the MRI environment and allow for the measurement of varying degrees of task difficulty. Additionally, in order to examine the effects of age within older adults, age was treated as a continuous variable and predictor in our analyses. Given past evidence, as well as evidence of dedifferentiation in aging (Li & Lindenberger, 2002), we anticipated that both working memory and motor tasks would engage similar regions in frontoparietal cortices. Since task-related activation, otherwise known as neuromodulation, has been consistently observed in healthy aging as a function of task difficulty (Cabeza, Anderson, Locantore, & McIntosh, 2002; Reuter-Lorenz & Cappell, 2008), we also expected activation within these regions to increase as a function of task difficulty. Lastly, due to the recruitment of additional neural resources implicated with increasing age in working memory and motor tasks (Heuninckx, 2005), we predicted that age would be related to parametric increases in neural activation related to task difficulty. Thus, the aim of the present work is to bridge the understanding of the relationship between working memory and motor function in healthy older adults, and examine how the neural substrates of these abilities are modified by task difficulty and age.

Design & procedure

Participants

Thirty community-dwelling adults between 60 and 85 years old were initially recruited to participate in this two-day study. One participant withdrew from the study before completing the functional magnetic resonance imaging session and was subsequently replaced by an additional recruit. Three others were removed from the final analysis due to scoring below accepted range (>26) in the MMSE (1) and feeling uncomfortable in the scanner (2), leaving a final group of 27 older adults (11 males, M_{age} = 69.89 years, SD_{age} = 5.96 years). All participants were right-handed (confirmed via both phone and in-take interviews), native English speakers, and had normal or corrected-to-normal vision. No participants reported a personal or family (first-degree relation) history of neurological or psychological disorders, any major medical conditions (e.g., diabetes, heart disease), or any musculoskeletal disorders. No participants reported taking any medication that might affect cerebral blood flow (Lassen & Christensen, 1976), or motor control (Reilly, van Donkelaar, Saavedra, & Woollacott, 2008). For an overview of participant demographics and cognitive measures, see Table 1. Written informed consent was obtained from all participants and the Institutional Review Board at The Pennsylvania State University approved all procedures.

Day 1 procedure

Testing occurred across two days. On the first day, participants completed a battery of cognitive assessments including the vocabulary section of the Wechsler Adult Intelligence Scale (WAIS, version III; Kreiner & Ryan, 2001), computerized tasks to measure nonverbal working memory (recall and word recognition tasks), verbal fluency (letter fluency and category fluency; (Kempler, Teng, Dick, Taussig, & Davis, 1998), and a Stroop task (Stroop, 1935). Additionally, processing speed was evaluated using simple and choice RT tasks, and the Purdue Pegboard Test (Tiffin & Asher, 1948) was used evaluate manual dexterity and bimanual coordination. IN ADDITION TO THE COGNITIVE BATTERY, PARTICIPANTS COMPLETED THE Barratt Impulsiveness Scale (BIS-11; Patton, Stanford, & Barratt, 1995) and the Freiburg Visual Acuity & Contrast Test (FrACT, vs 3.7.1; Lange et al., 2009). Last, participants completed several precision grip force tasks, which are reported elsewhere (e.g., Neely et al., 2017).

Day 2 procedure

Day 2 took place at the MRI imaging center. Participants performed three tasks including a grip force task, an n-back working memory task, and a language production task (the results of the language task are reported in Gertel et al. (under review)). Task order was counter-balanced across participants. Participants completed two consecutive runs of each task. Each fMRI run was composed of six alternating task (30s) and rest (15s) blocks,

Table 1. Demographics and cognitive assessment scores.

	M (SD)
Demographics	
Age (Years)	69.89 (5.96)
Education (Years)	17.65 (2.35)
Cognitive assessment tasks	
MMSE	29.00 (1.00)
NVWM	
Immediate Recall	11.11 (2.31)
Delayed Recall	9.51 (2.87)
Stroop Accuracy	98.71% (.01%)
Processing Speed	
Simple Reaction Time	272.72ms (39.96ms)
Choice Reaction Time	342.85ms (50.20ms)
Verbal Fluency Total	63.96 (15.33)
WAIS-III Vocabulary	53.67 (6.46)
Purdue Pegboard Test Total	35.22 (5.10)
Barratt Impulsiveness Scale (Self-Control)	10.11 (2.53)
Freiburg Visual Acuity & Contrast Test	40.70 (14.44)

Key: M, mean; SD, standard deviation; MMSE, Mini-Mental State Examination; NVWM, Non-verbal working memory; WAIS-III, Weschler Adult Intelligence Scale-III.

including two blocks from each of three levels of task difficulty (described below). Within each task, difficulty was operationalized by progressively increasing the cognitive demand at each level (again described below). Block order was pseudorandomly arranged with the constraint that two blocks of the same level of difficulty could not occur in a row.

Visually guided grip force task. The force task protocol described here is similar to that reported in Neely, Coombes, Planetta, and Vaillancourt (2013). Participants produced force against a custom-designed Bragg-grating fiber-optic force transducer with a resolution of 0.025 N (Neuroimaging Solutions, LLC). The transducer was housed in an MR-safe precision grip apparatus held between the thumb and index finger of the right hand. An sm130 Dynamic Optical Sensing Interrogator (Micron Optics, CITY) digitized force output produced by the participant at 62.5 Hz. Custom LabVIEW (National Instruments, CITY) software converted the digitized force to Newtons. Participants were provided continuous (60 Hz) visual feedback about their force during the task.

Prior to the experimental task in the scanner, each participant's maximum voluntary contraction (MVC) was measured using a pinch grip dynamometer (Lafayette Hydraulic Pinch Gauge, Model J00111). The average of three trials determined each participant's MVC in Newtons. Target amplitudes were normalized to 15% of each participant's MVC because the amplitude of force output influences brain activation.

During the visually guided grip force task, participants viewed two bars against a black background: a red/green force bar that moved up with increasing force and down with decreasing force, and a white, static target bar. The color of the force bar cued the onset and offset of force. The force task included three levels of difficulty. In the easy condition, or "static" task, participants produced constant force for 30s to a predictable target. In the medium condition, or "dynamic-same" task, participants produced 2s force pulses separated by 1s of rest to a predictable target. In the difficult condition, or "dynamic-different" task, participants produced 2s force pulses separated by 1s of rest to an unpredictable target (See Figure 1 for a visualization of each condition). All participants completed a brief training session to become familiar with the tasks immediately before the experimental session.

Working memory task. Working memory was measured using an n-back task. The n-back requires participants to continuously remember the last *n* of a series of letters. In this case, participants were instructed to respond under three separate conditions of task difficulty. In the easy condition, a target letter appeared on the screen (0-back). Medium difficulty was operationalized as responding when the target matched a cue that appeared immediately before the target (1-back), and hard when the cue appeared two letters before the target (2-back). The 0-back condition used an "x" as the target letter (6 targets per block), whereas targets in the 1- and 2-back conditions were chosen at random (7 targets per block). The letters were presented in a block of 15 letters for 500 ms followed by a 1500 ms delay, during which letters were replaced by a fixation cross. Across all conditions, target letter comprised 50% of the trials. The letters used in the n-back task were presented in black font, size 48 font, on a white background. Prior to the start of each block an instruction screen was presented for 3000 ms cueing participants to the upcoming condition.

Prior to scanning, instructions for each condition in the n-back task were provided to the participant. Participants were instructed to press with their index finger for a target

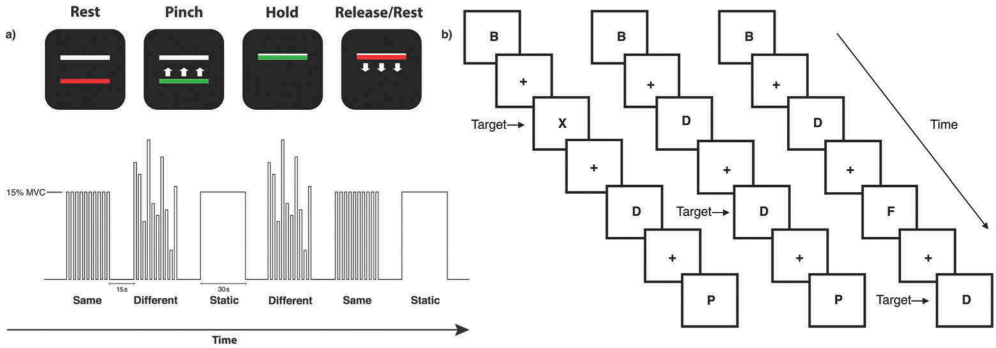

Figure 1. Depiction of visually guided grip force task and n-bask task. (a) depicts the visually guided grip force task. The visual display contains two horizontal bars presented against a black background. The target bar (white) is stationary and the red/green force bar provides real-time visual feedback. (b) depicts the n-back task. Letters appear on the screen for 500ms. Each trial is separated by a 1500ms interstimulus interval.

and their middle finger for a non-target letter. Following instructions for each condition participants completed two practice blocks. The first practice was designed to make sure participants understood the instructions and thus was self-paced to allow experimenter feedback. The second practice block was designed to acquaint participants with the timing of task parameters to be used in the scanner.

MRI data acquisition protocol

Magnetic resonance images were collected using a 20-channel head coil with a Siemens 3T Magnetom Prisma Fit (Siemens, Berlin, Germany). Head position was stabilized with adjustable padding on both sides of the head. Scanner noise was attenuated with a combination of earplugs and earphones. Visual stimuli were displayed on a visor using mirror-geometry. Functional images were obtained using a T2*-weighted, echo-planar pulse sequence with the following parameters: repetition time = 2500 ms, echo time = 25 ms, flip angle = 90°, field of view = 240 mm^2, voxel size = 3 mm isotropic with no gap between slices (n = 41). A three-dimensional T1-weighted image was collected with the following parameters: repetition time = 2300 ms, echo time = 2.28 ms, flip angle = 8°, field of view = 256 mm^2, acquisition matrix = 240 × 240mm, voxel size = 1 mm isotropic with no gap between slices (n = 192). Following functional scans, DTI data was collected but was not included in current analyses.

Behavioral analyses

All behavioral data was analyzed using RStudio using the dplyr package (Wickham, François, & Müller, 2018). Continuous force data was time-locked to the onset of each scan. The force time series data was digitally filtered using a tenth-order Butterworth filter with a 15-Hz low-pass cutoff frequency. Visual inspection of force output was performed, and four time-points were determined for each trial: force onset, beginning of steady-state force, and force offset. The 15s rest periods were omitted from analysis. Root mean square error was calculated for each trial and then averaged across runs for each participant. Signal processing and root mean square error calculations were conducted with custom-written algorithms in MATLAB (MathWorks) and were z-scored using RStudio. The working memory task was scored based on whether a participant accurately identified a target trial. Error rates were calculated by subtracting the percentage incorrect from the overall possible accuracy (100%). Error rate for force and working memory data was analyzed within and across tasks. Paired sample t-tests were used to confirm differences in difficulty across easy, medium, and hard task conditions. All p values were considered significant if less than 0.05. Pearson's r values were also computed to determine whether there was a relationship between difficulty level performance and participant age. Last, Pearson's r values were also calculated between overall error rate on force task and activation in each ROI identified in the imaging analysis (see below) in order to examine the relationship between task performance and increases in neural activation.

fMRI data processing and analysis

Data processing and analysis were performed using Statistical Parametric Mapping (SPM12; Wellcome Department of Cognitive Neurology, http://www.fil.ion.ucl.ac.uk/spm). Raw data was visually inspected, and the origin was set to the anterior commissure. Realignment was conducted by registering each volume of the functional data to the first volume of the first scan run using a 6-parameter rigid body affine transformation. Functional scans were then slice time corrected, co-registered with each subject's T1-weighted anatomical scan, and normalized to the MNI template. To do this, the raw T1 MPRAGE images were co-registered to the mean realigned functional image, and then the co-registered T1MPRAGE image was segmented and registered to the MNI template. Finally, smoothing of the functional scans was performed with a Gaussian kernel of 6 mm full width at half-maximum (FWHM). Participants (N = 1) with greater than 3 mm translation in any direction were excluded from further analysis.

The data were analyzed by creating analogous but separate general linear models (GLMs) for each of the force, working memory, and language tasks. Specifically, for each task, the data were modeled by convolving SPM's hemodynamic response function with a 30s boxcar function for each of the 12 task blocks. To evaluate the linear trends related to increasing task difficulty, each task block was modeled using a linear parametric analysis. This allowed for the identification of voxels in which the BOLD signal correlated linearly with increasing levels of task difficulty. In a second model, age was entered as a continuous predictor to determine whether increasing age affects the correlation between parametrically increasing BOLD signal and increasing levels of task difficulty. Finally, regressors of no interest were created to control for cofounding variables, including a regressor for the memory task's instruction screen, six regressors corresponding to motion parameters (x, y, z, pitch, roll, and yaw) derived from realignment, and gray matter volume, which was computed using volBrain (Manjón & Coupé, 2016).

Random effects analyses were performed to examine BOLD responses that significantly correlated with task difficulty at the group level within each task. Group analyses were thresholded at $p < .05$ FWE, using a 10-voxel extent and an implicit whole brain mask created from the MNI template that ensured all identified activation fell within gray matter regions. In order to examine common activation across tasks, conjunction analyses were performed in SPM12. As a first step, a conjunction of both tasks was computed and thresholded at $p < .05$ FWE. Age was then applied as a predictor in this conjunction model.

Results

Behavioral results

Visually guided force task

Participants had an overall accuracy on the grip force task of 98.4% ($M_{ErrorRate}$ = 1.6%). With respect to differences across task difficulty, paired samples t-test determined that there was no significant difference between the easiest condition (static condition; $M_{ErrorRate}$ = 1.30%, $SD_{ErrorRate}$ = .54%) and the medium difficulty condition (same condition; $M_{ErrorRate}$ = 1.0%, $SD_{ErrorRate}$ = .40%), $t(24) = 1.14$, $p = .26$, 95% CI [0.00, 0.00]. However, there was a significant difference between the easiest condition and the most difficult condition (different condition; $M_{ErrorRate}$ = 3.0%, $SD_{ErrorRate}$ = .57%), $t(24) = -12.43$, $p < .001$, 95% CI [–.02,-.01], as well as between the medium and most difficult conditions, $t(24) = -14.61$, $p < .001$, 95% CI [–.02, –.01]. The results support our manipulation of difficulty across task levels. Pearson's r values were calculated in order to examine the relationship between overall error rate on the force task and age. There was a nonsignificant relationship between overall error rate and age ($r = 0.21$, $p = 0.302$; Figure 2(b)). Lastly, the relationship between error rates on the force grip task and neural activation across all ROIs was nonsignificant (all p's > .05).

Working memory

Participants had an overall accuracy rate of 88.8% on the n-back task ($M_{ErrorRate}$ = 11.2%). Paired samples t-test determined that there was no significant difference between the error rate on the easiest (0-back; $M_{ErrorRate}$ = 6.68%, $SD_{ErrorRate}$ = 8.03%) and medium difficulty conditions (1-back; $M_{ErrorRate}$ = 7.56%, $SD_{ErrorRate}$ = .12%), $t(24) = -.53$, $p = .60$, 95% CI [–.04, .03]. However, there were significantly more errors in the most difficult condition (2-back; $M_{ErrorRate}$ = 15.28%, $SD_{ErrorRate}$ = 8.54%) compared to the easiest condition, $t(24) = -6.26$, $p < .001$, 95% CI [–.11, –.06] and medium difficulty condition, t

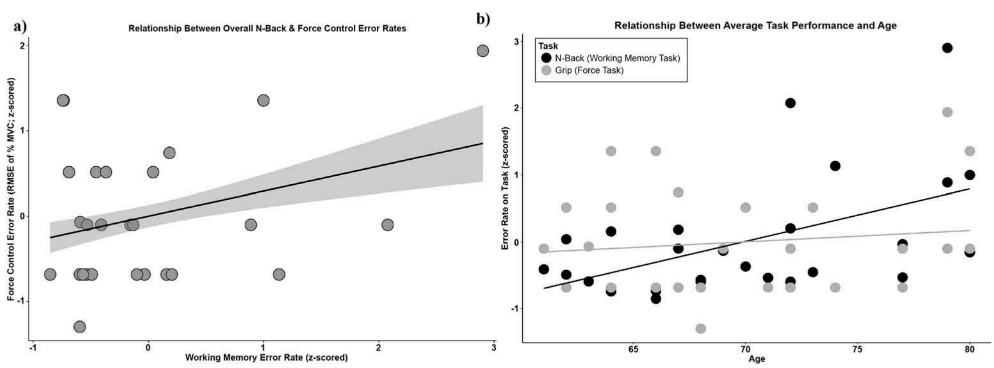

Figure 2. Relationship between performance on working memory and force tasks. (a) depicts the overall positive but nonsignificant relationship between error rate on force and working memory tasks ($r = 0.27$, $p = 0.125$). (b) depicts the overall error rates associated with age in the WM task ($r = 0.52$, $p = 0.006$) and force task ($r = 0.21$, $p = 0.302$).

(24) = −5.84, p < .001, 95% CI [−.10, −.05]. Results support our manipulation of difficulty across task levels. Pearson's r values were calculated in order to examine the relationship between overall error rate on the working memory task and age. There was a significant relationship between overall error rate and age ($r = 0.52$, $p = 0.006$; Figure 2(b)). Lastly, the relationship between error rates on the working memory task and neural activation across all ROIs was also nonsignificant (all p's > .05).

Finally, when comparing behavior across tasks, there was a positive but nonsignificant relationship between error rate on the force grip and working memory tasks ($r = 0.27$, $p = 0.125$; Figure 2(a)).

Imaging results

When task difficulty parametrically increased in working memory and motor tasks, a conjunction of activity was observed in bilateral dorsal and left ventral premotor cortices, left precentral gyrus, bilateral supramarginal gyri, and left angular gyrus (Table 2, Figure 3(a)). All aforementioned regions with the exception of the left ventral premotor cortex and left precentral gyrus were also identified in a separate conjunction analysis that included age as a predictor. As shown in Figure 3(b), this analysis also revealed activation in left precentral gyrus. Despite this overlap in task difficulty, there was no relationship between task activation and performance (see above). Activation maps for each task compared to rest are reported in the supplemental materials, as are maps examining increases in difficulty for each task individually.

Discussion

The present study investigated the underlying neural activation associated with working memory and motor control as a function of both task difficulty and age in a group of older adults. Based on past research involving individuals with ASD (Neely et al., 2019) and ADHD (Neely et al., 2016), which reported deficits in working memory and motor output we posited that the two tasks were reliant on common cognitive and neural mechanisms (see also Marvel et al., 2019). We further posited that this overlap would be most apparent in a population that exhibited variability and decline in working memory functioning, such as older adults. The results provided mixed evidence for this position. While

Table 2. Conjunction of neural activity between working memory and force tasks.

			Parametric increase in task difficulty					Parametric increase in task difficulty Including age as a regressor				
			Coordinates					Coordinates				
Region	H	BA	x	y	z	t	mm^3	x	y	z	t	mm^3
Dorsal premotor cortex	R	6	30	4	58	7.70	2,160	30	4	58	7.63	1,782
	L	6	−26	2	58	7.40	729	−26	2	58	7.26	459
Ventral premotor cortex	L	44	−46	8	32	7.08	378					
Precentral gyrus	L	6	−50	6	42	7.08	432					
Supramarginal gyrus	R	40	42	−40	46	6.60	459	46	−38	44	6.83	378
	L	40	−44	−42	44	8.83	2,592	−44	−42	44	8.76	2,187
Angular gyrus	L	40	−30	−50	42	8.03	2,268	−28	−50	42	7.90	1,971

H = hemisphere (L = left, R = right); BA = Brodmann's area; Coordinates (x, y, z) represent peak MNI coordinates; t = statistical t value; mm^3 represents voxel extent.

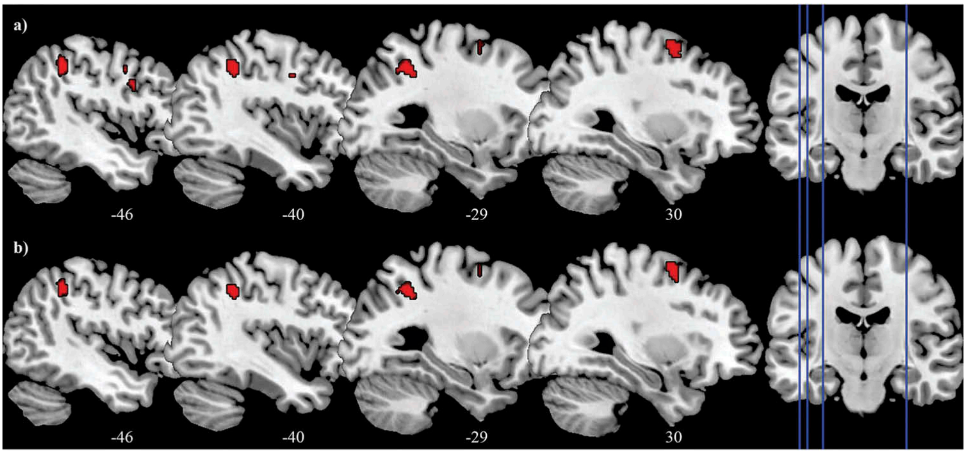

Figure 3. Depiction of conjunction for working memory and force activity for increasing task difficulty. (a) depicts the spatial overlap of neural activity for the conjunction analysis of parametric increases in difficulty across working memory and force tasks. (b) depicts the spatial overlap of neural activity for the conjunction analysis of parametric increases in difficulty across working memory and force tasks when age is included as a predictor.

behavior, measured by error rates, across the two tasks was positively correlated, this correlation failed to reach significance. However, we did identify a set of neural regions that exhibit common activity as a function of increases in task difficulty for both working memory and motor tasks throughout old age. Specifically, we observed common neuromodulation in bilateral dorsal and left ventral premotor cortices, left precentral gyrus, bilateral supramarginal gyri, and left angular gyrus. This overlap suggests a reliance on similar neural resources for both working memory and motor task as task difficulty increases in each task. These same regions also exhibited neuromodulation as a function of increasing age within older adults. The current work adds to previous work that has observed neuromodulation for working memory (Cappell et al., 2010; Reuter-Lorenz & Park, 2010; Schneider-Garces et al., 2009) and motor control (Heuninckx, 2005; Heuninckx et al., 2010; Mattay et al., 2002) in older adults. While neuromodulation associated with task difficulty has been observed in both tasks previously, the current study is the first to observe overlapping regions of activation and neuromodulation across a working memory and motor skill task in older adults. As such, the current results expand upon this earlier work by suggesting that common resources are needed for task execution within older adults when task difficulty increases.

Behaviorally, performance in both the working memory and motor task declined as task difficulty increased, supporting previous aging research that finds reductions in performance as a function of task difficulty (Li, Lindenberger, Freund, & Baltes, 2001; Lindenberger et al., 2000; Yogev-Seligmann et al., 2008). Despite this decrease in performance, indexed by increasing error rates, we observed increases in neural recruitment across frontoparietal regions as a function of difficulty. While frontoparietal modulation in response to task difficulty has been observed previously in both working memory (Anguera, Reuter-Lorenz, Willingham, & Seidler, 2011; Anguera, Seidler, & Gehring, 2009; Li, Lindenberger et al., 2001; Lindenberger et al., 2000) and motor control tasks in aging

(Noble et al., 2011), this is the first study to identify overlap across both task domains in the same sample of older adults. Previous work from Anguera and colleagues reported overlapping neural activity in frontoparietal regions in young adults (Anguera, Reuter-Lorenz, Willingham, & Seidler, 2010) across a spatial working memory task and a visuomotor adaption task, but not in older adults (Anguera et al., 2011), with the authors concluding that older adults were not able to recruit working memory resources while performing a motor control task. In contrasts to Anguera et al. (2011), the current results showed frontoparietal overlap within older adults across the n-back and grip force tasks, suggesting that both tasks recruit similar neural resources. Moreover, this overlap was observed as a function of parametrically increasing task difficulty. Differences in working memory and motor tasks used across the two studies may account for conflicting results across studies. Additionally, an important novel contribution of the current work is the examination of task difficulty in both working memory and motor tasks. As such, the current findings suggest that it may be the neural response to task difficulty that result in a need to recruit working memory resources in a motor control task in older adults.

The idea of increased recruitment of neural activity as a function of task difficulty has long been considered in the aging literature. Specifically, the PASA theory (posterior-to-anterior-shift-in-aging; Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008; Dennis & Cabeza, 2008) suggests that older adults upregulate frontoparietal activity compared to younger adult in order to successfully complete cognitive tasks. Additionally, the CRUNCH model (Compensation-Related Utilization of Neural Circuits Hypothesis; Reuter-Lorenz & Cappell, 2008) posits that such over recruitment tends to be more prominent at lower levels of task difficulty, with older adults unable to upregulate neural activity as task difficulty reaches higher levels. This theory been applied to working memory tasks (Cappell et al., 2010; Reuter-Lorenz & Park, 2010; Schneider-Garces et al., 2009) and also to increased neural activation on motor tasks (e.g., Heuninckx, 2005; Heuninckx et al., 2010; Noble et al., 2011). Consistent with this work that compares across age groups, in our sample of older adults, it was the oldest-old who exhibited the greatest increases in neural recruitment across levels of task difficulty, in both the working memory and motor control tasks. Although the idea of upregulation in aging has typically been discussed in the context of compensation, the current results do not support this interpretation. That is, the increased activation in frontoparietal regions was not associated with improvements in task performance for either task. To this end, the current study extends work depicting neuromodulation (Cabeza et al., 2002; Reuter-Lorenz & Cappell, 2008) in the absence of behavioral benefits (Chein, 2001; Marvel & Desmond, 2010, 2012) to include common activation across both working memory and motor domains. Given that increases in neural recruitment were observed as a function of both task difficult and increased age within our sample of older adults, the results also suggest that this increased recruitment may reflect nonselective recruitment. Expanding on the conclusions reached in Seidler et al. (2010), we surmise this nonselective recruitment reflects an inefficient response to task difficulty that worsens with increased aged within commonly recruited frontoparietal regions across tasks. Given relatively high performance in the current sample of older adults, more work in need, across larger ranges of difficulty, in order to fully investigate this theory. To further test the nature of compensatory neural activity, future studies should include an increased sample of older adults, including those over the age of 85 to see if there is any drop in recruitment in the "oldest old" (Salthouse, 1985). Given the increased activation and decline in performance from the easiest level of task difficulty to the most challenging level, the current results may be better accounted for by a dedifferentiation account of aging than compensatory recruitment.

With respect to the interpretation of overlapping frontoparietal activity for working memory and motor control tasks (specifically the n-back and force grip tasks used in the current study), we had posited that both tasks required the maintenance and application of information in working memory stores for completing task goals. Specifically, maintaining letters in the n-back task for comparison across trials and maintaining a representation of force output in the grip force task to be applied to the motor output indicated on each force output trial. While this interpretation is supported by Anguera and colleagues (Anguera et al., 2011), others have suggested that activity in motor regions during working memory tasks reflect a motor trace that serves to support rehearsal of the stored information (Marvel et al., 2019). While the two interpretations are closely linked in theory, current work cannot disentangle them. The use of non-verbal working memory tasks may help in identifying whether overlap reflects motor traces in memory tasks or the more basic maintenance of information across the two types of tasks.

Conclusions

The hypothesis that there is shared neural activation for working memory and motor tasks as a function of both task difficulty and age was supported. This finding extends previous literature noting that working memory may underlie motor capabilities (Anguera et al., 2010, 2009; Neely et al., 2016, 2019, 2017). At the neural level, these findings extend previous work showing older adults engage common frontoparietal regions to support cognitive monitoring and motor execution (Heuninckx, 2005). However, lack of correlations between neural activity and behavior in either task do not support a conclusion of compensation. Finally, upregulation of neural activity among the oldest participants in our sample suggest that neuromodulation in response to changes in task difficulty exists throughout advanced aging. This finding has implications for theories of aging and intervention research, suggesting that age is not a limiting factor with regard to plasticity of neural recruitment.

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Disclosure statement

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