



Lifespan differences in visual short-term memory load-modulated functional connectivity

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ABSTRACT

Working memory is critical to higher-order executive processes and declines throughout the adult lifespan. However, our understanding of the neural mechanisms underlying this decline is limited. Recent work suggests that functional connectivity between frontal control and posterior visual regions may be critical, but examinations of age differences therein have been limited to a small set of brain regions and extreme group designs (i.e., comparing young and older adults). In this study, we build on previous research by using a lifespan cohort and a whole-brain approach to investigate working memory load-modulated functional connectivity in relation to age and performance. The article reports on analysis of the Cambridge center for Ageing and Neuroscience (Cam-CAN) data. Participants from a population-based lifespan cohort ($N = 101$, age 23–86) performed a visual short-term memory task during functional magnetic resonance imaging. Visual short-term memory was measured with a delayed recall task for visual motion with three different loads. Whole-brain load-modulated functional connectivity was estimated using psychophysiological interactions in a hundred regions of interest, sorted into seven networks (Schaefer et al., 2018, Yeo et al., 2011). Results showed that load-modulated functional connectivity was strongest within the dorsal attention and visual networks during encoding and maintenance. With increasing age, load-modulated functional connectivity strength decreased throughout the cortex. Whole-brain analyses for the relation between connectivity and behavior were non-significant. Our results give additional support to the sensory recruitment model of working memory. We also demonstrate the widespread negative impact of age on the modulation of functional connectivity by working memory load. Older adults might already be close to ceiling in terms of their neural resources at the lowest load and therefore less able to further increase connectivity with increasing task demands.

1. Introduction

Visual short-term memory (VSTM), or the capacity to temporarily retain a limited amount of visual information (Logie, 1989), is critical in our interactions with our environment and supports higher-order executive processes. Unfortunately, VSTM declines throughout the adult lifespan (Brockmole and Logie, 2013). Given the importance of VSTM in everyday functioning, a thorough understanding of the relation between VSTM and age is essential. A large number of studies have shown differential patterns of regional brain activation by memory load related

to age, mainly expressed by greater activation in older adults, that can be interpreted by several accounts including the compensation-related utilization of neural circuits hypothesis (CRUNCH; Reuter-Lorenz and Cappell, 2008; but see Jamadar, 2020, for a conflicting finding and a systematic review). Regional activation studies typically report increased activity in the frontoparietal, dorsal attention, and salience networks and decreased activity in the default mode network in response to increased working memory load (e.g., Rottschy et al., 2012, Zuo et al., 2019). Modulation of activation by load is related to performance and is weakened with increasing age (Cappell et al., 2010;

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Heinzel et al., 2017; Kaup et al., 2014; Kennedy et al., 2017). While there is no doubt that frontoparietal regions are critical for VSTM, studies using multivoxel pattern analysis (MVPA) show that the contents of VSTM can be decoded from the visual cortex (e.g., Olmos-Solis et al., 2021) and that there is a decrease in classification performance as a function of load related to individual task performance (Emrich et al., 2013). Thus, it has been suggested that working memory maintenance arises from interactions between frontoparietal control regions and perceptual processing regions, where representations are maintained (e.g., Olmos-Solis et al., 2021; for an overview on this account see for example Eriksson et al., 2015; for a lifespan perspective see review Sander et al., 2012). Synchronization of activity in distributed networks is critical for working memory (D'Esposito and Postle, 2015) and recent developments in connectivity methods have led to a shift in focus from relating working memory processes to local brain responses to interactions in widespread networks (Soreq et al., 2019). However, the effect of age on functional connectivity related to working memory is still understudied. The current study contributes to our understanding of age differences in working memory by using a large lifespan cohort, a continuous response task with different working memory loads, and a task-based, whole brain, functional connectivity approach.

Load-modulated functional connectivity refers to the connectivity strength (positive or negative) between regions of interest for the contrast of high versus low load. In young adults, VSTM load has been associated with within-network connectivity in the frontoparietal, dorsal attention, ventral attention, and visual networks (Eryilmaz et al., 2020; Liang et al., 2016; Soreq et al., 2019; Zuo et al., 2019), and between-network coupling among frontoparietal, dorsal attention, ventral attention and default mode networks (Eryilmaz et al., 2020; Liang et al., 2016). Furthermore, due to its role in sustaining attention, interactions between the dorsal attention network and other networks, is thought to be critical to memory performance at higher cognitive loads (Zuo et al., 2019).

A limited number of studies with mixed results have investigated the effects of age on working memory load-modulated functional connectivity. Pongpipat et al. (2021) showed that functional connectivity within frontoparietal and default mode regions was strengthened as working memory load increased. With increasing load, the negative connectivity between the frontoparietal and default mode network also increased. Crucially, this pattern was invariant across the lifespan, but better performance only related to stronger negative coupling between these networks in middle-aged and older adults, not in younger adults or the oldest old. The youngest adults performed well, and the oldest adults poorly, regardless of connectivity between frontoparietal and default mode regions. The authors suggested that for adults in the middle and older age range, brain maintenance or compensation strategies are most important. In contrast, Heinzel et al. (2017) and Nagel et al. (2011) both showed reduced working memory load-dependent modulation of connectivity between the dorsolateral prefrontal cortex and other regions in older adults. Increasing this connectivity with increasing load was related to higher performance in younger and older adults. A limitation of these studies is that they only included a very limited subset of brain regions or seeds. Some studies have used whole-brain activation results to define a working memory network for their connectivity analysis. For instance, Burianova et al. (2015) reported modulation of connectivity by memory load in the working memory network in younger adults but not in older adults. Crowell et al. (2020) investigated network integration, defined as the ratio of connectivity within the task network versus between the task network and all other regions. While younger adults increased within-network connectivity with increasing load in the task network, older adults recruited a more distributed cortical network. This is in line with previous findings of reduced within-network specificity in older adults (Bethlehem et al., 2020; Chan et al., 2014; Geerligs et al., 2015) and the concept of age-related neural dedifferentiation (for a review, see Koen and Rugg, 2019).

Although these recent findings give some insight on how age affects load-modulated functional connectivity in a predefined working memory network, a comprehensive investigation of the relationship between whole-brain connectivity in relation to VSTM load across the lifespan is missing. A whole-brain approach may be particularly critical, as a recent study showed that task-modulated connectivity not only involves task-active regions but also regions that are not activated or deactivated by the task (Di and Biswal, 2019). Furthermore, regions that are coactivated during a task do not necessarily have higher connectivity during task than rest, indicating that both regions might be involved in the task but work independently of one another (Di and Biswal, 2019). Crowell et al. (2020) showed age-related differences in working memory load-related connectivity. Older adults demonstrated higher connectivity between the task-related network and other areas. These effects might be missed when preselecting regions of interest. Additionally, selecting regions of interest based on activation is suboptimal as peak activation studies typically report overactivation in older adults, making it difficult to select a shared set of regions across age groups (Reuter-Lorenz and Cappell, 2008). A second limitation of previous studies is that most use an extreme group design (i.e., comparing young and older adults). Thus, in the present study we address these issues by using a whole-brain approach to characterize age-related differences in load-modulated functional connectivity in a large, adult lifespan cohort.

Participants from the population-based Cambridge center for Ageing and Neuroscience (Cam-CAN) lifespan cohort ($N = 111$, age 23–86) performed a visual short-term memory (VSTM) task during functional magnetic resonance imaging (fMRI). VSTM was measured with a delayed recall task for visual motion with three different loads. Recall precision has been found a highly sensitive measure to investigate working memory and has been used in clinical and healthy aging populations (e.g., Lugtmeijer et al., 2021; Mitchell et al., 2018; Tas et al., 2020; Zokaei et al., 2015). Using a delayed recall task, as opposed to the commonly used n-back task, allowed us to compare task-related interactions during both encoding and maintenance periods. A previous study using a similar task design reported differences in brain activity during stimulus presentation and maintenance in relation to working memory load, with visual regions showing an effect of load during encoding and frontoparietal regions during maintenance (Emrich et al., 2013). These findings suggest that it is relevant to analyze the encoding and maintenance periods separately. Whole-brain load-modulated connectivity was estimated using psychophysiological interactions in a hundred regions of interest, sorted into seven networks (Friston et al., 1997; Schaefer et al., 2018; Yeo et al., 2011). We expected: 1) increased load to be associated with increased functional connectivity, particularly in frontoparietal, attentional control and visual regions in line with regional activation and decoding studies, 2) no effect of age on load-modulated functional connectivity between the frontoparietal and default mode network (based on Pongpipat et al., 2021) and decreased load-modulated connectivity between frontal and parietal regions with increasing age (based on Heinzel et al., 2017), and 3) better performance to be associated with higher load-modulated functional connectivity in networks modulated by VSTM load (based on Heinzel et al. (2017) and Nagel et al. (2011)). These hypotheses only concern regions included in previous studies. Using a whole brain approach we aim to determine whether load-modulated functional connectivity extends to other regions across the cortex.

2. Materials and methods

2.1. Participants

A population-based sample of 280 healthy adults participated in Stage 3 of the Cam-CAN project. Participants completed a series of neuropsychological and neuroimaging experiments, of which the VSTM fMRI task is analyzed in this study. Half of the participants in Stage 3 were assigned to the VSTM task, of which 125 completed it. Eight

Table 1
Demographics.

Age group	Younger	Middle	Older
<i>N</i>	36	35	40
Age range (years)	23–40	41–60	61–86
Sex (male/female)	18/18	16/19	23/17
Handedness (right/left)	33/3	35/0	38/2
Highest education			
University	32	27	22
A' levels	1	5	11
GCSE grade	3	3	3
None > 16	0	0	4
MMSE <i>M</i> (<i>SD</i>)	29.36 (1.02)	28.91 (1.48)	28.40 (1.34)

Note. Sex based on self-report. Handedness = score on the Edinburgh Handedness Inventory (Oldfield, 1971). MMSE = Mini Mental State Examination.

participants were excluded based on poor performance on the lowest memory load trials of the task (single item, mean absolute error $>30^\circ$), two had incomplete EPI data, and four failed preprocessing of fMRI data. The final sample consisted of 111 participants with an age range of 23–86 years old (demographic information in Table 1, only grouped by age for illustrative purposes, not for analyses). MMSE scores ranged from 25 to 30. Eight participants had a missing MMSE score from the Stage 3 testing phase. Thus, for those participants, we used their MMSE score from Stage 1 for the means reported in Table 1 (the mean number of days between Stages 1 and 3 for these participants was 698 days, range 279–1317 days). Ethical approval for the Cam-CAN study was obtained from the Cambridgeshire 2 (now East of England – Cambridge Central) Research Ethics Committee. Participants gave written, informed consent before participating.

2.2. Experimental design

The stimuli and task were adapted from Emrich et al. (2013). In short, VSTM was measured with a delayed recall task for visual motion with three different loads based on set size (Fig. 1). Participants were asked to fixate on a dot in the center of a screen during a 7 second intertrial interval. Then three patches of coherently moving dots were presented sequentially, each in a different color. Patches were presented for 500 ms with a 250 ms blank interval. Depending on the set size, one, two or three patches displayed dots moving in a linear direction. Participants had to remember the motion direction and the corresponding color. The remaining patches showed dots moving in a circular motion at the same speed and could be ignored. During an 8 s blank interval, participants were to keep the motion direction(s) in mind. Finally, the probe display consisted of a circle with a line pointing to a random

point on the circle, in one of the three colors that indicated which of the motion directions needed to be reported. Participants indicated the corresponding direction by rotating the line clockwise or counterclockwise by means of pressing keys on a button box. After confirmation of the direction by pressing a third key, or after 5 s, the next trial began.

The task consisted of 3 runs of 30 trials. Each run had 10 trials of each memory load (1, 2, and 3), counterbalanced with serial position (first, second, or third) and color (red, yellow, or blue). Trials within each run were presented in random order. On 27 trials per run, the motion direction of the probed patch was one of the three directions (7, 127, or 247°). To prevent participants from noticing this pattern, random directions were used for the 3 remaining trials, as well as all the unprobed patches throughout the task (i.e., that needed to be memorized but were not tested).

2.3. Behavioral analysis

Response error, or the angular difference between the target value and the reported value, was used as a model-free measure of performance. The effects of load, age, and their interaction was analyzed using mixed effects modeling, with subject as random effect, and as fixed effects load and age. Analyses were conducted in R (version 4.2.0) using the lme4 package (Bates et al., 2015). Four models were built hierarchically such that effects were added one by one to see if additional predictors improved model fit (e.g., Sommet and Morselli, 2017). Predictors were added in the following order: subject, age, load, and age \times load. Response error captures the mean absolute deviation from the target and was used instead of model estimates (such as precision; Zhang and Luck, 2008) because we found that model fit (log-likelihood) declined with age (Pearson correlation, set size 1 $r(109) = -0.36$, $p < .001$, set size 2 $r(109) < -0.46$, $p < .001$, set size 3 $r(109) = -0.53$, $p < .001$).

Nevertheless, for completeness, we also report the results from a three-component mixture model (Zhang and Luck, 2008, modified by Bays et al., 2009) that distinguishes between different types of errors. This provides estimates of how many items (directions) were stored in memory (K), the precision of each item held in memory (κ), the proportion of non-target errors (reporting a direction that corresponded to an unprobed patch), and the proportion of guess responses. The model described responses by a probabilistic mixture of errors centered on the target feature, centered on one of the non-target features, or distributed uniformly (guesses). Errors centered on the target or non-target features were described by a Von-Mises distribution (a circular analogue of the normal distribution). Further, because there is a significant response bias away from cardinal and towards oblique angles that increased with age, we subtracted the mean response bias per direction from each response prior to running the mixture model. Finally, the correlation be-

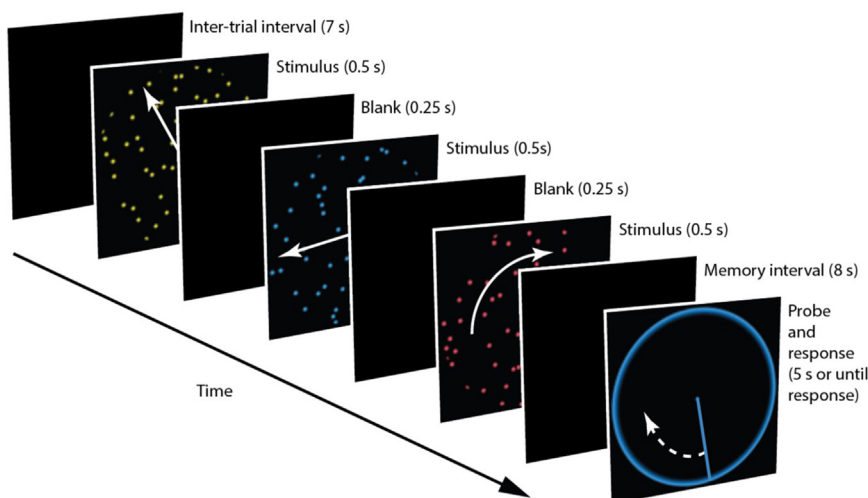


Fig. 1. Example trial from the delayed-recall task. Participants were shown three patches of moving dots and were cued after a blank interval with a color of which the corresponding direction of motion needed to be reported.

tween different performance measures and age was analyzed per set size. Outliers on the response error measure were identified with a boxplot, based on a value higher than 1.5 times the interquartile range above the upper quartile (Tukey, 1977).

2.4. MRI acquisition

The MRI data were collected using a Siemens 3 T TIM TRIO system. During each of three functional runs while the participant was performing the task, T2*-weighted Echo Planar Images were acquired using the following parameters: Repetition time (TR) = 2 s, three echo times (TE = 12 ms, 25 ms and 38 ms), flip angle = 78°, 34 axial slices of 2.9 mm thickness acquired in descending order with an inter-slice gap of 20%, in plane field of view (FOV) = 224 mm × 224 mm, and voxel-size = 3.5 mm × 3.5 mm × 3.48 mm. There were a variable number of scans per run, depending on reaction time, ranging from 294 to 349 (median 320).

A structural image was acquired for each participant, on a different day (median 49 days apart, range 75 to 1039). This used a T1-weighted 3D Magnetization Prepared Rapid Gradient Echo (MPRAGE) sequence with the following parameters: TR = 2250 ms, TE = 2.98 ms, inversion time = 900 ms, 190 Hz per pixel, flip angle 9°, FOV = 256 × 240 × 192 mm, and GRAPPA acceleration factor 2, voxel size 1 mm isotropic.

2.5. MRI preprocessing

Imaging data were preprocessed with the automatic analysis (AA, release 3) batching system (<https://imaging.mrc-cbu.cam.ac.uk/imaging/AA>) using Statistical Parametric Mapping software (SPM12 release 7771; Wellcome Trust center for Neuroimaging, London, UK) and MATLAB (MATLAB version 9.10.0.1739362 (R2021a). Natick, Massachusetts: The MathWorks Inc.). The structural images were rigid-body registered with an MNI template brain, bias corrected, segmented, and warped to match a study-specific anatomical template based on the whole CamCAN Stage 3 sample using the DARTEL procedure (Ashburner, 2007; Taylor et al., 2017), which was subsequently normalized into MNI space. The functional images were then realigned, corrected for slice-time acquisition, rigid-body coregistered to the structural image, transformed to MNI space using the warps and affine transforms from the structural image, smoothed (8 mm FWHM Gaussian kernel), and resliced to 3 × 3 × 3 mm voxels.

The first-level GLM for each participant comprised three neural components per trial: (1) encoding, modeled as an epoch of 2 s duration at onset of the first moving dot pattern; (2) maintenance, modeled as an epoch of 8 s from the onset of the blank screen; and (3) probe, modeled as an epoch of the duration from the onset of the probe till response. Each of these components were modeled separately for the three memory load levels and convolved with the canonical hemodynamic response function (HRF). Two block regressors were added to model the three different runs.

2.6. Head motion

To assess whether there was an interaction between VSTM load and age on head motion, realignment parameters from the preprocessing were used to calculate framewise displacement per scan (Power et al., 2012, 2014). As a within-subject contrast (set size 3 > set size 1) is used for the functional connectivity analyses, only an interaction between set size and age would be a confound for our results. Rotational displacements were converted to millimeters to approximate displacement on the surface. Next, the sum of the absolute values from all six realignment parameters was calculated. This resulting time series for the framewise displacement was then multiplied by the normalized task regressor of interest (for set size 1 and 3 separately) to get the displacement per condition based on the onset times corrected for the hemodynamic response function. The mean of these vectors represents the average framewise

displacement per condition during maintenance. Only the maintenance period was included as the encoding phase only lasted for 2 s (with a TR of 2 s) and only at the time of the presentation of the third stimulus is the set size of that trial clear. The probe phase is not included in our analysis of framewise displacement as none of our connectivity analyses included the probe phase and we wanted to avoid the confound of motion from giving a response. Mixed effects modeling (lme4 package in Rstudio) was used to analyze the effects of load, age, and their interaction on head motion. Subject was the random effect in the model, load and age were fixed effects. Head motion appears to be especially problematic in resting state designs, compared to task-based designs (Huijbers et al., 2017). Nevertheless, subjects with head motion greater than 2SD above the group mean were excluded from the functional connectivity analyses.

2.7. Correlational PPI

Whole-brain functional connectivity matrices were estimated for the contrast set size 3 > set size 1, for each subject by using a correlational psychophysiological interaction (cPPI) approach as implemented by the cPPI toolbox (Fornito et al., 2012; Friston et al., 1997). Since we had no a priori predictions about directionality we used cPPI which is based on partial correlations between ROIs to isolate task-related changes in functional coupling between regions, resulting in symmetrical connectivity matrices. This avoids the arbitrary distinction between seed and target as is required in traditional PPI (Wang et al., 2018). The cPPI method has recently been used in other studies to examine effects of set size (Davis et al., 2018; Crowell et al., 2020). We obtained connectivity terms for 100 ROIs corresponding to the cortical Schaefer parcellation (Schaefer et al., 2018; in line with Heffernan et al., 2021; Pervaiz et al., 2020; Rieck et al., 2021). The ROIs were sorted into seven networks from Yeo et al. (2011): visual, somatomotor, dorsal attention, ventral attention, limbic, frontoparietal, and default mode. As the “limbic network” only consisted of the orbitofrontal cortex and temporal pole, we used the term OFC-TP to refer to this network for the sake of clarity. Within- and between-network connectivity was defined based on these networks. The PPI terms were obtained by modeling the task effects, the physiological signal, and their interaction following the manual of the cPPI toolbox (Fornito et al., 2012). For each participant, average time series over all voxels were extracted from each ROI based on the first-level GLM design matrix using an F-contrast that included all task regressors for the effect of interest and no threshold (following the steps of the SPM12 manual). In the cPPI toolbox, for each pair of ROIs, the HRF was deconvolved from the time courses of both ROIs using the same code as implemented in SPM (in `spm_peb_ppi.m`). Deconvolution is recommended as interactions between task and brain signals occur at the neural level rather than in the hemodynamic response (Gitelman et al., 2003). Both deconvolved time courses were multiplied by the unconvolved task regressor for the contrast of interest (set size 3 > set size 1) to generate the deconvolved PPI terms. Note that the contrast of interest is set size 3 > set size 1 (in line with Nagel et al., 2011); this is not a comparison to an implicit baseline. The PPI terms were reconvolved with the HRF. Finally, the partial correlation between these two PPI terms was computed adjusting for: the raw time courses of the two ROIs, all task regressors (encoding, maintenance, and probe for set sizes 1, 2, and 3) except for those creating the contrast of interest, the time-courses of the remaining ROIs, and nuisance signals. Thirty-two nuisance regressors were added, representing six motion parameters estimated in the realignment stage, time-series from white matter tissue and cerebrospinal fluid (CSF), their derivatives, plus quadratic functions of those 16 parameters. Masks for white matter and CSF were based on the FieldMap toolbox in SPM12 (probability maps were thresholded at 0.8 and 0.5 respectively, based on visual inspection for no overlap with the Schaefer cortical atlas). This was done for all ROI pairs, resulting in a 100 × 100 symmetrical partial correlation matrix for each subject for encoding and maintenance separately. The resulting matrices express load-modulated

functional connectivity strength for the contrast set size 3 > set size 1, in this manuscript referred to as an increase (or decrease) in connectivity strength with increasing load.

2.8. Group-level analysis

Group-level analysis on the cPPI matrices were conducted using the Network Based Statistics (NBS) toolbox (Zalesky et al., 2010). We first ran, for the partial connectivity between each pair of ROIs, a one-sample *t*-test for the effect of task load for the contrast set size 3 > set size 1, with a threshold of $t = 0.5$ (this value is based on partial correlations in the connectivity matrix) to identify which ROI pairs showed a medium to large effect of memory load. Subsequently, per ROI pair, we ran three GLMs, in a stepwise manner, to assess the relationship between age, performance, and the age-by-performance interaction and brain-wide load-modulated connectivity (Capogna et al., 2022). For performance we used response error from set size 3 (in line with Nagel et al., 2011), as using the difference score between set sizes 3 and 1 would be noisier and performance at set size 3 is most sensitive to individual differences. As supplementary analysis (S3) we included the results based on the difference score. Performance and age were mean-centered before calculating the interaction term. In the first model we tested the effect of age on the load-dependent changes in connectivity (cPPI ~ age). In the second model we added performance as a regressor to test the effect of performance on modulation of connectivity by load, while controlling for age (cPPI ~ age + performance). The third model tested for the interaction between age and performance (cPPI ~ age * performance). The GLM models are based on a design matrix that contains regressors for age, performance, and age × performance, and a contrast vector for the statistical test (separate for a positive and negative effect). As effect sizes of associations between neural measures and cognition are small (Marek et al., 2022) and our whole-brain approach necessitated correction for many tests, we added an exploratory analysis by repeating the analyses of the second and third model restricted to network pairs where load-modulated functional connectivity was strongest in either the encoding or maintenance connectivity matrix.

Both the one-sample *t*-test and the three GLM models were controlled for the family-wise error rate (FWE) using the NBS toolbox. The first step in NBS is mass univariate testing at every connection in the connectivity matrix. In the second step, connections with a value exceeding a threshold are selected. For the one-sample *t*-test of the main effect of load, the threshold is $t = 0.5$, which corresponds to a medium to large effect, for the GLMs testing the effect of age, performance, and their interaction, the threshold is $t = 2.365$ (corresponding to a *p*-value of 0.01 with a DF of 100). The third step is to identify topological clusters among the connections that exceeded the threshold. In the final step, an FWE-corrected *p*-value is computed based on 5000 permutations (Freedman and Lane, 1983). For each permutation the first three steps are repeated. Graph component significance is at $p < .025$ (2 comparisons, positive and negative contrast). Results are reported as the number of significant edges. NBS has been found to offer more power than FDR correction for identifying distributed networks of edges (Fornito et al., 2013) and has been used to identify functional networks associated with memory performance and age before (Capogna et al., 2022). BrainNet Viewer was used for visualization of networks on a 3D-brain (Xia et al., 2013, <http://www.nitrc.org/projects/bnv/>).

3. Results

3.1. Behavioral results

Using mixed linear models, we analyzed the effects of age and VSTM load on response error. The first model contained only subject as random effect and confirmed that accuracy across memory loads was correlated within individuals (ICC = 0.40). Adding age to the model improved the model fit ($\chi^2(1)=28.53, p < .001$), as did load ($\chi^2(1)=173.14, p < .001$),

and the age × load interaction ($\chi^2(1)=41.58, p < .001$). Pairwise contrasts showed that response error on set size 1 was different from that of set size 2 and set size 3, and there was a difference between set size 2 and set size 3 ($p < .001$, Fig. 2A). The positive correlation between age and response error is significant at all loads (Table 2), but as can be seen in Fig. 2B, the effect of age was more pronounced at higher loads. As the boxplot identified one outlier on response error at set size 3 (i.e., our outcome measure of interest for fMRI analyses), we reran all analyses excluding this subject (age 54, female). This did not lead to different results.

To evaluate the contribution of different sources of error, we applied a three-component mixture model (Bays et al., 2009). Most of these measures correlated significantly with age (Table 2, Fig. 2C-F), except for estimated item capacity at set size 1, guess rate at set size 1 and 2, and proportion of non-target errors at set size 2 (adjusted alpha $0.05 / 14 = 0.0036$; note that non-target errors are not possible for set size 1). A decrease in precision, and an increase in guess rate and non-target errors, all contribute to a higher response error with increasing age at a high memory load. However, as already mentioned, increasing age was associated with a lower model fit at all three loads and thus, we decided to use raw response error in relating performance to functional connectivity.

3.2. Head motion

Using mixed linear models, we analyzed the effects of age and VSTM load on head motion to make sure that our functional connectivity results are not confounded by differences in head motion. The first model contained age as fixed effect and showed that adding age to a model with only subjects (random effect) improved the model fit ($\chi^2(1)=36.35, p < .001$). In the second model load was added, but this did not improve the model fit ($\chi^2(1)=1.58, p > .05$), and neither did adding the age × load interaction in the third model ($\chi^2(1)=2.58, p > .05$). Head motion was comparable for the different conditions and there was no interaction effect, so it is unlikely that the observed age difference in load-modulated connectivity is the result of differential head motion across conditions with age. With increasing age, head motion increased (tested continuously, but to illustrate, mean framewise displacement was 0.21, 0.26, and 0.45, for young, middle, and old adults respectively, based on the age groups of Table 1). Therefore, we excluded ten subjects based on mean framewise displacement of higher than 2SD above the mean of the total sample (resulting in a mean framewise displacement per group of 0.21, 0.26, and 0.32, respectively). All further analyses report on a final sample of 101 subjects. Exclusion of these 10 subjects did not affect any of the results below.

3.3. Whole-brain functional connectivity

Calculating whole-brain load-modulated functional connectivity for the contrast of load (set size 3 > set size 1), we assessed the effect of memory load, and how this modulation by load is associated with age, performance, and their interaction. Results in the main manuscript are based on the 100-region-parcellation. To examine the impact of different levels of coarseness of brain atlases on functional connectivity estimates we additionally report results for the Schaefer 200- and 400-region-parcellations, which largely yielded a similar pattern of results (see supplementary materials, S4).

3.3.1. Main effect of load

Load-modulated functional connectivity strengthened with increased positive connections at higher load both within and between networks (Fig. 3A and D). An NBS-based one-sample *t*-test with a threshold of $r > 0.5$ was applied to identify edges that showed a medium to large effect of load (FWE-corrected, number of significant edges for encoding = 500, and maintenance = 724, Fig. 3B and E). The strongest

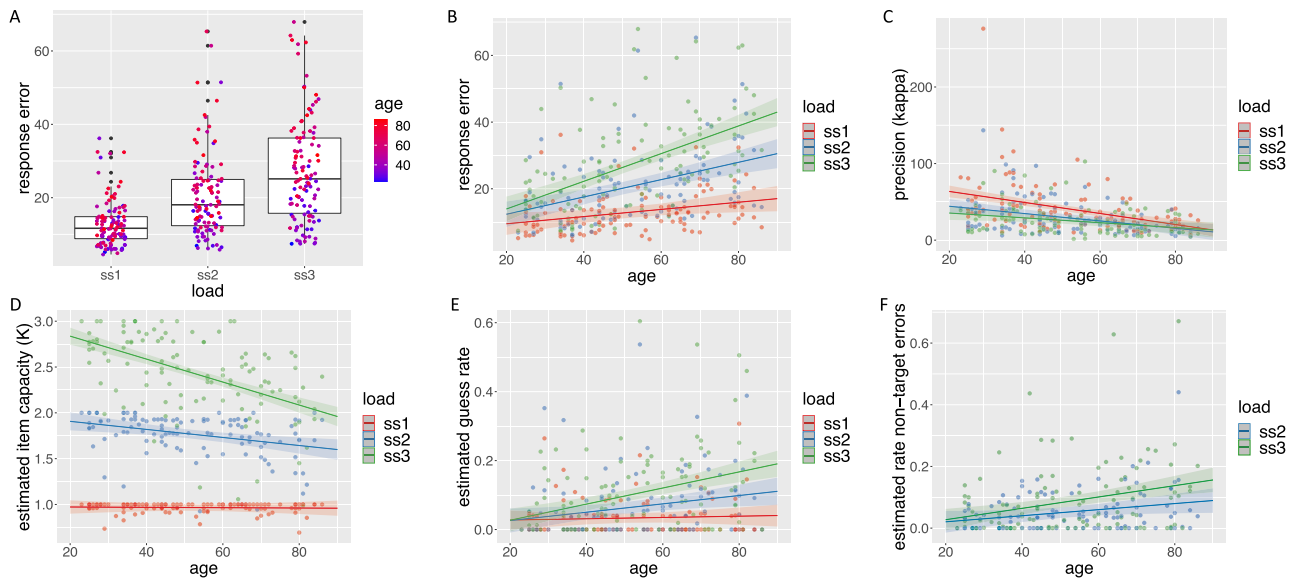


Fig. 2. Effects of memory load and age on VSTM performance. A) response error shown as boxplot per load with age on a color scale from young in blue to old in red. In panels B to F, the linear regression line for the effect of age is shown per set size, along with its 95% confidence interval, for the B) response error, C) precision (kappa), D) item capacity (K), E) estimated guess rate, and F) estimated rate of non-target errors.

Table 2
Correlations between VSTM performance measures and age per memory load.

Measure	Load 1 (<i>r</i> , <i>p</i>)		Load 2 (<i>r</i> , <i>p</i>)		Load 3 (<i>r</i> , <i>p</i>)	
Response error	.30	.001	.41	< 0.001	.52	< 0.001
Precision (kappa)	−0.38	< 0.001	−0.38	< 0.001	−0.30	.002
Item capacity (K)	−0.06	.537	−0.35	< 0.001	−0.51	< 0.001
Proportion of guesses (pG)	.06	.537	.23	.016	.34	< 0.001
Proportion of non-target errors (pNT)	-	-	0.27	.004	.28	.003
Model fit (LL)	−0.3	< 0.001	−0.46	< 0.001	−0.53	< 0.001

Note: significant results in bold.

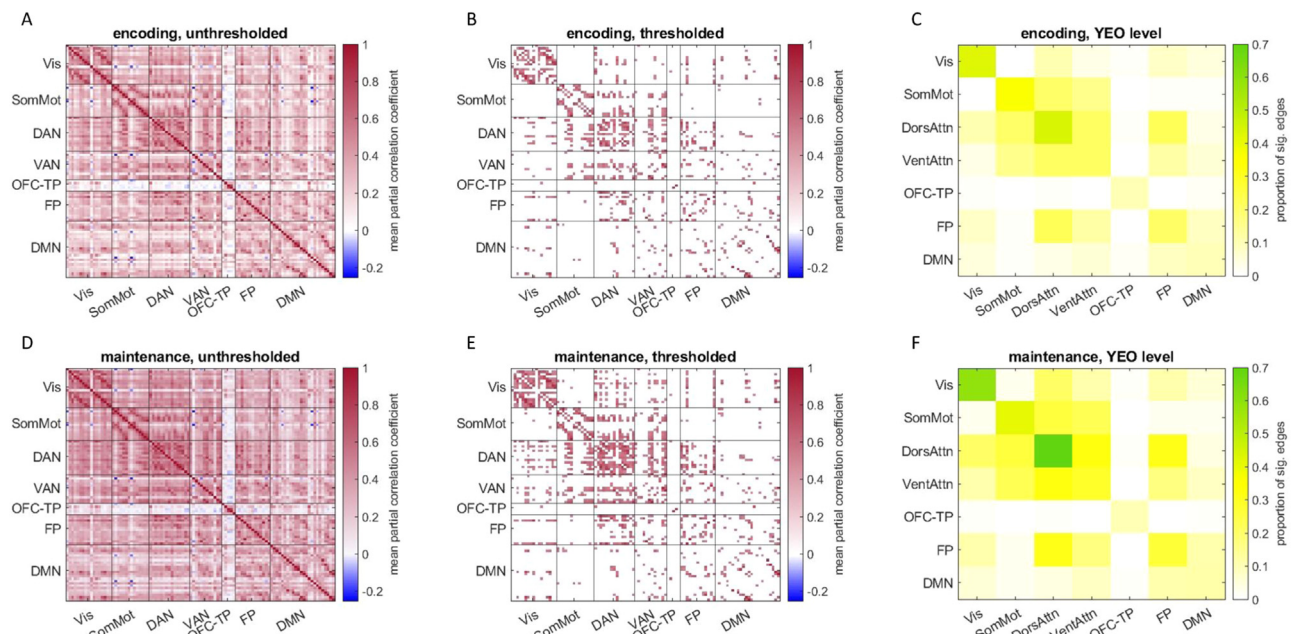


Fig. 3. Partial correlation coefficient matrices for mean encoding (A and B) and maintenance (D and E) connectivity for the contrast set size 3 > set size 1. ROIs are sorted into seven networks from Yeo et al. (2011): visual (Vis), somatomotor (SomMot), dorsal attention (DAN), ventral attention (VAN), orbitofrontal-temporal pole (OFC-TP), frontoparietal (FP), and default mode (DMN). Red colors indicate a positive partial correlation, while blue colors indicate a negative partial correlation. Panels A and D show the unthresholded matrices. Panels B and E show the results of a one-sample *t*-test for a medium to large effect size (thresholded $r > 0.5$, FWE-corrected $p < .025$). Panels C and F show the proportion of edges that survive thresholding per network cell, with green indicating a higher proportion.

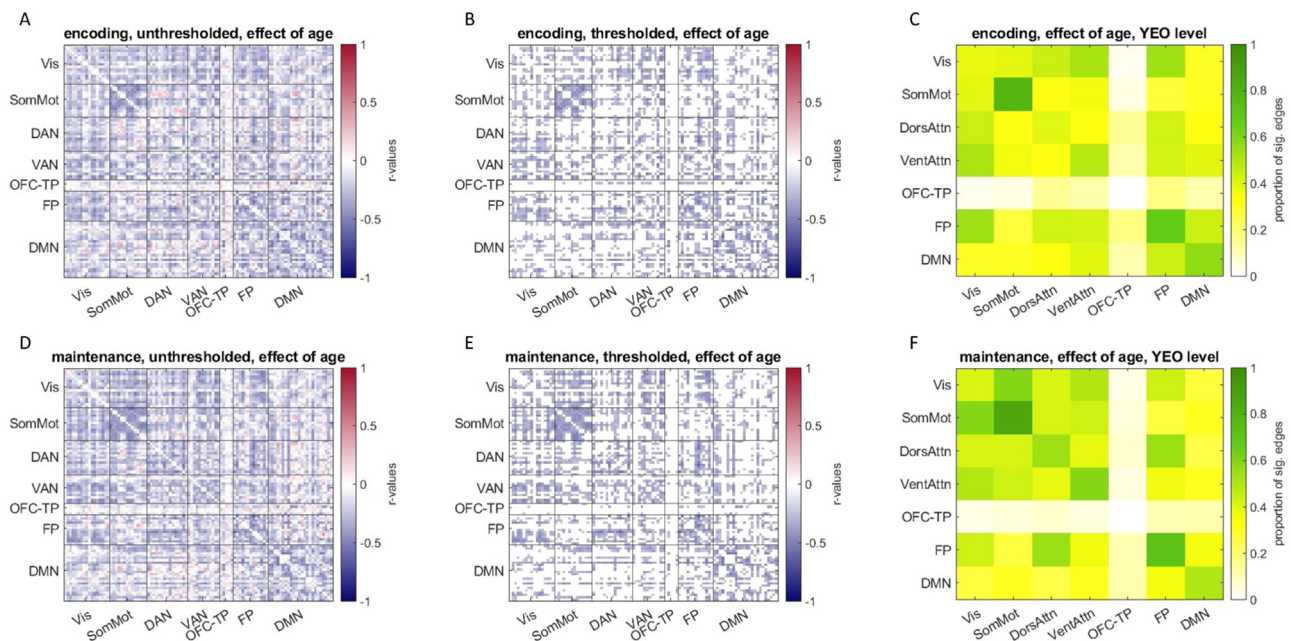


Fig. 4. Correlation matrices for encoding (A and B) and maintenance (D and E) for the correlation between age and load-modulated connectivity strength. Red colors indicate a positive correlation, while blue colors indicate a negative correlation. Panels A and D show the unthresholded matrices. Panels B and E show only edges where the effect of age is significant based on an NBS based t -test (FWE-corrected, $p < .025$). Panels C and F show the proportion of edges that show a significant effect of age per network cell, with green indicating a higher proportion.

within-network connectivity was in the dorsal attention network followed by the visual network, and to a lesser extent the somatomotor, ventral attention, and frontoparietal networks (see Fig. 3C and F, which show the proportion of edges that survive thresholding per network). Between-network connectivity increased primarily between the somatomotor, dorsal attention, and ventral attention networks, and between the dorsal attention and the frontoparietal networks. The pattern of high positive correlations for the contrast of set size 3 > set size 1, was highly comparable for encoding and maintenance.¹

3.3.2. Effect of age

With increasing age, there was a significant decrease in load-modulated connectivity (weakening of positive correlations with increasing task load) for the contrast of high versus low memory load throughout the brain. Fig. 4A and D show the correlation between age and load-modulated connectivity for each ROI pair (number of significant edges based on NBS for encoding = 1871 and maintenance = 1849, Fig. 4B and E). Age-related declines were most pronounced within the somatomotor, frontoparietal, and default mode networks, and between the visual network and the ventral attention and frontoparietal networks (Figs. 4C and 4F show the proportion of significant edges per network pair). During encoding there was additionally a pronounced decline in load-modulated functional connectivity strength with age between the frontoparietal and visual and default mode networks. Dur-

¹ The effect of load may seem stronger during the maintenance period compared to the encoding period. This may be partly due to the difference in duration between encoding and maintenance (2 versus 8 s, respectively, see supplementary materials S1., Figures S1.1 and 1.2). The pattern of load-modulated connectivity is highly similar to that of encoding in the last two seconds of the maintenance interval suggesting that it is not just spillover effects. Furthermore, when analyzing the encoding and maintenance phases together, the overall connectivity pattern remains the same, with the number of significant edges (585 for the combined analysis) in between that of encoding and maintenance separately (500 and 724, respectively, Figure S1.3). This suggests that the stronger load-modulated connectivity during maintenance is not purely an artefact caused by the difference in timing.

ing maintenance the decline in load-modulated functional connectivity was more pronounced within the dorsal and ventral attention network, and between the visual network and the somatomotor and ventral attention networks, and the dorsal attention and frontoparietal networks. There were no significant positive effects of age (graph component FWE-corrected $p = .23$ and $p = .22$ for encoding and maintenance respectively); that is, no connections showed a load-dependent increase in connectivity that was stronger in older compared to younger adults. Older adults do still show positive load-modulated functional connectivity but to a lesser extent compared to younger adults, as illustrated in Fig. 5 for average within-network connectivity by age group (young: 20–40; middle: 41–60; old: older than 60 years).

3.3.3. Effect of performance

Running the model (predicting connectivity from performance, controlling for age) on the full matrices for encoding and maintenance did not result in any effects of performance that survived correction (see supplementary materials S2.1 for whole brain unthresholded and non-significant thresholded results). We ran an exploratory analysis restricted to the two networks where load-modulated connectivity strength was highest, the visual and dorsal attention networks (Fig. 3C and F). Unthresholded results of these two networks showed positive and negative associations between performance and connectivity within the visual network, and negative associations in the dorsal attention network (Fig. 6A and D). After NBS thresholding, lower response error (i.e., better performance) was associated with an increase in load-modulated connectivity strength within the dorsal attention network, controlling for the effect of age (number of significant edges for encoding = 22, and maintenance = 32, Fig. 6B and E; scatterplot of the relationship between average load-modulated connectivity in the dorsal attention network and performance controlled for age in supplementary materials S2, Figure S2.2). The effect was more left lateralized during encoding compared to during the maintenance phase (Fig. 6C and F). Using the difference score of response error (set size 3 - set size 1) resulted in a similar pattern of connectivity strength in the unthresholded results. In this analysis, none of the edges survived FWE correction (supplementary materials S3).

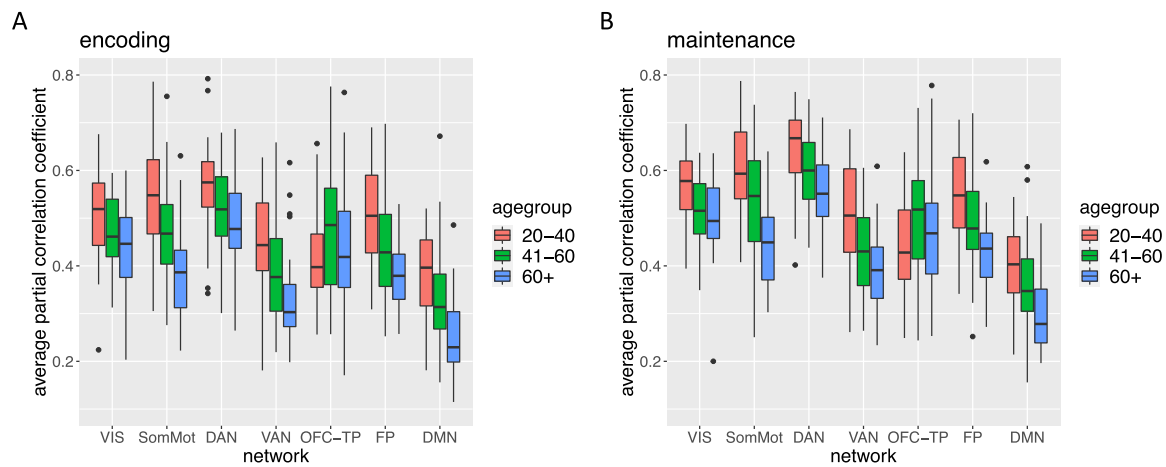


Fig. 5. Average load-modulated connectivity strength (partial correlation coefficient) within each network per age group. Participants are split into young (20–40 years old), middle (41–60 years old), and older (60+) adults for illustrative purposes. Left during encoding (A), right during maintenance (B). The lower and upper ends of the colored boxes correspond to the first and third quartiles with the black line indicating the median. The error bars are set at $1.5 \times$ the inter-quartile range. Data points that exceed this value are indicated by the black dots.

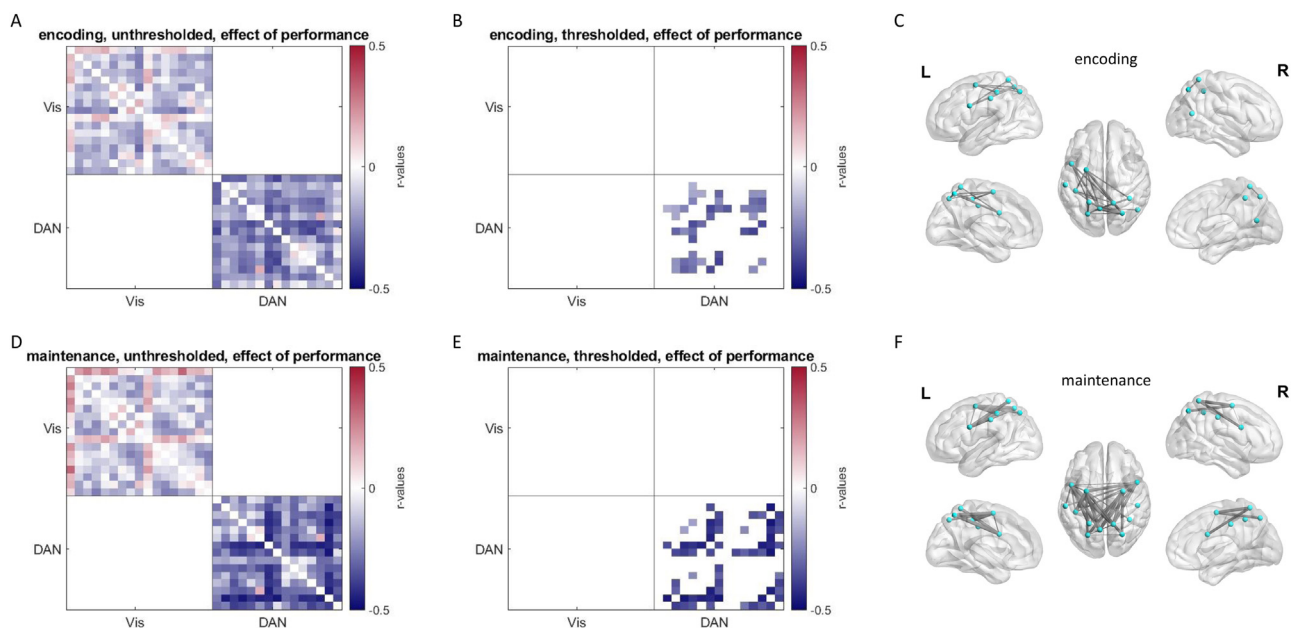


Fig. 6. Results of an exploratory analyses of the effect of performance in restricted networks. Correlation matrices for encoding (A and B) and maintenance (D and E) for the correlation between performance (response error at set size 3) and load-modulated connectivity strength in the visual and dorsal attention networks. Red colors indicate a positive correlation, while blue colors indicate a negative correlation. Panels A and D show the unthresholded matrices. Panels B and E show only edges where the effect of performance is significant based on an NBS based t -test (FWE-corrected, $p < .025$). Panels C and F show the significant edges overlaid to a 3D-brain.

3.3.4. Interaction effect of age \times performance

Last, we tested the interaction effect of age \times performance over all edges and restricted to the visual and dorsal attention networks. This yielded no significant results.

4. Discussion

In this study, we found that load-modulated connectivity strength increased in response to VSTM load, especially within the dorsal attention and visual networks. Age was associated with reduced load-modulated connectivity strength across the cortex, especially within the frontoparietal and somatomotor networks. Finally, while there were no significant associations between performance and load-modulated connectivity at the whole-brain level, exploratory analyses within the networks most sensitive to task load suggested that better performance may be related

to load-modulated connectivity in the dorsal attention network, in an age-invariant way. As we discuss below, our results provide additional support to the sensory recruitment model of working memory and lend further support to the CRUNCH hypothesis of neurocognitive aging.

4.1. VSTM load-modulated functional connectivity

Load-modulated functional connectivity effects were most pronounced within the dorsal attention and visual networks, both during encoding and maintenance. According to the sensory recruitment account of working memory (e.g., D'Esposito and Postle, 2015), the same cortical regions involved in perceptual processing are recruited for maintenance during working memory. Compelling evidence for this account derives from studies using MVPA that show that the visual cortex supports representations of visual features during the delay period,

despite mean activity in the visual cortex dropping to baseline levels during that same period (reviewed in D'Esposito and Postle, 2015; and in Teng and Postle, 2021; Emrich et al., 2013). In contrast, the intraparietal sulcus shows load-dependent delay-period activity, but working memory content cannot be readily decoded from this region at higher loads (Emrich et al., 2013). Based on delay-period activity and MVPA studies, the parietal cortex has been associated with attentional control needed for context-binding, prioritization of items, and resistance to distraction (e.g., Gosseries et al., 2018; Teng and Postle, 2021). Our results contribute to this literature by showing that functional connectivity in both the visual and dorsal attention networks is modulated by working memory load during both encoding and maintenance (see also Soreq et al., 2019, for similar findings with young adults). It is important to note that an increase in load-modulated connectivity strength within the visual network cannot be easily explained by more visual input, as the amount of visual input and average motion per item was matched at all three set sizes.

Another key network in the sensory recruitment framework is the frontoparietal network which has been associated with top-down control and abstract representations (Scimeca et al., 2018). Activation studies have shown increased activity in frontoparietal regions related to working memory load (e.g., Manoach et al., 1997; Rottschy et al., 2012; Zuo et al., 2019). In contrast, functional connectivity studies report mixed results, some reporting increased connectivity within the frontoparietal network with increasing load (Liang et al., 2016; Pongpipat et al., 2021), while others report an increase relative to baseline but no additional modulation by load (Soreq et al., 2019; Zuo et al., 2019). Most of these studies used variations of the n-back task, while the current paradigm manipulated the number of directions being held in mind, and we found only moderate load-modulated connectivity strength within the frontoparietal network for the contrast of set size 3 > set size 1. Functional connectivity within the frontoparietal network may reflect the need for top-down control, which likely differs more moving from baseline to task than it does moving from lower to higher loads. This is an important question for future research.

Strikingly, we found pronounced load-modulated connectivity within the somatomotor network. Changes in connectivity specifically within the supplementary motor area have been associated with working memory load effects (Nagel et al., 2011; Steffener et al., 2012). In contrast, Eryilmaz et al. (2020) examined connectivity during a Sternberg short-term memory task with letters, but did not observe a load effect within the somatomotor network. Load-modulation in the somatomotor network might be related to the spatial aspect of the task used here. Participants likely maintained a spatial representation of each motion direction in order to respond correctly. Other work also suggests a link between working memory and motor planning; for instance, locations held in working memory can affect eye movements (Theeuwes et al., 2015). Connectivity within the somatomotor network has been associated with prospective motor coding during a spatial delayed recall task (Purg et al., 2022), with greater connectivity seen when there is a predictable relation between the motor response and the location of the memorized target (motor response from center to target > motor response from random location to target). Prospective motor coding can be used to execute a spatial response but also to support rehearsal and evaluate a memory probe (Postle, 2006). To stress the coupling between sensory maintenance and motor intention, D'Esposito and Postle (2015) argue for the use of the label "sensorimotor recruitment" instead of the more common label "sensory recruitment" models.

In addition to these *within* network changes, we also observed several *between* network changes, including between the dorsal attention, ventral attention, and somatomotor networks, and between the dorsal attention and frontoparietal networks. The functions of these networks include visuospatial attention, processing salience, somatosensory and motor processing, and working memory and inhibition (respectively; reviewed in Uddin et al., 2019). Higher working memory load plausibly results in stronger connectivity between these networks as more top-down

control is required. Interestingly, load-modulated connectivity strength between the visual and dorsal attention networks was limited (in line with Eryilmaz et al., 2020). It might be that functional connectivity between these networks is consistent across different memory loads. A second possible explanation is that between-network connectivity is only modulated by load during the response phase when a comparison is made between the memorized items to select a response (Xu, 2017).

The main discrepancy between our results and previous studies is the limited effect of working memory load on default mode network connectivity (Eryilmaz et al., 2020; Liang et al., 2016; Pongpipat et al., 2021). Pongpipat et al. (2021) reported an increase in negative connectivity between the frontoparietal and default mode network as load increased. This effect was stronger when comparing task with a control condition than for the linear effect of load. Further, a study by Zuo et al. (2019), showed that while the default mode network was strongly associated with performing an N-back, this was to a similar extent in the contrasts of baseline vs 0-back, and 0-back vs 2-back. Possibly our lowest load condition (which required remembering a single direction while ignoring rotating dots in two other colors) was more demanding than that of other studies using, for example, a 0-back task. It might be that functional connectivity of the default network (much like the frontoparietal network) is mainly modulated by the presence or absence of a task.

4.2. Age effects on load-modulated functional connectivity

Older age in our study was related to greater response error, which at the highest load, the mixture model suggests was due to lower precision, lower item capacity, and a higher rate of non-target errors and guess responses. Lower precision and item capacity suggests an age-related decline in the ability to maintain multiple high-resolution representations, while a higher rate of non-target errors and guesses might relate to a decline in inhibition and attentional control.

We found negative effects of age on the modulation of functional connectivity by load in widespread networks throughout the cortex except for the orbitofrontal and temporal pole ROIs. Older adults showed less increase in load-modulated connectivity strength as task demands increased, as has been reported in activation studies (Cappell et al., 2010; Heinzel et al., 2017; Kaup et al., 2014; Kennedy et al., 2017). Reduced connectivity with age in the default mode network is a consistent finding in the literature across both task-based and resting state studies (Andrews-Hanna et al., 2007; Bethlehem et al., 2020; Damoiseaux et al., 2008; Geerligs et al., 2012, 2015; Grady et al., 2010; Sambataro et al., 2010; Samu et al., 2017; Tsvetanov et al., 2016), one that we replicate here. Our study additionally shows a novel finding of decreased load-modulated connectivity with increasing age within the somatomotor, dorsal attention, ventral attention, and frontoparietal networks, and between the visual network and other networks and between the dorsal attention and frontoparietal networks. Decreases in within and between-network connectivity across the cortex with increasing age have been reported in a language task (Zhang et al., 2021) and within networks supporting higher level cognitive functions during resting-state (Geerligs et al., 2015).

One possible explanation for reduced modulation in network functional connectivity by working memory load in older adults is that they may already be close to ceiling in terms of neural resources at set size one. We found that older adults do still show positive load-modulated connectivity (Fig. 5), but to a lesser extent than younger adults. At the same time, the difference in performance between a lower and higher set size is much larger in older adults than it is in young (Fig. 2b). This suggests that younger adults increase functional connectivity moving from set size 1 to 3 in response to increased task demands, resulting in only a slight decrease in performance. Older adults show less of an increase in connectivity strength with increasing demands and their performance declined more. In a previous study, older adults showed a large change in functional connectivity moving from baseline to a simple task, while connectivity was comparable when moving from a simple task to a more

demanding task; in contrast, younger adults showed the largest change from a simple to a more demanding task (Geerligs et al., 2013). According to the CRUNCH model (Reuter-Lorenz and Cappell, 2008), older adults need to recruit more neural resources at lower levels of demand compared to younger adults. This has the consequence that they reach the ceiling of their neural resources at a lower task load (Dørum et al., 2017). Our results are compatible with CRUNCH, if older adults were already expending close to maximum resources at set size one of our task, they would not show much further increase with additional task load.

The resting-state literature describes decreased segregation of functional networks with increasing age, with weaker within-network connectivity and greater connectivity between networks (Chan et al., 2014; Geerligs et al., 2012, 2015). Our result of weaker positive load-modulated connectivity strength with increasing age within and between all networks except for the orbitofrontal-temporal pole network, show that findings from resting-state data do not easily translate to task-modulated connectivity. This stresses the relevance of a task-based approach for understanding how age affects cognitive functioning (Campbell and Schacter, 2016). The relevance of task-based approaches has also been stressed (e.g., by Rosenberg and Finn, 2022) in response to Marek et al. (2022), who suggested larger sample sizes are needed to relate resting state connectivity to behavioral performance.

4.3. Performance effects on load-modulated functional connectivity

Effects of performance on neural measures are much smaller than those of age. When testing the relationship between performance and connectivity across the whole brain, controlling for age, the effects of performance did not survive correction for FWE. As we hypothesized that the effects of performance would be most pronounced in the networks that showed the strongest effect of task load, we conducted an exploratory analysis restricted to those networks. By basing our exploratory analysis on whole-brain connectivity results, we made a data-driven choice in our selection of networks to further examine in relation to performance. Previous studies have often based their selection of ROIs on activation results which has led to a strong focus on the frontoparietal network; however, in our connectivity results, the frontoparietal network was only moderately modulated by task load. Results from our exploratory analysis suggest that while both the visual and dorsal attentional networks are highly sensitive to load, individuals with a lower response error (i.e., better performance) are those who show a higher load-modulated functional connectivity strength only within the dorsal attention network (controlling for age).

The dorsal attention network is primarily associated with visuospatial attention. Various models of memory have indicated attention as crucial for working memory (Baddeley and Hitch, 1974; Cowan, 1988). There is a large body of research which suggests that individual differences in working memory performance are determined for a large part by variability in attentional control (for a review, see Erikson et al., 2015). As we did not modulate attention, we cannot determine whether the involvement of the dorsal attention network means that attention is the mechanism causing the differences in performance in our study. It is interesting that load-modulated connectivity in the dorsal attention network might be related to performance, given the mixed evidence on decoding the content of working memory from areas like the intraparietal sulcus despite this region showing sustained load-sensitive delay-period activity (Emrich et al., 2013; D'Esposito and Postle, 2015). Previous studies have also associated task-related increases in functional connectivity with better performance (between the premotor cortex and the dorsolateral prefrontal cortex, Nagel et al., 2011; between the supplementary motor areas, cingulate, precuneus and some frontal areas, Steffener et al., 2012), though in some cases in an age-dependent manner (within a frontoparietal network, Burianova et al., 2015; negative connectivity between the frontoparietal and default mode network, Pongpipat et al., 2021). These studies used a priori selection of ROIs

or a network based on activation to study the effects of performance. We used our connectivity results to select networks for our exploratory analysis as task-modulated connectivity not only involves task-active regions but also regions that are not activated or deactivated by the task (Di and Biswal, 2019). This might explain the difference in results. We found no significant interaction effect between age and performance on load-modulated connectivity.

As the effect of performance was non-significant in our whole-brain analysis, the results from our exploratory analysis should be interpreted with care. Both our main analysis and supplementary analyses using different parcellations suggest opposite effects of performance on load-modulated functional connectivity in the visual and dorsal attention network (see the unthresholded results in Figure S4.4). These exploratory analyses only hint at possible mechanisms. Future studies, preferably in the form of a preregistered report, can use these results for a priori selection of networks to further study the relation between functional connectivity and performance.

4.4. Limitations and methodological remarks

In this study we investigated the modulation of functional connectivity by working memory load. There are many confounds when studying age-related differences in functional connectivity, like head motion (Geerligs et al., 2017), vascular health (Tsvetanov et al., 2020), and motor skill for task-based connectivity. By using a contrast for two different task loads, we obtained a measure that showed the difference within each individual between two conditions. This within-individual measure is less sensitive to between-individual confounds, and demonstrates that the difference in connectivity from low to high load is smaller in older adults. However, this does not give information on whether older adults have higher connectivity strength at low load compared to younger adults, as CRUNCH would predict (discussed above; Reuter-Lorenz and Cappell, 2008), and/or lower connectivity strength at high load. We could not test this here due to our lack of a zero-load condition or a separable resting baseline in the task. Thus, it is important to keep in mind when interpreting these findings that an ROI or network pair that does not show a modulation by task load might still change in strength of connectivity between rest and task. Furthermore, the modulation in connectivity strength reported here is only based on the contrast of set size 3 > set size 1. This does not exclude the possibility that the relationship with load is U-shaped or that findings depend on these specific loads.

A second limitation is that the patterns of connectivity during encoding and maintenance cannot fully be dissociated. The encoding period always preceded maintenance, and as is typical for most working memory paradigms, the delay-period had a fixed length without jitter (Crowell et al., 2020). We included regressors for the events that we were not interested in for each specific contrast (e.g., regressors for the encoding and response periods when examining the maintenance phase), but this had no influence on the connectivity matrices (i.e., partial correlations did not change). Thus, in the current design we cannot exclude the possibility of some contamination from the encoding period during maintenance. A related issue typical for working memory task designs, is the difference in duration of the encoding and maintenance period. A longer period might have a better signal-to-noise ratio and therefore, result in stronger effects. However, analyzing the encoding and maintenance phase together did not lead to stronger load-modulated connectivity, which suggests that the stronger load-modulated connectivity during maintenance is not only an artifact of different timing and may reflect a true increase in load-modulated connectivity when maintaining information in working memory. Supplementary analyses showed that the stronger effect held up for all four 2 s windows of the maintenance interval. A closer look at the effects of age and performance on connectivity patterns suggests that there are slightly different patterns of connectivity during encoding and maintenance. Specifically, stronger effects of age between the frontoparietal and the visual and de-

fault mode network were observed during encoding. This suggests that the design is to some extent able to detect differences between the two task periods, and that the highly similar patterns are not just due to spill-over effects.

Third, the advantage of a whole-brain approach is that we were able to demonstrate how widespread the effect of age is on load-modulated functional connectivity. However, it does come at the cost of multiple comparisons. Whereas effects of age were clearly detectable, the effects of cognition on neural signals are often weaker (see for a review on brain-wide association studies Marek et al., 2022), made worse here by the need to control for age. Therefore, we focused on the effect of performance only in the network cells that showed the strongest effect of task load. This exploratory analysis suggests that an increase in connectivity strength within the dorsal attention network might be related to better performance, while controlling for age. Our whole brain results that did not survive correction for FWE pointed in the same direction.

Nevertheless, our study had several strengths which include a large, adult lifespan sample, a highly sensitive measure for working memory with a continuous response, a separate encoding and maintenance phase, the same amount of visual input per trial across loads, a whole-brain approach, a within-subject connectivity measure based on the contrast of high versus low working memory load, and replication of our main findings using different parcellation schemes. Future studies need to validate our findings using interventional and longitudinal studies.

5. Conclusion

The current study confirms that functional connectivity strengthens in response to increasing working memory load. This was especially true in the dorsal attention and visual networks during encoding and maintenance. The similarity between patterns of connectivity during encoding and maintenance and the strong load modulation in the visual network provide additional support for the sensory recruitment model of working memory. A novel finding was that VSTM load-modulated functional connectivity decreased with age across most of the cortex both within and between networks, possibly because older adults are already close to ceiling in terms of neural resources at the lowest load. Our exploratory analyses give suggestions for future research to further investigate the relation between working memory performance and functional connectivity in the visual and dorsal attention networks.

Data availability

Derived neuroimaging data, behavioral data, and code are available in the Open Science Framework at <https://osf.io/w3s74/>. Raw data can be requested from the Cam-CAN access website (<https://camcan-archive.mrc-cbu.cam.ac.uk/dataaccess/>). For a complete description of Cam-CAN data and pipelines, see Shafto et al. (2014) and Taylor et al. (2017).

Declaration of Competing Interest

The authors declare no conflict of interests.

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Credit authorship contribution statement

Selma Lugtmeijer: Conceptualization, Data curation, Formal analysis, Methodology, Project administration, Visualization, Writing – original draft. **Linda Geerligs:** Conceptualization, Supervision, Writing – review & editing. **Kamen A. Tsvetanov:** Methodology, Writing – review & editing. **Daniel J. Mitchell:** Conceptualization, Data curation, Formal analysis, Methodology, Software, Writing – review & editing.

Cam-CAN: Investigation, Data curation. **Karen L. Campbell:** Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:[10.1016/j.neuroimage.2023.119982](https://doi.org/10.1016/j.neuroimage.2023.119982).

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