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Openness to Experience is associated with neural and performance measures of memory in older adults

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Abstract

Age-related decline in episodic memory performance is a well-replicated finding across numerous studies. Recent studies focusing on aging and individual differences found that the Big Five personality trait Openness to Experience (hereafter: Openness) is associated with better episodic memory performance in older adults, but the associated neural mechanisms are largely unclear. Here, we investigated the relationship between Openness and memory network function in a sample of 352 participants (143 older adults, 50-80 years; 209 young adults, 18-35 years). Participants underwent functional magnetic resonance imaging (fMRI) during a visual memory encoding task. Functional memory brain-network integrity was assessed using the similarity of activations during memory encoding (SAME) scores, which reflect the similarity of a participant's memory network activity compared to prototypical fMRI activity patterns of young adults. Openness was assessed using the NEO Five-Factor Inventory. Older vs young adults showed lower memory performance and higher deviation of fMRI activity patterns (i.e. lower SAME scores). Specifically in older adults, high Openness was associated with better memory performance, and mediation analysis showed that this relationship was partially mediated by higher SAME scores. Our results suggest that trait Openness may constitute a protective factor in cognitive aging by better preservation of the brain's memory network.

Keywords: Openness to Experience; episodic memory; aging; fMRI; subsequent memory effect

Introduction

Episodic memory is often defined as the ability to encode and recall information about experienced previous events (Baddeley et al., 2001; Tulving, 2002). A decline in episodic memory performance has been widely characterized as a hallmark symptom of a number of age-related neurological conditions, particularly Alzheimer's disease (AD; Tromp et al., 2015; El Haj et al., 2016), but it has also been associated with neurocognitive aging in healthy adults (Cansino, 2009; Grady, 2012; Salthouse, 2010). Despite the age-related episodic memory decline, there is considerable interindividual variability in memory performance in older adults, presumably due to protective factors for age-related neurocognitive declines (Cansino, 2009), such as physical activity (Lee et al., 2010; Bherer et al., 2013), education (Hendrie et al., 2006) and intelligence capacities (Bråthen et al., 2021). At the personality trait level, the Big Five trait Openness to Experience (hereafter: Openness) has been associated with episodic memory performance (Gregory et al., 2010; Terry et al., 2013; Curtis et al., 2015; Luchetti et al., 2016; Sutin et al., 2019), with older adults scoring high in this trait showing better memory performance. While the association between Openness and episodic memory performance in older adults is a well-replicated finding, the underlying brain processes are still largely unknown.

In neuroimaging studies, episodic memory encoding and retrieval have been associated with activations of the medial temporal lobe system (i.e. hippocampus, parahippocampal and perirhinal cortices), as well as of prefrontal, parietal and occipital cortices (Davachi, 2006; Rugg and Vilberg, 2013; Nenert et al., 2014). Collectively, these brain regions can be considered to constitute a human memory network (Soch et al., 2021a). Notably,

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older subjects not only do show reduced activations in this network, particularly in occipital and fusiform cortices, but also reduced deactivations in brain regions of the default mode network (DMN) like the precuneus and posterior cingulate cortex (Maillet and Rajah, 2014; Fjell et al., 2016; Damoiseaux, 2017; Soch et al., 2021a,b). These memory-related regions are also subject to age-related structural changes in both gray and white matter volumes (Raz and Rodrigue, 2006; Head et al., 2008; Fjell and Walhovd, 2010). However, results are mixed regarding the relationship between age-related structural differences and cognitive performance (Salthouse, 2011; Oschwald et al., 2019). In a recent study, we showed that chronological age is generally better predicted by structural magnetic resonance imaging (MRI), whereas functional MRI (fMRI) data and particularly single-value scores are superior in predicting individual memory performance in older adults (Soch et al., 2022), possibly due to individual differences in compensatory mechanisms to maintain cognitive abilities (Raz and Lindenberger, 2011; Tang et al., 2018; Cabeza et al., 2018a; Bråthen et al., 2021). As such, functional age-related differences are often but not always accompanied by cognitive decline (Cansino, 2009; Wong et al., 2012; Richter et al., 2023) and they may also reflect adaptive strategies that are employed as a compensatory mechanism (Cabeza et al., 2002, 2018b; Grady and Craik, 2000; Maillet and Rajah, 2014; Stern, 2009). It was proposed that the onset of declining behavioral performance during aging is closely associated with an individual's capacity to compensate for age-related physiological changes (e.g. Stern, 2009). While previous behavioral studies indicate that personality facets associated with Openness positively influence the maintenance of higher cognitive functioning including memory (Sharp et al., 2010; Ihle et al., 2019; Karsazi et al., 2021), a possible relationship of Openness with the recruitment of the functional brain networks during successful encoding is yet widely unknown.

To quantify the degree of age-related deviation of fMRI activation patterns from prototypical activity in young adults, singlevalue scores of activation (and deactivation) patterns during episodic memory encoding have been proposed as a potential tool for the quantification of neurocognitive aging (Düzel et al., 2011; Soch et al., 2021a). Düzel et al. (2011) described the functional activity deviation during encoding (FADE) score, a measure of deviation from prototypical memory network activations. More recently, Soch et al. (2021a) introduced the similarity of activations during memory encoding (SAME) score, which measures similarity with prototypical brain activity of young adults and reflects both brain activation (i.e. inferior and medial temporal structures, particularly of the parahippocampal cortex, occipital and fusiform cortices) and deactivation patterns (i.e. midline cortical structures). The SAME score correlates positively with memory performance in older adults, that is, higher similarity of encodingrelated activations is predictive for better episodic memory performance. This holds for dependent measures (i.e. obtained from the same fMRI task; Soch et al., 2021a) as well as for independent measures (Richter et al., 2023) of memory performance. As reductionist measures, these single-value scores are suitable for investigating correlations with other variables, offering a distinctive opportunity to investigate the complex interplay of age-related functional differences, memory decline and personality traits (Allen and DeYoung, 2015; DeYoung and Allen, 2019).

Openness reflects the tendency to be creative, imaginative, curious and open to new ideas and art (Costa and McCrae, 1989). Highly open individuals have been characterized to show a predisposition toward cognitive flexibility and exploration (DeYoung et al., 2005; DeYoung, 2013, 2015). Openness is considered a highly

cognitive trait (DeYoung, 2013, 2014) and has been linked to better performance in cognitive abilities such as working memory, inhibitory control and fluid and crystallized intelligence (DeYoung et al., 2005; Chamorro-Premuzic and Furnham, 2008). An fMRI study showed that trait Openness was related to working memory accuracy, and this effect was fully mediated by activity in left lateral prefrontal and medial frontal cortices (DeYoung et al., 2009). In addition to replicating the positive relationship between Openness and intelligence measures, Soubelet and Salthouse (2010) reported that individuals scoring high on trait Openness also showed better episodic memory performance. Large cohort studies examined links between individual differences in Big Five personality traits and age-related episodic memory performance. In a meta-analysis focusing on older adults (>50 years), Luchetti et al. (2016) reported that high Openness, high Conscientiousness, and low Neuroticism were associated with better memory performance and lower memory decline over a 4-year longitudinal follow-up. The cross-sectional result pattern was replicated in another sample (Sutin et al., 2019), and another longitudinal study showed that individuals scoring high on Openness and low on Neuroticism performed better in an episodic memory task 20 years later (Stephan et al., 2020). While there were slightly different correlation patterns of Big Five personality traits and episodic memory performance among those studies, low Neuroticism and high Openness were consistently reported to be associated with better memory performance in older adults. This overall supports the notion of trait Openness as a potential protective factor (and Neuroticism as a potential risk factor) for memory function in aging.

While there is evidence supporting a relationship of better episodic memory performance in older adults with both high trait Openness and better-preserved episodic memory brain-network activity, it is yet unclear whether brain activity patterns could serve as a link between individual differences in Openness and memory performance. To this end, the present study aimed to investigate the relationship between Openness, episodic memory performance and neural episodic memory encoding in young and older adults using personality assessment and fMRI in a visual memory encoding task. Based on previous studies, we hypothesized that trait Openness would be positively related to (i) episodic memory performance and (ii) preserved levels of memory brain-network activity (i.e. higher SAME scores) in older adults. Moreover, we also want to answer the question if (iii) the relationship between trait Openness and episodic memory performance is mediated by the levels of memory-related brain activity in older adults. While the present study focuses on Openness and memory contrasts, we additionally explored other Big Five personality traits and fMRI novelty contrasts.

Methods

Participants

We investigated and combined two previously described study cohorts of 117 (Assmann et al., 2021) and 259 (Soch et al., 2021b) healthy adults. As we were interested in personality traits, participants were included only if personality questionnaire data were available. These personality attributes have not been analyzed or published previously. The total sample of 352 adults was split up into the groups of young (n = 209, 18-35 years old; age:M = 24.30, s.d. = 3.29) and older adults (n = 143, 50–80 years old; age: M = 63.80, s.d. = 6.68). Participants were recruited via flyers at the local academic institutes, via advertisements in local newspapers and during public events of the Leibniz Institute for Neurobiology (e.g. 'Long Night of the Sciences'). All participants were right-handed, were fluent in German language and did not report any neurological or mental disorder in a standardized neuropsychiatric interview. The local ethics committee of the Faculty of Medicine at the Otto-von-Guericke University Magdeburg approved the study. All participants signed informed consent in accordance with the Declaration of Helsinki (World Medical Association, 2013) and received financial compensation for participation.

Visual memory encoding task

In an fMRI session, participants performed an incidental visual memory encoding task (Düzel et al., 2018; Assmann et al., 2021; Soch et al., 2021b). More specifically, participants viewed images of indoor and outdoor scenes and were asked to classify the photos as indoor or outdoor via button press. The task consisted of 132 trials, including unknown indoor and outdoor images (44 trials each; 'novel' images) and two images that were pre-familiarized to the participants (one indoor and one outdoor, each presented in 22 trials; 'master' images). Each trial started with the presentation of an image for 2500 ms followed by a fixation cross for a variable delay between 500-2300 ms in the first cohort (Assmann et al., 2021) and 700-2650 ms in the second cohort (Soch et al., 2021b).

Approximately 70 min after the start of the fMRI session, participants underwent a surprise recognition memory test outside the scanner. In this test, the 88 images from the fMRI session ('old') and 44 at this time unknown images ('new') were presented. Participants were asked to rate the familiarity of each image on a Likert scale from 1 ('definitely new') to 5 ('definitely old'). Data were collected using custom code written in Presentation (Version 0.55, Neurobehavioral Systems, www.neurobs.com).

Memory performance score A

To evaluate the memory test results from the pictures observed during fMRI scanning, the performance was quantified as A-prime (A'), which represents the area under the curve derived from the receiver-operating characteristic (ROC; Soch et al., 2021a). This characteristic describes the relationship between false alarms (FAs; incorrectly identifying new items as old) and hits (correctly identifying previously seen items as old).

As previously described in Soch et al. (2021a, appendix B), let o_1, \dots, o_5 represent the counts of old stimuli, and n_1, \dots, n_5 represent the counts of new stimuli, rated during the retrieval phase on a scale of 1 ('definitely new') to 5 ('definitely old'). The hit and FA rates, as functions of a threshold value $t \in \{0,1,...,5\}$, are determined as the proportions of old stimuli and new stimuli, respectively, that received ratings higher than t:

$$\mathsf{H}(t) = \frac{1}{O} \sum_{i=t+1}^{5} o_i$$

$$\mathrm{FA}(t) = \frac{1}{N} \sum_{i=t+1}^5 n_i$$

where $O = o_1 + \cdots + o_5$ and $N = n_1 + \cdots + n_5$. Consider that H(0) =FA(0) = 1 and H(5) = FA(5) = 0. Note the hit rate as a function of the FA rate:

$$y = f(x)$$
, such that $y = H(t)$ and $x = FA(t)$ for each $t = 0, 1, ..., 5$

By that, the area under the ROC curve is determined as the integral of this function from 0 to 1:

$$A' = \int_0^1 f(x) \, \mathrm{d}x = \int_0^1 \mathrm{H}(\mathrm{FA}) \, \mathrm{dFA}$$

A' ranges from 0 to 1 with A' = 0.5 indicating random guessing and A' = 1 perfect memory performance.

fMRI data acquisition and preprocessing

The fMRI data were acquired using two Siemens 3T MR tomographs (Verio and Skyra). fMRI was assessed as 206 T2*-weighted echo-planar images (EPIs; first cohort: repetition time TR = 2.4 s, echo time TE = 30 ms, flip- α = 80°; 40 slices, 104 × 104 in-plane resolution, voxel size = $2 \times 2 \times 3$ mm, for details see Assmann et al., 2021; second cohort: TR = 2.58 s, TE = 30 ms, flip- $\alpha = 80^{\circ}$; 47 slices, 64×64 in-plane resolution, voxel size = $3.5 \times 3.5 \times 3.5$ mm, for details see Soch et al., 2021b) in interleaved-ascending slice order (1, 3, ..., 47, 2, 4, ..., 46). Structural MRI was acquired as a T1-weighted MPRAGE image (TR = 2.5 s, TE = 4.37 ms, flip- α = 7°; 192 slices, 256×256 in-plane resolution, voxel size = $1 \times 1 \times 1$ mm) for later co-registration.

Data preprocessing and analysis were performed using Statistical Parametric Mapping (SPM12; Wellcome Trust Center for Neuroimaging, University College London, London, UK; https://www. fil.ion.ucl.ac.uk/spm/software/spm12/). EPIs were corrected for acquisition delay, head motion and, in the second cohort additionally, magnetic field inhomogeneities using voxel-displacement maps derived from the field maps. Finally, unwarped EPIs were normalized to a common voxel size of $3 \times 3 \times 3$ mm and eventually spatially smoothed using an isotropic Gaussian kernel of 6 mm at Full Width at Half Maximum (FWHM).

Extraction of single-value FADE and SAME fMRI scores

FADE and SAME scores were calculated following the protocol of previous studies (Soch et al., 2021a; Richter et al., 2023). First, we generated single-subject contrast images representing effects of novelty processing (contrasting novel with master images) and subsequent memory effects (parametrically modulating the BOLD response to novel images as a function of arcsine-transformed subject's responses ranging from 1 to 5 in the subsequent recognition memory test). Second, we computed a reference map showing significant activations (and, for the SAME score, additionally significant deactivations) on each of the two fMRI contrasts (i.e. novelty processing or subsequent memory) within young adults. Third, we calculated summary statistics for every participant and fMRI contrast: the FADE score (indicating the amount of deviation of activations from young subjects) and the SAME score (indicating the amount of similarities of activations and deactivations with young subjects). The SAME score additionally accounts for the inter-individual variability within the reference sample of young subjects via dividing by their standard deviation.

Single-value fMRI scores were extracted as described previously (Soch et al., 2021a; Richter et al., 2023): if we define J_+ as the set of voxels demonstrating a positive effect in young subjects at a predetermined significance threshold (in this case, P<0.05, family-wise error (FWE)-corrected, extent threshold k = 10 voxels), and t_{ij} as the t-value of the ith older subject in the jth voxel for the same contrast, the FADE score for this subject can be calculated as follows:

$$\mathsf{FADE}_i = \frac{1}{v} \sum_{j \notin L} t_{ij} - \frac{1}{v_+} \sum_{j \in L} t_{ij}$$

where v_+ represents the count of voxels within J_+ , and v corresponds to the count of voxels outside J_{\perp} .

Next, we define J_{-} as the set of voxels demonstrating a negative effect in young subjects at a predetermined significance threshold. If we have $\hat{\beta}_i$ as the average contrast estimate in young subjects, $\hat{\sigma}_j$ as the standard deviation of young subjects for a contrast at the jth voxel and $\hat{\gamma}_{ij}$ as the contrast estimate for the ith older subject at the jth voxel, the SAME score can be calculated as follows:

$$\mathsf{SAME}_i = \frac{1}{v_+} \sum_{j \in J_+} \frac{\hat{\gamma}_{ij} - \hat{\beta}_j}{\hat{\sigma}_j} + \frac{1}{v_-} \sum_{j \in J_-} \frac{\hat{\beta}_j - \hat{\gamma}_{ij}}{\hat{\sigma}_j}$$

where v_+ represents the count of voxels within J_+ , and v_- corresponds to the count of voxels within J_- .

Hereafter, we refer to the scores as follows:

- FADE score computed from the novelty contrast: FADE novelty score,
- (ii) SAME score computed from the novelty contrast: SAME novelty score,
- (iii) FADE score computed from the memory contrast: FADE memory score and
- (iv) SAME score computed from the memory contrast: SAME memory score.

Assessment of trait Openness

Openness that reflects self-reports of being imaginative, curious and having a wide range of interests was assessed using the German version (Borkenau and Ostendorf, 1993; Körner et al., 2008) of the NEO Five-Factor Inventory (NEO-FFI; Costa and McCrae, 1989), a shortened version of the NEO-PI-R (Costa and McCrae, 1992). The NEO-FFI is a 60-item questionnaire (12 items for each scale) that measures the Big Five personality traits: Neuroticism, Extraversion, Openness, Agreeableness and Conscientiousness. The items are rated on a five-point Likert scale (strongly disagree to strongly agree). The internal consistency of the scales ranged between a Cronbach's α of 0.71 and 0.85 (Borkenau and Ostendorf, 1993; Schmitz et al., 2001; Körner et al., 2008).

Statistical analysis

Data were analyzed using custom code written in MATLAB R2022a and IBM® SPSS® Statistics, Version 28. Comparisons of mean A', FADE/SAME novelty and memory scores and personality scores between young vs older adults were performed using t-tests. For nominal scale variables (gender and education), the χ^2 test for independence was used. All reported correlation coefficients were Pearson's r if not stated otherwise.

To examine the independent effects of Openness on A' and the FADE/SAME memory scores in older adults, multiple regression analyses were calculated. Since previous studies reported substantial covariations of Openness with demographic variables and a range of cognitive functions (DeYoung et al., 2005; Gregory et al., 2010; Soubelet and Salthouse, 2010), we included age, gender (male vs female), education (with vs without German university entrance diploma, 'Abitur') and crystallized intelligence measured with the multiple-choice vocabulary intelligence test [Mehrfachwahl-Wortschatz-Intelligenztest B (MWT-B); Lehrl, 1999] as explanatory variables in the analyses.

Mediation models with Openness as an independent variable, A' as a dependent variable and FADE/SAME memory scores as a mediator variable were calculated using the 'lavaan' package (Rosseel, 2012) in (R Core Team, 2013). The reported path estimates for the mediation model were standardized estimates using all path information (Std.all). The reported effect sizes were standardized beta coefficients (β) and Cohen's d. To control for covariations with demographics and crystallized intelligence, the analyses described earlier were also conducted with adjusted variables.

Table 1. Demographic information and mean (s.d.) memory, imaging and personality trait scores in the young vs older adult groups

Variable	Young adults	Older adults	Test statistics
Demographics			
Age	24.30 (3.29)	63.80 (6.68)	t = 65.49, P < 0.001
Gender	112/97 f/m	87/56 f/m	$\chi^2 = 1.82,$ $P = 0.178$
Education (Abitur)	203/6 with/without	65/78 with/without	$\chi^2 = 124.79$, $P < 0.001$
MWT-B	26.73 (3.15)	30.20 (3.26)	t = 8.13, P < 0.001
Memory and imagin	g scores		
Memory performance (A')	0.81 (0.08)	0.77 (0.08)	t = -5.20, P < 0.001
FADE memory score	-1.30 (0.57)	-0.86 (0.50)	t=7.58, P<0.001
SAME memory score	-0.07 (0.85)	-1.13 (0.53)	t = -14.29, $P < 0.001$
FADE novelty score	-1.77 (0.66)	-1.89 (0.62)	t = -1.73, P = 0.084
SAME novelty score	-0.08 (0.71)	-0.39 (0.53)	t = -4.66, P < 0.001
Big Five personality	scores		
Neuroticism	28.53 (6.39)	27.09 (5.34)	t = -2.28, P = 0.023
Extraversion	42.33 (5.35)	40.01 (4.82)	t = -4.16, P < 0.001
Openness	43.14 (5.74)	40.97 (4.51)	t = -3.97, P < 0.001
Agreeableness	46.17 (5.40)	45.61 (4.38)	t = -1.08, P = 0.283
Conscientiousness	45.66 (6.09)	47.50 (5.25)	t = 2.94, P = 0.004

Therefore, multiple regression analyses were run including age, gender, education and MWT-B scores on Openness, A', FADE memory score and SAME memory score, and residuals were saved for further mediation analyses.

As an exploratory analysis, we computed voxel-wise regressions of the fMRI subsequent memory contrast with Openness in older adults. Results are reported at $P_{\rm cluster}$ < 0.050 using the FWE rate cluster-level correction and an uncorrected cluster-forming threshold of $P_{\rm voxel}$ < 0.001 (Eklund et al., 2016).

Results

Demographic information and trait Openness

Young and older adults did not differ significantly with respect to the gender ratio (Table 1). As reported previously, older vs young adults less frequently had a university entrance diploma (education, 'Abitur'), most likely due to historical differences in educational systems (for a detailed discussion, see Soch et al., 2021a). Using the MWT-B (Lehrl, 1999), a screening of crystallized intelligence, we found higher MWT-B scores in older vs young participants. In the NEO-FFI, older vs young adults showed lower scores for Openness [t(350) = -3.97, P < 0.001, d = -0.43; Figure 1], Neuroticism [t(350) = -2.28, P = 0.024, d = -0.25] and Extraversion [t(350) = -4.16, P < 0.001, d = -0.45], and higher scores for Conscientiousness [t(350) = 2.94, P < 0.001, d = 0.25]. There was no significant group difference for Agreeableness [t(350) = -1.08, P = 0.283, d = -0.25, Table 1].

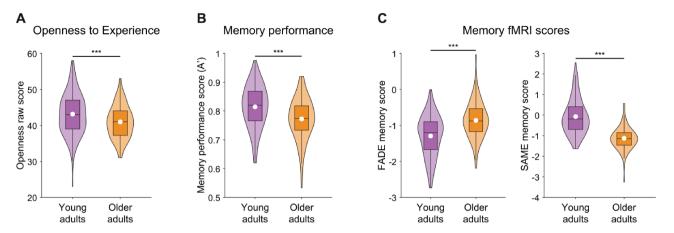


Fig. 1. Violin plots of the (A) Openness raw scores, (B) memory performance and (C) FADE/SAME memory scores in young vs older adults. The white dot indicates the mean value and the box outlines the interquartile range and median. ***P < 0.001.

Table 2. Correlation coefficients between the Big Five personality traits and the memory performance (A') and fMRI scores for the young and older adults

		Neur.	Extr.	Open.	Agre.	Cons.	A'
Young adults	A'	-0.07	0.17	0.09	0.14	0.04	1
	FADE memory score	-0.04	-0.07	-0.03	-0.14	-0.04	-0.27 ^{**}
	SAME memory score	-0.03	0.05	0.04	0.10	-0.01	0.39
	FADE novelty score	-0.09	0.11	0.07	0.06	0.03	0.09
	SAME novelty score	0.04	-0.06	-0.09	-0.12	-0.08	0.02
Older adults	A′	-0.14	0.25	0.27**	0.01	-0.02	1
	FADE memory score	0.01	-0.17 [*]	-0.25 ^{**}	0.11	0.10	-0.33 ^{**}
	SAME memory score	0.01	0.17*	0.29	-0.07	-0.13	0.41
	FADE novelty score	-0.04	0.04	0.12	0.15	-0.07	-0.04
	SAME novelty score	-0.01	0.13	-0.09	-0.03	0.15	0.24**

Note: Neur. = Neuroticism, Extr. = Extraversion, Open. = Openness to Experience, Agre. = Agreeableness, Cons. = Conscientiousness.

Age differences for memory performance and FADE/SAME scores

A' was significantly lower in older (M = 0.77, s.d. = 0.73) vs young adults [M = 0.81, s.d. = 0.75; t(350) = -5.20, P < 0.001, d = -0.57;Table 1 and Figure 1]. As shown in Figure 1, there was a significant difference between older vs young adults in the FADE [young: M = -1.30, s.d. = 0.57; older: M = -0.86, s.d. = 0.50; t(350) = 7.38, P < 0.001, d = 0.80 and SAME memory scores [young: M = -0.07, s.d. = 0.85; older: M = -1.13, s.d. = 0.53; t(350) = -13.17, P < 0.001, d = -1.43]. Taken together, this suggests a higher deviation (FADE) and lower similarity (SAME) of the memory brain-network activity in older adults compared to the reference of prototypical young adult activity with a particularly large effect size for the SAME score. While the SAME novelty score was significantly different between the age groups [young: M = -0.08, s.d. = 0.71; older: M = -0.39, s.d. = 0.54; t(350) = -4.43, P < 0.001, d = -0.48, there was no significant group difference in the FADE novelty score [young: M = -1.77, s.d. = 0.66; older: M = -1.89, s.d. = 0.62; t(350) = -1.73, P = 0.084, d = -0.19]. This might be due to differences in the underlying brain networks and their association with aging (e.g. a rather specific association of the FADE novelty score with MTL regions vs more widespread associations for all other scores; for illustration, see Richter et al., 2023; Supplementary Figure S2; for a detailed discussion, see Soch et al., 2021a).

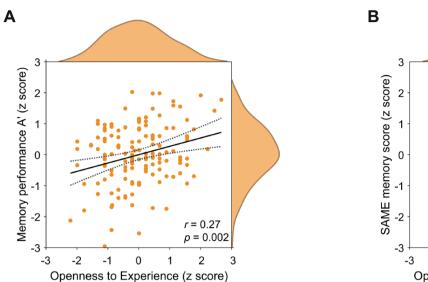
Correlations of memory performance and imaging scores with Big Five personality traits

While we observed significant correlations between the FADE/SAME memory scores with A' in both age groups, personality scores particularly correlated with memory performance and fMRI scores in older adults (Table 2). The largest correlations were found for Openness with A' (r = 0.27, P = 0.001), FADE (r = -0.25, P = 0.002) and SAME memory scores (r = 0.29,P<0.001), suggesting that older adults scoring high on Openness show better memory performance and more prototypical memory network activity (Figure 2). In the exploratory analysis for the other personality traits, a similar pattern was observed for Extraversion (Table 2). For exploratory correlations between the single NEO-FFI items of Openness, A' and the FADE/SAME memory scores in older adults, see Supplementary material A. The largest correlation between Openness and A' was found for 'Philosophical discussions', which belongs to the NEO-PI-R Openness facet 'Ideas'. For FADE/SAME memory scores, the largest correlations with Openness were found for 'Wave of excitement to art/literature', which belongs to the NEO-PI-R Openness facet 'Aesthetics' (Costa and McCrae, 1992; Ostendorf and Angleitner,

Trait Openness within the group of older adults

As Openness was correlated with A' and the FADE/SAME memory scores in older adults only, further analyses are focused on this group. In older adults, Openness was significantly positively correlated with education (point-biserial: r = 0.22, P = 0.008) and MWT-B test results (r = 0.18, P = 0.036), but not with age (r = 0.04, P = 0.658) or gender (point-biserial: r = -0.04, P = 0.656). Multiple regression analyses revealed that there was a substantial direct effect of Openness as predictor on A', the FADE memory score and the SAME memory score as criterion, independently of the

^{*}P < 0.05.



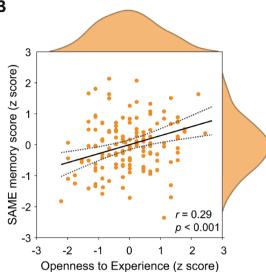


Fig. 2. Scatter plots including 95% confidence intervals and the data distribution for the correlations of Openness (here shown as z scores) with (A) the memory performance and (B) the SAME memory score within the group of older adults.

Table 3. Multiple regression analysis of the direct effects of Openness on memory performance and FADE/SAME memory scores controlled for demographic variables (age, gender and education) and crystallized intelligence (MWT-B scores) in older adults

	A′			FADE memory score		SAME memory score	
	β	P	β	P	β	P	
Openness	0.24**	0.005	-0.22*	0.009	0.26**	0.002	
Age	-0.10	0.250	0.17	0.048	-0.09	0.297	
Gender	0.03	0.730	-0.07	0.415	0.15	0.075	
Education	0.09	0.321	-0.11	0.213	0.18*	0.048	
MWT-B	0.10	0.288	-0.09	0.351	0.03	0.707	

Note: One participant was excluded from all analyses involving the MWT-B due to missing value.

demographic variables (age, gender and education) and MWT-B scores (Table 3).

As shown in Table 4, the mediation analysis with the FADE memory score as mediator on the relationship between Openness as an independent variable and A' as a dependent variable revealed a partial mediation effect (total effect: $\beta = 0.27$, P = 0.001; indirect effect: $\beta = 0.07$, P = 0.020). This suggests that the FADE memory score mediated 26.29% of the total effect between Openness and A'.

The mediation analysis with the SAME memory score as mediator on the relationship between Openness as an independent variable and A' as a dependent variable also revealed a partial mediation effect (total effect: $\beta = 0.27$, P = 0.001; indirect effect: $\beta = 0.11$, P = 0.004; Table 4; Figure 3). This suggests that the SAME memory score mediated 40.74% of the total effect between Openness and A'.

Control analyses on the associations between Openness, memory performance and fMRI measures

To ensure the observed mediation effects were not due to covariations with demographics and crystallized intelligence, the analyses described earlier were also conducted for Openness, A'

Table 4. Mediation analysis within the group of older adults with FADE/SAME memory scores as mediators of the association between Openness and episodic memory performance (A')

	β	P
FADE memory score		
Total effect: Openness \rightarrow A'	0.27	0.001
Direct effect: FADE memory score \rightarrow A'	-0.25	0.002
Direct effect: Openness \rightarrow A'	0.20	0.013
Indirect effect: Openness \rightarrow FADE memory	0.07 (26.29%)	0.020
$score \rightarrow A'$		
SAME memory score		
Total effect: Openness \rightarrow A'	0.27	0.001
Direct effect: SAME memory score \rightarrow A'	0.37	< 0.001
Direct effect: Openness \rightarrow A'	0.16	0.036
Indirect effect: Openness \rightarrow SAME memory score \rightarrow A'	0.11 (40.74%)	0.004

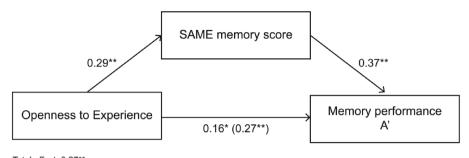
and FADE/SAME memory scores adjusted for age, gender, education and MWT-B scores. We were able to confirm the partial mediation effects in these additional analyses (Supplementary material B).

Since Extraversion showed a similar correlational pattern with memory performance and fMRI scores as Openness, mediation analyses including Extraversion instead of Openness were calculated, which did not reach statistical significance (Supplementary material C). Moreover, partial correlations between Openness, A' and FADE/SAME memory scores were still statistically significant after controlling for Extraversion (0.22 \leq |r| \leq 0.25, P < 0.001), while Extraversion (controlled for Openness) was only significantly correlated with A' (r = 0.20, P = 0.019), but not with FADE/SAME memory scores (FADE: r = -0.11; SAME: r = 0.10; $P \ge 0.204$; Supplementary material D1). A mediation analysis including Openness (controlled for Extraversion), A' and fMRI memory scores revealed full mediation effects for FADE (indirect effect: 33.33% of the total effect) and SAME memory scores (47.52%; Supplementary material D2).

Additionally, trait theories suggest a meta-trait Plasticity, which is defined as the shared variance of Openness and

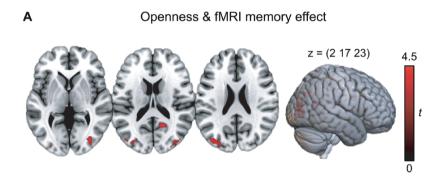
^{**}P<0.01;

Mediation model in older adults (N = 143)



Total effect: 0.27** Indirect effect: 0.11** (partial mediation 40.74%)

Fig. 3. Mediation analysis within the group of older adults shows that the relationship between trait Openness and memory performance (A') is partly mediated (40.74% of the total effect) by the SAME memory fMRI score. *P<0.05; **P<0.01.



В Mediation model with left MOG in older adults (N = 143)

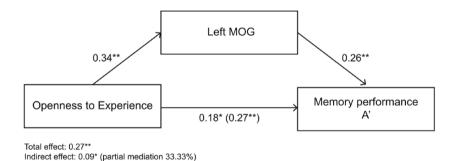


Fig. 4. (A) Regression analysis of Openness and fMRI memory effect (positive effect) in older adults. P < 0.05, FWE-corrected at cluster level, cluster-defining threshold P<0.001, uncorrected. All activation maps are superimposed on the Montreal Neurological Institute Neurological (MNI) template brain provided by MRIcroGL (https://www.nitrc.org/projects/mricrogl/). (B) Mediation analysis showed that the relationship between Openness and memory performance (A') was partially mediated (33.33% of the total effect) by activity in the left MOG. *P<0.05; **P<0.01.

Extraversion (DeYoung, 2006, 2013, 2015). We further ran mediation analyses with the latent factor Plasticity as an independent variable (Supplementary material D3). These analyses revealed a significant indirect effect with the SAME memory scores (21.20% of the total effect), but not the FADE memory scores (11.81% of the total effect) as mediation variables.

Voxel-wise association of fMRI contrasts with Openness

As an exploratory analysis, we computed voxel-wise regressions of the fMRI memory contrast with Openness in older adults. We observed significantly positive associations of Openness with successful memory encoding activations in the left $\beta = 0.21$, s.d. = 0.20; t(141) = 4.35, P = 0.009, x y z = -42 -79 23; 47 voxels] and right $[\beta = 0.08, s.d. = 0.16; t(141) = 4.15, P = 0.025, x y]$ z = 33-79 2; 38 voxels] medial occipital gyrus (MOG; FWE clusterlevel correction; Figure 4A). Additionally, the analysis revealed a positive association with the precuneus/posterior cingulate cortex ($\beta = 0.14$, s.d. = 0.25), which, however, did not reach corrected statistical significance [t(141) = 4.50, P = 0.080, x y z = 15-58 17; 28]voxels; FWE cluster-level correction; Supplementary material E; Supplementary Figure S1].

Correlations between the left and right MOG peak-voxel activity and personality traits as well as the FADE/SAME memory

Table 5. Pearson's correlations between occipital gyrus peakvoxel activity (left and right MOG), Big Five personality traits and memory-related brain activity and performance

	Lef	t MOG	Right MOG		
	r	P	r	Р	
Neuroticism	0.04	0.615	-0.15	0.079	
Extraversion	0.16	0.061	0.10	0.242	
Openness	0.34	< 0.001	0.33**	< 0.001	
Agreeableness	-0.01	0.905	0.04	0.667	
Conscientiousness	-0.05	0.556	0.05	0.527	
FADE memory score	-0.47 ^{***}	< 0.001	-0.37 ^{***}	< 0.001	
SAME memory score	0.42***	< 0.001	0.31***	< 0.001	
Memory performance A'	0.33***	< 0.001	0.07	0.440	

^{***}P < 0.001.

scores and A' are shown in Table 5. A mediation analysis including Openness as an independent variable, A' as a dependent variable and the left MOG peak-voxel activity as a mediation variable revealed a partial mediation (total effect: $\beta = 0.27$, P = 0.001; indirect effect: $\beta = 0.09$, P = 0.01; 33.33% of the total effect; Figure 4). Openness was positively related to A' ($\beta = 0.18$, P = 0.03) and the left MOG ($\beta = 0.34$, P<0.001). There was a significant positive association between the left MOG and A' ($\beta = 0.26$, P = 0.002).

Discussion

The goal of the present study was to investigate to what extent differences in memory encoding-related brain activity explain the frequently reported relationship between Openness and memory performance in older adults. To this end, trait Openness was correlated with single-value fMRI scores reflecting deviations from or similarities with prototypical memory encoding brain activity in a visual memory encoding task. Consistent with our hypotheses, high trait Openness in older adults was related to both, better memory performance and more prototypical brain activity (low FADE/high SAME score). A mediation analysis revealed that the relationship between Openness and memory performance in older adults was substantially mediated by FADE/SAME fMRI scores. This overall provides the first evidence that older adults scoring high on trait Openness show better memory performance, which is mediated by a more prototypical memory brain-network activity during encoding.

Mediation of Openness and episodic memory performance by neural activity

Across all subjects, the age group (older vs young adults) had a significant effect on episodic memory performance and memoryrelated fMRI activity as indicated by FADE and SAME scores. This converges with previous studies demonstrating age differences in memory performance and functional brain activity (Düzel et al., 2011; Maillet and Rajah, 2014; Fjell et al., 2016; Damoiseaux, 2017; Morcom and Henson, 2018; Soch et al., 2021a,b).

The link between Openness and episodic memory retrieval in older adults was mediated by activity in memory brain networks during memory encoding. Specifically, older adults who scored high in trait Openness also showed more prototypical brain activity during memory encoding, which was directly related to better episodic memory performance. These results converge with studies reporting a positive relationship between Openness and episodic memory performance in older adults (Terry et al., 2013; Luchetti et al., 2016; Sutin et al., 2019; Stephan et al., 2020). One possible explanation for this may be that highly open older adults are more likely to engage in intellectually stimulating activities such as traveling, attending cultural events and seeking novel or aesthetic experiences (Kraaykamp and van Eijck, 2005; Chamorro-Premuzic and Furnham, 2008; Soubelet and Salthouse, 2010; Jackson et al., 2020; Talpain and Soubelet, 2022). Increased exposure to cognitive-stimulating life experiences may delay agerelated manifestation of memory deficits (Stern, 2009; Franchow et al., 2013). Additionally, Openness is related to a broad range of cognitive abilities, including fluid and crystallized intelligence, and working memory capacity (Gregory et al., 2010; Schretlen et al., 2010; Sharp et al., 2010; Chapman et al., 2012; Nishita et al., 2019). In this context, high Openness may reflect a protective factor at the personality trait level, indicating preserved memory-related cognitive functioning in older age.

At structural brain levels, there are overlapping reports that high Openness is related to a decrease in cortical thickness, particularly in frontal (orbitofrontal, superior and posterior frontal and prefrontal) and parietal (inferior parietal and precuneus) regions (Wright et al., 2007; Kapogiannis et al., 2013; Vartanian et al., 2018). Other structural measures linked high Openness to increased orbitofrontal cortex folding and surface area (Vartanian et al., 2018) and a lower integration of structural brain networks (Talaei and Ghaderi, 2022). In contrast, other studies found small-to-no associations between Openness and structural brain measures (DeYoung et al., 2010; Bjørnebekk et al., 2013; Avinun et al., 2020; Hyatt et al., 2022). These null findings were further supported by recent meta-analyses that did not discover any replicable relationship between Openness (and other Big Five traits) and cortical thickness, gray matter volume and surface areas (Chen and Canli, 2022). At functional levels, the neural basis of Openness has largely been associated with resting state fMRI activity. These studies showed that individual differences in Openness can be predicted by functional connectivity matrices (Dubois et al., 2018) and have repeatedly been related to activity in the DMN (Horn et al., 2014; Blain et al., 2020), suggesting that highly open individuals show a more efficient DMN functioning (Beaty et al., 2016, 2018). Another recent study reported a decreased withinnetwork DMN functional connectivity in highly open individuals, which was mainly driven by the Fantasy sub-facet of Openness (Marstrand-Joergensen et al., 2021). DMN activity also was related to cognitive functions with particular relevance for trait Openness (e.g. creativity, imagination and divergent thinking; DeYoung et al., 2012; DeYoung, 2014) and episodic memory retrieval. The DMN is subject to age-related changes, indicating alterations in the DMN such as reduced activity in medial temporal and parietal regions and increased activity in frontal areas, which often have been assumed to reflect compensatory reactions to age-related brain alterations (Desgranges et al., 2011; Andrews-Hanna et al., 2014; Mohan et al., 2016; Mak et al., 2017). The mentioned regions in the DMN also have a qualitative overlap with brain regions whose activity was measured using FADE/SAME memory scores, such as the precuneus and posterior cingulate cortex. Overall, it may be that high Openness reflects a protective factor when it comes to successful aging of neural structures associated with episodic memory functioning. In the present study, this might be reflected by a higher similarity of highly open older adults' brain activity to the prototypical functional brain responses during memory encoding.

Exploratory analysis: associations between Openness and medial occipital brain activity

In an exploratory, voxel-wise analysis within older adults, we found that high Openness and better memory performance were related to amplified activations in the MOG. Converging with our results, the MOG shows robust activations during encoding (Maillet and Rajah, 2014) and recognition (Yonelinas et al., 2001) as well as increased functional connectivity with the hippocampus during successful memory formation (Ranganath et al., 2005). Hence, the MOG is considered part of a visual memory and perception network, which is active during both episodic memory encoding and retrieval (Slotnick, 2004; Slotnick and Schacter, 2006; Thakral and Slotnick, 2015; Waldhauser et al., 2016). This is in line with a proposed model for visual memory encoding, which demonstrated an early involvement of the MOG driven by the primary and secondary visual areas (Nenert et al., 2014). These areas are also affected by aging, indicating decreased occipital activity during working memory, visual attention and episodic retrieval tasks (Cabeza et al., 2004; Davis et al., 2008) and a disproportionate recruitment of the left vs right visual cortex during encoding of visual episodic information (Maillet and Rajah, 2014). There is preliminary evidence suggesting that high Openness is related to different low-level visual perceptual experiences (Antinori et al., 2017). Accordingly, Blake and Palmisano (2021) reported differences in perceptual processing of ambiguous visual stimuli in high creativity/divergent thinking, two features that are also related to individual differences in Openness (DeYoung et al., 2012; Kaufman et al., 2016). This overall raises the question whether the age-related associations between Openness and successful memory encoding may rely not only on preserving neurocognitive functioning by intellectual engagement and activities but also on personality-related differences in early visual processing during memory encoding.

Clinical relevance

In a recent meta-analysis, AD patients showed lower levels of selfreported and informant-obtained Openness and Extraversion, and higher levels of Neuroticism compared to controls (D'Iorio et al., 2018). A similar personality profile was considered a risk factor and predictor for developing AD (Caselli et al., 2018; Duberstein et al., 2011) and assumed to change before vs after the AD diagnosis (Robins Wahlin and Byrne, 2011). Other studies proposed that specifically low Openness was a pre-clinical marker of incipient cognitive decline (Williams et al., 2013) and that high Openness may protect from memory decline (Terry et al., 2013). This suggests that Openness is part of a personality profile in which high Openness may constitute a protective factor in the transition from healthy memory functioning to risk stages for AD and personality changes that go along the development of AD. Our study is thus of high clinical relevance, as it provides novel evidence that the presumably protective effect of Openness on episodic memory functioning is reflected by functional brain-network differences. This should encourage conducting similar studies in individuals at risk of developing AD to better understand the beneficial characteristics of personality traits on brain alterations before and after AD onset.

A potential role for the mesolimbic dopamine system and Openness in preserved cognition

In the present study, memory network activity and performance in older adults were both specifically correlated with Openness and Extraversion, which may potentially emphasize the influence of the dopamine system. This converges with empirical and theoretical references that ascribe dopaminergic functioning a major role in the cognitive and behavioral expressions of Openness and Extraversion (Depue and Lenzenweger, 2001; DeYoung, 2010, 2013; Pickering and Pesola, 2014; Wacker and Smillie, 2015).

Extraversion has previously been linked to dopamine-rich brain regions (Li et al., 2019) and cortical reward processing (Cooper et al., 2014; Smillie et al., 2019). In an fMRI study, Passamonti et al. (2015) reliably linked high Openness to increased functional connectivity of the prefrontal cortex and substantia nigra/ventral tegmental area. Moreover, a recent pharmacological study linked Openness and divergent thinking to dopamine activity (Käckenmester et al., 2019). Furthermore, in the Cybernetic Big Five Theory, Openness and Extraversion are considered a metatrait Plasticity whose neuromodulator is dopamine (DeYoung et al., 2005; DeYoung, 2013, 2015). Our analyses including Plasticity (Supplementary material D) indicated a mediation effect solely for the SAME memory score, which may suggest an involvement of dopamine. Dopamine has also often been implicated in episodic memory functioning (Wittmann et al., 2005; Adcock et al., 2006; Düzel et al., 2010), and impaired dopaminergic neurotransmission is associated with cognitive aging and longitudinal memory decline (Bäckman and Farde, 2009; Morcom et al., 2010; Chowdhury et al., 2012; Papenberg et al., 2014; Nyberg et al., 2016). Düzel et al. (2010) proposed that an increase of mesolimbic dopaminergic activity promotes exploratory behavior and ultimately memory performance in older adults. In line with this framework, our results suggest links between Openness/Extraversion and age-related differences in neural memory functioning.

Relevance of Openness facets

A major limitation of the present study was that personality traits were assessed with only one questionnaire (NEO-FFI), which ultimately did not allow to examine by which trait sub-facet the age-related Openness effects on memory were mainly driven. Accordingly, previous studies reported that Openness facets (e.g. Fantasy, Feelings, and Ideas) had different longitudinal trajectories (Bleidorn et al., 2009) and varying associations with psychometric intelligence (Moutafi et al., 2006). Other studies that divided Openness into the sub-facets 'Openness' (fantasy and aesthetics) and 'Intellect' (intellectual engagement; DeYoung, 2014) linked Intellect to creative achievements in the sciences (Kaufman et al., 2016), fluid intelligence (Nusbaum and Silvia, 2011) and increased working memory-related prefrontal activity (DeYoung et al., 2009). In contrast, the sub-facet Openness, but not Intellect, was related to implicit learning (Kaufman et al., 2010) and reduced cortical thickness in fronto-temporal gyri (Vartanian et al., 2018). In the development of the Big Five Aspects Scale (BFAS; DeYoung, 2013, 2014; DeYoung et al., 2013), the sub-facets Openness and Intellect were correlated with the NEO-PI-R Openness scale, indicating that NEO Openness total scores may strongly reflect the BFAS sub-facet Openness than Intellect (DeYoung et al., 2007). An exploratory analysis of single-item correlations (Supplementary material A) showed that memory performance was particularly related to an item of the NEO-PI-R Ideas facet (i.e. open-mindedness, open to new ideas and intellectual engagement), and FADE/SAME memory scores to an item of the Aesthetics facet (i.e. open to and interests in art, music and poetry). According to the independent associations of Openness subfacets with individual differences at cognitive, behavioral and neural levels, it seems very encouraging for follow-up studies to assess personality traits with a higher resolution (e.g. NEO-PI-R or BFAS; DeYoung et al., 2007). Such studies would not only provide a better understanding of the Openness sub-facets, but would also shed more light on the specific cognitive processes (e.g. creativity us intellect) involved in the protective effects of Openness on neurocognitive aging. In the context of the present study, it might be conceivable that the effects of Openness on cortical memory encoding and memory performance may be even stronger represented in one of the facets than in the global Openness domain.

Specificity of trait activation

The associations of Openness with neural memory encoding were only supported in the older adult age group. This might be due to group-related differences in average Openness and memory performance. In line with other research, in the present study, older vs young adults showed lower Openness scores (Schaie et al., 2004; Roberts et al., 2006; Allemand et al., 2007; Bleidorn et al., 2009) and a declined memory performance (Oschwald et al., 2019). It is conceivable that the memory task was not challenging enough for young adults, such that it did not pose an optimal situation to activate the influences of personality traits (McNaughton and Smillie, 2018; Taconnat et al., 2022) and thus masked potential shared variance between memory encoding and trait Openness. Moreover, the FADE/SAME scores are by definition contrasted with the memory-related fMRI activity of the young group. Thereby, the FADE/SAME scores might further conceal potential trait correlations within the group of young adults and rather reflect highly suitable single scores for the investigation of personality in neurocognitive aging.

Conclusion

Our study provides novel evidence that the personality trait Openness is associated with episodic memory performance, and this effect was substantially mediated by memory-related brain activity in older adults. Specifically, those older adults with high Openness showed better memory performance and this was due to a higher similarity to brain activity patterns of young adults. To the best knowledge of the authors, this is the first report linking the relationship between trait Openness and memory performance to actual brain activity in an episodic memory task. The present study further shows the utility of single-value fMRI scores in personality neuroscience with a high statistical power.

End notes Supplementary data

Supplementary data are available at SCAN online.

Data availability

Due to data protection regulations, sharing of the entire data set underlying this study in a public repository is not possible. We have previously provided Generalized Linear Models (GLM) contrast images as a NeuroVault collection (https://neurovault.org/ collections/QBHNSRVW/) and MATLAB code for imaging scores as a GitHub repository (https://github.com/JoramSoch/FADE_SAME) for an earlier article using the same dataset (Soch et al., 2021a). Access to de-identified raw data will be provided by the authors upon reasonable request.

Conflict of interest

The authors declared that they had no conflict of interest with respect to their authorship or the publication of this article.

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