

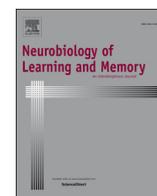
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# The neural basis of individual differences in memory performance in young and older adults: Using the encoding/retrieval flip account as framework



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## ABSTRACT

Aging is associated with cognitive decline, specifically in episodic memory. However, there are large individual differences in the extent of this decline and previous research suggests that these are associated with differences in executive functioning (EF). These EF differences, and associated differences in the encoding and retrieval of episodic information, have been linked to differences in the activation of particular brain regions. The “encoding/retrieval flip” (E/R flip) framework assumes deactivation and activation of specific brain regions during successful encoding and retrieval, respectively. The present study assessed whether this framework can be used to explain EF-based individual differences in memory performance of young and older participants. Young adults ( $N = 19$ ) and older adults ( $N = 39$ ) performed an incidental semantic encoding and memory recognition task in an fMRI setting, focusing on brain regions that show the E/R flip. The association between an index of EF and fMRI activity in brain regions showing the E/R flip was tested in each age group. EF predicted E/R flip activity in the older, but not young adults. These findings underscore the importance of individual differences in ageing research and provide empirical evidence for the association between EF and the E/R flip.

## 1. Introduction

Aging is an inevitable path in nature. Although deterioration in cognitive abilities has been widely reported in older adults, studies have shown that some individuals are able to maintain their cognitive functioning until late adulthood. These individuals demonstrate strong cognitive plasticity in terms of effectively using environmental support to achieve better performance (Cheke, 2016; Kessels & de Haan, 2003).

In a recent study, we found that older adults (OAs) displaying high executive functioning (EF) were able to form deeper memory traces that were promoted by the task demands during semantic encoding (i.e., effortful semantic encoding) and later achieved the same memory performance as younger adults (YAs; Fu, Maes, Kessels, & Daselaar, 2017). In contrast, OAs with relatively weak EF were unable to form such deeper memory traces potentially prompted by the increased task demand. We explained this using the framework of the Compensation-Related Utilization of Neural Circuits Hypothesis (CRUNCH; Reuter-Lorenz, 2008). Accordingly, relative to YAs, OAs need a stronger activation of additional brain areas to compensate for their overall weaker cognitive abilities, and in order to cope with the task demands to the

same extent as YAs. However, importantly, there is a limit to this presumed compensatory brain activation; presumably, OAs with lower EF reach this limit earlier than OAs with higher EFs (see also Fu, Kessels, & Maes, 2020).

Although the notion of differential brain activations provides a compelling explanation for individual differences in cognitive abilities in normal aging, the exact neural underpinnings remain unclear. In the current study, we aimed to map the patterns of brain activity associated with this hypothesis, using the same memory paradigm as in Fu et al. (2017). There is abundant evidence that neural networks supporting encoding and retrieval of information decline with age (Daselaar & Cabeza, 2008; Nyberg & Bäckman, 2011) and that aging-related changes in brain function underlie cognitive aging. We hypothesized that different levels of brain activity and associated differences in memory performance are related to differences in EF of the OAs. However, concerning the direction of the link between EF and brain activity there are two possibilities that may depend on task difficulty. Starting from the premise that individuals with stronger cognitive resources have a larger capacity for recruiting (additional) brain regions and associated stronger activity when needed, we argue that in the case

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of relatively complex tasks and looking within a sample of OAs, those with relatively little cognitive resources might be confronted with a task demand that exceeds their capacity for such recruitment (i.e. the system has reached its maximum). Instead, OAs with more cognitive resources can cope with these demands by recruiting the necessary brain regions. This would imply a positive association between EF capacity and brain activation. In the case of relatively easy tasks, the task demands and associated required brain activations might be well within the limits of the cognitive capacity of most or all OAs. In this case, individual differences in cognitive resources might be expressed as differences in the extent of brain activation, with the higher functioning participants requiring *less* neural activity for reaching the same performance level than the lower functioning individuals. This implies a negative association between cognitive capacity and brain activity. These reasonings are supported by previous research on brain activations, providing evidence for an interaction between cognitive capacity and task demands (e.g., Barulli & Stern, 2013; Schneider-Garces et al., 2010; Stern et al., 2012). Because we used the same relatively demanding episodic memory task as in Fu et al. (2017), we hypothesized that individuals with higher EF would have higher amplitudes of neural activities related to successful memory events.

Although encoding and retrieval of episodic information are two temporally separated events, they are strongly interdependent (Rugg, Johnson, Park, & Uncapher, 2008). In the past few decades, with the development of neuroimaging tools, a framework has been developed regarding neural activities underlying successful memory performance that is built on the notion of the “encoding/retrieval flip” or E/R flip (Amlien, Sneve, Vidal-Piñeiro, Walhovd, & Fjell, 2018; Daselaar, 2009; Gilmore, Nelson, & McDermott, 2015; Huijbers et al., 2012). In this notion, specific brain regions, including the posterior midline region (PMR) and ventral parietal cortex (VPC), are deactivated during successful episodic memory encoding, and activated during successful retrieval. Although the precise mechanism of the E/R flip is still under investigation, researchers argue that the E/R flip can be seen as the representation of brain systems collaborating functionally to increase the likelihood of successful memory performance (Buckner, Andrews-Hanna, & Schacter, 2008; Huijbers et al., 2012).

Given the expected positive association between EF and brain activation in the case of demanding tasks, one would hypothesize high-EF OAs showing a higher amplitude of the E/R flip than low-EF OAs. For the YAs, one possible hypothesis is that they would subjectively experience the task as relatively simple, because they all would have sufficient cognitive resources, and a corresponding capacity of activating necessary brain regions. If anything, this could imply a negative association between EF and E/R flip related brain activity. An alternative hypothesis is that, for the YAs, there will be no large inter-individual differences in recruited brain resources, implying no strong association between EF and E/R flip activity.

The current study applied the same semantic encoding and retrieval tasks as described in Fu et al. (2017) in an fMRI experimental setting, with the aim to obtain neural evidence for the hypothesis of EF-capacity related differential brain activations. Based on previous studies (Daselaar, 2009; Vannini et al., 2013), we took the PMR and VPC as regions of interest (ROIs) for the E/R flip. We hypothesized that the total amplitude of the E/R flip can be explained by the EF of OAs, reflecting a positive relation, whereas this relation is negative or close to zero for YAs.

## 2. Methods and materials

### 2.1. Participants

Twenty-one YAs aged 19–44 years ( $M = 24.4$ ,  $SD = 5.1$ , 11 women) and 42 OAs, aged 60–79 years ( $M = 66.9$ ,  $SD = 3.7$ , 16 women) were recruited by an advertisement in local newspapers. All participants were native Dutch speakers who did not have a history of

neurological or psychiatric illnesses (self-report). All OAs scored higher than 27 on the Mini Mental State Examination (MMSE, Folstein, Folstein, & McHugh, 1975;  $M = 29.3$ ,  $SD = 0.8$ , range = 28–30). Three OAs were excluded from the analyses due to incidental findings in the MRI data. One YA was excluded from the analyses due to not adhering to the task instruction and another YA was excluded because his age (44) deviated two standard deviations from the rest of the YAs (and OAs). All participants signed an informed consent form before the start of the experiment and received €30 as remuneration afterwards. The study was approved by the Ethics Committee of the Faculty of Social Sciences of the Radboud University and all experimental manipulations were performed in accordance with the approved guidelines and the declaration of Helsinki.

### 2.2. Neuropsychological tests

Similar to the study by Glisky, Polster, and Routhieaux (1995), three neuropsychological tests were used to measure EF: (1) Backward Digit Span from the Wechsler Adult Intelligence Scale – Fourth Edition (WAIS-IV, Wechsler, 2014), (2) Mental Arithmetic, and (3) Mental Control from the Wechsler Memory Scale – Fourth Edition (WMS-IV, Wechsler, 2009). However, we did not use the participants’ performance on the Mental Control test for determining the composite EF score due to a ceiling effect (Full score = 8, Median = 8, Mean = 7.9,  $SD = 0.3$ ). Participants’ performances on the other two EF tests were converted to a  $z$  score. Subsequently, the average of the two  $z$  scores was taken as composite EF score, representing each individual’s EF capacity. Moreover, education level was recorded using seven categories based on the Dutch educational system (Verhage, 1964; 1 = less than primary school, 7 = academic degree), and verbal intelligence was assessed by the Dutch version of the National Adult Reading Test (NART) (Schmand, Bakker, Saan, & Louman, 1991).

### 2.3. Semantic encoding task

The semantic encoding task comprised 360 trials, each beginning with a fixation cross (300 ms), followed by a word triplet. Participants were asked to indicate which of the two words displayed at the bottom of the screen was semantically more related to the target word at the top by pressing corresponding buttons on a button box. Word triplets were taken from Fu et al. (2017). Participants had 3500 ms to make their own judgment for each triplet and every trial ended with a jitter of 0–2500 ms blank screen (see Fu et al., 2017, for more details). This incidental encoding task is similar to the one used in Daselaar (2009) and a recent study by Amlien et al. (2018), in which the E/R flip was demonstrated in OAs.

### 2.4. Recognition memory task

The 360 target words from the encoding task were intermixed with 180 new words and randomized for the recognition memory task. Participants were asked to judge whether a word had been presented in the previous encoding task (old) or not (new), taking their confidence level into consideration, by pressing corresponding buttons on the button box (see Amlien et al., 2018; Daselaar, 2009; Huijbers et al., 2013, for similar tasks). Four options were presented together with the target word: “old!”, “old?”, “new?”, “new!”. For all analyses, we combined responses “old!” and “old?” as “old” and “new?” and “new!” as new judgment. Trials started with a fixation cross of 300 ms, proceeded with a 3500 ms response limit and short breaks after every 135 trials and ended with a jitter (randomized durations, ranging from 0 to 2500 ms).

### 2.5. Procedure

The neuropsychological tests were administered first in each

participant, after which they acquainted themselves with the semantic encoding task. The semantic encoding task consisted of two runs in the MRI scanner, each lasting about 15 min. After this task, T1-weighted structural images were collected in a 6-min interval. Participants were then taken out of the scanner to have a 3–5-min break and to be instructed for the recognition memory task which consisted of 4 runs of 11 min in the scanner. The recognition memory task started immediately after the break. All tasks were designed and presented using Presentation® and conducted in Radboud University research labs and lasted three hours.

### 2.5.1. fMRI data acquisition

For the current study, images were collected using a 3T Siemens scanner. High-resolution T1-weighted structural images were obtained with a 30 ms echo time (TE), a 2300 ms repetition time (TR), a 256 × 256 mm field of view (FOV), a 256 × 256 matrix, and a slice thickness of 1 mm. Functional scanning involved a T2\*-weighted gradient-multi-echo-planar imaging (EPI) sequence with a 2240 ms TR, a 224 × 224 mm FOV, a 64 × 64 matrix, a slice thickness of 3 mm, 32 slices (interleaved sequence), a 90 degree flip angle, and TEs at 9, 19, 29, 39, and 49 ms. Earplugs were used to decrease scanner noise and foam pads and headbands were applied to minimize head motion.

### 2.6. fMRI data analysis

#### 2.6.1. Pre-processing

fMRI data were pre-processed using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>). We discarded the first 5 successive images (29 for the first run of each task) in each run to allow the magnetization to reach equilibrium. As preliminary analyses, following previous approaches (Daselaar, 2009), we took images with TE = 29 ms to proceed further analyses. Standard pre-processing procedures were implemented: slice-timing was corrected for differences in slice acquisition times, motion was corrected by aligning to the first image volume, data were normalized to the standard SPM 8 EPI template and resliced into 3 × 3 × 3 mm<sup>3</sup> resolution in Montreal Neurological Institute space, smoothing was applied with an 8-mm full-width half-maximum isotropic Gaussian kernel.

#### 2.6.2. fMRI models

To access trial-related activity, we convolved a vector of the onset times of the stimuli with a synthetic hemodynamic response function (HRF). To correct for head motion artefacts, six rigid body parameters of realignment entered the design matrix as nuisance regressors. For encoding, there were three trial types: hits, misses, no-response; for retrieval, two more types were added: correct rejection and false alarm. The standard general linear model (GLM) were used to model the effects of interest and the nuisance effects. To identify statistical parametric maps for each participant, linear contrasts to the parameter estimates (beta weights) for the events of interest were implemented, resulting in a *t*-statistic for each voxel.

We followed the same methods as reported in Daselaar (2009) to quantify the E/R flip. Four steps were taken: (1) we selected regions of interest (ROIs) in PMR (consisting of the precuneus and posterior cingulate, BA7/29/30/31) and VPC (consisting of the inferior parietal lobe, and supramarginal and angular gyri, BA39/40) using the Wake Forrest PickAtlas toolbox (<http://fmri.wfubmc.edu/software/pickatlas>); (2) To locate regions within the ROIs demonstrating a phase (encoding, retrieval) × success (hit, miss) interaction, we calculated the contrasts encoding deactivation (hits < misses), and retrieval activation (hits > misses), at an uncorrected threshold of  $\alpha < 0.05$ ; (3) a conjunction analysis of these contrasts was performed by inclusively masking the resulting *t* maps; (4) the mean cluster activity (parameter estimates) for encoding deactivation and retrieval activation of each individual participant were extracted using the Conbar toolbox (<http://cabezalab.org>). To assess the E/R flip, we

extracted encoding and retrieval activity of each ROI. Because deactivation is represented as negative parameters, the “delta” of neural activity was calculated as encoding activity subtracted by retrieval (Vannini et al., 2013). A larger absolute value reflects stronger activity.

### 2.7. Regression analyses

To test whether EF capacity differentially explains the successful memory neural activity of OAs compared to YAs, we first performed two regression analyses (using SPSS 25) in which the Age Group × EF score interaction was used as predictor and the overall neural activity in each of the two E/R flip regions as criterion. For each of these analyses, we identified and removed influential data points using Cook’s distance (*D*) as criterion (cut-off:  $D > 0.1$ ). After establishing a significant predictive power of the interaction term in each of the two analyses, we performed multi-regression analyses (backward method) separately for each group, for the corresponding E/R flip regions. In these analyses we used EF, age, education, and verbal intelligence as predictors, and Cook’s *D* > 0.1 as criterion to remove influential data points.

## 3. Results

### 3.1. Behavioral performance

We calculated general performance on the memory encoding and retrieval task using *d*-prime as measure and the performance of OAs and YAs on the neuropsychological tests. As illustrated in Table 1, independent sample *t*-tests revealed a significant difference in NART-IQ score ( $t(58) = 6.74, p < .001$ ), suggesting that the OAs had a higher estimated verbal intelligence. However, there was no significant difference regarding education level, EF, and memory performance, although the difference in memory performance was at trend level.

### 3.2. Regression analyses

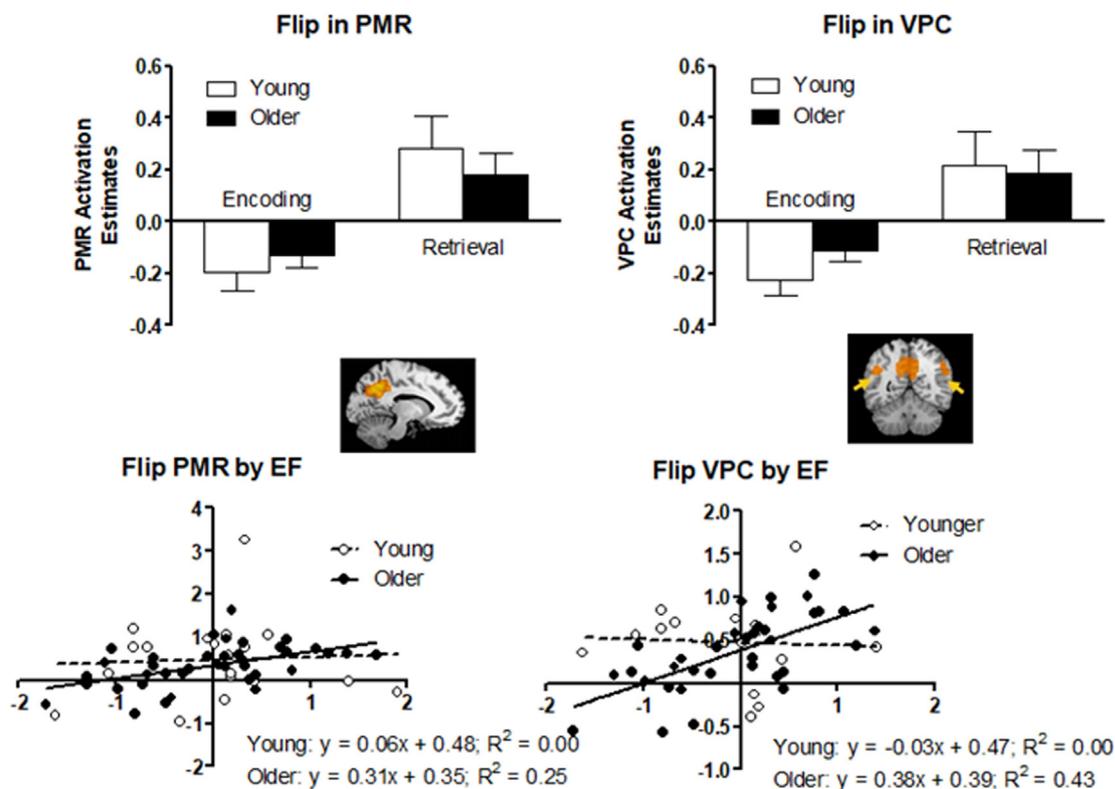
Initial regression analyses with the Age Group × EF score interaction as predictor revealed two influential data points for each of the two analyses (one OA and one YA). After removal of these data points, the interaction effect significantly predicted the amplitude of the E/R flip PMR activity ( $R^2 = 0.12, F(1, 54) = 7.32, p = .009, \beta = 0.35$ ), as well as VPC activity ( $R^2 = 0.13, F(1, 54) = 7.86, p = .007, \beta = 0.36$ ). The significance of the interaction term for the PMR and VPC E/R flip activity motivated follow-up multiple regression analyses for each age group separately. For the analysis of PMR and VPC activity in the OAs, there was one influential data point, respectively, three influential data

**Table 1**

Behavioral performance comparison between older and younger adult; Mean (SD) or *N*.

	Younger adults	Older adults	<i>t</i> (df = 56)	<i>p</i> (2-tailed)
<i>N</i>	19	39		
Sex (women)	10	16		
Age	23.47 (2.50)	66.92 (3.69)	53.90	
NART-IQ	93.44 (5.71)	119.51 (16.78)	8.66	< 0.001
Education level*	6.33 (0.69)	6.00 (0.95)		0.235
MMSE		29.27 (0.79)		
Backward Digit Span	8.68 (2.00)	8.15 (1.99)	−0.95	0.346
Mental Arithmetic	14.58 (3.65)	13.74 (2.70)	−0.89	0.382
<i>d</i> -prime	0.91 (0.39)	0.73 (0.23)	−1.80	0.084

\* Education level was calculated based on the Dutch educational system using a 7-point scale, with 1 = less than primary education and 7 = academic degree. The comparison between two groups was conducted using a Mann-Whitney *U* test. NART = National Adult Reading Test; IQ = intelligent quotient; MMSE = Mini-Mental State Examination



**Fig. 1.** EF capacity significantly predicted the amplitude of the “E/R flip” in older adults but not the young adults. Brain regions showing the locations of E/R flip (PMR and VPC) as identified by Daselaar (2009). Upper plots: encoding success activity and retrieval success activity in both younger and older adults. Bottom plots: the x-axis represents the composite z-scores that represent individuals’ executive functioning, and the y-axis represents parameter estimates by the fMRI analysis. PMR is posterior midline region, VPC is ventral parietal cortex.

points, which were removed. The analyses revealed that only EF survived as significant predictor of E/R flip PMR activity ( $R^2 = 0.25$ ,  $F(1, 36) = 12.28$ ,  $p = .001$ ,  $\beta = 0.50$ ) and of VPC activity ( $R^2 = 0.43$ ,  $F(1, 34) = 26.10$ ,  $p < .001$ ,  $\beta = 0.66$ ). However, for the YAs, no factor significantly predicted the amplitude of the E/R flip in PMR, whereas for VPC activity, only education level survived as predictor (after removal of three influential data points;  $R^2 = 0.46$ ,  $F(1, 13) = 11.21$ ,  $p = .005$ ,  $\beta = 0.68$ ). See Fig. 1 for an illustration.

#### 4. Discussion

In a previous study, we found that when provided with external support for the purpose of achieving better memory performance, only OAs with relatively high EF benefited (Fu et al., 2017). In this previous study, we used the CRUNCH framework to explain this phenomenon, suggesting that OAs with higher EF could enhance the activity of relevant brain regions in order to cope with the task demands of the effortful encoding conditions. The current fMRI study investigated the underlying neural basis of this hypothesis and specifically focused on the E/R flip activity in the PMR and VPC. We hypothesized that the EF capacity of the OAs should contribute to the amplitude of this neural activity. More specifically, stronger EF was hypothesized to be associated with a larger E/R flip amplitude linked to successful memory performance. At the same time, we expected EF to be either a negative or no predicting factor in YAs because of their sufficient capacity for recruitment of the necessary brain regions. The results supported our hypotheses. In the OAs, multiple regression analyses established the significant role of EF with activity in both PMR and VPC regions as criterion. In contrast, in the YAs, EF could significantly predict neither PMR nor VPC E/R flip activity.

In accordance with our hypothesis, OAs with relatively high EF displayed a larger amplitude for the E/R flip in PMR and VPC,

indicating that more neural activation contributes to successful memory performance. The E/R flip was firstly proposed by Daselaar (2009), based on an observation of neural activity associated with successful memory performance. This proposal was supported by a later fMRI study (Huijbers et al., 2012). One of the explanations for the E/R flip is the attention to memory (AtoM) account (Daselaar & Cabeza, 2008). This account states that deactivations during encoding are due to top-down attention, voluntary attention towards the study items. Activations during retrieval result from bottom-up attention, that is, voluntary attention towards the memory cue that is redirected to the internal mnemonic associations evoked by the memory cue (Daselaar, 2009; Huijbers et al., 2012). Our findings are consistent with this account. Unlike low-EF OAs, high-EF OAs are able to use their resources not only by devoting more top-down attention during encoding, but also by directing more bottom-up attention during retrieval, as evident by the amplitude of the E/R flip. We assume that we did not observe this phenomenon in the group of YAs because they have ample cognitive resources, implying little EF-related variation in brain activations.

It is worthy of note that, although we only found a trend towards a significant difference between OAs and YAs in their memory performance, this is not in conflict with our previous claim that OAs display episodic memory decline and that only OAs with relatively high EF benefit from external support. This is because in the present study OAs were all relatively high functioning. Moreover, the scores of the OAs on verbal IQ even surpassed those of the YAs. In fact, when we divide the OAs group into high and low EF groups (based on a median split, as in Fu et al., 2017), we again observed a trend difference in memory performance between YAs and low EF OAs ( $t(35) = -1.85$ ,  $p = .07$ ), whereas there was no difference between YAs and high EF OAs ( $t(38) = -1.56$ ,  $p = .13$ ). This provides further evidence for the importance of taking individual differences into consideration in ageing studies.

Elaborating on our previous study (Fu et al., 2017), the current study investigated the neural basis of the association between EF and memory performance. Results from the regression analyses confirmed that stronger EF abilities in late adulthood, putatively indicating a stronger capacity for using limited cognitive resources, were significantly and positively associated with E/R flip-associated neural activity.

#### CRedit authorship contribution statement

**Li Fu:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing - original draft, Visualization, Funding acquisition. **Joseph H.R. Maes:** Conceptualization, Formal analysis, Writing - review & editing, Visualization, Project administration. **Roy P.C. Kessels:** Writing - review & editing, Supervision, Project administration. **Willem Huijbers:** Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Supervision, Project administration.

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#### Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.nlm.2020.107251>.

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