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Depressive symptoms are associated with reduced positivity preferences in episodic memory in aging

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ABSTRACT

Age-related positivity preferences are represented as greater memory benefits for positive and/or reduced benefits for negative material with age. It is unknown if positivity preferences are limited to older adults without depressive symptoms. In this fMRI study, adults across the lifespan with a range of depressive symptoms were scanned as they rated emotional intensity of images and subsequently completed a recognition memory task. Behavioral, univariate, and functional connectivity analyses provided evidence for interactive effects between age and depressive symptoms. With low depressive symptoms, typical age-related emotional preferences emerged: younger age was associated with better memory for negative images, and this benefit was reduced with older age. With increasing depressive symptoms in older age, positivity preferences were reduced, manifesting as improvements in negative memory. The neural data highlighted potential underlying mechanisms, including reductions in prefrontal cortex connectivity reflecting diminished ability to engage regulatory processes to reduce negative affect in older participants with higher depressive symptoms. These findings suggest that depressive symptoms in older adulthood reduce positivity preferences through alterations in neural networks underlying emotion regulation.

1. Introduction

While emotional content is often better remembered than neutral content across adulthood (LaBar and Cabeza, 2006), older age has been associated with both enhanced benefits for positive and reduced benefits for negative material relative to neutral material—a pattern known as positivity preference (Murphy and Isaacowitz, 2008). Enhanced positivity and reduced negativity are often explained in terms of the socioemotional selectivity theory (SST; Carstensen et al., 1999; Carstensen et al., 2006), which states that the relative importance of life goals shifts as actual, and perceived, time left in one's life diminishes. In early adulthood, individuals may prioritize future goals as they make long-term plans for their lives. Over time, these goals realign such that priorities in late life focus on present-oriented goals such as maintaining meaningful relationships and emotional well-being. One method for promoting these goals is engagement in emotion regulation to increase positive affect and decrease negative affect (Barber et al., 2016; Carstensen et al., 2003).

Emotion regulation at the neural level involves recruitment of prefrontal regions that modulate activity in emotional appraisal and perceptual processing regions (Ochsner et al., 2012). For example, positive reappraisal has been shown to engage lateral and medial prefrontal cortical (PFC) areas (Dore et al., 2017; Halfmann et al., 2021). When engaging emotion regulation to reduce negative affect, this increase in PFC activity is associated with a reduction in amygdala activity (for reviews, see Berboth and Morawetz, 2021; Etkin et al., 2015).

Our lab previously conducted an fMRI study to assess emotional memory differences between young and older adults and the neural mechanisms involved not only in stimulus processing, but also in anticipation of the stimulus (Corbett et al., 2020). Consistent with SST, older adults showed worse memory for negative than neutral images, while young adults' memory did not differ between valence conditions. Further, only older adults showed inverse functional connectivity between ventromedial PFC (vmPFC) and amygdala during emotional anticipation, suggesting that older adults engaged spontaneous emotion regulation strategies to re-

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duce the negative affect and memory of the upcoming stimulus[1]. These findings are in line with other work showing amygdala activity is modulated by vmPFC regulation processes to a greater extent in older than in younger adults (Leclerc and Kensinger, 2011; Roalf et al., 2011; Sakaki et al., 2013; St Jacques et al., 2010). In addition to vmPFC, dorsomedial PFC (dmPFC) has also been associated with emotion regulation, playing a role in up- or downregulating emotional responses in the appraisal of experiences (for review, see Kensinger and Ford, 2021). Previous work has shown inverse connectivity between dmPFC and hippocampus in older adults for negative events (Ford and Kensinger, 2018), which may be related to reduced vividness of memory for negative events.

The literature reviewed thus far pertains to healthy adults. However, there is reason to believe processes underlying positivity preferences may be disrupted by symptoms of depression. Individuals with both clinical and subclinical depression show substantially better memory for negative than for positive or neutral material (for meta-analysis and review, see James et al., 2021). A frequently cited explanation for such findings is that material which is congruent with one's mood state is better remembered than that which is incongruent (for reviews, see Holland and Kensinger, 2010; Matt et al., 1992). Onset and maintenance of negative mood states in depression have been linked to dysfunctional emotion regulation. Depression is frequently associated with use of minimally effective or even maladaptive emotion regulation strategies, such as rumination, and with difficulty engaging the more effective strategies like reappraisal (Joormann and Stanton, 2016). Depression has been associated with amygdala hyperactivity in response to negative stimuli that is not modulated by prefrontal regions the way it is in healthy controls (for meta-analysis and review, see Hamilton et al., 2012). Even when depressed individuals are able to downregulate amygdala activity comparably to controls, this effect is reduced with higher symptom severity (Erk et al., 2010). Similar effects have also been reported during the anticipation of negative events (Abler et al., 2007).

Few studies investigating emotional episodic memory in depression have included older participants in their samples (for review, see James et al., 2021). Furthermore, even when studies include older adults, comparisons are often made between depressed and healthy control groups. It may, however, be more informative to assess depression as existing along a continuum because while prevalence of diagnosed major depressive disorder (MDD) decreases with age, clinically significant symptoms that do not meet the threshold of MDD are quite common among older adults (Polyakova et al., 2014). Additionally, a number of barriers may stand in the way of individuals obtaining a diagnosis of MDD, such as poor access to healthcare (Williams et al., 2017) and stigma associated with mental illness (Conner et al., 2010). Thus, we believed it was important to consider not only cases of diagnosed depression in the current study, but also levels of depressive symptoms that may or may not meet the criteria for diagnosis.

In Corbett et al. (2020), young adults had significantly greater levels of depressive symptoms compared to older adults. Because depression is known to impact emotion regulation, we could not rule out the possibility that young adults' failure to downregulate negative affect was due to their depressive symptoms. Similarly, the intact emotion regulation effects for older adults may have been a consequence of the low levels of depressive symptoms in this group. Furthermore, because Corbett et al. only used negative and neutral images, they could not test whether older adults also showed greater memory benefits for positive relative to neutral images than the young—a pattern that would provide additional support for positivity preference in older age. The design used in the current fMRI study elucidates these uncertainties and allowed us to directly investigate the interactive effects of age and depressive symptoms on memory for emotional events and associated neural processes. While undergoing scanning, participants ages 18-76 with a range of depressive symptom severity rated the emotional intensity of positive, neutral, and negative images that were preceded by audio cues to signal the valence. Participants then completed a recognition task for the images outside of the scanner.

We predicted the memory preference for negative events should be reduced with age, and the memory preference for positive events should increase with age, in line with SST. We predicted these relationships would be weaker with higher levels of depressive symptoms, which would support the idea that depressive symptoms reduce the positivity preference in older adults. To investigate how age and depressive symptoms uniquely and jointly affected stimulus processing, we conducted univariate analyses in regions of interest (ROIs). Similar to the behavioral predictions, we expected age-related positivity preferences to be reduced with higher levels of depressive symptoms, as exhibited by reductions in preferential processing of positive images and/or increases in processing of negative images. To investigate emotion regulation, we assessed functional connectivity during the cue period using generalized psychophysiological interaction (gPPI) analyses. Seed regions in vmPFC and dmPFC were selected based on findings in prior work of their role in exerting regulatory control to increase or decrease activity in other regions. We predicted that higher level of depressive symptoms in older age would be associated with diminished upregulation of positive affect and downregulation of negative affect.

2. Materials and methods

Complete methodological details are presented in the *Supplemental Materials*.

2.1. Participants and procedure

Participants were 24 females and 32 males, ages 18–76 (mean 40.55 ± 16.99; mean education 14.73 ± 2.38 years; race: 41.1% White/Caucasian, 39.3% Black/African American, 7.1% Asian, 7.1% multiracial, 1.8% Middle Eastern, 1.8% Pacific Islander, 1.8% Hispanic/Latino; ethnicity: 80.4% not Hispanic/Latino, 7.1% Hispanic/Latino, 12.5% not indicated). Twenty-three participants had been diagnosed with major depressive disorder (MDD), and of these, 14 indicated they were taking medication[2] for depression at the time of study (see *Supplemental Materials* for details).

Participants were administered a series of questionnaires and neuropsychological assessments, including the Revised Center for Epidemiological Studies Depression Scale (CESD-R; Eaton et al., 2004) to assess depressive symptomology. The CESD-R has been validated for assessing depressive symptoms in the general population (Van Dam and Earleywine, 2011) and in older adults (Katz et al., 2020). Unlike the original CES-D, which uses a cut-score of 16 to identify those at risk for depression, the CESD-R uses an algorithmic approach based on DSM criteria to classify scores into five categories, from "no clinical significance" (i.e., scores under 16) to "meets criteria for major depressive episode" (i.e., anhe-

[1] This conclusion was drawn from the imaging data only; participants were not explicitly asked to engage specific regulation strategies, nor were they asked about their use of regulation strategies after the task.

[2] Medication was not significantly correlated with age, $r(56) = .05$, $p = 0.72$, or CESD-R, $r(56) = .05$, $p = 0.74$. When added as a covariate of non-interest to the analyses, the pattern of results remained the same.

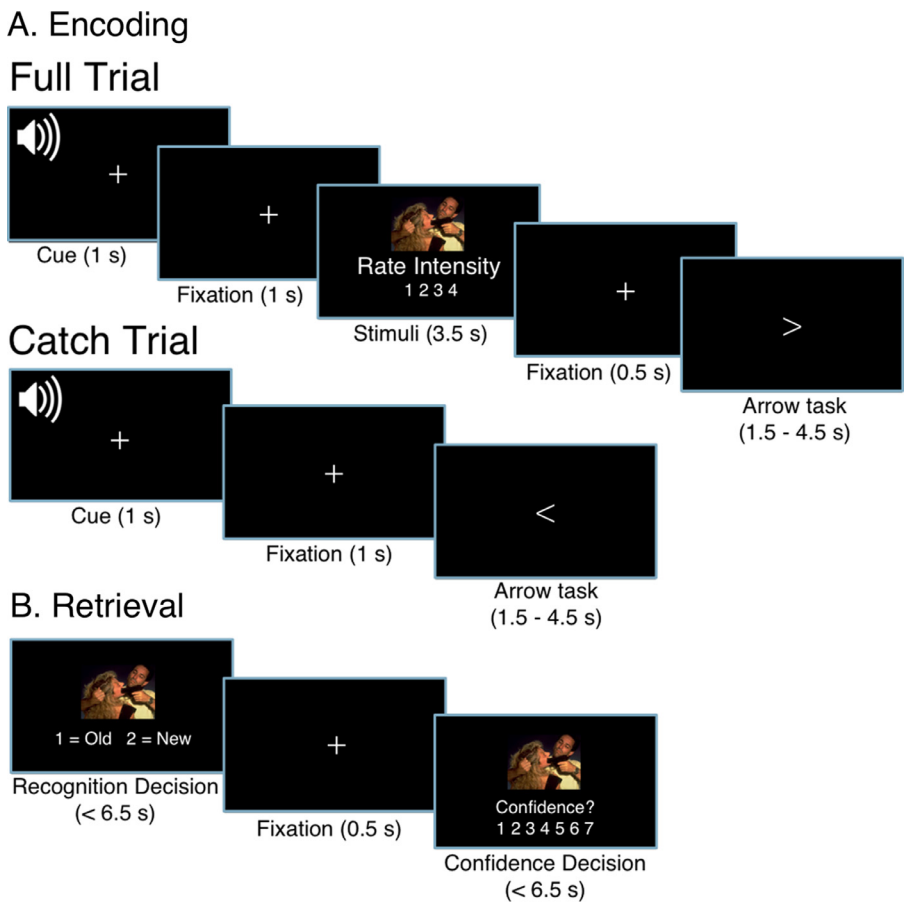

Fig. 1. Experimental Design for Encoding (A) and Retrieval (B).

donia or dysphoria, plus an additional four symptoms endorsed as occurring nearly every day for two weeks). CESD-R scores in the sample ranged from zero to 52 (mean 23.67 ± 14.83).

The incidental encoding task (completed in an fMRI scanner) consisted of 252 positive, neutral, and negative images from the Nencki Affective Picture System (NAPS; Marchewka et al., 2014) and International Affective Picture System (IAPS; Lang et al., 2008). As illustrated in Fig. 1A, all trials started with the auditory cue that signaled the valence of the upcoming stimulus, followed by a brief fixation period. The positive cue was the sound of a winning slot machine, the neutral cue was a whistling tone, and the negative cue was the sound of tires screeching. For the full trials (75% of trials), the stimulus was then presented, and participants were tasked with rating the emotional intensity of the image on a 1–4 scale, with 1 being the least intense and 4 being the most intense. Participants were informed that cues were always valid indicators of the stimulus valence. For the remaining 25% of trials ("catch trials"), no image followed the audio cue (see Fig. 1A). Catch trials were included to estimate unique cue-related activity, as has been done in previous studies (e.g., Corbett et al., 2020; Corbetta et al., 2000; Sussman et al., 2017; Wheeler et al., 2006). One might wonder if there are any carryover effects of emotional arousal from prior stimuli. This is possible in any event-related emotional study, not just ours. However, the trial order was randomized, so any lingering effects from the emotionally-valenced stimuli would not affect one valence condition more than the others.

In the retrieval task, participants first made a recognition decision to indicate whether the image had been shown during encoding, then they rated their confidence on a 1–7 scale (see Fig. 1B). Retrieval stimuli consisted of all 252 old images and 126 new images. Stimuli were counterbalanced across participants such that the new images at retrieval differed across participants. Participants completed practice trials for both encoding and retrieval. Practice was repeated until participants demonstrated understanding of the task. For additional task details, see the *Supplemental Materials*.

As noted in Corbett et al. (2020), our use of valenced auditory cues differs from the visual cues (e.g., X and O) and neutral tones used in many previous studies with young adults (e.g., Grupe et al., 2013; Mackiewicz et al., 2006; Nitschke et al., 2006; Sarinopoulos et al., 2010) to signal the valence of the upcoming stimuli. Initial piloting revealed that older participants experienced difficulty mapping the associations between these kinds of visual cues and the valence categories in our task. This led us to use naturalistic sounds (1 for each valence condition) with preexisting associations to the valence conditions that they signaled (e.g., screeching tires can precede the negative event of a car wreck), which made it easier for both young and older participants to remember the associations. Furthermore, using visual cues would have made it more challenging to disentangle anticipatory visual perceptual neural signals from those associated with perception of the cue.

2.2. Behavioral analyses

Memory performance was estimated using the *Pr* discrimination index: p(hit) – p(false alarm) and memory bias was estimated using the *Br* bias index: p(false alarm)/(1 – *Pr*) (Snodgrass and Corwin, 1988). To investigate the influence of age and depressive symptoms on emotional memory discriminability and bias, we cre-

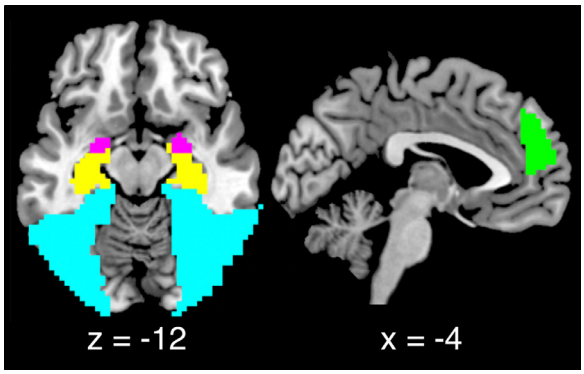

Fig. 2. ROIs Used in Imaging Analyses.
Note. Magenta = amygdala, yellow = hippocampus, cyan = ventral occipitotemporal cortex (VOTC), green = dorsomedial prefrontal cortex (dmPFC) (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

ated positive – neutral and negative – neutral difference scores. These values were entered into separate hierarchical regression equations as the outcome variables, with age and CESD-R score (both continuous variables) entered as predictors in Model 1. The interaction between these 2 variables was added in Model 2. The predictor variables were centered around their respective means. Similar steps were taken to investigate age and depressive effects on intensity ratings.

2.3. fMRI analysis

See the *Supplemental Materials* for information on fMRI acquisition and additional details about the imaging analyses (e.g., preprocessing, first level modeling).

2.3.1. Region of Interest (ROI) definition

Four bilateral ROIs were generated from the Anatomical Automatic Labeling (AAL) system (Tzourio-Mazoyer et al., 2002) implemented in the WFU Pickatlas toolbox (Maldjian et al., 2003)––amygdala, hippocampus, and ventral occipitotemporal cortex (VOTC; consisting of fusiform, parahippocampal, inferior occipital, middle occipital, and inferior temporal AAL regions). One functional dmPFC ROI was identified from a task > baseline univariate F contrast (center at [0, 53, 29], 369 voxels). The ROIs are shown in Fig. 2. These ROIs were selected to investigate the effects of age and depressive symptoms on regions associated with emotion (amygdala; Pessoa and Adolphs, 2010; Sergerie et al., 2008), memory encoding (hippocampus; Dahlgren et al., 2020; Murty et al., 2010), visual processing (VOTC; Fusar-Poli et al., 2009; Sambuco, 2022), and regulation (dmPFC; Berboth and Morawetz, 2021; Pico-Perez et al., 2017).

2.3.2. Univariate analysis

For univariate analysis, neural activity was modeled to the onset of the stimulus image. A valence (positive, neutral, negative) ANOVA model was created for the encoding period using only subsequent hit full trials. Mean activity within each ROI was extracted for the 3 valence conditions for each participant. To investigate whether age and depressive symptoms uniquely or interactively predicted encoding differences between valence conditions, we created positive – neutral and negative – neutral difference scores for each ROI to serve as the outcome variable. Hierarchical regressions were conducted as described above.

2.3.3. Functional connectivity analysis

We examined functional connectivity during catch trials using vmPFC and dmPFC seeds (6mm spheres around [18, 66, -3] and [12, 60, 21], respectively; regions identified in Corbett et al. (2020). Because only catch trials were used for this analysis, neural activity was modeled to the onset of the audio cue. The SPM12 generalized psychophysiological interactions (gPPI) toolbox (http://brainmap.wisc.edu/PPI) (McLaren et al., 2012) was used to estimate whole-brain connectivity with the seed regions. Parameter estimates of connectivity were extracted from left and right amygdala (separately for left and right hemispheres due to prior findings of lateralization for different types of regulation; for review, see Barreiros et al., 2019; Vrticka et al., 2011), bilateral hippocampus, and VOTC regions. Age, depressive symptoms, and their interaction were examined as predictors of functional connectivity using hierarchical regression as described above. It should be noted that due to signal dropout, 3 participants did not have data in the vmPFC sphere. The 53 participants with sufficient vmPFC data were used in this analysis. All 56 participants were used in the dmPFC connectivity analysis.

4. Results

All effects for positive and negative valence conditions are presented relative to the neutral valence condition.

4.1. Behavioral

Age significantly moderated the relationship between depressive symptoms and negative memory discriminability (i.e., negative *Pr* – neutral *Pr*; see Table 1). No significant effects were found for positive memory discriminability or any of the bias analyses. Fig. 3 presents the simple slopes for visualization of the moderator effect: at the mean age of the sample, CESD-R score did not have much of an effect on memory benefits for negative images. However, at older ages (1 standard deviation above the mean), higher CESD-R score was associated with larger memory benefits for negative images. Younger individuals (1 standard deviation below the mean) tended to show the opposite trend: lower CESD-R score was associated with larger memory benefits for negative images.

For intensity ratings, older age predicted lower negative intensity ratings (see Table 1). That is, older participants tended to provide lower intensity ratings for negative relative to neutral images. No effects were significant for positive intensity ratings.

Our diverse sample allowed us to explore whether race contributed to any observed effects. Though our Black/African American and White/Caucasian participants did not differ on positive or negative discriminability or bias ($t(42)$s <1.18, $ps > .246$), we dummy coded race and used it as a covariate in our behavioral analyses. The significance of the results remained unchanged, with no significant effects found for positive memory discriminability or any of the bias analyses ($ps > 0.058$ for all effects); the moderator effect remained significant for negative memory discriminability ($p = 0.034$), suggesting race did not play a major role in these effects.

4.2. Imaging

4.2.1. Univariate

Univariate analyses examined the influence of age, depressive symptoms, and their interaction on activity associated with event encoding during full trials. In the amygdala, higher CESD-R score was associated with lower activity for emotional (both positive and negative) relative to neutral trials, while older age was associated with lower activity only for negative relative to neu-

Table 1
Results for regression analyses with age and CESD-R predicting memory performance and intensity ratings.

	Model 1			Model 2		
	B	*SE B*	*β*	*B*	*SE B*	*β*
Positive *Pr*						
Age	-0.00008	0.001	-.016	0	0.001	.041
CESD-R	0	0.001	.034	0	0.001	.029
Age x CESD-R	—	—	—	0.00008	0	.269
R^2		.002			.071	
F for ΔR^2		0.047			3.856	
Negative *Pr*						
Age	0.00001	0.001	.002	0	0.001	.073
CESD-R	0	0.001	.024	0	0.001	.018
Age x CESD-R	—	—	—	0	0	.333[a]
R^2		.001			.106	
F for ΔR^2		0.015			6.146[a]	
Positive *Br*						
Age	0.002	0.001	.229	0.002	0.001	.232
CESD-R	0.001	0.001	.142	0.001	0.001	.142
Age x CESD-R	—	—	—	0.000006	0	.011
R^2		.052			.052	
F for ΔR^2		1.448			0.006	
Negative *Br*						
Age	0	0.001	-.048	-0.001	0.001	-.064
CESD-R	0	0.002	.038	0	0.002	.040
Age x CESD-R	—	—	—	-0.00005	0	-.074
R^2		.005			.01	
F for ΔR^2		0.133			0.276	
Positive Intensity Rating						
Age	-0.006	0.003	-.259	-0.005	0.003	-.246
CESD-R	-0.006	0.004	-.247	-0.006	0.004	-.247
Age x CESD-R	—	—	—	0.0001	0	.064
R^2		.088			.092	
F for ΔR^2		2.502			0.22	
Negative Intensity Rating						
Age	-0.008	0.004	-.287[a]	-0.007	0.004	-.240
CESD-R	-0.006	0.005	-.199	-0.006	0.004	-.200
Age x CESD-R	—	—	—	0	0	.229
R^2		.086			.136	
F for ΔR^2		2.446			2.957	

Note. All conditions presented in the table are relative to the neutral valence condition.
[a] $p < 0.05$

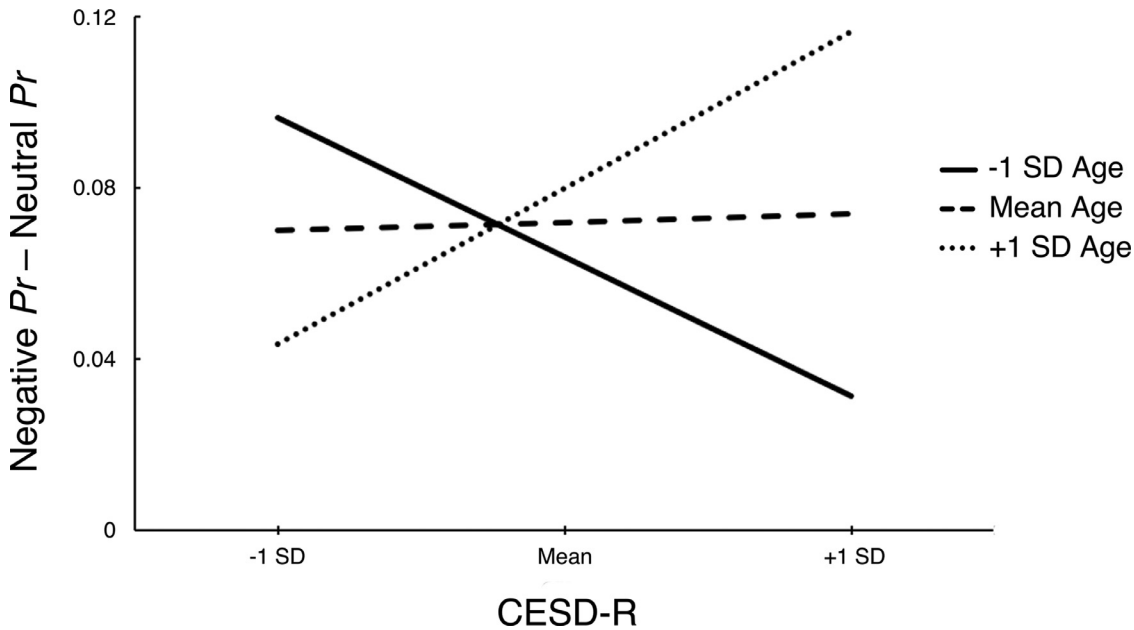

Fig. 3. Simple Slopes for Age and CESD-R Predicting Negative Memory Discriminability.
Note. The lines represent age: mean (dashed), - 1 SD (solid), + 1 SD (dotted). The p value for the interaction term: $p = .016$.

Table 2
Results for regression analyses with age and CESD-R predicting univariate activity.

	Model 1			Model 2		
	B	*SE B*	*β*	*B*	*SE B*	*β*
Amygdala						
Positive						
Age	-0.003	0.003	-0.172	-0.003	0.003	-0.185
CESD-R	-0.008	0.003	-0.344[a]	-0.008	0.003	-0.343[a]
Age x CESD-R	—	—	—	-0.00008	0	-0.062
R^2		.110			0.114	
F for ΔR^2		3.275[a]			0.212	
Negative						
Age	-0.01	0.003	-0.395[a]	-0.011	0.003	-0.415[a]
CESD-R	-0.009	0.004	-0.307[a]	-0.009	0.004	-0.305[a]
Age x CESD-R	—	—	—	0	0	-0.092
R^2		.173			0.181	
F for ΔR^2		5.529[a]			0.512	
Hippocampus						
Positive						
Age	-0.001	0.002	-0.051	-0.001	0.002	-0.088
CESD-R	-0.003	0.002	-0.198	-0.003	0.002	-0.194
Age x CESD-R	—	—	—	0	0	-0.174
R^2		0.035			0.064	
F for ΔR^2		0.968			1.602	
Negative						
Age	-0.003	0.002	-0.186	-0.003	0.002	-0.189
CESD-R	-0.003	0.003	-0.185	-0.003	0.003	-0.185
Age x CESD-R	—	—	—	-0.00001	0	-0.014
R^2		0.047			0.047	
F for ΔR^2		1.301			0.01	
VOTC						
Positive						
Age	-0.00004	0.005	0.001	-0.002	0.005	-0.058
CESD-R	-0.006	0.006	-0.139	-0.006	0.006	-0.133
Age x CESD-R	—	—	—	-0.001	0	-0.278[a]
R^2		0.019			0.093	
F for ΔR^2		0.523			4.215[a]	
Negative						
Age	-0.002	0.006	-0.048	-0.004	0.006	-0.087
CESD-R	0.001	0.007	0.021	0.001	0.007	0.025
Age x CESD-R	—	—	—	-0.001	0	-0.186
R^2		0.003			0.036	
F for ΔR^2		0.089			1.785	
dmPFC						
Positive						
Age	-0.006	0.007	-0.128	-0.006	0.007	-0.125
CESD-R	-0.006	0.008	-0.122	-0.006	0.008	-0.123
Age x CESD-R	—	—	—	0.00004	0	0.015
R^2		0.021			0.022	
F for ΔR^2		0.578			0.011	
Negative						
Age	-0.012	0.007	-0.246	-0.014	0.007	-0.281
CESD-R	0.001	0.008	0.013	0.001	0.008	0.016
Age x CESD-R	—	—	—	-0.001	0	-0.162
R^2		.063			.088	
F for ΔR^2		1.778			1.429	

Note. All conditions presented in the table are relative to the neutral valence condition.
Key: dmPFC, dorsomedial prefrontal cortex; VOTC, ventral occipitotemporal cortex.
[a] $p < 0.05$

tral trials (see Table 2). Within VOTC, age significantly moderated the relationship between CESD-R and activity during positive trials. The simple slopes for this moderator effect are shown in Fig. 4. At low levels of depression (-1 SD CESD-R), older participants (+1 SD age) showed greater VOTC activity for positive than neutral trials than did younger participants (-1 SD age). With increasing levels of depression, older participants showed a reduction in VOTC activity during positive trials, while younger participants showed a slight increase. No other univariate effects were significant.

4.2.2. Functional connectivity

Functional connectivity analyses examined the influence of age and depressive symptoms on emotional anticipation/preparation during catch trials. Results are presented in Table 3. Older age predicted greater positive vmPFC-left amygdala coupling during positive relative to neutral event anticipation (i.e., cue period). No other effects with the vmPFC seed were significant. For dmPFC, higher CESD-R scores predicted greater positive connectivity with right amygdala for positive relative to neutral catch trials. Older age was associated with lower dmPFC-hippocampus positive connectivity for negative relative to neutral trials. Older age was also predictive lower dmPFC-VOTC positive connectivity negative relative to neutral trials, and notably, this relationship was moderated by CESD-R. The simple slopes (Fig. 5) reveal minimal age differences in connectivity with high depressive symptoms (+1 SD CESD-R). With low depressive symptoms (-1 SD CESD-R), younger participants (-1 SD age) showed positive connectivity between

Table 3
Effects of age and depressive symptoms on functional connectivity.

	Model 1			Model 2		
	B	*SE B*	*β*	*B*	*SE B*	*β*
vmPFC						
Left Amygdala						
Positive						
Age	0.015	0.006	0.343[a]	0.014	0.006	0.330
CESD-R	0.014	0.007	0.275	0.014	0.007	0.278
Age x CESD-R	—	—	—	0	0	-0.057
R^2		0.139			.142	
F for ΔR^2		4.04[a]			0.176	
Negative						
Age	0.002	0.006	0.055	0.001	0.006	0.017
CESD-R	0.004	0.007	0.076	0.004	0.007	0.089
Age x CESD-R	—	—	—	0	0	-0.151
R^2		0.006			0.027	
F for ΔR^2		0.160			1.047	
Right Amygdala						
Positive						
Age	0.006	0.005	0.168	0.006	0.006	0.166
CESD-R	0.010	0.006	0.222	0.010	0.006	0.222
Age x CESD-R	—	—	—	-0.00002	0	-0.008
R^2		0.056			0.056	
F for ΔR^2		1.480			0.003	
Negative						
Age	0.001	0.004	0.020	0	0.005	-0.004
CESD-R	0.0001	0.005	0.001	0	0.005	0.010
Age x CESD-R	—	—	—	0	0	-0.096
R^2		0			0.009	
F for ΔR^2		0.010			0.422	
VOTC						
Positive						
Age	0.002	0.008	0.036	0.002	0.008	0.040
CESD-R	0.00002	0.009	0	-0.00005	0.009	-0.001
Age x CESD-R	—	—	—	0.00005	0	0.014
R^2		.001			0.001	
F for ΔR^2		0.033			0.008	
Negative						
Age	-0.003	0.008	-0.060	-0.002	0.008	-0.036
CESD-R	-0.001	0.009	-0.018	-0.002	0.009	-0.027
Age x CESD-R	—	—	—	0	0.001	0.098
R^2		0.003			0.012	
F for ΔR^2		0.084			0.437	
Hippocampus						
Positive						
Age	0.002	0.004	0.085	0.001	0.004	0.059
CESD-R	0	0.004	0.014	0.001	0.004	0.023
Age x CESD-R	—	—	—	0	0	-0.105
R^2		.007			0.017	
F for ΔR^2		0.171			0.503	
Negative						
Age	-0.004	0.003	-0.163	-0.004	0.003	-0.194
CESD-R	-0.001	0.004	-0.033	-0.001	0.004	-0.022
Age x CESD-R	—	—	—			
R^2		0.025			0.039	
F for ΔR^2		0.631			0.712	
dmPFC						
Left Amygdala						
Positive						
Age	-0.003	0.006	-0.066	-0.003	0.006	-0.079
CESD-R	0.005	0.007	0.094	0.005	0.007	0.095
Age x CESD-R	—	—	—	0	0	-0.063
R^2		0.017			0.021	
F for ΔR^2		0.463			0.199	
Negative						
Age	-0.006	0.006	-0.141	-0.007	0.006	-0.157
CESD-R	0.010	0.007	0.201	0.010	0.007	0.202
Age x CESD-R	—	—	—	0	0	-0.078
R^2		0.078			0.084	
F for ΔR^2		2.250			0.328	
Right Amygdala						
Positive						
Age	0.006	0.005	0.159	0.006	0.006	0.162
CESD-R	0.016	0.006	0.345[a]	0.016	0.006	0.345[a]

(*continued on next page*)

Table 3 (*continued*)

	Model 1			Model 2		
	B	*SE B*	*β*	*B*	*SE B*	*β*
Age x CESD-R	—	—	—	0.00004	0	0.015
R^2		0.109			0.109	
F for ΔR^2		3.25[a]			0.012	
Negative						
Age	0.001	0.006	0.028	0.001	0.007	0.034
CESD-R	0.009	0.007	0.178	0.009	0.007	0.177
Age x CESD-R	—	—	—	0.0001	0	0.026
R^2		0.029			0.030	
F for ΔR^2		0.796			0.034	
VOTC						
Positive						
Age	-0.004	0.008	-0.078	-0.003	0.008	-0.065
CESD-R	0.006	0.009	0.093	0.006	0.009	0.092
Age x CESD-R	—	—	—	0	0	0.058
R^2		0.019			0.023	
F for ΔR^2		0.522			0.173	
Negative						
Age	-0.024	0.009	-0.358[a]	-0.020	0.009	-0.301[a]
CESD-R	-0.008	0.010	-0.100	-0.008	0.010	-0.105
Age x CESD-R	—	—	—	0.001	0.001	0.266[a]
R^2		0.115			0.182	
F for ΔR^2		3.444[a]			4.273[a]	
Hippocampus						
Positive						
Age	-0.002	0.004	-0.061	-0.003	0.004	-0.099
CESD-R	0.005	0.005	0.137	0.005	0.005	0.141
Age x CESD-R	—	—	—	0	0	-0.179
R^2		0.028			0.058	
F for ΔR^2		0.760			1.677	
Negative						
Age	-0.011	0.004	-0.350[a]	-0.011	0.004	-0.358[a]
CESD-R	-0.002	0.005	-0.069	-0.002	0.005	-0.068
Age x CESD-R	—	—	—	-0.0001	0	-0.033
R^2		0.112			0.113	
F for ΔR^2		3.346[a]			0.063	

Note. All conditions presented in the table are relative to the neutral valence condition. Seed regions appear in bold text.
Key: dmPFC, dorsomedial prefrontal cortex; vmPFC, ventromedial prefrontal cortex, VOTC, ventral occipitotemporal cortex.
[a] $p < 0.05$

dmPFC and VOTC while older participants (+1 SD age) showed inverse connectivity.

5. Discussion

With this study, we sought to determine whether depressive symptoms in older age diminish the behavioral and neural correlates of positivity preferences that are often exhibited in healthy aging. The data provide support for the hypothesis that depressive symptom severity can reduce age-related positivity preferences in memory discriminability, perceptual processing, and anticipatory emotion regulation. These findings are discussed in detail below.

5.1. Interactive effects between age and depressive symptoms

We predicted the memory preference for negative events and positive events would be reduced and increased with age, respectively, consistent with the SST, and that these relationships would be weaker with higher levels of depressive symptoms. Our results showed that at low levels of depressive symptoms, older age predicted lower memory benefits for negative material—consistent with prior studies in healthy aging (Charles et al., 2003; Gruhn et al., 2007; Leclerc and Kensinger, 2011). The majority of studies investigating positivity preferences in aging have been conducted on samples without depression. In the present study, behavioral results showed that when depressive symptoms are evident, there is a reversal in the pattern of age effects such that older participants with higher CESD-R scores show greater negative memory benefits than young, middle-aged adults, and older adults with low CESD-R scores. This suggests that higher levels of depressive symptoms in older adults are associated with weakened positivity preferences in memory discriminability. One prior study (Barber et al., 2020) showed that depressive symptoms did not moderate positivity preferences. However, their study was not designed to test the role of depression, thus depression scores tended to be lower among their participants (16% of their participants scored above the cutoff of 5 on the 15-item Geriatric Depression Scale vs. 66% of ours who scored above the CESD-R cutoff of 16). These differences may have contributed to the discrepancy in the findings.

With low levels of depressive symptoms, positive memory discriminability was essentially equivalent across age. This finding may seem at odds with the idea of positivity preferences, in which one might expect greater positive memory with age. However, a meta-analysis (Reed et al., 2014) found that older adults' bias for positive information is most consistently observed when their attention is unconstrained versus constrained by task (e.g., "Does the stimulus present an indoor or outdoor scene?"). Carstensen and DeLiema (2018) suggest that passive viewing of experimental stimuli does not interfere with the activated goals that, according to the SST, differ for younger and older adults. Requiring participants to actively engage with the material, on the other hand—as we did in this study—essentially assigns new goals that may override, at least temporarily, the goal of older adults to prioritize positive information. It should be noted, however, that other studies

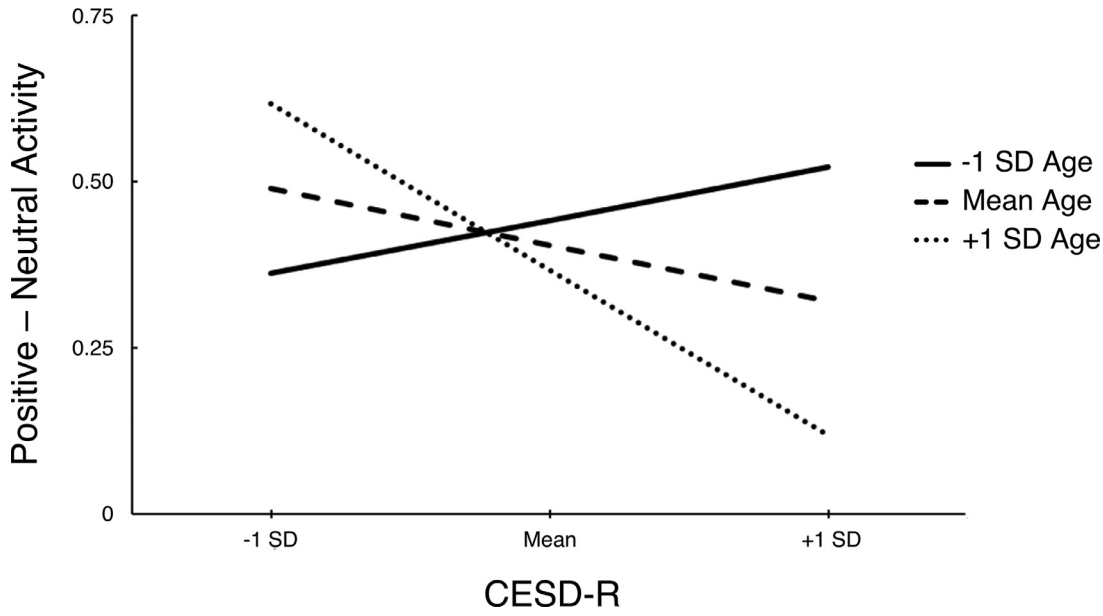

Fig. 4. Simple Slopes for Age and CESD-R Predicting VOTC Positive Activity.
Note. The lines represent age: mean (dashed), - 1 SD (solid), + 1 SD (dotted). Univariate activity for the positive condition is presented relative to the neutral condition. The p value for the interaction term: $p = 0.045$. VOTC, ventral occipitotemporal cortex (bilateral fusiform, parahippocampal, inferior occipital, middle occipital, and inferior temporal AAL regions).

have shown the magnitude of the positivity effect to be unaffected by experimental manipulations such as incidental versus intentional encoding (Hess et al., 2013) or passive viewing versus active engagement with the stimuli (Emery and Hess, 2008; Gong and Fung, 2020; Tomaszczyk et al., 2008). The differences in the results between our study and those cited in the previous sentence cannot be explained by differences in valence and arousal ratings, as these ratings were similar across studies. Likewise, the delay between encoding and retrieval was roughly similar across studies. It remains unclear why our results differed from those in the studies cited here, but characteristics such as the diversity of our sample and the presence of depressive symptoms may have been contributing factors.

An unexpected finding is that for younger participants, higher level of depressive symptoms was associated with worse memory for negative relative to neutral images. A reduction in experienced arousal could account for this finding. Though the Age x CESD-R interaction only marginally predicted negative intensity ratings ($\beta = .23$, $p = .09$), examination of the simple slopes (*Supplemental Figure S2*) revealed that in younger age, higher CESD-R score predicted lower intensity rating for negative images. Anhedonia has been associated with reduced emotional experience (Mathews and Barch, 2006) and with reduced emotional memory for negative material (Olsen et al., 2015). While the current study did not show that anhedonia symptoms as measured by the CESD-R were correlated with age ($r = -0.09$, $p = 0.492$), it is possible that the 2 anhedonia items on the CESD-R[3] were insufficient to measure trait anhedonia. To further explore this question, future studies may wish to include more extensive measures of anhedonia (for review, see Rizvi et al., 2016).

Interactive effects of age and depressive symptoms were also seen in the univariate imaging results in the VOTC. Previous work has highlighted the role of the ventral visual stream in emotional memory encoding and retrieval (Bowen et al., 2018; Clewett and Murty, 2019). Similar to our behavioral hypotheses, we predicted that visual processing would be increased for positive and reduced for negative events with older age, but that these effects would be reduced with higher levels of depressive symptoms. The finding that positive VOTC activity decreased with increasing depressive symptoms in older age supported our hypothesis. At low levels of depressive symptoms, older participants demonstrated positivity preferences in neural recruitment of perceptual processing regions. This finding is consistent with previous work showing higher positive versus neutral BOLD signal in perceptual processing regions in healthy older adults than in younger adults (Kehoe et al., 2013). However, with increasing levels of depressive symptoms, these positivity preferences were reduced in older participants, such that engagement of these ventral visual processing regions during positive trials looked more like that during neutral trials. This may suggest that higher levels of depressive symptoms in older age reduce the preferential perceptual processing of positive material that is typically found in healthy aging (Gronchi et al., 2018; Isaacowitz et al., 2006).

For functional connectivity, we predicted that depressive symptoms would alter the anticipatory emotion regulation effects previously observed in healthy older adults (Corbett et al., 2020). When cues indicated an upcoming negative image, low-depressive older participants showed inverse connectivity between dmPFC and VOTC. This inverse connectivity pattern was reduced with greater depressive symptoms. The strength and vulnerability integration (SAVI) model (Charles, 2010) suggests that healthy older adults are able to maintain positive emotional states by employing regulation strategies prior to the onset of a negative stimulus. By providing cues to signal the valence of the upcoming stimulus, our experimental paradigm allowed participants to engage the necessary strategies to reduce negative affect, such as directing attention away from the upcoming stimulus (i.e., distraction). Corbett et al. (2020) previously showed that older adults with low levels of depressive symptoms spontaneously downregulated negative affect when anticipating a negative image. This downregulation was accomplished via vmPFC exerting top-down control to reduce activity in several regions including those important for perceptual processing and memory encoding (e.g., inferior occipital,

[3] These items were “Nothing made me happy” (item #8) and “I lost interest in my usual activities” (item #10).

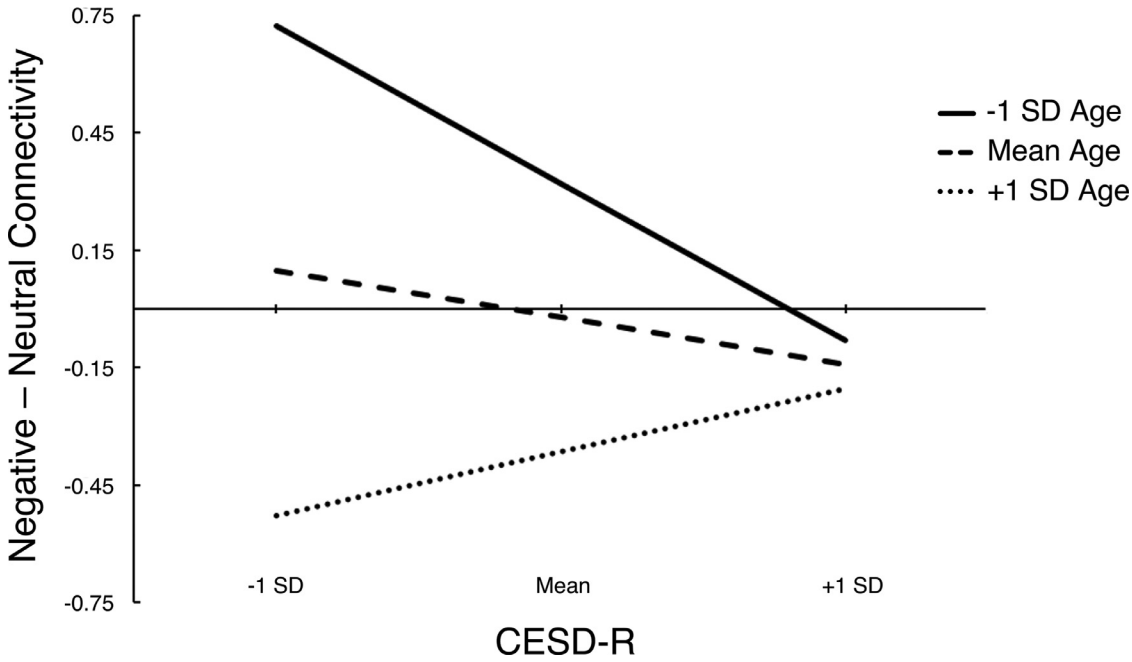

Fig. 5. Simple Slopes for Negative Functional Connectivity Between dmPFC and VOTC.
Note. The lines represent age: mean (dashed), - 1 SD (solid), + 1 SD (dotted). Functional connectivity for the negative condition is presented relative to the neutral condition. The p value for the interaction term: $p = 0.044$. The dmPFC region was used as the seed and the VOTC region was used as the target. The dmPFC ROI was a 6mm sphere around [12, 60, 21]. dmPFC, dorsomedial prefrontal cortex, VOTC, ventral occipitotemporal cortex.

parahippocampal gyrus). Notably, this effect was absent in their young adults. However, it was unclear from their study whether these differences between age groups were due to age or higher levels of depressive symptoms in young than older adults. Findings in the current study elucidate this uncertainty by showing that this inverse coupling is observed *only* for older adults with low levels of depressive symptoms. This suggests that depressive symptoms interfere with older adults' ability to spontaneously engage regulation processes in the face of impending negative stimuli. This is consistent with behavioral findings in that the older participants who were more attuned to the upcoming negative stimulus (i.e., those with higher depressive symptoms) also showed better memory for negative images compared to their counterparts with lower depressive symptoms.

In younger participants, higher depressive symptoms were associated with reduced positive connectivity between dmPFC and VOTC during negative trials. Previous research has shown reduced connectivity in young depressive patients during anticipation of negative stimuli, suggestive of enhanced bottom-up perceptual processing co-occurring with attenuated top-down regulatory processing (Manelis et al., 2016; Strigo et al., 2013), which may be reflective of executive dysfunction that is common in depression (Disner et al., 2011; Li et al., 2018). Feeser et al. (2013) linked reduced prefrontal responses during emotional anticipation in young depressed individuals versus controls to environmental disengagement associated with loss of motivation that is characteristic of depression (Franzen and Brinkmann, 2016; Frey and McCabe, 2020). This account provides a link to the behavioral finding in the current study of reduced memory discriminability and intensity ratings for negative relative to neutral images in younger participants with higher levels of depressive symptoms, as discussed above. Depressive symptoms in these individuals may contribute to impaired anticipatory processing that ultimately hurts their ability to effectively attend to and encode to-be-remembered information.

While older participants with low levels of depressive symptoms showed inverse connectivity, younger participants with low levels of depressive symptoms showed positive connectivity. If the inverse connectivity represents suppression of perceptual processing and memory encoding, does positive connectivity suggest the opposite—that is, are young adults with low depressive symptoms less able to suppress? It is certainly possible this is the case; however, we believe it is more likely that this positive connectivity represents enhanced attention toward the upcoming stimulus. In line with the SST, unlike older adults, younger adults are not necessarily motivated to dampen the impact of upcoming negative images, therefore they may have no need to engage suppression mechanisms spontaneously. Had we explicitly asked participants to suppress their responses to the upcoming stimulus, we may have found few age differences among these low depressive symptom individuals—in line with prior studies which show young and old alike are able to suppress emotion when instructed to do so (Livingstone and Isaacowitz, 2018; Lohani and Isaacowitz, 2014).

One point worth noting is that the Age x CESD-R interactions in the univariate analyses were found for positive images, while the interactions in the functional connectivity analyses were for negative images, similar to the behavioral results. We did expect that the univariate analyses would reflect differences in memory encoding processes that would complement the behavioral findings. Why might the pre-stimulus connectivity patterns better parallel the behavioral data than the stimulus-related activity? One possibility is that because cues allowed participants to anticipate the valence of the stimuli, and emotion regulation processes could be engaged prior to stimulus encoding, demands on these processes were reduced during stimulus presentation. Assuming older individuals with low levels of depression were motivated to engage them, particularly for negative stimuli, and these processes were negatively impacted by depression, the Age x CES-D interactions would be more evident in the pre-stimulus than stimulus encoding period for negative events. These depression-related moderations

of emotion regulation activity may have contributed more to negative memory preferences than did processes related to perception and elaboration of the stimuli. Future studies incorporating explicit manipulations of emotion regulation at pre- and post-stimulus periods could be useful in testing these hypotheses.

5.2. Age-related positivity preferences

While the results discussed in the previous section offer compelling evidence for depression-related reductions in positivity preferences in older age, some age-related positivity preferences that were not moderated by depressive symptoms were also observed. Controlling for CESD-R scores, age was associated with reductions in experienced arousal, as measured by participants' intensity ratings, of negative relative to neutral images. This finding is consistent with the idea that older adults are better able than their younger counterparts to employ effective emotion regulation strategies (John and Gross, 2004). Further supportive of this idea is the finding of lower amygdala activation for negative than neutral trials with older age. This is consistent with SST and aligns with previous literature showing reduced amygdala activity for older compared to younger adults for negative stimuli (Fischer et al., 2010; Leclerc and Kensinger, 2011; Mather et al., 2004; Tessitore et al., 2005). In the current study, functional connectivity analyses revealed greater positive coupling between vmPFC and left amygdala for positive than neutral events with age. This finding may represent enhancement of positive affect during the anticipation period for older participants regardless of depressive symptoms. While a true replication of the findings in Corbett et al. (2020) would have been observed in the current study as greater negative coupling between vmPFC and amygdala for negative than neutral events, Corbett et al. interpreted their findings as evidence of positivity preferences in line with SST. That is, their older adults suppressed processing of the upcoming negative stimulus in an attempt to promote emotion regulation goals. We believe the findings in the current study also serve as evidence for positivity preferences in older age. It is important to note that Corbett et al. (2020) did not use positive images as we did in the current study, and they used behavioral partial least squares analyses as opposed to the approach we took with our functional connectivity analyses. These differences may have precluded exact replications.

Findings in the current study also showed that older age was associated with greater inverse coupling between dmPFC and hippocampus for negative than neutral trials, consistent with prior work showing age-related increases in dmPFC and decreases in hippocampal activity for negative events (Ford and Kensinger, 2018). The dmPFC and hippocampus are part of the episodic memory network (Benoit and Schacter, 2015). The finding of a positive relationship between these regions in younger age could suggest greater priming of this network, readying the individual to encode the upcoming image. With older age, the pattern shifts to greater inverse connectivity, suggestive of older individuals engaging regulatory processes to reduce encoding of upcoming negative events.

It is important to discuss the distinct roles that dmPFC and vmPFC play in emotion regulation. While both of these frontal regions are densely interconnected with the amygdala, the dmPFC has been implicated in mediating cognitive control over emotional responses and maintaining goal-relevant regulation strategies, while the vmPFC is believed to play a larger role in emotion detection and affective valuation, or integration of affective meaning from presented stimuli with internal emotion regulation goals (Berboth and Morawetz, 2021; Koush et al., 2019). It is possible that the greater coupling between vmPFC and amygdala with older age for positive cues observed in the current study is reflective of older individuals' promotion of positive well-being goals (Koush et al., 2019). The greater inverse connectivity between dmPFC and hippocampus with older age for negative cues may reflect cognitive control being exerted that serves to reduce the vividness of the memory trace for the to-be-encoded negative event (Ford and Kensinger, 2018).

Why were these age effects in connectivity not moderated by depressive symptoms? It is possible that the relatively low levels of depressive symptoms among older participants compared to younger participants precluded our ability to detect moderation effects in these specific processes. That is, depressive symptoms may play less of a role in anticipatory emotional experience and encoding preparation than in anticipatory attentional processes (i.e., connectivity between dmPFC and VOTC, in which age effects *were* moderated by depressive symptoms). Another non-mutually exclusive possibility is that the influence of depressive symptoms is stronger during stimulus processing than during preparation. While beyond the scope of the current paper, this is a hypothesis we or others could explore moving forward.

5.3. Depression-related effects

Controlling for age, higher CESD-R score was associated with lower bilateral amygdala activity for positive and negative versus neutral events, across age. Lower amygdala activity for emotional events is consistent with meta-analytic findings of reduced emotional reactivity across valence contexts in depression (Bylsma et al., 2008). For example, in 1 study (Ferri et al., 2017) where participants labeled the emotion displayed on face stimuli, higher symptom severity in depressed participants was associated with reduced amygdala response. Reduced emotional reactivity has also been found to correlate with depressive symptoms (Benning and Ait Oumeziane, 2017). In the current study, CESD-R score showed a trend of negatively predicting intensity ratings for positive images across age (β = -0.247, p = 0.08) and for negative images in younger age (see discussion above). Given that depression is a heterogeneous disorder (Monroe and Anderson, 2015), future studies may wish to explore how the different symptoms of depression differentially contribute to emotional reactivity (Saxena et al., 2017) and how these contributions differ with age.

5.4. Limitations and future directions

One limitation of the study was the sample size may have been insufficient to detect some small moderation effects. An additional limitation was that age and CESD-R were negatively correlated. Though these predictors were centered for all regression analyses to reduce multicollinearity, it could not be eliminated, and thus likely reduced the power of the regression models. The heterogeneous sample was both a limitation and a strength of the study. By recruiting adult participants with a range of depressive symptom severity, we were able to test the unique and interactive effects of these 2 variables. However, including some individuals who were diagnosed with MDD and some who were receiving treatment may have attenuated some effects. Future studies may wish to take these factors into consideration when recruiting participants.

Several studies of aging examine positivity effects in memory, defined as benefits for positive over negative material (Murphy and Isaacowitz, 2008). While we did examine positivity effects in our own data, these effects were reduced compared to the positivity and negativity preferences that we presented in the results. To avoid redundancy and keep our results succinct, we focused on

emotional preference (positive vs. neutral, negative vs. neutral) in the current paper. One possibility for finding fewer differences between positive and negative events compared to emotional versus neutral events is that the latter reflects differences in both valence and intensity. Because intensity ratings were more similar for positive and negative events across participants (2.43 [$SD = 0.55$] and 2.67 [0.47], respectively) than neutral events (1.83 [0.49]), this may have contributed to fewer positive versus negative effects. Thus, the difficulty with separating valence from arousal is a limitation for our study as well as other studies of emotional memory.

High memory performance, particularly among younger participants, left us underpowered to run difference in memory analyses on the imaging data (i.e., hits vs. misses). To make such analyses possible, future studies may make the memory task more challenging by including a greater number of stimuli, including lures similar to the studied images at retrieval, or increasing the retention period between encoding and retrieval. Another limitation of the study is that we were unable to predict memory performance using the neural signals. To do this, the neural signals, age, CESD-R score, and the interaction between these variables would have been necessary to include as predictors of memory outcome. However, our small sample meant that we were underpowered to consider all of these factors in combination.

Though having a diverse sample meant we were sufficiently powered to test the influence of race on positivity preferences, we did not find any of the behavioral results to change when race was added as a covariate. However, age and race were correlated in our sample ($r(44) = 0.45$, $p = 0.002$), such that Black/African American participants tended to be older than White/Caucasian participants, which could have confounded the results. No studies, to our knowledge, have explicitly investigated racial differences in positivity preferences (though Charles et al., 2003 mention that in an exploratory analysis, they found no significant interactions involving race). Therefore, race influences on positivity preferences should be a priority of future research.

5.5. Conclusions

The current study provides novel supporting evidence for the hypothesis that positivity preferences in memory exhibited in healthy aging are reduced with depressive symptoms. This reduction coincides with alterations in neural recruitment of a network of regions underlying emotion regulation. These neural findings suggest that ability to engage regulatory processes to dampen negative affect in older age is diminished with higher levels of depressive symptoms. This study is the first to show interactive effects of age and depressive symptoms on positivity preferences in memory and the neural mechanisms involved in anticipating and responding to emotional events. The findings underscore the importance of investigating depressive symptoms throughout adulthood. This study lays the groundwork for future individual differences research to continue exploring these relationships and their associated factors (e.g., treatment, comorbidities) in larger samples.

CRediT authorship contribution statement

Taylor A. James: Conceptualization, Methodology, Software, Validation, Formal Analysis, Investigation, Data Curation, Writing–Original Draft, Writing–Review and Editing, Visualization, Project Administration. **Audrey Duarte:** Conceptualization, Resources, Writing–Review and Editing, Supervision, Funding Acquisition.

Disclosure statement

The authors have no actual or potential conflicts of interest.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neurobiolaging.2022.10.006.

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