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Behavioral/Cognitive

Age-Related Positivity Bias in Emotion Recognition Is Linked to Lower Cognitive Performance and Altered Amygdala–Orbitofrontal Connectivity

Noham Wolpe,[1,2,3] **Daniel Harlev,**[1,4] **Eyal Bergmann,**[4] **Cam-CAN**[3] **and Richard N. Henson**[3]

[1]Department of Physical Therapy, The Stanley Steyer School of Health Professions, Gray Faculty of Medical & Health Sciences, Tel Aviv University, Tel Aviv 6997801, Israel, [2]Sagol School of Neuroscience, Tel Aviv University, Tel Aviv 6997801, Israel, [3]MRC Cognition & Brain sciences Unit, Department of Psychiatry, University of Cambridge, Cambridge CB2 7EF, United Kingdom, and [4]Department of Psychiatry, Rambam Health Care Campus, Haifa 3109601, Israel

Changes in emotion recognition are observed in aging, in dementia, after brain lesions and as a function of mental health factors, such as depression. In aging, older adults have been argued to show a "positivity bias," which has been associated with a relatively spared recognition accuracy for positive emotion and an increased tendency to label emotions as positive. This bias has been suggested to support mental well-being. However, it has also been found in association with cognitive decline and brain lesions. Here, we investigated the behavioral and brain correlates of this age-related positivity bias. We used multimodal brain imaging in a large group of human adults ($n = 665$, 333 females) drawn from a population-derived cohort across the lifespan, together with a psychometric analysis of an emotion recognition task using facial expressions. Beyond reductions in expression recognition accuracy, older adults showed increased perceptual thresholds for negative emotions and a reduced threshold for the positive emotion, even after accounting for general face recognition abilities. This positivity bias in labeling emotions was strongly associated with lower cognitive performance in older people, but not with (nonclinical) depressive symptoms. It was also associated with reduced gray matter volume in the bilateral anterior hippocampus–amygdala and increased functional connectivity between these regions and the orbitofrontal cortex. Together, age-related positivity bias is associated with cognitive decline and structural and functional brain differences. A positivity bias in emotion recognition may therefore reflect an early marker of neurodegeneration, a hypothesis that could be tested in future longitudinal studies.

Key words: aging; cognitive decline; depression; emotion recognition; neurodegeneration; positivity bias

Significance Statement

Emotion recognition changes with age, with older adults showing a "positivity bias," reduced recognition of negative emotions, and a tendency to label emotions as positive. While this has been theorized as an adaptive mechanism supporting emotional well-being, emerging evidence suggests it may instead signal cognitive decline or neurodegeneration. Using a large population-based cohort ($n = 665$), multimodal brain imaging, and a psychophysical emotion recognition task, we found that age-related positivity bias was strongly linked to cognitive decline but not depressive symptoms. Moreover, this bias was associated with differences in the structure and functional connectivity of the anterior hippocampus–amygdala. These findings suggest that positivity bias may be a marker of neurodegeneration, with implications for early detection of age-related cognitive decline.

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Correspondence should be addressed to Noham Wolpe at nwolpe@tau.ac.uk.

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Introduction

Aging affects emotion recognition abilities, including the interpretation of facial expressions and vocal cues (Ruffman et al., 2008). Research indicates that older adults are less accurate at recognizing emotions compared with younger adults, particularly negative emotions (anger, fear, and sadness, but not disgust), while a smaller effect is found for happiness (Hayes et al., 2020). In tasks requiring explicit emotion recognition, older adults demonstrate a greater tendency to label stimuli as positive and a reduced tendency to label them as negative (Johnson and Whiting, 2013). These effects have been suggested to reflect a positivity bias, wherein older adults focus more on positive over negative stimuli.

Socioemotional selectivity theory (SST) provides a theoretical explanation for the positivity bias observed with age. SST proposes that, when people perceive their future as limited, they selectively shift their attention toward positive information (Reed and Carstensen, 2012; Stretton et al., 2022). This shift is thought to reflect preserved cognitive control (Sakaki et al., 2019) and to maintain emotional (Mather and Carstensen, 2003; Stretton et al., 2022; Kennedy and Mather, 2024) and motivational (Carstensen and Mikels, 2005) well-being, possibly through reappraisal—that is, cognitively reframing negative stimuli in a more positive light (Li et al., 2011). A key prediction of SST therefore is that positivity bias should be associated with both better improved cognitive functioning and emotional well-being.

However, an alternative perspective suggests that positivity bias may instead be linked to cognitive decline and poorer mental health. Some studies have reported associations between positivity bias and age-related cognitive decline (Virtanen et al., 2017; Glinka et al., 2020; Kong et al., 2022) as well as increased depressive symptoms (Anderson et al., 2011; Dalili et al., 2015), casting a less sanguine interpretation of the age-related positivity bias. Moreover, decline in emotion recognition, particularly for negative emotions, is a well-documented early sign of neurodegenerative diseases, such as Alzheimer's, Parkinson's, and Huntington's disease, where they are associated with broader cognitive impairments (Assogna et al., 2008; Henley et al., 2012; Klein-Koerkamp et al., 2012).

Despite extensive research on the brain basis of emotion recognition in both healthy individuals and clinical populations (Adolphs, 2002), what mediates the above age-related differences remains unknown. Lesion and functional imaging studies consistently highlight the amygdala, orbitofrontal cortex (OFC), anterior cingulate cortex, and insula as key regions for recognizing and differentiating facial emotions (Hornak et al., 1996; Adolphs et al., 1999; Phillips et al., 2003; Barrett and Wager, 2006; Fusar-Poli et al., 2009; Lindquist et al., 2012). However, it remains unclear whether these brain regions also underpin age-related differences in emotion recognition in the general population and whether their involvement reflects an adaptive shift toward positivity (as proposed by SST) or emerging neural vulnerability (as suggested by dementia research).

Here, we address this gap by combining a large population-based cohort, a psychophysical facial emotion recognition task, and multimodal structural and functional brain imaging. Importantly, we accounted for potential confounders, including general face recognition ability. Participants labeled morphed emotional expressions (anger, disgust, fear, happy, sad, surprise) that blended pairs of emotions in varying proportions (Calder, 1996). We fit psychometric functions to each participant's responses to examine biases in emotion recognition computed as the psychometric thresholds.

We hypothesized that older adults would exhibit higher recognition thresholds for the negative emotions of anger, fear, and sadness but a lower threshold for the positive emotion of happiness, consistent with previous research (Johnson and Whiting, 2013). Critically, we tested whether this age-related positivity bias would be related to improved (according to SST) or worse (according to dementia studies) depressive symptoms and cognitive performance (Schmid and Schmid Mast, 2010; Anderson et al., 2011; Virtanen et al., 2017; Krause et al., 2021). Lastly, we hypothesized that the positivity bias would be associated with reduced gray matter volume in the amygdala (Adolphs et al., 1999) and possibly altered functional connectivity with OFC, anterior cingulate cortex, and insula (Barrett and Wager, 2006; Lindquist et al., 2012).

Materials and Methods

Participants. A population-based cohort of healthy adults ($n = 665$) was recruited as part of the Cambridge Centre for Ageing and Neuroscience (Cam-CAN; Shafto et al., 2014; Taylor et al., 2015). The study was approved by the Cambridgeshire 2 (now East of England—Cambridge Central) Research Ethics Committee, and all participants provided a written informed consent prior to the study.

Behavioral tasks and scales. Participants completed the "Emotion Hexagon" task, which is a face emotion recognition task (Calder, 1996). The task examines emotion recognition of faces. Stimuli were created from the Ekman and Friesen Pictures of Facial Affect series (Ekman and Friesen, 1976), using a single identity (model JJ), which allowed us to isolate emotion-specific effects without introducing variability related to facial identity. The task includes morphed images, created by combining six pairs of the emotional expressions: happiness–surprise, surprise–fear, fear–sadness, sadness–disgust, disgust–anger, and anger–happiness. Each pair consists of five morphed images with the following ratios: 90–10%, 70–30%, 50–50%, 30–70%, and 10–90%. For example, the five anger–happiness images included the following ratios of anger to happiness expressions: 90–10%, 70–30%, 50–50%, 30–70%, and 10–90%. The complete stimulus set consists of 30 images (six emotional pairs × five morphed face ratios).

On each trial, one of the 30 morphed images was displayed on a computer screen. Participants were asked to select the emotion label (happy, sad, anger, fear, disgust, or surprise) that best described the facial expression shown by clicking on one of the emotion labels displayed on the screen using a computer mouse. At the start of each trial, both the image and emotion labels appeared. After 3 s, the image disappeared, and the emotion labels remained visible throughout the trial, with no time limit for the response. After responding, there was a 2 s delay, after which the next trial began. No feedback was provided regarding response accuracy. Participants completed five blocks of trials, with each block presenting the 30 morphed faces in a randomized order (150 trials in total). Before the first block, a practice block consisting of 15 trials was completed to familiarize participants with the task; this practice block was excluded from all analyses. The task was administered using E-Prime (Psychology Software Tools).

To control for general age-related decline in face recognition abilities, including potential sensory impairments (Baltes and Lindenberger, 1997), participants completed the Benton Facial Recognition Test (Levin et al., 1975; Benton et al., 1983), which is designed to evaluate the ability to match images of unfamiliar faces. The task consisted of 27 trials, and on each trial participants are scored 0 or 1 if they incorrectly or correctly matched a target face, respectively (Shafto et al., 2014). In addition, cognitive performance was assessed using the Cattell Culture Fair test (Cattell and Cattell, 1960), which is a normative test that measures fluid intelligence as a continuous score. For completeness, in a supplementary analysis, we also report the results with Addenbrooke's Cognitive Examination Revised version (ACE-R; Mioshi et al., 2006), which assesses key cognitive domains for dementia screening. Depression symptoms were assessed using the Hospital and Anxiety Depression Scale (HADS; Zigmond and Snaith, 1983). Handedness was evaluated as a continuous variable using the Edinburgh Handedness Inventory (Oldfield, 1971). Education was assessed as an ordinal variable (Table 1), and sex was recorded as a binary variable.

Behavioral analyses of emotion recognition. Our behavioral analyses examined emotion recognition in the Emotion Hexagon task. We excluded trials with implausibly short RTs < 200 ms (0.14% of trials removed), as such rapid responses likely reflect anticipatory reactions rather than genuine decision-making (Ratcliff, 1993). As there was no time limit on the participant's response, we also excluded trials with extremely long RTs > 10 s (0.53% of trials removed), as these trials might reflect potential lapses in attention as well as introduce a short-term memory confound. The 10 s threshold was chosen to retain as much valid data as possible while removing only the most extreme outliers, which are unlikely to represent typical task engagement.

Similar to previous studies (Calder, 1996), we first computed the mean accuracy and median RT for the 70 and 90% stimulus levels for each emotion across participants. However, as our primary aim was to understand biases in emotion recognition, rather than performance accuracy alone, we analyzed responses across the whole morph levels, to capture tendencies to label emotions even when the presented stimulus was ambiguous (Johnson and Whiting, 2013). To this end, we fit each participant's responses with a psychometric function. Specifically, for each participant and for each emotion, we identified the images where the emotion was present and categorized them into 10, 30, 50, 70, and 90% levels of that emotion. As each stimulus was presented five times and each emotion was included in two emotional pairs (see above), there were 10 data points per emotion level, making up a total of 50 trials for fitting. For each level, we calculated the probability that the participant selected that specific emotion. These data points were then fit with psychometric functions using *psignifit* version 3 (Wichmann and Hill, 2001). Considering the nature of the task, where low stimulus level for one emotion meant high stimulus level for another emotion, we fixed the guess rate parameter (lower asymptote) to zero. Gaussian, logistic, and Weibull functions were used, and the function with the best fit in terms of Bayesian information criterion across participants was selected. Our main parameter of interest was the recognition threshold, i.e., the emotion level (%) required for a 50% probability of choosing that specific emotion. For completeness, we also reported the recognition sensitivity, i.e., the psychometric slope at 50% morph level. While this approach fits a separate psychometric function for each emotion (modeling the probability of choosing that emotion across morph levels), which assumes conditional independence of choices, it provides an intuitive estimate of emotion-specific threshold and slope. This would not be directly available from a more parsimonious model, such as a single multinomial logistic model. This trade-off was acceptable given our aim to quantify valence-specific bias rather than full categorical choice patterns.

To examine the effect of age on biases in emotion recognition, we conducted partial Spearman correlation analyses between recognition thresholds and age for the six emotions, adjusting for confounding variables, namely, sex and performance, in the Benton task to control for visual/perceptual ability. We next performed a principal component analysis (PCA) on the recognition thresholds for the four emotions typically showing the strongest positivity bias, namely, "sad," "anger," "fear," and "happy." The PCA had three principal aims: (1) to address inherent dependencies between emotions in the task design (e.g., the angry–happy continuum contributes to both angry and happy thresholds) by summarizing shared variance between emotion thresholds into orthogonal components; (2) to test for a consistent positivity bias by examining whether an increased tendency to label faces as "happy" (reduced threshold) was associated with a reduced tendency to label faces as negative, namely, "sad," "anger," and "fear" (increased thresholds), by examining loadings across emotions; and (3) if evidence for (2) is found, to use the first principal component (PC1) as a composite measure of positivity bias for subsequently investigating associations with cognition, depression, and structural and functional brain imaging data. For the behavioral associations with cognition and depression, this composite measure was entered as the dependent variable in a multiple regression analysis, with Cattell score, and HADS as the predictors of interest, while sex, education, age, and the total score on the Benton task were included as covariates of no interest.

Structural imaging. Participants were scanned using a 3 T Siemens TIM Trio System equipped with a 32-channel head coil. T1-weighted MPRAGE images were acquired with the following parameters: TR, 2,250 ms; TE, 2.99 ms; TI, 900 ms; flip angle, 9°; FOV, 256 × 240 × 192 mm; and isotropic 1 mm voxels. Both structural and functional images (described below) were preprocessed using the automatic analysis batching system (http://imaging.mrc-cbu.cam.ac.uk/imaging/AA) in SPM12 (Taylor et al., 2015). For voxel-based morphometry (VBM) analysis, we first segmented the images using SPM12's tissue priors, followed by diffeomorphic anatomical registration through exponentiated lie algebra (DARTEL) to enhance intersubject alignment (Ashburner, 2007). Specifically, segmented images from all participants scanned in the Cam-CAN project ($n = 651$) were normalized to a project-specific template. The images were then normalized to the Montreal Neurological Institute (MNI) space, modulated to maintain estimates of volume, and smoothed with a 8 mm full-width at half-maximum Gaussian kernel, as done in our previous work (Wolpe et al., 2016, 2020). MRI data from 14 participants were excluded due to technical issues during scanning, preprocessing errors, or brain structural abnormalities. After excluding three participants based on behavioral data (as described above), 642 participants had complete behavioral and structural neuroimaging data.

The analyses followed a similar logic and steps to our previous studies (Wolpe et al., 2016, 2020). The structural imaging analysis aimed to use an unbiased whole-brain approach to identify brain regions associated with age-related differences in recognition of negative emotion. A multiple regression analysis was conducted to generate a statistical parametric map, with the interaction term between the emotional PC1 and age as the primary interest. The interaction term was orthogonalized with respect to the main effects of age and PC1, since the main effect of emotion recognition (PC1) was also of interest. Additional covariates of no interest included sex, handedness, education, total score in the Benton task, and "trait" head motion, calculated as the root mean square volume-to-volume displacement, averaged across functional MRI (fMRI) sessions for each participant, as done previously (Geerligs et al., 2015, 2017; Bergmann et al., 2024). An inclusive mask with an absolute threshold of 0.15 was applied to the preprocessed images to ensure the inclusion of gray matter voxels. All variables were Z-scored before entry into the regression models. A threshold of $p < 0.001$, uncorrected, was used to identify significant clusters, with a family-wise error (FWE) correction performed at the cluster level with statistical significance determined at $p < 0.05$, which was further Bonferroni-corrected to account for four directional T-contrasts: positive and negative directions for the interaction effect and positive and negative effects of age.

Functional imaging. During the same scanning session, participants underwent T2*-weighted fMRI scanning using a gradient-echo echoplanar imaging (EPI) sequence (TR, 1,970 ms; TE, 30 ms; flip angle, 78°; FOV, 192 × 192 mm; voxel size, 3 × 3 × 4.44 mm). A total of 261 volumes were acquired (the first five volumes were discarded to allow for T1 equilibration), each comprising 32 axial slices (in descending order) with a 3.7 mm thickness and a 20% interslice gap.

These functional images were obtained during task-free "resting state," where participants were passively awake with their eyes closed for 8 min and 40 s. The preprocessing and analysis followed a similar procedure to our previous work (Geerligs et al., 2015; Wolpe et al., 2016). Motion effects were minimized through the procedure: T2*-weighted EPI images were corrected for distortions using fieldmaps and subsequently motion- and slice-time corrected in SPM12. Mean EPI images were coregistered to the T1 structural image and normalized to MNI space using the DARTEL template created in earlier steps. A wavelet despiking technique was applied to mitigate motion artifacts (Patel et al., 2014). Participants whose mean spike percentage exceeded

2 SD from the group mean were excluded; based on this criterion, 7 out of 651 participants with valid structural and functional data were excluded (1.23%). The remaining 644 despiked functional images were smoothed using a 10 mm full-width at half-maximum Gaussian kernel (Taylor et al., 2015).

To investigate differences in functional connectivity in relation to age-related emotion recognition, we conducted a seed-based functional connectivity analysis using the results from the VBM analysis as the seed. Specifically, a sphere 9 mm (3 voxel) in diameter was centered on the peak voxel for which the relationship between gray matter volume and PC1 depended on age (i.e., the above age × PC1 interaction). The rationale for this analysis followed our previous work (Wolpe et al., 2016), with the assumption that task-free activity and connectivity patterns are relevant for task-based measures (Tavor et al., 2016).

Whole-brain analysis identified voxels with timeseries that were positively correlated with the mean time series of the seed region for each participant. Motion artifacts were further controlled for by including (1) the six motion parameters; (2) mean white matter signal; (3) mean cerebrospinal fluid signal; (4) first-order temporal derivatives, squares, and squared derivatives of the above signals (Satterthwaite et al., 2013); and (5) a high-pass filter (<0.1 Hz). The resulting beta images from each participant were entered into a group analysis, which included the composite emotion recognition measure (PC1) and its interaction with age, as well as the covariates age, handedness, sex, education, performance in the Benton task, and total motion (calculated as the root mean square of volume-to-volume displacement; Yan et al., 2013). All variables were *Z*-scored before entry into the regression analysis. As in the structural imaging analyses, clusters were identified at $p < 0.001$, uncorrected, with an FWE correction performed at the cluster level at $p < 0.05$, further Bonferroni-corrected to account for two directional T-contrasts: positive and negative directions of any interaction effects. Significant clusters were labeled using the Harvard-Oxford atlas in MRIcron (https://www.nitrc.org/projects/mricron).

Results

Participant sample

Demographic details are summarized in Table 1. Of the 665 participants who performed the behavioral task, 642 had valid structural brain data, while 644 participants had valid fMRI data.

Effect of age on emotion recognition

In line with previous studies (Calder, 1996), we first examined mean accuracy and median reaction time in the task for the 70 and 90% stimulus level conditions (Text S1, Figs. S1, S2). Our findings replicated the results of a large meta-analysis (Hayes et al., 2020), showing a strong negative effect of age on emotion recognition accuracy for fear, sadness, and anger, moderate effect for surprise, small effect for happiness, and no consistent effect for disgust. There were also significant associations between age and median reaction time for the six emotions, whereby older adults were slower in the task. However, as our primary aim was to understand biases in emotion recognition, we analyzed responses across the whole morph levels to capture tendencies to label emotions for different stimulus levels by fitting a psychometric function.

For our principal analyses, we examined performance across "all" stimulus levels (Text S2, Table S1). We fitted a psychometric function to each participant's responses for each of the six emotions (Fig. 1). The winning model used a Weibull function (Text S3), and we computed each participant's recognition threshold as the stimulus level for which 50% response is observed for that emotion.

We examined the associations between age and recognition thresholds (Fig. 2). We used Spearman correlations considering some extreme values in recognition threshold estimates (see further consideration below) and potential nonlinearities in their relationship with age. Importantly, we adjusted for confounding variables using partial correlations, particularly for performance in a nonemotional face matching task, in order to control for visual/perceptual ability (see Materials and Methods). There were positive associations between perceptual threshold and age for negative emotions, with Spearman correlation highest for fear ($\rho = 0.432$; $p < 2.2 \times 10^{-16}$), followed by anger ($\rho = 0.323$; $p < 2.2 \times 10^{-16}$) and sad ($\rho = 0.138$; $p = 3.8 \times 10^{-4}$). In contrast, perceptual thresholds decreased with age for the emotions happy ($\rho = -0.179$; $p = 3.55 \times 10^{-6}$) and surprise ($\rho = -0.123$; $p = 0.001$). No association was found between age and recognition threshold for disgust ($\rho = -0.061$; $p = 0.116$). For completeness, we report the relationship between recognition sensitivity—measured as the slopes of individual psychometric function—and age (Text S4, Fig. S3). This analysis showed no valence-specific pattern and a general decline in recognition sensitivity across the six emotions with age.

Together, these results suggest that age was associated with a reduced tendency to label face expression as negative emotions, namely, "fear," "anger," and "sad," but an increased tendency to label them as "happy" and "surprise." These results are consistent with an age-related positivity bias in emotion recognition (Johnson and Whiting, 2013).

Table 1. Summary of participant demographics across age deciles

Age	*N*	Gender M/F	Handedness R/L	Education			
				None	GCSE	A Levels	Higher
18–29	70	30/40	64/6	1	21	6	42
30–39	94	51/43	86/8	1	19	7	67
40–49	117	54/63	107/10	0	29	5	83
50–59	95	50/45	86/9	5	19	10	61
60–69	114	60/54	103/11	7	35	8	63
70–79	109	53/56	103/6	16	25	7	61
80–89	66	34/32	61/5	12	17	5	32
Total	665	332/333	609/55	42	165	48	409

Handedness was assessed the using the Edinburgh Handedness Inventory (Oldfield, 1971) as a continuous variable. However, for simplicity, it is reported here as a binary measure, with a positive score on the Edinburgh Handedness Inventory indicating right-hand dominance. Education was categorized according to the English education system: "none," no education over the age of 16 years; "GCSE," General Certificate of Secondary Education (typically at 16 years of age); "A Levels," General Certificate of Education Advanced Level (typically at 18 years of age); "Higher," university or professional education post A Levels (typically at 21 years of age).

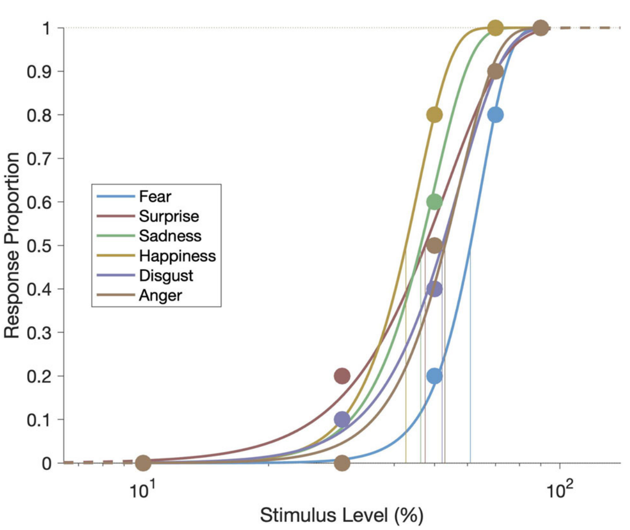

Figure 1. Psychometric function fit. Model fit across the six emotions for a representative participant.

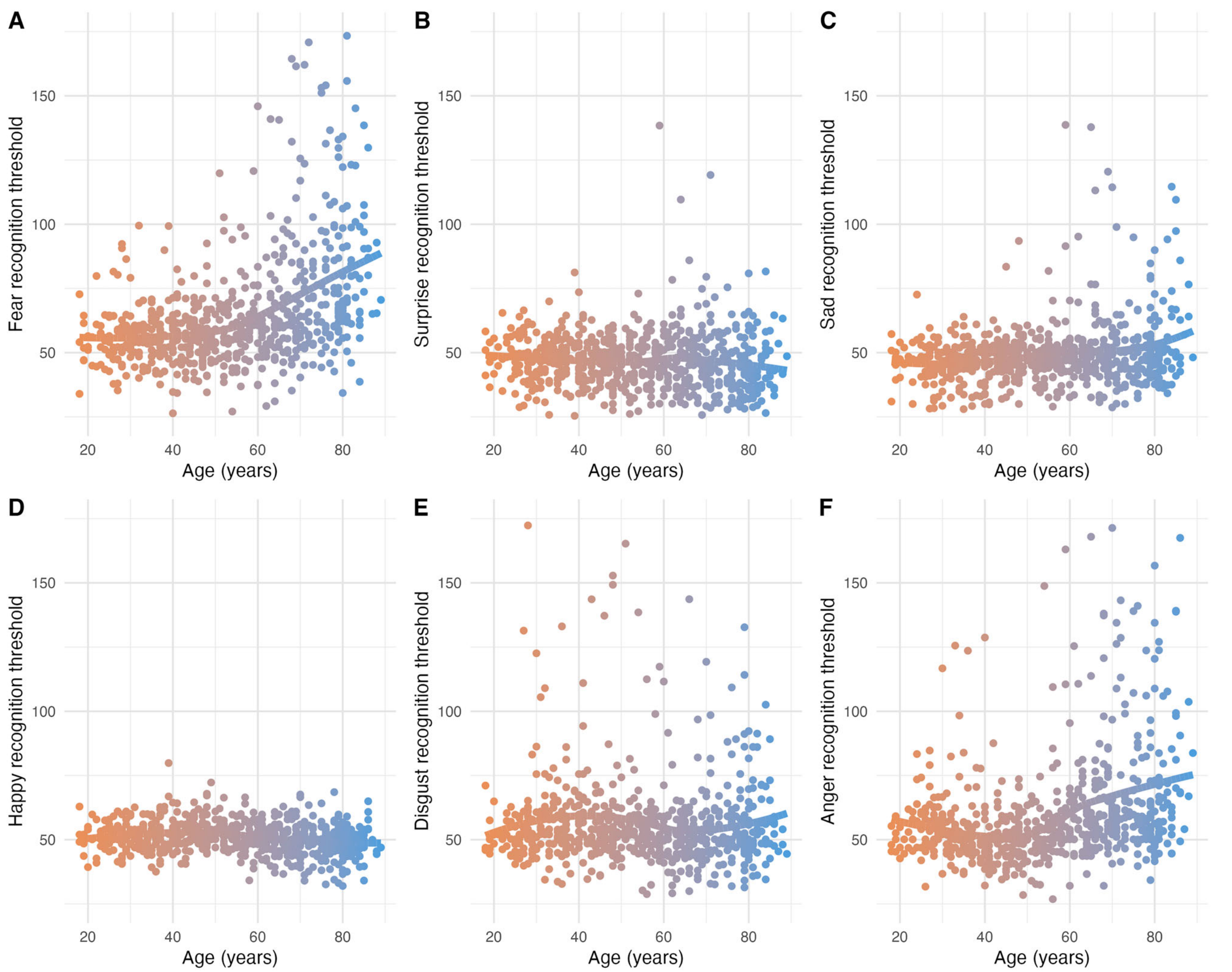

Figure 2. Emotion recognition thresholds. ***A***, Fear recognition threshold by age, where recognition threshold was computed by fitting a Weibull function to each participant's responses across the five stimulus levels. The line represents locally estimated scatterplot smoothing, used to visualize the age-related trend. ***B–F***, Same as ***A*** but for surprise, sad, happy, disgust, and anger, respectively.

We conducted a PCA on emotion recognition thresholds of the three negative emotions "fear", "anger" and "sad" and positive emotion "happy" to (1) address the dependency between thresholds; (2) confirm that reduced labeling of negative emotions was associated with increased labeling of positive emotion by examining their loadings; and (3) compute a composite measure for this behavioral pattern in order to test for its behavioral and brain correlates. The first principal component (PC1) explained 42% of the variance and loaded on all four emotions (anger, 0.62; fear, 0.54; happy, −0.34; sad, 0.44). Importantly, the loadings had opposite signs for negative emotions and the positive emotion, suggesting that PC1 does not simply reflect overall task performance but rather an increased tendency to label faces as "happy" coupled with reduced tendency to label them as negative emotions ("angry," "fear," "sad"). In other words, higher PC1 scores indicate a stronger positivity bias.

As there were some extreme values in threshold which may reflect poorer psychometric fits, excluding thresholds >3 robust SD and recomputing the first principal component revealed similar first PC ($r = 0.93$). Similarly, a PCA on all six emotions yielded comparable results. Five emotions loaded strongly on PC1, with happy and surprise showing opposite signs relative to the three negative emotions (anger, 0.56; fear, 0.63; happy, −0.25; sad, 0.36; surprise, −0.29). The sixth emotion disgust had a weak loading (0.08). Importantly, PC1 scores for the four-emotion and six-emotion models were highly correlated ($r = 0.953$), demonstrating that the inclusion of all six emotions does not substantially change the interpretation of the principal component. Consistent with these findings and our a priori interest in the four core emotions, we therefore used the four-emotion PC1 as a composite measure of positivity bias in the task, measured as the tendency to label faces as positive ("happy") at the expense of labeling them as negative emotions ("anger," "fear," "sad").

Behavioral correlates of positivity bias

We tested whether age-related increase in positivity bias in emotion recognition would be associated with better cognitive performance and fewer depressive symptoms (as predicted by SST) or with worse cognitive performance and more depressive symptoms (as predicted by dementia studies). To this end, we conducted two separate linear regression models predicting positivity bias, one with cognitive performance (Cattell test of fluid intelligence) by age as the main predictor and another with depressive symptoms (HADS total score) by age as the main predictor. We further accounted for potential confounders, namely,

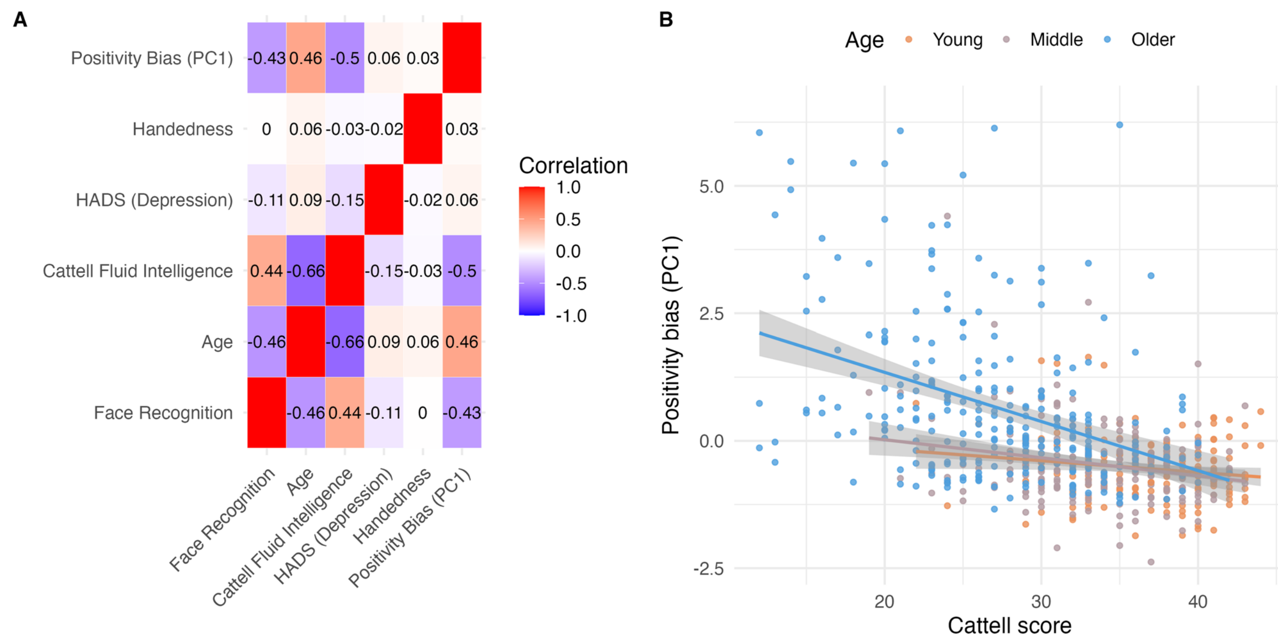

Figure 3. Behavioral correlates of positivity bias. ***A***, A correlation plot illustrating the Pearson's correlation coefficients between variables included in the regression model predicting positivity bias. ***B***, A scatterplot illustrating the significant negative Cattell × age interaction predicting positivity bias (PC1 from emotion recognition thresholds). Age was split to three groups: young (aged 40 and younger), middle (aged 40–60), and older (age 60 and older) for illustration purposes only, since it was included as a continuous variable for the analyses.

Table 2. Results of linear regression models predicting positivity bias

Variable	Standardized coefficient	SE	*t* statistic	*p* value
PC1 ∼(Intercept)	−0.019	0.051	−0.385	0.700
Benton	−0.192	0.037	−5.237	2.231×10^{-7}
Age	0.183	0.044	4.124	4.222×10^{-5}
Cattell	−0.243	0.044	−5.489	5.879×10^{-8}
Sex_female	−0.225	0.063	−3.553	4.088×10^{-4}
Handedness	0.027	0.031	0.853	0.393
Cattell × age	−0.182	0.036	−5.093	4.675×10^{-7}
PC1 ∼(Intercept)	0.086	0.047	1.820	0.069
Benton	−0.277	0.038	−7.231	1.407×10^{-12}
Age	0.327	0.038	8.516	1.225×10^{-15}
HADS	−0.005	0.034	−0.159	0.873
Sex_female	−0.200	0.068	−2.957	0.003
Handedness	0.007	0.041	0.173	0.863
HADS × age	0.018	0.037	0.484	0.628

HADS, Hospital Anxiety and Depression Scale; PC1, first principal component from PCA; SE, standard error of the mean.

sex and general face matching performance (Fig. 3*A*). The results of the linear regression analysis are summarized in Table 2. Notably, there was a significant negative Cattell × age interaction (as well as a significant negative main effect of Cattell), suggesting that older adults had more negative association between positivity bias and cognitive performance (Fig. 3*B*). Similar results were found when using the ACE-R as a measure of cognitive performance (Text S5, Table S2). In contrast, there were no associations between positivity bias and depressive symptoms or depressive symptoms by age interaction. Very similar results were found when including both cognitive performance and depressive symptom severity in a single regression model.

Brain correlates of age-related positivity bias

To investigate the brain correlates of age-related differences in biases in emotion recognition, we conducted structural and functional brain imaging analyses. First, we performed a VBM analysis to identify brain regions where gray matter volume was associated with positivity bias in emotion recognition thresholds in an age-dependent manner. Across the whole group, positivity bias was negatively associated with gray matter volume in a cluster within the intracalcarine cortex ($k = 3{,}494$; cluster-level FWE–corrected $p = 3.122 \times 10^{-8}$; Bonferroni-corrected for four contrasts). However, similar to our behavioral analysis above, our primary contrast was the negative interaction between age and positivity bias, to identify brain regions in which gray matter volume was associated with an increased positivity bias with age. This contrast revealed two clusters in the right ($k = 1{,}190$; cluster-level FWE–corrected $p = 0.003$; Bonferroni-corrected for four contrasts) and left ($k = 774$; cluster-level FWE–corrected $p = 0.044$; Bonferroni-corrected for four contrasts) hippocampus/amygdala (Fig. 4*A–C*). The negative direction of this interaction meant that gray matter volume in these clusters was more negatively correlated with positivity bias in older participants (Fig. 4*D*). No significant results were found for a positive association with the interaction term.

We next sought to investigate how individual differences in functional connectivity with bilateral anterior hippocampus/amygdala were related to the increased positivity bias with age. The two bilateral anterior hippocampus/amygdala clusters showing an association with age-related increase in positivity bias were combined into a single seed for functional connectivity analyses on the BOLD timeseries during task-free "resting state" scans. As in the structural brain imaging analysis, we included several covariates, including age, sex, handedness, performance in the Benton task, and head motion.

The results are summarized in Table 3. We found that age × positivity bias (measured as PC1 from the PCA on recognition thresholds) was positively associated with functional connectivity between the bilateral anterior hippocampus/amygdala and other temporal regions, namely, bilateral parahippocampal gyrus and inferior and middle temporal gyri (Fig. 5*A*). A third distal cluster was identified in the bilateral OFC/frontal pole. The positive interaction meant that increased positivity bias in older adults was associated with increased functional connectivity between these regions and the seed (Fig. 5*B*).

Discussion

Our study combined a face emotion recognition task, cognitive/mood assessments, and multimodal imaging to investigate age-related biases in emotion recognition. Controlling for face recognition abilities in a large population-based cohort ($n = 665$), older adults showed an increased tendency to label faces with the positive emotion of happiness but a reduced tendency to label faces with the negative emotions anger, fear, and sadness. This positivity bias was strongly associated with an age-related reduction in cognitive performance, but not with depressive symptoms.

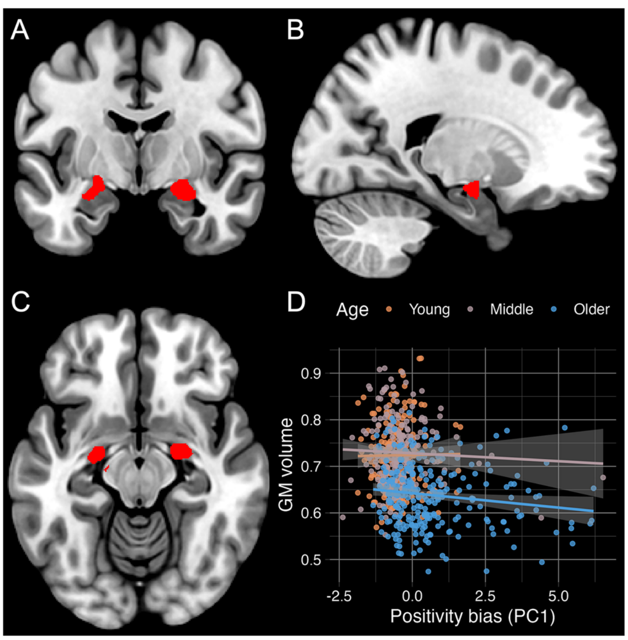

Figure 4. Structural correlates of age-dependent positivity bias in emotion recognition. ***A***, Coronal, (***B***) sagittal, and (***C***) axial view of the brain, with the two bilateral anterior hippocampus/amygdala overlaid. Gray matter (GM) volume in these regions showed a significant negative association with the positivity bias in emotion recognition (measured as the first principal component, PC1, of emotion recognition thresholds) by age. ***D***, A scatterplot illustrating the significant PC1 × age interaction predicting GM volume in the peak voxel of the right hippocampus cluster. Age was split to three groups: young (aged 40 and younger), middle (aged 40–60), and older (age 60 and older) for illustration purposes only, since it was included as a continuous variable for the analyses.

Importantly, it was linked to structural differences in the bilateral anterior hippocampus/amygdala regions and to the functional connectivity of these regions with OFC bilaterally.

Age-related biases in emotion recognition and their behavioral correlates

Our findings revealed significant age-related differences in emotion recognition, even when accounting for confounding variables such as general face recognition ability. We found a greater reduction in recognition accuracy for negative emotions anger, fear, and sadness, compared with happiness, with no age-related differences for disgust, which is consistent with previous research (Hayes et al., 2020). Examining the psychometrics of emotion recognition, older adults showed higher recognition thresholds for negative emotions (anger, fear, and sadness) but reduced recognition thresholds for positive emotion (happiness) and for surprise. The valence of surprise is debated: some consider it positive, while others find it context-dependent (Matsumoto et al., 2000; Lin et al., 2017). Indeed, our task included only a subset of emotion pairs, which can influence errors and response biases in the task (see Strengths and Limitations). In addition to these biases, we found that recognition sensitivity was reduced across all emotions, rather than disproportionately reduced for negative emotions. Together, these findings support the idea that older adults tend to label (subjectively) ambiguous stimuli as positive rather than negative (Johnson and Whiting, 2013), consistent with a positivity bias.

While SST frames positivity bias with age as adaptive (Mather and Carstensen, 2003; Stretton et al., 2022), aging and dementia research suggests it is associated with cognitive decline (Horning et al., 2012; Virtanen et al., 2017). Our results are consistent with the latter account. We estimated individual differences in positivity bias as the first principal component of recognition thresholds for anger, fear, sad, and happy (which was similar to the principal component across all thresholds). We found that this measure of positivity bias and cognition became more negative with age. These results were consistent across two independent cognitive measures (Cattell test and ACE-R) and did not change when including depressive symptoms in the model.

How might age-related cognitive decline lead to a distinct valence-dependent effect on emotion recognition thresholds? Negative emotions are generally considered more difficult to distinguish between: As the number of negative emotion categories increases, the recognition rates decrease significantly, suggesting the blurred boundaries between negative emotions can make them harder to recognize (Wang et al., 2023). This is partly supported by our supplementary analysis of specific responses to

Table 3. Summary of seed-based functional connectivity analyses

Brain region		*K*	Coordinates at peak voxel *x*	*y*	*z*	*t* statistic	*p* value
R	Parahippocampal gyrus/inferior temporal gyrus/middle temporal gyrus	367	30	−6	−21	4.51	4.42×10^{-4}
			42	0	−30	4.25	
			60	−3	−39	4.06	
R/L	Orbitofrontal/frontal pole cortex	253	24	39	−18	4.39	0.004
			−9	39	−24	4.34	
			18	33	−24	4.09	
L	Parahippocampal gyrus/temporal fusiform gyrus/frontal orbital cortex	175	−21	−6	−30	4.44	0.022
			−27	−15	−42	3.96	
			−24	6	−18	3.41	

Clusters where functional connectivity with bilateral anterior hippocampus/amygdala seed showed a significant positive association with age × positivity bias (first principal component of recognition thresholds). *K* indicates the cluster size in number of voxels. *P* values computed with FWE correction at the cluster level (cluster-forming threshold, $p < 0.001$, uncorrected), with additional Bonferroni's correction applied to account for two contrasts: positive and negative correlations with the interaction term.

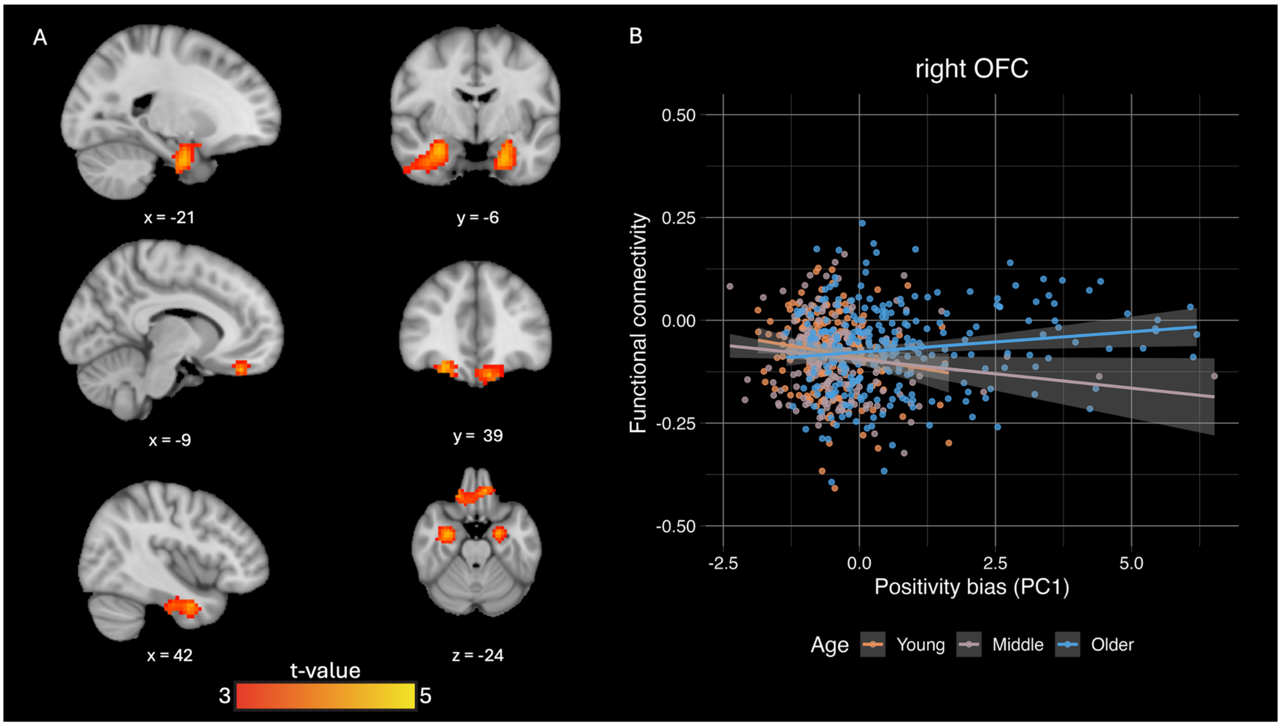

Figure 5. Functional correlates of age-dependent positivity bias in emotion recognition. ***A***, Clusters where functional connectivity with the bilateral anterior hippocampus/amygdala region showed a significant positive association with age × positivity bias. Positivity bias was measured as the first principal component (PC1) of emotion recognition thresholds. $P < 0.05$, FWE-corrected, with a cluster-forming threshold of $p < 0.001$, uncorrected. ***B***, A scatterplot illustrating the significant age × PC1 interaction associated with functional connectivity of the bilateral anterior hippocampus/amygdala seed with the right orbitalfrontal/frontal pole cortex (OFC). As above, age was split to three groups, young (aged 40 and younger), middle (aged 40–60), and older (age 60 and older) for illustration purposes only, and was included as a continuous variable for the analyses.

each emotion, showing that older confused anger and fear. Nonetheless, we adjusted for basic perceptual ability in face recognition ability. Moreover, this cognitive/perceptual explanation for the bias would not explain the more general confusion pattern for the sadness emotion and the response pattern for happiness. Furthermore, it is not clear how this cognitive account would relate to the neural results considered later, which suggest a more fundamental role of emotional processing, possibly related to neurodegeneration. Together, the results suggest there are other, noncognitive contributors to age-related positivity bias (Kong et al., 2022).

Testing for other affective contributors, we found no significant relationship between bias in emotion recognition and depressive symptoms, and this did not change when adjusting for cognitive differences. Age-related positivity bias is thus independent from current affective state. This result contrasts with previous studies (Schmid and Schmid Mast, 2010; Anderson et al., 2011; Krause et al., 2021), and the null results should be interpreted with caution. The discrepancy between studies could reflect differences in methodology, as we used a composite measure of positivity bias, rather than only happiness and sadness. Additionally, the relatively mild depressive symptoms in our population-based cohort may have limited our ability to detect associations, as previous work found that emotion recognition deficits are more pronounced in individuals with greater symptom severity (Dalili et al., 2015). Interestingly, in a subset of the same individuals from this study, we previously found a relationship between an implicit emotion processing task, depressive symptoms, and functional activity in the insula (Nagrodzki et al., 2023). This suggests that explicit emotion recognition may engage a distinct affective–cognitive process. Finally, the tight linkage between age-related cognitive decline and depressive symptoms may further confound independent associations with positivity bias (Bergmann et al., 2024).

Brain structural and functional correlates of age-related positivity bias

Our imaging results show the anterior hippocampus/amygdala is associated with age-related positivity bias in recognition thresholds. As we used cluster-based inference, we cannot disentangle whether these effects are specific to one or both regions. Moreover, our seed-based functional connectivity analysis found that connectivity between the anterior hippocampus/amygdala and bilateral clusters in the OFC were associated with age-related positivity bias. Connectivity was also found with clusters in parahippocampal and lateral temporal cortex; however, these regions were close to the seed and could thus be an artifact of spread from the seed, given the smoothness in the data.

Increased connectivity between anterior hippocampus/amygdala and OFC was associated with increased age-related positivity bias. The direction of this positive interaction was opposite to the negative interaction found in the structural imaging analysis. Such a difference in directionality for association with structure and function is commonly reported both in our previous studies (Wolpe et al., 2014, 2016) and others' (Morcom and Johnson, 2015; Sheng et al., 2021). The exact mechanism for the increased functional connectivity in the context of reduced gray matter is not fully known but has been suggested to represent a form of compensation (Hafkemeijer et al., 2012).

The amygdala is a key structure involved in the generation and regulation of emotional responses (Calder, 1996; Adolphs et al., 1999; Rosen et al., 2002; Adolphs and Tranel, 2004).

Its connectivity with the medial prefrontal cortex, particularly the OFC and anterior cingulate cortex, is essential for modulating these emotional responses. Specifically, OFC–amygdala functional connectivity has been linked to reappraisal (Ochsner et al., 2012; Gao et al., 2021), which involves reframing negative experiences in a more positive light. Increased top–down modulation from the OFC to the amygdala in older adults may reflect such an emotion regulation mechanism, whereby ambiguous expressions are more likely to be labeled positively, paralleling the goal of reappraisal to dampen negative affect.

Emotion recognition and neurodegeneration

Positivity bias in emotion recognition is an early feature of neurodegenerative conditions, such as Alzheimer's disease and Parkinson's disease (Gray and Tickle-Degnen, 2010; Klein-Koerkamp et al., 2012). Our findings support the hypothesis that increased positivity bias with age may similarly reflect neurodegeneration. This is supported by the consistent associations we found with age-related reduction in cognitive performance. Moreover, the associations we found with structural differences in anterior hippocampus/amygdala and its functional connectivity with OFC mirror findings reported in people with brain lesions, stroke (Adolphs et al., 1999), and dementia-related neurodegeneration (Rosen et al., 2002).

This intriguing hypothesis would need to be validated in large longitudinal studies, measuring emotion recognition in older adults over time. Interestingly, the lack of association with depressive symptoms suggests that positivity bias could help distinguish cognitive decline from depression in old age (Bergmann et al., 2024).

Strengths and limitations

This study benefits from several strengths, including the use of a large, population-based cohort that spans the adult lifespan, a validated emotion recognition task, continuous analysis of recognition thresholds, and multimodal brain imaging. The inclusion of the Benton Facial Recognition Test allowed us to control for basic face recognition abilities, unlike previous research. However, several limitations must be acknowledged. First, our results are cross-sectional, limiting inferences about causality or the progression of age-related changes. Second, the behavioral task included only a subset of all possible emotion pairs (two emotional combinations or pairs per emotion), which meant that accuracy for each emotion could be influenced by the specific pairs that were presented. The threshold and sensitivity measures from the psychometric fit are thus not a pure, context-independent estimate of that emotion. Third, our functional connectivity analysis was on task-free "resting–state" data, and the lack of task-based fMRI data limited our ability to test for active processes involved while recognizing emotions. Finally, the relatively mild depressive symptoms may explain the lack of associations. Future research should include clinical populations to further explore the interaction between depression and age-related changes in emotion recognition.

Conclusion

We found that positivity bias in emotion recognition—reduced tendency to label stimuli as negative emotions at the expense of increased tendency to label then as positive—is increased with age, which is in turn associated with worse cognitive performance and structural differences in the anterior hippocampus/amygdala and its functional connectivity with OFC. Our study supports the idea that age-related positivity reflects neurodegeneration, but this requires confirmation in future longitudinal studies.

Data Availability

All data used for this work, including behavioral, structural, and functional imaging, are publicly available upon signing data sharing agreement on https://opendata.mrc-cbu.cam.ac.uk/projects/camcan/. The code used to analyze the data and generate the figures is available on https://github.com/nwolpe/emotion_recognition.

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