Emotion

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Behavioral and Brain Differences in the Processing of Negative Emotion in Previously Depressed Individuals: An Exploratory Analysis of Population-Based Data

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Depressed individuals show significant biases in the processing of emotional stimuli, focusing attention on negative facial expressions (termed "attentional negativity bias"). Some of these biases persist in previously depressed individuals, but their mechanisms remain largely unknown. Here, in a population-based study in which participants (n = 134, 68 females; 21–92 years) were recruited as part of the Cambridge Centre for Ageing and Neuroscience in 2010–2014, we explored (a) the cognitive process underlying attentional negativity bias; (b) whether this process is associated with a self-reported history of depression; and (c) the neural correlates of this process. Participants completed an implicit emotion processing task, while functional MRI was acquired. Drift-diffusion modeling was used to calculate each participant's tendency for sustained task-irrelevant attention on negative (angry) compared to neutral faces. In the cohort, 14% of participants reported a history of depression. Drift-diffusion modeling showed reduced drift rate for angry compared to neutral faces. The magnitude of this reduction was associated with self-reported depression history. Across the whole group, drift rate for angry faces was associated with increased brain activity when processing angry versus neutral faces in areas of bilateral insula/inferior frontal gyrus and bilateral parietal cortex. Our results suggest that attentional negativity bias is explained by slower task-relevant drift rate for negative (angry) stimuli. This slower drift rate is associated with the difference in brain activity when processing these stimuli, possibly reflecting increased emotional engagement. Such altered processing may persist even after a depressive episode, but this finding should be validated in clinical samples.

Keywords: depression history, emotional processing, attentional bias, drift-diffusion model, functional MRI

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All behavioral and imaging data are available through the Cambridge Centre for Ageing and Neuroscience data repository at https://camcan-archive.mrc-cbu.cam.ac.uk/dataaccess. All analysis scripts are available via a GitHub repository under the Massachusetts Institute of Technology license agreement at https://github.com/jaknag/angry-faces-prev-depressed-labcopy/tree/main. The authors have no conflicts of interest to disclose.

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Depressed individuals process emotional stimuli differently from people without depression. Considerable evidence for this comes from neuroscience studies showing that depressed individuals have an attentional bias toward faces expressing negative emotions, even when these are irrelevant to the task at hand (Kanske & Kotz, 2012; Leppänen, 2006; Leyman et al., 2007). This attentional bias has also been reported in people who were previously depressed (Bhagwagar et al., 2004; Leppänen et al., 2004; Ruhe et al., 2019) and has been suggested to be involved in the development of depression and risk of depression relapse (De Raedt & Koster, 2010; Ruhe et al., 2019). These negative emotions predominantly include sadness and anger (Elgersma et al., 2018; Suslow et al., 2020). Specifically, when processing angry faces, depressed individuals have increased attentional engagement compared to nondepressed individuals (Ao et al., 2020; Leyman et al., 2007). Moreover, previously depressed individuals are particularly sensitive to recognizing anger compared to never depressed individuals (Anderson et al., 2011).

Experimentally, emotional processing biases can be demonstrated in a variety of ways, such as increased reaction time (Gilboa-Schechtman et al., 2004; Leyman et al., 2007) and sustained eye gaze (Belopolsky et al., 2011). Task performance, such as task accuracy (Surguladze et al., 2004), is also typically affected, where increased emotional processing biases manifest as a performance enhancement when the emotional content is task-relevant or as a performance impairment when it is task-irrelevant (Kanske, 2012). The mechanism underlying these behavioral effects has been suggested to involve the allocation of cognitive processing to emotional content (Pessoa, 2009). However, what mechanisms are implicated, and their relevance for depression is largely unknown.

Sequential sampling models, such as the drift-diffusion model (DDM), have been widely used in recent years to investigate the underlying latent cognitive processes that explain changes in both reaction time and accuracy (Milosavljevic et al., 2010; Ratcliff & Rouder, 1998). The DDM assumes a stochastic accumulation of evidence until a threshold is crossed, at which point an individual commits to a decision (Ratcliff & McKoon, 2008). On this account, the attentional negativity bias in depression could be explained by a slower accumulation of evidence for negative emotional stimuli (smaller drift rate) or a more cautious behavior requiring more evidence to be accumulated to make decisions about negative stimuli (higher decision boundary).

Here, we sought to test which cognitive variable explains attentional negativity bias using DDM. We further asked whether differences in this variable would be present in previously depressed individuals. Finally, we investigated the neural correlates of this measure. To this end, we combined an implicit emotion processing task, DDM, and functional MRI (fMRI). We explored data from a population-based cohort of currently healthy participants across the adult lifespan. Participants performed a task which involved viewing emotionally neutral or angry faces, requiring them to discriminate their gender (Passamonti et al., 2008), while undergoing fMRI scans.

We hypothesized that attentional negativity bias would be associated with a smaller drift rate for gender discrimination for angry faces, rather than changes in decision boundary, in line with research showing a distractor-like effect of stimulus emotion for the task at hand (Todorova et al., 2020). Moreover, we predicted that this tendency for slower accumulation would be more pronounced in previously depressed individuals. Finally, we predicted that this behavioral effect would be associated with differences in brain activity in the limbic system, including the amygdala, which is thought to be sensitive to the emotional valence of stimuli (Kanske, 2012; Kanske & Kotz, 2011), and regions in the attentional network, including the inferior frontal gyrus (IFG), which are thought to modulate attention allocation (Hampshire et al., 2010).

Method and Materials

Participants

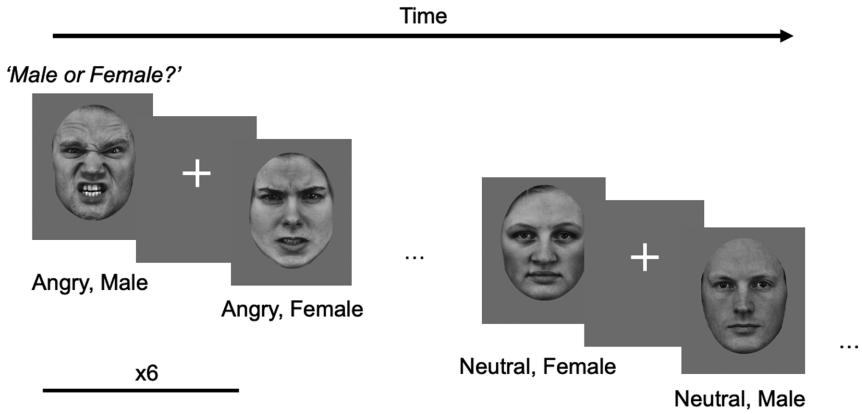
A population-based cohort of healthy adults (n = 136) was recruited as part of the third stage ("CC280") of the Cambridge Centre for Ageing and Neuroscience (Cam-CAN; Shafto et al., 2014; Taylor et al., 2017). The initial recruitment process in Cam-CAN involved residents in particular geographical areas through sampling from the population registered in primary care. This is the closest possible to being truly population representative in nature in the United Kingdom since registration with general practitioners is nearly universal in the United Kingdom. General practitioners made the initial referrals to potential participants, who were overall stable with no acute episodes of physical or mental conditions. Data collection took place between 2010 and 2014. Exclusion criteria are described at length in (Shafto et al., 2014) including significant cognitive impairment (Mini-Mental State Examination score of 24 or less), communication difficulties, significant medical problems (full list in Table 1 in Shafto et al., 2014), mobility problems, substance abuse, and MRI/magnetoencephalography safety and comfort issues. Ethical approval was granted by the local ethics committee, Cambridgeshire 2 (now East of England—Cambridge Central) Research Ethics Committee (Reference No. 10/H0308/50). Written informed consent was obtained from all participants before commencing the study. The study conforms to the provisions of the Declaration of Helsinki.

We identified previously depressed and never depressed individuals through self-report, by asking participants whether, and if so when, they had been diagnosed with depression requiring medication treatment. One participant who reported a depressive episode requiring medication within the same year of the study was excluded, to further minimize the risk of an overlap with their depressive episode. Demographic information, including age, sex, level of education, and handedness, was obtained. Participants were also administered the Benton Test of Facial Recognition (Levin et al., 2010) to control for general face recognition abilities. Current depressive symptoms were assessed using the Hospital Anxiety and Depression Scale (HADS; Zigmond & Snaith, 1983), while cognitive performance was assessed using the Addenbrooke's Cognitive Examination–Revised (ACE-R; Mioshi et al., 2006).

Behavioral Task

Participants completed a gender discrimination task of emotional faces, requiring them to identify the gender of a face showing an angry or a neutral facial expression (Figure 1; Passamonti et al., 2008). Visual instructions and stimuli were back-projected onto a screen and viewed through a mirror mounted on the MRI head coil. The experiment consisted of 24 blocks (12 angry and 12 neutral), each lasting 21 s. Within each block, there were six face trials and six null events (central fixation cross), pseudorandomly interleaved to

Figure 1
Task Illustration



Note. An angry or neutral face, followed by a fixation cross, was presented. Participants were asked to indicate whether the face displayed was male or female. Occasional null events were displayed, which consisted of a central cross displayed for 1,750 ms. Face pictures used in the task were taken from Karolinska Directed Emotional Faces (Lundqvist et al., 1998), which permits use for academic research and publication.

ensure no more than three consecutive trials of the same type (face or null).

During each face trial, a face was displayed for 1,000 ms, followed by a fixation cross for 750 ms. Participants responded with a button press to indicate whether the face was male or female. They were instructed to respond as quickly and accurately as possible and were only able to respond while the face was presented (up to 1,000 ms). On average, participants failed to respond in 2.63% of the trials. During each null event, the fixation cross was displayed for 1,750 ms. Each trial, whether a face trial or null event, lasted 1,750 ms, based on the scan repetition time (TR). The face stimuli consisted of 60 faces (30 identities, with an equal number of male and female identities), each showing either an angry or neutral expression.

The principal measures for each trial were reaction time (RT) and accuracy, that is, whether the participant correctly identified the gender of the face stimulus. In terms of median RT and mean accuracy across participants, an exclusion criterion of ±3 interquartile ranges identified one participant (accuracy ~60%) who was excluded from further analyses. The data from the remaining participants (n = 134) were used for the behavioral and imaging analyses.

Drift-Diffusion Modeling

To investigate the cognitive components of the decision-making process contributing to the variability in responses and RTs, DDM was used with the HDDM toolbox for Python, v0.9.2 (Wiecki et al., 2013). HDDM considers the responses and RTs of all trials to compute key parameters of a decision-making process, where responses are modeled either as correct/incorrect or based on their stimulus identity (male or female faces in our task). In the main analyses, we used the accuracy-coding approach, as we wanted to fully capture the attentional negativity bias, that is, both slower and less accurate decisions, when processing angry faces compared to neutral faces (Gilboa-Schechtman et al., 2004; Leyman et al., 2007; Surguladze et al., 2004). For completeness, we also report the results of stimulus coding models (see Supplemental Material).

In accuracy-coded HDDM, each trial is modeled as a decision-making process where evidence is accumulated over time at an average rate (drift rate "v"). This drift rate reflects the speed and direction of evidence accumulation, with higher drift rates indicating faster accumulation of evidence toward a correct decision. The process continues until the accumulated evidence reaches one of two decision thresholds (boundary separation "a"). The boundary separation parameter reflects the level of decision caution, with a larger boundary separation indicating more caution and more evidence required to reach a decision, and vice versa. Once a decision boundary is reached, there is a fixed delay (nondecision time "t"), which reflects other cognitive processes that are unrelated to the decision itself, such as sensory encoding (processing the stimulus) and motor response time (executing the decision).

In principle, changes to all three parameters could lead to increased RT typically observed for processing stimuli of negative emotional valence. Specifically, reduced drift rate, increased boundary separation, and increased nondecision time would all lead to increased RTs, although only the former two are related to the decision-making process. To identify which parameter best explains attentional negativity bias, we adopted a data-driven approach, by fitting different models with these different parameters explaining the attentional bias, and tested which model best explains the data.

We employed a pragmatic restriction on model complexity for interpretability, with one model parameter dependent on stimulus emotion (angry vs. neutral) per model: Model 1 (the null model) with all parameters independent of stimulus emotion; Model 2 with drift rate ("v") dependent on stimulus emotion; Model 3 with boundary separation ("a") dependent on stimulus emotion; and Model 4 with nondecision time ("t") dependent on stimulus emotion.

We identified the parameter which best explained attentional negativity bias in the task, by comparing the different models.

Hierarchical Bayesian model fitting was used to estimate each participant's model parameters, as drawn from a group distribution. In line with previous studies in the field, ultrafast RTs shorter than 250 ms were removed (Wiecki et al., 2013). Overall, 3.3% of the total trials were excluded in this way. Each model was estimated 5,000 times using the Markov chain Monte Carlo method, discarding the first 1,000 samples to minimize the effect of initial values on posterior inference and with a thinning factor = 2 to reduce autocorrelations. To select the best fitting model, the deviance information criterion (DIC) was computed for each model. DIC is a well-established and widely used metric for model comparison in hierarchical Bayesian modeling in general and in HDDM in particular (Wiecki et al., 2013). It balances model fit and complexity by penalizing models with a greater effective number of parameters, thus avoiding overfitting. The DIC is computed by adding up the deviance, which is defined as two times the negative log likelihood of the observed data given the estimated model parameters (Wiecki et al., 2013). The model with the lowest DIC, indicating the best trade-off between goodness of fit and simplicity, was selected for further analyses. The best fitting model was run with five chains, 10,000 samples each. The first 2,000 samples were discarded as burn-in and a thinning factor of 5 was used. Posterior convergence was assessed with the potential scale reduction statistic $\hat{R}$ (<1.1 for all parameters) and with inspection of posterior plots. To compare parameters across groups, the mean from each of the 8,000 resulting model parameter estimates was used. Group comparisons were conducted using *t* test or the Mann–Whitney *U* test for comparing ranks where the normality assumption was violated. Logistic regression models were conducted to test for the association between depression history (previously vs. never depressed) and model parameters while accounting for other covariates, namely current depressive symptoms (measured using the HADS), age (considering the large age range of participants and potential influence on depression history), and cognitive performance (measured using the ACE-R). All behavioral analyses were conducted in R (R Core Team, 2021) or Python with SciPy package (Virtanen et al., 2020).

Functional Brain Imaging Acquisition and Analyses

While participants performed the behavioral task, fMRI data were acquired on a 3T Siemens TIM Trio System, employing a 32-channel head coil, using T_2*-weighted contrast from a Gradient echo echo-planar imaging sequence. A total of 381 volumes were obtained per participant, each containing 32 axial slices (in descending order). Slice thickness was 3.7 mm with an interslice gap of 20%; TR = 2 s; time to echo = 30 ms; flip angle = 78°; field of view = 192 × 192 mm; voxel size = 3 × 3 × 4.44 mm. Total acquisition time was 12 min and 27 s. Seven participants were excluded due to technical problems, resulting in 127 participants with behavioral and imaging data.

The fMRI data were preprocessed and analyzed using SPM12 (https://www.fil.ion.ucl.ac.uk/spm/) in MATLAB (Mathworks, Massachusetts). Details of the Cam-CAN preprocessing pipelines have been described at length previously (Taylor et al., 2017). In short, data were unwarped using field-map images, realigned to correct for motion, high pass filtered (cutoff of 128 s), slice-time corrected, and coregistered to each participant's T_1-weighted image. The normalization parameters from applying Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra to the structural image (Ashburner & Friston, 2005) were then applied to warp functional images into the Montreal Neurological Institute space. The scans were smoothed with an 8-mm isotropic Gaussian kernel.

Although the emotional condition (angry vs. neutral) remained consistent within each block, our primary focus was on capturing trial-by-trial variability in brain activity related to individual decisions. We therefore used an event-related design, modeling trial-by-trial variations in brain responses to attentional and emotional processing. A generalized linear model (GLM) was fit to the fMRI time series in each voxel, which included regressors formed by convolving the estimated neural activity for each condition with a canonical hemodynamic response function. Neural activity for each trial was modeled as a boxcar with duration equal to the reaction time for that trial. Three binary regressors were defined: two for the experimental conditions (angry, neutral), as well as an "invalid" regressor for trials with no button press, or ultrafast trials with RT < 250 ms (see above). To correct for head motion, from the realignment stage of preprocessing, Cam-CAN derived six head motion parameters (three for translation: *X*, *Y*, *Z* and three for rotation: pitch, roll, yaw). These parameters were included in the first-level model as regressors. In total, the first-level model included nine regressors. An autoregressive model was used to estimate autocorrelation in the data and inverted to prewhiten the data and model.

The difference in activity between angry and neutral faces was used for a second-level GLM. We first tested for group difference (previously depressed vs. never depressed) in a GLM that included an intercept term and group, but considering the difference in sample size between groups, we focussed on whole-group correlations in the main analysis. In the main analysis, we tested for an association between activity in the angry versus neutral condition and drift rate for angry faces. This GLM included the drift rate for neutral faces and the drift rate for angry faces as regressors. We opted for a correlation between activation and drift rate across the whole study population to maximize the power. Using the large sample size across all participants allowed us to perform the more stringent whole-brain analysis.

To control for family-wise error at $p < .05$, random field theory was used for cluster-level inference, given an initial cluster-forming threshold of $p < .001$, uncorrected. An explicit gray matter mask was obtained from the Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra template and applied to the results. Mapping of clusters to anatomical areas was performed using the automated anatomical labeling atlas 3 extension for SPM12 (Rolls et al., 2020).

Transparency and Openness

We report how we determined our sample size, all data exclusions (if any), all manipulations, and all measures in the study. All data are available at https://cam-can.mrc-cbu.cam.ac.uk/dataset/. Analysis code is available at https://github.com/jaknag/angry-faces-prev-depressed-labcopy/tree/main (Nagrodzki, 2024). Face pictures used in the task were taken from Karolinska Directed Emotional Faces (https://kdef.se/), which permits use for academic research

and publication. Data were analyzed using SPM12 in MATLAB (Mathworks, Massachusetts); HDDM toolbox for Python, v0.9.2 (Wiecki et al., 2013); and in R (R Core Team, 2021). Ethical approval for the original data collection was granted by the local ethics committee, Cambridgeshire 2 (now East of England—Cambridge Central) Research Ethics Committee (Reference No. 10/H0308/50). This study's design and its analysis were not preregistered.

Results

Participants

A summary of the demographic details of participants and basic performance in the task is reported in Table 1 for previously depressed and never depressed participants. The two groups differed only on HADS depression scores, with the previously depressed group having a median score higher by 2 points in the HADS compared to never depressed group.

Emotional Processing and Drift-Diffusion Modeling

Across all participants, the reaction time was not significantly different between angry faces ($Mdn = 0.74$; interquartile ranges = [0.64, 0.89]) and neutral faces (0.74; [0.65, 0.89]), $U = 9.96e07$, $p = .317$. Moreover, the accuracy of responses was greater in the neutral versus angry condition, $\chi^2(1, N = 28{,}274) = 308$, $p < .001$. To identify which cognitive process underlies this effect, we next used DDM with accuracy coding, which models both changes in reaction time and accuracy.

To identify the specific cognitive process underlying the attentional bias for angry faces, we fit a set of DDMs to the behavioral data, varying the fixed and free parameters (see the Method section). That is, we used a data-driven approach to identify which DDM parameter best explains the attentional bias, by comparing goodness of fit for models with different parameters explaining the attentional bias. The model with the best fit (lowest DIC) included a different drift rate for angry and neutral, but one boundary separation "a" and nondecision time "t" fixed across both conditions (Figure 2A). Confirming this, across all participants, the drift rate was indeed significantly lower for angry faces, $t(265) = -4.75$, $p < .001$ (visualisation with simulated data, Figure 2B). Together, the results suggest that attentional negativity bias was best explained by slower drift rate in the angry condition compared to the neutral condition.

We next tested whether individual differences in attentional negativity bias as quantified by the drift rates were associated with a history of depression. We first examined the drift rates as a function of self-reported depression history. To illustrate this, we plotted the difference between drift rate for angry faces and drift rate for neutral faces for each individual across the two groups (Figure 2C). The difference, which accounts for individual differences in basic processing speed by subtracting drift rate for neutral faces, showed a negative tendency, in line with the attentional negativity bias. Moreover, there was variability in both groups, but an overall subtle tendency for previously depressed to have lower differences than never depressed individuals. The raw differences, however, do not account for covariates such as age, current depression scores, and other factors, for which we turned to a logistic regression analysis.

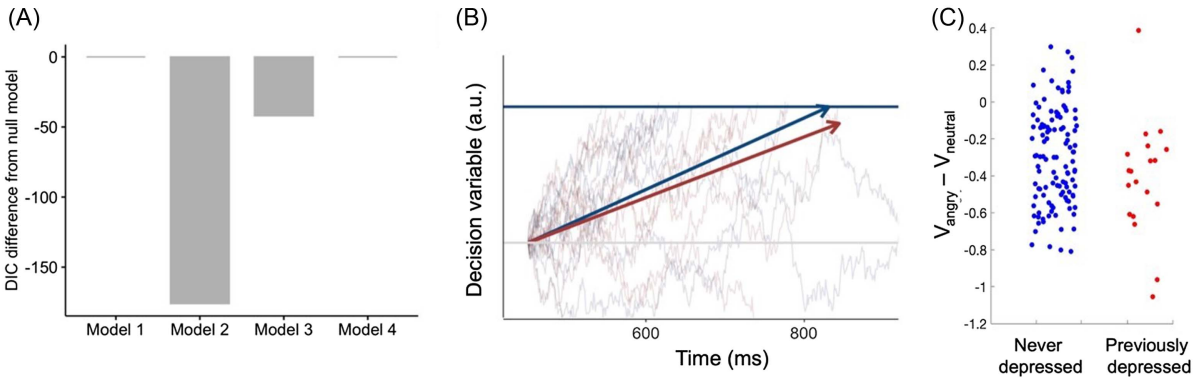
A logistic regression was performed, with drift rates for angry faces predicting participant depression history (never depressed vs. previously depressed). We further included HADS depression as a covariate to rule out current depressive symptoms contributing to this difference (see above) and age given the large age range in the study (Table 1). The logistic regression model was statistically significant, $\chi^2(6, N = 134) = 17.40$, $p = .004$. The model explained 21.8% (Nagelkerke's R^2) of the variance in self-reported depression history. Age was negatively associated with a history of depression, with an increase in age by 1 year decreasing the likelihood of self-reported depression history by 4.9%, 95% CI [1.2%, 8.4%], $t(128) = -2.54$, $p = .011$. By contrast, an increase in the HADS depression score by 1 point increased the likelihood of self-reported depression history by 24.6%, 95% CI [7%, 54%], $t(128) = 2.67$, $p = .008$. Cognitive performance measured by the ACE-R was not associated with depression history, $OR = 0.98$, 95% CI [0.85, 1.15], $t(128) = -0.23$, $p = .822$. Importantly, slower drift rate for angry faces was significantly associated with increased likelihood of self-reported depression history, $OR = 0.09$, 95% CI [0.01, 0.88], $t(128) = -1.98$, $p = .047$, while drift rate for neutral faces was not significantly associated with depression history, $OR = 5.12$, 95% CI [0.59, 52.95], $t(128) = 1.44$, $p = .149$. These findings suggest that a slower drift rate for angry faces is a persistent finding in previously

Table 1
Summary of the Demographic Information of Participants Included in the Study

Characteristic	Previously depressed	Never depressed	Total	Statistic	*p*
N	19	115	134		
Age	47.04 [38.11, 59.76]	58.16 [40.64, 73.35]	54.75 [39.18, 71.93]	$U = 845$	.058
Female	11 (58%)	57 (50%)	68 (51%)	$\chi^2(1, N = 134) = 0.18$	.617
Highest level of education					
Before GCSE	2 (10%)	4 (3%)	6 (4%)		
GCSE	1 (5%)	7 (6%)	8 (6%)	$\chi^2(3, N = 134) = 3.04$	.386
A-Level	3 (15%)	10 (9%)	13 (10%)		
University	13 (68%)	94 (82%)	107 (80%)		
HADS depression	4 [3, 6.5]	2 [1, 4]	2 [1, 4]	$U = 663.5$	.003
BFR	23 [22, 25]	23 [21, 25]	23 [21, 25]	$U = 1{,}039$	.245
ACE-R	97 [92, 99.5]	96 [94, 98]	96 [93.25, 98]	$U = 1{,}032$	.350
Reaction time (s)	0.75 [0.69, 0.82]	0.74 [0.68, 0.81]	0.74 [0.68, 0.82]	$U = 1{,}096$	.370
Accuracy (% correct)	0.92 [0.89, 0.95]	0.91 [0.87, 0.94]	0.92 [0.87, 0.94]	$U = 1{,}056$	.281

Note. Number of participants (%) or median (interquartile range) is presented. GCSE = General Certificate of Secondary Education; HADS = Hospital Anxiety and Depression Scale; BFR = Benton Face Recognition score; ACE-R = Addenbrooke's Cognitive Examination–Revised score.

Figure 2
Drift-Diffusion Model



Note. (A) Comparison of goodness of fit (DIC = deviance information criterion, lower value = better fit) across the models in comparison to Model 1 (the null model specifying all parameters independent of stimulus emotion). The models differed in terms of the parameter allowed to vary with stimulus emotion, namely drift rate "v" (Model 2), boundary separation "a" (Model 3), and nondecision time "t" (Model 4). (B) Simulation of the drift-diffusion process, based on the drift rate for neutral (blue) and angry (red) faces. The gray horizontal line represents the starting point of the drift process, and the blue horizontal line represents the decision threshold. Twenty trials were simulated for illustration. The arrows represent the mean of all traces for neutral faces (blue) and angry faces (red). (C) Difference between drift rate for angry and drift rate for neutral faces for each individual across the never depressed (blue circles) and previously depressed individuals (red circled). See the online article for the color version of this figure.

depressed individuals. This effect size for drift rate for angry faces predicting depression history was $f^2 = 0.05$, which is considered small to medium (Cohen, 1988). The effect persisted even after accounting for individual differences in current use of antidepressant medication, time since last depression episode, sex, education, and Benton face recognition score. Moreover, for completeness, in subsidiary analyses, we found no associations between other model parameters and depression history, for "a": $t(128) = 0.82$, $p = .414$, for "t": $t(128) = 0.80$, $p = .422$.

Functional Brain Imaging Results

The results of the fMRI analyses are summarized in Table 2.

Viewing angry compared to neutral faces showed widespread increased activity in bilateral occipital and temporal areas, including the left fusiform gyrus, as well as in the IFG. Decreased activity was observed in a large cluster encompassing bilateral orbitofrontal cortex and anterior cingulate cortex (Figure 3A). There was no significant difference in these activity patterns between previously depressed and never depressed individuals. However, considering the small number of individuals reporting a previous history of depression, our principal neuroimaging analysis focussed on the association between drift rate and brain activity across the whole group.

In our main neuroimaging analysis, we examined the relationship between individual differences in drift rate for angry faces (while accounting for drift rate for neutral faces) and brain activity when processing angry versus neutral faces (Table 2, Contrasts 3 and 4). We found regions where activity when processing angry versus neutral faces showed a significant negative correlation with drift rate for angry faces. Specifically, we found that participants with a lower drift rate for angry faces demonstrated increased activations in the bilateral insula/IFG and bilateral parietal cortex when viewing angry compared to neutral faces (Figure 3B; scatterplots for each cluster shown in Supplemental Material). Removing participants with high head motion, including the remaining demographic factors (age, sex, education, Benton face recognition score, HADS depression), or other DDM parameters did not change the results (Supplemental Material).

Discussion

Our study examined the persistence of emotional processing biases and their neural correlates in an exploratory analysis of a population-based study. Our results showed that (a) attentional negativity bias was explained by slower drift rate or accumulation of task-relevant evidence; (b) slower task-relevant drift rate for emotional stimuli (angry faces) was associated with depression history while accounting for drift rate for neutral faces; and (c) drift rate for angry faces was associated with brain regions previously associated with activity in bilateral insula/IFG and bilateral parietal cortex, which were previously implicated in emotion processing, as we discuss below.

People spend longer looking at emotionally negative stimuli, such as threatening or angry facial expressions (Belopolsky et al., 2011). The presentation of emotional stimuli leads to slower and less accurate responses when the emotional content acts as a distractor (Kanske & Kotz, 2012). This behavioral phenomenon has been termed attentional negativity bias, which is particularly pronounced in individuals currently (Huang et al., 2023; Leyman et al., 2007) or previously depressed (Bhagwagar et al., 2004; Leppänen et al., 2004; Ruhe et al., 2019). Our study found that the cognitive process underlying this phenomenon is slower evidence accumulation for task-relevant information for emotional (angry) stimuli. That is, when completing a task, such as deciding the gender of a face, individuals' attention can be diverted toward task-irrelevant emotional features of the stimuli, such as emotion. Due to its cognitive salience, the emotional content of the stimulus may attract

Table 2
Summary of Functional MRI Results

Contrast/cluster	MNI coordinates of peak (mm)	AAL3 label	Cluster size
Contrast 1: Main effect of stimulus emotion Angry—Neutral			
Cluster 1	30 −90 6	Right middle occipital gyrus	1,801
Cluster 2	−27 −93 6	Left middle occipital gyrus	1,280
Cluster 3	54 33 6	Right inferior frontal gyrus, triangular part	203
Cluster 4	−42 −42 −18	Left inferior temporal gyrus Left fusiform gyrus	107
Cluster 5	42 12 −36	Right middle temporal pole Right superior temporal pole	95
Cluster 6	−48 30 0	Left inferior frontal gyrus, triangular part Left inferior frontal gyrus, orbital part	87
Cluster 7	−51 12 −21	Left superior temporal pole Left middle temporal pole	51
Contrast 2: Main effect of stimulus emotion Neutral—Angry			
Cluster 1	21 30 −12	Right medial orbitofrontal cortex Right posterior orbital gyrus	669
Contrast 3: Positive correlation between drift rate for angry faces and activity in Angry—Neutral			
No significant clusters			
Contrast 4: Negative correlation between drift rate for angry faces and activity in Angry—Neutral			
Cluster 1	−42 12 6	Left insula Left inferior frontal gyrus, opercular part	81
Cluster 2	36 21 9	Right insula Right inferior frontal gyrus, triangular part	139
Cluster 3	−39 −48 42	Left inferior parietal gyrus	61
Cluster 4	48 −33 39	Right supramarginal gyrus	67

Note. AAL3 = automated anatomical labeling atlas 3; MNI = Montreal Neurological Institute.

attentional resources and engagement (Pessoa, 2009), even if it is irrelevant to the task at hand. This hypothesis is further supported by the observed association in our study between slower drift rate for angry faces and brain regions known to be involved in emotional processing (see below).

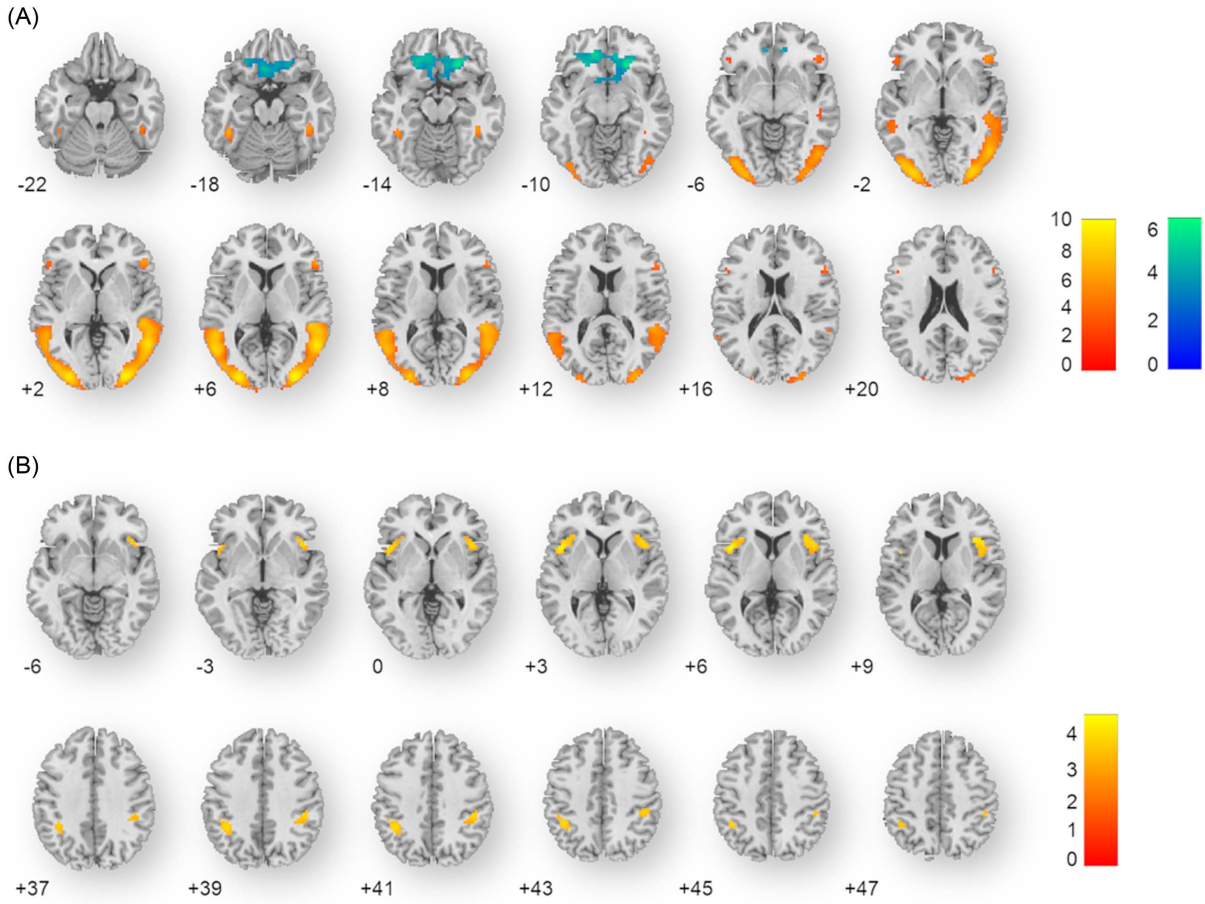
The slowing of task-relevant evidence accumulation was associated with a self-reported history of depression, with previously depressed individuals showing more slowing of task-relevant evidence accumulation compared to never depressed individuals. Importantly, this effect was above and beyond the individual's current depressive symptoms. The finding is consistent with previous research demonstrating that biased processing of emotional information persists in remitted depression (Anderson et al., 2011; Leppänen, 2006; Leyman et al., 2007). One possibility is that slower evidence accumulation rate for angry stimuli reflects an individual trait, rather than a state that is only present during a depressive episode (Ruhe et al., 2019), but this intriguing hypothesis remains to be tested in a larger clinically validated sample.

The lack of clinical validation is a significant limitation in our study (see the Limitations section). Individuals in our study were recruited in a manner close to population-representative sampling (see the Method section), which is a key strength. However, our study did not collect medical records and instead relied on self-reported diagnoses. Participants were asked if they had ever been diagnosed with depression for which they took antidepressant medication, in an effort to increase consistency and meet a threshold of clinical severity. We also asked when they last experienced a depressive episode that required medication, aiming to reduce potential biases. Despite these efforts, retrospective self-reports of depressive diagnoses are known to be biased (Tam et al., 2020). Several factors influence these biases. For example, the accuracy of recalling depressive episodes is reduced with time (Patten et al., 2012). This bias likely explains the negative association between age and self-reported depression history in our study, despite the increased cumulative likelihood of a depression diagnosis with age. This bias might also explain the relatively low number of previously depressed individuals in our study compared to some estimates of >20% lifetime prevalence of depression (Tam et al., 2020; Xu et al., 2024). Moreover, current depressive symptoms also influence recall biases, such that more depressive symptoms at present increase the likelihood of recall (Schraedley et al., 2002), as indeed found in our study. Finally, the severity of the depressive episode, which we did not evaluate in our study, also influences recall bias (Birk et al., 2020; Wells & Horwood, 2004). Thus, a natural follow-up to our study would be to replicate our findings in a clinically validated sample of patients in remission.

In addition to the association of drift rate for angry faces and depression history, across the whole group (never depressed and previously depressed), we found a relationship between this brain response to angry versus neutral faces and the degree to which angry faces slowed down evidence accumulation. This association was found in several areas, including the insula, IFG, and parietal cortex—all bilaterally. These regions have all been previously linked with emotional processing and depression, as we describe below.

The insula is part of the "rich club" of highly connected brain regions (Z. J. Dai et al., 2015; Harriger et al., 2012) and is frequently reported in imaging studies in healthy individuals and in people with

Figure 3
Visual Illustration of Functional MRI Results



Note. (A) Axial slices showing areas of increased (warm color scale) and decreased (cold color scale) activation in the angry versus neutral condition across all participants. Numbers indicate slice *z* coordinates. (B) As in (A), but for areas showing increased activation with decreasing drift rate for angry faces when processing angry versus neutral faces. See the online article for the color version of this figure.

mental health disorders, including depression and other mood disorders (Drysdale et al., 2017; Janiri et al., 2020; Schnellbächer et al., 2022). It also forms part of the salience network, where it is suggested to prioritize salient information for neural processing (Michel, 2017; Uddin, 2015). Given this role, its activity in our study may reflect involvement in processing emotionally salient stimuli (angry faces). Moreover, the IFG, particularly the right IFG, is commonly associated with behavioral inhibition (right IFG, Aron et al., 2003; Duann et al., 2009), and activity in this region has also been linked to treatment response in depression (D. Dai et al., 2020; Gorka et al., 2019; Marwood et al., 2018). While our findings indicate IFG activity, further research is needed to clarify its specific functional contribution in this context. Finally, some studies have reported changes in the parietal cortex in major depressive disorder (Mel'nikov et al., 2018), and this region has also been implicated in evidence accumulation during decision-making tasks in humans (FitzGerald et al., 2015; Sestieri et al., 2014; Yao et al., 2020) and nonhuman primates (Shadlen & Newsome, 2001; Steinemann et al., 2022; Stine et al., 2022; Zhang et al., 2022).

Together, these findings suggest that the brain regions identified in our study may form part of a broader network involved in both cognitive and emotional processes. It is possible that the prefrontal cortex modulates parietal-mediated evidence accumulation (Hanks et al., 2015; Pedersen et al., 2015), potentially influenced by emotional salience or valence signaled by the insula (Uddin, 2015). However, the precise interactions among these regions in the context of our task remain to be fully elucidated.

In contrast to our hypotheses, we did not find an association between amygdala activity and processing of angry versus neutral faces or drift rate for angry faces (Kanske, 2012; Kanske & Kotz, 2011). The amygdala plays a crucial role in the processing of angry facial expressions. Neuroimaging studies have demonstrated that the amygdala shows increased activity in response to angry faces (Sato et al., 2004). While caution is needed when interpreting null findings in general and the lack of association in our exploratory study in particular, it is possible that baseline amygdala reactivity in the gender discrimination task is reduced because the emotion of the stimuli was irrelevant to the task itself (Pessoa et al., 2002).

Moreover, we used whole-brain correction, which, while more statistically rigorous, reduces sensitivity to detecting regions associated with drift rate.

Limitations

Our study has several limitations one should consider when interpreting the results. First, given the exploratory nature of the study, focussing on people from the general population recruited for a study on healthy aging, only 19 individuals reported a previous diagnosis of depression, leading to a small group size. Together with the relatively small effect size, this limits reproducibility of our results and emphasizes the need to replicate our results in larger better balanced studies. Second, we rely on self-reported depression history, rather than clinical records. The accuracy of self-reported depression history is clearly limited, mainly in underestimating depression prevalence (Takayanagi et al., 2014). Interestingly, in our study, increasing age was associated with a reduced likelihood of reporting a history of depression. This suggests either poor recall of historical diagnoses or a generational effect of lower rate of incidence, diagnosis, or self-report in the older participants. However, the prevalence of prior depression diagnosis in our population-based sample (14.2%) was similar to that in some population-representative studies (Smith et al., 2013), but smaller than other estimates (Tam et al., 2020; Xu et al., 2024). Moreover, an inaccurate recall of depression history would lead to incorrect group classification in our study (e.g., wrongly classifying a previously depressed individual to the never depressed group), thereby making it more difficult to detect a significant group effect. Third, depression history as defined here yields a highly heterogeneous group in terms of severity, clinical characteristics, treatment received, and psychosocial factors. We did not collect data on the number of previous depressive episodes or their severity, and these were therefore not considered in the analyses. Last, our study is cross-sectional in nature and does not provide follow-up clinical information, for example, on recurrence of depression. Longitudinal studies are paramount for establishing the ability of our measures to predict clinical factors, such as risk of relapse.

Conclusion

In summary, we find that previously depressed individuals show a persistent difference in the processing of negative emotional stimuli and that, regardless of depression history, the degree of this effect is related to brain activity in distinct regions for emotional processing. These findings have implications for understanding cognitive biases in depression and, once validated in a larger clinical population, may have clinical relevance for treating individuals with significant negative biases.

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