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ORIGINAL ARTICLE

Emotional processing and positive affect after acute exercise in healthy older adults

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Abstract

The well-elucidated improvement of mood immediately after exercise in older adults presumably involves adaptations in emotion-processing brain networks. However, little is known about effects of acute exercise on appetitive and aversive emotion-related network recruitment in older adults. The purpose of this study was to determine the effect of acute exercise, compared to a seated rest control condition, on pleasant and unpleasant emotion-related regional activation in healthy older adults. Functional MRI data were acquired from 32 active older adults during blocked presentations of pleasant, neutral and unpleasant images from the International Affective Pictures System. fMRI data were collected after participants completed 30 min of moderate to vigorous intensity cycling or seated rest, performed in a counterbalanced order across separate days in a within-subject design. The findings suggest three ways that emotional processing in the brain may be different immediately after exercise (relative to immediately after rest): First, reduced demands on emotional regulation during pleasant emotional processing as indicated by lower precuneus activation for pleasant stimuli; second, reduced processing of negative emotional stimuli in visual association areas as indicated by lower activation for unpleasant stimuli in the bilateral fusiform and ITG; third, an increased recruitment in activation associated with regulating/inhibiting unpleasant emotional processing in the bilateral medial superior frontal gyrus (dorsomedial prefrontal cortex), angular gyri, supramarginal gyri, left cerebellar crus I/II and a portion of right dorsolateral prefrontal cortex. Overall, these findings support that acute exercise in active older adults alters activation in key emotional processing and regulating brain regions.

KEYWORDS
cognitive aging, emotion, fMRI, international affective picture system, mood, physical activity

1 | INTRODUCTION

With older age comes a considerable prevalence of mental health problems such as anxiety and depression (Reynolds et al., 2015). In the United States, 20% of people aged 55 years or older are estimated to experience some types of mental health concern (Centers for Disease Control and Prevention and National Association of Chronic Disease Directors, 2008). There is also evidence that this alarmingly pervasive issue is being further exacerbated, given that anxiety and depression rates have increased in older adults during the COVID-19 pandemic (Webb & Chen, 2022). However, greater levels of leisure time physical activity during the peak of the COVID-19 shutdown were associated with lower symptoms of depression among older adults (Callow et al., 2020). Understanding how behavioral interventions such as exercise may impact brain circuits that govern mental health is therefore particularly pertinent, especially since the world population of older adults is continuing to expand rapidly (Mitchell & Walker, 2020). Here, we report the effects of a single session of exercise on brain activation in response to the viewing of affective images in older adults.

Studying older adults' emotional reactivity is important due to its crucial implications for this population's long-term mental health and well-being. For example, aging-related emotional problems can lead to negative mood-related cognitive biases and worsened mental health outcomes in older adults (Knight & Durbin, 2015). Emotional responsiveness can be measured in the laboratory through the use of International Affective Picture System (IAPS) images (Lang et al., 2008). IAPS pictures aim to engage a large breadth of human experiences and vary widely on dimensions of valence and arousal (Mikels et al., 2005). Namely, these pictures can have a pleasant, unpleasant, or neutral valence and range from not arousing at all to highly arousing. Valence and arousal are classically regarded as the two key dimensions of emotion, and their implementation is not limited to IAPS pictures—these dimensions were also built into the Self-Assessment Manikin (SAM) rating scale, a nonverbal scale that measures an individual's subjective emotional responses (Lang, 1980). Within this framework of emotion, discrete networks process pleasant and unpleasant stimuli, and these networks may be independent of or covary and overlap with networks that encode arousal level (Lang et al., 1998). Several cross-validation studies have affirmed that emotionally provocative IAPS pictures reliably induce expressive and physiological emotional responses (Marchewka et al., 2014).

Previous research suggests that there are discrete and non-overlapping appetitive and aversive brain circuits that are engaged during exposure to pleasant and unpleasant IAPS images, respectively (Lang & Bradley, 2010). Specifically, the bilateral amygdalae are primarily involved in processing unpleasant stimuli, at a level that is stronger when the unpleasant stimulus is more arousing (Gerdes et al., 2010). Unpleasant emotional processing is also classically noted at regions including the hippocampus, parahippocampal gyri, temporal lobe, visual cortex, fusiform gyri, prefrontal cortex, and anterior cingulate gyrus (Aldhafeeri et al., 2012). Pleasant emotional processing involves significant activation in prefrontal cortex, anterior and posterior cingulate gyri, the temporal lobe, and occipital regions (Aldhafeeri et al., 2012; Gerdes et al., 2010), as well as right caudate and left medial and dorsolateral prefrontal cortex activation (Gerdes et al., 2010).

A growing body of research indicates that aerobic exercise is beneficial for improving the mental health of older adults in both chronic and acute time frames (Rhyner & Watts, 2016; Yao et al., 2021). Moderate-intensity aerobic exercise training has been shown to reduce anxiety, depression, and negative mood and boost self-esteem and cognitive function (Sharma et al., 2006). Furthermore, a single moderate-intensity session of aerobic exercise has been shown to provide anti-panic and anxiolytic effects, shift attentional bias toward pleasant stimuli and away from unpleasant stimuli while this physical activity is being performed, and influence connectivity between the anterior insula and hippocampus while increasing positive affect (Smith, 2013; Ströhle et al., 2005; Tian & Smith, 2011). In particular, in a previous study published from the same protocol and participants reported here, we found that improvements in positive affect were related to reductions in resting state functional connectivity within the cingulo-opercular network (Alfini et al., 2020). Nevertheless, little is known about the specific effects of exercise on pleasant and unpleasant emotion-related network recruitment in healthy older adults, which we hypothesize could represent the neural mechanisms that support the subjective mood improvements after acute exercise.

Impact Statement

Our fMRI findings contribute novel insight on several possible regional mechanisms that could underlie improved emotional processing after acute exercise in healthy older adults. We complement previous evidence that acute exercise can improve mood and suggest such effects may implicate activity changes at nodes of both appetitive and aversive emotion-related networks.

The aim of the present study was to determine if acute exercise, compared to a seated rest control condition, impacted pleasant and unpleasant emotion-related network recruitment in healthy older adults, as measured by task-related functional MRI. For this purpose, we used a meta-analysis informed ROI analysis to compare activation between conditions within each a priori emotion-related ROI, a meta-analysis informed mask analysis to compare activation between conditions in each voxel of a single mask containing all a priori emotion-related ROIs, and an exploratory functional region of interest (ROI) MRI analysis to compare activation between conditions in any post-condition active region. Finally, we aimed to determine whether exercise-related changes in brain activation were correlated with pre- to post-condition changes in self-reported affect.

2 | METHOD

2.1 | Participants

Thirty-two physically active, healthy, cognitively normal, and community-dwelling older adults (aged 55–81 years) were recruited for participation in the present study. To be included in the study, participants were required to be prescreened using a structured interview questionnaire. The prescreening and recruitment process ensured inclusion of participants that would be able to safely participate in acute exercise and an MRI scan. Briefly, participants were recruited from in-person informational sessions at local recreation centers, study fliers on university listservs and regional newspaper advertisements. Interested individuals were screened using a structured telephone interview to determine health history and identify potential contraindications for completion of study procedures. Individuals were excluded if they reported a history of heart attack, stroke, transient ischemic attack, seizures, brain tumor, epilepsy, closed head injury, alcohol or substance abuse, psychosis, current visual or auditory limitations, or a current diagnosis of Alzheimer's disease, cardiovascular disease, atrial fibrillation, coronary artery disease, diabetes, hypertension, or Parkinson's disease. We also attempted to exclude individuals with probable obstructive sleep apnea using the snoring tiredness observed pressure-body age neck gender questionnaire (scores >4) (Chung et al., 2016), elevated depression using the beck depression inventory-II (>13) (Beck et al., 1996), elevated trait anxiety using the state trait anxiety inventory (>54) (Spielberger et al., 1970), significant cognitive impairment using the mini-mental status examination (<24) (Folstein et al., 1983), left-handedness using the Edinburgh handedness inventory (<0) (Oldfield, 1971), severe obesity (body mass index ≥40 kg/m^2), low physical activity (<30 min of physical activity three times per week during the past 6 months), limited English language proficiency, and magnetic resonance imaging (MRI) contraindications. Health-related exclusion criteria generally helped to ensure a sample that could safely complete a bout of moderate to vigorous intensity aerobic exercise. Exclusion of left-handed individuals, mental health conditions, and cognitive impairment was particularly important in cutting potential sources of variation in emotional brain processing, as well (Brookshire & Casasanto, 2012; Bylsma et al., 2008; Costanzo et al., 2015; Li et al., 2020; Liu et al., 2022). Exclusion of individuals with probable obstructive sleep apnea was performed to exclude those with characteristically worsened sleep, since wrist actigraphy-based sleep data were also analyzed for the present sample (Alfini et al., 2020). Finally, those with limited English language proficiency and MRI contraindications were excluded to ensure that included individuals could understand instructions and undergo MRI. Individuals who qualified after telephone screening then obtained physician approval for moderate- to vigorous-intensity exercise and participated in a laboratory screening session in which participants were familiarized with study procedures, interviewed for seven-day physical activity recall (Sallis et al., 1985), and asked to provide informed consent. This study was approved by the Institutional Review Board of the University of Maryland in accordance with the Helsinki Declaration of 1975 (World Medical Association, 2013). All participants were instructed to maintain normal eating habits. Moreover, participants were told to refrain from eating for 4 h prior, drinking alcohol for 12 h before, and drinking caffeine for 4 h in advance to participation each testing day. Participants were given this advice so that confounding influences could be avoided, as caffeine and alcohol can alter neurotransmission and confound brain function (Ferré & O'Brien, 2011), while eating a short period before exercise can lead to gastrointestinal distress. Participants who completed all experimental sessions were paid for their participation. Subject recruitment and inclusion processes have been detailed for this sample previously [see Alfini et al., 2020 and figure 1 in Won et al., 2019].

2.2 | Acute exercise and rest conditions

In this within-subjects design study, participants completed exercise and rest conditions in a counterbalanced order across two testing days (intersession interval, mean = 12.21 days, standard deviation = 17.81 days). Counterbalancing of condition order effectively enables possible confounds from factors such as room familiarity

to be distributed equally across the conditions. The exercise protocol included 30 min of pedaling on a stationary bike at a moderate to vigorous intensity. The moderate to vigorous intensity of cycling was implemented by instructing participants to self-select their pace to correspond with a Borg's Rating of Perceived Exertion (RPE) of 15 (i.e., which is associated with the verbal anchor of "Hard") and a pedal cadence of 60–80 revolutions per minute (rpm) (Borg, 1990). As detailed by previous publications from our group and others, the 30-min acute exercise condition used an established protocol containing 20 min of steady-state exercise bounded by a 5-min self-paced warm-up and cooldown (Alfini et al., 2020; Won et al., 2019). The acute exercise was performed on a mechanically braked cycle ergometer (Monark 828 E, Monark Exercise AB, Vansbro, Sweden). After the completion of the cycling cooldown, participants were offered a towel and dry clothing.

For the rest condition, participants engaged in 30 min of wakeful seated chair rest at a target RPE of 6. Participants were not permitted to read, write, talk, listen to music, or use any electronic devices during their seated rest. The rest condition was completed in the same testing room that was used to perform the acute exercise condition.

During both conditions, participants were provided water ad libitum. Before, during, and after the conditions, valence, arousal, heart rate (HR), and RPE were measured at 5-min intervals. This process helped verify that participants were reaching prescribed intensities for each condition. While valence and arousal were assessed using the Self-Assessment Manikin (Bradley & Lang, 1994), HR was recorded using a HR monitor (Polar RS800CX, Polar Electro Oy, Kempele, Finland) and RPE was recorded using Borg's 6–20 scale (Borg, 1990).

2.3 | Behavioral assessments

Positive affect (PA) and negative affect (NA) were measured using the state version of the positive and negative affect schedule (PANAS) (Watson et al., 1988). The PANAS is a psychometrically sound 20-item index of PA and NA. State anxiety was also measured using the state trait anxiety inventory (STAI), a common tool used in both research and clinical settings that can measure state and trait anxiety (Spielberger et al., 1970). These behavioral measures were completed before and after each experimental condition. Behavioral findings based on the current sample plus four more participants excluded in the present analyses ($n = 32$) were identified and reported previously (Alfini et al., 2020).

2.4 | MRI assessment

Following each condition, participants were prepared for MRI and MRI data were then acquired using a Siemens 3.0 Tesla MR scanner and a 32-channel head coil. Participants were instructed to remain motionless, keep their eyes open, and gaze at a fixation crosshair. Sagittal T1-weighted anatomical images were acquired roughly 10 min after each experimental condition using a magnetization prepared rapid gradient echo (MPRAGE) sequence (repetition time [TR] = 1900 ms; echo time [TE] = 2.3 ms; inversion time [TI] = 900 ms; flip angle = 9°; slice thickness = 0.9 mm; in-plane resolution = 0.9 mm × 0.9 mm; matrix = 256 mm × 256 mm; field of view = 230 mm × 230 mm; duration = 4 min 26 s).

To assess emotional brain activation during functional data acquisition, emotionally provocative or neutral international affective pictures system (IAPS) pictures were presented electronically using E-Prime 2.0 (Psychology Software Tools). IAPS images vary on dimensions of valence and arousal and are used to reliably induce expressive and physiological emotional responses in lab settings (Lang & Bradley, 2010). Echo planar imaging (EPI) volumes were collected during the task approximately 40 minutes after the completion of the MPRAGE scan, using a multi-band sequence (repetition time = TR = 2000 ms; echo time = TE = 24 ms; flip angle = 70°; slice thickness = 3.0 mm; distance factor = 30%; 36 slices; in-plane resolution = 3.0 mm × 3.0 mm; matrix = 64 mm × 64 mm; field of view = 192 mm × 192 mm; volumes = 246; duration = 8 min 18 s). IAPS pictures were shown in 20-s blocks of either pleasant, neutral, or unpleasant stimulus valence—a given block contained only one of these valences and had 10 pictures presented for a repetition time (TR) of 2 s each. The full order of blocks for all subjects was neutral, pleasant, unpleasant, pleasant, unpleasant, pleasant, neutral, pleasant, unpleasant, unpleasant, neutral, and neutral. After each 20-s stimulus block, there was a 20-s rest block that involved the participant focusing on a fixation crosshair. For any given participant, the task version used after each experimental condition differed with unique sets of pictures, such that no specific image would be viewed more than once across the two testing days. Like condition order, the order of task version across testing days was counterbalanced across participants. To ensure that the visual stimuli were being attended to, participants were instructed to press buttons at their right index and middle fingers in response to indoor and outdoor images, respectively. The total duration of the IAPS task was 8 min 18 s.

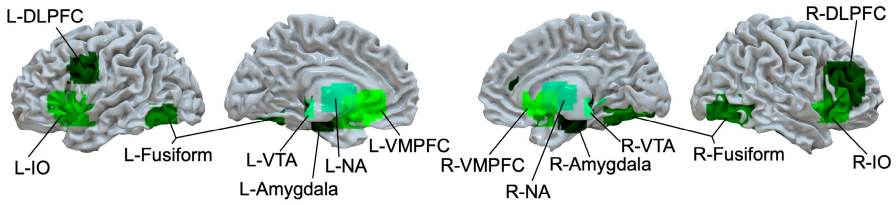

FIGURE 1 Meta-analytic emotional processing regions: Colored areas represent the 14 meta-analytic regions where activation to pleasant stimuli (pleasant minus neutral) and activation to unpleasant stimuli (unpleasant minus neutral) were compared between the exercise and rest conditions ($n = 28$). "L-", left; "R-", right; DLPFC, dorsolateral prefrontal cortex; IO, inferior orbital region; NA, nucleus accumbens; VMPFC, ventromedial prefrontal cortex; VTA, ventral tegmental area.

2.5 | fMRI data preprocessing

For each participant and condition, a structural T1 file and an IAPS-task-related functional e-prime data file were each located. Prior to data preprocessing, the structural and functional files were converted from DICOM to NifTI format. Functional images were processed using the Analysis of Functional NeuroImages (AFNI) software package (Cox, 1996). Functional images were aligned to an MNI template. Next, the anatomical data were skull-stripped and warped to the MNI template. Anatomical data were then run through Freesurfer's recon-all and @SUMA_Make_Spec_FS functions to generate a lateral ventricle mask and an anatomical follower file. The lateral ventricle mask was used in the afni_proc.py command to regress out the top three principal components from cerebrospinal fluid. The first two volumes of e-prime time-series data were removed using the tcat function. Other steps included in the afni_proc.py command included removal of outlier spikes in the data, slice timing correction to account for differences in data acquisition timings, alignment of functional data to the anatomical image, warping the anatomical data to standard space, volume registration for motion correction, blurring or spatial smoothing of each volume, creation of a brain mask from functional data, scaling the time series in each voxel individually to a mean of 100, and perform the regression analysis. The head motion censoring threshold in the afni_proc.py script was set as .5 mm.

Several fMRI contrasts of interest were calculated, including pleasant block-associated activation minus neutral block-associated activation, as well as unpleasant activation relative to neutral activation, as well. Neutral, pleasant, and unpleasant block-associated activation were set to be computed with reference to the off periods that involved viewing a fixation crosshair and no other stimulus. Three subjects were excluded from the analysis due to excessive head motion that was characterized as having 22% or more of fMRI task-associated TRs censored after either condition. A fourth subject was also excluded due to missing fMRI data. Thus, for any of the fMRI or behavioral analyses, $n = 28$ subjects. For these 28 included subjects, a paired t-test revealed that the percentage of task TRs censored after the acute exercise condition was not significantly different from the percentage of task TRs censored after the seated rest control condition ($p = .383$). As a result of data preprocessing, structural voxel dimensions were resampled to 1 mm × 1 mm × 1 mm, and functional voxel dimensions were resampled to 3 mm × 3 mm × 3 mm.

2.6 | fMRI data analysis

2.6.1 | Meta-analysis informed approach

The overall objective for the meta-analysis informed approach was to search for between-condition emotional activation differences in brain regions that have been established in the literature to be involved with emotional processing or regulation. After preprocessing steps, two meta-analysis-focused analyses were run—a meta-analytic region of interest (ROI) analysis and a meta-analytic mask analysis. To prepare for these analyses, meta-analytic regions involved with pleasant and unpleasant emotional processing were identified in an a priori fashion using a literature search and term-based activation maps in neuroquery.org. The pleasant emotional activation map was based on the search term "reward," whereas the unpleasant emotional activation map was based on the search terms "emotion regulation" and "emotional faces". A total of 14 unilateral meta-analytic ROIs were created and constrained to gray matter using MRIcron drawing tools—these ROIs are all shown in Figure 1. The eight cortical meta-analytic ROIs, as well as the search terms, valence (pleasant or unpleasant), and intensity ("I," in z-score units) and cluster size ("C," in number of voxels) thresholds associated with each of them are as follows: left and right fusiform regions ("emotional faces," unpleasant valence, I = 9, C = 10); left and right ventromedial prefrontal cortex regions, left and right dorsolateral prefrontal cortex regions, and left and right inferior orbital regions ("emotion regulation," unpleasant valence, I = 4, C = 10).

The six subcortical meta-analytic ROIs, and the search terms and valence associated with each of them, are left and right amygdala regions ("emotional faces," unpleasant valence); left and right nucleus accumbens regions ("reward," pleasant valence); and finally, the left and right ventral tegmental area regions ("reward," pleasant valence). Importantly, intensity and cluster-size thresholds were not applied to subcortical meta-analytic ROIs, since subcortical meta-analytic ROIs were created using an AAL3 atlas as the underlay. All 14 meta-analytic ROIs were created and constrained to cortical gray matter using MRIcron drawing tools. Additionally, all 14 meta-analytic ROIs were resampled to functional data resolution to enable mean beta extractions to be completed. It was hypothesized that the 14 meta-analytic emotion ROIs would show between-condition differences in pleasant (P-N) or unpleasant (U-N) activation.

For the meta-analytic ROI analysis, signal was averaged across a given ROI's voxels. Mean pleasant and unpleasant activation betas were extracted from each meta-analytic ROI, and mixed effects models were then utilized to compare emotional activation between the experimental conditions. For the meta-analytic mask analysis, first, a single mask containing all 14 meta-analytic emotion ROIs was constructed. Then, signal was analyzed in each mask voxel separately. Finally, paired *t*-tests were run to compare emotional activation between study conditions.

2.6.2 | Exploratory functional ROI analysis

The exploratory functional ROI analysis approach was a data-driven approach that involved a whole-brain voxel-wise analysis for each condition separately, and then comparisons between the conditions on the activated regions in either condition. As a result of the cluster-corrected voxel-wise analysis for the exercise and rest conditions, 17 regions of significant pleasant (P-N) or unpleasant (U-N) activation either post-exercise or post-rest were identified as functional regions of interest (ROIs) for further analysis to determine differences between the exercise and rest conditions. It was hypothesized that these functional ROIs would show between-condition differences in pleasant (P-N) or unpleasant (U-N) activation. These ROIs were saved using AFNI's interface.

From each of the 17 functional ROIs, activation beta weights were extracted for each subject after each condition. Next, between-condition comparisons for each ROI using paired *t*-tests were completed to determine significant between-condition activation differences. Group-wise false discovery rate (FDR) thresholds were applied to each significant *p*-value. FDR thresholds were calculated for each significant finding within the meta-analysis group of results or the exploratory functional ROI analysis group of results. Finally, pre- to post-condition changes in positive affect, negative affect, and state anxiety were investigated using paired *t*-tests.

3 | RESULTS

3.1 | Participants

We previously reported demographics for all 32 participants that completed the study protocol [see table 1 in Alfini et al., 2020]. The present sample of $n=28$ participants is highly similar and predominantly female ($n=20$, 71.4%), white ($n=22$, 78.6%), and highly educated with more than 12 years of schooling ($n=26$, 92.9%). Furthermore, the mean ± standard deviation for several baseline measures describing the current sample are as follows: Age (years) = 65.9 ± 7.6; body mass index (kg/m^2) = 25.9 ± 4.3; beck depression inventory II score = 1.9 ± 2.0; state–trait anxiety inventory form Y-2 (trait) score = 46.6 ± 4.1; total kcal/kg/week (expended for 7-day physical activity) = 223.8 ± 29.0. No adverse events were reported for any participant throughout the study.

3.2 | Manipulation check

As a precursor to hypothesis testing, we verified that there were significant differences in ratings of perceived exertion (RPE) and heart rate (HR) between the acute exercise and seated rest conditions [similar to table 2 in Alfini et al., 2020]. Mean ± standard deviation as well as results of paired *t*-tests comparing each measure between conditions are as follows: exercise RPE = 14.6 ± 1.2, rest RPE = 6.1 ± 0.2, $p=2.2\times10^{-16}$; exercise HR = 137.5 ± 19.4, rest HR = 66.5 ± 8.8, $p=7.2\times10^{-16}$. Subjective ratings of valence and arousal for each condition, and *p*-value for differences between conditions, were as follows: exercise SAM-V = 5.7 ± 2.0, rest SAM-V = 6.7 ± 2.1, $p=.022$; exercise SAM-A = 5.2 ± 2.0, rest SAM-A = 4.3 ± 2.1, $p=.087$.

3.3 | Behavioral assessments

Behavioral data (PA, NA, state anxiety) were imputed by respective sample means for one participant who had instances of missing data. A mixed-effects model using condition (exercise, rest), time (pre, post), sex (M, F), mean-centered age, and the interaction of condition and time as fixed effects and subject as a random effect revealed a nonsignificant condition × time interaction for PA (95% confidence interval [CI] = −0.24 to 5.36,

$p = .073$, $n = 28$) and a significant fixed effect of condition ($p = .005$). The acute exercise intervention missed significance in amplifying PA (95% CI = −0.06 to 2.06, $p = .064$, $n = 28$), whereas acute rest missed significance in diminishing PA (95% CI = −3.20 to 0.08, $p = .061$, $n = 28$). However, PA was significantly higher after acute exercise compared to after rest (95% CI = 0.86 to 4.93, $p = .007$, $n = 28$) and there were no differences in precondition baseline PA levels between exercise and rest (95% CI = −2.06 to 2.73, $p = .773$, $n = 28$). No significant effects were found for negative affect (NA) and state anxiety. Previous analysis of the full sample of 32 participants revealed a significant condition × time interaction for PA, significant enhancement of PA by acute exercise, and significant diminishment of PA by acute rest [see Alfini et al., 2020].

3.4 | Meta-analysis informed results

The meta-analysis informed ROI analysis did not reveal significant between-condition differences in unpleasant (U-N) or pleasant (P-N) activation (see Tables 1 and 2). The mixed models used to identify this lack of differences included gray matter mean activation beta as the outcome variable, condition, hemisphere, order, and age as fixed effects, and hemisphere and subject as random effects.

Meanwhile, the meta-analysis informed mask analysis showed that a portion of the right DLPFC meta-analytic ROI had greater unpleasant (U-N) activation after exercise compared to rest (cluster size-corrected, significant at a p threshold of $p = .01$, and corrected for multiple comparisons in AFNI). A paired t-test comparing mean activation betas between conditions at this subregion of the right DLPFC meta-analytic ROI was significant at $p = .001$ (see Table 3). Only this result from the meta-analysis informed approach survived the FDR threshold. Unpleasant (U-N) activation intensity at this result region, however, was not correlated with PA, NA, nor state anxiety behavioral score. For pleasant (P-N) activation, there were no differences between the exercise and rest conditions using the meta-analysis informed mask analysis.

3.5 | Exploratory functional ROI analysis

Among the 17 ROIs identified using the whole brain voxel-wise functional ROI analysis, seven showed significant between-condition activation differences that survived the FDR threshold. The bilateral precuneus ($p = .009$) demonstrated a significant between-condition difference for *pleasant* (P-N) activation (see Table 4 and Figure 2; also shown in Figure 4, right-most panel). However, pleasant (P-N) activation intensity at bilateral precuneus was not correlated with PA, NA, or state anxiety behavioral score.

For activation to unpleasant stimuli (U-N), the left fusiform gyrus (FG) and inferior temporal gyrus (ITG), right FG and ITG, left angular gyrus (AG) and supramarginal gyrus (SMG), left and right medial superior frontal gyrus (SFG in dorsomedial prefrontal cortex [DMPFC] area), right AG and SMG, and left cerebellum crus I and II all showed significant between-condition differences. Among these six ROIs, the left FG and ITG ($p = .007$) and right FG and ITG ($p = .022$) exhibited *reduced* activation to unpleasant stimuli (U-N) after exercise relative to rest. The left AG and SMG ($p = .014$), left and right medial SFG ($p = .002$), right AG and SMG ($p = .001$), and left cerebellum crus I and II ($p = .002$) all showed *greater* activation to unpleasant stimuli (U-N) after exercise relative to rest (see Table 5 and Figure 3; also shown in Figure 4, in all but the right-most panel). For each of the six result regions showing between-condition differences in unpleasant (U-N) activation, unpleasant (U-N) activation intensity was not correlated with PA, NA, or state anxiety behavioral score.

4 | DISCUSSION

These findings provide fMRI evidence that an acute bout of moderate to vigorous intensity aerobic cycling exercise, compared to a seated rest control condition, may influence neural circuits involved in visual emotional processing in healthy older adults. These effects were observed in regions known to be involved with both pleasant and unpleasant emotion processing. Importantly, this pattern aligns with previously published work from our group where the effects of acute exercise on semantic memory activation were localized to nodes of the semantic memory network (Won et al., 2019). In summary, following acute exercise relative to after seated rest, there was less activation for pleasant stimuli at the bilateral precuneus, less activation for unpleasant stimuli in the bilateral fusiform and inferior temporal gyri, and more activation for unpleasant stimuli in the bilateral medial superior frontal, angular, and supramarginal gyri, the left cerebellar crus I/II, and a portion of right dorsolateral prefrontal cortex. These results suggest less emotional regulation during pleasant emotional experience, reduced processing of negative emotional stimuli, and increased emotion regulation during unpleasant emotion, respectively (see Sections 4.1 and 4.2). These findings support that acute moderate to vigorous intensity exercise in active older adults alters activation in key brain regions associated with emotional processing and regulation.

Behavioral results of the present study are generally consistent with the post-exercise mood improvement

TABLE 1 Results of ROI analysis on meta-analytic emotional processing regions: No significant between-condition differences in intensity of activation for unpleasant emotional stimuli for any meta-analytic ROI ($n = 28$).

						Rest		Exercise		Exercise–rest	
Region label	***x***	***y***	***z***	**BA**	**Vox**	**Mean**	**SD**	**Mean**	**SD**	**Mean difference**	***p*-Value**
Frontal											
L-IO &	−26	13	−26	47	110	0.01	0.08	0.04	0.06	0.03	**.0447**
R-IO	28	25	−26	47, 11	92						
L-IO	−26	13	−26	47	110	0.03	0.06	0.04	0.05	0.01	.5280
R-IO	28	25	−26	47, 11	92	0.00	0.09	0.04	0.07	0.04	.0672
L-DLPFC &	−56	16	19	9, 46	63	0.01	0.05	0.03	0.06	0.02	**.0467**
R-DLPFC	34	40	−14	10, 46	217						
L-DLPFC	−56	16	19	9, 46	63	0.03	0.05	0.04	0.06	0.01	.4490
R-DLPFC	34	40	−14	10, 46	217	−0.01	0.05	0.02	0.06	0.03	.0627
L-VMPFC	−2	22	−26	11	123	0.00	0.06	0.01	0.07	0.01	.5087
R-VMPFC	4	28	−17	11	30	−0.02	0.10	0.01	0.05	0.03	.1468
Occipital, temporal											
L-FG	−50	−56	−29	37	77	0.05	0.09	0.02	0.09	−0.03	.1500
R-FG	40	−44	−29	37	139	0.03	0.10	0.04	0.08	0.01	.8340
Subcortical											
L-VTA	−5	−23	−17	–	2	0.02	0.09	0.01	0.09	−0.01	.7075
R-VTA	4	−23	−17	–	2	0.00	0.09	0.01	0.08	0.01	.5060
L-NA	−11	7	−14	–	45	0.00	0.05	0.01	0.06	0.01	.6950
R-NA	7	7	−11	–	38	−0.01	0.04	−0.01	0.05	0.00	.9760
L-Amygdala	−29	−5	−29	–	66	0.03	0.12	0.05	0.08	0.02	.5060
R-Amygdala	31	−2	−32	–	73	0.03	0.06	0.02	0.05	−0.01	.7830

Note: Activation for unpleasant emotional stimuli is the unpleasant minus neutral contrast for each experimental condition. The (*x*), (*y*), and (*z*) represent peak activation in neurological coordinates on MNI space; BA, Brodmann area; vox, number of voxels in cluster; vol, cluster volume in mm^3; mean, mean activation intensity post-condition beta; SD, standard deviation of mean activation intensity post-condition beta; *p*-value, *p*-value of the condition effect from mixed-effects models using mean activation intensity as the outcome variable, condition, hemisphere, scan order, and age as fixed effects, and subject as a random effect (note that the mixed models testing the pairs of meta-analytic ROIs uniquely had Hemisphere as a random effect, too); "L/R-", left and right; "L-", left; "R-", right; DLPFC, dorsolateral prefrontal cortex; FG, fusiform gyrus; IO, inferior orbital region; NA, nucleus accumbens.; VMPFC, ventromedial prefrontal cortex; VTA, ventral tegmental area. Comparisons in bold font had $p < .05$ but lack an asterisk (*) because they did not survive the false discovery rate (FDR) threshold—thus, these findings were not statistically significant.

we previously reported in the full sample of 32 subjects (Alfini et al., 2020). In the current analysis, we confirmed a significantly greater positive affect after exercise relative to after seated rest in the current sample of 28 participants, and the effect sizes were similar compared to our previous report (Alfini et al., 2020). Increased positive affect in older adults has been associated with greater physiological well-being, improved mental health, increased interaction with the environment, increased participation in leisure activities, effective stress coping, and social connectedness (Fredrickson, 2001; Steptoe et al., 2008). Importantly, greater positive affect has also been correlated with patterns of thought that are notably more flexible, creative, integrative, open to information, and efficient (Estrada et al., 1997; Isen et al., 1987, 1991; Isen & Daubman, 1984; Isen & Means, 1983). Thus, it appears that greater positive affect can improve older adult's mental health and cognition—two domains that commonly worsen with increased age, even for otherwise healthy older adults (Dumas, 2017; Jokela et al., 2013; Petrova & Khvostikova, 2021; Sinha et al., 2021).

4.1 | Meta-analysis informed approach

We observed from the meta-analysis informed mask analysis approach that a portion of the right DLPFC meta-analytic ROI had greater unpleasant activation after 30 min of stationary cycling, when compared to after seated rest ($p = .001$ in meta-analytic mask analysis). Prior evidence suggests that this region may be involved in the control and regulation of the valence of emotional experiences (Nejati

TABLE 2 Results of ROI analysis on meta-analytic emotional processing regions: No significant between-condition differences in intensity of activation for pleasant emotional stimuli for any meta-analytic ROI ($n = 28$).

						Rest		Exercise		Exercise–rest	
Region label	***x***	***y***	***z***	**BA**	**Vox**	**Mean**	**SD**	**Mean**	**SD**	**Mean difference**	***p*-Value**
Frontal											
L-IO	−26	13	−26	47	110	0.03	0.06	0.02	0.04	−0.01	.3303
R-IO	28	25	−26	47, 11	92	0.02	0.08	0.03	0.05	0.01	.7040
L-DLPFC	−56	16	19	9, 46	63	0.02	0.05	0.02	0.05	0.00	.7200
R-DLPFC	34	40	−14	10, 46	217	0.02	0.06	0.03	0.05	0.01	.4580
L-VMPFC	−2	22	−26	11	123	0.02	0.07	0.02	0.06	0.00	.9960
R-VMPFC	4	28	−17	11	30	0.01	0.08	0.01	0.06	0.00	.9590
Occipital, temporal											
L-FG	−50	−56	−29	37	77	0.02	0.11	0.01	0.09	−0.01	.8630
R-FG	40	−44	−29	37	139	0.03	0.10	0.04	0.09	0.01	.5160
Subcortical											
L-VTA	−5	−23	−17	–	2	0.01	0.08	0.00	0.09	−0.01	.5161
R-VTA	4	−23	−17	–	2	0.00	0.08	0.01	0.07	0.01	.7630
L-NA	−11	7	−14	–	45	0.02	0.05	0.01	0.05	−0.01	.2784
R-NA	7	7	−11	–	38	0.01	0.05	0.00	0.05	−0.01	.4720
L-Amygdala	−29	−5	−29	–	66	0.01	0.11	0.02	0.06	0.01	.7170
R-Amygdala	31	−2	−32	–	73	0.00	0.06	0.00	0.05	0.00	.9870

Note: Activation for pleasant emotional stimuli is the pleasant minus neutral contrast for each experimental condition. The (*x*), (*y*), and (*z*) represent peak activation in neurological coordinates on MNI space; BA, Brodmann area; vox, number of voxels in cluster; vol, cluster volume in mm^3; mean, mean activation intensity post-condition beta; SD, standard deviation of mean activation intensity post-condition beta; *p*-value, *p*-value of the condition effect from mixed-effects models using mean activation intensity as the outcome variable, condition, hemisphere, scan order, and age as fixed effects, and subject as a random effect; "L-", left; "R-", right; "L/R-", left and right; IO, inferior orbital region; DLPFC, dorsolateral prefrontal cortex; VMPFC, ventromedial prefrontal cortex; FG, fusiform gyrus; VTA, ventral tegmental area; NA, nucleus accumbens.

TABLE 3 Results of mask analysis on meta-analytic emotional processing regions: Significant between-condition differences in intensity of activation for unpleasant emotional stimuli for a subset of one meta-analytic ROI ($n = 28$).

						Rest		Exercise		Exercise–rest	
Region label	***x***	***y***	***z***	**BA**	**Vox**	**Mean**	**SD**	**Mean**	**SD**	**Mean difference**	***p*-Value**
Frontal											
R-DLPFC	31	58	4	46, 10	14	−0.03	0.07	0.04	0.07	0.07	**.0005***

Note: Activation for unpleasant emotional stimuli is the unpleasant minus neutral contrast for each experimental condition. The (*x*), (*y*), and (*z*) represent peak activation in neurological coordinates on MNI space; BA, Brodmann area; vox, number of voxels in cluster; vol, cluster volume in mm^3; mean, mean activation intensity post-condition beta; SD, standard deviation of mean activation intensity post-condition beta; *p*-value, *p*-value for paired *t*-test of post-exercise and post-rest activation intensity mean betas at this region (99% confidence); DLPFC, dorsolateral prefrontal cortex; "R-", right. The comparison in bold font is significant at $p < .05$, and an asterisk (*) is appended to this significant finding since it survived the false discovery rate (FDR) threshold.

et al., 2021). The DLPFC also exhibits increased connectivity with the amygdala when it is contributing to emotion regulation (Berboth & Morawetz, 2021). Moreover, excitatory transcranial direct stimulation of the DLPFC has been shown to enhance intentional upregulation of positive emotional reactivity and downregulation of negative emotional reactivity (Hansenne & Weets, 2020). Thus, the literature therefore supports that the DLPFC may play a general role to assist in attenuating negative emotional reactivity due to its inhibitory projections onto subcortical emotional circuitry, including the amygdala. The present meta-analysis result suggests that there may be increased emotion regulation during unpleasant emotional processing after exercise when compared to rest.

TABLE 4 Exploratory functional ROI analysis results: Significant between-condition differences in intensity of activation for pleasant emotional stimuli for one functional ROI ($n = 28$).

						Rest		Exercise		Exercise–rest	
Region label	***x***	***y***	***z***	**BA**	**Vox**	**Mean**	**SD**	**Mean**	**SD**	**Mean difference**	***p*-Value**
Parietal											
L/R-precuneus	−2	−65	49	7	80	0.07	0.06	0.02	0.07	−0.05	**.0091***
Parietal, temporal											
R-AG, R-STG, R-MTG, R-TPJ	52	−53	22	40, 39, 13	15	0.06	0.06	0.04	0.07	−0.02	.1265

Note: Activation for pleasant emotional stimuli is the pleasant minus neutral contrast for each experimental condition. The (*x*), (*y*), and (*z*) represent peak activation in neurological coordinates on MNI space; BA, Brodmann area; vox, number of voxels in cluster; vol, cluster volume in mm^3; mean, mean activation intensity post-condition beta; SD, standard deviation of mean activation intensity post-condition beta; *p*-value, *p*-value for paired *t*-test of post-exercise and post-rest activation intensity mean betas (99% confidence); "L-", left; "R-", right; "L/R-", left and right; AG, angular gyrus; MTG, middle temporal gyrus; STG, superior temporal gyrus; TPJ, temporoparietal junction. The comparison in bold font is significant at $p < .05$, and an asterisk (*) is appended to this significant finding since it survived the false discovery rate (FDR) threshold.

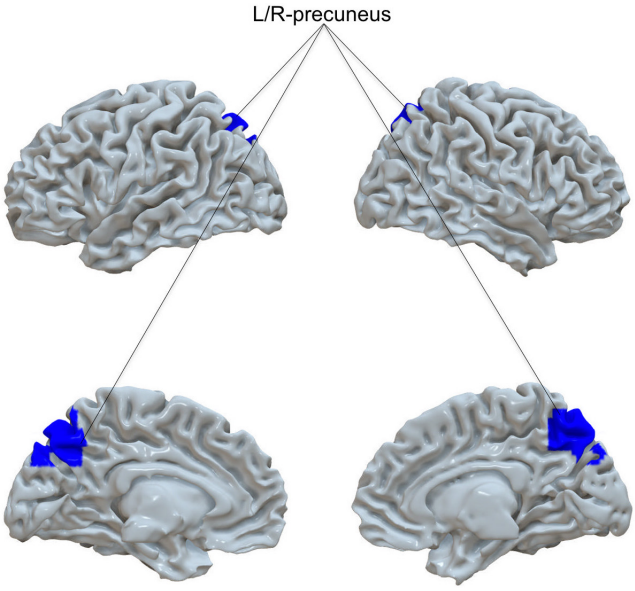

FIGURE 2 Exploratory functional ROI analysis results: Between-condition differences in activation for pleasant emotional stimuli in one functional ROI. Activation for pleasant emotional stimuli is the pleasant minus neutral contrast for each experimental condition. The colored area and label represent the sole region where intensity of activation for pleasant emotional stimuli (Pleasant minus Neutral) was significantly different between the exercise and rest conditions ($n = 28$). The blue color indicates that the intensity of activation for pleasant emotional stimuli was significantly lower after exercise relative to after rest. This significant finding survived the false discovery rate (FDR) threshold and is presented in Table 4.

4.2 | Exploratory functional ROI approach

The exploratory functional ROI analysis showed significantly less activation to pleasant stimuli after exercise compared to after rest in the bilateral precuneus. The bilateral precuneus is known to support a wide array of highly integrative functions, including visuospatial memory, episodic memory retrieval, first-person perspective taking, and the experience of agency (Cavanna & Trimble, 2006). Relevant to the present study, there is also evidence that the precuneus may play a vital role in neural circuits involved in different emotion regulation strategies (Bendall, 2017). For example, the precuneus exhibits greater connectivity with the amygdala when an individual is regulating their emotions by redirecting their attention when facing unpleasant emotional stimuli (Ferri et al., 2016). Along these lines, previous literature indicates that the precuneus may be a hub for emotion inhibition-related activity that is more active when emotion inhibition demands are high (Bartholomew et al., 2019). Less activation to pleasant stimuli relative to neutral (P-N) in the bilateral precuneus after exercise may reflect a lowering of emotional inhibition during pleasant emotional experience. Individuals diagnosed with a mood disorder and suicidal behavior have previously been shown to have abnormally high functional connectivity from the amygdala to the paracentral lobule and precuneus (Zhang et al., 2020). In our study, subjective positive affect increased after exercise relative to rest. Our finding of lower bilateral precuneus activation during pleasant picture viewing suggests that improved regulation of precuneus-driven emotional inhibition may be one of the effects of exercise in emotion-related neural networks that *collectively* underlie the therapeutic effect of exercise on mood.

Six regions displayed significant differences in activation to unpleasant stimuli (U-N) between the two experimental conditions. Four of those regions showed greater unpleasant activation after exercise when compared to

TABLE 5 Exploratory functional ROI analysis results: Significant between-condition differences in intensity of activation for unpleasant emotional stimuli for six functional ROIs ($n = 28$).

						Rest		Exercise		Exercise–rest	
Region label	***x***	***y***	***z***	**BA**	**Vox**	**Mean**	**SD**	**Mean**	**SD**	**Mean difference**	***p*-Value**
Frontal											
L/R-mSFG (DMPFC)	1	55	25	9, 10	105	0.02	0.04	0.08	0.07	0.06	**.0023***
L-Broca's area	−56	22	10	45, 44	16	0.03	0.05	0.06	0.05	0.03	**.0440**
Temporal											
R-anterior STS, R-STG, R-MTG	49	−11	−11	22, 21	15	0.03	0.05	0.07	0.06	0.04	.0531
R-MTG	67	−47	4	22, 21	49	0.09	0.12	0.12	0.09	0.03	.2620
Parietal											
R-AG, R-SMG	64	−56	28	40, 39, 22	38	0.02	0.06	0.08	0.06	0.06	**.0007***
L-AG, L-SMG	−50	−59	28	39, 40	70	0.03	0.05	0.07	0.06	0.04	**.0143***
L-SMG	−65	−47	28	40	15	0.03	0.06	0.06	0.06	0.03	.0776
Occipital, temporal											
L-FG, L-ITG	−41	−56	−14	37	17	0.08	0.08	0.02	0.08	−0.06	**.0075***
R-FG, R-ITG	37	−53	−14	37	19	0.08	0.07	0.03	0.08	−0.05	**.0219***
L-IOG, L-FG	−50	−74	−17	19, 18, 37	15	0.16	0.13	0.12	0.19	−0.04	.3546
R-IOG, R-MOG, R-V5/MT, R-ITG	52	−80	−2	19, 18, 37	28	0.13	0.16	0.15	0.13	0.02	.4652
L-IOG, L-MOG, L-V5/MT, L-ITG	−53	−74	−8	19, 37, 18	20	0.09	0.12	0.13	0.11	0.04	.2124
L-IOG, L-MOG, L-ITG	−47	−83	−5	19, 18	16	0.08	0.12	0.13	0.12	0.05	.1199
R-IOG, R-MOG, R-V5/MT, R-ITG	43	−80	−11	19, 18	58	0.11	0.10	0.08	0.08	−0.03	.1463
Cerebellum											
L-cerebellum crus I & II	−32	−89	−29	18, 19	20	0.02	0.10	0.11	0.11	0.09	**.0018***

Note: Activation for unpleasant emotional stimuli is the unpleasant minus neutral contrast for each experimental condition. The (x), (y), and (z) represent peak activation in neurological coordinates on MNI space; BA, Brodmann area; vox, number of voxels in cluster; vol, cluster volume in mm^3; mean, mean activation intensity post-condition beta; SD, standard deviation of mean activation intensity post-condition beta; p-value, p-value for paired t-test of post-exercise and post-rest mean betas (99% confidence); "L/R-", left and right; "L-", left; "R-", right; AG, angular gyrus; DMPFC, dorsomedial prefrontal cortex; FG, fusiform gyrus; IOG, inferior occipital gyrus; ITG, inferior temporal gyrus; MOG, middle occipital gyrus; MTG, middle temporal gyrus; SFG, superior frontal gyrus; SMG, supramarginal gyrus; STG, superior temporal gyrus; STS, superior temporal sulcus; V5/MT, middle temporal visual area. The comparisons in bold font are significant at $p < .05$, and asterisks (*) are appended to the significant findings that survived the false discovery rate (FDR) threshold. The sole comparison in bold font lacking an asterisk (*) had $p < .05$ but did not survive the false discovery rate (FDR) threshold—thus, this finding was not statistically significant.

after rest—namely, the left angular gyrus and supramarginal gyrus, right angular gyrus and supramarginal gyrus, bilateral medial superior frontal gyrus (in DMPFC), and left cerebellum crus I/II. These four regions have a myriad of roles, but each has been implicated in processes of emotion regulation (Kensinger & Ford, 2021; Opialla et al., 2015; Snow et al., 2014; Tanaka & Kirino, 2019). Furthermore, angular gyrus damage can be associated with depressive symptoms, abnormally high medial superior frontal gyrus activation has been associated with stronger emotional reactivity to unpleasant stimuli, and inhibitory transcranial magnetic stimulation of the cerebellum has been correlated with emotion dysregulation (Nagaratnam et al., 2002; Powers et al., 2017; Schutter & van Honk, 2009). Supramarginal gyrus volume has itself been positively associated with efficacy of emotion recognition performance into older age—which is consistent with an emotion regulation-related role since emotion recognition has been suggested to be a precursor to emotion regulation (Wada et al., 2021; Yoo et al., 2006). Another noteworthy point is that the angular gyrus and supramarginal gyrus are located within the inferior parietal lobule, a brain region involved in detecting and responding to behaviorally relevant environmental stimuli as part of

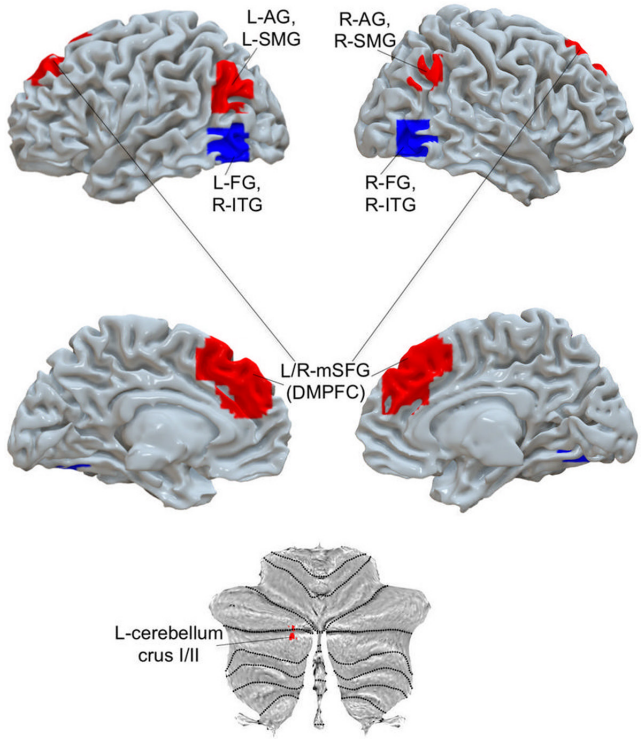

FIGURE 3 Exploratory functional ROI analysis results: Between-condition differences for unpleasant emotional stimuli. Colored areas and labels depict six regions where intensity of activation for unpleasant emotional stimuli (unpleasant minus neutral) intensity was significantly different between the exercise and rest conditions ($n = 28$)—these depicted significant clusters survived the false discovery threshold (FDR). Blue indicates that the intensity of activation for unpleasant emotional stimuli was significantly lower after exercise relative to after rest, whereas red conveys that the intensity of activation for unpleasant emotional stimuli was significantly greater after exercise when compared to after rest. The first and second rows show lateral and medial views of the left and right hemispheres, respectively. The third row depicts a flatmap of the cerebellum. The cluster size on the cerebellar flatmap is not to scale with cluster sizes in the lateral and medial hemisphere views—for reference, the size of the cluster in the cerebellum is 20 vox, whereas the size of the R-AG/SMG cluster is 38 vox. The findings depicted in this figure are included in Table 5. "L/R-", left and right; "R-", right; AG, angular gyrus; DMPFC, dorsomedial prefrontal cortex; FG, fusiform gyrus; ITG, inferior temporal gyrus; L-", left; mSFG, medial superior frontal gyrus; SMG, supramarginal gyrus.

the salience network (Uddin et al., 2019). Taken together, greater activation during the viewing of unpleasant stimuli after exercise compared to after rest at the left angular gyrus and supramarginal gyrus, right angular gyrus and supramarginal gyrus, bilateral medial superior frontal gyrus, and left cerebellum crus I/II may reflect ascribing greater salience to unpleasant external stimuli and/or increased emotion regulation during unpleasant emotion. Both potential effects are possible, but we speculate the latter could be more likely given that all regions play a role in emotion regulation and subjective positive affect increased after exercise relative to rest.

The two regions that showed significantly lower activation to unpleasant stimuli following exercise when compared to after rest were the left FG and ITG as well as the right FG and ITG. The fusiform gyrus has been implicated in high-level visual functions such as face processing (Kanwisher et al., 1997; Weiner & Zilles, 2016). There is evidence that the fusiform gyrus exhibits stronger responses to emotional than neutral faces, and this may be explained by extensive bidirectional connectivity between the fusiform gyrus and the amygdala (Herrington et al., 2011; Monroe et al., 2013). The FG and ITG may thus encode emotional salience. In support of this interpretation, while abnormal fusiform activation level may be one of the factors that underlies increased sensitivity to unpleasant emotional content for schizophrenia and social anxiety disorder patients, inferior temporal gyrus volume has been positively correlated with level of recognition of negative emotions (Frick et al., 2013; Li et al., 2010; Rosen et al., 2006). The present finding of less activation to unpleasant stimuli at the left FG and ITG as well as the right FG and ITG after exercise relative to rest may reflect reduced signals to/from the amygdala in response to unpleasant stimuli. In support of this view, prior work suggests that higher positive affect is associated with lower amygdala reactivity to unpleasant stimuli, which given previously described bidirectional connectivity relations would suggest that higher positive affect may also be associated with reduced fusiform reactivity to unpleasant stimuli (Sanchez et al., 2015). In the present study, the exercise-specific effect of reduced unpleasant activation at left FG and ITG and right FG and ITG was complemented by the behavioral effect of significantly greater positive affect after exercise when compared to rest.

4.3 | Potential mechanisms and limitations

The cellular mechanisms by which acute aerobic exercise influences emotional activation levels and mood remain inconclusive. One possibility is that change in emotional activation level at a given region after exercise is mediated by change in amount of galaninergic inhibition of noradrenergic circuits (Sciolino & Holmes, 2012). Regarding mood improvement after exercise, evidence suggests that acute aerobic exercise may enhance positive affect by significantly reducing cortisol response during subsequent stressful tasks (Chen et al., 2019). Acute exercise may also improve mood via opioid or serotonin systems (Dietrich & McDaniel, 2004). There is

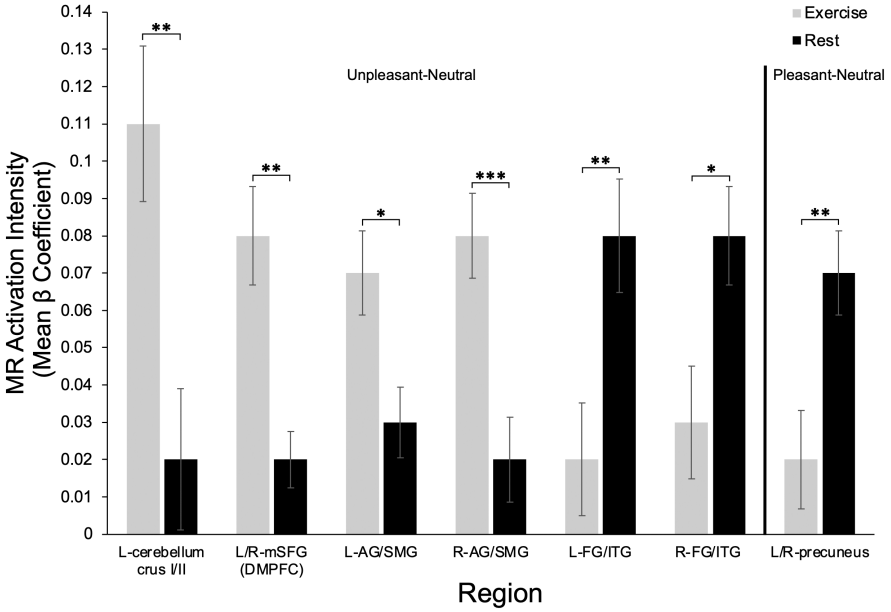

FIGURE 4 Mean intensity of activation for unpleasant emotional stimuli (unpleasant minus neutral, mean activation intensity β coefficient) for six regions and mean intensity of activation for pleasant emotional stimuli (pleasant minus neutral, mean activation intensity β coefficient) for one region, after each condition. All regions from the exploratory functional ROI analysis that showed a significant between-condition activation difference which survived the false discovery rate (FDR) threshold are depicted. Error bars = standard error of the mean (SEM); "L/R-", left and right; "L-", left; "R-", right; AG, angular gyrus; DMPFC, dorsomedial prefrontal cortex; FG, fusiform gyrus; ITG, inferior temporal gyrus; mSFG, medial superior frontal gyrus; SMG, supramarginal gyrus. Asterisks indicate statistical significance as follows: "*", $p < .05$; "**", $p < .01$; "***", $p < .001$.

reason, however, to suspect that neurochemical changes do not explain the *entirety* of mood improvement after acute exercise, and that regional activation changes also contribute. For instance, excitatory transcranial direct stimulation of the ventromedial prefrontal cortex has been shown to influence the processing of emotional stimuli (Junghofer et al., 2017). Moreover, major depressive disorder patients exhibit activation level abnormalities in regions including the prefrontal cortex and amygdala, and these abnormalities may correlate with attention and memory biases toward unpleasant stimuli and away from pleasant stimuli (Davidson et al., 2002; Drevets, 1998; Groenewold et al., 2013). Interestingly, in healthy young adults, we have shown that during moderate- to vigorous-intensity cycling exercise, attentional bias toward pleasant faces increases and attentional bias toward unpleasant faces decreases (Tian & Smith, 2011). Mental health does crucially depend on different affective states, such as emotions, and dysregulated emotional circuitry might lead to maladaptive, detrimental effects on mental well-being (Gross et al., 2019). Our findings are consistent with a protective effect from a single session of exercise in healthy older adults.

To our knowledge, our study is the first to elucidate specific activation changes at emotion-processing brain regions after acute exercise in active older adults. These effects may underlie the classically observed improvement of mood after acute exercise. Furthermore, our study utilized two analytic approaches; one that was informed by and restricted to a meta-analysis of the existing neuroimaging literature and a second data-driven whole brain voxelwise analysis that was unconstrained. These two approaches revealed convergence with the existing literature on emotion and also revealed effects that may be specific to the metabolic impacts of exercise. Moreover, our fMRI contrasts for pleasant and unpleasant emotional activation were made relative to neutral stimulus processing in order to account for any generalized effects of exercise on visual processing. However, our work is not without limitations. Specifically, while engagement with IAPS pictures is an effective approximation of real-life emotional situations, these stimuli do not produce a flawless emulation of human emotional experience. The IAPS images are encountered in the specific context of the scanner, which is socially, environmentally, and bodily an entirely different experience compared to spontaneous life experience. Second, although we observed significant pleasant- and unpleasant-related activation differences between the exercise and rest conditions, differences between conditions in subjectively rated affect were not correlated with differences in activation magnitude. In our previous work (Alfini et al., 2020) which involved a separate resting state fMRI scan in the same participants, we found that decreased resting state functional connectivity between

the bilateral insula and the hippocampus was related to increased positive affect after exercise. The lack of such associations in the ROI approach employed in the current study suggests that emotion networks, as opposed to isolated brain regions involved in emotion processing, may play a more prominent role in the mood enhancing effects of exercise [see (Won et al., 2021) for detailed review]. It is also possible that parts of the brain not involved with emotional picture processing support mood changes following acute exercise. Third, we did not observe significant between-condition activation differences in subcortical regions, such as the amygdala. Nevertheless, this is consistent with previous work that supports that acute exercise does not affect the amplitude of the acoustic startle eyeblink response, which is linked to amygdala circuits (Lang et al., 1998), nor corrugator muscle activation during IAPS picture viewing (Smith et al., 2002; Smith & O'Connor, 2003). Future studies should explore amygdala connectivity after acute exercise and include sedentary older adults and those diagnosed with depression and/or anxiety. Fourth, post hoc power analyses revealed that any findings with $p < .05$ that did not pass FDR-correction (see Tables 1 and 5) had power between 0.52 and 0.56, suggesting that a more well-powered study with a greater sample size is still needed to clarify whether such findings are statistically significant. Given the small sample size, the effects that met FDR-correction should be considered preliminary and should be replicated. Finally, 55–81 years is a large age range to consider as older adults, and it is possible that age-based differences might have influenced findings. However, we examined the correlations between age and activation intensity after each condition and found that only one region (left angular gyrus and supramarginal gyrus after rest) was negatively correlated with age, but this association was not statistically significant after correction for multiple comparisons. Thus, we did not observe any evidence for a consistent association between age and brain activation after exercise or rest in our study.

5 | CONCLUSION

The present study suggests that an acute bout of exercise may influence brain activation during the viewing of pleasant and unpleasant images in healthy older adults via regional upregulation or downregulation of activation in emotion-related neural circuits. These effects may support improved emotional reactivity, given that subjective positive affect was significantly greater after exercise compared to after rest. Our findings provide mechanistic evidence to support the widely reported recommendation that exercise may be useful as a lifestyle intervention to address the public health challenge of mental health service for an ever-expanding world population of older adults. Although the durability and longitudinal impact of acute exercise on emotion-related neural networks remains uncharacterized, our data suggest that a single session of acute exercise may benefit healthy older adults via amplification of pleasant emotional experience and attenuation of unpleasant emotional processing. Future work should replicate these preliminary findings and determine if regular engagement in exercise produces adaptations within emotion-related networks that lead to long-term protection of mental health and prevention of mood disorders in older adults.

AUTHOR CONTRIBUTIONS

Yash Kommula: Formal analysis; investigation; visualization; writing – original draft; writing – review and editing. **Jeremy J. Purcell:** Supervision; visualization; writing – review and editing. **Daniel D. Callow:** Writing – review and editing. **Junyeon Won:** Data curation; project administration; writing – review and editing. **Gabriel S. Pena:** Writing – review and editing. **J. Carson Smith:** Conceptualization; data curation; funding acquisition; methodology; project administration; resources; supervision; validation; writing – review and editing.

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CONFLICT OF INTEREST

All authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and analysis code that support the findings of this study are available from the corresponding author upon reasonable request.

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