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Neural correlates of changing food choices while bypassing values

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ABSTRACT

Current theories suggest that altering choices requires value modification. To investigate this, normal-weight female participants' food choices and values were tested before and after an approach-avoidance training (AAT), while neural activity was recorded during the choice task using functional magnetic resonance imaging (fMRI). During AAT, participants consistently approached low- while avoiding high-calorie food cues. AAT facilitated low-calorie food choices, leaving food values unchanged. Instead, we observed a shift in indifference points, indicating the decreased contribution of food values in food choices. Training-induced choice shifts were associated with increased activity in the posterior cingulate cortex (PCC). In contrast, the medial PFC activity was not changed. Additionally, PCC gray matter density predicted individual differences in training-induced functional changes, suggesting anatomic predispositions to training impact. Our findings demonstrate neural mechanisms underlying choice modulation independent of valuation-related processes, which has substantial theoretical significance for decision-making frameworks and translational implications for health-related decisions resilient to value shifts.

1. Introduction

Optimizing dietary patterns is essential for aiding humans (Cureau et al., 2018; Ebbeling et al., 2004; Forouzanfar et al., 2015; Romieu et al., 2017) and global environmental health (Clark et al., 2019; Mason and Lang, 2015; Willett et al., 2019). In a recent framework, Rangel et al. (2008) categorized computational processes involved in value-based decision-making into five stages: representation, valuation, action selection, outcome appraisal, and learning. Accordingly, even in the most straightforward decision, an agent first needs to identify possible actions, calculate the value of each option, and finally select the one with the highest value. Conspicuously, valuation plays a central role in decision-making (for review, see Balleine et al., 2008; Balleine and O'Doherty, 2010). Similarly, to choose which food item to consume, one heavily relies on their existing values (i.e., food preferences). Current theories assume that changing choices are accompanied by modifying values associated with targeted items (Balleine et al., 2008; Balleine and Dickinson, 1998; Balleine and O'Doherty, 2010; Rangel et al., 2008). However, the necessity of shifting values for altering choices has recently become a matter of intense debate (Bakkour et al., 2016; Becker et al., 2015; Kakoschke et al., 2017b; Knudsen and Wallis, 2022; Mehl et al., 2018; Schonberg et al., 2014; Schonberg and Katz, 2020; Schumacher et al., 2016). Whether choice can be affected regardless of value has substantial theoretical significance for understanding the cognitive and neural mechanisms of decision-making (Knudsen and Wallis, 2022; Rangel et al., 2008) and translational implications for strategies used to optimize health-related decisions, such as food choices in clinical and normal populations (Bongers et al., 2015; Guerrieri et al., 2008; Nederkoorn et al., 2009, 2010).

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Choices are simultaneously affected by multiple factors (Balleine et al., 2008; Balleine and Dickinson, 1998; Balleine and O'Doherty, 2010; Rangel et al., 2008). The most intuitive feature is the expected reward value associated with possible options, leading to choosing the item with the highest subjective value (Bradfield and Balleine, 2013; Colwill, 1993; Colwill and Delamater, 1995; Thrailkill et al., 2021). Alternatively, choices can also be affected in the absence of value modification, a procedure that is largely uninvestigated in terms of underlying cognitive processes and neural substrates (Rangel et al., 2008). For example, direct training to approach certain food cues could lead to a higher frequency of choosing the targeted item, independent of the value associated with the response (Hershberger, 1986). Notably, the difference between value- and non-value-based mechanisms is not related to their automaticity. That is, once well-trained, both mechanisms can lead to automatic responses (Strack and Deutsch, 2004; Thrailkill et al., 2021) that are not resource-consuming (Cooper and Shallice, 2000; Norman and Shallice, 1986). Additionally, if enough cognitive resources are available, both mechanisms can be overridden by using inhibition (Diamond, 2013). Still, since inhibition, like other forms of cognitive control, requires an immediate mental effort, it is aversive. Consequently, we prefer to rely on cognitive control processes as little as feasible (Botvinick and Braver, 2015; Shenhav et al., 2017), highlighting the importance of regimens that can affect choices without resorting to inhibition (Froehlich et al., 2021; Guerrieri et al., 2008; Nederkoorn et al., 2009; Zahedi et al., 2020).

One approach to change choices in the absence of value modification is employing approach-avoidance training (AAT; Kakoschke et al., 2017a; Wiers et al., 2011), in which targeted stimuli are consistently associated with approach or avoidance. For instance, Wiers et al. (2011) showed that a short AAT, associating alcoholic beverages with avoiding response, induced an avoidance bias toward alcohol in alcohol-dependent participants. Importantly, this avoidance bias was accompanied by symptom improvement in these patients. AAT can be considered a nonreinforced learning procedure (Schonberg and Katz, 2020) since the targeted stimuli are not connected to reward or punishment contingencies but to specific responses. Consequently, even though AAT modifies behavior, it is largely unknown how this is related to value. Hence, AAT, a canonical training regimen for affecting choices, is highly appropriate for assessing the necessity of shifting values when altering choice behavior.

Although the neural underpinnings of AAT in the healthy population remain uninvestigated (Mehl et al., 2019; Wiers et al., 2015), the neural substrates of values and choice behavior allow us to draw hypotheses. In the last decades, the ventromedial prefrontal cortex (vmPFC), orbitofrontal cortex (OFC), and posterior cingulate cortex (PCC) have been shown to be associated with choices (Bartra et al., 2013; Kable and Glimcher, 2009). Notably, tasks that target final choices seem to strongly engage PCC (Kable and Glimcher, 2007; Paulus and Frank, 2003), but value signals are represented in vmPFC and OFC (Plassmann et al., 2007, 2010). Additionally, PCC has been discussed as the neural hub that detects changes in the environment and motivates shifts in behavior (Pearson et al., 2011). For instance, Kable and Glimcher (2007) found that PCC activity can predict participants' final choices in an intertemporal choice task. Also, Cousijn et al. (2012) showed that approach bias toward cannabis-related images correlates with increased activity in PCC when comparing heavy users and non-users. Further, PCC and precuneus have been shown to be more activated in internet-gambling-dependent participants than in the control group, and their BOLD activities are correlated with their gaming urge (Ko et al., 2013). Together, these results suggest that compared to vmPFC and OFC, which encode values and integrate them in decision-making-related networks, PCC activity might encode and incorporate internally motivated (Leech and Sharp, 2014) behavioral tendencies in decision-making processes.

In the current study, we investigate the necessity of shifting values for altering choices. Further, we elucidate how such a choice modification without value change is potentially incorporated into decision-making networks at the neural level. We hypothesize that even though AAT affects choices, it leaves reward value unaffected. These hypotheses came from two sources: (1) other forms of behavioral modification techniques, such as cue-approach training, have been shown to change choices independent of explicit values (e.g., Bakkour et al., 2017; Schonberg et al., 2014). (2) Previous AAT studies using implicit association tasks did not find a significant effect of AAT on implicit values while choices were modulated (Kakoschke et al., 2017). Further, we assess whether the relationship between choices and ratings is modulated by AAT such that the same values would be less critical for final choices after AAT compared to baseline (McKerchar et al., 2009; Scherbaum et al., 2012). Accordingly, we expect that at the neural level, mPFC that encodes values would not be affected by AAT. In contrast, PCC, which is the neural hub that incorporates behavioral tendencies in choice behavior, would be modulated by AAT. We further explore anatomical predispositions to behavioral modifications by conducting voxel-based morphometry. Finally, to test if the AAT training effect can be transferred to real-life food intake, participants underwent a breakfast-buffet test at the end of each testing session.

2. Method

2.1. Participants and stimuli

Thirty-four normal-weight (i.e., 18 < BMI < 25) right-handed subjects (mean age = 25.14 years, SD = 4.01 years; mean BMI = 21.46, SD = 1.77) participated in the study. The sample size was chosen based on a priori power analysis with $\alpha = 0.05$, $1 - \beta = 0.95$ (Cohen, 1988, 2016), and expected effect sizes of $Cohen's\ \ f = 0.35$ (equivalent to $\eta_p^2 = 0.1$) derived from previous studies(Jones et al., 2018; Kakoschke et al., 2017b; Mehl et al., 2018; Schumacher et al., 2016). The power analysis indicated that the total sample size $N \geq 29$ were required. Participants did not report any history of mental illnesses. It has been reported that there are gender differences in metabolism (Dionne et al., 1999), eating behavior (Manippa et al., 2017; Rolls et al., 1991; Wardle et al., 2004), and neural responses to food cues (Manippa et al., 2017). Therefore, only female subjects were recruited for the study. Food intolerances or allergies and any diet restriction (i.e., being vegan or vegetarian) were exclusion criteria during recruitment. Prior to the experiment, all subjects were informed about the procedure and personal data handling, and their written consent was collected according to the declaration of Helsinki. Participation was compensated with 8€ per hour. The study was approved by the ethics committee of the University of Lübeck. One subject was excluded from data analyses completely, as she did not show any variance in the data (i.e., no accepted response in the food-choice task). Two more participants were excluded from analyses that required food ratings as they had more than 50% missed responses in the subjective rating task.

We selected 80 food images from the database of Blechert et al. (2014), containing 40 low- (mean = 70.15 kcal/100 g, SD = 44.24 kcal/100 g) and 40 high-calorie food items (m = 236.59 kcal/100 g, SD = 59.24 kcal/100 g). Since the perception of sugar can interfere with and mask the perception of fat (Bolhuis et al., 2018; Drewnowski and Schwartz, 1990), only savory items were selected. The selected food stimuli were divided into two stimulus stets, each containing 20 high- and 20 low-calorie items. To increase the training effect's generalizability, one stimulus set was used exclusively for the pre- and post-tests and the other for AAT (i.e., the training session), making the results independent of the specific food items. The assignment of stimulus sets to tasks (i.e., test vs. training) was counterbalanced across participants. The use of different stimulus sets for training (i.e., AAT) and test (i.e., the choice and subjective rating tasks) ensured that the observed training effects are generalized over the stimuli, task, and context (i.e., in vs. outside of the MRI scanner).

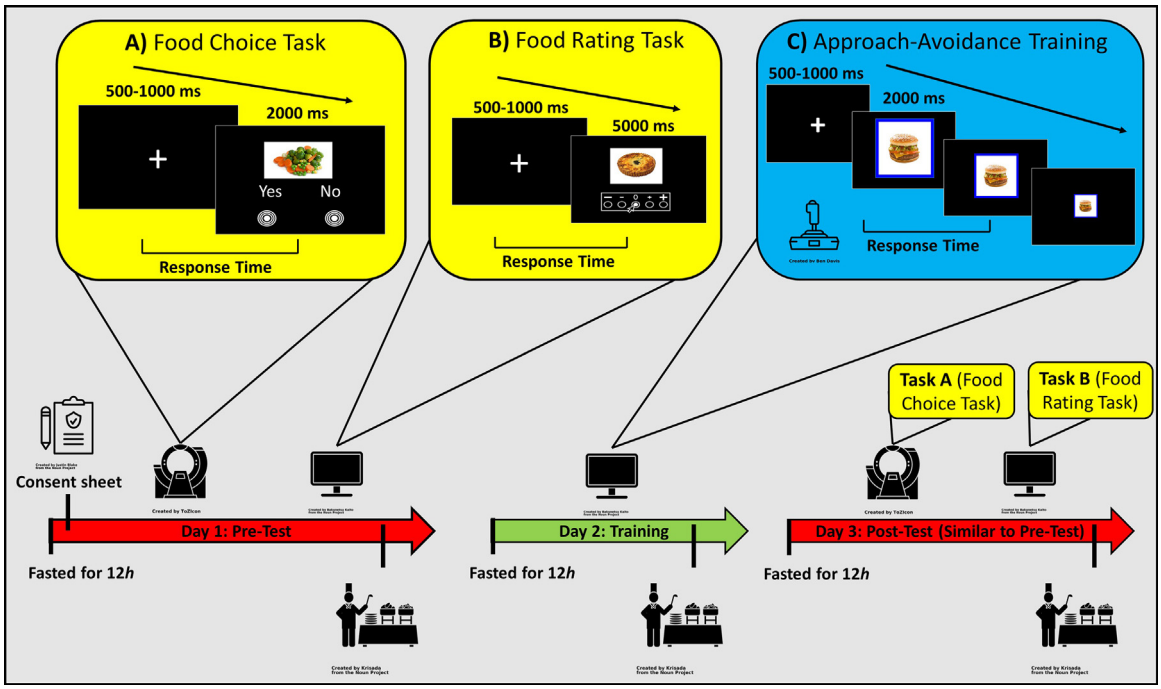

Fig. 1. Schematic representation of the experimental paradigms. As stimuli, 80 food images (Blechert et al., 2014) containing 40 low- and 40 high-calorie food items were employed. To test training effect generalizability, two sets of food images, each containing 20 low- and 20 high-calorie food cues, were used; one exclusively for the pre- and post-tests and the other for AAT (i.e., the training session). During Days 1 and 3, subjects participated in a food choice task, while neuroimaging data were recorded using fMRI, and a food rating task, which took place outside of the scanner. A) In the choice task, participants indicated whether they wanted to consume the presented food. The choice task consisted of 160 trials, divided into four blocks of 40 trials. The order of stimuli was pseudorandomized so that in each block, each stimulus would be presented once. B) In the rating task, participants were instructed to indicate how appealing they found the presented picture using a continuous slider. All images in the test set were rated using a continuous scale. C) For AAT, participants were instructed to consistently pull [toward their body] or push [away from their body] the presented food items in response to the color of stimulus frames (i.e., blue or yellow) using a joystick. Notably, low-calorie stimuli were consistently cued to be approached and high-calorie stimuli to be avoided. For optimal approach and avoidance resemblance (Rinck and Becker, 2007), the employed AAT had an embedded zooming feature. AAT consisted of five blocks of 40 trials (each picture in the training set was presented five times). The order of images was pseudorandomized so that each image would be presented once during each block. Additionally, participants were instructed not to drink or eat anything besides water for 12 h before each session. At the end of each session, they could choose as many items as they wanted from a breakfast buffet where multiple food options were available.

2.2. Choice and subjective rating tasks

All tasks were programmed in MATLAB (r2020b; MathWorks Company) via Psychtoolbox v3 (Brainard, 1997). In the subjective rating task (Fig 1-B), participants were asked to indicate how appealing they find a presented item on a continuous scale of 1–7, representing “not appealing at all” and “very appealing”, respectively, using a mouse. Each trial started with a fixation cross, randomly presented between 500 and 1000 msec. Afterward, a food item accompanied by the continuous Likert scale below the image was presented. Each trial would terminate either after the participants’ response or the maximum of 5000 msec. No response or responses after 5000 msec were considered as missed trials. Further, the order of images was completely randomized. Images (660×660 pixels) were presented against a black background.

In the food-choice task (Fig 1-A), participants indicated whether they were willing to consume a presented item or receive the equivalent amount of money instead. Two options (i.e., Yes and No) could be chosen by moving an MRI-compatible joystick (Fiber Optic Joystick, Current Designs) to the left or right. In order to avoid motor confounds on imaging data, the position (i.e., being on the left or right) of the “Yes” and “No” responses were counterbalanced across trials. Each trial was started by a fixation cross, randomly presented for 2, 4, 6, or 8 s (mean intertrial intervals = 4 s) to ensure hyperbolically distributed intertrial intervals (Miezin et al., 2000). Afterward, each stimulus was presented for 2000 msec, during which participants could respond. No response or responses after 2000 msec were considered as missed trials. Each image in the test set was presented four times during the food-choice task, yielding 160 trials in total. The task was split into four blocks of 40 trials, each consisting of 20 low- and 20 high-calorie images. The order of images was pseudorandomized so that each image would be presented only once during each block. The inter-block interval was 20 s. Images (660×660 pixels) were presented in a white frame against a black background.

2.3. Approach-Avoidance training

For AAT (Fig 1-C), participants were instructed to pull [toward their body] or push [away from their body] in response to the color of stimulus frames (i.e., blue or yellow) using an MRI-compatible joystick. Frame color to response assignment was counterbalanced across participants. For optimal approach and avoidance resemblance (Rinck and Becker, 2007), the employed AAT had an embedded zooming feature: pulling and pushing the joystick, depending on the approach or avoidance assignment, either increased or decreased the size of the presented image. In AAT, all low-and high-calorie stimuli were cued to be approached and avoided, respectively. Each picture in the training set was presented five times, yielding 200 trials in total. Further, AAT was split into five blocks of 40 trials, consisting of 20 low- and 20 high-calorie images. The order of images was pseudorandomized so that each image would be presented only once during each block. The trial structure (i.e., intertrial, inter-block intervals, and response time) was similar to the food-choice task.

2.4. Procedure

The study consisted of three sessions on three consecutive days (Fig. 1). Prior to the study, participants were instructed to fast (i.e., not eat and drink anything rather than water) and not consume alcohol or caffeine for at least 12 h before each session. Every session started between 08:00 and 9:00 in the lab. In the beginning, participants received written instructions about the experimental procedure and the tasks of the respective day. On Days 1 and 3 (i.e., the pre- and post-training sessions), the food-choice task was administered in the MRI scanner, followed by the subjective rating task, which was completed outside the scanner. Furthermore, on Day 2 (i.e., the training session), AAT was conducted outside the MRI scanner. Pre- and post-training sessions lasted approximately one hour, and the AAT session took place in 30 min. At the end of each session, participants were offered a breakfast, where they could choose as many food items as they wanted from multiple available low- and high-calorie options. The number of the low- and high-calorie items that participants selected in pre- and post-session was recorded. All presented results are related to the comparisons of pre- vs. post-sessions.

2.5. fMRI acquisition and preprocessing

Functional and anatomical images were acquired using a 3T Trio (Siemens) scanner equipped with a 12-channel head coil. In each of the four functional scanning runs, 127 T2*-weighted echo-planar images containing 33 slices, with 3 mm thickness and separated by a gap of 0.75 mm, were acquired. The order of acquisition was descending. Imaging parameters, resulting in an isotropic voxel size of 3 mm, were as follows: repetition time (TR), 2000 msec; echo time (TE), 30 msec; flip angle, 78°; matrix size, 64 × 64; field of view (FOV), 192 × 192 mm^2. Further, a high-resolution T1-weighted magnetization prepared rapid gradient-echo image (MPRAGE) was collected for each subject. The parameters were as follows: TR, 1900 msec; TE, 2.52 msec; matrix size, 256 × 256; FOV, 256 × 256 mm^2; 192 slices (1 mm thick); flip angle, 9° Preprocessing, first-level, and group-level analysis of the functional data were conducted using SPM12 (The Wellcome Department of Imaging Neuroscience, Institute of Neurology, London, UK). During preprocessing, scans were spatially realigned, slice-time corrected, co-registered to their structural images, and subsequently normalized to the standard Montreal Neurological Institute (MNI) EPI template using deformation fields. Finally, images were smoothed using an 8-mm full-width at half-maximum (FWHM) Gaussian kernel. None of the participants moved more than 3 mm/rad within each run.

2.6. Statistical analysis

All behavioral statistical analyses were conducted via R programming language (http://www.R-project.org/). Only correct responses (i.e., produced during the designated response time) were used for statistical analyses. The results of the food-choice and subjective rating tasks were analyzed using a 2 × 2 repeated measure ANOVA, with Session (pre vs. post) and Calorie (high vs. low) as within-subject factors. All the behavioral data were checked to conform to ANOVA's assumptions: normal distributions, no extreme outliers [i.e., outside $Quartile\ 1(Q1) - 3 * interquartile(IQR), Q3 + 3 * IQR$], and linearity of relations. Further, indifference points were calculated using logistic regression modeling. Indifference points in binary choices are referred to estimated positions where agents might accept or reject an item with similar probability (McKerchar et al., 2009; Scherbaum et al., 2012). For each participant in each condition, choices were entered into the model as a binary input (i.e., yes = 1, no = 0) and subjective ratings as a continuous predictor. The model's output represents the probability of choosing an item giving the subjective rating for that item, as described in Eq. (1).

$$p_{j,i,k}(Y) = \frac{1}{1 + exp^{(\beta_0 + \beta_1 x)}} \tag{1}$$

In Eq. (1), x designates subjective rating, Y choice, j participant number, i session (e.g., pre-training), k calorie content (e.g., low-calorie), and finally β_0 and β_1 are the parameters of the model. For each of the participants at each condition, the indifference points were defined as the subjective rating that predicts choosing an item with a probability of 50%. Notably, indifference points are the prediction of computed models and represent a combined picture of choice biases (i.e., $\beta 0$ in the model) and rating values contribution (i.e., $\beta 1$ in the model) in final choices. For five participants, the rating associated with 50% was outside acceptable boundaries (i.e., [1,7]); therefore, these participants were eliminated in the final analysis of indifference points. The calculated indifference points were entered in a 2 × 2 repeated measure ANOVA similar to the one used for the subjective rating and food-choice tasks.

For participants' breakfast choices, the output (i.e., the count of selected low- and high-calorie food items) had a quasi-Poisson instead of a Gaussian distribution. Therefore, for analyzing the breakfast data, we utilized a quasi-Poisson mixed model with log as the link function. In the model, Participants were included as random, and Session (pre vs. post) and Calorie (high vs. low) as fixed effects, as follows:

$$Outcome\ \sim\ 1\ +\ Calorie * Session,\ random + (1|\ ID) \tag{2}$$

For calculating and analyzing the model, the MASS package in R was used (Ripley et al., 2013). The statistical inference was made based on chi-square tests and type II sum of squares. Further, the total calorie consumed and ordered for each session was analyzed by using the Wilcoxon test, as these values were not normally distributed.

The statistical analyses of fMRI data were conducted using MATLAB (r2020b; MathWorks Company), SPM12 (The Wellcome Department of Imaging Neuroscience, Institute of Neurology, London, UK), and R programming language (http://www.R-project.org/). The effects of interest were calculated for each participant and session using general linear models (GLM), including all four runs. In GLM1, the food-choice task trials were assigned to four event-related conditions: accepted and rejected items of low- (n = 80) and high-calorie images (n = 80). The resulting vectors were convolved with a canonical hemodynamic response function. Further, we used a high-pass filter with a 180 Hz cutoff and an explicit brain mask. For finding functional ROIs, p values were corrected for multiple comparisons using the family-wise error correction at the cluster level (FWE_c). Based on the suggestions of Woo et al. (2014), we chose a high primary threshold (i.e., $p\langle 0.001,\ contigueous\ voxels\rangle 40$) to enhance spatial localization and interpretability. This approach has been discussed to provide the best balance between the type I and II errors in fMRI studies (Lieberman and Cunningham, 2009; Woo et al., 2014). Extracted neural activities of selected ROIs were assessed using a 2 × 2 × 2 repeated measure ANOVA, with Session (pre vs. post), Calorie (high vs. low), and Decision (accepted vs. reject) as within-subject factors. For calculating correlations between neural activities and behavioral measures, the repeated-measure correlation package (rmcorr) in R was used (Bakdash and Marusich, 2017).

Further, to assess whether there can be a predisposition to AAT, we conducted voxel-based morphometry (VBM) using the computational anatomy toolbox (CAT12). For VBM, T1 images are spatially normalized using geodesic shooting templates (Ashburner and Friston, 2011) and segmented into gray matter (GM), white matter (WM), and cerebrospinal fluid (CSF). Total intracranial volumes (TIV) were calculated and used as a nuisance regressor in VBM-GLM. Afterward, images were smoothed using an 8-mm FWHM. Finally, the extracted gray matter densities of the selected regions of interest (ROI) were correlated with the BOLD activity of those same regions. Since we did not assume a linear relationship between BOLD activity and gray matter density, instead of Pearson's correlation, ranked Spearman's correlation was assessed.

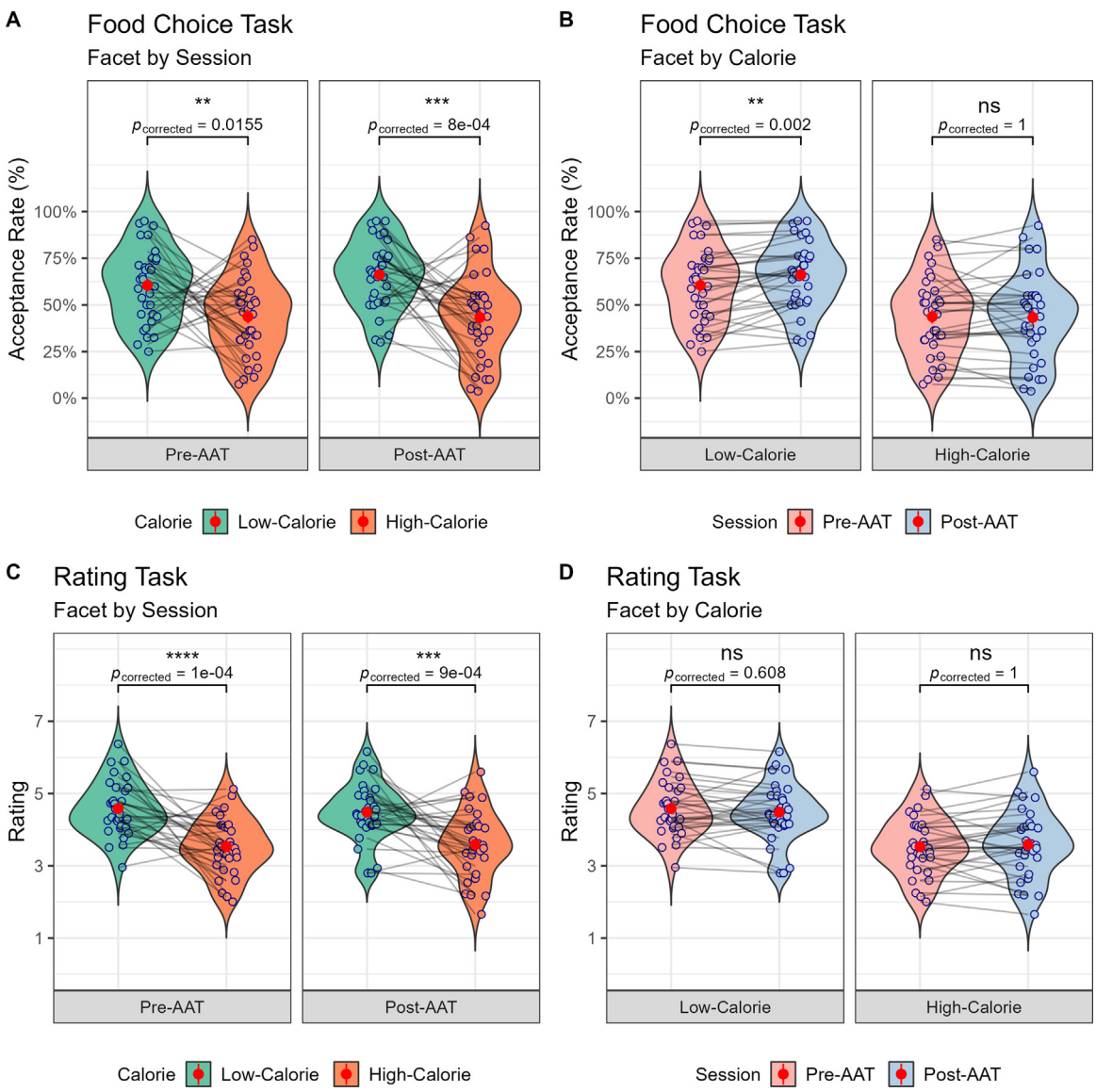

Fig. 2. The violin diagrams of the behavioral results for (A & B) the food-choice task and (C & D) the subjective rating task. Red dots and lines represent means and 95% confidence intervals (CI), calculated based on the standard error of the mean (SEM). All *p* values are Bonferroni-corrected.

3. Results

3.1. The impact of AAT on choices and values

In order to investigate whether AAT affected food choices, we tested the acceptance rates via a 2 × 2 ANOVA with Calorie (low- vs. high-calorie) and Session (pre- vs. post-test) as within-subject factors. The interaction between Session and Calorie was significant ($F(1,32) = 6.22$, $\boldsymbol{p} = 0.017$, $\eta_p^2 = 0.16$), suggesting a significant change in choice as a function of training (Fig. 2-A). Notably, after the training, participants chose low-calorie food items significantly more often ($t(32) = 3.56, \boldsymbol{p} = 0.001, Cohen's\ d = 0.62$, Bonferroni-corrected), whereas the high-calorie items were not significantly affected by AAT ($t(32) < 1$, $n.s$). Further, the main effect of Session was marginally significant ($F(1,32) = 3.66$, $p = 0.064$, $\eta_p^2 = 0.10$). Also, participants chose significantly more low-calorie ($mean = 0.633$, $SD = 0.190$) than high-calorie ($mean = 0.435$, $SD = 0.220$) food items, as shown in the significant main effect of calorie ($F(1,32) = 12.00$, $\boldsymbol{p} < 0.001$, $\eta_p^2 = 0.27$).

Next, we tested whether the values associated with the food items changed after training (Fig. 2-B). Notably, food values were measured by the subjective rating tasks, where participants indicated how appealing they found the presented pictures. Importantly, neither the interaction between Session and Calorie was significant ($F(1,30) = 1.23$, $p = 0.27$, $\eta_p^2 = 0.03$), nor the main effect of Session ($F(1,30) < 1$, n.s.), showing that AAT did not affect food values. Further, with the Bayesian equivalent of paired *t*-test, we tested the changes in food values from the pre- to post-test for high- ($B_{10} = 0.2223751 \pm 0.04\%$) and low-calorie items ($B_{10} = 0.3157722 \pm 0.03\%$), which showed moderate evidence favoring null hypotheses (i.e., there was no change in these food values from pre- to post-AAT). In general, participants rated low-calorie food items ($mean = 4.53, SD = 0.78$) significantly higher compared to high-calorie food items ($mean = 3.55, SD = 0.85$; $F(1,30) = 21.65$, $\boldsymbol{p} < 0.001$, $\eta_p^2 = 0.41$).

Afterward, to assess whether AAT effects are transferred to real-life food choices, we analyzed the breakfast choices using a quasi-Poisson mixed model with Calorie (low- vs. high-calorie) and Session (pre- vs. post-test) as fixed and Participant as a random effect. We could find a marginally significant change in real food choice as a function of training, as unveiled by the marginally significant interaction of Session and Calorie ($\chi^2(1, N = 132) = 3.28, p = 0.069$). In gen-

eral, participants chose more low- ($mean = 6.72, SD = 2.29$) than high-calorie items ($mean = 4.69, SD = 2.37, \chi^2(1, N = 132) = 38.57, \boldsymbol{p} < 0.001$). We did not observe a significant main effect of Session ($\chi^2(1, N = 132) = 0.31, p = 0.576$). Notably, low-calorie breakfast choices were numerically increased ($mean = 0.36,\ SD = 2.07$), and high-calorie ones decreased ($mean = -0.72,\ SD = 2.73$) in post- compared to pre-test. However, these numerical changes, either for low-calorie ($Wilcoxon(32) = 68, p = 0.168, r = 0.24$, Bonferroni-corrected) or high-calorie breakfast choices ($Wilcoxon(32) = 258, p = 0.211, r = 0.20$, Bonferroni-corrected), were not significant. Next, we analyzed the calories consumed and ordered for each session to investigate whether the effects of AAT were translated to participants' ecologically valid consumption behavior. However, neither ordered calories ($Wilcoxon(32) = 222, p = 0.304, r = 0.18$) nor consumed calories ($Wilcoxon(32) = 183, p = 0.08, r = 0.303$) were significantly affected by Session.

3.2. The contribution of values to choice shifts as a function of training

Next, we tested how food values contribute to choices before and after AAT. To do so, we employed individual indifference points, which indicate the estimated value at which participants chose food items with a 50% probability (McKerchar et al., 2009; Scherbaum et al., 2012). Here, we observed a significant interaction between Session and Calorie ($F(1, 25) = 4.69,\ \boldsymbol{p} = 0.040,\ \eta_p^2 = 0.15$), indicating that indifference points were modulated as a function of training. The contrast analysis (Fig. 3-A, B) showed that although there was no significant difference between low- and high-calorie indifference points in the pre-training session ($t(25) = 1.13, p = 0.536, Cohen's\ \ d = 0.22$, Bonferroni-corrected), this difference became significant in the post-training session ($t(25) = 3.75, \boldsymbol{p} = 0.001, Cohen's\ \ d = 0.72$, Bonferroni-corrected). Further, although high-calorie indifference points were not changed after AAT ($t(25) < 1$, n.s.), the low-calorie indifference points decreased significantly ($t(25) = 2.47, \boldsymbol{p} = 0.040, Cohen's\ d = 0.48$, Bonferroni-corrected). These findings suggest that after training, novel behavioral tendencies were formed, which resulted in participants' willingness to accept low-calorie food at a lower value.

Further, the indifference points were not significantly changed by Session ($F(1, 25) = 1.52,\ p = 0.229,\ \eta_p^2 = 0.05$). However, we observed significantly lower indifference points for low- ($mean = 3.70, SD = 0.98$) vs. high-calorie images ($mean = 4.17, SD = 0.99$) in general ($F(1, 25) = 6.45,\ \boldsymbol{p} = 0.017,\ \eta_p^2 = 0.20$). This result might indicate that participants' choices of high-calorie compared to low-calorie food cues were influenced by other factors, such as inhibition.

To confirm that alterations in acceptance rates were related to changes in indifference points, we calculated the repeated-measure correlation coefficient. The results showed a strong correlation between the acceptance rates and indifference points ($r(77) = -0.688,\ 95\%\ CI\ [-0.790\ \ -0.549\ ],\ \boldsymbol{p} < .001$), confirming that alterations in acceptance rates were indeed associated with changes in indifference points. This result clearly shows the validity of indifference point estimations (Eq. 1), which are the logistic regression models' outputs (i.e., the 50/50 probability estimations for a given participant and category).

3.3. Identifying brain regions of interest sensitive to calorie and choice

We first identified brain regions that code the caloric value (Bongers et al., 2015; Meule and Kubler, 2014) (i.e., high- vs. low-calorie) in the pre-test (Fig. 4). The reason for calculating this specific contrast was that high- compared to low-calorie images are better detectors of impulsive choices that heavily depend on behavioral tendencies (Bongers et al., 2015; Meule and Kubler, 2014). Two areas showed significant differences: PCC [$MNI:\ \ x = -3, y = -16, z = 35$, ($t(32) = 5.47, \boldsymbol{FWC_c} = 0.035$)], and ACC [$MNI = x = 9, y = 26, z = 26$, ($t(32) = 4.60, \boldsymbol{FWE_c} = 0.007$)]. Next, we tested for decision-sensitive regions (i.e., accept versus reject) in the pre-test (Fig. 4). In line with the previous findings (Bartra et al., 2013; Kable and Glimcher, 2009; Plassmann et al., 2007, 2010), mPFC was identified as the only region reflecting choice [$MNI = x = 6, y = 41, z = -7$, ($t(32) = 6.29, \boldsymbol{FWE_c} = 0.015$)]. The following analyses will thus specifically target the activities within these regions of interest.

3.4. The effects of behavioral modifications on brain activity

To address whether brain activity was modulated by the experimental manipulations, we analyzed the BOLD activities of the functional ROIs, which were specified in the whole-brain analysis. That is, we first conducted a whole brain analysis only for the pre-AAT session (see section 3.3). Based on this analysis, several functional ROIs were detected. Afterward, the beta values (i.e., BOLD signals) were extracted from each of these functional ROIs for both pre- and post-tests. Using general linear models (GLM), we included Decision (Accept vs. Reject), Calorie (high- vs. low-calorie), and Session (pre- vs. post-test) as within-subject regressors. To see the results of the parametric modulation analysis regarding value encoding, please see the supplementary materials.

In the mPFC ROI, the main effect of Decision was significant as expected (Bartra et al., 2013; Kable and Glimcher, 2009; Plassmann et al., 2010) ($F(1, 32) = 22.95,\ \boldsymbol{p} < 0.001,\ \eta_p^2 = 0.41$), suggesting that mPFC (Plassmann et al., 2007, 2010) is involved in choice behavior. However, mPFC activity was not significantly affected by Calorie ($F(1, 32) = 3.12,\ p = 0.086,\ \eta_p^2 = 0.08$), Session ($F(1, 32) = 3.16,\ p = 0.084,\ \eta_p^2 = 0.08$), or by interactions between the factors ($Fs(1, 32) < 1,\ n.s.$).

Next, we turned to PCC to investigate its role in the decision-making network. In the PCC ROI (Fig. 5), the interaction between Calorie and Session (Fig 5-A, B) was significant ($F(1, 32) = 4.94,\ \boldsymbol{p} = 0.033,\ \eta_p^2 = 0.13$), indicating that PCC activity was modulated as a function of AAT. The contrast analysis showed that although activity in response to low- compared to high-calorie food items was significantly lower in the pre-training session ($t(32) = 5.05, \boldsymbol{p} < 0.001, Cohen's\ \ d = 0.87$, Bonferroni-corrected), there was no significant difference between them after AAT ($t(32) < 1, n.s.$). Further, even though AAT significantly affected activity in response to low-calorie images ($t(32) = 2.46, \boldsymbol{p} = 0.038, Cohen's\ d = 0.42$, Bonferroni-corrected), it did not significantly affect high-calorie items ($t(32) < 1, n.s.$). Together, these results suggested that PCC is a strong candidate for integrating newly formed behavioral tendencies in choice behavior, which leads to an increase in the frequency of choosing low-calorie food items. This result might have been expected based on the whole brain analysis conducted only for the pre-test session to find the functional ROIs. However, with these functional ROIs, we searched for the training-dependent effect, which is the comparison of pre- and post-AAT. To confirm this postulation, we investigated whether the activities in response to low-calorie food items were correlated with the acceptance rate of these food images by calculating a repeated-measure correlation. Notably, the results revealed a significant correlation between PCC activity and low-calorie acceptance rates ($r(32) = 0.352,\ 95\%\ CI\ [0.003,\ 0.624], \boldsymbol{p} = .041$; Fig. 5-C).

Additionally, Calorie significantly affected PCC activity ($F(1, 32) = 6.85,\ \boldsymbol{p} = 0.013,\ \eta_p^2 = 0.17$), possibly showing that, in general, choosing high-calorie food items relies more on behavioral tendencies than low-calorie items (Bongers et al., 2015; Meule and Kubler, 2014). No other main effect (Session: $F(1, 32) = 1.81,\ p = 0.186,\ \eta_p^2 = 0.05$; Decision: $F(1, 32) = 3.03,\ p = 0.090,\ \eta_p^2 = 0.08$) or interaction (Decision * Session: $F(1, 32) = 2.79,\ p = 0.104,\ \eta_p^2 = 0.08$; others: $Fs(1, 32) < 1, n.s.$) was significant.

Finally, in the ACC, the interaction between Calorie and Session was marginally significant ($F(1, 32) = 3.72,\ p = 0.062,\ \eta_p^2 = 0.10$), suggesting that AAT possibly affected the activity of ACC. To understand this marginal interaction, we conducted a series of contrast analyses. The results showed that even though BOLD activity in response to low- compared to high-calorie food items was significantly lower before AAT ($t(32) = 4.66, \boldsymbol{p} < 0.001, Cohen's\ \ d = 0.81$, Bonferroni-corrected), there was no significant difference between low- and high-calorie BOLD activity after AAT($t(32) < 1, n.s.$). However, there was no significant repeated-

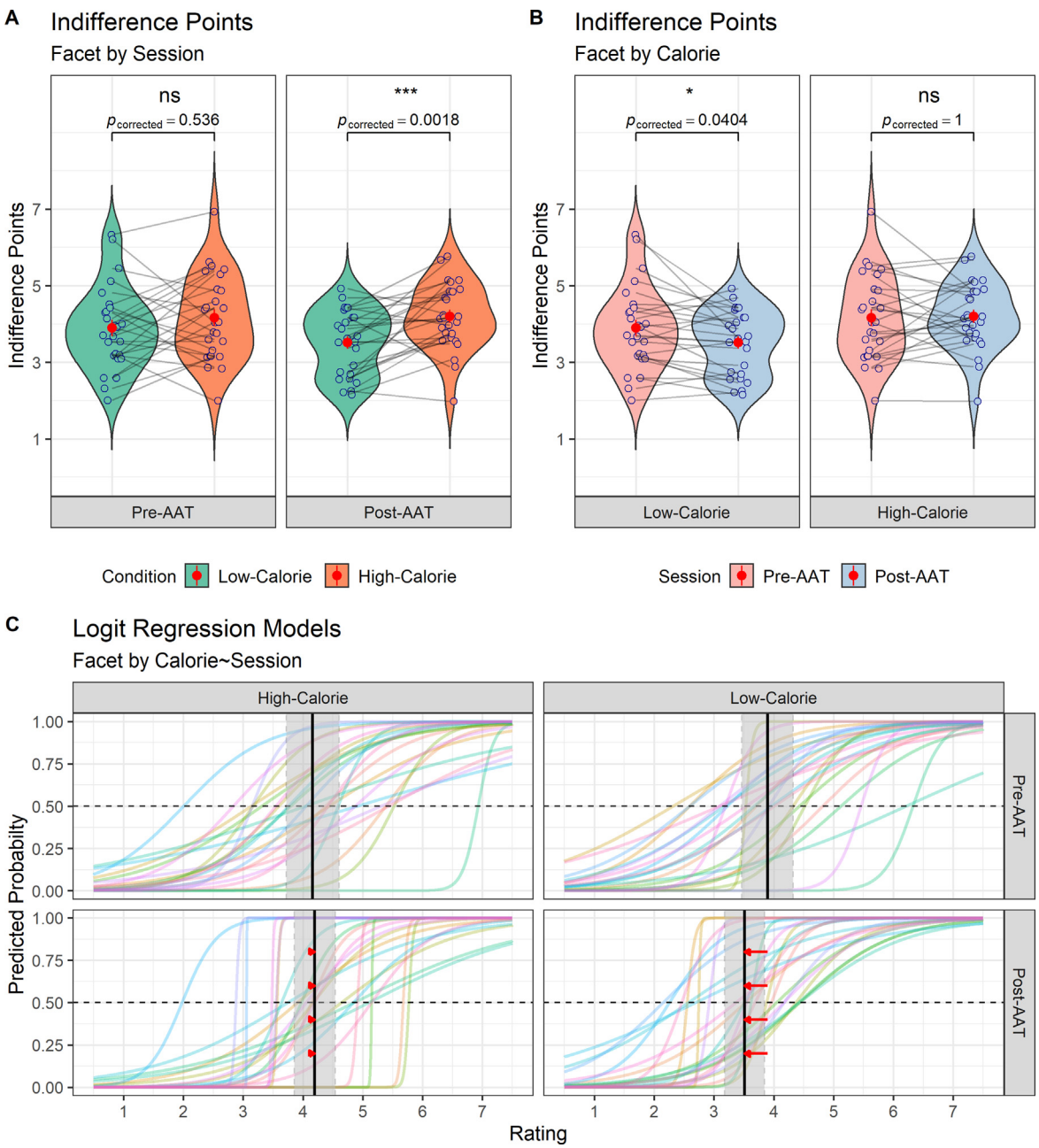

Fig. 3. The violin diagrams of the indifference point analysis, grouped by (A) Calorie and (B) Session. Red dots and lines represent means and 95% CIs, calculated based on the standard error of the mean (SEM). All p values are Bonferroni-corrected. (C) The predicted probabilities based on logit regression models. Dashed horizontal lines mark 50% predicted probability, used for calculating indifference points for each participant and condition. Solid vertical lines mark indifference points, and gray highlighted areas represent 95% CIs, calculated based on the standard error of the mean (SEM). Red arrows in the post-training panels show the changes in mean indifference points from pre- to post-AAT sessions.

measure correlation between the ACC BOLD activities and acceptance rates ($r(32) = 0.024$, $95\%\ CI\ [-0.327,\ 0.369], p = 0.891$). Further, the main effect of Calorie was significant ($F(1,32) = 9.44$, $\boldsymbol{p} = 0.004$, $\eta_p^2 = 0.22$). However, no other main effect (Decision: $F(1,32) = 2.96$, $p = 0.094$, $\eta_p^2 = 0.08$; Session: $F(1,32) < 1, n.s.$) or interaction was significant (Session * Decision: $F(1,32) = 1.90$, $p = 0.176$, $\eta_p^2 = 0.05$, others: $Fs(1,32) < 1, n.s.$).

3.5. Understanding individual differences in brain activity alterations based on the anatomical predisposition

After finding that PCC might play an essential role in integrating behavioral tendencies in choice behavior, we were curious whether anatomical differences in PCC can potentially explain individual differences in brain activity changes. VBM results showed that there is a significant correlation between activity changes from the pre- to post-test and the gray matter density of PCC ($r_{Spearman}(31) = 0.353$ $[0.011,\ 0.621], \boldsymbol{p} = 0.044$**)**. Notably, applying more conservative outlier criteria ($i.e.$, $[Quartile\ 1(Q1) - 1.5 * interquartile(IQR), Q3 + 1.5 * IQR]$) did not change the results. ($r_{Spearman}(28) = 0.388$ $[\ 0.033,\ 0.656], \boldsymbol{p} = 0.034$; Fig. 5-D**)**.

4. Discussion

Current decision-making theories assume that changing choices are dependent on modifying values associated with targeted items

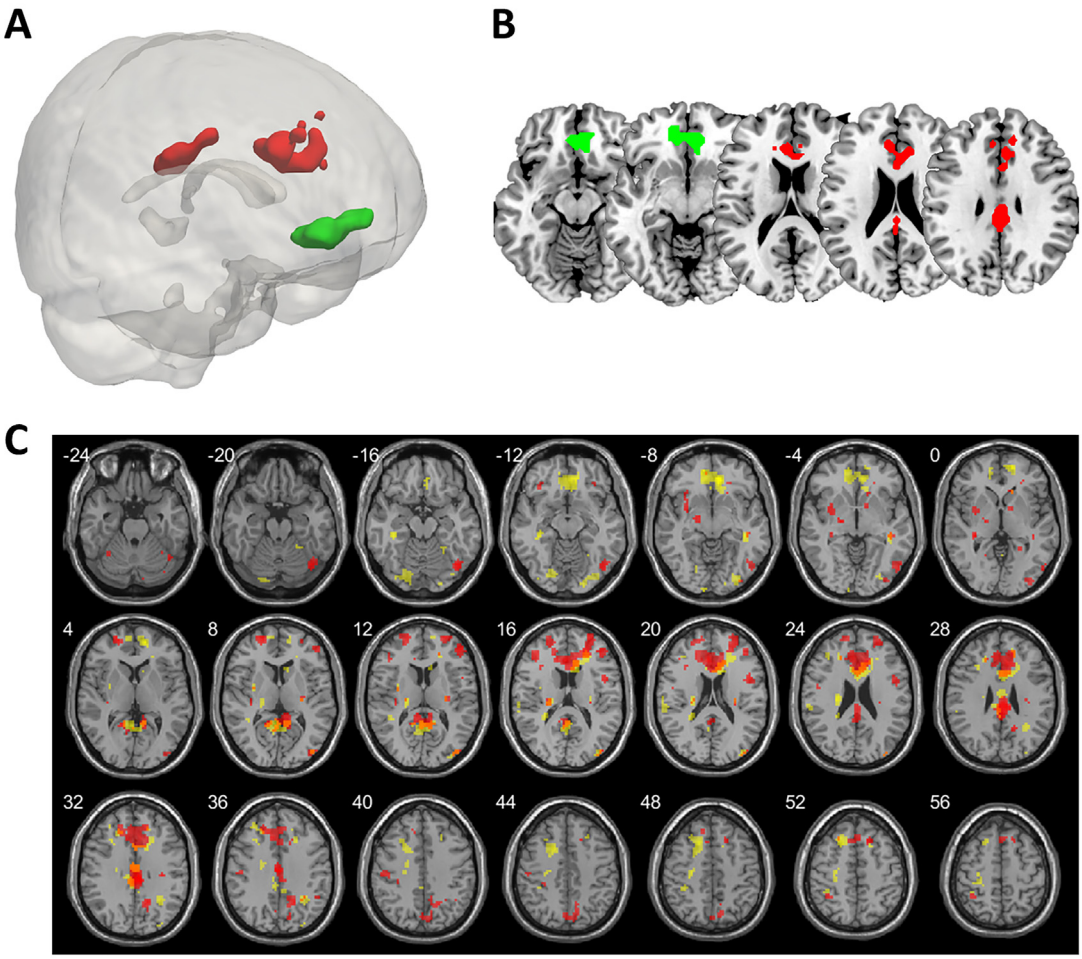

Fig. 4. Functional ROIs derived from high- vs. low-calorie (red) and accept vs. reject (green) contrasts in the pre-training session. A) The 3D rendition of the ROIs. B) The multiple-slice rendition of axial slices at $z = -12, -8, 18, 22, and\ 30$. Green: decision-sensitive area (i.e., mPFC); Red: habit-sensitive areas (i.e., ACC and PCC). C) The corresponding whole-brain analyses of high- vs. low-calorie (red) and accept vs. reject (yellow). For visualization, the uncorrected images ($p\langle 0.005,\ k\rangle 10$) are shown (Lieberman and Cunningham, 2009).

(Balleine et al., 2008; Balleine and Dickinson, 1998; Balleine and O'Doherty, 2010; Rangel et al., 2008; Schonberg and Katz, 2020). In the current study, we challenge this assumption by investigating the effects of AAT on choice behavior, during which low-calorie food items were consistently associated with approach and high-calorie food items with avoidance. The behavioral results showed that although after AAT, subjective ratings of food items were not changed, participants chose low-calorie food items more frequently. Further, logit regression modeling of indifference points revealed that AAT induced a positive bias toward low-calorie food items, making the participants choose these items at a lower value level. Hence, our behavioral results strongly corroborated our hypothesis that AAT modulates choices without value modification. The fMRI results indicated that the BOLD activity of PCC, but not mPFC, was modulated as a function of AAT. Notably, PCC activity in response to low-calorie images during pre- and post-tests was correlated with participants' acceptance rates, indicating a fundamental role of PCC in integrating behavioral tendencies in choice behavior.

The current study builds upon insights from previous studies (e.g., Bakkour et al., 2017; Mehl et al., 2019; Schonberg et al., 2014) to timely address the debate on the relationship between subjective value and choice. So far, several studies (e.g., Becker et al., 2015; Kakoschke et al., 2017b; Mehl et al., 2019, 2018) have investigated the applicability of AAT in counteracting obesity and overweight. However, the underlying cognitive and neural mechanisms of AAT in healthy humans remained mostly unknown. In some of these studies (e.g., Becker et al., 2015; Mehl et al., 2019, 2018; Schumacher et al., 2016), subjective food values were unassessed, making the results difficult to interpret beyond conferring the applicability of AAT. Others investigated obese individuals (e.g., Mehl et al., 2019, 2018) that are shown to cognitively process food stimuli differently compared to normal-weight participants (Nummenmaa et al., 2012; Volkow et al., 2011).

Our behavioral findings are in line with replicated findings in the AAT (Becker et al., 2015; Dickson et al., 2016; Jones et al., 2018; Kakoschke et al., 2017a, 2017b; Mehl et al., 2019, 2018; Schumacher et al., 2016) and other nonreinforced learning literature (Aridan et al., 2019; Bakkour et al., 2016, 2017; Botvinik-Nezer et al., 2020). For instance, Kakoschke et al. (2017b) found that AAT decreases unhealthy food choices compared to cognitive-control training (where a go-nogo task was used to increase inhibitory control for unhealthy food cues) and the control condition. However, in their study, AAT did not affect food items' implicit associations (IAT). Another form of nonreinforced learning is cue-approach training. In cue-approach training, targeted stimuli [e.g., low-calorie food images] are consistently associated with a cue [e.g., a high-pitch tone], which signals that the presented item should be chosen [e.g., pressing a button]. Multiple studies showed cue-approach training boosts choices of trained items (Aridan et al., 2019; Bakkour et al., 2016, 2017; Botvinik-Nezer et al., 2020), although the increase in choices is not accompanied by an increase in subjective rat-

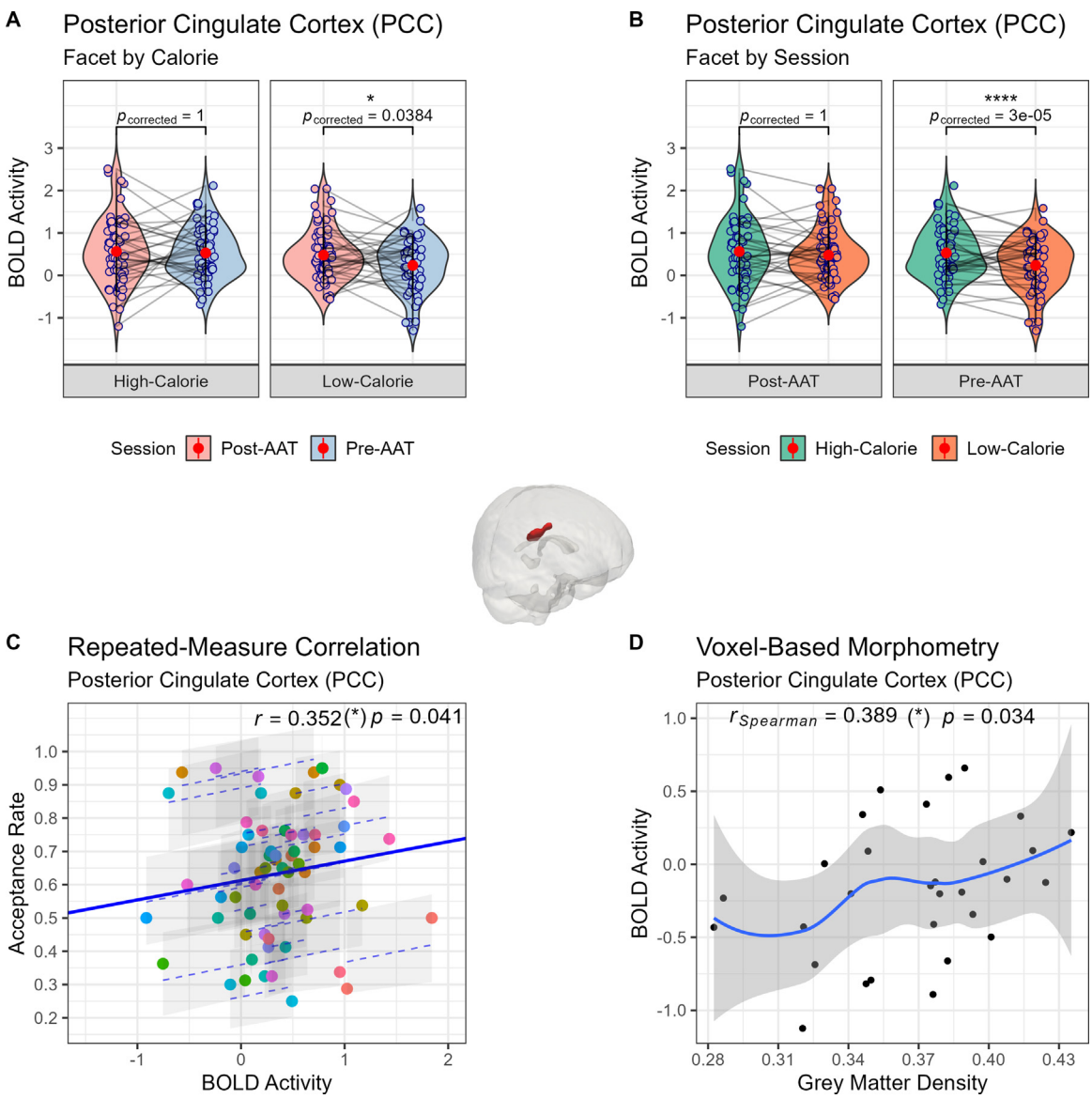

Fig. 5. The violin diagrams of the BOLD activity of PCC faceted by (A) Calorie and (B) Session. Red dots and lines represent means and 95% CIs, calculated based on the standard error of the mean (SEM). All p values are Bonferroni-corrected. (C) Correlation between the BOLD activity of PCC in response to low-calorie food items and the acceptance rate of low-calorie food items in the food-choice task. (D) Correlation between gray matter density and BOLD activity of PCC in response to low-calorie food items (depicted for 29 participants in the range: $Q1 - 1.5 * IQR, Q3 + 1.5 * IQR$. Blue lines and gray areas show the fitted curve and 95% CI, respectively. The presented curve is computed based on locally estimated scatterplot smoothing (LOESS). Notably, we could not assume a linear relationship between gray matter density (related to a three-dimensional volume) and functional activity, and therefore, we used Spearman's rank correlation coefficient and not Pearson's correlation, which assumes linearity.

ings of the targeted items (Bakkour et al., 2016, 2017; Schonberg et al., 2014). In the cue-approach training, participants are asked to respond based on the presence of a cue by pressing a corresponding button (Schonberg et al., 2014), whereas no active avoidance behavior is exerted. Comparing the no-response to the response condition will introduce, among others, motor confounds. In contrast, AAT incorporates both approach and avoidant motor responses and therefore is ecologically valid (Kakoschke et al., 2017b; Wiers et al., 2011) and controls for confounds that are pertinent to cue-approach training.

Notably, our results showed that alterations in indifference points were correlated with choice shifts. When one considers that the indifference points of low-calorie items are the only differentiating variable between the pre- and post-AAT, our suggested account becomes even more credible. That is, our results indicate that alteration in choices is the consequence of the formation of novel behavioral tendencies rather than shifting values associated with the targeted items. This suggestion is supported by findings in the cue-approach training literature that indicate the consciously perceivable association between specific stimuli and responses is crucial for the effectiveness of nonreinforced learning (Bakkour et al., 2016; Schonberg et al., 2014).

Secondly, our results indicated that the effects of food-related AAT in normal-weight participants are restricted to elevating the choices of low-calorie items. This finding is in line with other studies; for instance, Mehl et al. (2018), using a multi-session training design, compared obese and normal-weight subjects. They observed that in the healthy group, AAT only increased the approach bias toward healthy food items; in contrast, in the obese group, AAT only decreased the approach bias toward unhealthy food images. Assessing the impact of other nonreinforced learnings, such as cue-approach training, offers a similar pattern. For instance, even though cue-approach training can increase the

frequency of choosing liked items, it cannot decrease the frequency of selecting neutrally or positively-valenced items (Bakkour et al., 2016; Botvinik-Nezer et al., 2020; Schonberg et al., 2014; Schonberg and Katz, 2020). These results can be understood if one considers that behavioral tendencies are one variable that affects choices and interacts with other factors, such as value associations. Although a short AAT session can increase choices of approach-trained items that are appetitive or positively valenced, it would not decrease choices of avoid-trained images when they are appetitive or liked. It is still feasible that multiple-session or longitudinal AAT would negate the effects of other factors, such as existing values. In other words, low-calorie items are, on average, liked, and hence, approach bias is congruent with the existing values; therefore, AAT is effective. In contrast, high-calorie items are not disgusted, and therefore, avoidance bias is incongruent with existing values. This might explain why a short AAT training was ineffective in inducing avoidance bias toward high-calorie items in our study and others (e.g., Mehl et al., 2018). The distinction between values and behavioral tendencies is further corroborated by the effects of evaluative conditioning (Levey and Martin, 1975), where it is repeatedly shown that changes in preferences are not necessarily accompanied by alterations in the choice behavior (Corneille and Stahl, 2019; Hofmann et al., 2010; Hutter and Rothermund, 2020).

By assessing participants' breakfast choices, we investigated the translational effects of AAT on real-life food choices. Our results showed that participants' breakfast choices are modulated by AAT depending on the calorie content of food items, highlighting a numerical increase in low-calorie and decrease in high-calorie choices in the post- compared to the pre-test. Considering these results, one might infer the translational effects of AAT on real-life decisions. However, the results of previous studies investigating AAT effects on real-life food choices are mixed, as some show that AAT can significantly affect real-life choices (Schumacher et al., 2016), but others failed to find these effects (Becker et al., 2015; Dickson et al., 2016). Considering the mixed findings by other groups and our marginally significant results, one should cautiously interpret these results before future studies with larger samples investigate the reliability and stability of these effects.

Our results also indicated that low-calorie food items were preferred before AAT to high-calorie food items. This finding is in accordance with other studies with mixed-gender and multinational samples (Blechert et al., 2014; Zahedi et al., 2022). The reason for this initial difference, however, might be related to a multitude of factors (Scaglioni et al., 2018), the discussion of which is outside the scope of the current study.

Our fMRI results not only corroborate the behavioral modification account but also provide a new framework for understanding previous fMRI results. Considering that in our results, there is a correlation between acceptance rates of low-calorie images and the activity of PCC, one can suggest PCC as the neural hub that integrates behavioral tendencies during decision-making. This proposition is entirely in line with value-based decision-making literature, where it is shown that PCC activity is especially crucial in tasks that measure choices (Bartra et al., 2013; Kable and Glimcher, 2007, 2009; Paulus and Frank, 2003) but PCC might not be engaged in tasks that measure values and preferences such as willingness to pay (Plassmann et al., 2007, 2010). Notably, the observed results highlight the significance of PCC activity in behavioral modifications, as a similar neural pattern can be observed in other non-reinforced learning procedures. The increase in the frequency of choosing an item is correlated with the increase in the activation of posterior parietal areas, including PCC and precuneus (Cousijn et al., 2012; Voigt et al., 2019; Zhou and Freedman, 2019), and frontal areas such as ACC (Mehl et al., 2019), which proceeds changes in the values of the targeted item (Voigt et al., 2019). Even though value-encoding areas, such as vmPFC and orbitofrontal cortices (Baumgartner et al., 2011; Smith et al., 2014, 2010), and cognitive-control-related areas, such as dlPFC (Wang et al., 2020; Yan et al., 2016), might be engaged in later stages (Cousijn et al., 2012; Wiers et al., 2013), their role might not be as essential in initial nonreinforced learning (Aridan et al., 2019; Mehl et al., 2019).

If PCC integrates behavioral tendencies, one should expect that PCC would be involved in guiding attention and initiating behavior regardless of external rewards and punishments. Remarkably, PCC, a central node in the default mode network, has been discussed as the neural hub that detects changes in the environment and motivates shifts in behavior (Pearson et al., 2011). Further, Leech and Sharp (2014) argued that PCC plays a vital role in directing the focus of attention and supports internally-directed cognition.

Our VBM results show that PCC gray matter density predicts PCC BOLD activity changes. This finding may explain individual differences in responsiveness to behavioral modification training. In other words, participants who rely more heavily on behavioral tendencies in their daily life potentially have higher PCC gray matter density and are also more susceptible to AAT. This suggestion aligns with the idea that addiction might alter the importance and organization of neural activity in different brain areas (Volkow et al., 2010). However, this speculation should be treated cautiously before future studies replicate these results.

A limitation of the current study was that the utilized version of AAT did not have a condition where stimuli would be associated with approach and avoidance with 50% probability (Dickson et al., 2016; Kakoschke et al., 2017a). However, three points should be noted when considering the impacts of this limitation. First, the stimulus set (Blechert et al., 2014) used in the current study (i.e., low- versus high-calorie food items) did not allow for forming a readily distinguishable third category. This issue is also noticeable in the other comparable studies that used similar stimulus sets (e.g., Mehl et al., 2019). Hence, as realistic food stimuli were crucial for generalizing the observed effects to real-life choices, this limitation was partly forced upon the current study. Second, the observed behavioral effects were restricted to the approach condition, probably showing that the obtained effects cannot be simply related to demand characteristics. And finally, the correlation between behavioral and neuronal results shows that our interpretation regarding PCC is reasonably independent of the AAT conditions.

Further, the current study only used female participants due to gender differences in metabolism (Dionne et al., 1999), eating behavior (Manippa et al., 2017; Rolls et al., 1991; Wardle et al., 2004), and neural responses to food cues (Manippa et al., 2017). Specifically, we were interested in whether the behavioral modification training is effective in female participants, who were shown to apply more cognitive control when choosing food (Wardle et al., 2004). However, the current results need to be replicated across genders to increase their generalizability.

In the current study, we used a binary choice task for measuring participants' choice behavior. Alternatively, one could use a between-two-item choice task (i.e., a low- versus high-calorie image) for measuring participants' responses. However, using between-two-item choices might lead to an outcome that is not readily interpretable. In other words, if participants choose low-calorie more frequently than high-calorie items after AAT, it might be because they are less willing to choose high-calorie items or, alternatively, more willing to choose low-calorie ones. Nevertheless, in the case that one uses such a paradigm, we expected to see increased low-calorie food choices after AAT and a simultaneous decrease in high-calorie choices. The reason for this speculation is that in our study, low-calorie items were, on average, more appealing than high-calorie ones, both in the pre- and post-AAT sessions, and further, AAT induced a behavioral tendency toward low-calorie items. Therefore, after AAT, all the known factors (i.e., values and behavioral tendencies) congruently favor low-calorie choices over high-calorie items.

Conclusion

In the current study, we challenged the assumption that value modification is necessary for altering choice behavior by investigating the effectiveness of AAT in facilitating choices of low-calorie food images.

In line with other studies (Kakoschke et al., 2017b; Mehl et al., 2018), our results showed that AAT can effectively alter participants' choice behavior. The observed behavioral modulations were related to alterations in indifference points and not subjective ratings, suggesting behavioral tendencies affected choice behavior while bypassing existing values. Our fMRI data revealed that the acceptance rates of low-calorie food items were correlated with PCC activity, which suggests PCC is the neural hub that integrates behavioral tendencies in decision-making processes. Finally, a correlation between BOLD activity changes and PCC gray matter density suggested a possible anatomical predisposition to behavioral modifications. Significantly, the current study indicates the possibility of affecting choice behavior regardless of value modification. This finding calls for a revision of existing frameworks used for understanding nonreinforced learning and value-based decision-making. Finally, our results offer a viable approach for improving health-related choices regardless of associated values, which is of great advantage for optimizing health-related decisions, such as food choices (Bongers et al., 2015; Guerrieri et al., 2008; Nederkoorn et al., 2009, 2010).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data and scripts used in the current study are stored in an institutional repository at the German Institute of Human Nutrition (DIfE). The repository is composed of anonymized fMRI datasets, behavioral log files, and scripts. Access to them can be requested by contacting the corresponding authors.

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Data and Code Availability Statement

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2023.120134.

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