

The Impact of Emotional States on Cognitive Control Circuitry and Function

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Abstract

■ Typically in the laboratory, cognitive and emotional processes are studied separately or as a stream of fleeting emotional stimuli embedded within a cognitive task. Yet in life, thoughts and actions often occur in more lasting emotional states of arousal. The current study examines the impact of emotions on actions using a novel behavioral paradigm and functional neuroimaging to assess cognitive control under sustained states of threat (anticipation of an aversive noise) and excitement (anticipation of winning money). Thirty-eight healthy adult participants were scanned while performing an emotional go/no-go task with positive (happy faces), negative (fearful faces), and neutral (calm faces) emotional cues, under threat or excitement. Cognitive control performance was enhanced during the excited state relative to a nonarousing control condition. This enhanced performance was paralleled by heightened activity of frontopari-

etal and frontostriatal circuitry. In contrast, under persistent threat, cognitive control was diminished when the valence of the emotional cue conflicted with the emotional state. Successful task performance in this conflicting emotional condition was associated with increased activity in the posterior cingulate cortex, a default mode network region implicated in complex processes such as processing emotions in the context of self and monitoring performance. This region showed positive coupling with frontoparietal circuitry implicated in cognitive control, providing support for a role of the posterior cingulate cortex in mobilizing cognitive resources to improve performance. These findings suggest that emotional states of arousal differentially modulate cognitive control and point to the potential utility of this paradigm for understanding effects of situational and pathological states of arousal on behavior. ■

INTRODUCTION

Emotions are pervasive in our everyday life experiences, present in many decisions we make and actions we take. For example, how we react in traffic on our commute to work may vary by whether we just got cut off or just got let into moving traffic by another commuter. Although we each experience lability of emotional states in our daily lives, persistence of these emotions is a distinguishing feature of many psychopathologies (e.g., anxiety, depression, bipolar disorder, borderline personality; Sheppes, Suri, & Gross, 2015; Gross & Jazaieri, 2014; Carpenter & Trull, 2013; Jazaieri, Urry, & Gross, 2013; Townsend & Altshuler, 2012; Cisler & Olatunji, 2010; Joormann & Gotlib, 2010). Understanding influences of emotional states on cognitive and neural processes may help elucidate emotional conditions and processes that alter typical and atypical behavior.

The interaction of emotion and cognition is typically examined by how well one can redirect attention from,

or reappraise, emotional information presented in the form of brief emotional sounds, words, faces, or pictures. These emotional stimuli are often embedded within well-established cognitive control tasks like the go/no-go (Hare, Tottenham, Davidson, Glover, & Casey, 2005), Stroop (Whalen, Bush, Shin, & Rauch, 2006; Bush, Luu, & Posner, 2000; Bush et al., 1998; Whalen et al., 1998; George et al., 1994), dot probe (MacLeod, Mathews, & Tata, 1986) and matching tasks (Bishop, Duncan, Brett, & Lawrence, 2004; Vuilleumier, Armony, Driver, & Dolan, 2001) to test for either interference or facilitation of attention and actions. Explicit instructions may also be given to reappraise emotional information as nonemotional or neutral (Heller et al., 2013; Wager, Davidson, Hughes, Lindquist, & Kevin, 2008; Ochsner & Gross, 2005). Successful redirection of attention from, or reappraisal of, emotional stimuli has been associated with cognitive control circuitry involving the prefrontal, parietal, and anterior cingulate cortical regions (Wager et al., 2008; Ochsner & Gross, 2005), whereas focusing attention on this information has been associated with limbic brain regions (Buhle et al., 2014; Silvers et al., 2014; Hartley & Phelps, 2010; Wager et al., 2008; Ochsner & Gross, 2005). Frontoparietal and frontostriatal circuitry have been

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implicated broadly in cognitive control tasks (e.g., go/no-go, *n*-back) irrespective of the presence of emotional or motivational content (Shackman, Maxwell, Greischar, & Davidson, 2009; Simmonds, Pekar, & Mostofsky, 2008; Vincent et al., 2008; Owen, McMillan, Laird, & Bullmore, 2005). Taken together, these studies implicate these control systems in regulating emotional and motivational processes (Buhle et al., 2014; Chiew & Braver, 2011; Hare et al., 2005; Ochsner & Gross, 2005; Davidson, Putnam, & Larson, 2000; Hariri, Bookheimer, & Mazziotta, 2000).

The previously described studies involve brief or momentary emotional stimuli rather than lasting emotional states of arousal. Emotion has also been examined across longer timescales in studies that induce an emotional state. For instance, mood induction studies use recollection of positive or negative autobiographical memories, guided imagery, film clips, or self-referential statements (Kohn et al., 2014; Zhang, Yu, & Barrett, 2014; Wagner, Boswell, Kelley, & Heatherton, 2012; Jallais & Gilet, 2010; Westermann, Stahl, & Hesse, 1996) to engage and sustain an emotional state. Mood induction procedures have been shown to be relatively effective in inducing mood states but rely on subject control rather than experimental control, with variability among individuals (Kohn et al., 2014; Larcom & Isaacowitz, 2009). Other paradigms manipulate the uncertainty or timing of an outcome or event (Schlund, Hudgins, Magee, & Dymond, 2013; Somerville et al., 2013; Alvarez, Chen, Bodurka, Kaplan, & Grillon, 2011; Somerville, Whalen, & Kelley, 2010) to induce periods of sustained anticipatory anxiety, as measured by self-report, psychophysiological, or imaging measures of mood and arousal. Few if any of these studies, however, have investigated how these sustained emotional states specifically impact cognitive control. Examining decision-making under emotional states of a longer timescale, with experimental control, may provide a more ecologically valid framework with which to understand the effects of real-life emotional situations and/or pathological states of arousal on behavior.

The valence of emotional stimuli and states may differentially impact cognitive processes. A number of studies using discrete emotional stimuli have found that both appetitive and threat cues can interfere with cognitive control (Teslovich et al., 2014; Chiew & Braver, 2011; Hare et al., 2005; Hariri et al., 2000). Meanwhile, studies exploring the cognitive impacts of sustained emotional states have found differential effects dependent on the valence of the emotion. Specifically, positive mood states have been shown to broaden the scope of attention and improve cognitive performance in problem solving, memory recall, and decision-making (Padmala & Pessoa, 2011; Fredrickson & Branigan, 2005; Ashby, Valentin, & Turken, 2002; Isen, 2002; Ashby, Isen, & Turken, 1999), whereas negative emotional states are associated with narrowing of attentional focus and decreased cognitive capacity that results in diminished task performance (Van Steenbergen, Band, & Hommel, 2011; Liston, McEwen, &

Casey, 2009; Fredrickson & Branigan, 2005; Chajut & Algom, 2003; Easterbrook, 1959).

The current study tests dissociable effects of both positive and negative emotional cues and sustained emotional states on cognitive control and neural processes within a variation of the emotional go/no-go task (Hare et al., 2005). Participants perform this task when “excited” about possibly winning up to \$100 and when feeling “threatened” by the anticipation of an aversive sound. We hypothesized that negative and positive cues would similarly impact cognitive control capacity, whereas negative and positive mood states would differentially affect cognitive control (i.e., negative emotional states would diminish cognitive performance whereas positive emotional states would enhance performance). Likewise, we hypothesized that prefrontal and parietal control circuitry would be differentially modulated by sustained emotional states. We tested for dissociable differences in behavioral performance and brain activity to sustained emotional states and emotional cues and then explored interactive effects of emotional state and emotionally valenced cues on cognitive control.

METHODS

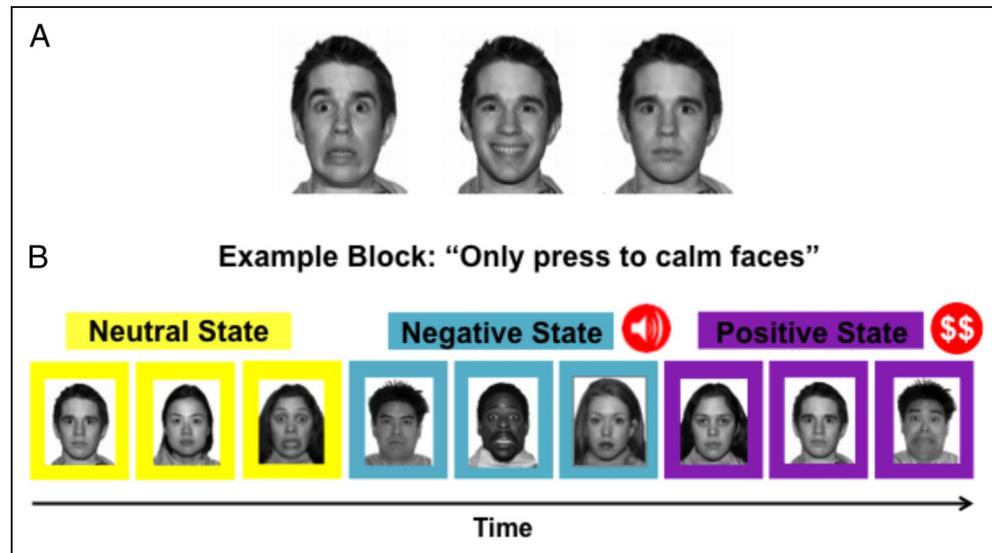
Participants

Fifty healthy right-handed adults, ages 21–25 years, were scanned. Data from two participants were excluded because of poor overall performance (more than 2 *SDs* below the group’s average performance as measured by *d*-prime). Data from four participants were excluded because of excessive head motion (greater than 10% of time points censored as defined by >1.56 mm translational or 1° rotational motion within a run), and data from six participants were excluded because of technical problems. A total of 38 usable scans (18 men and 20 women; mean age = 23.61; *SD* = 1.34) are reported in the final analyses. Participants were recruited from a diverse community sample in New York City and Los Angeles as part of an ongoing multisite project and self-identified as White (31.6%), Black (28.9%), Asian (23.7%), and Hispanic (15.8%). Participants reported no use of psychotropic medications or past diagnoses of, or treatment for, psychiatric or neurological disorders. All participants provided informed written consent approved by the institutional review boards at both data collection sites.

Experimental Task

During the fMRI scan, participants completed a modified emotional go/no-go paradigm (Hare et al., 2005) that consisted of happy, fear, and calm emotional expressions as both targets and nontargets (Figure 1A)—the Cognitive Control Under Emotion task. The task was performed under three emotional state conditions: while anticipating a negative event (threat), a positive event (excitement), or

Figure 1. Experimental paradigm. (A) Examples of each facial type used in the paradigm: fear, happy, and calm. (B) Schematic of one run of the emotional go/no-go imaging task with emotional cues as targets (go) or nontargets (no-go). Cues occur within blocks of sustained negative emotion (unpredictable aversive noise), positive emotion (unpredictable reward), and neutral (no event), indicated by the background color of the screen (yellow, blue, or purple).



no event (neutral). Each condition was denoted with a distinctly colored background (Figure 1B). Participants practiced the task before entering the scanner to ensure that they understood the instructions and conditions.

The negative emotional state of threat (depicted on the blue background) was induced using verbal instruction of an unpredictable aversive auditory stimulus, previously used successfully in fear conditioning (Pattwell et al., 2012; Soliman et al., 2010), paired with an image representing a megaphone. The unpredictable nature of the potential to hear the noise maintains the sustained state of potential threat (Davis, Walker, Miles, & Grillon, 2010; Phelps, Connor, Gatenby, Gore, & Davis, 2001). Verbal instruction of the possibility of winning up to \$100 (depicted on the purple background) was used to induce a sustained positive emotional state of arousal (excitement) and was paired with the image and sound of a slot machine. Participants were instructed that the probability of an event occurring, the volume of the noise, or the amount of money won, was not tied to their performance, but rather, was determined by the computer and would occur randomly, only when the background screen was the instructed color. In reality, participants heard the noise and won \$20 exactly once over the course of the task in a pseudorandomized order. The relevant event always occurred near the end of an experimental run so that the sustained emotional state associated with anticipation of the event would have maximal duration and so that repetition times (TRs) occurring subsequent to the event could be excised from analyses (to remove any potential artifact of the event). During a third state (depicted with a yellow background), participants were told that there was no chance of any event occurring as they completed the task. Each state (75-sec duration) occurred twice during each run.

Data were acquired in six 8-min 2-sec runs representing each combination of emotional expression (calm, fear, happy) as a go or no-go stimulus using a mixed

block/event-related design. Run orders of the emotional go/no-go were pseudocounterbalanced and background color/emotional state pairings were counterbalanced. At the beginning of each run, participants were instructed which emotional expression was the target and reminded of the colored background/emotional state pairings. Participants answered a series of four questions to assure they were aware of each of these contingencies before the outset of each run. Participants were queried about the potential event associated with each of the three colored backgrounds in a yes/no format (e.g., "Does this color screen mean that you could win up to \$100?") and were asked to confirm the target facial expression type (e.g., "Which face are you pushing for?"). Feedback was provided after each question, reiterating the contingencies. For each trial, a face appeared for 500 msec followed by a jittered intertrial interval (2–7 sec). A total of 114 trials were presented in each run in a pseudorandomized order (84 go, 30 no-go across all cue types). In total, 60 no-go and 168 go trials, across all three cue types, were acquired for each emotional state for a total of 48 min 12 sec.

Behavioral and Psychophysiological Data Acquisition

Participants completed a final screening for MRI safety before being positioned in the scanner, with a five-button (NY) or four-button (LA) MR-compatible button box. The experimental task was presented using E-Prime 1.0 (NY) or 2.0 (LA) and was projected onto a flat screen mounted in the scanner bore. Participants viewed the screen via a mirror mounted on a 12-channel head coil. Skin conductance response (SCR) was acquired using disposable, isotonic gel electrodes, which were attached to the first and second fingers of the left hand between the first and second phalanges. The electrode cables were grounded through an RF filter panel. The skin conductance signal

was recorded and amplified using a Biopac recording system and AcqKnowledge 4.0 (Biopac, Goleta, CA) software during fMRI scanning (200 Hz sampling). E-Prime software was used to indicate the onset/offset of the emotional state during the task (Lim et al., 1997). SCR data were acquired from 48 of the 50 participants.

After exiting the scanner, participants were asked to answer debriefing questions about the believability of task conditions. Participants were asked how much they expected to win money or hear the noise during the block color that corresponded to the verbal instruction (e.g., “Did you expect to win money more during the purple blocks than the blue or yellow blocks?”). Each question consisted of a 7-point scale (1 = *not at all*, 7 = *very much*). Thirty-eight participants completed the postscan questionnaire.

fMRI Data Acquisition

Whole-brain fMRI data were acquired using Siemens Magnetom Trio 3.0-T scanners located at the Citigroup Biomedical Imaging Center at Weill Cornell Medical College or at the University of California, Los Angeles. Scanning parameters were identical across data collection sites. A high-resolution, T1-weighted magnetization-prepared rapid-acquisition gradient-echo sequence scan was acquired using BIRN optimized sequences (Jovicich et al., 2006; TR = 2170 msec, echo time = 4.33 msec, field of view = 256 mm, 160 slices, 1.0 mm × 1.0 mm × 1.2 mm sagittal slices). Functional images were acquired using T2*-sensitive echo-planar pulse sequences covering the full brain. Thirty-eight 4-mm thick axial slices were acquired per 2500 msec TR (echo time = 30 msec, field of view = 200 mm, flip angle = 90°, 3.1 × 3.1 × 4.0 mm voxels).

Behavioral Data Analysis

Behavioral data were analyzed for accuracy using the sensitivity index d' that incorporates both accurate hits and false alarms (Macmillan & Creelman, 2004). D-prime was calculated by subtracting normalized false alarm rate from normalized go accuracy. Behavioral data, stimulus timing, and emotional state timing information were extracted and calculated using MATLAB and Statistics Toolbox Release 2013b. All statistical analyses were conducted using R (release 3.1.0). Main effects of emotional cue and state and the emotional cue by state interaction were analyzed using repeated-measures ANOVAs models controlling for sex and scanning site as between-subject variables and with Bonferroni-corrected post hoc t tests to determine statistical significance between conditions.

We examined responses to debriefing questions and SCR to assess the efficacy of our emotional state manipulation. A 1-Hz filter was applied to raw SCR data. Data were smoothed for each participant, and individuals with

no discernable variation in SCR across runs were excluded, leaving 31 of the 48 participants in the analyses. SCR slope was extracted for each emotional state block within each run and was z-scored within each participant to account for individual differences in SCR. Slope values across each emotional state (excite, threat, and neutral) were then averaged. Change in skin conductance was computed as a difference scores between SCR slope values in an emotional state versus neutral. Given the directionality of our hypotheses with respect to these validation measures, one-tailed one-sample Student's t tests were performed to test whether debriefing questions were significantly different from one (the lowest value on the 7-point scale) and whether SCR differences were significantly different from zero.

fMRI Data Analysis

Image Processing

Functional imaging data were preprocessed and analyzed using Analysis of Functional NeuroImages (AFNI) software (Cox, 1996). Preprocessing of functional scans included correction for slice time acquisition using sinc interpolation, volume registration using six-parameter rigid body transformation to account for head motion, and normalization to Montreal Neurological Institute 152 1-mm T1 template using 12-parameter affine transformation and nonlinear transformations (*3dQWarp*) were performed. Data were resampled to 3-mm isotropic voxels and were smoothed using a FWHM Gaussian kernel of 6 mm. Signal intensity of each voxel time series was normalized to percent signal change. Three individual general linear models (GLMs) were created for each participant to estimate separate aspects of the task: (1) activation to emotional cues and sustained emotional states, (2) cue–state interactions, and (3) functional connectivity for the cue–state interactions.

Image Analysis

To disentangle the neural responses to the cues and to the sustained states, which were presented simultaneously, each participant's GLM included 16 regressors: Six task regressors consisting of correct responses to the emotional cues (fear, happy, and calm go trials and fear, happy, and calm no-go trials). In the same model, three regressors were included to model the longer (30 TRs) sustained emotional states (i.e., the threat, excite, and neutral sustained states). We also included a regressor corresponding to the incorrect trials (both go and no-go), as well as six motion parameters. Baseline trends were estimated to capture shifts in signal change. Cues were modeled using a three-parameter SPM gamma hemodynamic response function (HRF); the sustained states were modeled using a single-parameter block HRF. Time points with >1.56 mm (half voxel) of motion

were censored as well as the preceding and following time points.

To examine cue–state interactions, a second GLM was run and consisted of 19 task regressors. In this GLM, each task regressor corresponded to the specific cue and sustained state. For example, the regressors incorporated information for each task and state (e.g., Threat-Calm-Go, Threat-Calm-No-go, Threat-Happy-Go, Threat-Happy-No-go). Incorrect trials were modeled as a separate regressor, six motion regressors, motion censoring, and baseline trend estimations were incorporated in this model, as in the previous model. Regressors were convolved with a three parameter SPM gamma HRF.

These individual level GLMs were submitted to group linear mixed-effects (LME) analyses using the AFNI *3dLME* function (Chen, Saad, Britton, Pine, & Cox, 2013), which is robust to small amounts of missing data. All group level analyses included a random intercept for each participant as well as sex and scanning site as between-subject covariates. The first group level LME model assessed the main effect of the transient cues (the go as well as the no-go trials). The second group level LME model assessed the main effect of the sustained state (threat, excite, neutral). Lastly, given the observed behavioral interaction between emotional state and happy cue, a third group LME model directly paralleling the behavioral performance finding assessed the neural interaction of the sustained emotional state (threat and excite) with positive cue (happy). Group analyses were thresholded at $p < .05$ corrected for multiple comparisons using Monte Carlo simulation via the *3dClustSim* program in AFNI. Individual subject regression coefficients were extracted from regions with significant main effects of emotional state and submitted to offline post hoc analyses in R.

Psychophysiological Interaction Analysis

A generalized psychophysiological interaction (gPPI) analysis (McLaren, Ries, Xu, & Johnson, 2012; Cisler, Bush, & Steele, 2014) was conducted in AFNI to examine task-dependent connectivity across the whole brain. The seed region was identified in the activation contrast of threat versus excite state to happy cue—the posterior cingulate cortex (PCC). Briefly, the gPPI analysis was carried out by removing sources of noise and artifact, deconvolving the neural signal, extracting the functional time course within the seed region (5-mm sphere around peak activation), and convolving the time course data with task timings and the canonical HRF (Cisler et al., 2014; McLaren et al., 2012). The 19 task regressor individual GLM examining cue–state interactions, described above, was implemented, but for the gPPI analysis also included the seed time course and each time course/task interaction regressor for a total of 39 regressors plus the six motion regressors. Consistent with the analysis yielding the seed region, a group LME model, also controlling for sex and scanning site, was used to test the specific

interaction of emotional state (threat and excite) with positive cue (happy). Group results for the threat state versus excitement state across target type contrast were thresholded at $p < .05$, corrected for multiple comparisons at the whole-brain level using *3dClustSim*, as described previously.

RESULTS

Validation of Paradigm

To ensure that performance did not drop because of the long duration of the task, we examined differences in overall d' between the first and last run and found no significant differences in performance ($t(37) = 0.15, p > .25$). We examined self-report measures and psychophysiology to assess the efficacy of the experimental manipulation. Self-reported responses to debriefing questionnaires and SCR slope differences to emotional states were tested independently, so we used a Bonferroni adjusted alpha less than 0.025 to assess questionnaire response statistical significance and to assess change in SCR significance. Participants expected both the money ($t(37) = 14.96, p < .0001$) and loud noise ($t(37) = 15.48, p < .0001$) to occur during the instructed blocks (Figure 2A). Participants showed positive mean slope differences of SCR to both emotional states relative to neutral (Figure 2B). Although only the difference between the excite state and neutral was statistically significant ($t(30) = 2.23, p = .016$; threat – neutral, $t(30) = 1.11, p = .14$), SCR difference scores for the excite and threat conditions were not significantly different from each other ($t(30) = 1.14, p = .26$).

Behavioral Results

To tease apart the effects of emotional cue versus emotional states on task performance, we examined d' -prime to cues within the neutral state and d' -prime to calm cues across emotional states. Repeated-measures ANOVAs

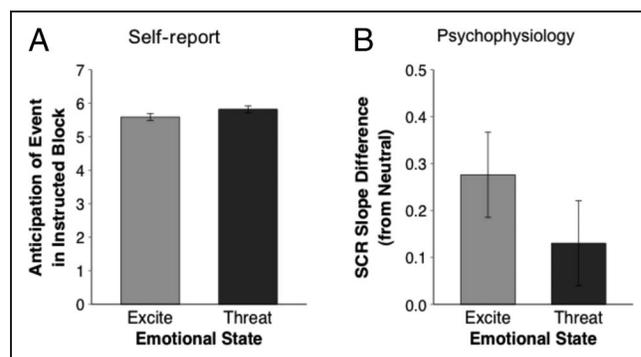


Figure 2. Validation of paradigm. (A) Participants expected to both win money and hear the loud noise during the instructed block. (B) Participants also showed similar effects in SCR in the emotional states relative to neutral. Means \pm SE presented.

showed no main effect of Cue type on performance ($F(2, 74) = 1.58, p = .21$; Figure 3A) but did reveal a main effect of Emotional state ($F(2, 74) = 4.38, p = .016$; Figure 3B). Post hoc Bonferroni-adjusted t tests showed that this main effect was primarily driven by the difference between the state of excitement and neutral ($t(37) = 2.87, p = .02$; threat versus neutral $t(37) = 1.59, p > .25$; excite vs. threat $t(37) = 1.39, p > .25$). Assessing across all emotional cues and states, a two-way repeated-measures ANOVA showed an Emotional state \times Cue interaction ($F(4, 148) = 3.57, p = .008$; Figure 3C). The largest effect of emotional state appeared to be on performance to happy cues across the three emotional states of excite, threat, and neutral (Figure 5A). Thus, we submitted these data to post hoc tests. Bonferroni-adjusted t tests revealed that participants showed enhanced performance to happy cues in the excite condition relative to neutral ($t(37) = 3.05, p = .013$), diminished performance in the threat condition relative to neutral ($t(37) = 2.61, p = .039$), and a pronounced difference in performance between excite and threat ($t(37) = 6.29, p < .0001$).

Imaging Results

Main Effects of Emotional State and Cue

Consistent with previous imaging studies using go/no-go tasks, in this variation we observed greater ipsilateral cerebellum ($Z = 7.34, p < .01$, corrected) and contralateral precentral gyrus ($Z = 4.12, p < .01$, corrected) activation to go trials relative to no-go trials and increased right ($Z = -3.81, p < .05$, corrected) and left ($Z = -4.15, p < .01$, corrected) inferior frontal gyrus (IFG) activation to no-go trials relative to go trials (Table 1). In studies implementing the emotional go/no-go task across development, we have previously observed a correlation of right IFG BOLD signal change on no-go versus go trials and overall proportion of false alarms across ages (Somerville,

Hare, & Casey, 2011). In this sample of adult participants, we find a similar association ($r(36) = 0.31, p = .0549$) that was not observed for frontoparietal regions ($r(36) = 0.199, p = .230$; parietal $r(36) = 0.255, p = .121$). In line with behavioral findings, no brain regions showed a main effect of Cue that survived correction for multiple comparisons. The activation map for the main effect of Emotional state revealed 11 regions showing differences in sustained activation (Table 2).

Given the behavioral findings of enhanced performance under a state of excitement, post hoc tests were performed on the beta values extracted from the four largest regions of activation, comparing activations between states using Bonferroni-adjusted t tests (Figure 4). These regions all showed relatively increased sustained activity in the excite state as compared with both the neutral and threat states: right parietal cortex (excite vs. neutral $t(37) = 4.55, p < .001$; excite vs. threat $t(37) = 4.73, p < .0001$; threat vs. neutral $t(37) = 0.18, p > .25$), right dorsolateral PFC (excite vs. neutral $t(37) = 5.11, p < .0001$; excite vs. threat $t(37) = 3.93, p = .001$; threat vs. neutral $t(37) = 2.32, p = .077$), right IFG and insula (excite vs. neutral $t(37) = 3.97, p < .001$; excite vs. threat $t(37) = 4.01, p < .001$; threat vs. neutral $t(37) = 0.06, p > .25$), and left striatum (excite vs. neutral $t(37) = 4.49, p < .001$; excite vs. threat $t(37) = 4.26, p < .001$; threat vs. neutral $t(37) = 0.43, p > .25$). Of these regions, only activation of the striatum was positively correlated with performance as measured by d' ($r(36) = 0.355, p = .029$). Sustained activity in this region was positively correlated with sustained activity in the prefrontal ($r(36) = 0.625, p < .0001$) and parietal regions ($r(36) = 0.446, p = .005$) during the excite state.

Interactive Effects of Emotional State and Cue

We focused our analysis on the observed behavioral interaction between Emotional cue and State (Figure 5A).

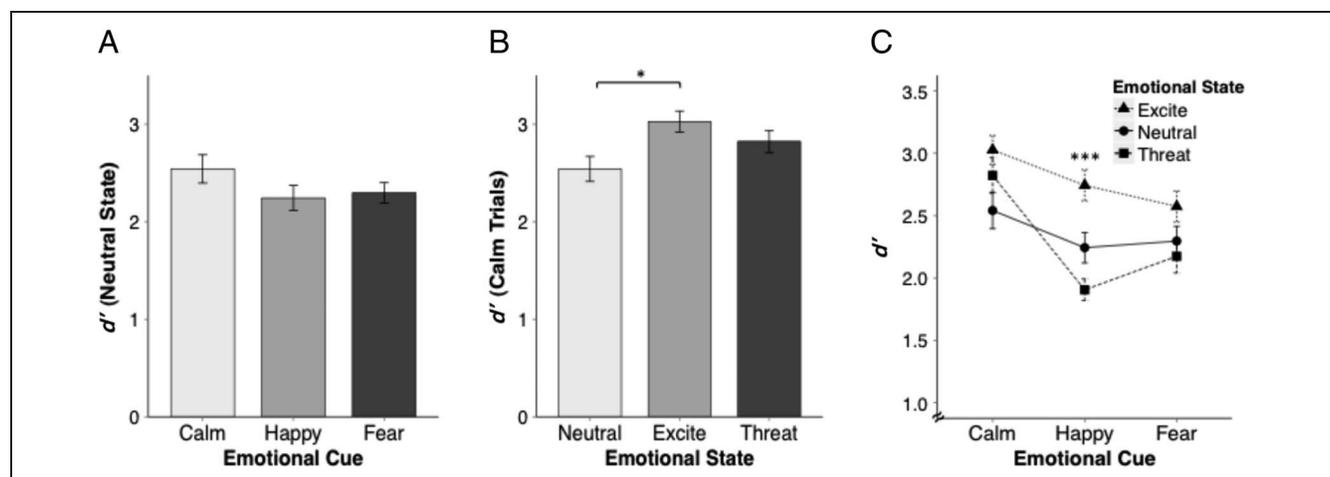


Figure 3. Sustained states of emotion influence performance to nonemotional and emotional cues. Behavioral performance dissociating emotional cue (A) from emotional state (B) and interactions between emotional states and cues (C). Means \pm SE presented. * $p < .05$, *** $p < .0001$.

Table 1. Response Type Activation Map (Go > No-go)

<i>Region</i>	<i>Brodman's Area</i>	<i>Peak Coordinate</i>	<i>Voxels, n</i>	<i>Z Statistic</i>
R cerebellum		-14.5, +53.5, -20.5	384	+7.34
R cerebellum		-14.5, +68.5, -47.5	50	+4.80
R lingual gyrus	18	-11.5, +98.5, -14.5	270	+4.68
R cingulate	24	-11.5, -12.5, +33.5	79	-4.57
R lateral PFC	3, 4, 6, 9	-44.5, +26.5, +63.5	359	-4.53
R superior temporal	22	-65.5, +38.5, +6.5	356	-4.53
R precentral	6	-17.5, -9.5, +63.5	50	-4.33
R SMA	6	-14.5, +5.5, +69.5	31	-4.33
L insula		+33.5, +2.5, -11.5	51	-4.26
L IFG	45	+27.5, -27.5, +0.5	38	-4.24
L temporal cortex	37	+39.5, +47.5, -11.5	44	-4.22
L superior temporal	22	+60.5, +59.5, +18.5	344	-4.21
L cerebellum		+30.5, +68.5, -20.5	73	+4.17
L precentral	6	+48.5, +2.5, +48.5	57	-4.15
L insula		+30.5, -12.5, +6.5	36	-4.15
R lateral PFC	10	-26.5, -48.5, +24.5	102	-4.13
L precentral	4	+36.5, +26.5, +60.5	75	+4.12
R mid temporal	19	-35.5, +47.5, +0.5	28	-3.99
L cingulate	24	+9.5, -3.5, +51.5	32	-3.88
R IFG	47	-41.5, -15.5, -2.5	29	-3.81
R parietal	40	-41.5, +41.5, +42.5	27	-3.72

Cluster FWE-corrected $p < .05$, individual voxel threshold 0.005, size ≥ 27 voxels.

Specifically, we compared BOLD signal to happy cues under threat versus under excitement. A single cluster survived whole-brain correction, showing greater activation for the threat than excite state, in the PCC ($x = -11.5$, $y = 44.5$, $z = 27.5$, $Z = 4.33$, cluster: 38 voxels, $p < .01$, corrected). PCC activation was enhanced when successfully engaging cognitive control on trials for which participants showed the most difficulty in performance.

A whole-brain generalized PPI analysis yielded seven clusters of voxels showing significantly greater functional connectivity with the PCC in the threat versus the excite condition to happy faces (see Table 3). Areas showing greater functional coupling included frontoparietal regions (Figure 5B) as well as dorsal anterior and middle cingulate regions. Functional connectivity parameter estimates were extracted from the frontoparietal clusters, and post hoc t tests were performed on lateral PFC ($t(37) = 5.01$, $p < .0001$) and both parietal regions (right and left betas collapsed; $t(37) = 4.91$, $p < .0001$). Functional connectivity parameter estimates did not show significant correlations with behavioral data. These findings show greater positive coupling between the PCC and frontoparietal con-

trol circuitry when the emotional cue and emotional state are in conflict (i.e., a smiling face when under threat).

DISCUSSION

Emotional triggers and prolonged emotional states are believed to influence thoughts and actions, yet there has been relatively little investigation of how different emotional states directly influence cognitive control capacity and the underlying neural circuitry. The current study shows that, in healthy adults, brief presentations of emotional cues do not significantly enhance or diminish cognitive control capacity, whereas sustained states of emotion alter this capacity. Under sustained states of excitement, when participants thought they could win as much as \$100 irrespective of their task performance, they showed enhanced cognitive performance. This finding is consistent with previous research suggesting that positive affect may broaden the scope of attention on cognitive tasks and improve performance (Fredrickson & Branigan, 2005; Ashby et al., 1999, 2002; Isen, 2002).

Table 2. Emotional State Main Effect Activation Map

Region	Brodmann's Area	Peak Coordinate	Voxels, n	F Statistic
R parietal cortex	40	-35.5, +56.5, +48.5	244	17.24
R dorsolateral PFC	9	-35.5, -36.5, +45.5	106	13.49
L striatum		+9.5, -3.5, +3.5	92	12.02
R IFG/insula	45, 13	-32.5, -21.5, +6.5	122	11.76
R lateral PFC	10	-41.5, -51.5, +15.5	40	11.43
Middle cingulate	23	-2.5, +23.5, +27.5	66	11.42
L cerebellum		+6.5, +77.5, -29.5	65	10.80
Middle cerebellum		-2.5, +53.5, -35.5	49	10.06
R dACC	32	-5.5, -27.5, +33.5	44	9.91
L IFG/insula	47, 13	+36.5, -18.5, -2.5	34	9.68
R caudate		-14.5, -3.5, +12.5	39	9.16

Cluster FWE-corrected $p < .01$, individual voxel threshold 0.005, size ≥ 34 voxels.

Improved performance under excitement was paralleled by increased sustained BOLD activation of frontoparietal and frontostriatal circuitry during this positive emotional state. Activation of these circuitries has been associated with performance in various cognitive control tasks (Buhle et al., 2014; Shackman et al., 2009; Simmonds

et al., 2008; Vincent et al., 2008; Liston et al., 2006; Owen et al., 2005). Specifically, frontoparietal circuitry has been implicated widely in cognitive control and attention processes, whereas frontostriatal activity, including that in the IFG, has been implicated more specifically in response inhibition (Aron, Robbins, & Poldrack, 2014; White et al.,

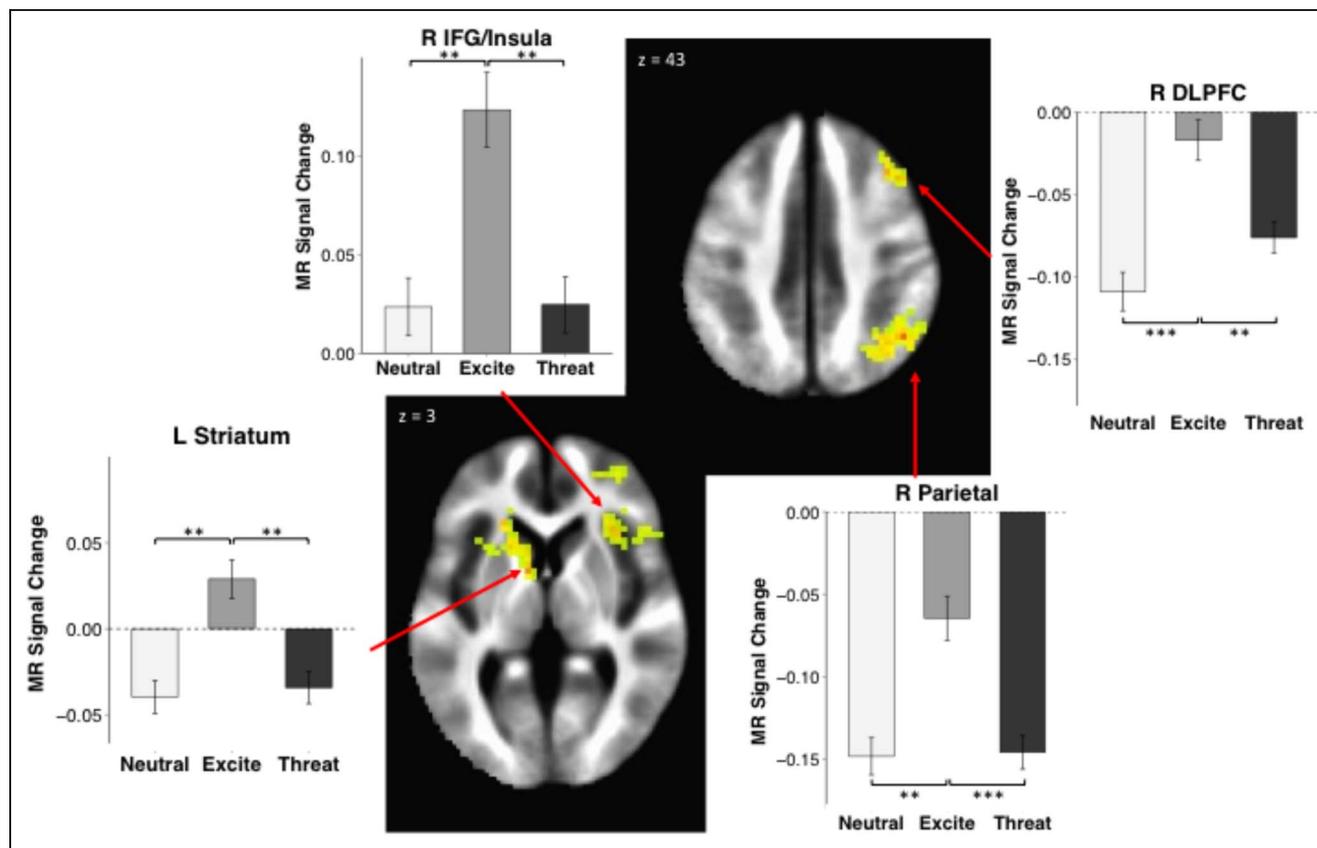


Figure 4. Heightened frontostriatal and frontoparietal activity under excitement. Representative axial images and extracted beta weights from regions showing a main effect of emotional state at $p < .01$, whole brain-corrected. All brain regions show a similar pattern of increased sustained activation under a state of excitement relative to neutral and threat conditions. Means \pm SE presented. $**p < .001$, $***p < .0001$.

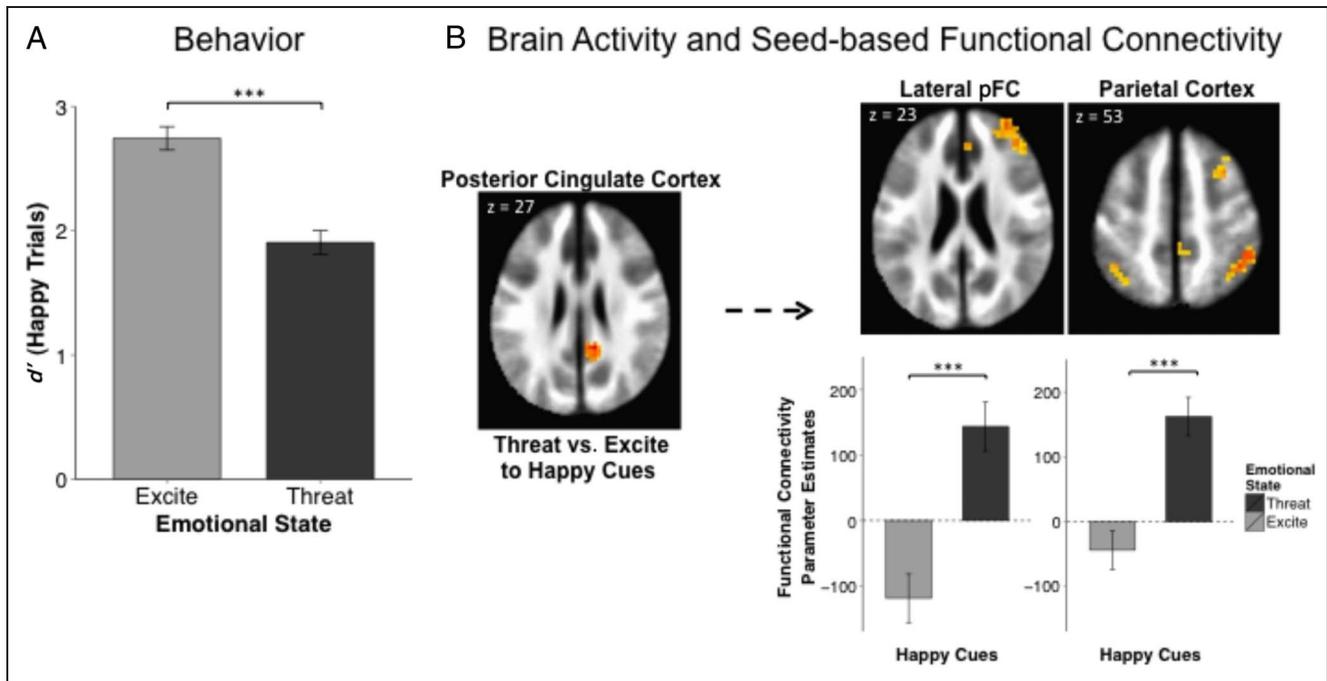


Figure 5. Diminished processing of positive information under threat. (A) Behavioral performance as indexed by d' to happy cues during states of excitement versus threat. (B) Localization of brain activity in PCC and seed-based functional connectivity with this region in dorsolateral prefrontal cortex and bilateral parietal cortex to happy cues during states of threat versus excitement. Means \pm SE presented. *** $p < .0001$.

2014; Dodds, Morein-Zamir, & Robbins, 2011; Heatherton & Wagner, 2011; Shackman et al., 2009; Vincent et al., 2008; Liston et al., 2006; Hare et al., 2005). Activity in the striatum was positively correlated with performance and with activity in prefrontal and parietal regions. The sustained increase in recruitment of these circuits throughout the state of excitement together with enhanced performance is consistent with heightened representation of task demands (Waskom, Kumaran, Gordon, Rissman, & Wagner, 2014; Miller & Cohen, 2001) that in turn facilitates cognitive control capacity.

In contrast to the improvement in cognitive control under a positive state of excitement, this ability was diminished under sustained threat. However, this diminished capacity was dependent on the type of emotional informa-

tion being processed. When the emotional cue conflicted with the emotional state (e.g., a smiling face under threat), behavioral performance declined. The presence of an emotional cue like a smiling face when under a state of potential threat is strikingly inconsistent with the negative emotional experience. This conflict at the emotional level is not dissimilar from cognitive conflict observed when two cognitive inputs compete for attention, resulting in the need for more cognitive control (Casey et al., 2000; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999). In the cognitive control literature, the ACC has been implicated in resolving this form of conflict (Fan, Hof, Guise, Fossella, & Posner, 2008; Bush et al., 2000; Casey et al., 2000; Botvinick et al., 1999). In the current study, the conflict is between an emotional input and an emotional state.

Table 3. PCC Functional Connectivity Activation Map (Threat > Excite to Happy Cues)

Region	Brodmann's Area	Peak Coordinate	Voxels, <i>n</i>	Z Statistic
R parietal cortex	40	-53.5, +44.5, +48.5	192	+5.31
R middle cingulate	31	-8.5, +29.5, +36.5	58	+5.28
R lateral PFC	10	-35.5, -57.5, +21.5	134	+4.59
L parietal cortex	40	+48.5, +53.5, +39.5	49	+4.36
R mid frontal	6	-47.5, -0.5, +42.5	66	+4.12
R lateral PFC	9	-53.5, -15.5, +39.5	42	+3.88
R dACC	32	-5.5, -36.5, +18.5	61	+3.81

Cluster FWE-corrected $p < .01$, individual voxel threshold 0.005, size ≥ 34 voxels.

We show that this form of emotional conflict is associated with PCC activity.

The PCC is a major hub of the default mode network (DMN) that has been implicated in processing positive and negative affect in the context of self (Brewer, Garrison, & Whitfield-Gabrieli, 2013; Maddock, Garrett, & Buonocore, 2001, 2003). Nonhuman primate research has shown that the PCC has diffuse structural connections throughout the brain, including other parts of cingulate cortex and association cortices in the frontal and parietal lobes (Leech & Sharp, 2013; Parvizi, Van Hoesen, Buckwalter, & Damasio, 2006). Although there is still little consensus regarding the computational functions of the PCC (Leech & Sharp, 2013), evidence from nonhuman primate research suggests that the neuronal firing in the PCC is involved in complex processes such as performance monitoring and salience detection in motivated goal-directed cognition (Heilbronner & Platt, 2013; Leech & Sharp, 2013; Heilbronner, Hayden, & Platt, 2011; Pearson, Heilbronner, Barack, Hayden, & Platt, 2011). It is hypothesized that a role of the DMN may be to flexibly allocate cognitive resources in cognitively demanding situations to facilitate changes in behaviors that lead to successful task performance (Heilbronner & Platt, 2013; Leech, Braga, & Sharp, 2012; Heilbronner et al., 2011; Pearson et al., 2011; Pearson, Hayden, Raghavachari, & Platt, 2009; Hayden, Nair, McCoy, & Platt, 2008).

When the emotional cue conflicted with the negative emotional state, the PCC showed positive coupling with frontoparietal control circuitry. Consistent with the work in nonhuman primates, recent converging evidence in humans shows positive functional connectivity of DMN hubs, including the PCC, with frontoparietal networks when participants are engaged in a goal-directed task. This heightened task-based connectivity is thought to represent the phenomenon proposed in nonhuman primate research of the PCC potentially mobilizing additional cognitive resources when necessary (Heilbronner & Platt, 2013; Leech et al., 2012; Pearson et al., 2011; Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010). Thus, during this condition of conflicting emotional information, where participants are exhibiting the most difficulty performing the task, we observe relatively increased activity in the PCC and positive functional coupling with cingulate and frontoparietal circuitry for correct trials. These results are consistent with a role for the PCC in mobilizing neural resources in cognitively taxing conditions.

An alternative interpretation of these data comes from the human resting-state fMRI literature. Studies of resting-state functional connectivity shed light on the functional organization and architecture of neural networks. Healthy participants generally show negative connectivity or inverse coupling between DMN regions and task-relevant networks. Due in part to the high resting-state activity of DMN regions such as the PCC, it is thought that the commonly observed negative coupling is a reflection of redirecting attention outward from focusing inward on

self (Leech & Sharp, 2013; Whitfield-Gabrieli & Ford, 2012; Uddin, Kelly, Biswal, Castellanos, & Milham, 2009). Many psychiatric disorders characterized by cognitive control problems show the opposite pattern of positive connectivity between default and control networks, including schizophrenia and depression (Leech & Sharp, 2013; Whitfield-Gabrieli & Ford, 2012). These alterations in resting-state neural circuitry are thought to reflect components of the pathology, such as difficulties with redirection of attention and increased rumination. Thus, the heightened functional connectivity observed when emotional input and emotional state conflict in combination with diminished cognitive control is reminiscent of altered resting-state connectivity in psychiatric populations characterized by cognitive control problems.

Although simultaneous processing of conflicting negative and positive emotions diminished cognitive control capacity and elicited greater activity in the PCC for correct trials in the context of smiling faces under threat, the opposite pattern of behavior was shown when a fearful face occurred in the positive state of excitement. One potential explanation for this seemingly conflicting result is that fearful faces may be ambiguous stimuli that do not provide contextual information (Davis & Whalen, 2001). Several studies have suggested that positive or negative emotional context can bias the interpretation of ambiguous facial expressions (Neta, Davis, & Whalen, 2011; Kim et al., 2004). In this study, the prevailing positive emotional context (anticipation of winning money) may influence the interpretation of ambiguous stimuli such as a fearful face as surprise rather than threat, thus reducing the degree of conflict in the different forms of emotional information. Specifically, performance was enhanced to fearful relative to neutral faces in the positive emotional state. This interpretation is consistent with general improvements in cognition when experiencing positive affect (Fredrickson & Branigan, 2005; Ashby et al., 1999, 2002; Isen, 2002).

Although healthy adults show diminished performance and differential recruitment of task-related circuitry when faced with conflicting emotional information, it is still unclear how competing emotional inputs may differentially influence cognitive control and neural processes in different conditions, such as in developmental or psychiatric populations. Adolescence is a time of heightened sensitivity to emotional and social inputs (Casey, 2015), thus understanding complex influences of emotions on cognitive and neural processes during this typical stage of development may provide further insights into situational effects on behavior. Furthermore, emotional problems are hallmarks of a wide range of psychopathologies (Carpenter & Trull, 2013; Townsend & Altshuler, 2012; Cisler & Olatunji, 2010; Joormann & Gotlib, 2010) that peak during this developmental period with one in five adolescents meeting criteria for a mental illness (Merikangas et al., 2010; Kessler & Wang, 2008), highlighting the importance of developmental considerations in this line of research

(Casey, Glatt, & Lee, 2015; Lee et al., 2014). The influence of emotions on cognitive and neural processes in developmental and psychiatric populations is a primary area of empirical investigation and one that may have important implications for clinical assessment and interventions that may improve outcomes (Sheppes et al., 2015; Gross & Jazaieri, 2014; Lee et al., 2014; Davidson et al., 2002). The behavioral paradigm reported in this study may be useful in probing the complex interactions between cognition and emotion in developmental and psychiatric populations.

The findings reported here must be considered in light of their limitations. We here refer to the sustained states of positive arousal and negative arousal as “excitement” and “threat,” respectively. However, we do not have a measure of these mood states to directly assess how the participants were feeling. Additionally, although we observed significantly increased skin conductance across the excite state relative to neutral, the increase in skin conductance in the threat state relative to neutral was not significantly different from zero. Much of the SCR data collected were not usable, and there was significant variability in the data. Data may have been particularly noisy because they were acquired in the scanner and because participants viewed brief emotional cues throughout each state block. Examining SCR data in a larger sample may help to increase power and reduce noise. It is also possible that some participants did not find the loud noise as aversive as others did, although this stimulus has been validated as aversive in previous imaging research (Soliman et al., 2010; Levita, Hare, Voss, Ballon, & Casey, 2009). Investigating individual differences in responses to these induced emotional states may yield further insight into how emotion differentially impacts cognitive control among individuals.

This study implements a novel neuroimaging paradigm for examining how emotional information and states impact attention and actions, for better or worse. We demonstrate that emotional states and cues have dissociable and interacting influences on cognitive control processes and on the underlying neural circuitry. Our findings suggest that sustained positive states are associated with improvements in performance in healthy adults whereas conflicting positive emotional information under a negative state diminishes performance and alters neural activation and connectivity. Understanding complex influences of emotions on cognitive and neural processes in healthy participants is a first step toward delineating conditions (e.g., pathological, developmental, or environmental) for which emotional processes may alter behavior.

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