

When Is an Adolescent an Adult? Assessing Cognitive Control in Emotional and Nonemotional Contexts

Psychological Science
2016, Vol. 27(4) 549–562
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DOI: 10.1177/0956797615627625
pss.sagepub.com


**Alexandra O. Cohen¹, Kaitlyn Breiner², Laurence Steinberg³,
Richard J. Bonnie⁴, Elizabeth S. Scott⁵, Kim A. Taylor-Thompson⁶,
Marc D. Rudolph⁷, Jason Chein³, Jennifer A. Richeson^{8,9},
Aaron S. Heller¹⁰, Melanie R. Silverman¹, Danielle V. Dellarco¹,
Damien A. Fair⁷, Adriana Galván², and B. J. Casey¹**

¹Department of Psychiatry, Sackler Institute for Developmental Psychobiology, Weill Cornell Medical College;

²Department of Psychology, University of California, Los Angeles; ³Department of Psychology, Temple University;

⁴University of Virginia School of Law, University of Virginia; ⁵Columbia Law School, Columbia University;

⁶New York University School of Law, New York University; ⁷Department of Behavioral Neuroscience and

Psychiatry, Oregon Health & Science University; ⁸Department of Psychology, Northwestern University;

⁹Institute for Policy Research, Northwestern University; and ¹⁰Department of Psychology, University of Miami

Abstract

An individual is typically considered an adult at age 18, although the age of adulthood varies for different legal and social policies. A key question is how cognitive capacities relevant to these policies change with development. The current study used an emotional go/no-go paradigm and functional neuroimaging to assess cognitive control under sustained states of negative and positive arousal in a community sample of one hundred ten 13- to 25-year-olds from New York City and Los Angeles. The results showed diminished cognitive performance under brief and prolonged negative emotional arousal in 18- to 21-year-olds relative to adults over 21. This reduction in performance was paralleled by decreased activity in fronto-parietal circuitry, implicated in cognitive control, and increased sustained activity in the ventromedial prefrontal cortex, involved in emotional processes. The findings suggest a developmental shift in cognitive capacity in emotional situations that coincides with dynamic changes in prefrontal circuitry. These findings may inform age-related social policies.

Keywords

adolescence, cognitive control, development, emotion, fMRI, legal policy, young adult

Received 8/6/15; Revision accepted 12/28/15

Definitions of adulthood in the United States differ according to state law and policy. Although most states set the age of majority at 18, the legal age for purchasing alcohol is 21 (Institute of Medicine & National Research Council, 2014), and the minimum age for criminal prosecution is 14 or younger in most states (Taylor-Thompson, 2014). In scientific studies, 18 is often used as the cutoff for adulthood even though government research policies, until recently, considered individuals under 21 to be minors. Thus, the legal definition of adulthood is fluid and imprecise. One consideration in defining adulthood is when behavior, and the underlying neural circuitry, can be said

to have reached maturity. Extant studies suggest that this may vary depending on the context in which adolescents are assessed. In the current study, we compared the development of cognitive control in neutral and emotionally arousing situations because the latter seem highly relevant to many policies relating to definitions of adulthood.

Corresponding Author:

B. J. Casey, Weill Cornell Medical College, Sackler Institute for Developmental Psychobiology, 1300 York Ave., Box 140, New York, NY 10065

E-mail: bjc2002@med.cornell.edu

Although a large developmental literature shows that adolescents' speed and accuracy on simple cognitive tasks can resemble adults' (Luna, Marek, Larsen, Tervo-Clemmens, & Chahal, 2015), mounting evidence suggests that contextual factors influence performance differentially as a function of age. Studies show that adolescence, typically defined as ages 13 through 17, is a time of heightened sensitivity to motivational, social, and emotional information (Casey, 2015; Steinberg, 2010). Specifically, during adolescence, cognitive-control capacities and decision making appear to be especially influenced by incentives (Galvan et al., 2006; Geier, Terwilliger, Teslovich, Velanova, & Luna, 2010; Somerville, Hare, & Casey, 2011; Van Leijenhorst et al., 2010), threats (Cohen-Gilbert & Thomas, 2013; Dreyfuss et al., 2014; Grose-Fifer, Rodrigues, Hoover, & Zottoli, 2013; Hare et al., 2008), and peers (Chein, Albert, O'Brien, Uckert, & Steinberg, 2011; Gardner & Steinberg, 2005). Behavioral regulation in response to these inputs has been shown to rely on prefrontal circuitry (Dreyfuss et al., 2014; Hare et al., 2008; Somerville et al., 2011), which shows marked change into the early 20s (Gogtay et al., 2004; Sowell et al., 2004).

Prominent neurobiological theories of adolescence suggest that dynamic and asymmetric trajectories in structural and functional development of limbic and prefrontal circuitry are implicated in motivated behavior and its control, respectively, and may lead to a propensity toward risky and impulsive actions (Casey, 2015; Casey, Getz, & Galvan, 2008; Ernst, Pine, & Hardin, 2006; Mills, Goddings, Clasen, Giedd, & Blakemore, 2014; Steinberg, 2010). Phylogenetically older brain regions, such as subcortical limbic regions, show nonlinear developmental changes and appear to be functionally sensitized during adolescence (Galvan et al., 2006; Hare et al., 2008; Raz-nahan et al., 2014), whereas development of prefrontal cortex (PFC) exhibits a roughly linear trajectory (Galvan et al., 2006; Gogtay et al., 2004; Sowell et al., 2004). Resting-state functional-connectivity data show prolonged development of long-range cortical connectivity that does not stabilize until the 20s (Dosenbach et al., 2011; Fair et al., 2009). Together, these results suggest continued refinement of brain circuitry, particularly prefrontal cortical circuitry, into young adulthood, but the behavioral implications of this protracted brain development remain unclear.

The current study compared the development of cognitive control under brief and prolonged states of emotional arousal and nonemotional states. We focused on the 18-to-21 age range given the protracted development of prefrontal circuitry and the particular legal and social relevance of this age group. Our key premise was that responses in emotional situations would provide insight on cognitive capacities relevant to social and legal policy,

such as those related to criminal responsibility and accountability. Prior research examining motivational and social influences on cognitive capacities in young adults has used varying age ranges and experimental manipulations that have produced mixed results (Chein et al., 2011; Cohen-Gilbert et al., 2014; Silva, Shulman, Chein, & Steinberg, 2015; Steinberg et al., 2009). We attempted to control for several of these variables by testing the impact of both brief and sustained positive and negative emotional states on cognitive control, using predefined age groups as well as age as a continuous variable. We hypothesized that there would be a developmental shift in cognitive control in emotional situations that would correspond to dynamic changes in prefrontal circuitry. Specifically, we predicted that young adults 18 to 21 years old would differ from adults over age 21 in cognitive control in emotionally arousing conditions (as teens do) but not in neutral conditions.

Method

Participants

Participants were 110 individuals from a larger sample of 147 healthy, right-handed 13- to 25-year-olds who underwent functional MRI (fMRI) while performing an adapted emotional go/no-go task (Hare et al., 2008) under sustained emotional states of threat and excitement and under nonemotional states (Cohen et al., 2016). Data from 5 participants were excluded because of their poor overall performance ($> 2 SD$ below the group's average performance as measured by d'). Data from 14 participants were excluded because of excessive head motion (more than 10% of time points within a run censored because of translational motion > 1.56 mm, or half a voxel, or rotational motion $> 1^\circ$), and data from 18 participants were excluded because of technical problems that led to errors in coding and recording of behavioral data in the scanner. A total of 110 usable scans were included in the final analyses reported here (41 teens—23 females and 18 males, ages 13–17 years, $M = 16.19$, $SD = 1.20$; 35 young adults—17 females and 18 males, ages 18–21 years, $M = 19.88$, $SD = 1.09$; 34 adults—17 females and 17 males, ages 22–25 years, $M = 24.08$, $SD = 1.04$). Portions of the data from 38 adults in this sample are included in a separate report (Cohen et al., 2016) focusing on different experimental questions.

Participants were a diverse community sample recruited from New York City and Los Angeles as part of an ongoing multisite project. They self-identified as Caucasian (32.7%), African American (27.3%), Hispanic (24.6%), Asian (12.7%) and "other" (2.7%). The recruitment target for this portion of the study was 125 participants, in anticipation of 20% attrition due to excessive

head motion, poor performance, or technical issues. Because of exclusions due to poor task performance and technical issues in the scanner environment, 22 additional participants were run. Participants reported no use of psychotropic medications or past diagnoses of or treatment for psychiatric or neurological disorders. Adults and parents provided informed written consent, and minors provided assent. The institutional review board at each site approved the study.

Experimental task

Participants completed a modified emotional go/no-go paradigm (Hare et al., 2008) called the Cognitive Control Under Emotion (CCUE) task (Cohen et al., 2016). In this task, happy, fearful, and calm emotional expressions (Fig. 1a) are presented as targets, which participants are instructed to respond to (go trials), and nontargets, which participants are instructed not to respond to (no-go trials). The task is performed in blocks of sustained anticipation of a negative event (aversive sound), a positive event (winning up to \$100), and no event; each type of block is denoted with a different background color on the screen (Fig. 1b). (Further descriptions of this task and task-related neural activations are available in other

reports: Cohen et al., 2016; Dreyfuss et al., 2014; Hare et al., 2008; Somerville et al., 2011). Participants practiced the task prior to entering the scanner, so that they understood the instructions and conditions.

We included both blocks with a sustained state of threat and blocks with a sustained state of excitement in order to dissociate effects of arousal and effects of valence. Threat was induced by telling participants that they might experience an unpredictable aversive auditory stimulus. Excitement was induced by telling participants that they had a chance of winning up to \$100. Participants were instructed that the probability of an event occurring, the volume of the noise, and the amount of money won would not be tied to their performance, but rather would be determined by the computer. They were also told that events of a given type would occur randomly, only when the background screen was a particular color (blue for one event and purple for the other). In reality, each participant heard the noise once and won \$20 once over the course of the task, and these events occurred in a pseudorandomized order. Each event always occurred near the end of an experimental run, so that these time points could be eliminated from the analyses. During blocks of a sustained neutral state (depicted with a yellow background), participants were told there

a



b

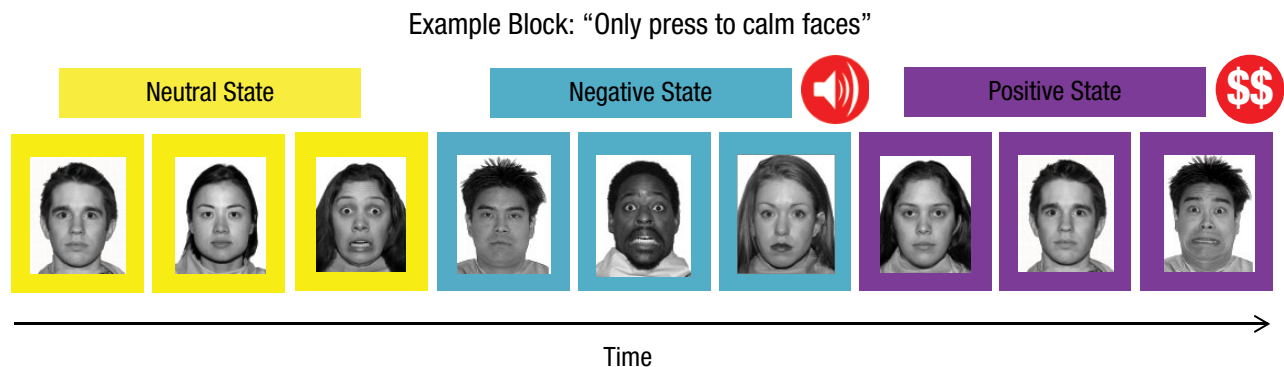


Fig. 1. The Cognitive Control Under Emotion (CCUE) paradigm (from Cohen et al., 2016): (a) examples of the fearful, happy, and calm faces used as cues and (b) schematic of one run of the task. In a given run, participants were instructed to respond to one type of cue (go trials) and not to respond to another (no-go trials). These cues were presented within blocks of sustained negative emotion (anticipation of an unpredictable aversive noise), positive emotion (anticipation of an unpredictable monetary reward), and neutral emotion (no event anticipated); the block type was indicated by the background color of the screen (yellow, blue, or purple).

was no chance of either event occurring as they performed the task. Each state (75-s duration) was induced twice during each run.

Data were acquired in six 8-min 2-s runs (total of 48 min 12 s). Each run consisted of a unique combination of the emotional expressions that served as go and no-go cues (calm-go/fearful-no go, calm-go/happy-no go, happy-go/fearful-no go, happy-go/calm-no go, fearful-go/calm-no go, fearful-go/happy-no go), in a mixed-block event-related design. Run orders were pseudocounterbalanced, and pairing of the background color and emotional state was counterbalanced. Before each run, participants were told which type of emotional expression was the target and reminded of the meaning of each colored background. We then asked participants a series of four questions to be sure they were aware of each of these contingencies. On each trial, a face appeared for 500 ms; the intertrial interval was jittered (2–7 s). A total of 114 trials were presented in each run, in a pseudorandomized order (84 go trials and 30 no-go trials). For each emotional state, we acquired data on a total of 168 go trials and 60 no-go trials.

Behavioral and psychophysiological data acquisition

Participants completed a final screening for MRI safety before being positioned in the scanner, with a five-button (New York) or four-button (Los Angeles) MR-compatible button box. The experimental task was presented using E-Prime 1.0 (New York) or 2.0 (Los Angeles; Psychology Software Tools, Inc., <http://www.pstnet.com>) 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 a radio-frequency filter panel. During fMRI scanning, the skin conductance signal was recorded (200-Hz sampling) and amplified using a Biopac recording system and AcqKnowledge 4.0 software. E-Prime software was used to indicate the onset and offset of the emotional states during the task. SCR data were acquired from all the participants.

After exiting the scanner, participants were asked debriefing questions about the believability of task conditions. Specifically, they were asked how much they expected to win money or hear the noise during the blocks in which the background color signaled the possibility of those events (e.g., “Did you expect to win money more during the purple blocks than the blue or yellow blocks?”). Each question was answered using a 7-point Likert scale (1 = *not at all*, 7 = *very much*).

Collection of debriefing data from 2 of the 110 subjects was accidentally omitted.

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 Staglin Center for Cognitive Neuroscience at the University of California, Los Angeles. Scanning parameters were identical at the two data-collection sites. A high-resolution, T1-weighted magnetization-prepared rapid-acquisition gradient-echo (MPRAGE) sequence scan was acquired using Biomedical Informatics Research Network (Jovicich et al., 2006) optimized sequences with the following parameters: repetition time (TR) = 2,170 ms, echo time (TE) = 4.33 ms, 256-mm field of view (FOV), 160 sagittal slices with a thickness of 1.2 mm. 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 2,500-ms TR (TE = 30 ms, FOV = 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' , which incorporates the rates of both hits and false alarms (Macmillan & Creelman, 2004). We calculated d' by subtracting the normalized false alarm rate from normalized accuracy on go trials. Behavioral data, stimulus timing, and emotional-state timing were extracted and calculated using MATLAB and Statistics Toolbox Release 2013b (The MathWorks, Natick, MA). All statistical analyses of the behavioral data were conducted using R (Release 3.1.0; R Core Team, 2014). We tested for age-related differences in performance (d') using analysis of variance (ANOVA) models that included sex and scanning site as between-subjects variables. To investigate performance responding to the emotional cues, without effects of emotional state, we tested for main effects of age group on performance with each cue type in the neutral state. To investigate performance during the emotional states, controlling for effects of the emotional cues, we tested for main effects of age group on performance responding to the calm face cues in each emotional state. A Bonferroni-adjusted alpha of less than .01 was used to correct for multiple comparisons in determining the statistical significance of these ANOVA results. Bonferroni-corrected post hoc t tests were used to determine the statistical significance of differences between age groups. Linear and quadratic models were also fitted to each dependent variable, with age modeled continuously. As in the age-group analyses, we used a Bonferroni-adjusted

alpha of less than .01 to determine statistical significance. All analyses were performed on the data from the 110 subjects with usable imaging and behavioral data.

We examined responses to the debriefing questions and the SCR data to assess the efficacy of our emotional-state manipulation. A 1-Hz filter was applied to the raw SCR data. Data were smoothed for each subject. Six subjects had no SCR data because of technical difficulties in the collection of these data, and 29 of the remaining 104 participants had no discernible variation in SCR across the experiment or individual runs and so were removed from the SCR analyses. SCR slope was extracted for each emotional-state block within each run and was z -scored within subjects to account for individual differences in SCR. Each individual's average slope was calculated for each emotional state (excitement, threat, and neutral). Change in skin conductance was computed as the difference between average SCR slope in an aroused state (excitement or threat) and average SCR slope in the neutral state. Given the directionality of our hypotheses with respect to these validation measures, we performed one-tailed one-sample Student's t tests to test whether responses to debriefing questions were significantly different from 1 (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 a 6-parameter rigid-body transformation to account for head motion, and normalization to the Montreal Neurological Institute (MNI) 152 1-mm T1 template using a 12-parameter affine transformation and nonlinear transformations (AFNI *3dQWarp* function). Data were resampled to 3-mm isotropic voxels and were smoothed using a full-width/half-maximum Gaussian kernel of 6 mm. Signal intensity of each voxel time series was normalized to percentage signal change.

Image analysis. A general linear model (GLM) was created for each participant to estimate activation in response to the emotional cues and sustained-emotional-state blocks. To disentangle the neural responses to the cues and to the sustained states, which were presented simultaneously, we included 16 regressors in each participant's GLM: 6 task regressors for correct responses to the emotional cues (fearful, happy, or calm faces on go trials and fearful, happy, or calm faces on no-go trials), 3 task regressors modeling the longer (30-TR) sustained

emotional states (i.e., the threat, excitement, and neutral sustained states), an additional regressor corresponding to trials with incorrect responses (both go and no-go trials), and 6 motion estimation parameters. Baseline trends were estimated to capture shifts in signal change. Activation in response to the face cues was modeled with a three-parameter gamma hemodynamic-response function (HRF); activation during the sustained states was modeled using a single-parameter block HRF. Time points with motion greater than half a voxel (1.56 mm) were censored, along with the preceding and following time points.

Individual-level regression coefficients for the 110 participants 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 and included sex and scanning site as between-subjects variables. Separate models were used to assess effects of transient cues (modeled as brief events) and sustained states (modeled as prolonged blocks) on brain activity. The first group-level LME model assessed effects of the transient cues (fearful, happy, and calm faces) on go and no-go trials. The second group-level LME model assessed effects of the sustained states (threat, excitement, and neutral). Age-group contrasts (general linear tests) were specified within each model to directly probe the neural correlates of behavioral findings. Two additional models assessed effects of the emotional cues and emotional states as a function of exact age as a continuous variable (i.e., interactions of emotional cues or states with exact age).

In group whole-brain analyses, individual voxels were thresholded at a p value of .005; the cluster-size threshold was a p value of .05 after correction for multiple comparisons (performed using Monte Carlo simulation via the *3dClustSim* program in AFNI). For the threat condition, given our a priori hypotheses regarding differences in prefrontal activation, we used an anatomical region of interest (ROI) for the PFC (obtained from the Harvard-Oxford probabilistic atlas in FSL; <http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/>; Smith et al., 2004). Similar to the PFC ROI in previous studies (e.g., Foerde, Steinglass, Shohamy, & Walsh, 2015), this ROI combined the frontal pole, superior frontal gyrus, middle frontal gyrus, inferior frontal gyrus (triangularis and opercularis), frontal medial cortex, subcallosal cortex, paracingulate gyrus, cingulate gyrus anterior division, and frontal orbital cortex bilaterally; a threshold of 50% probability was used for all subregions within the PFC. A p value of .005 was used as the threshold for individual voxels ($p < .05$ after PFC volume correction for multiple comparisons was performed using Monte Carlo simulation via the *3dClustSim* program in AFNI). Regression coefficients for individual participants

were extracted from regions with significant effects and were tested for brain-behavior correlations in R (Release 3.1.0; R Core Team, 2014).

Psychophysiological interaction analysis. Generalized psychophysiological interaction (gPPI) analyses (McLaren, Ries, Xu, & Johnson, 2012) were conducted in AFNI to examine task-dependent connectivity across the whole brain. Seed regions were the two PFC regions identified as having age-group effects. The gPPI analyses were carried out by removing sources of noise and artifact, deconvolving the neural signal, extracting the functional time course within the seed regions (5-mm spheres around peak activation), and convolving the time-course data with task timings and the canonical HRF (McLaren et al., 2012). The 16-regressor GLM used for the individual-level image analyses was implemented, but for the gPPI analyses, these models also included regressors for the seed time course and each Time Course \times Task Condition interaction, for a total of 27 regressors. The group-level LME model (controlling for sex and scanning site) was used to test the specific age-group contrasts. Specifically, group-level LME models tested the effects of transient cues (fearful, happy, and calm faces) and sustained states (threat, excitement, and neutral) separately. Age-group contrasts (general linear tests) were specified within each model. The models used a p threshold of .05, corrected for multiple comparisons at the whole-brain level using *3dClustSim*, as described previously.

Results

Behavioral results

Validation of the paradigm. Responses to the debriefing questions and SCR slope differences were tested independently, so we used a Bonferroni-adjusted alpha of less than .025 in our validation tests. These validation measures were collapsed across age. Participants expected both the money, $t(107) = 24.49$, $p < .001$, $d = 3.35$, and loud noise, $t(107) = 31.87$, $p < .001$, $d = 4.36$, to occur during the blocks in which they were led to anticipate these possibilities (Fig. 2a).

Participants' mean SCR difference scores (arousal state minus neutral state) were positive for both the excitement condition, $t(74) = 1.92$, $p = .029$, $d = 0.32$, and the threat condition, $t(74) = 1.65$, $p = .051$, $d = 0.27$ (Fig. 2b). SCR difference scores for the excitement and threat conditions were not significantly different from each other, $t(74) = 0.26$, $p > .250$, $d = 0.04$. These validation results replicate previous results for adults performing this same task (Cohen et al., 2016).

Main effects of age for each type of emotional cue.

In the neutral-state blocks, there were significant main effects of age group on performance in response to fearful cues, $F(2, 98) = 11.11$, $p < .001$, $\eta_p^2 = .16$; happy cues, $F(2, 98) = 10.90$, $p < .001$, $\eta_p^2 = .15$; and calm cues, $F(2, 98) = 7.81$, $p < .001$, $\eta_p^2 = .10$ (see Fig. 3a and Behavioral Results and Figs. S1a and S2a in the Supplemental

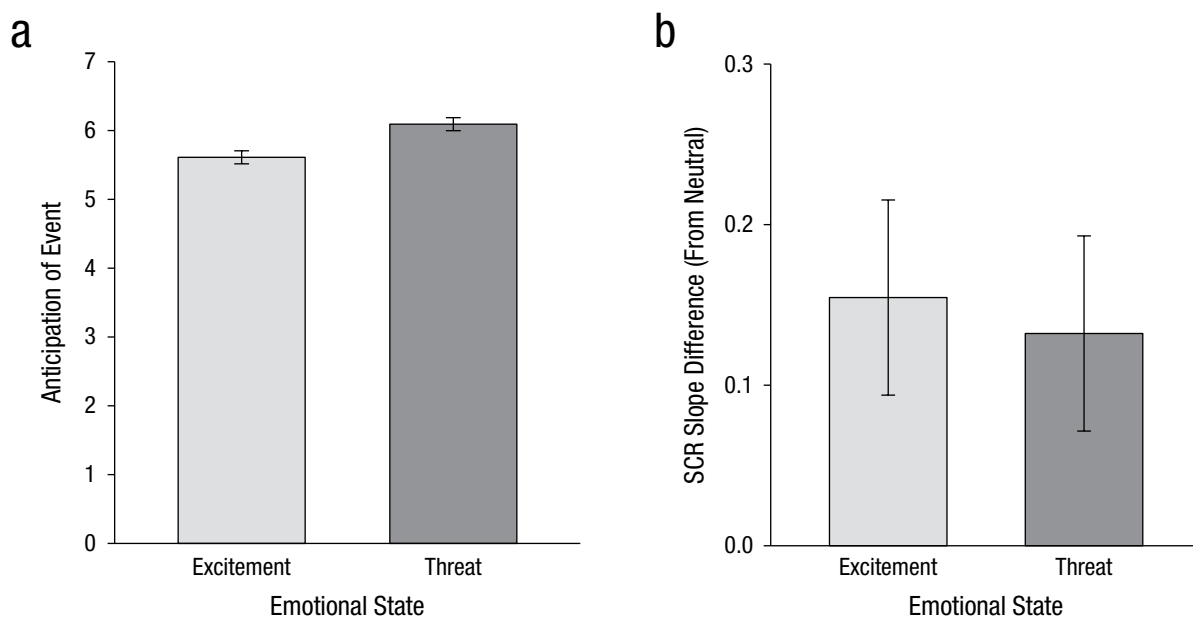


Fig. 2. Validation of the Cognitive Control Under Emotion (CCUE) paradigm: (a) participants' mean ratings of how likely they thought they were to win money and hear a loud sound in the excitement and threat blocks, respectively, and (b) participants' mean skin conductance response (SCR) during those blocks relative to the neutral blocks. Error bars represent ± 1 SE.

Material available online). Post hoc t tests revealed that teens and young adults showed diminished performance relative to adults in response to fearful cues—teens versus adults: $t(62.39) = 4.08, p < .001, d = 0.95$; young adults versus adults: $t(64.82) = 3.33, p = .0019, d = 0.80$; teens versus young adults: $t(70.09) = 0.61, p > .250, d = 0.14$. However, young adults and adults showed enhanced performance relative to teens in response to happy cues—teens versus adults: $t(71.15) = 4.14, p < .001, d = 0.96$; young adults versus adults: $t(65.77) = 1.79, p > .250, d = 0.43$; teens versus young adults: $t(73.96) = 2.55, p = .042, d = 0.59$ —and only teens and adults differed significantly in their performance with calm cues—teens versus adults: $t(64.05) = 3.54, p = .001, d = 0.82$; young adults versus adults: $t(64.60) = 1.56, p > .250, d = 0.38$; teens versus young adults: $t(71.54) = 2.14, p = .140, d = 0.49$.

We also examined effects of age as a continuous variable, fitting both linear and quadratic functions to performance with each cue type in the neutral-state blocks. Linear and quadratic functions significantly fit the data for all three cue types—fearful cues, linear: adjusted $R^2 = .12, p < .001, F(1, 108) = 15.68$; fearful cues, quadratic: adjusted $R^2 = .13, p < .001, F(2, 107) = 9.23$; happy cues, linear: adjusted $R^2 = .14, p < .001, F(1, 108) = 18.33$; happy cues, quadratic: adjusted $R^2 = .13, p < .001, F(2, 107) = 9.25$; calm cues, linear: adjusted $R^2 = .10, p < .001, F(1, 108) = 13.6$; calm cues, quadratic: adjusted $R^2 = .095, p = .002, F(2, 107) = 6.75$. However, the fit of the quadratic function completely overlapped with the fit of the linear function for the calm cues (see Fig. 4 for performance in response to calm cues in all three sustained emotional states and in response to fearful and happy cues in the neutral-state blocks).

Main effects of age for each emotional state. There were significant main effects of age group on performance in response to calm cues when participants were in emotionally arousing states of threat, $F(2, 98) = 17.57, p < .001, \eta_p^2 = .24$ (Fig. 5a), and of excitement, $F(2, 98) = 8.65, p < .001, \eta_p^2 = .13$ (Fig. S1b). Post hoc t tests revealed that, although young adults performed better than teens, teens and young adults both showed diminished performance relative to adults under the state of threat—teens versus adults: $t(60.47) = 5.40, p < .001, d = 1.24$; young adults versus adults: $t(59.51) = 2.75, p = .014, d = 0.66$; teens versus young adults: $t(73.25) = 3.25, p = .014, d = 0.64$. In contrast, only teens and adults' performance differed significantly under the state of excitement—teens versus adults: $t(58.52) = 4.28, p < .001, d = 0.98$; young adults versus adults: $t(66.95) = 2.03, p = .087, d = 0.49$; teens versus young adults: $t(61.39) = 1.83, p = .213, d = 0.42$.

We also examined effects of age as a continuous variable, fitting both linear and quadratic functions to performance in response to the calm cues in each emotional-state

condition. We found that both linear and quadratic functions significantly fit the data in both the threat condition—linear function: adjusted $R^2 = .23, p < .001, F(1, 108) = 34.08$; quadratic function: adjusted $R^2 = .24, p < .001, F(2, 107) = 17.78$ —and the excitement condition—linear function: adjusted $R^2 = .13, p < .001, F(1, 108) = 17.09$; quadratic function: adjusted $R^2 = .13, p < .001, F(2, 107) = 9.21$ (see Fig. 4).

Imaging results

To probe the neural correlates of the observed behavioral effects, we examined blood-oxygen-level-dependent (BOLD) activity in the age-group contrasts specified in the group LME models for each emotional cue and state. Specifically, general linear tests comparing brain activity (relative to implicit baseline, i.e., overall baseline brain activity) of teens and young adults with that of adults were specified for the relevant conditions. We also examined BOLD activity using group LME models in which age was modeled continuously. For these models, in the absence of any specific general linear tests, we examined activation maps showing the interactions of age with type of emotional cue and emotional-state condition.

Effects of emotional cues as a function of age. Two clusters survived whole-brain correction in the age-group analyses of response to fearful cues, showing less activity in teens and young adults than in adults: right dlPFC ($x = -41.5, y = -9.5, z = 36.5, 47$ voxels; $Z = -4.66, p < .02$, corrected; Figs. 3b and 3c) and right thalamus ($x = -20.5, y = 23.5, z = 6.5, 57$ voxels; $Z = -3.88, p < .02$, corrected). MR signal change in dlPFC was positively correlated with behavioral performance (in the neutral condition) responding to fearful cues across age, $r(108) = .203, p = .033$ (Fig. 3d), but this correlation did not remain significant when we controlled for age, $r(107) = .087, p = .365$. A general linear test corresponding to the behavioral result was performed for happy cues in the group-level emotional-cue model to compare brain activity (relative to implicit baseline) of teens with that of adults and young adults in response to happy cues. A single cluster in the right inferior frontal gyrus ($x = -32.5, y = -24.5, z = -11.5, 30$ voxels; $Z = -4.18, p < .02$, corrected) survived whole-brain correction, showing more activity in teens than in both young adults and adults (see Imaging Results and Figs. S2b and S2c in the Supplemental Material). No clusters survived whole-brain correction in the analyses of activation in response to calm cues, and no interactions of emotional cue with age group were observed.

Four clusters in the dorsal anterior cingulate cortex (dACC), parietal cortex, and right and left cerebellum survived whole-brain correction when we examined the

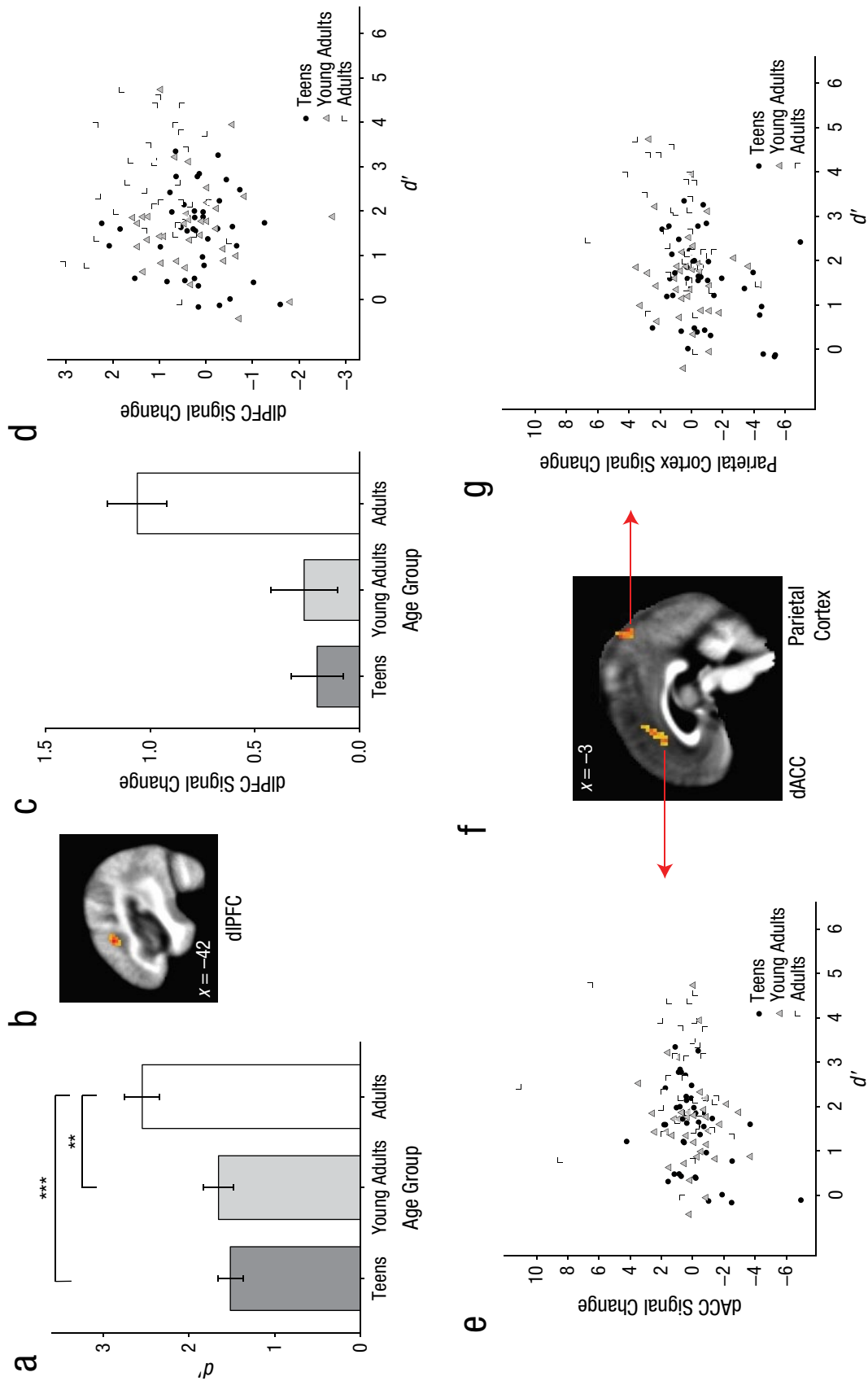


Fig. 3. Results for the fearful cues. The graph in (a) shows mean performance in response to the brief fearful cues in the neutral-state condition, as indexed by d' , for each of the age groups. The brain image in (b) shows the location of the region in the dorsolateral prefrontal cortex (dIPFC) for which signal-change results are presented. The graphs in (c) and (d) show mean signal change in the dIPFC in response to the fearful cues for each age group and as a function of d' in the neutral-state condition (separately for each age group), respectively. The brain image in (f) shows the location of the regions in the dorsal anterior cingulate cortex (dACC) and parietal cortex for which mean signal change in response to the fearful cues is graphed as a function of d' in the neutral-state condition, separately for each age group, in (e) and (g). Error bars represent ± 1 SE. Asterisks indicate significant differences (** $p < .01$, *** $p < .001$).

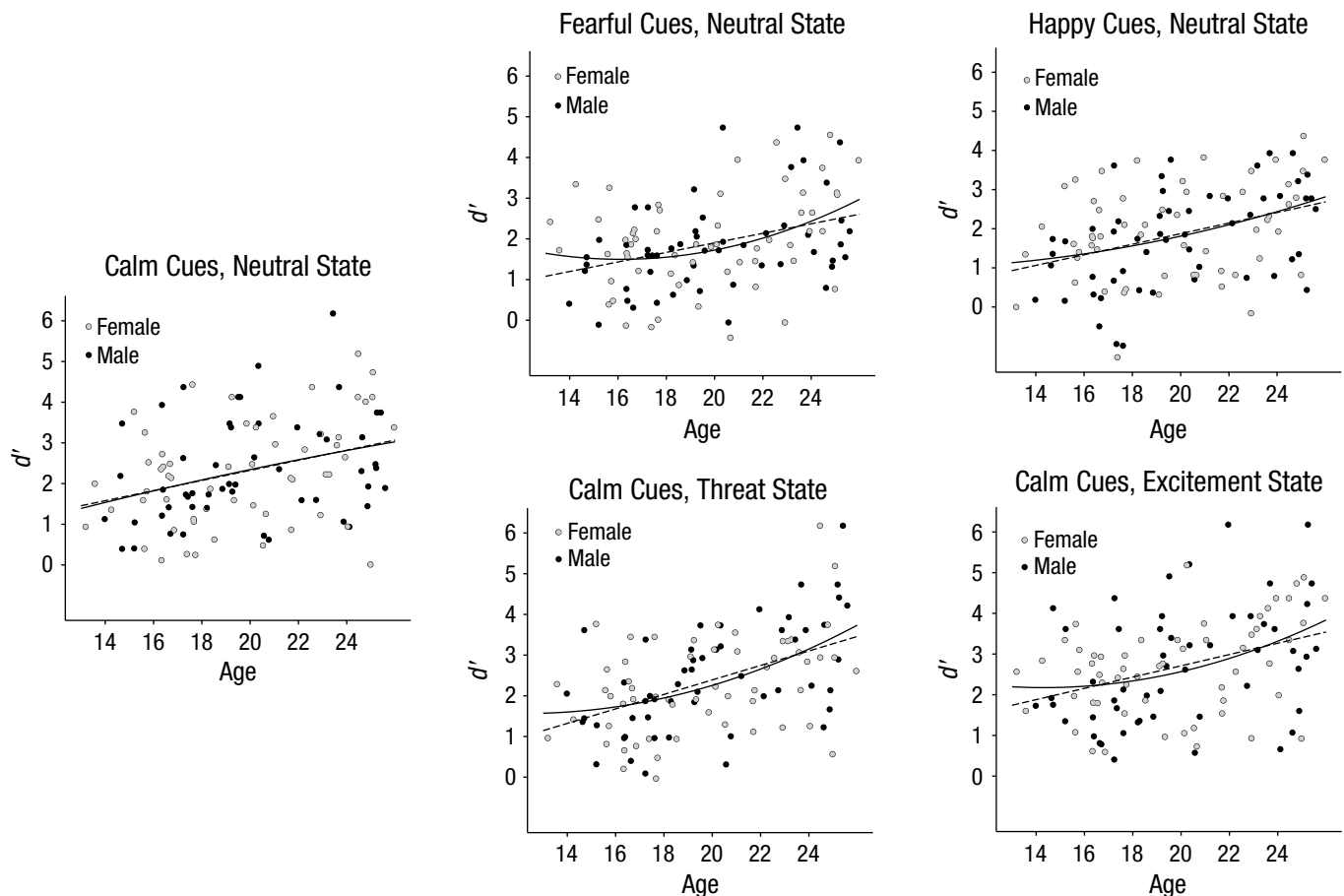


Fig. 4. Scatterplots showing male and female participants' performance, as indexed by d' , as a function of age, along with linear and quadratic functions fitted to the data. Results are shown for each kind of emotional cue in the neutral-state condition, as well as for calm cues in the threat and excitement conditions.

interaction of age as a continuous variable with type of emotional cue (see Table S1 in the Supplemental Material). In the two largest regions, the dACC and the parietal cortex (Fig. 3f), activity in response to fearful cues was positively correlated with age, $r(108) = .196, p = .040$, and $r(108) = .32, p < .001$, respectively. MR signal change in response to happy cues was negatively correlated with age in the dACC, $r(108) = -.189, p = .048$, but not in the parietal cortex, $r(108) = -.164, p = .087$. Activity in response to calm cues was not significantly correlated with age in either of these regions, $r(108) = -.088, p = .363$, and $r(108) = -.079, p = .412$, respectively.

We examined whether changes in dACC and parietal activity in response to fearful cues were correlated with behavioral performance. In both of these regions, MR signal change in response to fearful cues was positively correlated with d' in the neutral-state condition, $r(108) = .222, p = .020$, and $r(108) = .359, p < .001$, respectively (Figs. 3e and 3g). Similar patterns were observed even when we controlled for age, $r(107) = .166, p = .081$, and $r(107) = .277, p = .002$. These results suggest that these

regions are important for behavioral performance of the task.

Effects of emotional states as a function of age.

Although no activations survived whole-brain correction for the contrast of age groups in emotional states, a single cluster in the ventromedial PFC (vmPFC; $x = 3.5, y = -33.5, z = -17.5$, 13 voxels; $Z = 3.58, p < .05$, PFC corrected; Fig. 5b) survived PFC volume correction for responses in the state of threat. Teens' and young adults' BOLD activity in the vmPFC during the threat condition showed a sustained increase relative to adults' (Fig. 5c). MR signal change in this region in the threat condition was negatively correlated with behavioral performance (in response to the calm cues) in the threat condition, $r(108) = -.308, p = .001$ (Fig. 5d), and this correlation remained significant even when we controlled for age, $r(107) = -.215, p = .023$, and when we removed the one extreme outlier, $r(107) = -.253, p = .008$. No interactions of emotional state with age group were observed. In analyses for the excitement

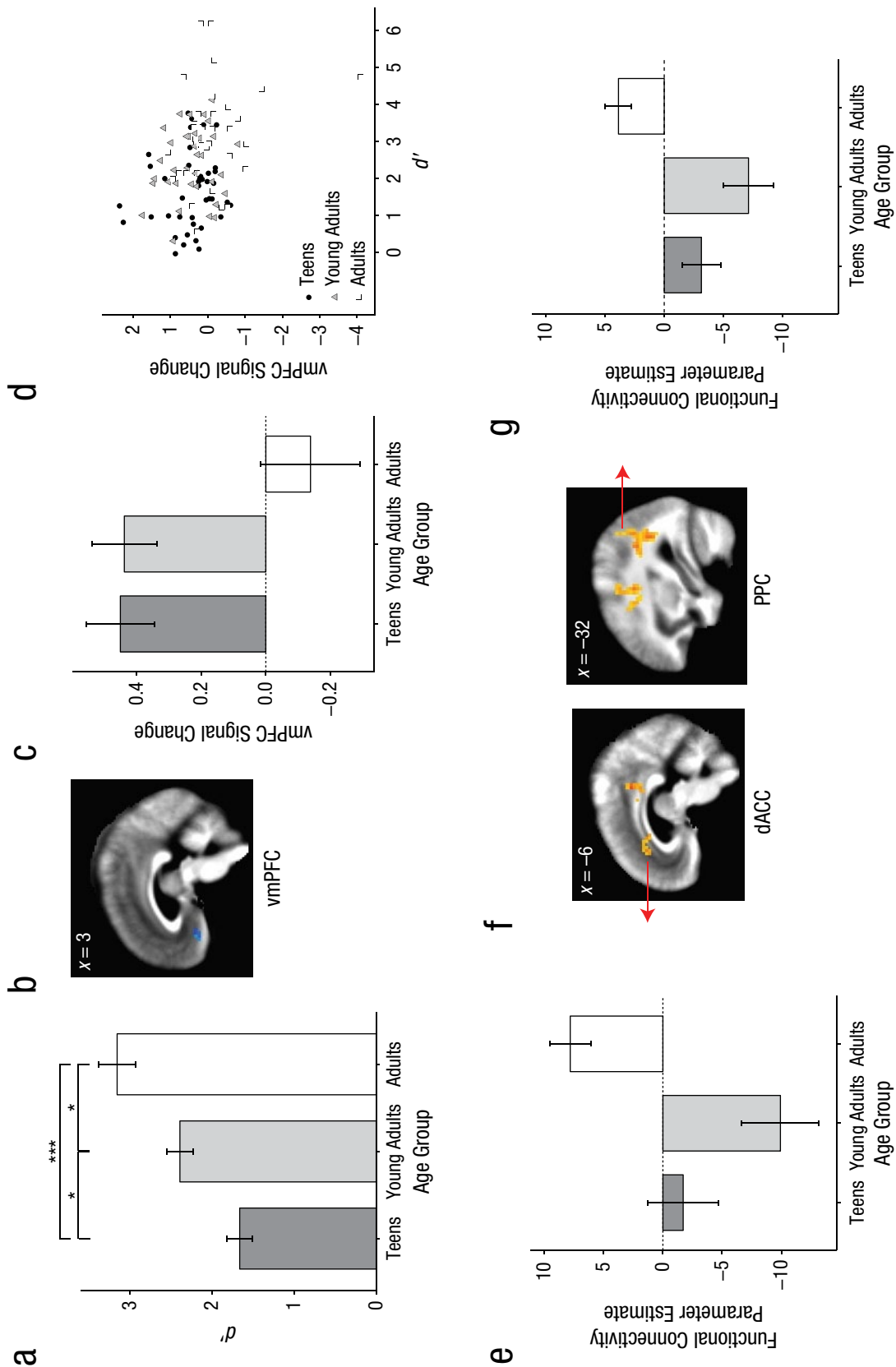


Fig. 5. Results for the sustained-threat condition. The graph in (a) shows mean performance on calm-cue trials, as indexed by d' , for each of the age groups under the sustained state of threat. The brain image in (b) shows the location of the region in ventromedial prefrontal cortex (vmPFC) for which signal-change results are presented. The graphs in (c) and (d) show mean signal change in the vmPFC in the threat condition for each age group and as a function of d' on calm-cue trials (separately for each age group), respectively. The brain images in (f) show the location of the regions in the dorsal anterior cingulate cortex (dACC) and posterior parietal cortex (PPC) for which functional coupling with the vmPFC is graphed for the three age groups in (e) and (g). The asterisk indicates a significant difference ($*p < .05$, $***p < .001$).

and neutral-state conditions, no clusters survived whole-brain or PFC volume correction.

A single cluster in the parietal cortex ($x = -2.5$, $y = 68.5$, $z = 54.5$, 29 voxels; $F = 11.90$, $p < .05$, corrected) survived whole-brain correction when we examined the interaction of emotional state and age as a continuous variable (see Fig. S3 in the Supplemental Material). MR signal change in this region showed similar positive associations with age in the threat and excitement conditions, $r(108) = .181$, $p = .058$, and $r(108) = .305$, $p = .001$, respectively, but not in the neutral-state condition, $r(108) = .151$, $p = .116$. Because BOLD activity in the threat and excitement conditions showed positive correlations with age, we collapsed the MR signal across these conditions and tested for associations between activation in this region and behavioral performance (in response to the calm cues) in these conditions. MR signal change was positively correlated with behavioral performance, $r(108) = .209$, $p = .028$ (see Fig. S3), but this correlation did not hold when we controlled for age, $r(107) = .11$, $p = .251$.

Seed-based functional connectivity with prefrontal regions in the three age groups. Whole-brain gPPI analyses were performed using the dlPFC and vmPFC regions as seeds. Nine clusters of voxels showing significantly less functional coupling with the vmPFC in teens and young adults than in adults across the threat condition were observed (see Table S2 in the Supplemental Material). Areas showing this pattern included the dACC (Figs. 5e and 5f) and posterior parietal cortex (Figs. 5f and 5g). No significant clusters were observed in the age-group contrast for fearful cues using the dlPFC seed.

Discussion

Our findings suggest a developmental shift in cognitive control in negative emotional situations during young adulthood that is paralleled by dynamic developmental changes in prefrontal circuitry. Specifically, young adults showed diminished cognitive control under both brief and prolonged negative emotional arousal relative to slightly older adults, a pattern not observed in neutral or positive situations. This behavioral pattern was paralleled by altered recruitment of lateral and medial prefrontal circuitry in young adults and adolescents, a finding consistent with structural imaging studies showing protracted development of prefrontal circuitry (Gogtay et al., 2004; Sowell et al., 2004).

Teens' and young adults' diminished cognitive control in response to negative cues was paralleled by their decreased activity in cognitive-control circuitry. When presented with fearful cues, teens and young adults showed less activity than older adults in dlPFC, a region implicated in affective and cognitive regulation (Silvers

et al., 2015; Vincent et al., 2008), and in the dACC and parietal cortex. The dlPFC and parietal cortex have reciprocal projections with the dACC, and all three regions have been implicated in cognitive control and are coactivated during cognitive-control tasks (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Platt & Glimcher, 1999; Roy, Shohamy, & Wager, 2012). Further, activity in these regions not only was consistently lower in younger participants, but also was positively correlated with task performance. Together, these findings are consistent with the hypothesis that lower levels of activity within this circuitry in younger individuals reflects diminished cognitive control in the face of negative emotional cues that signal potential threat in the environment.

Although under sustained states of negative emotional arousal (threat), young adults performed better than teens, they performed worse than adults. Teens' and young adults' diminished performance relative to adults in the threat condition was paralleled by increased activity in the vmPFC. This region has been implicated in various processes, including self-referential thought and integration of affective information, and is a proposed hub for affective computations and regulation (Roy et al., 2012). Increased sustained recruitment of the vmPFC under threat in teens and young adults may suggest heightened sensitivity to potential threat, leading to emotional interference and diminished cognitive control. This interpretation is supported in part by our finding of decreased functional coupling of the vmPFC with cognitive-control circuitry of the dACC and posterior parietal cortex in the threat condition among teens and young adults relative to adults. The negative functional connectivity between cognitive and emotional brain regions during this emotional state may underlie the poorer performance of the younger age groups.

Taken together, these findings suggest that young adulthood is a time when cognitive control is still vulnerable to negative emotional influences, in part as a result of continued development of lateral and medial prefrontal circuitry. This temporal developmental shift in cognitive-control capacity in negatively arousing situations relative to neutral (or positive) situations is consistent with the classic notion of developmental cascades in brain and behavior (Casey, Galván, & Somerville, 2015; Masten & Cicchetti, 2010). Accordingly, dynamic brain changes during late adolescence may enhance receptivity to or processing of emotional inputs in order to facilitate meeting changing socioemotional pressures that accompany adulthood (Casey et al., 2015).

Our findings have potential implications for informing age-related legal and social policies. Developmental findings based largely on teens have been referenced in several U.S. Supreme Court decisions regarding treatment of juvenile offenders over the past decade, with the Court

acknowledging immature cognitive functioning in juveniles as a mitigating factor in judgments of criminal culpability (Cohen & Casey, 2014; Scott, 2013; Steinberg, 2013). Scientific research has demonstrated that adolescents show heightened sensitivity to motivational and socioemotional information, which potentially renders them more vulnerable to poor decision making in these situations, compared with younger and older individuals (Chein et al., 2011; Cohen-Gilbert & Thomas, 2013; Dreyfuss et al., 2014; Galvan et al., 2006; Grose-Fifer et al., 2013; Hare et al., 2008; Somerville et al., 2011; Steinberg et al., 2009). The extension of this work to young adults, who show diminished cognitive control relative to slightly older adults in negative emotional situations, may have implications for legal policy. This is not to suggest that teens and young adults should not be held accountable for their actions, but rather, the boundaries of juvenile-court jurisdiction, criminal-court sentencing, and punishment may be informed by developmental considerations (Bonnie & Scott, 2013).

The implications of our findings must be considered within the limitations of the study. First, behaviors were measured within a controlled research setting. Although the emotionally arousing conditions may be relevant to emotional arousal in the real world, they were limited to experimentally manipulated emotional conditions that did not capture the complex real-world situations in which individuals typically make decisions. Second, the sample, although community based and representative of the racial and ethnic distribution in Los Angeles and New York City, was relatively small, with 110 participants 13 to 25 years of age; replication of these findings is warranted.

Prior research examining motivational and social influences on cognitive capacities in young adults as a unique age group has produced mixed results (Chein et al., 2011; Cohen-Gilbert et al., 2014; Silva et al., 2015; Steinberg et al., 2009). The present and previous findings suggest that teens' and young adults' cognitive capacities may be affected differently by various situations. For instance, although negative emotional arousal may diminish cognitive control in both teens and young adults, positive emotional arousal and the presence of peers may not influence young adults as strongly as teens (Chein et al., 2011). Identifying specific situations in which the behavior of young adults may differ from that of slightly older adults will be important in informing potential changes to existing policies and laws. Moreover, further examination of changes in brain structure, activity, and connectivity during this developmental period may provide clearer insights into why and when researchers may or may not observe group-level behavioral changes in young adults.

We examined the influence of emotional arousal on cognitive control from early adolescence through the mid 20s and found that negative emotional arousal, brief or

prolonged, affects this capacity in individuals ages 18 to 21 more than in older individuals. Few studies have examined cognitive capacities under emotional influences, and fewer still have taken this approach to study developmental differences in capacities of potential relevance to legal and social policies. Our findings provide support for consideration of contextual influences on behavior and brain function, such as the influence of emotional arousal, when evaluating appropriate age cut-offs for such policies. Although the data in this study do not speak directly to these policy issues, they may inform dialogues about the age of adulthood in a variety of social and policy contexts.

Author Contributions

B. J. Casey, A. Galván, and L. Steinberg developed the study concept. A. O. Cohen, K. Breiner, A. S. Heller, M. R. Silverman, and D. V. Dellarco collected the data and performed data analysis under the supervision of B. J. Casey and A. Galván. All authors contributed to interpretation of the data. A. O. Cohen and B. J. Casey drafted the manuscript, and all authors provided critical revisions and approved the final version of the manuscript for submission.

Acknowledgments

We gratefully acknowledge the assistance of Doug Ballon, Kristine Caudle, Jonathan Dyke, Hillary Raab, Ahrareh Rahdar, and the Citigroup Biomedical Imaging Center at Weill Cornell Medical College. We thank the anonymous reviewers for their constructive feedback.

Declaration of Conflicting Interests

B. J. Casey and L. Steinberg serve as paid consultants to the John D. and Catherine T. MacArthur Foundation. The authors declared that they have no other conflicts of interest with respect to their authorship or the publication of this article.

Funding

This work was supported by a National Science Foundation Graduate Research Fellowship (to A. O. Cohen). Preparation of this article was supported by a grant from the John D. and Catherine T. MacArthur Foundation to Vanderbilt University. Its contents reflect the views of the authors, and do not necessarily represent the official views of either the John D. and Catherine T. MacArthur Foundation or the MacArthur Foundation Research Network on Law and Neuroscience (www.lawneuro.org).

Supplemental Material

Additional supporting information can be found at <http://pss.sagepub.com/content/by/supplemental-data>

Open Practices

The data reported here are part of an ongoing multisite project. An optimized version of the Cognitive Control Under Emotion

(CCUE) task (both behavioral and jittered for use in the scanner) will soon be made available at https://www.sacklerinstitute.org/cornell/assays_and_tools/. The complete Open Practices Disclosure for this article can be found at <http://pss.sagepub.com/content/by/supplemental-data>.

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