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Social relevance modulates multivariate neural representations of threat generalization in children and adults

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Abstract

Few studies have examined threat generalization across development and no developmental studies have compared the generalization of social versus nonsocial threat, making it difficult to identify contextual factors that contribute to threat learning across development. The present study assessed youth and adults' multivoxel neural representations of social versus nonsocial threat stimuli. Twenty adults ($M_{age} = 25.7 \pm 4.9$) and 16 youth ($M_{age} = 14.1 \pm 1.7$) completed two conditioning and extinction recall paradigms: one social and one nonsocial paradigm. Three weeks after conditioning, participants underwent a functional magnetic resonance imaging extinction recall task that presented the extinguished threat cue (CS+), a safety cue (CS−), and generalization stimuli (GS) consisting of CS−/CS+ blends. Across age groups, neural activity patterns and self-reported fear and memory ratings followed a linear generalization gradient for social threat stimuli and a quadratic generalization gradient for nonsocial threat stimuli, indicating enhanced threat/safety discrimination for social relative to nonsocial threat stimuli. The amygdala and ventromedial prefrontal cortex displayed the greatest neural pattern differentiation between the CS+ and GS/CS−, reinforcing their role in threat learning and extinction recall. Contrary to predictions, age did not influence threat representations. These findings highlight the importance of the social relevance of threat on generalization across development.

1 | INTRODUCTION

Threat generalization is an adaptive associative learning mechanism whereby threat responses extend to a range of stimuli that resemble a past threat but have never themselves predicted an aversive experience (Dunsmoor & LaBar, 2013; Lissek et al., 2008). We may extrapolate from an angry encounter with one police officer to subsequent encounters with other officers, for example. The generalization of extinguished threat cues tests the retrieval of two related but incompatible memories: a threat memory and a safety memory. The ability to make precise threat/safety discrimination during extinction recall increases with age (Glenn et al., 2012) into adolescence (Lau et al., 2011). However, few studies have examined the neural substrates underlying the generalization of learned threat in youth, making it difficult to identify developmental mechanisms. We also know little about whether the shape of generalization gradients differs with contextual or stimulus features, especially among youth. To address these questions, we implemented functional magnetic resonance imaging (fMRI) in conjunction with multivoxel pattern analytical techniques to compare youth and adults' neural threat representations across social versus nonsocial threat cues during extinction recall. The examination of normative developmental threat and extinction learning processes across social and nonsocial threat stimuli may thus improve understanding of mechanisms underlying context-dependent responses in non-normative populations with impairments in extinction recall, like individuals with anxiety disorders.

Generalization enables humans and animals to respond adaptively to new threats based on perceptual or categorical features of a previously learned threat. Pavlovian conditioning and extinction paradigms have proven to be useful for experimentally testing threat learning and its generalization. In differential conditioning, a neutral stimulus (conditioned stimulus, CS+) is paired with an aversive, unconditioned stimulus (UCS) while a second, unreinforced stimulus (CS−) acts as a safety cue (Dunsmoor et al., 2009; Glenn et al., 2020; Lissek et al., 2008; Michalska et al., 2016, 2019; Shechner et al., 2018). During extinction, the CS+ is presented in the absence of the aversive UCS, usually resulting in a new CS+– safety association. Extinction generates a secondary memory that can inhibit retrieval and expression of the original fear memory and creates competition between the original threat conditioning memory and the extinction memory. Participants' recall and generalization of extinguished threat can be tested days or weeks following conditioning and extinction. During extinction recall, individuals may be presented with the extinguished CS and novel generalization stimuli (GS), which consist of CS−/CS+ blends. Extinction learning can influence responses to other stimuli via the generalization of extinguished threat cues (Vervliet et al., 2004). By testing the extent to which participants' conditioned threat response is elicited by perceptually similar stimuli that have not previously predicted the UCS, we can quantify the retention and generalization of extinction learning over time.

Several studies have observed developmental changes in extinction recall capacity (Britton et al., 2013; Lau et al., 2011; Michalska et al., 2016) and it is thought that extinction learning is impaired in youth with anxiety disorders (Britton et al., 2013; Glenn et al., 2020; Gold et al., 2020; Michalska et al., 2019; Shechner et al., 2018). Because several anxiety disorders and temperamental traits are linked with selective, threat-specific biases (LoBue & Pérez-Edgar, 2014; Ohman et al., 2001), extinction learning and generalization among nonclinical populations may also be context dependent. Furthermore, as many anxiety treatments depend on the generalization of safety cues to real-world scenarios, it is important to understand how different aspects of threat stimuli influence the generalization of extinction learning. The examination of normative developmental extinction learning processes across social and nonsocial contexts may thus improve understanding of potential mechanisms underlying associations between context-dependent responses and anxiety disorders. More generally, probing whether multivoxel generalization gradients narrow or broaden depending on the type of stimuli encountered can contribute to a nascent evidence base for extinction recall in youth and adults. Work with infants and children suggests there may be different developmental mechanisms for attentional biases to social versus nonsocial threats (LoBue et al., 2017; Shechner et al., 2017). For instance, youth displayed greater attention to social threats relative to adults but no developmental differences emerged for nonsocial threats (Shechner et al., 2017). If the ability to discriminate among similar features is more important in social contexts than nonsocial ones, or if developmental differences emerge in select contexts, this may provide more rich information about the nature of generalization during extinction recall tasks (Holt et al., 2014).

Several brain regions are reliably engaged in the acquisition, extinction, and generalization of conditioned threat responses, including the amygdala, anterior insular cortex (AIC), dorsal anterior cingulate cortex (dACC), and subregions of the prefrontal cortex (PFC; Antoniadis et al., 2009; Davis, 1997; Mechias et al., 2010; Phelps et al., 2004; Quirk & Beer, 2006; Schiller etal., 2008). Among healthy adults, as stimuli show increasing perceptual similarity to the CS+, activation in the amygdala, insula, and dorsomedial PFC (dmPFC) increases, whereas activation in the ventromedial PFC (vmPFC) decreases (Dunsmoor et al., 2011; Lissek et al., 2014; Schiller et al., 2008). Although some prior work has examined neural sources of threat generalization in both adults (Dunsmoor et al., 2011; Lissek et al., 2014; Onat & Büchel, 2015) and youth (Glenn et al., 2020; Michalska et al., 2019), direct comparisons between groups remain rare (see Gold et al., 2020 for a recent example). Given marked changes in threat-relevant neurocircuitry across age, modeling developmental aspects of threat generalization is essential to advance knowledge of its underlying mechanisms. Animal and human models suggest that, although threat learning is established early in development (Kim & Richardson, 2010; Rudy, 1993; Richardson & Hunt, 2010; Watson & Rayner, 1920), complex aspects of threat learning like generalization show developmental change (Glenn et al., 2012; Kim & Richardson, 2010; Rudy, 1993).

Behavioral research with children and adolescents suggests that the ability to differentiate between threatening and ambiguous or safe stimuli increases with age during middle childhood, from ages 8 to 12 (Glenn et al., 2012; Michalska et al., 2016; Schiele et al., 2016), with adolescents demonstrating poorer threat/safety discrimination than adults and distinctive neural responses to threat stimuli (Lau et al., 2011). Emerging

studies examining neural differences in threat learning between adults and adolescents have observed differences in the PFC that suggest adults may show greater PFC engagement in making threat/safety discriminations. Lau et al. (2011) found that adults but not adolescents displayed an association between dorsolateral PFC engagement and fear ratings during threat conditioning. In contrast, during the recall of learned threat, adolescents exhibited greater differentiation between threat and safety cues in amygdala and hippocampus, potentially due to a reliance on early-maturing subcortical structures. In addition, adults and adolescents display differential PFC engagement when processing extinguished threat cues, specifically in the vmPFC (Britton et al., 2013). Although limited research examines age differences in neural function during threat generalization directly, empirical evidence in anxious populations suggests that youth with anxiety exhibit alterations in functional connectivity of neural regions involved in extinction recall and that these anxiety-related alterations may be developmental in nature, highlighting the value of developmental approaches (Gold et al., 2020). Importantly, all these studies tested conditioning of face stimuli, which are inherently social. To date, no studies have directly compared neurodevelopmental differences in generalization of nonsocial threat stimuli across adolescents and adults. More research is needed to disentangle age-related changes in cortical and subcortical function during threat generalization, as well as how such changes might interact with the type of threat stimulus (i.e., social versus nonsocial).

The precision with which one processes similar-appearing stimuli may differ for social and nonsocial threats. For example, avoiding all people who resemble a former attacker and abstaining from potentially favorable interactions could bring greater personal cost than avoiding a broad category of objects (e.g., weapons) or nonhuman animals (e.g., bears). In line with this possibility, converging evidence suggests that social stimuli in general (Pitcher & Ungerleider, 2021), and faces in particular (Farah et al., 1998; Gauthier et al., 2003; Kanwisher et al., 1997; Pitcher & Ungerleider, 2021; Tsao et al., 2008), are processed in a specialized fashion by the brain. It is conceivable that unique features of social perception influence the generalization of threat responses across similar faces in ways that are distinct from the generalization of threat responses across similar objects. However, few adult studies and no developmental studies have directly compared threat generalization between social and nonsocial threat stimuli. Holt and colleagues (2014) compared adults' threat generalization gradients to faces and nonsocial "blobs" and found greater generalization for face stimuli when engaged in explicit memory, compared with nonsocial threat stimuli. However, physiological differences did not emerge across stimulus types and neural activity was not measured, so the neurobiological mechanisms that underlie differences in the subjective generalization of social versus nonsocial threat stimuli remain unknown. Additionally, the nonsocial "blobs" in this study were not members of a recognizable object category and did not pose any real-life threat. As threat-relevance influences threat conditioning (Öhman & Dimberg, 1978), it may be important that the social and nonsocial threat stimuli being compared are similar in threat relevance. The present study employed well-validated, child-friendly social and nonsocial conditioning paradigms that featured CS–UCS pairings that co-occur in dangerous real-life situations: a woman's neutral face predicting a fearful expression and scream and a colored bell (blue, yellow) predicting a red bell and an aversive alarm sound. To our knowledge, ours is the

first developmental study to examine neural effects of threat generalization to social and nonsocial threat stimuli during extinction recall.

We implemented representational similarity analysis (RSA) in conjunction with fMRI to characterize neural representations of social and nonsocial threat stimuli during extinction recall. Whereas univariate methods compare a region's average signal strength between conditions, RSA shifts the focus from mean activation differences to the information contained in distributed multivoxel patterns of brain activity (Kriegeskorte et al., 2008). With this analysis, we assessed how multivoxel neural representations of threat are influenced by social relevance among youth and adults. In our recent study in youth (Glenn et al., 2020), we found that neural patterns in vmPFC were best able to discriminate generalization accuracy, emphasizing the important role of this region in extinction recall and the utility of this method. In the current study, we leveraged our prior approach to (1) compare neural pattern representations of threat generalization gradients for faces and objects; and (2) test developmental differences in neural pattern similarity between adolescents and adults. First, because extensive prior evidence indicates that humans detect and distinguish between faces very rapidly due to experience (Bukach et al., 2006; Tarr & Gauthier, 2000), we predicted that participants would demonstrate an increased ability to perceptually distinguish between threatening and ambiguous social stimuli compared with nonsocial threat stimuli. We hypothesized that this would be accompanied by greater neural pattern similarity between threatening and ambiguous nonsocial threat stimuli, indicating greater threat generalization, compared with social threat stimuli. Because none of the included regions selectively respond to social or nonsocial threat stimuli (Adolphs et al., 1999; Birbaumer et al., 2005; Büchel et al., 1999; Isenberg et al., 1999), we hypothesized that we would see this effect across all regions of interest (ROIs). Second, as behavioral (Glenn et al., 2012; Klein et al., 2020; Lau et al., 2011; Michalska et al., 2016) and neural (Pattwell et al., 2012) evidence suggests that threat/safety discrimination increases with age, we predicted that youth would display increased threat generalization across both social and nonsocial threat stimuli compared with adults. Because all the regions included in our analyses show graded responses during generalization and are thought to act as a "fear circuit," we remained agnostic about differences in activation across ROIs (Dunsmoor et al., 2011; Lissek et al., 2014; Schiller et al., 2008).

2 | METHODS

2.1 | Participants

Child and adult participants were recruited through mailings and advertisements from the Washington, DC, metropolitan area. Written informed consent from adult participants and parents and written assent from youth participants were obtained. Participants were eligible to participate in the present study if they were medication free, had an IQ > 70, reported no contraindications for neuroimaging, were not colorblind, and were free from psychopathology requiring immediate treatment. The study consisted of two conditioning and extinction recall paradigms: a social threat paradigm and a nonsocial threat paradigm (see below).

As part of a larger study, 64 adults and 52 youth completed both social and nonsocial conditioning and extinction procedures. No adults aborted the task during conditioning procedures but several were dropped from the study due to technical issues ($n = 2$) and having a sibling in the study ($n = 1$). Children who aborted during conditioning ($n = 2$) and those that had siblings ($n = 6$) in the study were not eligible for the present study. A subset of these participants were invited to participate in extinction recall procedures, with the intended sample size of 20 participants from each age group. Participants who only completed one scan, social extinction recall ($n_{Adult} = 6$, $n_{Youth} = 7$) or nonsocial extinction recall ($n_{Adult} = 6$, $n_{Youth} = 6$) were not included in the present study. Twenty adults completed both social and nonsocial extinction recall procedures. No adults were excluded due to motion or experimenter error. Eighteen children participated in both social and nonsocial extinction recall procedures. Two of these children were excluded because they aborted the scan ($n = 1$) or due to experimenter error ($n = 1$), leaving 16 participants with complete data. This resulted in a final sample of 16 youth ($M_{age} = 14.1 \pm 1.7$, range $= 10$–17) and 20 adults ($M_{age} = 25.7 \pm 4.9$, range $= 20$–43) who contributed data. See Table 1 for demographic information. Study procedures were approved by the National Institute of Mental Health Institutional Review Board. A subset of the conditioning data from this sample of healthy controls was combined with conditioning data from anxious participants who were not included in this sample and reported by Shechner et al. (2015). The prior report did not examine fMRI data during extinction recall; thus, all brain imaging analyses presented in this paper are novel.

2.2 | Procedure

Participants completed two conditioning and extinction recall paradigms: a social threat paradigm (Britton et al., 2013) and a nonsocial threat paradigm (Shechner et al., 2015). Briefly, the social "screaming lady" paradigm paired a woman's face with an aversive scream and the nonsocial "bells" paradigm paired a colored bell with an aversive alarm. Thus, even though the paradigms differ on the social versus nonsocial dimension, both pair sets of pictorial and auditory stimuli that co-occur in real-life dangerous situations. All participants completed both paradigms and the order of the two procedures (social threat or nonsocial threat) was randomly determined. Each paradigm consisted of a conditioning component in the laboratory and an in-scanner extinction recall component, spaced approximately 3 weeks apart. Participants completed each component on a separate visit, totaling four visits per participant.

2.3 | Measures

2.3.1 | Threat conditioning

__Nonsocial threat: bells paradigm:__ We employed an uninstructed threat learning task that has successfully produced threat conditioning while maintaining an acceptable dropout rate in youth and adults (Ginat-Frolich et al., 2019; Glenn et al., 2020; Michalska et al., 2016, 2019; Shechner et al., 2015). A schematic representation of the nonsocial threat conditioning task is provided in Figure 1(a). The task consisted of three phases: preacquisition, acquisition, and extinction (Michalska et al., 2016, 2019; Shechner et al., 2015). During preacquisition, participants viewed the nonsocial conditioned stimuli (CS+

and CS−), blue and yellow cartoon bells. During baseline, or preacquisition, each CS was presented four times to allow participants to habituate to the stimuli. During acquisition, the CS+ predicted the UCS, a 1 s image of a red bell that coterminated with an aversive 95 dB alarm sound. Each CS was presented 10 times and the CS+ were followed by the UCS with an 80% reinforcement schedule. Participants were told that they could learn to predict when the UCS would occur but they were not explicitly told about the contingency. During threat extinction, each CS was presented eight times in the absence of the UCS. In all phases, the CS were presented for 7–8 s, followed by an interstimulus interval (ISI) of a gray screen presented for 8–21 s ($M = 15$ s). The CS+ and CS− assignment was pseudorandomized (two different orders counterbalanced across participants). Skin conductance response (SCR) to the CS was collected continuously using PsyLab psychophysiological recording system (PsyLab SAM System Contact Precision Instruments, London) using a sampling rate of 1000 Hz. Following each of the three phases, participants also rated the CS+ and CS− on several dimensions using a 10-point Likert scale (1 = none to 10 = extreme). Specifically, after preacquisition, participants rated how much they liked and feared each CS, as well as how pleasant and unpleasant the CS were. After conditioning and extinction, participants rated how much they liked each CS, how anxious they were, and how unpleasant each CS was.

Social threat: screaming lady paradigm: The social threat conditioning task followed the same conditioning procedures as the nonsocial threat conditioning task but used distinct audio and visual stimuli. The CS+ and CS− were black and white photos of two White female faces with neutral expressions (Tottenham et al., 2009). The CS+ predicted the UCS, a 1s presentation of a fearful face coterminating with an aversive 95 dB scream (Figure 1(b)).

2.3.2 | Extinction recall

Nonsocial threat: bells paradigm: Participants returned to complete an in-scanner extinction recall task approximately 3 weeks ($M = 22.22$ days ± 9.26) following threat conditioning. The time between conditioning and extinction recall did not significantly differ across tasks, $t(35) = 1.16$, $p = .255$. Participants viewed the CS+, CS−, and four GS that were morphed blends of the CS (GS20 [20% CS+], GS40 [40% CS+], GS60 [60% CS+], and GS80 [80% CS+]; Figure 2(a)). The task consisted of two runs, each with six blocks of 12 trials each. At the start of each block, participants were instructed to answer one of two questions: (1) How afraid are you of this bell now? (threat appraisal); (2) How likely was the bell to ring in the past? (explicit memory). Next, stimuli, task instructions, and response scales ranging from 0 to 6 were presented simultaneously for 4000 ms, followed by a 2000–10,000 ms jittered ISI. Participants viewed 12 presentations of each stimulus for each question (threat appraisal, explicit memory), totaling 144 trials. The task was programmed in E-prime (PST Inc., Pittsburgh, PA, USA). Participants viewed the screen via a mirror mounted on the head coil. A two-button box response device recorded the participants' responses. SCR was also collected from the index and middle fingers of the nondominant hand using an MRI-compatible MP-150 system (BIOPAC Systems, Inc., CA, USA) at a sampling rate of 1000 Hz. Because SCR data were not collected during the social extinction recall task and cannot be compared across tasks, SCR data are not included in this report.

Social threat: screaming lady paradigm: At a separate visit approximately 3 weeks following social threat conditioning ($M = 24.72$ days $\pm$ 10.44), participants returned to complete an fMRI extinction recall task of the social threat stimuli. Extinction recall for the social threat task replicated the nonsocial extinction recall procedure except participants viewed the CS+ and CS− and nine morphed images consisting of different blends of the CS (GS10–GS90: 10% CS+, 20% CS+, 30% CS+, 40% CS+, 50% CS+, 60% CS+, 70% CS+, 80% CS+, 90% CS+; Figure 2(b)). The task consisted of three runs, each with eight blocks of 11 trials each. As with the nonsocial threat task, at the start of each block, participants were instructed to answer one of two questions: (1) How afraid are you of this face now? (threat appraisal); (2) how likely was she to scream in the past? (explicit memory). Next, the stimuli, task instructions, and response scales (ranging from 0 to 6) were presented simultaneously for 4000 ms, followed by a 500–1500 ms jittered ISI. Participants viewed 12 presentations of each stimulus for each question (threat appraisal, explicit memory), totaling 264 trials. SCR was not collected during this task.

2.4 | Imaging data

2.4.1 | MRI data acquisition

Whole-brain neuroimaging data were collected using a 3 T General Electric 750 scanner and 32-channel head coil. For the nonsocial threat extinction recall task, 343 functional image volumes were collected during 2 runs of 23 min 9 s each. For the social threat extinction recall task, 272 functional image volumes were collected during 3 runs of 10 min 26 s each. For both social and nonsocial threat extinction recall tasks, functional image volumes with 47 contiguous interleaved axial slices (in-plane resolution 2.5 mm, 3 mm slice thickness) were obtained with a T2*-weighted echo-planar sequence (TR = 2300 ms; TE = 25 ms; flip angle = 50; field of view [FOV] = 240 mm; matrix $= 96 \times 96$). All functional data were anatomically localized and coregistered to a high-resolution T1-weighted volumetric scan of the whole brain, using a magnetization prepared gradient echo sequence (MPRAGE; TE = min full; TI = 425 ms; flip angle = 7; FOV = 256 mm; matrix $= 256 \times 256$; in plane resolution 1.0 mm).

2.4.2 | Image analysis

Individual echo-planar data were preprocessed and analyzed using Analysis of Functional NeuroImages (AFNI; Cox, 1996). Preprocessing included slicetime correction, motion correction, and smoothing with a 4 mm full-width halfmaximum kernel. All MRI data remained in individual space and did not undergo transformation to a standard template. BOLD data were scaled at the voxel-wise time series by their temporal means so that the effect estimates could be interpreted as percent signal change relative to the mean. Every TR on which motion exceeded 1 mm was censored. Participants were excluded for excessive motion if more than 20% of TRs for one stimulus were censored for motion/outliers ($n = 0$).

The preprocessed images for each participant were modeled using standard general linear model analysis. The present study focuses on examining the association between social relevance of threat and neural representation. Each stimulus was modeled as a unique regressor for each question type (threat appraisal, explicit memory), totaling to 12 regressors for extinction recall of nonsocial threat (CS−, GS20–GS80, CS+) and 22 regressors for extinction recall of social threat (CS−, GS10–GS90, CS+). Third-order Legendre

polynomials modeling baseline drift and six head motion parameters were modeled as covariates. This resulted in one whole-brain average voxel pattern for each regressor for each participant, each of which contained BOLD activity patterns for each morph (CS−, GS, CS+) averaged across trials in that condition.

2.4.3 | Region of interest selection—We examined participants' threat representations in five a priori anatomically defined bilateral ROIs: (1) amygdala, (2) AIC, (3) vmPFC, (4) dmPFC, and (5) dACC. These regions are recruited during threat conditioning and extinction recall. Specifically, the amygdala, AIC, dmPFC, and dACC contribute to the formation of threat associations and the production of threat-conditioned behaviors (Davis, 1992; Duvarci et al., 2009; Etkin & Wager, 2007; Fullana et al., 2016; Maier et al., 2012; Schiller et al., 2008; Schiller & Delgado, 2010), while the vmPFC is associated with fear inhibition to previously dangerous, but currently safe CS (Lissek et al., 2014; Schiller et al., 2008). The bilateral amygdala (label: amygdala), vmPFC (label: medial orbitofrontal cortex), dmPFC (label: superior frontal cortex), and dACC (label: caudal anterior cingulate cortex) were defined using the Desikan-Killiany atlas (Desikan et al., 2006). The left and right anterior circular sulci of the insula (label: anterior circular sulcus of the insula) were defined using the Destrieux atlas (Destrieux et al., 2010). Cortical and subcortical segmentations were performed on T1-weighted whole-brain volumetric scans using FreeSurfer-v6.0 image analysis suite (Fischl et al., 2002, 2004). This automated pipeline includes motion correction, skull stripping, B1 bias field correction, and gray and white matter segmentation. Segmentations were converted to volumetric data in AFNI space (@SUMA_Make_Spec_FS of SUMA). Mask fit was visually inspected in AFNI by overlaying converted Freesurfer segmentations on participants' T1 images.

2.5 | Data analysis

2.5.1 | Visit 1: threat conditioning—Prior analyses of social and nonsocial threat conditioning that include these data have been previously reported (Shechner et al., 2015). See Supplementary Material for details.

2.5.2 | Visit 2: extinction recall

Self-report: Mixed model regression analyses were used to analyze self-report ratings of each CS and GS during extinction recall (SPSS Version 27). To compare across tasks, our primary model was run only including the CS−, GS20, GS40, GS60, GS80, and CS+. Linear and quadratic trends of participant responses to the stimuli were examined for each question (threat appraisal, explicit memory) and age group (youth, adults) as well as the interaction between linear and quadratic trends and age group. Fixed effects included stimulus trend (linear, quadratic), task (social threat, nonsocial threat), question type (threat appraisal, explicit memory), and age group (youth, adult), as well as the interactions between these variables. Morph was included as a random effect. All possible interactions were included in the initial model. Nonsignificant interactions were omitted from the final model. Standardized values are reported.

To compare participants' self-reported fear and memory of each individual stimulus, pairwise comparisons were also conducted between each CS and all remaining stimuli

within each task. Finally, to examine the stability of responding across tasks, intraclass correlation analyses were conducted separately for each CS and GS across the social and nonsocial threat tasks. False discovery rate (FDR) correction was performed using the Benjamini–Hochberg (BH) method (Benjamini & Hochberg, 1995).

Multivoxel neural data: Representational dissimilarity matrices were created for each participant, task, and ROI using RSA with the rsatoolbox (https://github.com/rsagroup/rsatoolbox) in Matlab (Version 2020a). For each participant in each task, we extracted average voxel-wise responses to the CS+, CS−, and each GS within the anatomical masks created for each ROI. Pairwise dissimilarities were computed as one minus the Pearson correlation coefficient between multivoxel activation patterns elicited by each stimulus (Glenn et al., 2020; Kriegeskorte et al., 2008), resulting in one dissimilarity value for each pair of stimuli. From this, we obtained one dissimilarity matrix for each ROI (amygdala, AIC, vmPFC, dmPFC, dACC) in both tasks (social threat, nonsocial threat). Each dissimilarity matrix displayed pairwise dissimilarities between all stimuli within a given subject, task, question type, and ROI.

To review, our aim was to examine how neural responses to the learned threat stimulus (CS+) generalized to other safe (CS−) or ambiguous (GS) stimuli, and whether generalization was influenced by age, task, question type, and ROI. Therefore, we extracted only the comparison between the CS+ and the remaining stimuli (CS−/GS) from our neural dissimilarity matrices. Further, in order to use the same comparative models across tasks, we only included GS0 (CS−), GS20, GS40, GS60, and GS80 from the social threat task, as the nonsocial threat task did not include GS10, GS30, GS50, GS70, or GS90. However, post hoc analyses were run for all social threat stimuli to ensure the results remained consistent. Mixed model regression analyses were used to analyze the dissimilarity of neural patterns elicited by GS0–GS80 versus CS+ comparisons (SPSS Version 27). The dependent variable was the dissimilarity between neural patterns of activation elicited by the learned threat (CS+) versus the CS− and GS (i.e., 1–the correlation between CS+ neural patterns and GS20 neural patterns). Linear and quadratic trends of neural pattern differentiation were tested to quantify the shape of the generalization gradients. Fixed effects included the shape of the stimulus trend (linear, quadratic), task (social threat, nonsocial threat), question type (threat appraisal, explicit memory), ROI (amygdala, AIC, vmPFC, dmPFC, dACC), and age group (youth, adult), as well as two- and three-way interactions between these variables. ROI and morph were included as random effects. Nonsignificant interactions were not included in the final model. All tests were two-sided and significance was set at $\alpha < .05$. The reported statistics are standardized.

3 | RESULTS

3.1 | Visit 1: threat conditioning

Participants' self-reported fear during conditioning indicated successful conditioning followed by extinction across the whole sample with no interaction by age group or task. We also replicated findings from Shechner et al. (2015) that moderate to strong intraclass correlation coefficients (ICCs) were observed across tasks during conditioning for both

self-report and SCR. However, we did not observe similarly strong intraclass correlations during extinction. See Supplementary Material for full analyses of self-report and SCR during conditioning.

3.2 | Visit 2: extinction recall

3.2.1 | Self-report

Self-report generalization gradients: The linear mixed model revealed main effects of both linear and quadratic trends (linear: $B = .423$, SE $= 0.032$, $t(179.21) = 13.08$, $p < .001$; quadratic: $B = .057$, SE $= 0.011$, $t(817.99) = 5.10$, $p < .001$). Several significant interactions also emerged. Figure 3 plots self-report fear and memory ratings by age group and task.

Linear effects.: First, we observed a three-way task × question type × linear trend interaction, $F(1, 817.99) = 20.34$, $p < .001$, as well as significant task × linear and question type × linear two-way interactions ($ps < .001$). Follow-up linear mixed models were carried out within each task to probe the task × question type × linear interaction, which included question type and linear trend as fixed effects and morph as a random effect. For both the social and nonsocial threat tasks, we observed significant question type × linear interactions, such that the explicit memory questions elicited stronger linear effects than the threat appraisal questions (ps .001). Follow-up analyses for the nonsocial threat task revealed that participants exhibited a significant linear shape of self-reporting during nonsocial explicit memory, $B = .169$, SE $= 0.042$, $t(124.38) = 3.99$, $p < .001$, but not threat appraisal, $B = .031$, SE $= 0.021$, $t(71.74) = 1.49$, $p = .14$. In contrast to the nonsocial threat task, the social threat task elicited a significant linear shape of self-reporting for both threat appraisal, $B = .089$, SE $= 0.037$, $t(44.04) = 2.38$, $p = .022$, and explicit memory questions, $B = .441$, SE $= 0.045$, $t(79.68) = 9.76$, $p < .001$.

Quadratic effects.: The model also revealed several interactions with the quadratic generalization gradient. First, a two-way task × quadratic interaction emerged, such that the nonsocial threat task showed a stronger quadratic effect than the social threat task, $B = .040$, SE $= 0.013$, $t(817.99) = 3.07$, $p = .002$. Follow-up linear mixed models carried out within each task revealed a significant quadratic effect for the nonsocial threat task, $B = .068$, SE $= 0.011$, $t(214.00) = 6.21$, $p < .001$, but not the social threat task, $B = .028$, SE $= 0.015$, $t(214.00) = 1.84$, $p = .067$. The second quadratic interaction that emerged was a two-way question type × quadratic interaction, with the explicit memory questions eliciting stronger quadratic responses than the threat appraisal questions, $B = -.058$, SE $= 0.013$, $t(817.99) = -4.49$, $p < .001$. However, follow-up analyses within each attention state revealed that both attention states elicited both linear and quadratic trends (ps .001). No main effects of age, question type, or task emerged from the initial model ($ps > .15$).

Pairwise comparisons between CS and GS

Nonsocial threat.: BH corrected pairwise comparisons were conducted between each CS and all other stimuli during the nonsocial threat task (see Figure 4 and Table 2). We observed that for both threat appraisal and explicit memory questions, the CS+ was rated more highly than the CS− and all GS ($ps < .037$), meaning participants found the CS+ bell to be the most fear-inducing and the most likely to have rang compared with all other stimuli (CS−,

GS). During threat appraisal, participants reported being *more* afraid of the CS− than GS20 ($p = .02$), but no differences emerged between the CS− and GS40–GS80. Further, during explicit memory, participants reported that the CS− was *more* likely to have rang than GS20, GS40, and GS60 ($ps < .025$) but not GS80 ($p = .80$). These elevated ratings of the CS− for both threat appraisal and explicit memory questions are in line with the significant quadratic generalization gradients.

Social threat.: During the social threat task, pairwise comparisons between each CS and all other stimuli (see Figure 4 and Table 2) revealed that participants were more fearful of the CS+ face (threat appraisal) and rated it as more likely to have screamed (explicit memory) than the CS− and GS10–GS70 ($ps < .011$), but not GS80 or GS90 ($ps > .12$). For threat appraisal questions, participants reported less fear of the CS− than GS70–GS90 (all $ps < .01$), but no differences emerged between the CS− and GS10–GS60 (all $ps > .09$). For explicit memory questions, participants rated the CS− as less likely to have screamed than GS50–GS90 (all $ps < .025$). Explicit memory ratings did not significantly differ between CS− and GS10–GS40 (all $ps > .09$). Reported effects remain significant at the $p < .05$ level after applying a BH multiple comparisons correction.

Intraclass correlation between social and nonsocial threat tasks—Intraclass correlation analyses were conducted for threat appraisal and explicit memory ratings for the CS+, CS−, and all GS across the social and nonsocial threat tasks. Prior to FDR correction, averaged across groups, moderate ICCs were found for the CS+ for both threat appraisal, ICC = .53, $p = .013$, and explicit memory, ICC = .51, $p = .019$. Participants' explicit memory ratings revealed moderate intraclass correlations to the GS60, ICC = .58, $p = .007$. Finally, participants' threat appraisal ratings elicited significant intraclass correlations to the GS80, ICC = .48, $p = .030$. No significant effects remained following multiple comparisons correction using the BH method. See Table 3.

Intraclass correlation analyses were also conducted for each ROI's CS−/GS versus CS+ neural pattern differentiation for each question type (threat appraisal, explicit memory), across social and nonsocial threat tasks. Following multiple comparison correction using the BH method, one significant ICC value was observed. For the AIC, the GS40 versus CS+ comparison displayed moderate reliability in the explicit memory condition across social versus nonsocial threat tasks, ICC = .67, $p = .001$.

3.3 | Neural differentiation between the CS+ versus the CS− and GS

Several main effects emerged from the linear mixed model. Figure 5 plots neural pattern dissimilarity by age group, task, and ROI. First, there was a main effect of question type, $B = .211$, SE = 0.028, $t(3584.02) = 7.61$, $p < .001$, with threat appraisal eliciting overall greater neural pattern differentiation between the CS+ and the GS/CS− than explicit memory. In other words, when participants evaluated their fear of the stimulus, patterns of neural activation elicited by the ambiguous (GS) or safe (CS−) stimuli were more dissimilar to those elicited by the conditioned threat stimuli (CS+) than they were when they recalled whether the stimulus predicted the UCS. This suggests greater threat/safety discrimination during threat appraisal. Second, a main effect of ROI emerged, $F(4, 60.00) = 63.04$, $p <$

.001. Pairwise comparisons revealed that the amygdala and vmPFC did not differ from each other ($p = .97$) but had greater GS/CS+ neural pattern differentiation than the AIC, dACC, and dmPFC (all ps < .001). The AIC demonstrated greater GS/CS+ differentiation than the dmPFC ($p < .001$) but not the dACC ($p = .028$). Finally, the dACC demonstrated greater GS/CS+ differentiation than the dmPFC ($p = .001$).

We also characterized the shape of the generalization gradient, or the relations among the CS+, CS−, and GS, by including linear and quadratic trends in the model. Main effects emerged for the linear but not quadratic generalization gradient (linear: $B = .060$, SE = 0.017, $t(156.38) = 3.62$, $p < .001$; quadratic: $B = .010$, SE = 0.012, $t(3384.02) = 0.86$, $p = .39$). Both the linear and quadratic shape of the generalization gradient interacted with task (linear × task: $B = −.057$, SE = 0.020, $t(3384.02) = −2.90$, $p = .004$; quadratic × task: $B = .053$, SE = 0.017, $t(3384.02) = 3.21$, $p = .001$). Follow-up linear mixed models for the social threat task revealed a linear but not quadratic shape of neural activation across CS and GS (linear: $B = .060$, SE = 0.022, $t(139.33) = 2.74$, $p = .007$; quadratic: $B = .010$, SE = 0.015, $t(142.00) = .64$, $p = .52$). By contrast, a quadratic but not linear shape of neural activation across nonsocial threat stimuli was observed (linear: $B = .003$, SE = 0.026, $t(94.75) = .11$, $p = .91$; quadratic: $B = .063$, SE = 0.016, $t(142) = 3.95$, $p < .001$). These effects are largely in line with participants' self-report.

No main effects of task ($p = .28$) or age ($p = .75$) emerged, nor did age interact with any variables (all ps > .12). However, we conducted exploratory linear mixed models within each individual ROI to examine each brain region independently. When ROIs were examined separately, main effects of task emerged in the AIC, dACC, and dmPFC (see Supplementary Materials). A second post hoc linear mixed model was run with all social threat stimuli to replicate results from the full linear mixed model and ensure that removing stimuli from the analyses to compare across tasks did not alter the results. All significant effects were replicated (see Supplementary Materials).

4 | DISCUSSION

The aim of the present study was to leverage multivariate analyses to elucidate neural representations of previously extinguished social and nonsocial threat stimuli. The study also examined the extent to which these representations differ between adults and adolescents. Three key findings emerged. First, we observed that social and nonsocial threat stimuli elicited distinct shapes of neural pattern generalization gradients. For both multivoxel neural responses and self-reported fear and memory ratings, social threat stimuli elicited a linear generalization gradient while nonsocial threat stimuli elicited a quadratic generalization gradient. Second, we observed a main effect of brain region, such that the amygdala and vmPFC displayed the greatest neural pattern differentiation between the GS, CS−, and CS+, across tasks, followed by the AIC, dACC, and dmPFC. Finally, contrary to our expectations, we did not observe an effect of age group on threat representations during extinction recall.

Our first aim was to utilize multivariate pattern analysis to compare neural threat representations across social and nonsocial threat stimuli during extinction recall. For youth and adults, neural activity patterns exhibited a linear generalization gradient for social threat

stimuli and a quadratic generalization gradient for nonsocial threat stimuli. In other words, as socially relevant stimuli became increasingly similar perceptually to the CS+, neural activity patterns elicited were also more strongly correlated. By contrast, during nonsocial threat generalization, the stimuli that were most similar to *both* CS+ and CS− elicited greater neural pattern similarity to the CS+, indicating poorer discrimination or possible conflation of CS− and CS+. The quadratic shape of neural representational dissimilarity and self-report response during the nonsocial threat task suggests that participants confounded the CS+ and CS−, indicating enhanced threat/safety discrimination of social threat stimuli relative to nonsocial threat stimuli. The pattern of participants' self-reported fear and explicit memory paralleled that of the neural activity, with linear generalization gradients observed in ratings of social threat stimuli and quadratic generalization gradients in ratings of nonsocial threat stimuli. Of note, the self-report explicit memory ratings of the nonsocial threat stimuli could also be fit by a linear gradient.

That the trends of the generalization gradients observed in neural activity and behavioral ratings differed across tasks suggests that youth and adults may be better able to make threat/safety discriminations for socially relevant stimuli compared with nonsocial threat stimuli during extinction recall. Because humans have evolved to cooperate, we possess an ability to use our past experience to precisely differentiate friends from foes. And while nonsocial threats can pose a significant danger, they may be more easily categorizable as threatening or nonthreatening. For instance, it is safe to avoid most bears without differentiating among them. These superior discrimination abilities for socially relevant stimuli may be supported by human's unique face-processing abilities. Face processing mechanisms occur in specialized, anatomically separated neural pathways (Kanwisher et al., 1997; Tsao et al., 2008). Whereas most stimuli are processed in a piecemeal manner, based on their features, faces are processed holistically (Farah et al., 1998; Gauthier et al., 2003). This may allow better discrimination between subtle perceptual changes in facial identity than other types of stimuli. This is consistent with studies finding holistic processing is associated with superior face recognition abilities (Wang et al., 2012), and that training holistic processing in people with prosopagnosia, or face blindness, enhances their face perception abilities (DeGutis et al., 2014). More work examining the generalization of non-face social threat stimuli is needed to determine whether superior threat/safety discrimination during extinction recall is due to face processing abilities or social relevance more broadly.

Second, we aimed to probe which brain regions showed greater neural pattern differentiation between the learned threat stimulus (CS+) and other ambiguously threatening stimuli. We found that the vmPFC and the amygdala demonstrated the greatest neural pattern differentiation between the GS and the CS+, relative to the AIC, dACC, and dmPFC. In other words, within the amygdala and vmPFC, patterns of neural activation that were elicited by the CS+ were the most different from the patterns of activation elicited by all other GS, compared with all other tested regions. This is consistent with previous studies finding that the vmPFC and amygdala play a central role in threat learning and threat generalization (Davis, 1992; Dunsmoor et al., 2011; Duvarci et al., 2009; Lissek et al., 2014; Resnik & Paz, 2015; Schiller et al., 2008; Schiller & Delgado, 2010). The amygdala is critical in forming the CS–US association and producing conditioned fear behaviors (Davis, 1992), whereas the

vmPFC is involved in the recall of learned extinction (Lissek et al., 2014; Schiller et al., 2008). Aberrant recruitment of the vmPFC has been associated with deficiencies in threat generalization (Cha et al., 2014; Greenberg et al., 2013; Holt et al., 2012) and is linked to anxiety disorders in youth and adults (Cha et al., 2014; Glenn et al., 2020; Greenberg et al., 2013; Milad et al., 2009). Here, in a sample of healthy youth and children, we observed that neural activity patterns in the vmPFC and amygdala showed the greatest distinctiveness for the CS+, reinforcing their important role in distinguishing between extinguished safety and threat cues. We did not find that brain region interacted with task (social versus nonsocial threat), which may suggest that, during threat generalization, these regions are similarly engaged across social and nonsocial threat stimuli and, therefore, that differences in multivoxel neural response across tasks are associated with other regions. However, our small sample size precludes strong inferences and warrants replication in larger samples.

Finally, contrary to our hypothesis, we did not find that the shape or magnitude of threat generalization was significantly different between age groups. This is inconsistent with several previous studies, which have found that the ability to differentiate between threat and non-threat stimuli increases between adolescence and adulthood and that threat-related brain structures are engaged differentially across age groups (Lau et al., 2011; Pattwell et al., 2012). The null result we observed may be related to the fact that our sample of adults was fairly young, with over half being less than 25 years of age. Structures in the PFC responsible for cognitive control and executive function continue maturing for several years after age 18 (Cohen et al., 2016; Giedd, 2004). By contrast, it is also possible that developmental differences in threat/safety discrimination during extinction recall occur earlier in middle childhood (Glenn et al., 2012; Michalska et al., 2016; Schiele et al., 2016), in which case, our sample of mostly early adolescents may have been too old to detect age differences. However, several studies have found that adults and adolescents display differences in neural and behavioral responses during extinction recall (Britton et al., 2013; Lau et al., 2011) and future work with larger samples may want to examine age-related differences across a broader age range.

Though we believe the present study provides important preliminary data, several limitations should be noted. First, because this was a cross-sectional study with a relatively small sample size, we are limited in our ability to make inferences about developmental processes. Second, as noted previously, because all social threat stimuli were pictures of faces, we cannot determine whether superior threat/safety discrimination for social threat stimuli is driven by cognition of social relevance or to humans' unique face-processing abilities. Also, because we only included two exemplars of social and nonsocial threat stimuli, differences in neural activity could be due to the particular features of this stimulus set. Ideally, future studies would be longitudinal and include nonface social threat stimuli. Finally, comparisons across social and nonsocial threat stimuli might have been influenced by differences in experimental design across tasks, including smaller increments between morphs of the social relative to nonsocial threat stimuli. Post-hoc analyses were carried out with both the full set of social threat stimuli (increments of 10%) and with only the relevant morphs for comparison with nonsocial threat stimuli (increments of 20%), to rule out spurious results. The limitations of the present study were offset by the fact that all youth and adults completed a total of four (two conditioning, two extinction recall) paradigms, enabling

within-subject comparisons across social versus nonsocial threat stimuli. In summary, the current study leveraged multivariate analyses to examine the influence of age and stimulus type on the generalization of conditioned threat stimuli. The present results highlight the importance of the social relevance of a threat on generalization across development.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Funding information

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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FIGURE 1.

Conditioning paradigm with (a) nonsocial (Top) and (b) social (Bottom) threat stimuli. Nonsocial threat task: during acquisition, one bell (CS+) was repeatedly paired with a red bell and loud alarm sound (UCS); the other bell (CS−) was never paired with the UCS. Social threat task: during threat acquisition, one female face (conditioned stimulus; CS+) was paired with a fearful face coterminating with a scream (unconditioned stimulus; UCS). The other female face (CS−) was never paired with the UCS
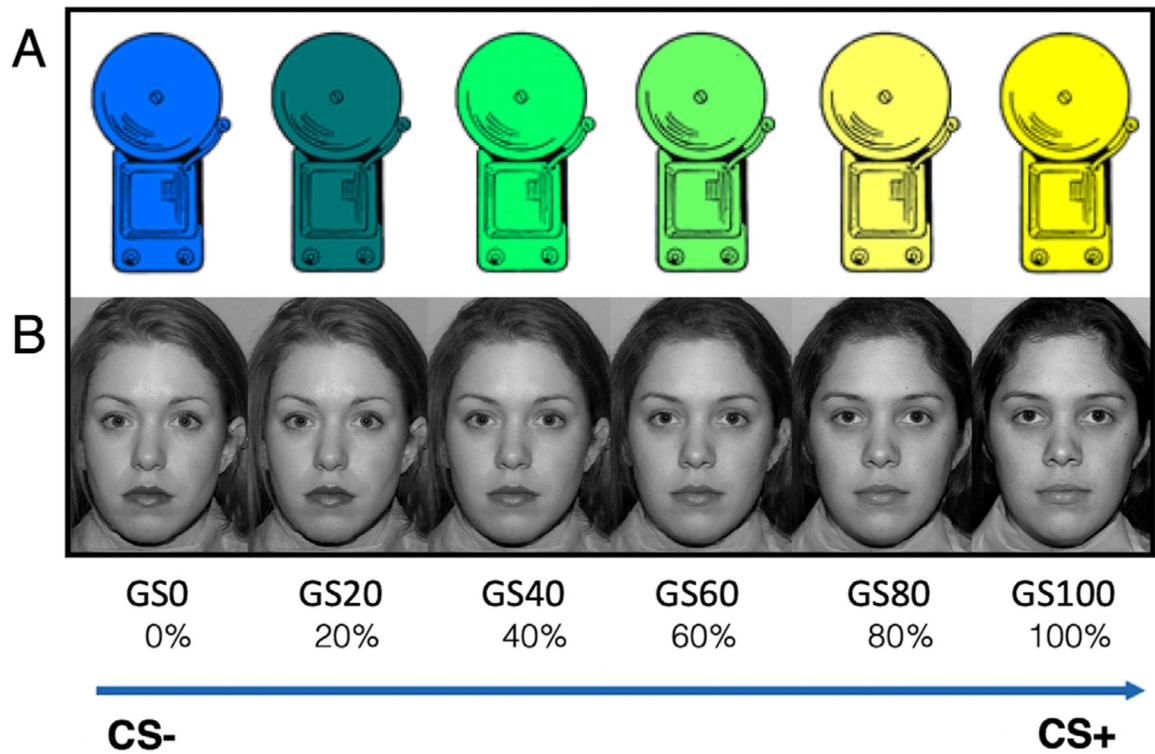
FIGURE 2.
Extinction recall paradigm with (a) nonsocial (Top) and (b) social (Bottom) threat stimuli. Participants viewed the CS− (GS0), CS+ (GS100), and generalization stimuli (GS) that were morphed blends of the CS− and CS+. The social threat task was morphed in steps of 10% but only steps of 20% are displayed here for ease of viewing. At the start of each block, participants answered one of two questions: (1) How afraid are you of this bell/woman? (threat appraisal); (2) How likely was the bell to ring/woman to scream? (explicit memory)
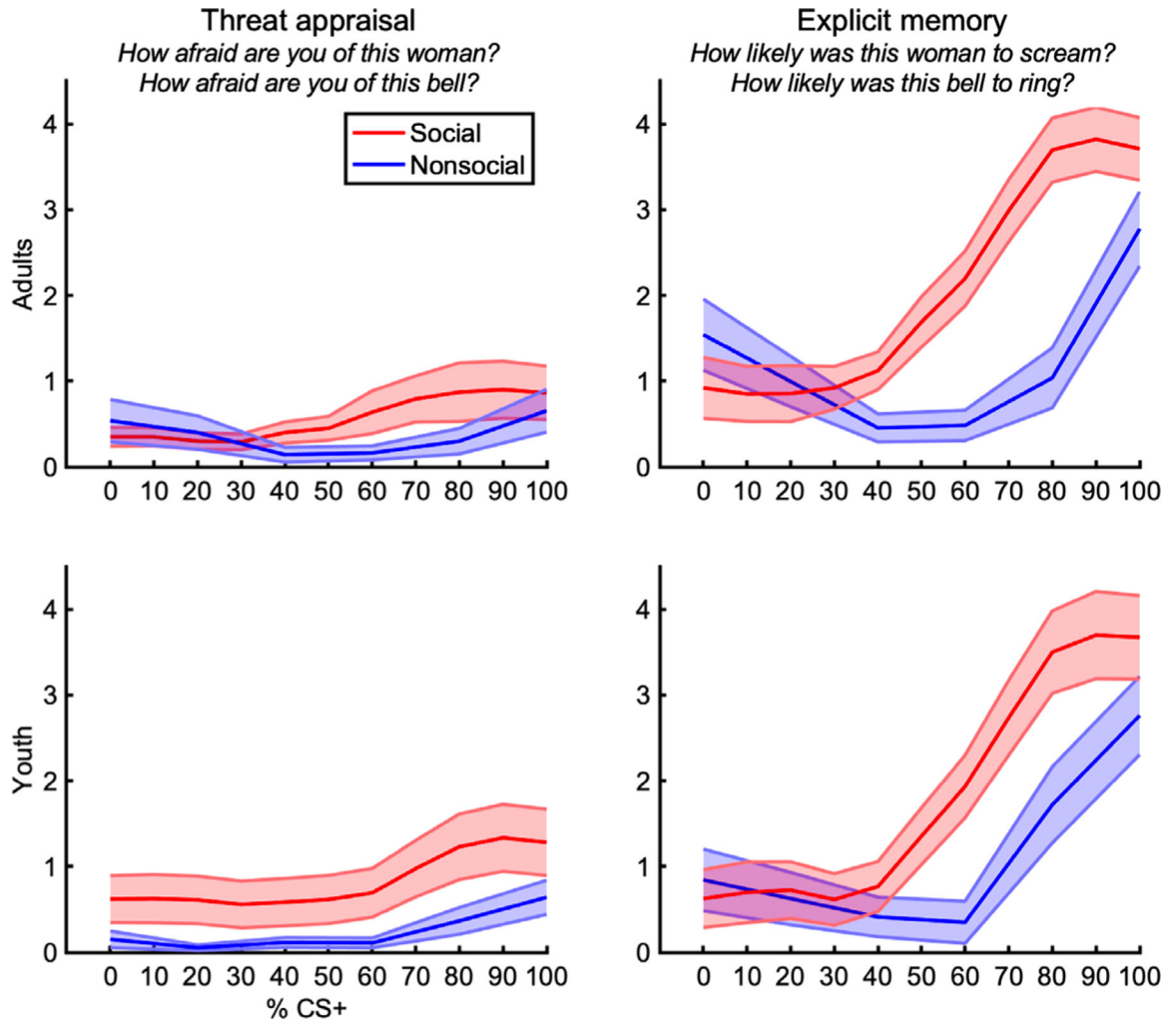
FIGURE 3.
Self-reported fear and memory ratings by stimulus. Participants completed in-scanner ratings (from 0 to 6) of their fear of each stimulus ("How afraid are you of this woman/ bell?") during threat appraisal blocks (Column 1) and their memory of the conditioning event ("How likely was this woman to scream/bell to ring?") during explicit memory blocks (Column 2)
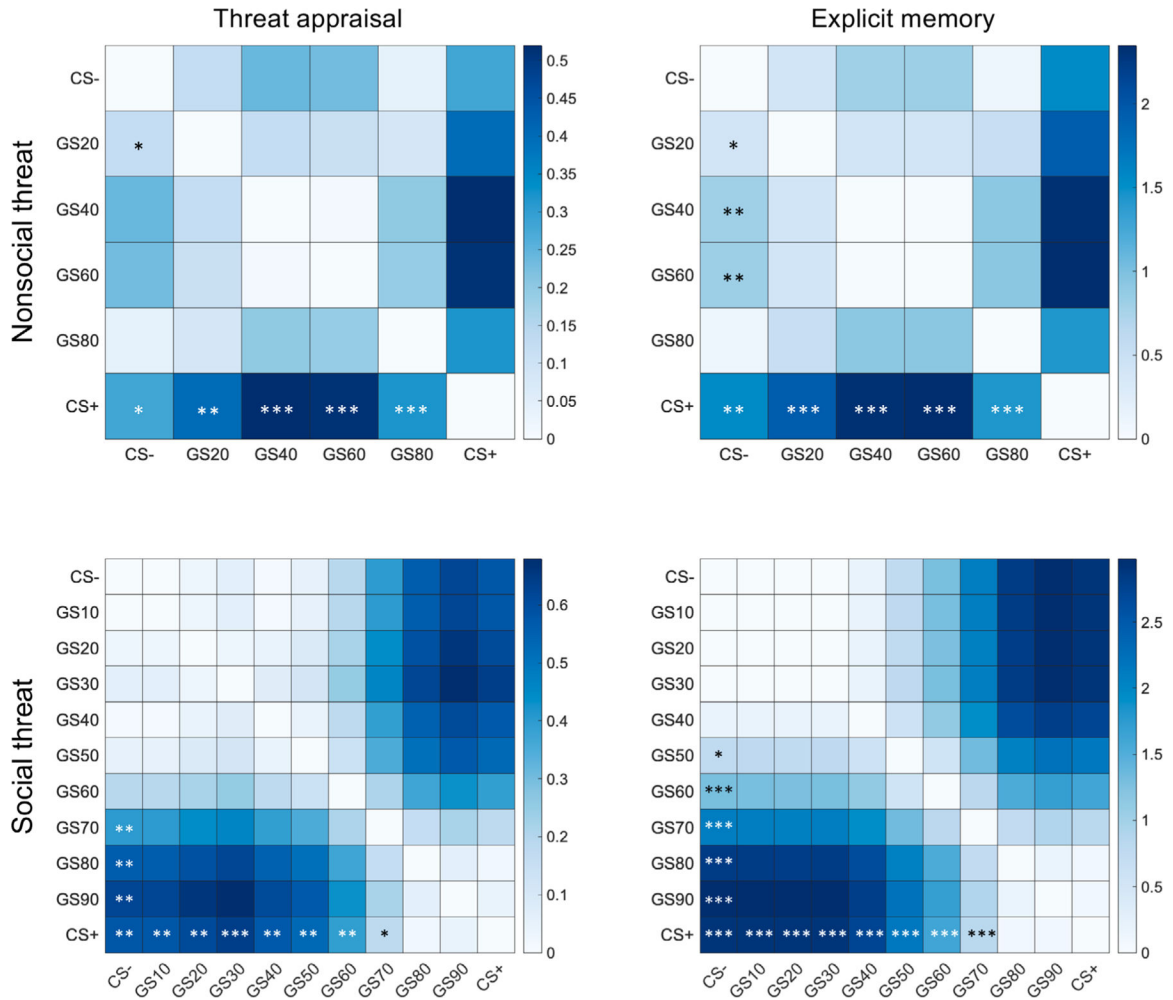
FIGURE 4.

Heatmap of pairwise dissimilarity between stimuli. Pairwise dissimilarity was calculated as the absolute value of the difference score between self-report ratings of each stimulus, averaged within each task (nonsocial threat, social threat) and question type (threat appraisal, explicit memory). Each dissimilarity value is represented by a cell in the behavior dissimilarity matrix. Within each condition, pairwise comparisons were conducted between each CS and the remaining stimuli (represented as the first column and last row of each matrix). Stimuli that significantly differed are marked with asterisks. Reported effects remain significant after FDR correction using the Benjamini–Hochberg method. Intraclass correlation analyses were conducted to assess cross-stimulus similarity between social and nonsocial threat stimuli, not depicted in this figure (see Table 3). Note: ***p .001; **p .01; *$p < .05$
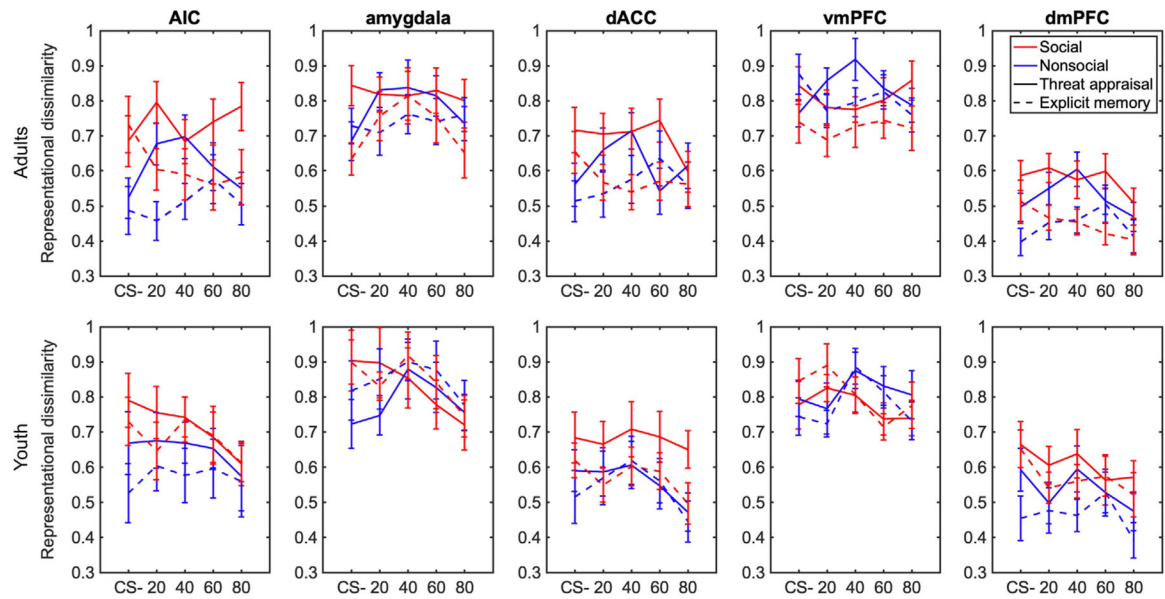
FIGURE 5.

Neural pattern dissimilarity by ROI and age. Task differences in neural pattern dissimilarity between CS−/GS versus CS+ for adults (top) and youth (bottom). Neural pattern dissimilarity (1 – Pearson correlation coefficient) was measured in the anterior insular cortex (AIC), amygdala, dorsal anterior cingulate cortex (dACC), ventromedial prefrontal cortex (vmPFC), and dorsomedial prefrontal cortex (dmPFC). See Methods for details regarding statistical analyses

TABLE 1

Sample demographic characteristics

| | N | Age in years (M, SD) | Female(%) | Latinx (%) | Race | | | |
					White(%)	Black(%)	Asian(%)	Multiracial(%)
Youth	16	14.1 (1.7)	62.5	12.5	37.5	31.3	6.3	25.0
Adults	20	25.7 (4.9)	60.0	5.0	50.0	15.0	25.0	10.0

TABLE 2

Means, standard deviations, and pairwise comparisons between self-report ratings of the CS+ and CS−/GS

	Threat appraisal					Explicit memory				
Social threat	M	SD	t	d	p	M	SD	t	d	p
CS+ vs.	1.05	1.46	—	—	—	3.69	1.75	—	—	—
CS−	0.47	0.81	3.25**	0.54	.003	0.79	1.47	6.40***	1.07	<.001
GS10	0.47	0.83	3.25**	0.54	.003	0.78	1.41	6.55***	1.09	<.001
GS20	0.44	0.81	3.18**	0.53	.003	0.80	1.38	6.54***	1.09	<.001
GS30	0.41	0.79	3.46***	0.58	.001	0.79	1.15	7.44***	1.24	<.001
GS40	0.48	0.83	3.27**	0.55	.002	0.96	1.07	8.01***	1.33	<.001
GS50	0.52	0.87	3.34**	0.56	.002	1.54	1.31	7.70***	1.28	<.001
GS60	0.66	1.11	2.90**	0.48	.006	2.08	1.43	6.26***	1.04	<.001
GS70	0.87	1.24	2.68*	0.45	.011	2.88	1.66	4.81***	0.80	<.001
GS80	1.03	1.52	0.54	0.09	.593	3.61	1.77	1.18	0.20	.247
GS90	1.09	1.51	−1.61	−0.27	.116	3.77	1.82	−1.35	−0.23	.186
Nonsocial threat	**M**	**SD**	**T**	**d**	**p**	**M**	**SD**	**t**	**d**	**p**
CS+ vs.	0.65	0.97	—	—	—	2.77	1.86	—	—	—
CS−	0.37	0.88	2.18*	0.36	.036	1.23	1.70	3.43**	0.57	.002
GS20	0.25	0.67	3.10**	0.52	.004	0.83	1.27	4.91***	0.82	<.001
GS40	0.13	0.32	3.83***	0.64	.001	0.44	0.81	6.82***	1.14	<.001
GS60	0.14	0.31	3.61***	0.60	.001	0.42	0.87	6.70***	1.12	<.001
GS80	0.33	0.64	3.60***	0.60	.001	1.34	1.68	4.92***	0.82	<.001

Pairwise dissimilarity was calculated as the absolute value of the difference score between self-report ratings of each stimulus, averaged within each task (nonsocial threat, social threat) and question type (threat appraisal, explicit memory). Within each condition, paired samples t-tests were conducted between the CS+ and the remaining stimuli. Reported effects remain significant after FDR correction using the Benjamini–Hochberg method. Note:

***
p .001;

**
p .01

*
$p < .05$.

TABLE 3

Intraclass correlations coefficients (ICC) between self-report across social and nonsocial threat stimuli during extinction recall

	CS−	GS20	GS40	GS60	GS80	CS+
Explicit memory	.36 [−.26–.67], $p = .10$	.40 [−1.74–.29], $p = .84$	.13 [−.70–.56], $p = .34$	.58 [.17–.78], $p = .007$	.22 [−.53–.60], $p = .23$	.51 [.04–.75], $p = .019$
Threat appraisal	.36 [−.26–.67], $p = .10$	−.01 [−.99–.48], $p = .52$	.33 [−.31–.66], $p = .12$	.26 [−.45–.62], $p = .19$	.48 [−.03–.73], $p = .030$	.53 [.09–.76], $p = .013$

ICC values are reported for social and nonsocial generalization stimuli [M ± SD]. Because social stimuli GS10, GS30, GS50, GS70, and GS90 cannot be compared with nonsocial stimuli, they have been omitted from the table. Confidence intervals for intraclass correlations are reported in brackets. No effects remain significant after multiple comparisons correction using the Benjamini–Hochberg method.