Development and Psychopathology (2025), **37**, 802–814
doi:10.1017/S0954579424000683

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Regular Article

Early life adversity is associated with greater similarity in neural representations of ambiguous and threatening stimuli

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Abstract

Exposure to early life adversity (ELA) is hypothesized to sensitize threat-responsive neural circuitry. This may lead individuals to overestimate threat in the face of ambiguity, a cognitive-behavioral phenotype linked to poor mental health. The tendency to process ambiguity as threatening may stem from difficulty distinguishing between ambiguous and threatening stimuli. However, it is unknown how exposure to ELA relates to neural representations of ambiguous and threatening stimuli, or how processing of ambiguity following ELA relates to psychosocial functioning. The current fMRI study examined multivariate representations of threatening and ambiguous social cues in 41 emerging adults (aged 18 to 19 years). Using representational similarity analysis, we assessed neural representations of ambiguous and threatening images within affective neural circuitry and tested whether similarity in these representations varied by ELA exposure. Greater exposure to ELA was associated with greater similarity in neural representations of ambiguous and threatening images. Moreover, individual differences in processing ambiguity related to global functioning, an association that varied as a function of ELA. By evidencing reduced neural differentiation between ambiguous and threatening cues in ELA-exposed emerging adults and linking behavioral responses to ambiguity to psychosocial wellbeing, these findings have important implications for future intervention work in at-risk, ELA-exposed populations.

Keywords: ambiguity tolerance; early life adversity; representational similarity analysis; threat hypervigilance; valence bias

(Received 14 February 2023; revised 26 February 2024; accepted 29 February 2024; First Published online 11 April 2024)

Introduction

Exposure to early life adversity (ELA), including experiences of abuse and neglect, is a potent risk factor for impaired psychosocial functioning. The implications of ELA are wide-reaching, increasing the risk of delinquency (Ford et al., 2010; Turner et al., 2016), behavioral problems (Choi et al., 2019; Schroeder et al., 2020), social dysfunction (McCrory et al., 2022; Salzinger et al., 1993), and psychopathology (Green et al., 2010; Kessler et al., 2010; McLaughlin et al., 2012) throughout the lifespan. ELA is hypothesized to disrupt healthy functioning in part by sensitizing neural circuitry to motivationally salient and threat-relevant cues (Callaghan & Tottenham, 2016; McLaughlin & Sheridan, 2016), resulting in heightened vigilance for potential threat (McLaughlin & Lambert, 2017; Nusslock & Miller, 2016; Silvers et al., 2017). This sensitization may result in a tendency to overestimate threat in ambiguous situations (Chen & Matthews, 2001, 2003; Lange et al., 2019; McLaughlin et al., 2019). Critically, in samples not selected for ELA exposure, the tendency to assume threat in the face of ambiguity has been linked to psychosocial challenges (Carleton, 2016; Chen & Lovibond, 2020; Dodge, 2006; Hirsch et al., 2016; Taghavi et al., 2000), whereas positive evaluations of ambiguity have been shown to mitigate risk for psychosocial challenges following ELA (Lange et al., 2019; Troller-Renfree et al., 2015, 2017; VanTieghem et al., 2017). Although an extensive literature has demonstrated ELA-based differences in neural responses to objectively negative cues (Doretto & Scivoletto, 2018; Herzberg & Gunnar, 2020; Saarinen et al., 2021; da Silva Ferreira et al., 2014), few studies have examined neural responses to ambiguous stimuli as a function of adversity exposure. Notably, work in clinical populations suggests that responses to ambiguous stimuli are more predictive of psychosocial health than responses to explicitly threatening stimuli (Lissek et al., 2010). While understudied, examining how ELA shapes responses to ambiguity stands to transform our understanding of how early experiences contribute to psychopathology and to eventually identify modifiable protective factors in vulnerable populations.

Prior behavioral studies suggest that ELA is associated with developmental differences in processing ambiguity. For instance, Bick et al. (2017) found that children with a history of institutional orphanage care differed from age-matched comparisons in recognition accuracy for ambiguous, but not unambiguous, facial expressions. Further research has demonstrated that ELA-exposed youth tend to interpret ambiguity as threatening more often than

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Cite this article: Saragosa-Harris, N. M., Guassi Moreira, J. F., Waizman, Y., Sedykin, A., Peris, T. S., & Silvers, J. A. (2025). Early life adversity is associated with greater similarity in neural representations of ambiguous and threatening stimuli. *Development and Psychopathology* **37**: 802–814, https://doi.org/10.1017/S0954579424000683

age-matched peers (Dodge et al., 1990) (although see Vantieghem et al., 2017, which finds the opposite). For instance, Chen and Matthews (2001, 2003) demonstrated that low SES youth were more likely than high SES youth to interpret ambiguous scenarios as threatening, whereas no group differences were observed when presented with explicitly threatening scenarios. Similarly, Pollak and Kistler (2002) found that, relative to comparison youth, abused children overidentified anger in morphed facial expressions. At present, little is known about how ELA exposure impacts ambiguity processing in adulthood, limiting our understanding of how enduring the effects of ELA are on interpretations of ambiguity.

Although several studies suggest that, on average, ELA-exposed individuals overestimate threat when evaluating ambiguity, there is marked heterogeneity amongst ELA-exposed individuals. Such individual differences may be particularly important for psychosocial functioning in ELA-exposed individuals. For example, VanTieghem et al. (2017) found that the tendency to evaluate ambiguous facial expressions positively mitigated risk for internalizing symptoms in previously institutionalized, but not comparison, youth, suggesting that this behavioral phenotype may be a uniquely protective factor for ELA-exposed populations. Ambiguous stimuli may thus be useful for probing hypersensitivity to potential threats (Neta et al., 2017; Pollak & Kistler, 2002) and more broadly indexing individual differences relevant to psychosocial functioning (Lissek et al., 2010; Neta & Brock, 2021; Petro et al., 2021; Puccetti et al., 2020; Vantieghem et al., 2017). Identifying such individual differences may be particularly important during the transition from adolescence to adulthood, a developmental stage characterized by heightened risk for psychiatric disorders (Arnett et al., 2014), especially among individuals exposed to ELA (van der Vegt et al., 2009).

The tendency to appraise ambiguity as threatening may stem in part from difficulty distinguishing between ambiguous and threatening stimuli. At the neural level, this may manifest in the brain representing ambiguous and threatening information similarly (Lecei & van Winkel, 2020), particularly within affective neural circuitry responsive to valenced stimuli. Although this possibility has received theoretical support (Lecei & van Winkel, 2020), prior empirical work examining neural discrimination among affective cues following ELA has largely relied on univariate analyses to capture average BOLD responses to affective stimuli (Green et al., 2016; Saarinen et al., 2021; Tottenham et al., 2011; van Harmelen et al., 2013). While useful, univariate approaches rely on averaging brain activity over several units into a single index of activity and thus cannot capture more detailed, distributed patterns of representations of ambiguity — or, crucially, how similar these distributed patterns are to representations of threat. Multivariate tools offer a unique opportunity to examine more detailed, distributed patterns of neural activity. Such methods are particularly sensitive to subtle variations in social and affective stimuli (Weaverdyck et al., 2020). For example, representational similarity analysis (RSA) is a technique that assesses representational overlap between stimulus types (e.g., ambiguous versus threatening) based on voxelwise, distributed patterns of neural activity (Dimsdale-Zucker & Ranganath, 2018; Kriegeskorte, 2008). Using RSA, recent studies in community samples demonstrate that multivariate representations within the amygdala track subtle variations in perceived trustworthiness of ambiguous social stimuli (FeldmanHall et al., 2018; Tashjian et al., 2019). RSA may similarly elucidate whether similarity between multivariate representations of ambiguity and threat differs as a function of adversity history.

In this study, we used RSA to investigate similarity in neural representations of ambiguous and threatening images as a function of ELA history. We chose to focus on the transition from adolescence to adulthood (i.e., "emerging adulthood") (Arnett et al., 2014) based on prior work suggesting that individual differences in responses to ambiguity are particularly important for shaping wellbeing during this period of development (Bardi et al., 2009; Silvers & Peris, 2023). This developmental stage is characterized by a number of ambiguous challenges (e.g., moving to a new and unfamiliar city for college or a first job, choosing a career path, living independently for the first time). The uncertainties associated with emerging adulthood are thought to be especially stressful during the earliest stages of this transitional period, when these novel stressors are the most unfamiliar and ambiguous (Bardi et al., 2009). For this reason, we recruited freshmen college students in order to capture this initial transition period in which ambiguity is thought to be most closely linked to wellbeing (Bardi et al., 2009). Our decision to focus on this developmental stage was additionally motivated by work demonstrating heightened risk for psychopathology during the transition to adulthood (Arnett et al., 2014), especially within populations with a history of caregiving adversity (van der Vegt et al., 2009).

A sample of 41 emerging adults with varying levels of ELA exposure underwent fMRI while viewing ambiguous, threatening, and nonthreatening images. Outside of the scanner, participants rated the images. We hypothesized that individuals with higher ELA would demonstrate greater sensitivity to threat, indicated by greater similarity (i.e., less differentiation) in their representations of ambiguous and threatening images. We expected this pattern to be specific to ambiguity and threat — that is, we did not hypothesize ELA-based differences in representational overlap between ambiguous and nonthreatening, or between threatening and nonthreatening, images. These hypotheses were tested in four a priori regions of interest, selected based on (1) their sensitivity to motivationally salient stimuli, especially ambiguous and potentially threatening signals, and (2) research demonstrating ELA-related differences in function within these regions: the amygdala (Fareri & Tottenham, 2016; FeldmanHall et al., 2018; Tashjian et al., 2019; Xu et al., 2021), nucleus accumbens (Fareri & Tottenham, 2016; Gee et al., 2018; Ray et al., 2020; Xu et al., 2021), anterior insula (Hein & Monk, 2017; Menon & Uddin, 2010; Tanovic et al., 2018; Xu et al., 2021), and ventromedial prefrontal cortex (vmPFC) (Chavez & Heatherton, 2015; Cohodes et al., 2021; Hart et al., 2018; Xu et al., 2021).

Given that ELA is associated with impairments across a broad range of domains, we also assessed global functioning, a construct that encapsulates mental health and other features of psychosocial functioning (Pirkis et al., 2005; Wing et al., 1998). We hypothesized that individuals exposed to greater levels of ELA would be more likely to appraise the ambiguous images negatively and would exhibit worse global functioning. While prior work has demonstrated robust effects of ELA on emotional outcomes, it has also revealed marked heterogeneity among ELA-exposed groups (Callaghan et al., 2019; Gee, 2021; Lange et al., 2019; Silvers et al., 2017; Stevens et al., 2021). Thus, we also tested whether individual differences in behavioral responses to ambiguity processing moderated links between ELA and global functioning. Based on prior work, we hypothesized that positive evaluations of ambiguity would be associated with better global functioning in

https://doi.org/10.1017/S0954579424000683 Published online by Cambridge University Press

high ELA individuals (Lange et al., 2019; Troller-Renfree et al., 2015, 2017; Vantieghem et al., 2017). Lastly, prior work demonstrates that taking longer to evaluate ambiguity is associated with more positive evaluations — potentially reflecting an adaptive regulatory process (Neta et al., 2022; Neta & Tong, 2016). We sought to replicate this finding and determine whether ELA moderates links between time spent evaluating ambiguity and global functioning, which ostensibly encompasses aspects of self-regulation.

Methods and materials

Data and code availability

All data, task scripts, and analysis scripts for this study are available on GitHub (https://github.com/nsaragosaharris/earlylifeadversity_ambiguity_study).

Participants

We recruited participants via flyers and online recruitment. An a priori, planned sample size of 40 was selected based on prior neuroimaging studies that used similar multivariate modeling techniques to the planned analyses (Dimsdale-Zucker & Ranganath, 2018; FeldmanHall et al., 2018; Stolier & Freeman, 2016). In total, 41 participants completed the neuroimaging and post-scan behavioral tasks ($N = 29$ females, age = 18 to 19 years old, $\overline{X}_{age} = 18.34$, $SD_{age} = 0.48$). Three participants did not complete the global functioning questionnaire (see *Questionnaires*). Sample demographics and summary statistics for questionnaire data are included in the Supplement (*Supplemental Table 1; Supplemental Figure 2*). Participants provided written consent. All study procedures were completed in accordance with the University of California Los Angeles Institutional Review Board (IRB# 19-001000).

Participants completed questionnaires at an initial lab session and subsequently underwent fMRI testing within two weeks of their lab session. Immediately after fMRI testing, participants completed a behavioral task. Participants were compensated for participation.

Participant inclusion criteria

Data were collected as part of a larger study investigating mental health in individuals transitioning from adolescence to adulthood. Eligibility for inclusion in the study was based on the following criteria and assessed via brief in-person interview and an MRI screening form: (1) individuals in their freshman year of college who were at least 18 years old; (2) no medical or psychiatric conditions contraindicating study participation (e.g., psychosis); (3) no current use of a psychiatric medication; (4) no current treatment for anxiety or depression; (5) no presence of metal in the body; (6) no current report of pregnancy; (7) no pressing mental health concern requiring immediate follow up (e.g. psychosis); and (8) no fear of enclosed spaces (claustrophobia).

Questionnaires

Early life adversity

Early life adversity (ELA) was measured using the Childhood Trauma Questionnaire Short Form (CTQ-SF) (Bernstein et al., 2003), a 28-item scale that assays experiences of emotional abuse, emotional neglect, physical abuse, physical neglect, and sexual abuse before age fourteen. The CTQ-SF has been validated in clinical and non-clinical samples and corresponds well to therapists' interview-based ratings of abuse and neglect (Bernstein et al., 2003). For each item, participants rated on a scale of 1 to 5 (1 = never true, 5 = very often true) how much they agreed with various statements (e.g., "I believe that I was physically abused"). Responses were totaled across subtypes of abuse and neglect, with higher scores indicating greater experiences of childhood trauma. Total scores were log-transformed and then z-scored to meet the assumptions of the planned statistical tests (i.e., normality).

Global functioning

Global functioning was measured by the self-rated version of the Health of the Nation Outcomes Scale for Children and Adolescents (HoNOSCA-SR) (Gowers et al., 2002), a 13-item measure based on the Health of the Nation Outcomes Scale (Wing et al., 1998) that assesses symptoms and functioning across four domains: behavioral problems (aggressive/antisocial, overactivity/attention, self-harm, substance misuse), impairment (scholastic/language skills, physical disability), symptomatic problems (hallucinations and delusions, non-organic somatic symptoms, emotional and related symptoms), and social problems (peer relationships, self-care and independence, family life and relationships, poor school attendance) (Pirkis et al., 2005). The HoNOSCA-SR has been validated (Pirkis et al., 2005) and correlates with a number of other mental health scales (Gowers et al., 2002). For each item on the HoNOSCA, participants used a 5-point Likert scale to indicate the degree to which they were affected by a given symptom or experience (e.g., "Have you been troubled by your disruptive behavior, physical or verbal aggression?") in the last two weeks (0 = "Not at all", 1 = "Insignificantly", 2 = "Mild but definitely", 3 = "Moderately", 4 = "Severely"). Responses across domains were totaled, with higher scores indicating poorer functioning.

fMRI task and analyses

fMRI paradigm

The fMRI task used an event-related design coded in PsychoPy2 (Peirce et al., 2019). Participants viewed a set of faces with 99 unique actors from the racially diverse affective expression dataset (Conley et al., 2018) while undergoing fMRI scanning. Actors in the selected images were 22% Asian, 32% Black/African American, 19% Hispanic or Latinx, and 26% White. 51% were female. Each of the 99 actors had three unique facial expression images (angry, happy, and surprised). Based on prior work, angry, happy, and surprised faces were considered the threatening, nonthreatening, and ambiguous stimuli, respectively (Neta et al., 2017; Pine et al., 2005; Pollak & Kistler, 2002; Vantieghem et al., 2017). In addition to the emotional expressions, participants viewed a blurred image on 27 trials, which was created by superimposing all of the 297 face images from the task and served as an attentional control. Participants viewed a single image per trial. Within each run (three total), participants viewed 33 threatening (angry), 33 non-threatening (happy), and 33 ambiguous (surprised) faces in addition to 9 blurred images (a composite of all face images), for a total of 108 trials per run and 324 total trials (Figure 1A). Every actor was shown three times (once per run), each time with a different facial expression (threatening, nonthreatening, or ambiguous). Participants were instructed to press the button box only when they saw the blurred image (attention check trials). Each stimulus was presented for 500 ms. Between trials, there was a jittered fixation cross. Jitter times were created in OptSeq2

https://doi.org/10.1017/S0954579424000683 Published online by Cambridge University Press

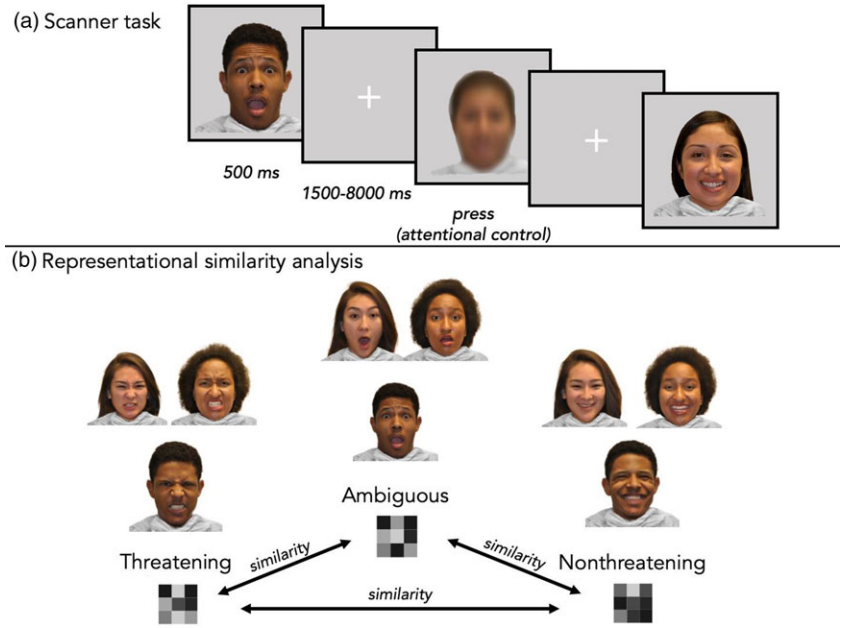

Figure 1. During the MRI task (a), participants passively viewed threatening, nonthreatening, and ambiguous faces. Catch trials included a blurred image and required a button box response. In representational similarity analyses (b), each expression type was modeled to create three multivoxel, vectorized patterns (within participant, run, and ROI). Pairwise correlations (indicated by arrows) were computed to index relative similarity between patterns of responses.

(https://surfer.nmr.mgh.harvard.edu/optseq/; mean length = 3 s, range = 1.5 to 8 s). Each run lasted 6 minutes and 36 s in total. Images within each of the three runs were shown in a randomized order and the order of runs was counterbalanced across participants.

fMRI acquisition

Data were acquired on a 3T Siemens Magnetom Prisma scanner using a 32-channel head coil. Functional data were acquired with 2.0 × 2.0 × 2.0 mm voxel size, 2.0 mm slice thickness, 60 interleaved slices, 2.0 mm slice thickness, 1000m repetition time (TR), 37 ms echo time, 60° flip angle, 208 mm field of view, and 6x multiband acceleration, and using Autoalign for slice positioning and alignment. Structural images were acquired using a high-resolution MPRAGE sequence (voxel size = 0.8 × 0.8 × 0.8 mm; TR = 2400 ms, echo time = 2.22 ms, field of view = 256 mm, slice thickness = 0.8 mm, 208 slices).

fMRI preprocessing. Preprocessing of fMRI data was carried out in FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl) using FEAT (FMRI Expert Analysis Tool) Version 6.00. Boundary based registration (Greve & Fischl, 2009) was used to register participants' functional data to their high-resolution structural images (i.e., to native space). FLIRT (FMRIB's Linear Image Registration Tool) (Jenkinson et al., 2002; Jenkinson & Smith, 2001) and FNIRT nonlinear registration (Andersson et al., 2007) were used to register high-resolution structural images to standard space (MNI 2.0 × 2.0 × 2.0 mm stereotaxic space) with 12 degrees of freedom. Preprocessing included motion correction using MCFLIRT (Jenkinson et al., 2002) using 24 standard and extended regressors, non-brain extraction using BET (Brain Extraction Tool) (Smith, 2002), grand-mean intensity normalization, and a 100 s high-pass temporal filter (Gaussian-weighted least-squares straight line fitting, with sigma = 50 s). Based on similar multivariate pattern analysis and RSA work (Glenn et al., 2020; Harry et al., 2013; Jin et al., 2015; Lee et al., 2020; Liang et al., 2017; Tashjian et al., 2019) and current recommendations (Dimsdale-Zucker & Ranganath, 2018; Misaki et al., 2013; Weaverdyck et al., 2020), in order to maintain fine-grained spatial details across voxels for RSA, we did not apply smoothing prior to multivariate analyses. Analyses were carried out using FILM (FMRIB's Improved Linear Model) prewhitening with local autocorrelation correction (Woolrich et al., 2001). Plots of temporal signal-to-noise ratios within these minimally preprocessed, unmodeled BOLD data by region are provided in the supplement (*Supplemental Figure 5*).

First level modeling

BOLD response patterns were modeled separately by trial expression type (threatening, nonthreatening, or ambiguous) in FSL using first level (i.e., within participant, within run) models, each of which included a regressor for each expression type. Blurred face trials (attention checks) were modeled but not further analyzed. Between-trial fixation crosses served as implicit baseline (i.e., were not explicitly modeled). This resulted in three general linear models (GLMs) per participant (one per run), each of which included BOLD estimates for threatening, nonthreatening, and ambiguous trials. Temporal derivatives for all regressors were included as covariates. Regressors were modeled using a double-gamma hemodynamic response function. To account for head motion, individual volumes with a framewise displacement greater than 0.9 mm were included as regressors (spike regressors created using 'fsl_motion_outliers'). Motion regressors and their derivatives were included as regressors of no interest.

Regions of interest

Four regions of interest (ROIs; amygdala, nucleus accumbens, anterior insula, and vmPFC) were selected a priori based on (1) their hypothesized role in responding to motivationally salient stimuli, especially ambiguous and potentially threatening signals (Tanovic et al., 2018), and (2) research demonstrating ELA-related functional differences within these regions (Fareri & Tottenham, 2016). An additional region, V1, was tested as a control region expected to respond to the affective visual stimuli (Kragel et al., 2019) but not expected to differ in functional activity based on

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ELA. The amygdala and nucleus accumbens were defined based on FSL's Harvard-Oxford atlas and were thresholded in MNI space using Harvard-Oxford's probabilistic masks, which specify the probability that a given voxel falls within the specified brain region. The amygdala was thresholded at $p = 0.50$ and the nucleus accumbens was thresholded at $p = 0.25$ based on prior work (Guassi Moreira et al., 2021; Tashjian et al., 2019) and visual inspection of anatomical alignment. V1 was defined based on FSL's Juelich atlas (Amunts et al., 2000) and thresholded at $p = 0.75$. The anterior insula and vmPFC were defined using anatomical masks from a relevant ROI-based meta-analysis (Xu et al., 2021). This meta-analysis examined neural responses to the dimensional emotions and valence portrayed in facial expressions (including angry, happy, and surprised faces). In the Xu et al. (2021) meta-analysis, the anterior insula and vmPFC were anatomically defined in MNI space using the automated anatomical labeling template (Tzourio-Mazoyer et al., 2002), and these ROIs were shared with our research team. All masks were originally defined in MNI space and transformed into participant-specific native space prior to multivariate (RSA) analyses. Because masks were participant-specific and in native space, there was variability in ROI size. In cases in which an ROI-based statistical estimate was significant, we conducted sensitivity analyses in which we controlled for the number of voxels within the ROI to ensure that differences in ROI size across participants did not affect statistical estimates.

Representational similarity analysis

The function 'NiftiMasker' in the Python package 'nilearn' (Abraham et al., 2014) was used to extract vectors of voxel-level coefficients within each ROI. All vectors were participant-specific, run-specific, ROI-specific, and condition-specific: Each vector corresponded to a regressor of interest (ambiguous, threatening, or nonthreatening) from the aforementioned GLMs for a given ROI per run (e.g., run 1 ambiguous vector, run 1 threatening vector, run 1 nonthreatening vector). These vectors were used to compute three pairwise Pearson correlations (ambiguous/threatening, ambiguous/nonthreatening, threatening/nonthreatening) for each run. Next, these correlations were averaged across runs, resulting in three correlations per ROI for a given participant (Figure 1B). Fisher's r-to-z transformation was then applied to the averaged Pearson correlation values (Dimsdale-Zucker & Ranganath, 2018). These z-transformed values represent similarity in patterns of representations between (1) ambiguous and threatening, (2) ambiguous and nonthreatening, and (3) threatening and nonthreatening facial expressions within a given ROI, with greater values indicating relatively greater similarity in voxelwise patterns of activation. Parallel analyses were run in a control region (V1). We hypothesized that individuals with higher ELA would demonstrate greater similarity ("overlap") in their representations of ambiguous and threatening images within the four ROIs (but not V1), and did not expect to see ELA-based differences in representational overlap between ambiguous and nonthreatening, or between threatening and nonthreatening, images. While hypotheses centered around RSA, in the interest of contributing to data sharing efforts, we report univariate methods and results in the supplement.

Post-scan categorization task

Paradigm

Participants completed a surprise, post-scan task in which they were shown a subset of images seen in the fMRI task. After completing six practice trials, participants were shown 200 images (100 ambiguous) over ten blocks (ten ambiguous, five threatening, and five nonthreatening faces per block). More ambiguous faces ($N = 100$) were shown because this was the primary condition of interest for this study. On each trial, participants pressed a button to indicate whether the person in the image "feels good" or "feels bad" (Vantieghem et al., 2017) by pressing a button on the keyboard (1 or 0, counterbalanced across participants). Each face was presented for 500 ms, followed by a screen with text requesting their response, which lasted for 1500 ms regardless of when they responded (*Supplemental Figure 1*). Early responses (during the initial 500 ms presentation screen) were accepted and included in analyses. If participants made more than one response, their final appraisal was used in analysis to minimize the possibility of analyzing responses made in error. A 200 ms fixation cross was included between trials. Block order was randomized and faces within each block task were shown in a randomized order. In between blocks, there was a ten second fixation screen.

Behavioral data analysis

To index an individual's propensity to interpret ambiguous faces negatively ("negativity bias"), we computed the percent of ambiguous trials in which participants selected the "feels bad" option. Based on prior work examining responses to ambiguity (Neta & Tong, 2016), we also computed average response times (RTs) by expression type (threatening, nonthreatening, ambiguous), as well as RT differences by expression type.

Sensitivity analyses of post-scan behavioral task. One participant demonstrated a decline in performance partway through the post-scan task, which resulted in five blocks in which this participant had low accuracy on angry trials due to repeated button presses. To account for these blocks in which this participant appeared not to be engaging with the task, we conducted sensitivity analyses for all statistical models involving data from the post-scan task. In these analyses, we excluded this participant's response data from the five blocks in which their accuracy on angry and happy trials was less than 80% ($N = 100$ usable trials). Unless otherwise stated, all reported results from behavioral analyses remained after excluding this participant's low-accuracy blocks.

Results

ELA, global functioning, and post-scan task behavior

ELA and global functioning

As hypothesized, individuals with greater self-reported ELA reported poorer global functioning (i.e., higher HoNOS scores; $\beta = 0.32$, 95% CI [0.02, 0.63], t (35) = 2.19, $p = 0.04$).

Post-scan task behavior

We conducted one-tailed t-tests to ensure that accuracy was significantly above chance performance (50%) on the threatening and nonthreatening (i.e., unambiguous) trials in the post-scan task. These analyses were conducted in order to verify that participants understood the task instructions. Results confirmed that participants correctly rated angry facial expressions negatively (mean accuracy = 0.93; t (40) = 30.6; $p < 0.001$) and happy facial expressions positively (mean accuracy = 0.96; t (40) = 71.5; $p < 0.001$; *Supplemental Figure 3*). This pattern of high accuracy and agreement in ratings also verified that the valences of these two types of images were indeed unambiguous. In line with prior work (Neta et al., 2009), participants took longer on average to evaluate surprised faces than angry (t (40) = 8.23, mean difference = 0.069

https://doi.org/10.1017/S0954579424000683 Published online by Cambridge University Press

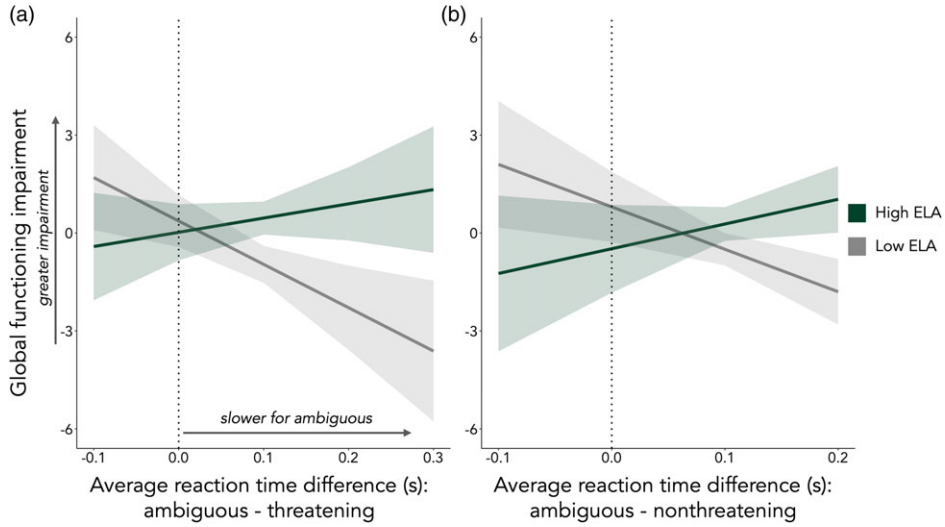

Figure 2. ELA interacted with reaction time to ambiguous cues to predict global functioning. For individuals exposed to lower levels of ELA, taking more time on average to evaluate ambiguous, relative to threatening (a) and nonthreatening (b) images was associated with better global functioning. The simple slopes for the association between ambiguous vs. threatening reaction difference and global functioning (a) are $b = 4.36$ and $b = -13.28$ for high and low ELA, respectively. The simple slopes for the association between ambiguous vs. nonthreatening reaction difference and global functioning (b) are $b = 7.58$ and $b = -13.01$ for high and low ELA, respectively. ELA was measured continuously, but is plotted categorically, at high ($z = 1.5$, in green) and low ($z = -1.5$, in gray) levels for visualization purposes only. Shaded regions represent 95% confidence intervals.

ms, 95% CI [0.05, 0.09], $p < 0.001$) or happy (t (40) = 9.85, mean difference = 0.097 ms; 95% CI [0.08, 0.12], $p < 0.001$) faces, supporting the idea that that surprised facial expressions are more ambiguously valenced.

We next tested whether ELA or global functioning related to negativity biases (i.e., the percent of ambiguous trials categorized negatively). After controlling for global functioning, individuals with greater ELA scores demonstrated a greater negativity bias (categorized a greater number of ambiguous faces negatively; $\beta = 0.34$, 95% CI [0.002, 0.68], t (34) = 2.04, $p = 0.049$). After excluding one participant's low-accuracy blocks in a sensitivity analysis (see *Sensitivity analyses of post-scan behavioral task* for description), this association was trending ($\beta = 0.34$, 95% CI [−0.005, 0.68], t (34) = 2.00, $p = 0.05$). Based on this sensitivity analysis and given that, on their own, neither ELA nor global functioning was associated with negativity biases (*Supplemental Tables 3 and 4*), we caution against strong interpretation of this finding. ELA and negativity biases did not interact to predict psychosocial functioning (*Supplemental Table 5*).

We next examined the relationship between reaction time (RT) and evaluations of the stimuli. Between-subject average RTs to ambiguous images did not predict negativity biases (*Supplemental Table 2*). However, in line with prior work (Neta & Tong, 2016), longer within-subject, trial-level RTs predicted more positive ratings of ambiguous stimuli in a multilevel model (OR = 1.95; 95% CI [1.44, 2.65], $z = 4.29$, $p < 0.01$).

Based on prior work suggesting that taking time to evaluate ambiguity may engage emotion regulation processes (Neta et al., 2022), we sought to determine whether ELA moderated association between time spent evaluating ambiguous (relative to unambiguous) stimuli and global functioning. We observed an interaction between RT differences and ELA exposure, such that taking more time on average to evaluate ambiguous, relative to threatening ($b = 5.88$, 95% CI [0.81, 10.95], t (33) = 2.36, $p = 0.02$; Figure 2A) and nonthreatening ($b = 6.86$, 95% CI [0.73, 12.99], t (33) = 2.28, $p = 0.03$; Figure 2B), images was associated with better global functioning, specifically in individuals with lower ELA scores.

ELA and similarity in neural representations of nonthreatening, threatening, and ambiguous stimuli

Using RSA, we tested our hypothesis that individuals with higher self-reported ELA would demonstrate greater similarity ("overlap") in representations of ambiguous and threatening stimuli within the regions of interest. We expected this association to be specific to ambiguous/threatening overlap — that is, we hypothesized no association between ELA and ambiguous/nonthreatening overlap or threatening/nonthreatening overlap.

Representational overlap: ambiguous and threatening stimuli

As hypothesized, individuals exposed to higher levels of ELA demonstrated greater similarity ("overlap") in multivariate representations of ambiguous and threatening stimuli bilaterally within the amygdala, nucleus accumbens, anterior insula, and vmPFC but not within the control region, V1 (Table 1; Figure 3). All associations remained significant after controlling for the number of voxels within a participant's ROI and after adjusting for multiple comparisons across different ROIs by using false discovery rate (FDR)-corrected q values (Table 1; Benjamini & Hochberg, 1995).

Representational overlap: ambiguous and nonthreatening stimuli

We next tested whether ELA was associated with representational overlap between ambiguous and nonthreatening stimuli. Contrary to our hypothesis, we found that ELA was positively associated with greater similarity in multivariate representations of ambiguous and nonthreatening stimuli in the right amygdala ($\beta = 0.03$; 95% CI [0.01, 0.06]; t (38) = 2.56, $p = 0.01$), even after controlling for participant-specific number of voxels within the region ($\beta = 0.03$, 95% CI [0.01, 0.06], t (37) = 2.51, $p = 0.02$). However, this was no

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Table 1. ELA was positively associated with greater similarity in multivariate representations of ambiguous and threatening stimuli in regions of interest. The same pattern was not evident in V1, the control region tested. Table includes the standardized beta coefficients and test statistics from a linear regression with z-scored log-transformed CTQ scores as the predictor and Fisher-*z*-transformed ambiguous/threatening RSA values as the outcome. Table includes false discovery rate (FDR)-corrected *q* values that adjust for multiple comparisons across different regions. Column on the right includes the same statistics after participant-specific ROI size was added as a covariate in the model.

Region	Standardized beta value	95% CI	*t* value	*p* value	*q* value	Adjusted for ROI size
Amygdala						
Right	$\beta = 0.05$	[0.02, 0.08]	$t\ (38) = 3.31$	$p < 0.01$	$q = 0.01$	$\beta = 0.05$ [0.02, 0.08], $t\ (37) = 3.26$, $p < 0.01$
Left	$\beta = 0.05$	[0.02, 0.08]	$t\ (38) = 3.07$	$p < 0.01$	$q = 0.01$	$\beta = 0.05$ [0.02, 0.08], $t\ (37) = 3.00$, $p < 0.01$
Nucleus accumbens						
Right	$\beta = 0.03$	[0.01, 0.06]	$t\ (38) = 2.44$	$p = 0.02$	$q = 0.04$	$\beta = 0.03$ [0.01, 0.06], $t\ (37) = 2.43$, $p = 0.02$
Left	$\beta = 0.04$	[0.01, 0.07]	$t\ (38) = 3.16$	$p < 0.01$	$q = 0.01$	$\beta = 0.04$ [0.02, 0.07], $t\ (37) = 3.20$, $p < 0.01$
Anterior insula						
Right	$\beta = 0.04$	[0.01, 0.07]	$t\ (38) = 2.78$	$p < 0.01$	$q = 0.02$	$\beta = 0.04$ [0.01, 0.07], $t\ (37) = 2.52$, $p = 0.02$
Left	$\beta = 0.04$	[0.003, 0.08]	$t\ (38) = 2.20$	$p = 0.03$	$q = 0.04$	$\beta = 0.04$ [0.0003, 0.08], $t\ (37) = 2.04$, $p = 0.049$
vmPFC						
Right	$\beta = 0.04$	[0.01, 0.07]	$t\ (38) = 2.36$	$p = 0.02$	$q = 0.04$	$\beta = 0.04$ [0.01, 0.08], $t\ (37) = 2.38$, $p = 0.02$
Left	$\beta = 0.04$	[0.003, 0.07]	$t\ (38) = 2.24$	$p = 0.03$	$q = 0.04$	$\beta = 0.03$ [0.003, 0.07], $t\ (37) = 2.18$, $p = 0.04$
V1 (control region)						
Right	$\beta = -0.01$	[−0.07, 0.05]	$t\ (38) = -0.27$	$p = 0.79$	$q = 0.88$	$\beta = -0.01$ [−0.07, 0.05], $t\ (37) = -0.24$, $p = 0.81$
Left	$\beta = 0.005$	[−0.06, 0.07]	$t\ (38) = 0.15$	$p = 0.88$	$q = 0.88$	$\beta = 0.01$ [−0.06, 0.07], $t\ (37) = 0.24$, $p = 0.81$

longer significant following FDR-corrected adjustments for multiple comparisons across different ROIs (FDR-adjusted $q = 0.14$; *Supplemental Table 7*). Although a similar pattern was observed in the right anterior insula, this association did not reach significance ($\beta = 0.03$; 95% CI [0.00, 0.06]; $t\ (38) = 1.96$, $p = 0.06$). This association was not evident within any of the other regions tested (*Supplemental Table 7*).

Representational overlap: threatening and nonthreatening stimuli

We next tested whether ELA was associated with representational overlap between threatening and nonthreatening stimuli. Contrary to our hypothesis, we found that individuals with higher ELA scores evidenced greater similarity in representations of threatening and nonthreatening stimuli within the right anterior insula ($\beta = 0.03$, 95% CI [0.003, 0.06], $t\ (38) = 2.23$, $p = 0.03$), even after controlling for the number of voxels within the region ($\beta = 0.04$, 95% CI [0.01, 0.06], $t\ (37) = 2.51$, $p = 0.02$). However, this was no longer significant following FDR-corrected adjustments for multiple comparisons across different ROIs (FDR-adjusted $q = 0.22$; *Supplemental Table 9*). This association was not evident in the left anterior insula or within any of the other regions tested (*Supplemental Table 9*).

Associations between brain, behavior, and global functioning

Representational overlap between ambiguous and threatening stimuli and global functioning

We hypothesized that greater representational overlap between ambiguous and threatening stimuli would be associated with poorer global functioning. However, we did not observe any significant associations between global functioning and representational similarity between ambiguous and threatening stimuli (*Supplemental Table 11*).

Representational overlap between ambiguous and threatening stimuli and post-scan task behavior

We hypothesized that greater representational similarity between ambiguous and threatening stimuli would predict greater negativity biases in the post-scan task, but we did not observe this hypothesized association (*Supplemental Table 12*).

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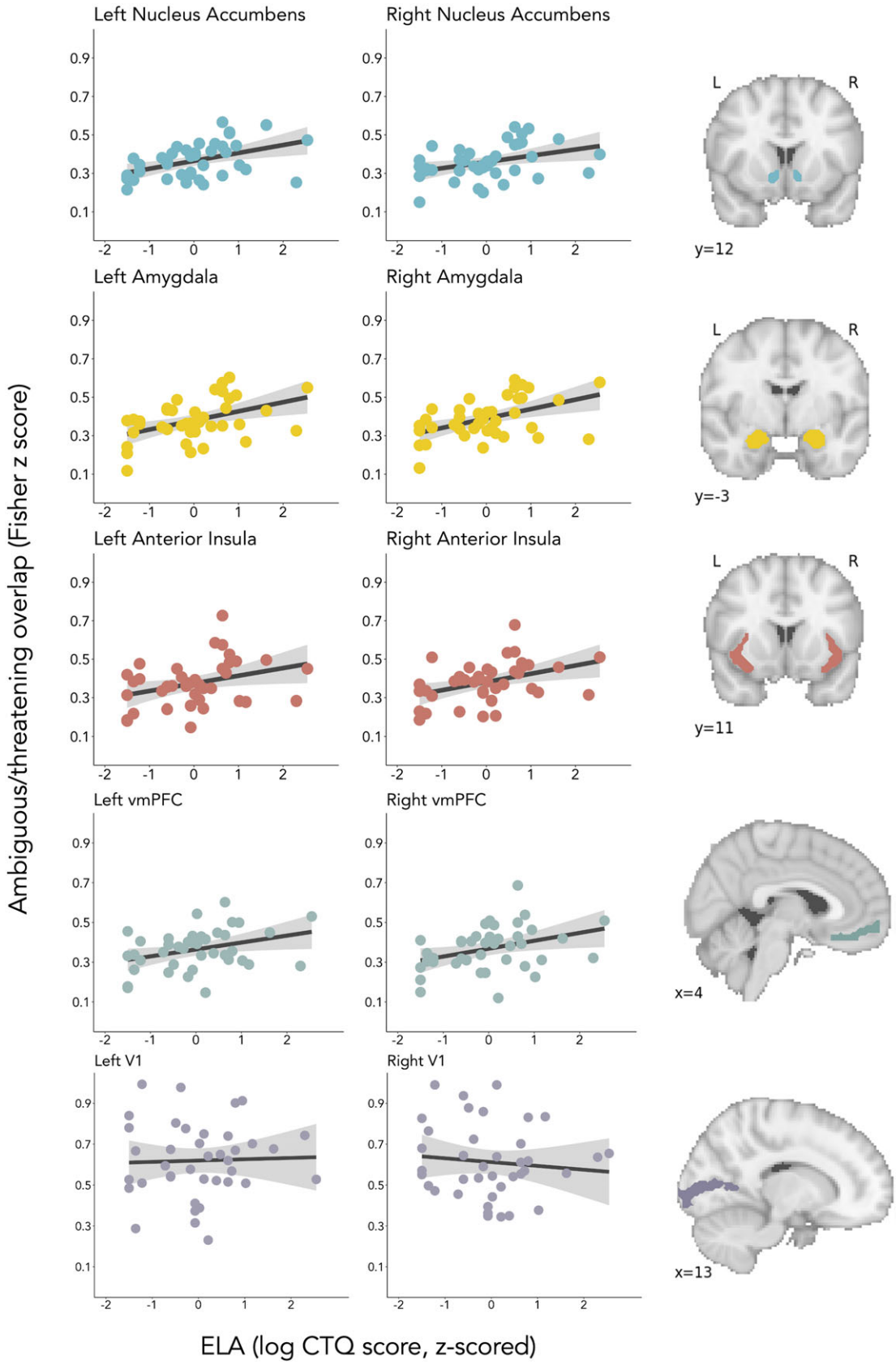

Figure 3. As hypothesized, individuals exposed to higher levels of ELA demonstrated greater representational overlap between ambiguous and threatening stimuli bilaterally within the nucleus accumbens, amygdala, anterior insula, and vmPFC, but not within V1.

https://doi.org/10.1017/S0954579424000683 Published online by Cambridge University Press

Discussion

Exposure to ELA impacts the development of threat-sensitive neural circuitry (Fareri & Tottenham, 2016; Herzberg & Gunnar, 2020). Altered functioning within these networks may underlie hypersensitivity to potential threat in the face of ambiguity, potentiating risk for impaired psychosocial functioning (Lecei & van Winkel, 2020; Nusslock & Miller, 2016). Leveraging RSA to characterize multivariate representations of affective stimuli, we found that emerging adults exposed to ELA demonstrated greater similarity ("overlap") in their representations of ambiguous and threatening images within affective and threat-sensitive circuitry. Notably, rather than a general effect in which individuals with a history of ELA simply exhibited general impairments in differentiating among affective cues, we found that ELA specifically related to attenuated discrimination between ambiguity and threat. These results were not evident in the tested control region (V1), suggesting specificity of the effect to threat-sensitive affective circuitry commonly found to be affected by ELA exposure (Cohodes et al., 2021; Fareri & Tottenham, 2016; Hein & Monk, 2017).

These results provide support for Lecei and van Winkel's (2020) theoretical model, which stipulates that ELA results in impaired pattern separation (i.e., impaired differentiation, or greater similarity) of emotional information, specifically in the presence of negative or ambiguous stimuli. In turn, this impairment is hypothesized to result in increased fear generalization, threat anticipation, and psychopathological symptoms. Our behavioral findings suggest that individual differences in processing ambiguity relate to global functioning, and that this association varies as a function of ELA exposure. Crucially, we examined these processes in individuals experiencing the transition from adolescence to adulthood. During this developmental stage, risk for psychopathology is heightened (Solmi et al., 2022) — especially within populations with a history of caregiving adversity (van der Vegt et al., 2009) — and responses to ambiguity are believed to have an increased effect on mental health (Bardi et al., 2009; Silvers & Peris, 2023). Results from the current study have implications both for basic models regarding how ELA shapes neural representations of threat and ambiguity, as well as for the role that ambiguity processing may play in psychosocial functioning following early life adversity.

Effects of ELA on representations of threat and ambiguity

The tendency to represent ambiguity similarly to threat following ELA may reflect an adaptive, learned response stemming from childhood experiences (Lecei & van Winkel, 2020). When repeatedly faced with threatening experiences, it is rational to infer threat when presented with an ambiguous scenario (Dunsmoor & Paz, 2015). Furthermore, having a low threshold for threat detection is an adaptive response that serves to protect an individual living in a high-threat environment from further harm (Boyce & Ellis, 2005; Chaby et al., 2015; Pollak & Kistler, 2002). The observed pattern of results, in which ELA-exposed individuals demonstrate impaired neural differentiation between ambiguous and threatening social cues, could stem from hypersensitive threat detection mechanisms. Notably, associations with ELA were only robustly observed when comparing neural representations of ambiguous and threatening cues, suggesting that ELA-exposed individuals do not simply exhibit general impairments in differentiating among affective cues. This specificity in observed results dovetails with existing theoretical models of hypersensitivity to threat (McLaughlin & Lambert, 2017), especially in the face of ambiguity (Lecei & van Winkel, 2020), following early life adversity. However, given that representational similarity did not predict subsequent appraisals of the ambiguous stimuli, it is possible that while rapid, initial responses to ambiguity are highly similar to responses to threat in ELA-exposed individuals, top-down compensatory mechanisms regulate responses in the decision-making phase. The role of potential regulatory mechanisms is especially important to consider given that participants were from a sample of college students with relatively healthy psychosocial functioning. Further research on how initial representations of ambiguity and regulatory processes interact to shape behavior is warranted.

Ambiguity processing and psychosocial functioning after ELA exposure

Contrary to our hypothesis, we did not observe a robust association between ELA and negativity biases in interpretations of ambiguity. Replicating prior work (Neta & Tong, 2016), we found that taking longer to evaluate ambiguous, relative to unambiguous, stimuli predicted subsequent positive appraisals, lending support to the idea that positive evaluations of ambiguity may require top-down regulatory mechanisms (Neta et al., 2022; Neta & Tong, 2016). Based on research linking responses to ambiguous stimuli to psychosocial outcomes (Lissek et al., 2010; Williams et al., 2007), we tested whether behavioral responses to ambiguity related to global functioning, and whether this differed as a function of ELA exposure. In line with the notion that slower responses to ambiguity reflect regulatory processes, taking longer to evaluate ambiguous relative to unambiguous images was associated with better global functioning, specifically in individuals with lower ELA levels. Research suggests that more deliberative and regulated responses are more advantageous in predictable environments (Kidd et al., 2013). In line with this reasoning, the observed interaction suggests that reliance on slower and ostensibly more calculated evaluations of ambiguity are associated with better functioning in individuals with low exposure to adversity. Investigation in a larger sample is needed to understand how this effect differs at various levels of ELA exposure and whether these group differences are driven by variations in self-regulation or other relevant mechanisms.

Strengths and limitations

The current study offers novel insights into the associations between ELA and neural processing of emotional information by leveraging multivariate pattern analyses. Our analytic approach enabled us to examine distributed patterns of brain activity within affective circuitry and, crucially, test similarity between multivariate representations of ambiguity and threat. This study design also allowed us to demonstrate specificity in our findings in that we provide evidence that these effects primarily pertain to ambiguity and threat, and within putatively affective, threat-sensitive circuitry. That said, given the limited sample size, the results from this study should be treated as provisional. Future studies replicating the current findings in a larger longitudinal sample could provide greater clarity into how ELA shapes representations of ambiguity.

Prior research suggests that negative responses to ambiguity may reflect hypersensitivity in the affective processes that govern rapid threat detection (Chen & Lovibond, 2016; Grupe & Nitschke, 2013; Mathews et al., 1997). Based on this work, we designed a task to probe rapid, uninstructed representations of ambiguity while participants were in the scanner. To this end, we asked participants to simply view

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the images while in the scanner and measured explicit categorizations of the images during the post-scan task. An important next step for future research is to characterize neural representations during the interpretation stage in which participants explicitly evaluate the valence of ambiguous stimuli. Moreover, based on similar prior work (Vantieghem et al., 2017), and to avoid biasing responses, participants rated whether the person in the image "feels good" or "feels bad". As a result, we did not capture explicit ratings of threat. Future work may benefit from a more precise measurement of the extent to which participants interpret the images as threatening.

Lastly, we measured ELA by incorporating retrospective reports of abuse and neglect into a broader summary measure. Examining ELA continuously via CTQ scores enabled us to demonstrate a linear relationship between severity of adversity history and the degree of similarity in representations of ambiguity and threat. While we did not have adequate power to investigate how different dimensions of experiences (e.g., threat or unpredictability in the caregiving environment) may differentially shape representations of ambiguity, this is an important avenue for future research.

Conclusion

Exposure to ELA, including experiences of abuse and neglect, is estimated to account for between 30% to 45% of psychopathologies worldwide (Green et al., 2010; Kessler et al., 2010; McLaughlin et al., 2012). Using multivariate pattern analysis, we provide novel insight into how ELA shapes threat-sensitive neural circuitry, evidencing reduced neural differentiation between ambiguous and threatening cues in ELA-exposed individuals, and link behavioral responses to ambiguity to psychosocial wellbeing during the transition to adulthood. Interventions that target responses to ambiguity may be particularly powerful in mitigating the detrimental effects of adverse early experiences.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0954579424000683.

Data and code availability. All data, task scripts, and analysis code for this study are available on GitHub (https://github.com/nsaragosaharris/earlylifeadversity_ambiguity_study).

Acknowledgements. This work was supported by the UCLA Academic Senate funds (JAS) and Semel Institute funds (TSP). During study design, data collection, and manuscript preparation, NMSH was supported by a Eugene V. Cota-Robles Fellowship Grant, a National Science Foundation Graduate Research Fellowship Program Grant (DGE-1650604), an Edwin Pauley Fellowship, a Graduate Summer Research Mentorship Program Grant, and National Institute of Child Health and Human Development T32 Predoctoral Training Program Grant. JFGM was supported by a National Science Foundation Graduate Research Fellowship (Fellow ID: 2016220797) and a National Institute of Child Health and Human Development T32 Predoctoral Training Program Grant during study design, data collection, and manuscript preparation. We thank our participants for taking part in this study and thank Maria Calderón, Elizabeth Campbell, Joyce Forster, Breanna Gomez, Casandra Gomez Alvarado, Ambar Hernandez, and Aayush Patel for help with recruitment, data collection, and data management.

Competing interests. The authors report no conflicts of interest.

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