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# An Exploration of Amygdala-Prefrontal Mechanisms in the Intergenerational Transmission of Learned Fear

Abbreviated title: Intergenerational fear

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Keywords: Neurodevelopment, learning, amygdala, parenting, emotion, fMRI



## RESEARCH HIGHLIGHTS

- Youth show stronger fear learning when observing parents compared to unfamiliar adults.
- Amygdala-mPFC circuitry supports observational learning in youth.
- Individual differences in parent brain (amygdala and mPFC recruitment during firsthand conditioning) and behavior (trait anxiety) correspond to youth brain and behavior during observational learning.

## ABSTRACT

Humans learn about their environments by observing others, including what to fear and what to trust. Observational fear learning may be especially important early in life when children turn to their parents to gather information about their world. Yet, the vast majority of empirical research on fear learning in youth has thus far focused on firsthand classical conditioning, which may fail to capture one of the primary means by which fears are acquired during development. To address this gap in the literature, the present study examined observational fear learning in youth ( $n=33$ ; age range: 6-17 years) as they watched videos of their parent and an “unfamiliar parent” (i.e., another participant’s parent) undergo fear conditioning. Youth demonstrated stronger fear learning when observing their parent compared to an unfamiliar parent, as indicated by changes in their self-reported liking of the stimuli to which their parents were conditioned (CS+, a geometric shape paired with an aversive noise; CS-, a geometric shape never paired with an aversive noise) and amygdala responses. Parent trait anxiety was associated with youth learning better (i.e., reporting a stronger preference for the CS- relative to CS+), and exhibiting stronger medial prefrontal-amygdala connectivity. Neuroimaging data were additionally acquired from a subset of parents during firsthand conditioning, and parental amygdala and mPFC activation were associated with youth’s neural recruitment. Together, these results suggest that youth preferentially learn fears via observation of their parents, and this learning is associated with emotional traits and neural recruitment in parents.

Keywords: Neurodevelopment, learning, amygdala, parenting, emotion, fMRI

## INTRODUCTION

As members of a social species, humans learn readily by observing conspecifics (Bandura, Blahard, & Ritter, 1969; Rachman, 1977). Observational learning may be especially important early in life when children turn to their parents to gather information about their world – including which stimuli are safe and which pose a threat (Debiec & Olsson, 2017; Sorce, Emde, Campos, & Klinnert, 1985). While emerging evidence from rodent models suggests that this learning pathway plays a crucial role in parent-to-offspring transmission of affective learning (Debiec & Sullivan, 2014), it remains understudied in humans. The present study sought to fill this knowledge gap by testing whether youth preferentially learn by observing their parents as opposed to other adults, and how amygdala-mPFC circuitry support this learning. We further sought to address what behavioral (i.e., trait anxiety) and neural phenotypes (i.e., recruitment of fronto-limbic circuitry involved in fear learning) in parents are associated with observational learning in youth.

Learning what cues constitute threat versus safety promotes surviving and thriving in one's environment. While the vast majority of fear learning research has historically focused on classical conditioning paradigms wherein a participant learns through firsthand experience to associate a neutral conditioned stimulus (CS) with an aversive unconditioned stimulus (US), both human and non-human animals can acquire learned fears by observing conspecifics exhibit fear behavior towards a stimulus (Bandura et al., 1969; Hygge & Ohman, 1978; Kavaliers, Choleris, & Colwell, 2001; Mineka & Cook, 1993; Mineka, Davidson, Cook, & Keir, 1984; Olsson, Nearing, & Phelps, 2007; Olsson & Phelps, 2004). While little behavioral research – and no neuroscientific research in humans – has examined observational fear learning in youth, two lines of evidence strongly suggest that youth can engage in this form of learning. First, youth can acquire an aversion to

neutral stimuli that are repeatedly paired with static fearful facial expressions (Askew, Dunne, Ozdil, Reynolds, & Field, 2013; Askew & Field, 2007; Dunne & Askew, 2013). Second, retrospective studies of adults with phobias suggest that childhood fears and phobias are often acquired vicariously (Ollendick & King, 1991; Öst, 1987).

Clinical and empirical data suggest that parents can potentiate observational fear learning in their offspring. For example, there is strong clinical evidence to suggest that fears, anxieties and phobias run in families, and that this link is at least partially mediated by parents modeling fearful or anxious behavior (Gerull & Rapee, 2002; Kendler, 2001; Thapar & McGuffin, 1995). Empirical data dovetails nicely with these findings by suggesting that parental fear expression influences approach and avoidance behaviors in youth (Egliston & Rapee, 2007; Gerull & Rapee, 2002; Muris, Steerneman, Merckelbach, & Meesters, 1996a; Sorce et al., 1985; Tamis-LeMonda et al., 2008), and that infants show preferential fear learning when their mothers model fear compared to when strangers do so (Zarbatany & Lamb, 1985). The tendency to readily learn about threats from parents appears to be evolutionarily conserved, as evidenced by the fact that rat pups acquire novel fear associations for a stimulus after observing their mothers express fear towards it (Debiec & Sullivan, 2014).

Several pieces of data hint at the possibility that the amygdala and medial prefrontal cortex (mPFC) support observational fear learning in youth and that this circuitry may be preferentially recruited during observation of one's parents. However, no prior work in humans has directly tested this hypothesis. Cross-species data indicate that amygdala-mPFC circuitry acquires, maintains and expresses firsthand fear learning (Burgos-Robles, Vidal-Gonzalez, & Quirk, 2009; Corcoran & Quirk, 2007; Etkin, Egner, & Kalisch, 2011; Herry, Vouimba, & Garcia, 1999; Laurent & Westbrook, 2009; Laviolette, Lipski, & Grace, 2005; Mechias, Etkin, & Kalisch, 2010), as well as observational fear

learning in adults (Olsson et al., 2007). This together with the fact that amygdala-mPFC circuitry supports firsthand fear learning in youth strongly implies that the same circuitry may underlie observational learning in youth (Silvers et al., 2016). While no research in humans has examined whether observing one's parent undergoing fear learning preferentially engages amygdala-mPFC circuitry in youth, there is evidence that amygdala-mPFC circuitry processes pictures of parents differently from strangers (Todd, Evans, Morris, Lewis, & Taylor, 2010; Tottenham, Shapiro, Telzer, & Humphreys, 2012). Moreover, across species it has been demonstrated that parental cues uniquely modulate the amygdala response during conditioning (Moriceau & Sullivan, 2006; Thompson, Sullivan, & Wilson, 2008), and that the amygdala supports observational fear learning via the mother's distress behaviors in juvenile rodents (Debiec & Sullivan, 2014).

The present study sought to test the hypothesis that parents enhance observational fear learning for their children, as compared to unfamiliar adults. We employed a wide age range because while it is clear that parents shape fear appraisals in early childhood (Sorce et al., 1985), less is known about whether older children and adolescents continue to reference parents when learning about potentially threatening stimuli. There are reasons to believe that they do not, given that youth seek greater autonomy from their parents during the transition to adolescence (Steinberg & Silverberg, 1986). However, it is also possible that older children and adolescents do reference parents during threat learning, given that parents continue to influence risk taking and emotion regulation to some degree in adolescence (Morris, Criss, Silk, & Houlberg, 2017; Telzer, Ichien, & Qu, 2015). Because of the amygdala's role in both firsthand and observational fear learning, it was hypothesized that parent-derived observational learning would be supported by amygdala recruitment and amygdala-



mPFC connectivity. Given behavioral research suggesting that parent-to-child transmission of fear is mediated by parental expression of fear (Muris, Steerneman, Merckelbach, & Meesters, 1996b) and that anxious behavior in a model facilitates observational learning in adults (Selbing & Olsson, 2019) and in rodents during development (Debiec & Sullivan, 2014), we sought to test whether parent anxiety might enhance fear learning in youth. The logic behind this was that parental anxiety might facilitate fear transmission between parents and offspring. Finally, we conducted exploratory analyses in a subset of parents and youth to examine whether parental recruitment of amygdala-mPFC circuitry during firsthand conditioning predicted youth's neural recruitment during observational learning about their parent.

## METHODS

### **METHODS RELATED TO YOUTH PARTICIPANTS**

#### **Overview and description of participants**

Participants completed a laboratory testing session that involved filling out questionnaires and participating in other behavioral tasks that are to be reported in forthcoming manuscripts. Approximately one month after the lab session, participants completed a fMRI testing session. 33 youth (21 female, 12 male) ranging in age from 6-17 years (Mean=12.45 years, S.D.=3.09) provided usable behavioral and neuroimaging data. 8 participants self-identified as African-American or Black, 3 as American Indian or Alaska Native, 6 as Asian-American, 8 as European-American or White, 8 as Hispanic or Latino(a) and 8 did not report their ethnic or racial identity (participants could select more than one race or ethnicity). 14 additional youth completed neuroimaging testing but were excluded from analyses due to excessive head motion (details on head motion are described below; 9 female, 5 male; Mean age=9.3 years, S.D.=1.6). Youth who were

excluded due to head motion were on average younger than the individuals comprising the final sample ( $t(45)=3.64, p<.001$ ), but did not differ in terms of gender ( $X^2(1,47)=.13, p=.72$ ). While age was included as a covariate in analyses, the primary goal of this study was to establish proof-of-concept evidence that parents modulate observational learning in youth rather than to examine age-related changes in observational learning. Youth trait anxiety was assessed using the parent report on the Screen for Childhood Anxiety Related Disorders (SCARED) in 25 participants (Mean score=11.48, S.D.=8.75) (Birmaher et al., 1999). Mean SCARED scores were not significantly different for the youth with usable fMRI data as compared to youth with unusable data (SCARED data was collected for 10 of the 14 youth with unusable data; Mean=13.2;  $t(33)=.43, p=.67$ ). The SCARED was not collected in 8 participants due to parents failing to complete the questionnaire or to experimenter error. All youth participants provided informed assent and procedures were approved by the Institutional Review Board at Columbia University. Data are hosted at <https://www.labarchives.com/> and can be obtained by emailing the senior author, [nlt7@columbia.edu](mailto:nlt7@columbia.edu).

### **Observational conditioning task**

**Paradigm.** Participants completed four runs of an observational conditioning task while undergoing fMRI scanning (Figure 1). This task was inspired by prior work in adults (Haaker, Golkar, Selbing, & Olsson, 2017; Olsson et al., 2007), and modified to test the hypothesis that observational learning is potentiated when youth observe their parents as opposed to an unfamiliar adult. Youth were told that they were going to watch a video of their parent and then another youth's parent ("unfamiliar parent" condition; order of parent and unfamiliar parent was counterbalanced across participants) completing a task that they themselves would soon complete. They were also told that when they completed the task themselves, they would see shapes and sometimes hear a loud

noise. The US, a loud unpleasant high-frequency white noise (Silvers et al., 2016; Tottenham, Shapiro, Flannery, Caldera, & Sullivan, 2019), was then played for the participant once before completing the task. Skin conductance data was collected but only 13 participants exhibited usable, non-zero data in any of the experimental conditions and thus it was not analyzed further.

Prior to observational conditioning (at “baseline”), participants rated how much they liked the CS+ and CS- on a scale of 1-5 (1=least liking, 5=most liking). Youth participants next completed the fear “acquisition phase” of the observational conditioning procedure wherein they watched a video of either their parent or the unfamiliar parent completing a firsthand conditioning task. In this task, parents were seated in front of a computer display and viewed two differently colored geometric shapes over the course of 16 trials while wearing headphones. The CS+ shape was paired with an aversive noise (unconditioned stimulus, US) on 75% of trials while the CS- shape was never paired with an aversive noise. On “reinforced” CS+ trials, the US was presented for the last 500 ms of the CS+ shape presentation. The CS- and CS+ were presented for a variable amount of time ranging from 500 to 19,000 ms (average=5,000 ms) and were separated by a variable fixation period (mean duration = 10,000 ms; range = 5,500-26,000 ms). CS- and CS+ trials were presented in a semi-randomized order created by Optseq. Importantly, youth participants could see the computer screen and their parent or unfamiliar parent’s face in the video, but could not hear the US (aversive noise) in the video (since the noise was delivered to parents via headphones).

Multiple versions of the conditioning task were programmed such that the CS+ and CS- could be a pink circle, blue diamond, green square or orange triangle. Shape assignment to the CS- or CS+ condition was counterbalanced across participants. The CS- and CS+ were always distinct for the parent and unfamiliar parent (i.e., if the parent

had a pink circle for either the CS+ or CS- the unfamiliar parent had it for neither condition). The unfamiliar parent was race, age and gender-matched as closely as possible to the youth participant's parent. Participants were instructed to press a button whenever they thought the adult (parent or non-parent) was about to hear the US. After completing the acquisition phase, participants again rated how much they liked the CS- and CS+ on a scale of 1-5.

After the acquisition phase, participants completed the "test phase" of the observational conditioning procedure. Participants were instructed that they would be completing the same task that they had seen in the video and were presented with 8 CS- and 8 non-reinforced (no US) CS+ trials. The CS- and CS+ were presented for a variable amount of time ranging from 500 to 11,500 ms (average=5,000 ms) and were separated by a variable fixation period (mean duration = 10,000 ms; range = 5,500-26,000 ms). CS- and CS+ trials were presented in a semi-randomized order created by Optseq (two different orders were created and presented in a counterbalanced manner across participants). The final (17<sup>th</sup>) trial featured a reinforced CS+ trial, which was discarded from analyses. At the conclusion of the test phase, participants again rated how much they liked the CS- and CS+ on a scale of 1-5. After completing the acquisition and test phases for their parent, participants completed the acquisition and test phases for the unfamiliar parent. Order of parent and unfamiliar parent was counterbalanced between participants.

**Behavioral analyses.** Behavioral analyses were carried out in SPSS 25.0. Participants' self-reported liking for the CS- and CS+ were subjected to a repeated measures univariate GLM with the following predictors: model (parent vs. unfamiliar parent), condition (CS- vs. CS+), study phase (baseline, post-acquisition and post-test), and mean-centered age. Sex did not constitute a main effect on stimulus liking nor did it

interact with any factors to predict liking ( $p$  values  $> .10$ ). Sex was thus not included in the results of this analysis reported here nor in any subsequent analyses in the interest of preserving degrees of freedom. Main effects and interactions were further interrogated using paired  $t$ -tests, when appropriate.

### **fMRI data acquisition and individual-level analyses**

**Acquisition.** Whole-brain imaging data were collected on a 3T GE SIGNA scanner using a NOVA 32-channel head coil. Participants completed a whole-brain high-resolution, T1\*-weighted anatomical scan (SPGR) and four functional runs. T2\*-weighted echoplanar images (ascending interleaved) were collected at an oblique angle ( $20^\circ$ ) (TR = 2000 ms; TE = 30 ms; flip angle =  $75^\circ$ ; FOV = 200 mm; 34 slices; 4 mm thick contiguous slices). For youth participants, the two acquisition runs were comprised of 122 TRs and the two test runs were comprised of 119 TRs (after the final trial was removed).

**Preprocessing.** Preprocessing was performed using SPM8 preprocessing tools (<https://www.fil.ion.ucl.ac.uk/spm/>) in NeuroElf (<http://neuroelf.net>). The first 4 volumes for each participant were discarded to allow for scanner signal stabilization. Preprocessing steps for the functional images included motion correction, slice-time correction and coregistration to the first functional image for each subject. Structural images were spatially normalized, using unified segmentation, to a standard template brain (MNI avg15T1.img) and warping parameters were applied to functional images for each subject. Normalized functional images were interpolated to 3 x 3 x 3 mm voxels and spatially smoothed with a 6-mm Gaussian filter. Volumes with 1 mm or more framewise head motion were censored (removed from the timecourse) and their preceding volume was removed. Participants were removed from analyses if 20% or more of their volumes were censored from any task run (or from the one task run, in the

case of parent participants). Among the 33 youth participants who were included in analyses, only 2.3% of volumes were censored.

**Individual fMRI analyses.** Task regressors were created for acquisition CS- trials, acquisition CS+ trials, test CS- trials and test CS+ trials. No separate task regressors were made for the presentation of US noise as this only occurred on the final test CS+ trial and was removed from the timecourse. Boxcar regressors for the different trial types were convolved with the hemodynamic response function in NeuroElf. A robust regression analysis was performed on the conditions of interest for each subject as well as estimates of global signal for each tissue type. Data were filtered using a high-pass filter. Six motion regressors (x, y and z displacement; pitch, roll and yaw rotation) and their 6 derivatives were included as covariates. Psychophysiological interaction (PPI) analyses were conducted using default settings in NeuroElf to examine amygdala-mPFC connectivity. The left amygdala ROI was used as a seed given results described below demonstrating differential activation for parents and strangers during observational learning over time. Separate regressors (generalized PPI) were made for the seed region time course as well as the interaction between the seed region time course and the CS+ and CS- conditions during the acquisition and test periods. The seed region timecourse was not deconvolved prior to the creation of regressors. Global signal estimates for each tissue type along with the six motion regressors and their derivatives were included as covariates of no interest. Once an estimate of the amygdala time course x condition interaction was calculated for each condition, connectivity estimates were extracted from the mPFC ROI for the CS+ and CS- conditions for each phase of the task.

**Group fMRI analyses.** Subject-level beta values were extracted from regions of interest (ROIs) in the bilateral amygdala and mPFC and analyzed in SPSS 25.0. Amygdala ROIs were defined using automated anatomical labeling in the MarsBaR toolbox for SPM8

(MNI: -24, -2, -18; 27, 1, -19). Prior work has suggested that parents exert a particularly powerful influence on the left amygdala, and thus this was the focus of our analyses (Tottenham et al., 2012). No significant main effects or interactions were observed in the right amygdala. The mPFC ROI was defined by placing a 8 mm sphere around mPFC coordinates (MNI: 1, 46, 24) reported in a prior fMRI study of observational conditioning (Olsson et al., 2007).

## **METHODS RELATED TO PARENT PARTICIPANTS**

### **Overview and description of participants**

The primary caregiver for each of the 33 youth completed a behavioral testing session wherein they completed questionnaires about themselves and their child and also underwent the firsthand conditioning task below (22 parents, 8 of whom had 2 or more children enrolled; Mean age=41.48 years; 18 female, 4 male). 17 of the 33 parents reported their trait anxiety using the State-Trait Anxiety Inventory (Mean score = 36.12; S.D.=9.07) (Spielberger, Gorsuch, Lushemne, Vagg, & Jacobs, 1983). Because 4 out of 17 parents had 2 or more youths in the study, parent trait anxiety scores were available for 21 youth participants. The other 16 parents did not complete due to experimenter error. 14 of the 33 parents completed neuroimaging testing in a separate testing session. 6 of the 14 parents who completed neuroimaging were the parent to 2 or more youths who completed neuroimaging testing, thus enabling us to analyze neuroimaging data in 23 parent-youth dyads. Parents who did not undergo scanning either did not participate because of contraindications (e.g., metal in the body) or because of time constraints. All parent participants provided informed consent and procedures were approved by the Institutional Review Board at Columbia University.

### **Firsthand conditioning task**

Parents completed the same conditioning task, but with different stimuli, during the behavioral session in the laboratory as well as inside the MRI scanner. Task details are described above in the section labeled “Observational conditioning task.” Skin conductance data was collected during the lab session but only 9 participants exhibited usable, non-zero data in any of the experimental conditions and thus it was not analyzed further.

### **Behavioral data analysis**

Participants rated how much they liked the CS+ and CS- on a 1-5 likert scale before and after completing the conditioning task (1=not at all, 5=very much).

### **fMRI data acquisition and analysis**

**Acquisition.** The parents conditioning task was comprised of 122 TRs and used the same parameters as the observational conditioning task described above.

**Preprocessing.** Preprocessing steps were identical to those described above for youth participants. No parents had to be removed due to excessive head motion.

**Individual and group-level fMRI analyses.** Task regressors were created for CS- trials, CS+ trials, and the US (at the end of reinforced CS+ trials). Analyses mirrored what was done in youths described above.

### **ANALYTIC PLAN**

#### **(Q1) Behavioral data: Do youth learn preferentially by observing their parents?**

As described above, a repeated-measures univariate GLM was implemented to examine youth participant’s self-reported liking for the CS- and CS+ presented during observational conditioning. Participants reported how much they liked the CS- and CS+ at baseline (prior to learning), after observing their parents learning (post-acquisition), and after being repeatedly presented with the CS- and CS+ (post-test). The data were subjected to a single model (parent vs. unfamiliar parent) x condition (CS- vs. CS+) x



study phase (baseline, post-acquisition, post-test) model. To test whether observing parents evoked better learning, we examined the model (parent vs. unfamiliar parent) x condition (CS+ vs. CS-) and model (parent vs. unfamiliar parent) x condition (CS- vs. CS+) x study phase (baseline, post-acquisition, post-test) interactions. Significant interactions were interrogated with follow-up paired t-tests, where appropriate, to examine whether individuals showed better learning (a larger difference in liking for CS- vs. CS+) for parents than strangers and whether this increased over the course of the experiment. All data were free of outliers, as defined by less than 3\*interquartile range beneath the 25<sup>th</sup> percentile or more than 3\*interquartile range above the 75<sup>th</sup> percentile.

**(Q2) fMRI data: Do youth preferentially activate amygdala-mPFC circuitry when observing their parents learn?**

Parameter estimates reflecting amygdala activation, mPFC activation and amygdala-mPFC connectivity were entered into separate repeated-measures univariate GLMs. Brain imaging data was collected during the acquisition and test phases of the observational conditioning procedure. In each case, the interactions of interest were the model (parent vs. unfamiliar parent) x condition (CS+ vs. CS-) and model (parent vs. unfamiliar parent) x condition (CS- vs. CS+) x study phase (acquisition and test) interaction. Significant interactions were interrogated with follow-up paired t-tests, where appropriate, to examine whether individuals showed better learning (a larger difference for CS+ vs. CS-) for parents than strangers and whether this increased over the course of the experiment. All data were free of outliers, as defined by less than 3\*interquartile range beneath the 25<sup>th</sup> percentile or more than 3\*interquartile range above the 75<sup>th</sup> percentile.

**(Q3) fMRI data: Does parental anxiety and youth neural activity correspond with better observational learning in youth?**

We tested this question in two steps.

First, we tested the hypothesis that parent anxiety was related to youth learning for the parent condition. Parent and youth trait anxiety (both mean-centered) were added as covariates to the repeated-measures univariate GLM examining liking for the CS+ and CS- described above so as to examine the parent anxiety x model (parent vs. unfamiliar parent) x condition (CS+ vs. CS-) and parent anxiety x model (parent vs. unfamiliar parent) x condition (CS+ vs. CS-) x study phase (baseline, post-acquisition and post-test) interactions. Parent and youth anxiety were positively, but not significantly, correlated with one another (partial correlation, controlling for youth age:  $r=.27$ ,  $p=.29$ ).

Second, we examined whether individual differences in neural recruitment and connectivity were associated with learning when observing one's parent. Learning was operationalized as the difference in CS- > CS+ liking post-acquisition and post-test. Partial correlations, controlling for age, were performed between these two learning metrics and left amygdala and mPFC activation and amygdala-mPFC connectivity.

Finally, based on results from the above analyses, we performed correlations between parent anxiety and youth amygdala and mPFC activation and connectivity. These were partial correlations that controlled for age.

**(Exploratory Q4) fMRI data: Does parental neural recruitment during firsthand conditioning predict their child's neural recruitment during observation?**

We tested this question by looking at correlations between each youth participant's mean left amygdala activation, mPFC activation and amygdala-mPFC connectivity during observational conditioning and their parent's respective measures during firsthand conditioning. These were partial correlations that controlled for age.

RESULTS

## **(Q1) Behavioral results: Do youth preferentially learn by observing their parents?**

Youth participants showed better observational learning for their parent relative to the unfamiliar parent, as indexed by self-reported liking for the CS+ versus CS-. This was specifically observed in the significant model (parent vs. unfamiliar parent) x condition (CS+ vs. CS-) interaction,  $F(1, 31)=4.24, p=.048$ ; Figure 2). Follow-up paired t-tests performed on average CS- and CS+ for parent across baseline, post-acquisition and post-test periods revealed that parents elicited significant discrimination between the CS+ and CS- ( $t(32)=3.39, p=.002$ ), whereas unfamiliar parent models did not ( $t(32)=.76, p=.45$ ). A significant condition x study phase interaction was also observed ( $F(2, 30)=7.13, p=.002$ ), and follow-up t-tests at each study phase revealed no discriminatory liking for the CS- and CS+ at baseline ( $t(32)=-.42, p=.68$ ) and a preference for the CS- over the CS+ post-acquisition ( $t(32)=2.09, p<.05$ ) and post-test ( $t(32)=3.64, p=.001$ ). The model (parent vs. unfamiliar parent) x condition (CS+ vs. CS-) x study phase (acquisition vs. test) interaction was not significant ( $F(2, 30)=.68, p=.51$ ). Although age marginally interacted with condition to predict learning ( $F(1,31)=3.59, p=.07$ ; age predicted less liking for the CS+, suggesting better learning in older participants), it did not interact with the model x condition interaction term nor the model x condition x study phase interaction term to predict learning ( $p$  values  $>.35$ ). Together, these findings suggest that youth discriminated between the CS+ and CS-, but particularly for parent, and that discriminant learning improved over time. Results comparing task responses for the final sample of 33 participants to the 14 participants excluded for head motion are provided in the supplement.

## **(Q2) fMRI results: Do youth preferentially activate amygdala-mPFC circuitry when observing their parents learn?**

Interactions between model (parent vs. unfamiliar parent) and condition (CS+ vs. CS-) as well as parent x condition x study phase (acquisition vs. test) were interrogated to test for neural evidence of preferential learning from parents. Youth demonstrated increased recruitment of the left amygdala for their parent relative to the unfamiliar parent over time, as reflected by the model (parent vs. unfamiliar parent) x condition (CS+ vs. CS-) x study phase (acquisition vs. test) interaction,  $F(1,31)=4.04$ ,  $p=.05$ ; Figure 3 and Figure 1S). No other significant model x condition or model x condition x time effects were observed ( $p$  values  $> .10$ ), nor were any age x model x condition or age x model x condition x time effects observed ( $p$  values  $> .14$ ).

To probe the parent x condition x study phase interaction, separate post-hoc model x condition repeated-measures GLMs were performed for the acquisition and test phases. At acquisition, no effect approached significance ( $p$  values  $> .28$ ). At test, the model x condition interaction approached significance ( $F(1,31)=3.43$ ,  $p=.07$ ). Follow-up paired t-tests on the test phase data revealed no significant differential amygdala response to CS+ relative to CS- for parent ( $p$  values  $> .14$ ). Instead, the model x condition interaction at test appeared to be due to the CS+  $>$  CS- contrasts trending in opposing directions (Parent<sup>Test</sup> CS+  $>$  CS- $=.06$ ; Unfamiliar Parent<sup>Test</sup> CS+  $>$  CS- $=-.04$ ).

## **(Q3) fMRI results: Does parental anxiety and youth neural activity correspond with better observational learning in youth?**

As described in the Methods, parent and youth trait anxiety were simultaneously added as covariates to the repeated-measures GLM to test the role that these psychological traits play in observational learning. Results revealed that self-reported

liking was predicted by a significant model (parent vs. unfamiliar parent) x test phase (baseline, post-acquisition, post-test) x condition (CS- vs. CS+) x parent anxiety (continuous, mean-centered) interaction,  $F(2,14)=7.20$ ,  $p=.003$ . To better understand this four-way interaction, we created two repeated-measure GLMs to separately test the test phase x condition x parent anxiety interaction for parent and unfamiliar parent, respectively (while still controlling for age and youth anxiety). The test phase x condition x parent anxiety interaction was significant for parent ( $F(2,14)=6.13$ ,  $p=.006$ ), but not for unfamiliar parent ( $F(2,14)=1.43$ ,  $p=.26$ ). Thus, all subsequent analyses related to parent anxiety focused on the parent condition. We next examined post-hoc correlations between parent anxiety and youths' degree of observational learning from parents (i.e., self-reported liking data for the parent condition only). Parent anxiety was associated with significantly better youth discrimination learning for their parent post-test (Figure 4 and Figure 2S;  $r_{\text{partial}}=.58$ ,  $p=.02$ ; partial correlation controlling for age and youth anxiety), but not at baseline or post-acquisition ( $p$  values  $> .26$ ).

We next sought to identify neural predictors of youth participants' learning from the parent model. In doing so, we examined whether youths' amygdala-mPFC activation and connectivity were associated with their own self-reported liking for the CS- and CS+ from the parent model condition. Partial correlations were performed, which controlled for age. Less amygdala reactivity in youth during acquisition was associated with better concurrent discrimination learning ( $r_{\text{partial}}=-.45$ ,  $p=.01$ ; CS-  $>$  CS+ self-reported liking post-acquisition), but not at test ( $r_{\text{partial}}=-.06$ ,  $p=.76$ ). Greater mPFC activation in youth was associated with marginally better learning during acquisition ( $r_{\text{partial}}=.30$ ,  $p=.09$ ) and significantly better discrimination learning post-test ( $r_{\text{partial}}=.40$ ,  $p=.02$ ). Thus, amygdala activation was only associated with CS-  $>$  CS+ liking ratings at acquisition, whereas mPFC activation was associated with CS-  $>$  CS+ liking ratings at both acquisition and

test. Youth amygdala-mPFC connectivity was not associated with concurrent discrimination learning at acquisition or test ( $p$  values  $> .10$ ).

Finally, we examined whether parent anxiety predicted neural recruitment and connectivity in youth participants when learning from their parents. Parent anxiety was associated with stronger negative amygdala-mPFC connectivity in youth during acquisition for the parent condition ( $r_{\text{partial}}=-.50$ ,  $p=.04$ ; controlling for age and youth anxiety; Figure 4 and Figure 2S), as well as less amygdala recruitment in youth at test ( $r_{\text{partial}}=-.52$ ,  $p=.03$ ; controlling for age and youth anxiety). No other amygdala or mPFC activation or connectivity values were associated with parent anxiety at ( $p$  values  $> .14$ ).

#### **(Exploratory Q4) fMRI data: Does parental neural recruitment during firsthand conditioning predict their child's neural recruitment during observation?**

As described in the Methods, a subset of parents completed firsthand conditioning while undergoing fMRI scanning. Youth observed their parents completing the same task (albeit in the non-MRI laboratory) during the acquisition period of their fMRI task. Parent mPFC activation during firsthand conditioning was negatively associated with their child's amygdala activation during the acquisition phase of observational learning ( $r_{\text{partial}}=-.47$ ,  $p=.03$ ; partial correlation controlling for age). Parent amygdala activation during firsthand conditioning was negatively associated with youth mPFC activity during the acquisition phase of observational learning ( $r_{\text{partial}}=-.44$ ,  $p=.04$ ; partial correlation controlling for age) (Figure 5 and Figure 3S). No other between-dyad activation or connectivity measures were significantly correlated ( $p$  values  $> .10$ ). In sum, these results indicate that parent amygdala-mPFC responses during firsthand learning are associated with their child's neural responses during observational learning.

## DISCUSSION

The present neuroimaging study provides preliminary evidence that parents produce stronger observational learning in their children than unfamiliar adults. While youth were able to learn from both their own parent and the unfamiliar parent, the parent model was associated with better fear learning at test. Consistent with parent-to-offspring transmission identified in non-human animal models, the current findings underscore the key role that parents play in emotional development (Debiec & Sullivan, 2014). The fact that youth recruited the amygdala during observational learning for their parents, and that intergenerational links in amygdala-mPFC recruitment were observed, further points to the role that parents play in shaping neurodevelopment relevant for emotional learning and regulation. Together with our findings linking parent anxiety with their children's learning, these results suggest that observational learning is an understudied yet important mechanism for both basic and clinical accounts of emotional development.

Findings from the present study strengthen and extend prior findings suggesting that parents play a privileged role in regulating emotional learning. Converging cross-species findings indicate that at key points in development, parents have the ability to buffer fear learning and stress neurobiology in their offspring (Gee et al., 2014; Hostinar, Johnson, & Gunnar, 2015; Moriceau & Sullivan, 2006). However, data from non-human animal studies suggest that parents can also facilitate fear learning during observational conditioning (Debiec & Sullivan, 2014). Our finding that youth showed enhanced observational learning for their parent compared to an unfamiliar adult, both at the level of self-report and amygdala responses, takes this prior animal work one step further by demonstrating *preferential* fear learning for parents. In doing so, these results broaden our understanding of how parenting sculpts fear learning. Specifically, our findings suggest that parents are not merely anxiolytic or safety-cuing for their offspring but

rather play a privileged role – at least by comparison to unfamiliar individuals – in both potentiating and ameliorating responses to threat in a context-dependent way. This dovetails nicely with the social referencing literature demonstrating that parents can encourage both approach and avoidance behaviors in infants (Sorce et al., 1985), and suggests that parents continue to impact emotional learning throughout childhood and adolescence.

The present study contributes to a growing body of literature indicating that parents shape the development of amygdala-mPFC circuitry in two key ways. First, our results provide initial evidence that amygdala-mPFC circuitry support youths' learning fear from observing parents. The present results supported our hypothesis that youth's amygdala-based observational learning would be enhanced for parents relative to an unfamiliar adult. Intriguingly, the parental enhancement of the amygdala response emerged most strongly post-encoding during the test phase. This is consistent with prior observational learning studies in adult humans (Haaker et al., 2017), and suggests that observational fear learning in youth may become magnified over time after initial encoding. Youth's amygdala and mPFC recruitment while observing their parents was associated with better behavioral indices of learning. These observations fit nicely with prior work linking caregiving experiences to development of this circuitry and the emotional learning processes it supports (Gee, Gabard-Durnam, et al., 2013; Pattwell & Bath, 2017; Silvers et al., 2016). Although our results warrant replication in a larger sample, our observation that parents potentiated activation specifically in the left amygdala, is consistent with prior studies examining parent-potentiating effects in the human brain (Tottenham et al., 2012). Second, the present study provides the first piece of data to suggest that parent recruitment of mPFC during fear learning predicts less offspring amygdala recruitment during observational learning and vice versa. These data



tentatively paint a picture of an intergenerational neurobiological association, whereby parents who strongly recruit prefrontal regulatory systems during affective learning indirectly buffer amygdala reactivity during observational learning in their children. It is worth noting, however, that while our results strongly suggest differences in learning from parents versus unfamiliar adults, future work with additional comparison conditions will be needed to conclusively determine whether parents preferentially enhance observational learning, whether unfamiliar adults impede such learning, or both.

Several results from the present study highlight the role that individual differences in anxiety may play in explaining the intergenerational transmission of fear learning. It is intriguing that parent anxiety, but not youth anxiety, corresponded with youth learning (as indexed by self-report) and points to the possibility that parental “models” with elevated anxiety emit a signal that facilitates observational learning. Recent work in adults suggests that unfamiliar models who exhibit more outward anxiety induce better observational learning in observers (Selbing & Olsson, 2019). The present study builds upon this prior research by suggesting that trait anxiety – not only experimentally manipulated expressed anxiety – in a model can potentiate observational learning, and that this might be particularly important in the context of parent-child relationships. Youth may be particularly prone to learn from anxious parents because they have ample opportunity to observe their parents in anxiety-provoking situations (Aktar, Majdandžić, de Vente, & Bögels, 2014; Maloney, Ramirez, Gunderson, Levine, & Beilock, 2015). Additional work is needed to parse the contributions of genetics and learned social experience in how youth interpret expressed fear in anxious parents. Parents in the present study were not part of a clinical sample and most had relatively low levels of trait anxiety. It is thus unknown what observational learning is like for children of parents with significantly elevated anxiety and additional work is needed in this space to

examine the clinical relevance of the present findings. It is noteworthy that higher levels of parent trait anxiety not only predicted stronger learning behavior in their children at test, but also stronger negative amygdala-mPFC connectivity in youth when observing their parents during acquisition. These findings are consistent with the notion that parental cues scaffold amygdala-mPFC circuitry and guide the nature of its development (Callaghan & Tottenham, 2015; Tottenham, 2015), perhaps explaining some of the variance in normative age-related changes in amygdala-mPFC circuitry across childhood and adolescence that support maturing emotion regulation (Gee, Humphreys, et al., 2013; Silvers et al., 2017). In further support of this idea, it has also been shown that severe parental deprivation is followed by altered maturation of amygdala-mPFC circuitry (Gee, Gabard-Durnam, et al., 2013; Silvers et al., 2016). Together with these past findings, the present study suggests that a range of more normative developmental experiences, including parent emotional traits, also sculpt amygdala-mPFC connectivity.

The present study has several limitations that warrant subsequent follow-up work. First, the sample size for the youth behavioral and neuroimaging findings is modest and the sample of parents for whom we collected anxiety and neuroimaging data is relatively small, due to the added difficulty of finding parent-youth dyads where both members could undergo MRI scanning. Thus, it is crucial that the present findings be replicated in a larger sample. A larger sample would also grant us the power to more adequately examine age effects, which we did not observe in the present study. Second, it is unknown whether the preferential learning effects observed for parents are truly unique to parents or whether similar results might be obtained if youth learned from another familiar individual such as a sibling or close friend. Relatedly, the distinct results obtained for a parent versus an unfamiliar adult could have arisen for a number of reasons (e.g., the parent eliciting empathic concern in their child, the unfamiliar adult

causing a sense of wariness) and thus further work with different “comparison” conditions is needed to isolate the unique effects of parents on observational learning. Third, as noted above, the parents in this study reported low to modest levels of anxiety and thus, it is unknown whether similar or different effects might be observed in youth of parents with clinical anxiety disorders. Addressing this question in future studies is of great import, given the fact that parent anxiety predicts offspring anxiety (Kendler, 2001; Muris et al., 1996b; Thapar & McGuffin, 1995). Fourth, the mechanisms underlying links between parent and child brain activation, as well as between parent anxiety and child learning, observed in the present study are unknown. Given that processes underlying fear conditioning are moderately heritable (Hettema, Annas, Neale, Kendler, & Fredrikson, 2003), and also that variations in parenting behavior predict function in fear learning circuitry (La Buissonnière-Ariza et al., 2019), both shared genetics and social learning may play important roles. Fifth, one reinforced CS+ trial concluded each test phase of the current paradigm. While this could have contributed to participant’s ratings of the CS+, it would have done so equivalently for the parent and unfamiliar parent conditions and thus is unlikely to explain why youth learned more effectively for their parent. However, future work might consider omitting reinforced trials to avoid conflating observational and firsthand learning.

The present study is the first to demonstrate in humans that fear learning in parents can be transmitted vicariously to their children. Converging evidence from parents and youth implicate amygdala-mPFC circuitry in supporting intergenerational observational learning. Our preliminary findings linking parent trait anxiety to youth learning and amygdala-mPFC connectivity suggest that this experimental approach possesses significant potential for informing models of both basic emotional development and clinical research on fear and anxiety disorders in youth.



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## Figure Legends

**Fig. 1. Observational conditioning task design.** The observational conditioning protocol is depicted with arrows indicating when behavioral and brain data were collected in youth participants.

**Fig. 2. Do youth learn preferentially by observing their parents? A.** Self-reported liking of the CS- versus CS+ are plotted as a function of model (parent vs. unfamiliar parent) and study phase (baseline, post-acquisition, and post-test). Error bars reflect 95% within-subject standard error. **B.** Difference scores for self-reported liking of the CS- versus CS+ are plotted as function of model (parent vs. unfamiliar parent) and study phase (baseline, post-acquisition, and post-test). Error bars reflect 95% within-subject standard error.

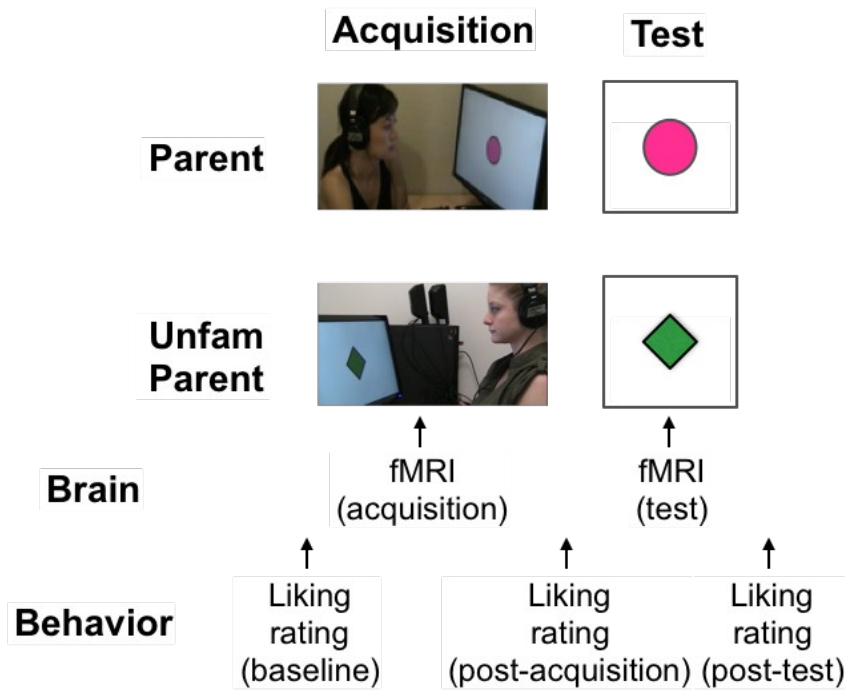
**Fig. 3. Do youth preferentially activate the amygdala when observing their parents learn?** Difference scores for amygdala responses to the CS+ and CS- are plotted as function of model (parent vs. unfamiliar parent) and study phase (post-acquisition, and post-test). Error bars reflect 95% within-subject standard error. CS- and CS+ results are plotted separately in Figure 1S in Supplement.

**Fig. 4. Does parental anxiety correspond with better observational learning in youth? A.** Difference scores for youth's self-reported liking of the CS- versus CS+ (post-test, parent observation condition) are plotted as function of parent anxiety. CS- and CS+ results are plotted separately in Figure 2S in Supplement. **B.** Parental anxiety corresponded with youth amygdala-mPFC connectivity during the acquisition phase of the parent condition. CS- and CS+ results are plotted separately in Figure 2S in Supplement.

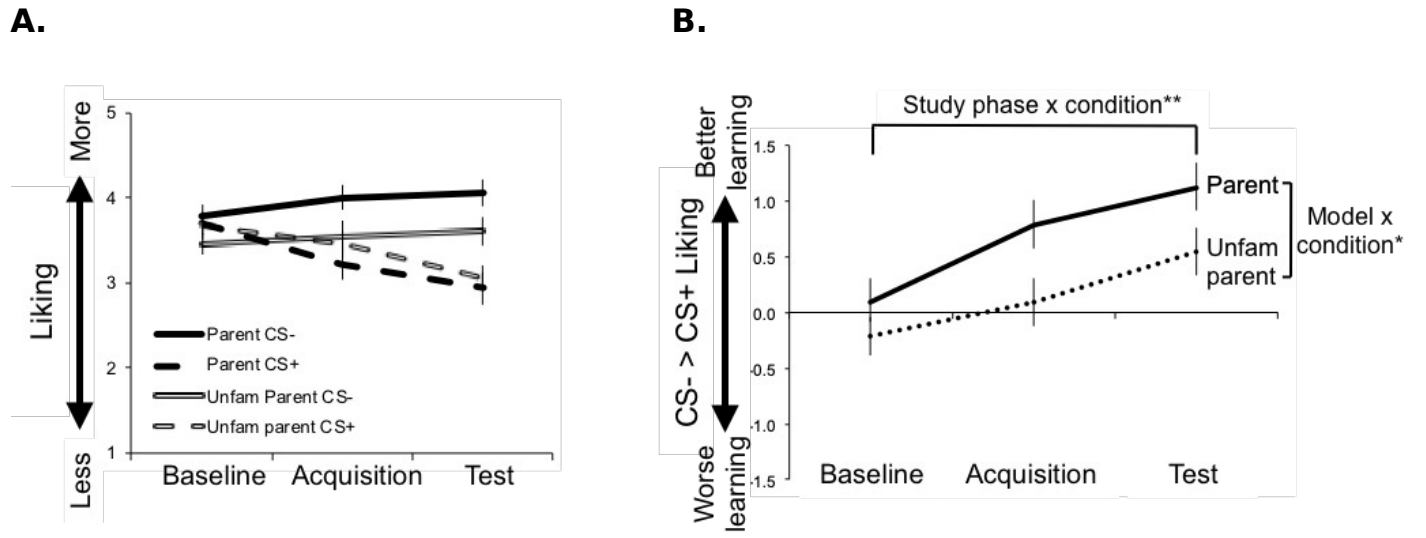
**Fig. 5. Does parental neural activity correspond with better observational learning in youth?** Arrows depict associations between parent neural activation during

firsthand conditioning and their child's neural activation while observing parent undergo firsthand conditioning. Parent and youth amygdala and mPFC recruitment were inversely associated. CS- and CS+ results are plotted separately in Figure 3S in Supplement.

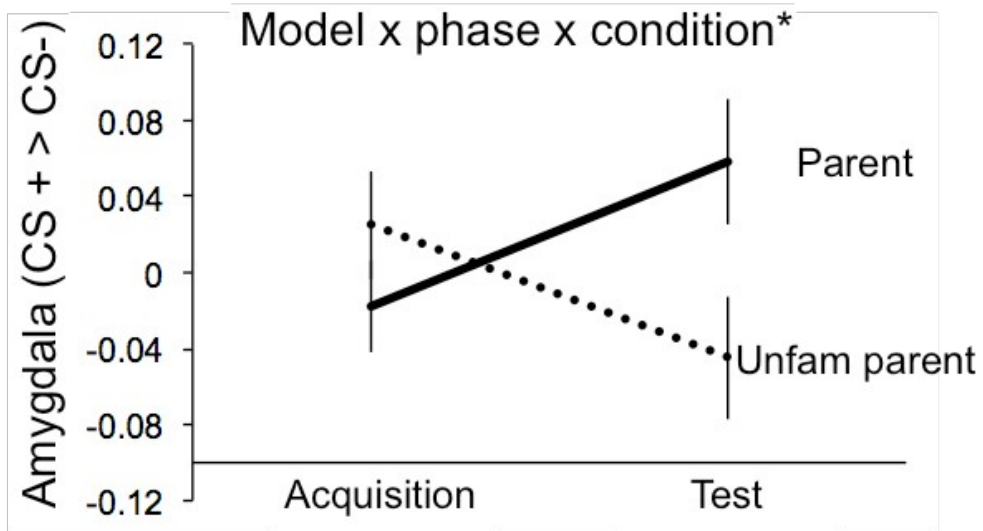
**Fig. 1. Observational conditioning task design.**



**Fig. 2. Do youth learn preferentially by observing their parents?**

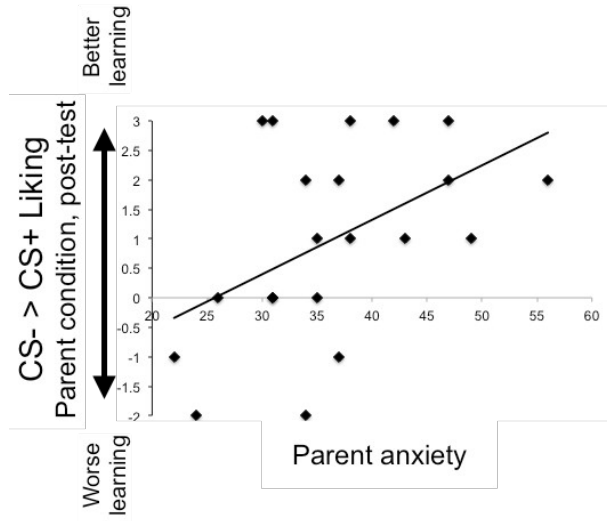


**Fig. 3. Do youth preferentially activate the amygdala when observing their parents learn?**

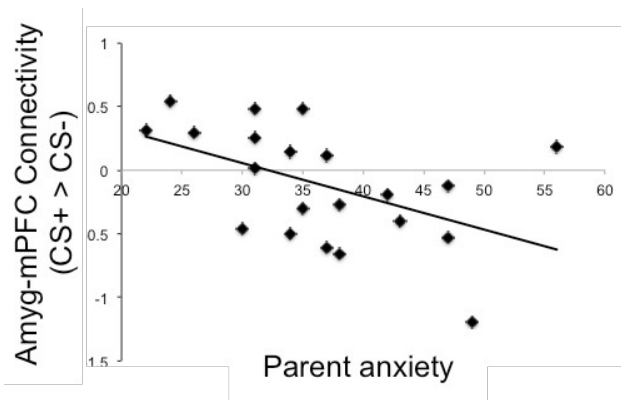


**Fig. 4. Does parental anxiety correspond with better observational learning in youth?**

**A.**



**B.**



**Fig. 5. Does parental neural activity correspond with better observational learning in youth?**

