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Lower neighborhood quality in adolescence predicts higher mesolimbic sensitivity to reward anticipation in adulthood

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ABSTRACT

Life history theory suggests that adult reward sensitivity should be best explained by childhood, but not current, socioeconomic conditions. In this functional magnetic resonance imaging (fMRI) study, 83 participants from a larger longitudinal sample completed the monetary incentive delay (MID) task in adulthood (∼25 years old). Parent-reports of neighborhood quality and parental SES were collected when participants were 13 years of age. Current income level was collected concurrently with scanning. Lower adolescent neighborhood quality, but neither lower current income nor parental SES, was associated with heightened sensitivity to the anticipation of monetary gain in putative mesolimbic reward areas. Lower adolescent neighborhood quality was also associated with heightened sensitivity to the anticipation of monetary loss activation in visuo-motor areas. Lower current income was associated with heightened sensitivity to anticipated loss in occipital areas and the operculum. We tested whether externalizing behaviors in childhood or adulthood could better account for neighborhood quality findings, but they did not. Findings suggest that neighborhood ecology in adolescence is associated with greater neural reward sensitivity in adulthood above the influence of parental SES or current income and not mediated through impulsivity and externalizing behaviors.

1. Introduction

Neighborhoods matter. Beyond individual or family socioeconomic status (SES), neighborhood level characteristics (e.g., crime, social disorder, physical deterioration) are associated with cognitive development, externalization and a variety of other mental health outcomes (Evans and English, 2002; Mair et al., 2008; Ross and Mirowsky, 2001). During adolescence, neighborhood environments may shape a variety of adolescent behaviors, including delinquency and risk taking (Sampson, 1997). In this same developmental period, neural structures supporting reward function and self-regulation are undergoing dramatic reorganization and pruning (Spear, 2000). Thus, adolescence may constitute a sensitive period during which neighborhood characteristics contribute to the development of adult reward anticipation and pursuit. Using functional neuroimaging, the current study draws on Life History Theory (LHT) (Cabeza de Baca et al., 2016; Gregory et al., 2009) to suggest that adolescent neighborhoods may play a role in adult neural sensitivity to the anticipation of rewards.

LHT describes individual development as a process of resolving competing biological challenges through tradeoffs. Environments with abundant and reliable resources encourage "slow" strategies that are low-risk and focused on long-term outcomes, encouraging delay of gratification. Conversely, environments with scarce and unreliable resources encourage "fast" strategies that are relatively high-risk and present-focused, encouraging delay discounting and immediate gratification (Ellis et al., 2009; Griskevicius et al., 2013; Wilson and Daly, 1997). LHT suggests that unreliable environments select for riskier, more reward sensitive, and more impulsive behaviors (Belsky et al., 1991; Ellis et al., 2009; Figueredo et al., 2006). Furthermore, since it is the developmental context that matters, adult access to resources should matter less in the development of these phenotypes.

1.1. Neuroimaging and life history

Empirical evidence for the LHT model is growing (e.g., Belsky et al., 2015, 2010; Simpson et al., 2012). Researchers working to adapt life history theory to human ontogeny propose that harshness and instability in formative environments calibrate biological systems to favor immediate rewards (Del Giudice et al., 2011). It follows that activity in neural systems supporting anticipation of reward would be similarly favored, while activity in systems sup-

porting the regulation of reward responding would be attenuated (Figueredo et al., 2006).

The striatum—and the nucleus accumbens (NAcc) specifically—is a mesolimbic area of the brain long associated with reinforcement learning and reward sensitivity (Olds and Milner, 1954; Robbins and Everitt, 1996). Human imaging studies support this view (Cooper and Knutson, 2008; Knutson et al., 2001; Liu et al., 2011). Moreover, ventral striatal activity (including the NAcc) in response to monetary gain is greatest among those who prefer small immediate rewards over bigger delayed rewards (Hariri et al., 2006). And, though not specifically implicating the NAcc, at least one study has documented altered sensitivity to potential rewards as a function of adolescent SES—in this case suggesting that lower SES corresponded with greater medial pre-frontal cortex (mPFC) responses to monetary reward anticipation (Romens et al., 2015).

Life history theorists are less clear about how childhood context should impact sensitivity to punishment or loss. One implicit hypothesis may be that decreased punishment sensitivity follows an increase in reward sensitivity and this further increases risk taking (e.g., Rossiter et al., 2012). However, individuals raised in abusive homes (a decidedly harsh and unstable ecology) develop a heightened vigilance for threat rather than habituation to it (Shackman et al., 2007). Possibly, a harsh and unreliable environment encourages sensitivity to punishment cues (vigilance). Lower neighborhood quality should therefore be associated, at least, with increased activation in the dorsal anterior cingulate cortex (dACC), an area involved in negative affect, cognitive control, and reward-based decision making (Bush et al., 2002). Previously dACC activation was noted during anticipation of monetary loss (Knutson et al., 2008; O'Doherty et al., 2001). However, the role of the dACC in reinforcement learning or rewards is comparatively less clear than that of the NAcc.

1.2. Third variables and mediators

In addressing the association between adolescent neighborhood quality and adult neural reward anticipation, it was important to include potential alternative explanations and, indeed, potential mediating variables, including parental socioeconomic status (pSES), current income, and externalizing behaviors. Measures of pSES have been associated with structural brain changes in both in adolescence (Hair et al., 2015) and in adulthood (Cavanagh et al., 2013), even while community level measures of current SES have at times failed to show structural differences (e.g., Gianaros et al., 2007). It is possible that the micro-environment of the home (reflected in pSES) may exert more influence on reward systems than neighborhood quality. Current resources too may impact reward systems, as we know that changes in resources in adulthood can impact cognitive performance in a state-dependent way (Mani et al., 2013). If current income is associated with greater sensitivity to the anticipation of rewards and punishment and not adolescent neighborhood or even pSES, it would put into question LHT hypotheses.

Importantly, children from lower SES contexts are often rated as more externalizing and impulsive (Bradley and Corwyn, 2002), though it is unclear whether this reflects impulsivity per se or relatively adaptive decision-making in resource-scarce and unreliable contexts (Michaelson et al., 2013; Otto et al., 2012; Sturge-Apple et al., 2016). One study found lower inhibition for adolescent girls whose parents had lower SES combined with greater ACC activation during an inhibition task (Spielberg et al., 2015). Adults higher in trait impulsivity/reward sensitivity also show increased activation in the striatum and OFC in response to the anticipation of monetary rewards (Hahn et al., 2009). It is certainly possible that resource-scarce and unreliable early environments could encourage externalizing behavior through decreased inhibition and greater impulsivity, and that, with repetition, these behaviors could in turn calibrate neural reward systems in trait-like ways that persist into adulthood. Given these possibilities, it is important to factor in measures of externalizing behavior into any discussion of increased reward anticipation.

1.3. Design and hypotheses

Our current study addresses LHT-based hypotheses using a multi-responder longitudinal sample. Participants' parents answered questions on neighborhood cohesion, deterioration, and risk as well as measures of pSES and their child's externalizing behaviors when participants themselves were 13 years of age. Approximately twelve years later participants completed the Monetary Incentive Delay (MID) task during functional magnetic resonance imaging (fMRI; c.f., Knutson et al., 2001), as well as a measure of current income, and a peer-nominated measure of externalizing behaviors. Drawing on LHT and previous neural research, we anticipated that 1) lower childhood neighborhood quality would correspond with greater mesolimbic activation in response to reward anticipation *and* punishment anticipation; and 2) that these associations would not be explainable by pSES, current income, or impulsivity.

2. Methods

2.1. Participants

Eighty-three healthy participants (41 Female) from the larger Virginia Institute for Development in Adulthood (VIDA; formerly Kids, Lives, Families, and Friends) longitudinal sample completed the current study (N = 184; c.f., Hare et al., 2011). Participants had been followed yearly since 13 years-of-age and were then scanned at around 25 years-of-age (m = 24.41, sd = 1.11). All participants from the larger sample were contacted via phone or e-mail. Participants were excluded if they could not bring an opposite-sex spouse, friend, or relationship partner to the scanning session because MID was added to the same sessions as an already running relationship-based fMRI study (c.f., Coan et al., 2013). Following safety standards for fMRI practice, possible participants were excluded if pregnant, claustrophobic, or if they had ferromagnetic items in their body. The sample was comprised of 53% (44) self-identified Caucasian participants and 39% (32) self-identified African American participants. About 7% of participants self-identified outside of these two prominent categories (2 Latino participants, 1 Asian participant, and 3 mixed-race participants). One participant declined to identify an ethnic background. Main effect analyses were completed on all 83 participants. Covariate analyses where completed for those with full data only (N = 77).

2.2. Measures

2.2.1. Questionnaires
2.2.1.1. Neighborhood quality questionnaire. Participant parents completed the Neighborhood Quality Questionnaire (NQQ) at wave 1 of the VIDA study when participants were 13 years old. The NQQ is a 22-item composite of three scales each assessing different aspects of neighborhood-quality (Buckner, 1988; Gonzales et al., 1996). The scale assesses neighborhood connectedness (e.g., "I believe my neighbors would help me in an emergency;" mother's $\alpha = 0.76$, 6 items), neighborhood crime and deterioration (e.g.,"In the past two years things in my neighborhood have gotten worse;" mother's $\alpha = 0.78$, 4 items), and neighborhood risk (e.g., "violent crimes that involve weapons occur in my neighborhood;" mother's $\alpha = 0.93$, 12 items) as reported by the participant's mother or father when

the mother was unavailable. Higher scores indicated greater connectedness, crime, and risk respectively. These scales were strongly correlated (average $r = 0.74$), allowing us to create a composite score. Risk and crime items were reversed scores and added to the connectedness scale. Thus, higher scores indicate greater neighborhood quality. Based on kernel density adolescent neighborhood quality was skewed left (-1.05), with most scores trending toward greater neighborhood quality ($M = -6.59$, $SD = 12.28$). Neighborhood quality was centered (demeaned) before being entered into the FSL covariate analysis.

2.2.1.2. pSES. In order to partial out variance due to socioeconomic factors outside of neighborhood quality we created a parental SES measure. Because father's reports of household income and education suffered from high missingness (39%) we used Mother's report of household income and mother's education to create the SES measure. Mother's picked from eight pre-tax income brackets (1 = under $5000 up to 8 = $60000 or more) and nine options for highest level of education achieved (1 = 8th grade or less up to 9 = post college degree). Education and income were strongly correlated ($r = 0.66$). Income and education scales were z transformed and the mean was calculated for the two scores. Three participants had father and not mother's report of income and education. SES was calculated based on the father's report for these three participants. Based on kernel density, pSES was slightly skewed left (-0.44) with less scores at the lower end of the created scale ($M = 0.65$, $SD = 0.26$).

2.2.1.3. Current income. Participants recorded their income bracket near the time of the fMRI study as part of the broader demographics questionnaire for the VIDA study. We considered creating an SES measure similar to the pSES measure in adolescence. However, income and education were not strongly correlated ($r = -0.27$) and we chose to use current income as a representative of current resources. Participants picked from nine pre-tax income brackets (1 = Student, no income, 2 = No income, 3, under $5000, 4 = $5000 − $9999, 5 = $10000 − $14999, 6 = $15000 −$19999, 7 = $20000–$29999, 8 = $30000–$39999, 9 = $40000 − $59999). Two participants in this sample were students (no income) and were removed from the income analyses given its categorical difference from the other brackets. Current income was fairly normally distributed (skew = -0.26) with most participants (n = 41) endorsing 5 ($10000 − $14999), 6 ($15000 − $19999), or 7 ($20000 − $29999). These results indicate that at the time of scanning most of our participants were below or at the median wage per person in the US and are representative of the 50th percentile and below in wage earnings ($26, 595; Social Security, 2011). These ordinal data were centered using the median (5).

Neighborhood Quality and Current Income were not significantly correlated ($r = 0.17$). However, both were significantly correlated with pSES at $r = 0.54$ and $r = 0.36$.

2.2.1.4. Externalizing behavior. To model adolescent and adult externalizing behavior we used the externalizing subscales of the Child Behavior Checklist (CBCL; Achenbach, 1991) and the Adult Behavioral Checklist (ABCL; Achenbach et al., 2003). The CBCL is a parent-rated questionnaire consisting of 118 items indicating various behavioral and emotional issues falling in the domain of internalizing (e.g., anxious or depressed) or externalizing (e.g., aggressive and hyperactive) problems. The CBCL was completed by the participant's mother at wave 1. The ABCL was then completed by a nominated peer around the time that fMRI was collected. The ABCL is an adult version of the CBCL and consists of 126 age-appropriate items. Again, we used only the externalizing raw scores and higher scores indicate greater externalizing behavioral problems. These scale were used to investigate whether personality

factors might better explain adolescent neighborhood quality associations with adult neural reward sensitivity.

CBCL externalizing subscale scores were skewed right with most mothers endorsing few externalizing behaviors in participants during adolescence (skew = 1.48, Median = 4, M = 5.5, SD = 5). ABCL externalizing subscales were also skewed right (skew = 2.5, Median = 3, M = 7.75, SD = 10) with few endorsements of externalizing behaviors from friends.

2.3. Procedure

Participants came in as part of a larger scanning session comprised of three tasks, one of which was the MID. All participants gave written informed consent in accordance with the University of Virginia's internal review board. The MID consists of three rewards cues, three punishment cues, and one neutral cue. Punishment and reward cues include three levels of expected monetary consequences as defined by the number of lines in a given cue (see Fig. 1). Reward and punishment cues are presented for 500 ms followed by a fixation cross and a white square. Participants are instructed to press a button when they see a small white square following the presentation of these cues. The button press serves to either avoid punishment in the form of losing money or receive a reward in the form of gaining money, depending on the cue. After each trial participants receive immediate feedback on their performance with an indication of current loss or gain and total money so far. As a motivator, participants were told that the money gained during the task would be "extra" from the original compensation promised. They could gain up to $40 dollars extra.

Participants were instructed three times on how the task worked: once by the experimenter before entering the scanner, once during a practice run, and again during the first of two experimental runs. The practice run produced an estimate of reaction time and calibrated the fixation cross (2000–2500 ms) and white square (160–260 ms) display times for the subsequent experimental runs, such that all participants would have a hit rate of ~66%. Structural scans were taken before any functional scans and a 10-min functional scan was taken during each of the two experimental runs of MID. Each run consisted of 72 trials with 27 reward cues, 27 punishment cues, and 18 neutral cues.

2.4. Data analysis

2.4.1. Neighborhood quality and pSES as predictors of externalizing behaviors

We conducted a multiple regression analysis predicting childhood externalizing behavior from Neighborhood Quality and PSES while controlling for current externalizing. Only complete cases were used (N = 69). All scales were centered and model was checked for assumptions of linearity, heteroscedasticity, normality of residuals, and influence.

2.4.2. MID behavioral data

In accordance with best practices to analyze reaction time data we conducted a linear mixed effects analysis. Behavioral data was analyzed using RStudio version 0.98.1028 and *lme4* version 1.1-9 (Bates et al., 2015), a linear mixed-effects modeling program in R. Individuals were modeled as random effects (adjusting for individual intercept) while cue-types (i.e., gain, neutral, loss) was modeled as a fixed effect. Raw reaction times were transformed into speed (1/reaction time) and all models were checked for influence using Cook's Distance and for normality using q-plots of residuals. Only accurate trials were used in the analysis. P-values for individual parameters were obtained using Satterthwaite approximation of degrees of freedom calculated through *lmerTest* version 3.1-120. Models were assessed for assumptions of the linear model and
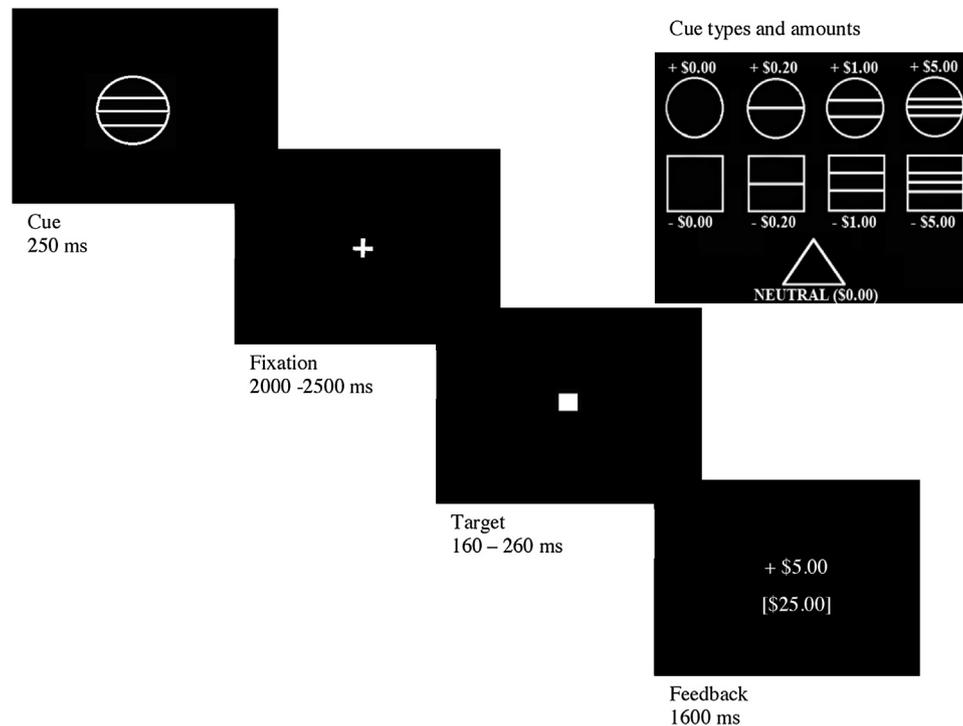
Fig. 1. Flow diagram of MID task. Cues signaling monetary gain, loss, or no consequence in the MID paradigm are on the upper right of the figure. Each run consisted of 72 trials with 27 reward cues, 27 punishment cues, and 18 neutral cues. The participants are taught the cues first by an experimenter and then by the practice run.

leverage. Four scores were consistently removed for undue influenced on the model as diagnosed by Cook's Distance. Removal of these scores improved model compliance with underlying assumptions, but interpretations did not change based on removal of these trials.

2.5. fMRI image acquisition and data analysis

Data were acquired using a Siemens 3.0 T MAGNETOM Trio high-speed magnetic resonance imaging device at the University of Virginia's Fontaine Research Park. Participants viewed the stimuli using the fMRI's CP transmit/receive head coil with an integrated mirror. One hundred and seventy-six high-resolution structural T1-weighted magnetization-prepared rapid-acquisition gradient echo images were obtained (1-mm slices, TR = 1900 ms, TE = 2.53 ms, flip angle = 90°, FOV = 250 mm, voxel size = 1 × 1 x 1 mm) before functional scans. Two hundred and twenty-four functional T2-weighted Echo Planar images (EPI's) sensitive to BOLD contrast were collected during each of the two MID tasks, each lasting 10 min. These functional images were collected in volumes of twenty-eight 3.5-mm transversal echo-planar slices covering the whole brain (1-mm slice gap, TR = 2000 ms, TE = 40 ms, flip angle = 90°, FOV = 192 mm, matrix = 64 × 64, voxel size = 3 × 3 x 3.5 mm).

Imaging data were preprocessed and analyzed using FMRIB Software Library (FSL) software (Version 5.98; www.fmrib.ox.ac.uk/fsl). We first corrected for motion artifacts using FMRIB's Linear Image Registration Tool (MCFLIRT; Jenkinson et al., 2002). Slice-timing differences were adjusted for using temporal interpolation, and signal to noise ratio was increased via a high-pass filter with a cutoff point of 100 s. Non-brain material in the fMRI data was removed using the BET brain extraction (Smith, 2002). We used a 5-mm full width at half-minimum Gaussian kernel, and grand-mean intensity normalization for spatial smoothing. Finally, functional imaging was registered to the Montreal Neurological Institute (MNI) standard space, using FLIRT (Jenkinson et al., 2002).

2.5.1. Lower-level analyses

After pre-processing, we used FSL's fMRI Expert Analysis Tool (FEAT) query to model reward and punishment anticipation. We subtracted the neural signal from each instance of a reward cue at all three levels from the neural signal during the neutral cue to obtain our model of anticipatory reward activation. The same was completed for the punishment trials to obtain our model of anticipatory punishment activation. Because our interests where in the overall neural activation in anticipation for reward and punishment, we collapsed across all three reward and punishment levels. We further aggregated both MID runs for each participant into a Level Two analysis using a fixed-effects model for greater signal to noise ratio.

2.5.2. Higher-level analyses

We completed main effect analyses for Reward and Punishment at the third level of analysis using the aggregate Reward > Neutral and Punishment > Neutral contrasts respectively. These images were corrected for multiple comparisons using a False Discovery Rate (FDR) at q = 0.01 and cluster corrected at Z = 2.3. To determine the associations between adolescent and current economic context on task-specific activity we then completed four whole-brain corrected cluster analyses using estimated smoothness and Gaussian Random Field Theory (GRF) to determine cluster size (Z = 2.3, p = 0.05). The covariate of interest (either Neighborhood Quality, pSES, or Current Income) were centered and entered into the models. Both positive and negative contrasts were computed. Covariate analyses can be summed into two models: Reward Anticipation > Neutral ∼ Neighborhood Quality + pSES + Current income, and Punishment anticipation > Neutral ∼ Neighborhood Quality + pSES + Current income. This yielded six activation maps: one map per each of the three explanatory variable showing the effect of each variable while adjusting for the effect the others for each of the two contrasts (3 variables x 2 contrasts = 6 statistical maps). Given theoretical precedent, we also conducted two structural region of interest (ROI) analyses looking for significant
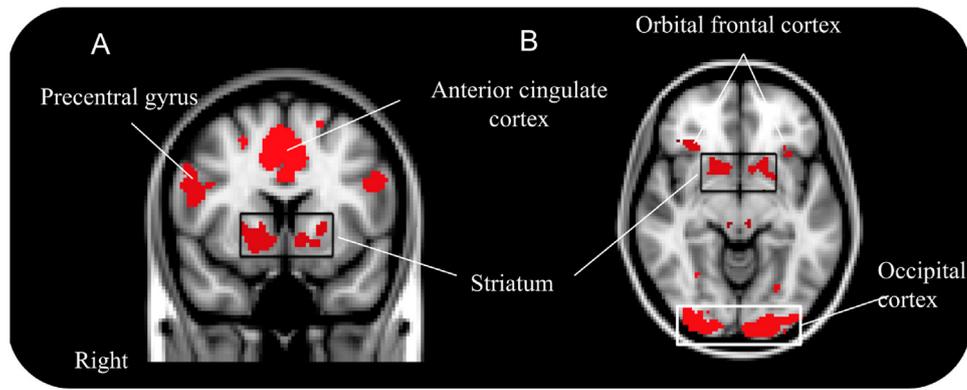
Fig. 2. Visualization of areas with greater activation in the Reward > Neutral contrasts at the group level. Images were FDR corrected (q = 0.01) and overlaid on to the MNI T1 wted high resolution anatomical image. Coronal (A) and Axial (B) slices located at Y = 16, Z = −8.

interactions in bilateral NAcc during reward anticipation. Specifically, we applied a binarized structural probability map of the NAcc from the Harvard-Oxford Subcortical Atlas and entered this as a pre-thresholding mask for both the Reward Anticipation model and the Punishment anticipation model. We then performed a small volume correction within this mask using voxel-wise thresholding in FSL while setting the individual voxel significance level at $p < 0.05$. FSL's voxel-wise thresholding employs GRF theory to determine the maximum height thresholding to correct for multiple comparisons.

3. Results

3.1. Behavioral results

3.1.1. Neighborhood quality and pSES as predictors of externalizing behaviors

Despite non-normality in the raw scores, transformation was not necessary given model diagnostics. Four cases were removed due to influence, though removal does not change the interpretation of the model. These cases were at the extreme ends of externalizing behaviors observed with one score at the minimum (0) and three scores where the highest scores observed in this sample (14, 23, and 25). The complete model was significant $(F(4,60) = 2.86, p < 0.05)$, with an R^2 of 0.10. Only PSES predicted externalizing such that higher PSES was associated with lower externalizing scores (B = −0.27).

3.1.2. MID behavioral analyses

Neighborhood quality, current income, childhood externalizing scores, and adult externalizing scores were not associated with MID performance. See Supplementary materials for greater detail.

3.2. Neuroimaging results

All coordinates given are in MNI space and the naming of structures is based on probability maps from the Harvard Oxford Cortical Atlas and the Harvard-Oxford subcortical atlas unless otherwise stated. Analyses where performed both by using the transformed reciprocal square root of Neighborhood Quality and with the measure simply mean centered. Since results and the interpretation does not change we report the untransformed data here.

3.2.1. Whole-brain analyses main effects

Reward Anticipation > Neutral. Replicating earlier MID studies (e.g., Knutson et al., 2001), we observed greater activation in the OFC extending to the anterior insula, ACC, precentral gyrus, occipital pole, lateral occipital cortex, bilateral NAcc and caudate, and

Table 1
Local maxima for clusters significantly activated in the Reward > Neutral contrast.

		Local Maxima Coordinates (mm)		
	Voxels	X	Y	Z
Dorsal Anterior cingulate cortex	3628	−2	2	50
L Latteral occiptital cortex	1680	−26	−54	38
R Occipital pole	1008	34	−90	6
L Occipital pole	897	−18	−96	−8
R Lateral occipital cortex	553	28	−64	52
Precentral gyrus	369	−48	6	24
L Occipital fusiform gyrus	314	−32	−70	−20
R inferior frontal gyrus	302	52	14	22
R Supramarginal gyrus	288	52	−34	52
R Nucleus accumbens	220	12	10	−6
L Putamen	177	−20	10	2
R Orbital frontal cortex	162	34	28	−6
L Insular cortex	158	−28	26	2
R DLPFC	152	42	50	8
R DLPFC	48	48	38	20
Posterior cingulate cortex	47	−2	−30	24
L Thalamus	36	−8	−20	10
R Thalamus	35	8	−14	2

portions of the brainstem, including the thalamus, during anticipatory gain (Table 1, Fig. 2).

Punishment Anticipation > Neutral Anticipation of punishment yielded three heterogeneous clusters broadly defined here as "motor/somatosensory," "left visual processing" and "right visual processing." Local maxima were found in the supplementary motor cortex (SMC), the paracingulate cortex, bilateral occipital pole, bilateral lateral occipital gyrus, the right occipital fusiform gyrus, and the left superior parietal lobule and supramarginal gyrus (Fig. 3, Table 2). Interestingly, we did not observe activation of the caudate and thalamus during punishment anticipation, as others have reported (Knutson et al., 2001). However, these areas do appear in covariate models.

3.2.2. Whole-brain analyses covariate effects

Six covariate analyses were run: Reward > Neutral x Neighborhood Quality, Reward > Neutral x Current Income, Punishment > Neutral x Neighborhood Quality, Punishment > Neutral x Current income, Reward > Neutral x PSES, and Punishment > Neutral x PSES (Table 3).

Null results: Neighborhood quality was not associated with punishment anticipation. pSES was not associated with reward anticipation nor to punishment anticipation. Current income was not associated with reward anticipation.

Reward Anticipation > Neutral x Neighborhood Quality. Lower neighborhood quality corresponded with greater activation
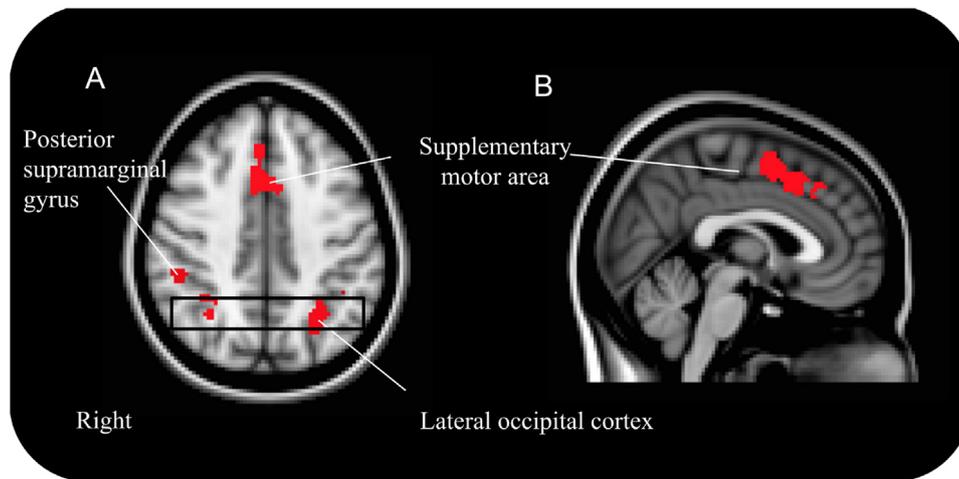
Fig. 3. Visualization of areas with greater activation in the Punishment > Neutral contrasts at the group level. Images were FDR corrected (q = 0.01) and overlaid on to the MNI T1 wted high resolution anatomical image. Axial (A) and Saggital (B) slices are located at X = 2, Y = 16, Z = 42.

Table 2
Local maxima for clusters significantly activated for Punishment > Neutral contrast.

Cluster Index	Voxels	Local Maxima Coordinates (mm)		
		X	Y	Z
Supplementary motor cortex	891	4	2	52
R Lateral occipital cortex	212	28	−64	50
L Lateral occipital cortex	204	−28	−62	42
L Occipital pole	140	−16	−92	−8
R Posterior supramarginal gyrus	106	48	−36	42
R Occipital pole	80	18	−92	−6
R Occipital pole	79	32	−90	4
R Middle frontal gyrus	48	28	2	52
R Insula	38	34	22	4
L Occipital pole	34	−30	−94	16
L Lateral Occipital cortex	21	−16	−70	52

in four clusters. Two clusters were comprised of portions of the left occipital pole and right lateral occipital cortex. A third cluster consisted of portions of the inferior temporal gyrus. Finally, there was a heterogenous cluster at the striatum comprised of bilateral portions of the NAcc and caudate (greater clustering on the right), portions of the right thalamus, and the right putamen, extending frontally towards the left OFC (Table 3, Fig. 4).

Punishment Anticipation > Neutral x Current Income. Lower current income corresponded with greater activations in two distinct clusters. The first cluster yielded a "visual processing" cluster comprised of bilateral portions of the occipital pole, the cuneal cortex, and the lateral occipital cortex. The second cluster yielded a "motor and somatosensory" cluster comprised of lateral areas of the precentral gyrus, the parietal operculum, and the central opercular cortex in the right hemisphere (see Table 3 and Fig. 5).

3.2.3. ROI covariate analyses

Null results: ROI analyses for the Punishment anticipation contrast were null. We looked both at the dACC and the NAcc and covariation with Neighborhood Quality and Income. Current income did not covary with NAcc response to reward anticipation.

3.3. Reward anticipation > Neutral x neighborhood quality in NAcc

Lower Neighborhood Quality corresponded with greater activation in response to reward anticipation in the NAcc (Fig. 6). Seventeen voxels on the right hemisphere near the caudate survived strict voxel-wise corrections while controlling for PSES and Current Income.
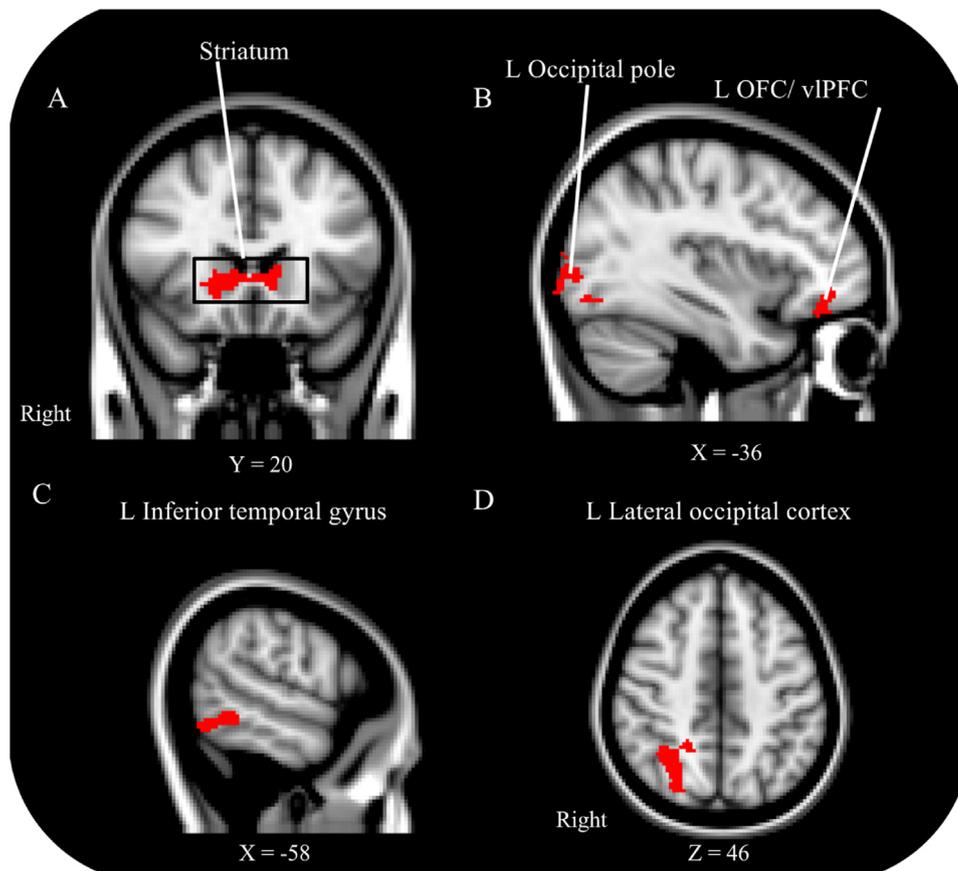
Table 3
Local maxima for clusters negatively correlated to covariates of interests for the both Reward Anticipation > Neutral and Punishment Anticipation > Neutral contrasts. Further thresholding was completed on the Reward Anticipation > Neutral contrast to break down large clusters. Models were adjusted for all socioeconomic variables.

Covariate Analyses Results					
			Local Maxima		
Reward > Neutral x Neighborhood Quality					
Cluster threshold Z > 2.5 (k > 20)[*]					
	Voxels	Max Z	X	Y	Z
R Caudate	561	4.02	14	22	0
L Occipital pole	262	4.15	−36	−94	4
R Lateral Occip cortex	228	3.39	26	−72	44
L Inferior temporal gyrus	157	3.69	−58	−60	−12
L Orbital frontal cortex/vlPFC	100	3.42	−32	42	−14
R Caudate	94	3.38	18	−2	26
L Lateral Occip	67	3.18	−50	−80	−4
L Lateral Occip	33	3.2	−46	−70	18
Punishment > Neutral x Current Income					
	Voxels	Z Max	X	Y	Z
R Parietal operculum	424	3.42	40	−24	22
Occipital Pole	360	3.61	−8	−94	24

[*] In order to further parcel the mesolimbic cluster a more stringent thresholding (Z = 2.5) was done using FSL's cluster tool. This is not meant to be inferential, only descriptive.

Fig. 4. Coronal (A), sagittal (B & C), and axial (D) visualizations of clusters negatively correlated with adolescent neighborhood quality in the Reward > Neutral contrast at the group level. Images' slice locations are below them. The "L Orbital frontal cortex" in image B is an extension of the "striatum" cluster in image A.
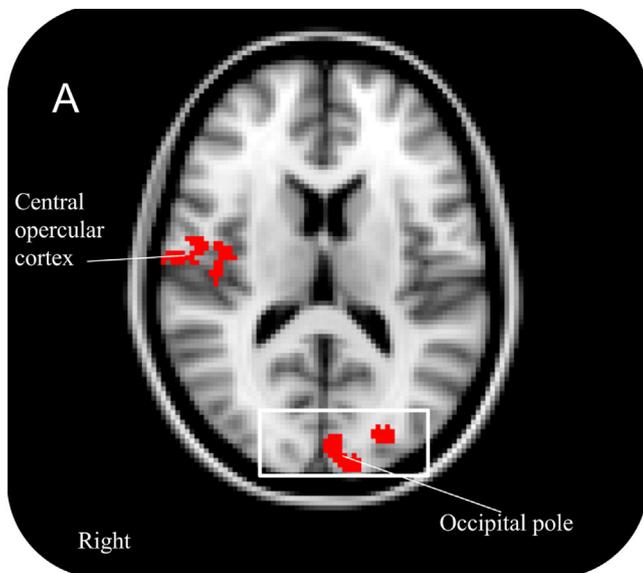

Fig. 5. Axial (A) slice of clusters negatively correlated with Current Income in the Punishment > Neutral contrast at the group level. Image located at Z = 18.

3.3.1. Mediation by externalizing behavior

We tested whether childhood CBCL score could account for the increased NAcc activation. Average Z stat scores where extracted from the NAcc mask in the reward anticipation contrast. We tested the association between both CBCL and ABCL scores on NAcc activation and these scores and NQQ and then entered the interaction in

a model. ABCL and CBCL were not associated with NAcc activation nor Neighborhood Quality ($F(1,76) = 0.00$, $p > 0.05$).

4. Discussion

We investigated the effects of adolescent socioeconomic context on a putative neural measure of reward anticipation, using LHT as a guide. Results provided mixed support for our initial hypotheses. As expected, adolescent neighborhood quality, but not current income, corresponded with mesolimbic activation during reward anticipation even after adjusting for pSES. Interestingly, lower current income corresponded with greater neural activation in anticipation of punishment in regions of the occipital and parietal lobes. Furthermore, although lower pSES was related to higher reported externalizing behaviors, externalizing behaviors did not account for the association between neighborhood quality and mesolimbic sensitivity to rewards. Below we consider possible explanations and implications for our results.

4.1. Developmental context and adult neural activation to secondary reinforcements

Harsh and unpredictable ecologies cannot be counted on to deliver higher rewards at a later time. Organisms in such environments should emphasize vigilance for, and quick responses to, immediate potential gains to increase survival. In this way, harsh developmental contexts may dispose adults to risky strategies in the face of resource uncertainty (Griskevicius et al., 2011; Griskevicius et al., 2013). While risk-taking behavior is almost certainly multiply determined, the current study suggests one
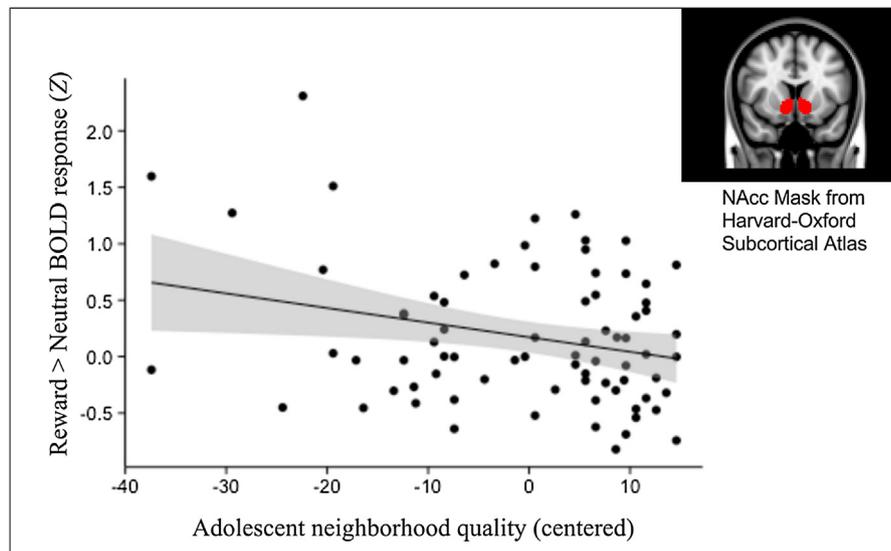
Fig. 6. Higher adolescent Neighborhood Quality (centered) is associated with lower average BOLD activation (displayed here in average Z statistic for the NAcc mask used). One outlier was removed due to excess leverage. Removal of this outlier does not change interpretation. Image on the right is a coronal slice (Y = 20) showing the binarized NaCC mask from the Harvard- Oxford Subcortical Atlas.

potential mechanism: when raised in a relatively harsh and unpredictable environment, we become more risk tolerant by way of increased sensitivity in neural systems supporting reward anticipation. Areas of the striatum, including the NAcc, and orbital and ventrolateral regions of the frontal cortex, were more sensitive to reward anticipation among participants who spent their early adolescence in lower quality neighborhoods. Interestingly, past research suggests that higher striatum activity during reward anticipation has also been associated with greater delay discounting—a preference for immediate rewards over rewards of greater value following a delay (Hariri et al., 2006).

We also found that lower adolescent neighborhood quality was associated with greater activation in areas of the occipital cortex and the precuneus, areas involved in visual processing and motor preparedness, respectively, during reward anticipation. Although not specifically predicted, this, too, may be consistent with LHT, which also suggests that increased uncertainty encourages vigilance and motor preparedness so that unpredictable resources may be more quickly acquired (Figueredo et al., 2006).

Because none of these observations are explained by current income, they likely reflect adaptations shaped by early developmental experiences. Which is not to say that current income is irrelevant—it is notable that lower current income was associated with greater neural activity in anticipation of monetary *punishments*. These effects were largely confined to areas associated with motor control and visual processing. Others have found that similar activations related to visual attention and motor preparation may track motivation (Padmala and Pessoa, 2011). Taken together, these results suggest that current income may still be exerting some influence on vigilance for, and motivated preparation to act on, potential monetary loss.

4.2. Externalizing behaviors and pSES

Individuals from lower parental SES backgrounds are often rated as more impulsive and more externalizing (Teasdale and Silver, 2009), and these factors are plausible alternative explanations for our adult neuroimaging results. Thus, we tested to see whether the association between adolescent neighborhood quality and adult reward anticipation was statistically dependent upon either externalizing or pSES, and finding in both cases that it was

not. Externalizing tendencies are therefore not likely what is driving the increased striatal sensitivity to reward anticipation that we observed for those from lower quality neighborhoods. Neither did we observe covariation between externalizing and areas putatively involved in inhibitory control and emotion integration, as others have reported (Romens et al., 2015; Spielberg et al., 2015).

As already noted, pSES was not related to adult neural reward anticipation. Although it remains possible that pSES is a proxy measure for the probability of having enriching or stressful life events, it may also be a less sensitive measure of harshness and instability. By contrast, neighborhoods, and other macro-ecologies such as schools, may be more important to the calibration of appetitive reward systems than parental education and income per se. Others have also observed that adolescents from lower quality neighborhoods as children show increased risk taking behavior later on (e.g., Carlson et al., 2014; Furr-Holden et al., 2012).

5. Conclusion

Taken together, the pattern found in our data is consistent with an LHT account of how early environments play a role in adult reward anticipation. Moreover, our results are consonant with work suggesting, for example, that midbrain dopaminergic activity associated with reward anticipation increases as the unpredictability of the reward increases (Fiorillo et al., 2003), or that, in rats, exposure to physical stress (e.g., glucocorticoid injections, restraints) reduces the number of inhibitory dopamine receptors in frontal regions of the brain, even while increasing the number of dopaminergic receptors in mesolimbic systems (El-Khodor and Boksa, 1997; McArthur et al., 2005). Importantly, these and similar effects are accompanied by increased locomotion, motivation, novelty seeking, and indiscriminant reward seeking behavior—all well-known behavioral correlates of heightened reward anticipation and impulsivity (Martinez-Tellez et al., 2009).

It is worth noting that, as applied to individuals from harsh and chaotic early life circumstances, potentiated activity in neural systems supporting reward anticipation can be viewed as a kind of central nervous system pathology—a *wound* (cf., McEwen and Gianaros, 2011). Indeed, heightened reward anticipation is implicated in several behavioral disorders (e.g., Beck et al., 2009; Plichta and Scheres, 2014; Sweitzer et al., 2016). In our view, however, one

advantage of the LHT perspective is its characterization of increased reward anticipation under harsh and unpredictable life circumstances not as a wound so much as an adaptive trade-off, which implies that more frequent and intense reward anticipation is an *advantage* under harsh and unpredictable circumstances—indeed, that those circumstances might result in additional adaptive advantages. Very recent work supports this view. For example, higher striatal reward anticipation may protect against depression following childhood neglect (Hanson et al., 2015), and children from low-resourced backgrounds who behave impulsively seem to have more robust cardiac vagal tone, a putative marker of resilience (Sturge-Apple et al., 2016). With these and related observations in mind, it may be useful in future work for researchers to elucidate the functional role of potentiated reward anticipation across a variety behaviors both adaptive and maladaptive.

5.1. Limitations and next steps

Neighborhoods matter. As predicted by LHT, we found increased mesolimbic activation in response to both reward anticipation as a function of lower childhood neighborhood quality, even after adjusting for current income and parental SES. Unfortunately, we were not able to adjust for current neighborhood quality, which would help clarify whether the neighborhood quality effect is relatively unique to adolescence. Similarly, we did not obtain fMRI scans during the period when the adolescent measure of neighborhood quality was obtained, which would help us to clarify whether differences in functional reward anticipatory mesolimbic-cortical activity were apparent at that time. Furthermore, the neighborhood quality measure we did leverage was skewed, and a broader distribution may have improved the reliability of our results. And, particularly because of our theoretical framework, the current study would have benefited much from the inclusion of a delay discounting task to determine if the connection between neighborhood quality and reward sensitivity extended to a behavioral measure of bias toward short-term rewards. Finally, our study did not prioritize mesolimbic resolution above whole-brain image acquisition as in some of the original MID work (Knutson et al., 2001), limiting our ability to specifically identify complex subregions of this area.

Despite these limitations, the present study brings us closer to understanding the conditions that drive phenotypic variability in neural systems putatively supporting reward anticipation—an understanding grounded here in LHT and sensitive to developmental context. Our neighborhood quality questionnaire captured both neighborhood deterioration and the predictability of access to social resources. Elsewhere, we have argued that the brain calibrates its efforts to access and utilize *personal* resources in inverse proportion to expected *social* resources (Beckes and Coan, 2011). LHT-specific designs that more precisely measure the impact of both micro and macro ecologies in development will, we expect, greatly enhance our understanding of a variety of neurodevelopmental phenotypes, including adult neural reward anticipation and its behavioral sequelae.

Conflict of interest

The authors declare no competing financial interests.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.dcn.2016.10.003.

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