Low Socioeconomic Status Is Associated with a Greater Neural Response to Both Rewards and Losses

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Abstract

■ Low socioeconomic status (SES) has been associated with distinct patterns of reward processing, which appear to have adverse implications for health outcomes, well-being, and human capital. However, most studies in this literature have used complex tasks that engage more than reward processing and/or retrospectively studied childhood SES in samples of adults. To clarify how SES relates to the development of reward processing tendencies, we measured income-to-poverty ratio (IPR) in 172 youth who subsequently underwent functional MRI while completing a passive avoidance task to assess neural responses to reward and loss information. Participants were 12–15 years old (mean = 13.94, SD = .52; 65.7% female) from a sample broadly representative of the Chicago area in terms of SES (IPR range = 0.1–34.53; mean = 3.90; SD = 4.15) and racial makeup (40.1% White 30.8% Black; 29.1% Hispanic). To the extent they had lower IPR, children displayed a trend toward worse behavioral performance on the passive avoidance task. Lower IPR also was associated with a greater response in attention brain regions to reward and loss cues and to reward and loss feedback. Lower IPR also was associated with reduced differentiation between reward and loss feedback in the ventromedial prefrontal and parietal cortex. The current data suggest that both increased salience of reward/loss information and reduced discrimination between reward and loss feedback could be factors linking SES with the development of human capital and health outcomes. ■

INTRODUCTION

Low socioeconomic status (SES) has been linked to variation in both cognitive and affective processes (Fry, Langley, & Shelton, 2017; Kobrosly et al., 2011; Hackman & Farah, 2009; Myerson, Rank, Raines, & Schnitzler, 1998; Kramer, Allen, & Gergen, 1995). Some of the most consistent findings involve a tendency toward risk-aversive decision-making and an increased preference for smaller immediate, relative to larger, but delayed rewards (Dohmen et al., 2011; Tanaka, Camerer, & Nguyen, 2010; Guiso & Paiella, 2008). It has been argued that material deprivation reduces an individual's ability to maximize rewards in the environment, because the relative costs of delayed reward and missed opportunities are much higher for those with severely limited reserve resources (Haushofer & Fehr, 2014). Notably, others have suggested that these changes in risk preferences are potentially adaptive in low-resource contexts (Frankenhuis & Nettle, 2020). In unpredictable and uncontrollable situations, like many low-resource contexts, the resources put aside for long-term goals may be lost or be wasted by changes in the situation. For example, in experimental paradigms with unpredictable contexts, a preference for small, immediate rewards yields greater success in the paradigm (see the work of Frankenhuis & Nettle, 2020).

Using functional neuroimaging, research has attempted to identify variations in brain responsivity that might underlie the risk preferences and cognitive tendencies associated with low SES. A recent meta-analytic synthesis of these findings indicates that lower SES is associated with an increased BOLD response in reward-responsive regions, but decreased activation in executive functioning regions (Yaple & Yu, 2020). These findings provide a potential mechanistic explanation for why low SES is consistently associated with adverse outcomes in life domains where reward processing is important, such as mental health problems (e.g., Takiguchi et al., 2015; Plichta & Scheres, 2014), risky behaviors (Galván, 2013; Kuhnen & Knutson, 2005), substance abuse (Lees et al., 2021), and antisocial behavior (Blair, Leibenluft, & Pine, 2014; Glenn & Yang, 2012).

However, in this literature, reward processing itself has actually been understudied. Of the 18 studies included in the Yaple and Yu (2020) meta-analysis, six used executive functioning paradigms, for example, stimulus response, working memory, mathematics, and language tasks. Four others used social tasks (e.g., social exclusion), and six employed emotion tasks (e.g., viewing emotional images). Although the executive functioning tasks generally had feedback phases, they did not specifically isolate reward processing in analyses.

A handful of the studies in the meta-analysis did, however, use paradigms that provide a "clean" measure of

reward processing. Gonzalez, Allen, and Coan (2016) utilized a monetary incentive delay task, and Gianaros et al. (2011) used a gambling task. Notably, the Gonzalez et al. study (2016) found an increased BOLD response among lower-SES youth within subcortical (caudate/striatum) and cortical (orbital frontal and parietal cortex) reward-related brain regions. Gianaros et al. (2011) found a reduced BOLD response in lower-SES youth within brain regions implicated in both reward and attention (dorsomedial frontal, subgenual anterior cingulate cortex, dorsolateral prefrontal, and parietal cortices). A third study administered a guessing task and observed a higher BOLD response in the dorsomedial frontal cortex to reward stimuli in disadvantaged youth (Romens et al., 2015).

In an important recent advance, Palacios-Barrios et al. (2021) focused on a sample of adolescents (age 15 years), in whom they had measured SES in childhood (age 10 years). A passive avoidance decision-making paradigm was used, where clear reward and loss of information are provided about which objects to approach and which to avoid (Newman, Widom, & Nathan, 1985). The authors found that lower SES was associated with a reduced representation of reward in the subgenual anterior cingulate cortex in response to approach, but not avoidant, stimuli. Limiting the generalizability of the findings, Palacios-Barrios et al. conducted ROI analyses, focusing only on brain regions implicated in reward processing (striatum, ventromedial prefrontal cortex [vmPFC], ACC), and the feedback phase of the task was not considered.

There are many possible reasons for the inconsistent findings in these studies of SES and reward processing. One explanation is that studies measured SES in a variety of different ways (ranging from subjective to objective, and from household to neighborhoods) at a variety of different life stages (childhood, adolescence, adulthood), which were not always concurrent with fMRI assessments. Notably, none of the previous studies examined SES as reflected in the income-to-poverty ratio (IPR). IPR as a measure of SES is better than neighborhood quality or simple income levels, as IPR considers the specific household (as opposed to a neighborhood average) and factors in the total number of people. A family of three living on $40,000 per year is financially better off than a family of seven living on that same income.

Here, we sought to build on these conflicting results by studying a racially and ethnically diverse group of children who were at a similar developmental phase: eighth grade. The youth were enrolled in Wave 1 of a longitudinal study. The age range was chosen to observe the changes that occur over the course of adolescence in reward processing (Galván, 2013) and in other domains. Each household's current financial situation was indexed by an IPR. Children then underwent an fMRI scan while completing a passive avoidance task that provided unambiguous feedback (as opposed to social feedback like exclusion) and allowed for cue and feedback phases of the task to be considered separately (White et al., 2016). Based on behavioral

evidence that shows greater reward sensitivity among persons of low SES (Dohmen et al., 2011; Tanaka et al., 2010; Guiso & Paiella, 2008), some fMRI data suggesting the same pattern (Gonzalez et al., 2016; Romens et al., 2015), and the theoretical argument that material deprivation disrupts reward processing (Haushofer & Fehr, 2014), we hypothesized that lower IPR would be associated with greater BOLD responses in both reward processing (vmPFC, striatum) and attention regions (dorsolateral frontal, dorsomedial frontal, and parietal cortices) in the cue phase of the paradigm. In addition, based on the same behavioral findings and theoretical accounts, we hypothesized that low IPR would be associated with larger BOLD responses during the feedback phase of the paradigm. We predicted these larger BOLD responses would be evident for both rewards and losses, because, in a low-resource context, all reward and loss information should have increased salience. Based on previous fMRI data (Yaple & Yu, 2020), we expected these BOLD responses to be observed in both reward processing and attention regions.

METHODS

Participants

The study involved 277 children from the Chicago area. To be eligible, they had to be in eighth grade (typically 13–14 years old), English-speaking, and in good health, defined as being (a) nonpregnant, (b) in good health, (c) without acute infectious disease for 2 weeks, and (d) without fMRI scanning contraindications. These criteria were assessed during a parental phone-screen, where youth were excluded if they ever had (i) been diagnosed with a serious medical illness or an Axis 1 psychiatric disorder, (ii) had been on any ongoing medication regimen in the previous 3 months; (iii) a hospitalization in the previous 12 months, or (iv) any history of pervasive developmental disorder. Each child gave written assent to participate, and a parent or guardian gave written consent. Northwestern University's institutional review board approved the protocol.

The study involved two sessions, typically spaced 1–4 weeks apart. Questionnaire and laboratory data were collected, whereas MRI data were acquired during the second session. Forty-four children did not complete the MRI session because they failed to attend the scanning session, arrived too late to complete the tasks, were too obese or too anxious to enter the scanner, or had previously unrecognized structural anomalies, which ended the MRI visit. No usable data were available from another 59 children because of technical problems with acquisition (e.g., brain outside field of view [FOV]), excessive motion (> 10% of repetition times [TRs] censored), or lack of variability in behavioral response (e.g., approach all stimuli). Thus, the final analytic sample was 172 youths.

The final sample was 40.1% White ($n = 69$), 30.8% Black ($n = 53$), 29.1% Hispanic ($n = 50$), and 65.7% ($n = 113$)

female with an average age of 13.94 (SD = .52) years. The final sample did not significantly differ from the youth who did not provide usable MRI data in terms of age ($t = -.786$, $p = .433$) or sex breakdown ($\chi^2 = 1.621$, $p = .203$). Comparisons indicated that children missing fMRI data were less likely to identify as White ($\chi^2 = 7.270$, $p = .007$).[1]

Socioeconomic Conditions

Children attended the initial session with a parent/guardian, who completed an interview regarding household finances and composition using the MacArthur Network Sociodemographic Questionnaire (Adler, Epel, Castellazzo, & Ickovics, 2000). Consistent with previous studies of brain development (Noble et al., 2015; Luby et al., 2013), we used household IPR as the primary indicator of socioeconomic conditions. Parents/guardians reported on the number of people living in the household, including dependent children. They also reported all sources of household income during the previous year, including job wages, government assistance, and workers' compensation. Using this information in conjunction with U.S. government thresholds for 2014, each child's IPR was computed. A higher IPR indicates greater economic resources. The final sample had an average IPR of 3.90 (SD = 4.15, range = 0.1–34.53). Consistent with the IPR of Chicago, the IPRs were positively skewed to a degree inconsistent with the assumption of a normal distribution (skewness = 3.45, SE = .185; kurtosis = 18.83, SE = .368; George & Mallery, 2019). To reduce the skewness and kurtosis of the data (Soloman & Sawilowsky, 2009), a Blom rank-order normalization transformation (Blom, 1958) was conducted on the IPR values reducing skewness to < .001, and kurtosis was reduced to −0.133. The final sample did not significantly differ in IPR from youth who did not provide usable MRI data ($t = -.584$, $p = .559$).

fMRI Paradigm

To assess reward processing, children performed a modified version of a passive avoidance task (White et al., 2016; Figure 1), where the goal is to learn which objects result in monetary rewards and respond accordingly. Each trial consisted of a "cue phase," where a colored, geometric shape was presented for 1500 msec. This was followed by a randomly jittered fixation period of 500–2500 msec, which preceded the "feedback phase." In the feedback phase, text feedback indicating reward or loss was presented for 1500 msec and was followed by another randomly jittered fixation period of 0–4000 msec. As soon as each shape was presented, children could "approach" the shape with a button press or "avoid" the shape via withholding a button response. In the feedback phase, approaching the shape triggered a reward or loss event, whereas avoiding the shape triggered a blank screen with no monetary outcome. In trials following a response, one of four outcomes occurred: high-magnitude win ($50), low-magnitude win ($10), high-magnitude loss (−$50), or low-magnitude loss (−$10). The feedback was probabilistic and pseudorandom, such that responding to two particular shapes earned money on 87.5% of trials and responding to the other two shapes lost money on 87.5% of trials. In total, children completed 24 trials of each of the four shapes (96 trials total) in one 9 min 55 sec run. Participants did not complete any practice trials outside the scanner. After completing the task, all participants were paid a $5 "performance bonus," regardless of their actual performance.

MRI Parameters and Preprocessing

Scanning took place at the Center for Translational Imaging at Northwestern University. A Siemens Prisma 3 Tesla scanner with a 64 phased-array head/neck coil was used. A

Figure 1. The passive avoidance task. Participants chose to respond (make a button press) or not respond (withhold a button press) to four objects (choice phase). Reinforcement was probabilistic such that over the course of the task, the selection of two objects would accrue money, and the selection of the other two objects would lose money (feedback phase). (A) A participant responds and receives rewarding feedback. (B) A participant responds and receives punishing feedback. (C) A participant chooses not to respond, and no feedback is provided. [graphic] = participant chooses object.
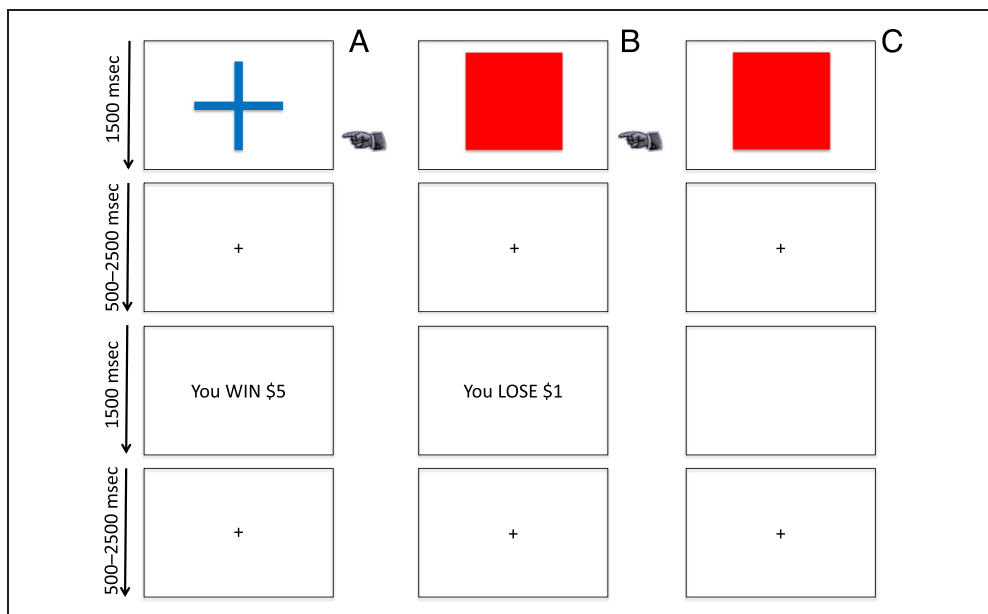
T2* weighted gradient EPI sequence (TR = 2000 msec; echo time = 27 msec; 240 mm FOV; 94 × 94 matrix; 90° flip angle) was utilized, collecting 300 total images for the reward paradigm. A whole-brain coverage was obtained with 43 axial slices (voxel size 1.694 × 1.694 × 1.7 mm³). Structural imaging consisted of a high-resolution navigated multi-echo magnetization prepared rapid acquisition gradient echo sequence (TR = 2300 msec, TE = 1.86, 3.78; flip angle = 7°; FOV = 256 × 256; matrix = 320 × 320; 208 slices; voxel size = 0.8 mm³).

fMRI data were analyzed using the standard *afni_proc.py* tool within the Analysis of Functional Neuroimages (AFNI; Cox, 1996) software. Functional images were despiked and slice-time and motion corrected. Anatomical scans were registered to the base volume of each child's functional images and warped to standard space (Talairach & Tournoux, 1988). Each volume of functional data was then aligned to this base volume and also warped to standard space. All volumes were resampled to 2 mm³. Functional images were spatially smoothed with a 6-mm FWHM Gaussian kernel. The time series were then normalized by dividing the signal intensity of a voxel at each time point by the mean signal intensity of that voxel for each run and multiplying the result by 100. The resultant regression coefficients represent a percentage of signal change from the mean.

Individual-level Analysis

Models included the six motion parameters from preprocessing (see above) and the following task regressors: (i) cue-phase trials when participants responded to the geometric shape (approach), (ii) cue-phase trials when participants did *not* respond to the geometric shape (avoid), (iii) rewarding feedback-phase trials, and (iv) punishing feedback-phase trials. All regressors were convolved with the AFNI default canonical gammavariate function to model the hemodynamic response. Linear regression was performed using models including motion and task regressors, as well as a task-specific baseline drift function to correct for slow movement during the scan. Volumes showing ≥ .5-mm movement from the previous volume were censored. This produced β coefficients and associated t statistics for each voxel and regressor.

Group-level Analysis

A whole-brain group-level analysis was conducted on the individual-level coefficients generated in the cue phase and feedback phase separately. IPR was entered as a covariate in a one-way (choice: approach, avoid) ANCOVA conducted on the cue-phase BOLD data. In the feedback phase, IPR was again entered as a covariate in a one-way (Feedback: win, loss) ANCOVA. In light of concerns within the neuroimaging literature regarding Type I error (Eklund, Nichols, & Knutsson, 2016), a simulation using the AFNI *3dClustSim* autocorrelation function (−acf) following the recommendations of AFNI's developers was

performed (Cox, Chen, Glen, Reynolds, & Taylor, 2017) to generate extent thresholds for a corrected *p* value of .05. An initial threshold of *p* = .002 was used yielding a whole-brain extent threshold of 68.2 voxels. All reported results exceeded this threshold. Post hoc testing was conducted on the average BOLD response extracted from the significantly activated voxels within clusters exceeding the extent threshold in size. Based on sample characteristics (see Descriptive Results section below), age and race/ethnicity were included as covariates in follow-up analyses. As the sample was 65.70% female, sex was also included as a covariate in the follow-up analysis.

RESULTS

Descriptive Results

Within the final sample, IPR did not significantly differ between male and female participants (Table 1). There was a trend toward a significant correlation between age and IPR (*r* = −.144, *p* = .060). A significant difference in IPR was also observed between ethnic/racial groups (*F* = 35.35, *p* < .001), where White youth had significantly greater IPR than Black youth (*t* = 7.07, *p* < .001) and

Table 1. Participant Descriptive Statistics for the Final Analytic Sample of 172 Youth

	Number	*Percentage*
Sex, female	113	65.7%
Race/Ethnicity		
Black	53	29.1%
White	69	40.1%
Hispanic/Latinx	50	30.8%
	Mean	*Standard Deviation*
Age, years	13.94	.52
Income-to-needs ratio	3.90	4.50
Relationships with IPR		
Correlation between age and IPR	*r* = −.144	*p* = .060
Sex differences in IPR	*t* = .916	*p* = .361
Race differences in IPR*	*F* = 35.35	*p* < .001
W > B*	*t* = 7.07	*p* < .001
W > H/L*	*t* = 7.32	*p* < .001
W > H/L	*t* = .104	*p* = .918

B = Black; W = White; H/L = Hispanic/Latinx.

* Indicates a significant difference at *p* < .05.

Hispanic/Latinx youth ($t = 7.32$, $p < .001$). Black and Hispanic/Latinx youth did not significantly differ ($t = .104$, $p = .918$).

Behavioral Results

A 2 (Valence: approach cue, avoid cue) × 2 (Magnitude: high [\$50], low [\$10]) ANCOVA covarying IPR was conducted on the accuracy data. A significant Valence × Magnitude interaction was observed, $F(1, 170) = 7.52$, $p = .007$, where participants' accuracy was significantly higher in high (85.7%) versus low-magnitude reward cues (79.3%) compared to high (64.9%) versus low-magnitude loss cues (64.7%, $t = 2.75$, $p = .007$). Significant main effects of Magnitude, $F(1, 170) = 8.98$, $p = .003$, and Valence, $F(1, 170) = 62.37$, $p < .001$ were also observed, where participants were more accurate to reward cues and more accurate to high-magnitude cues. A trending main effect of IPR was also observed, $F(1, 170) = 3.30$, $p = .071$, where greater IPR values were associated with increased accuracy ($r = .138$, $p = .071$).

A 2 (Valence: approach cue, avoid cue) × 2 (Magnitude: high [\$50], low [\$10]) × Sex (male, female) × 3 (Race/ethnicity: White Black, Hispanic/Latinx) ANCOVA covarying IPR and age was also conducted on the accuracy data. A significant Valence × Magnitude interaction was observed, $F(1, 166) = 8.73$, $p = .004$, where participants'

accuracy was significantly higher in high-magnitude reward cues (86.3%) relative to low-magnitude reward cues (79.4%) compared to high- (63.8%) versus low-magnitude loss cues (64.9%, $t = 2.75$, $p = .007$). Significant main effects of Magnitude, $F(1, 166) = 4.66$, $p = .032$, and Valence, $F(1, 170) = 49.28$, $p < .001$, were also observed, where participants were more accurate to reward cues and more accurate to high-magnitude cues. No other significant effects were observed ($F < 2.22$, $p > .138$), including the main effect of IPR, $F(1, 166) = 0.73$, $p = .395$.

fMRI Results

Choice-Phase Data

Choice × IPR Interaction. Significant Choice × IPR interactions were observed within left and right parietal cortex, as well as right anterior insula cortex (see Figure 2/Table 2). IPR was positively associated with the magnitude of the difference in BOLD response when choosing to approach versus choosing not to approach ($r = .294$–$.354$, $ps < .001$). In other words, to the extent that children had lower IPR values, they evidenced less neural distinction between cues associated with reward and loss.

Main Effect of IPR. Significant main effects of IPR were observed within regions including the left dorsolateral

Figure 2. Regions showing significant Income-to-Poverty Ratio × Choice Type interactions and a main effect of IPR in the choice phase. Significant Income-to-Poverty Ratio × Choice Type interactions were observed in right anterior insula cortex (A) and right inferior parietal cortex (C). In both regions, greater IPRs (reduced poverty) was associated with greater difference in BOLD response when responding relative to withholding a response in both regions (C/D). Greater IPR was associated with decreased BOLD response in dorsolateral pFC (E/F).
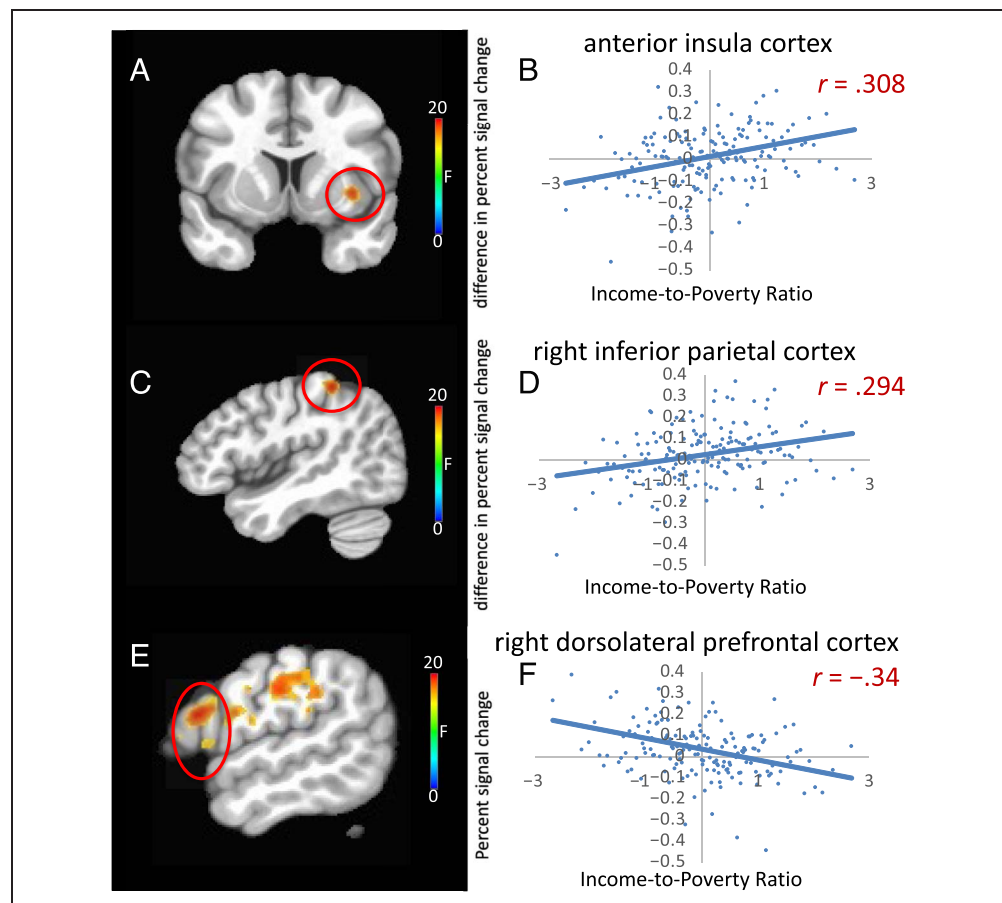
Table 2. Brain Regions Demonstrating Differential BOLD Responses during the Choice Phase

Region	Left/Right	x	y	z	F	p	Voxels
				Coordinates of Peak Activation[a]			
Choice Type × Income interaction							
Inferior parietal cortex	Left	−39	−35	38	25.287	< .0001	387
Inferior parietal cortex	Right	45	−37	50	19.040	< .0001	93
Anterior insula cortex	Right	33	9	2	17.056	< .0001	70
Main effect of IPR							
Dorsolateral pFC	Left	−53	19	20	21.853	< .0001	135
Inferior frontal gyrus	Left	−47	31	8	15.095	< .0001	109
Inferior parietal cortex	Left	−49	−17	30	20.448	< .0001	264
Inferior parietal cortex	Right	47	−21	46	16.762	< .0001	151
Precentral gyrus	Left	−57	−13	24	15.534	< .0001	214
Main effect of choice type							
Ventromedial prefrontal cortex	Left	−1	45	−4	17.647	< .0001	102
Caudate	Left	−9	7	12	22.352	< .0001	114
Caudate/thalamus	Right	13	−15	10	38.823	< .0001	794
Dorsal anterior insula cortex	Left	−29	17	12	20.784	< .0001	69
Inferior frontal gyrus	Right	43	−1	14	43.529	< .0001	492
Superior temporal gyrus	Left	−59	−11	0	23.137	< .0001	151
Temporal pole	Left	−25	9	−18	21.176	< .0001	277
Middle insula/postcentral gyrus	Right	51	−23	20	31.764	< .0001	595
Lingual gyrus	Left	−25	−43	−8	27.058	< .0001	133
Uncus	Right	27	7	−22	17.254	< .0001	73
Visual cortex	Left	−13	−95	−8	27.843	< .0001	622
Cerebellum	Right	13	−51	−14	67.058	< .0001	990
Cuneus	Left	−1	−81	26	14.901	< .0001	69
Motor cortex	Left	−35	−3	14	>99.99	< .0001	9216

[a] Based on the Tournoux & Talairach standard brain template.

pFC, left inferior parietal cortex, right inferior parietal cortex, left inferior frontal gyrus, and left postcentral gyrus (see Figure 2/Table 2)). In all regions, lower IPR values were associated with a larger BOLD response ($r = −.320$ to $−.399$, $ps < .001$).

Main Effect of Choice Type. Significant main effects of Choice were observed within regions including right caudate, left caudate, vmPFC, right inferior frontal gyrus, left anterior insula cortex, right superior temporal gyrus, and left temporal pole (see Table 2). When choosing to approach, relative to not choosing to approach, a greater BOLD response was observed in the left and right caudate, right inferior frontal gyrus, and left anterior insula cortex. When choosing to not approach (i.e., avoid), relative to choosing to approach, a greater BOLD response was observed in the vmPFC, right superior temporal gyrus, and left temporal pole.

Feedback-Phase Data

Feedback Type × IPR Interaction. A significant Feedback Type × IPR interaction was observed in the vmPFC where, again, IPR was positively associated with the difference in BOLD response to reward versus loss feedback ($r = .338$, $p < .001$; see Figure 3/Table 3). In other words,

Figure 3. Regions showing a significant Income-to-Poverty Ratio × Choice Type interaction and a main effect of IPR in the feedback phase. A significant Income-to-Poverty Ratio × Feedback Type interaction was observed in vmPFC (A). Greater IPRs (reduced poverty) was associated with greater difference in BOLD response to reward relative to loss trials (B). Greater IPR was associated with decreased BOLD response in inferior parietal cortex (C/D).
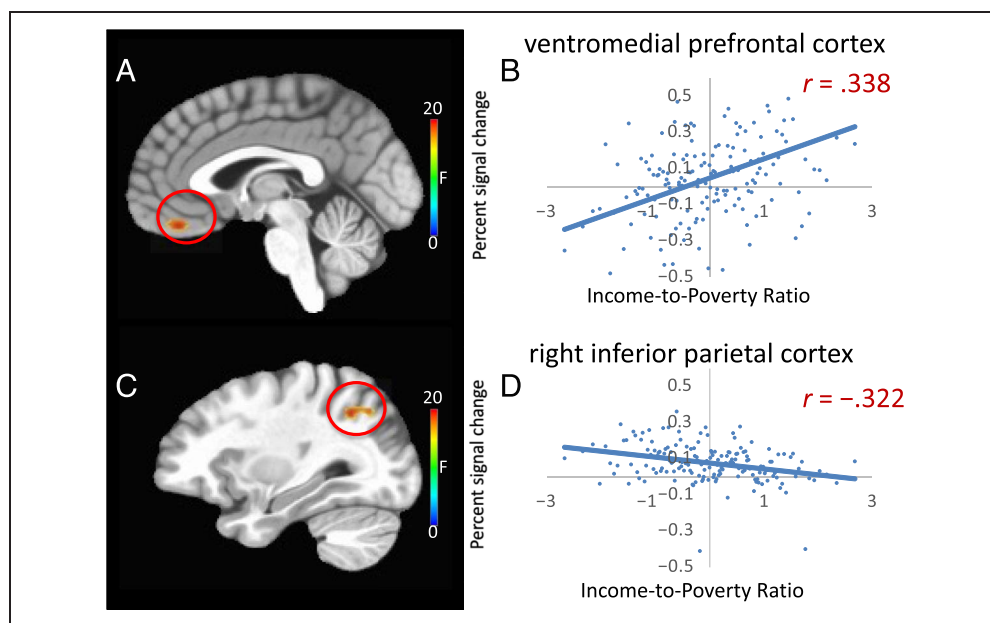
Table 3. Brain Regions Demonstrating Differential BOLD Responses during the Feedback Phase

Region	Left/Right	x	y	z	F	p	Voxels
			Coordinates of Peak Activation[a]				
Main effect of IPR							
Inferior parietal cortex	Right	29	−51	36	18.430	< .0001	108
Cerebellum	Left	−17	−43	−24	20.594	< .0001	85
Main effect of feedback type							
Dorsomedial frontal cortex	Right	9	13	62	51.147	< .0001	2381
Anterior insula cortex/motor cortex	Right	47	17	0	38.551	< .0001	1875
Anterior insula cortex/motor cortex	Left	−29	19	−8	42.382	< .0001	1350
Paracentral lobule	Right	13	−43	64	32.177	< .0001	1392
Superior temporal sulcus	Right	63	−17	14	30.828	< .0001	412
Inferior parietal cortex	Left	−35	−29	44	24.331	< .0001	310
Temporal–parietal junction	Left	−55	−47	30	34.449	< .0001	242
Superior temporal sulcus	Left	−47	−25	0	30.884	< .0001	267
Visual cortex	Left	−1	−87	−18	21.779	< .0001	91
Ventral striatum	Right	11	11	−6	27.274	< .0001	174
Ventral striatum	Left	−15	11	−4	33.928	< .0001	158
Inferior parietal cortex	Right	37	−33	46	19.173	< .0001	158
Superior temporal gyrus	Right	47	−25	0	30.828	< .0001	147
Temporal pole	Left	−47	7	−20	16.661	< .0001	119
Posterior thalamus	Left	−3	−25	0	17.726	< .0001	83
Dorsolateral middle frontal gyrus	Left	−25	43	34	18.478	< .0001	76

[a] Based on the Tournoux & Talairach standard brain template.

children with lower IPR showed less neural distinction between reward and loss information.

Main Effect of IPR. A significant main effect of IPR was observed within the right inferior parietal cortex, such that lower IPR was associated with a larger BOLD response ($r = -.322$, ps $< .001$; see Figure 3/Table 3).

Main Effect of Feedback Type. Significant main effects of Feedback Type were observed within regions including the left ventral striatum, right ventral striatum, dorsomedial frontal cortex, left dorsolateral pFC, right superior temporal sulcus, left superior temporal sulcus, right inferior parietal cortex, left inferior parietal cortex, left temporal–parietal junction, right superior temporal gyrus,

Table 4. Brain Regions Demonstrating Differential BOLD Responses during the Choice Phase Controlling for Age, Sex, and Race/Ethnicity

Region	Left/Right	x	y	z	F	p	Voxels
		Coordinates of Peak Activation[a]					
Choice Type × Income interaction							
Inferior parietal cortex	Left	−31	−31	40		< .0001	173
Inferior parietal cortex*	Right	43	−39	48		< .0001	6
Anterior insula cortex*	Right	33	9	0		< .0001	10
Main effect of IPR							
Dorsolateral pFC	Left	−57	19	12		< .0001	96
Inferior frontal gyrus*	Left	−53	29	10			16
Inferior parietal cortex	Left	−51	−17	32		< .0001	135
Inferior parietal cortex*	Right	43	−21	36		< .0001	42
Precentral gyrus	Left	−57	−13	24		< .0001	95
Choice Type × Race/Ethnicity interaction							
Visual cortex	Left	−9	−59	6		< .0001	272
Main effect of choice type							
Ventromedial prefrontal cortex*	Left	−5	39	−2		< .0001	47
Caudate	Left	−11	1	16		< .0001	101
Dorsal anterior insula cortex	Left	−29	15	14		< .0001	68
Inferior frontal gyrus	Right	43	−1	14		< .0001	511
Superior temporal gyrus	Left	−67	−5	4		< .0001	182
Temporal pole	Left	−47	11	−12		< .0001	336
Middle insula/postcentral gyrus	Right	55	−21	48		< .0001	628
Lingual gyrus*	Left	−25	−43	−8		< .0001	52
Uncus*	Right	25	5	−22		< .0001	13
Visual cortex	Left	−11	−97	4		< .0001	117
Cerebellum	Right	13	−51	−14		< .0001	947
Cuneus	Left	9	−83	26		< .0001	91
Motor cortex/caudate/thalamus	Left	−39	−5	16	>99.99	< .0001	12457

[a] Based on the Tournoux & Talairach standard brain template.

* Indicates a region failing to exceed the clustering threshold with the inclusion of additional covariates.

and left temporal pole (see Table 3). A greater BOLD response was observed to reward relative to loss feedback in the left ventral striatum, right striatum, right superior temporal sulcus, right inferior parietal cortex, and left inferior parietal cortex. A greater BOLD response was observed to loss relative to reward feedback in the dorsomedial frontal cortex, left dorsolateral pFC, left superior temporal sulcus, left temporal–parietal junction, right superior temporal gyrus, and left temporal pole.

Covariates

The above models were rerun adjusting for age, sex, and race/ethnicity. The inclusion of these covariates did not appreciably change findings for the cue phase (Table 4). The interaction in the left parietal cortex remained significant. Interactions in right parietal and anterior insula cortices also remained significant, albeit below the cluster threshold. The main effect of IPR remained significant in the left inferior parietal cortex, left dorsolateral pFC, and precentral gyrus. The right inferior parietal cortex and inferior frontal gyrus findings also remained, although the regions dropped below the clustering threshold. Regions showing a main effect of Choice Type in the initial analysis remained significant with the addition of the covariates, although the vmPFC region dropped below the cluster threshold. Significant Choice Type × Race/Ethnicity interactions were observed in the visual cortex, but not in attentional (or other) regions. No other significant main effects or interactions were observed. With respect to the feedback phase, the main effect of IPR remained significant within the right inferior parietal cortex, albeit below the clustering threshold (Table 5). In contrast, the IPR × Feedback Type interaction within vmPFC finding did not

Table 5. Brain Regions Demonstrating Differential BOLD Responses during the Feedback Phase Controlling for Age, Sex, and Race/Ethnicity

Region	Left/Right	Coordinates of Peak Activation [a]			F	p	Voxels
		x	y	z			
Feedback Type × Income Interaction							
Main effect of IPR							
Inferior parietal cortex*	Right	21	−55	32		< .0001	46
Cerebellum	Left	13	−41	−2		< .0001	204
Main effect of feedback type							
Dorsomedial frontal cortex	Right	9	15	62		< .0001	2738
Anterior insula cortex/motor cortex	Right	47	17	0		< .0001	1127
Anterior insula cortex/motor cortex	Left	−29	21	−6		< .0001	1264
Paracentral lobule	Right	13	−43	64		< .0001	1775
Superior temporal sulcus	Right	63	−17	16		< .0001	518
Inferior parietal cortex	Left	−41	−33	46		< .0001	445
Temporal–parietal junction	Left	−55	−47	30		< .0001	268
Superior temporal sulcus	Left	−47	−25	0		< .0001	223
Visual cortex	Left	1	−87	−16		< .0001	153
Ventral striatum	Right	17	11	−6		< .0001	126
Ventral striatum	Left	−15	11	−4		< .0001	152
Inferior parietal cortex	Right	29	−35	42		< .0001	158
Superior temporal gyrus	Right	47	25	0		< .0001	87
Temporal pole	Left	−45	7	−22		< .0001	74
Posterior thalamus*	Left	−5	−23	0		< .0001	53
Dorsolateral middle frontal gyrus*	Left	−25	43	34		< .0001	59

[a] Based on the Tournoux & Talairach standard brain template.

* Indicates a region failing to exceed the clustering threshold with the inclusion of additional covariates.

survive inclusion of additional covariates into the model. Regions showing a main effect of feedback type in the initial analysis remained significant with the addition of the covariates, although posterior thalamus and dorsolateral middle frontal gyrus dropped below the cluster threshold. No other significant main effects or interactions were observed after adding the additional covariates to the model.

DISCUSSION

The current study examined the association between SES and reward processing, using a passive avoidance task that allowed us to assess neural activity to both reward and loss stimuli. Three principal findings emerged. First, consistent with hypotheses, lower IPR was associated with a larger response in brain regions implicated in attention to reward and loss cues and to reward and loss feedback. Second, and contrary to hypotheses, lower IPR was associated with reduced differentiation between reward and loss information in the vmPFC, although this effect did not survive including race/ethnicity into the model. Finally, lower IPR was associated with reduced differentiation between reward and loss cues in attentional regions (bilateral parietal cortex). Collectively, these findings provide some insight into the mechanisms by which socioeconomic disadvantage might contribute to variations in the development of reward processing in children.

Consistent with hypotheses, both cues and receipt of reward and loss were associated with larger BOLD response in attentional regions (e.g., dorsolateral prefrontal, parietal cortices) in those with lower IPR. This pattern is consistent with the results observed in a variety of different decision-making and executive function paradigms (see the work of Yaple & Yu, 2020), as well as the results of studies that focus specifically on reward processing (Gonzalez et al., 2016; Romens et al., 2015), although see the works of Gianaros et al. (2011) and Palacios-Barrios et al. (2021). These patterns are also consistent with behavioral findings and theoretical positions suggesting that reward and loss information are particularly salient for those in low-resource settings, where even small changes in reward and loss can have a relatively large impact on an individual's circumstances (Haushofer & Fehr, 2014). However, studies that experimentally manipulate the amount and content of cognitive load during reward processing will be needed to fully test this. Notably, it has been argued that material deprivation reduces cognitive capacity by reducing available cognitive resources (Mani, Mullainathan, Shafir, & Zhao, 2013). Alternatively, it has been argued that alterations in reward processing, including changes in the salience of reward information, is part of an adaptive response to a low-resource environment (Frankenhuis & Nettle, 2020) The current findings of increased activation in attentional regions are not inconsistent with either of these positions.

Notably, lower IPR was also associated with a reduced distinction between reward and loss cues in attention/salience regions (bilateral parietal cortex, anterior insula cortex). These findings may be consistent with a scenario where material disadvantage increases sensitivity to both reward and loss information (Haushofer & Fehr, 2014). Those with higher IPR may feel free to look to maximize opportunities in their environment, whereas those with lower IPR may need to more actively avoid losses they cannot afford at the expense of maximizing relative opportunity. This is potentially reflected in the trend in the behavioral data toward poorer task accuracy as a function of lower IPR. The increased salience of reward and loss information may be adaptive in a low-resource context (Frankenhuis & Nettle, 2020). This is speculative, however, and will need to be tested in future work.

We observed associations within the vmPFC, but in an unanticipated direction. Lower IPR was associated with a reduced distinction between reward and loss receipt in this region. The vmPFC is a critical structure for reward processing (e.g., O'Doherty, 2011) and previously has been implicated in reward processing during passive avoidance (e.g., Kosson et al., 2006; White et al., 2013). Given previous findings (Yaple & Yu, 2020), we expected increased vmPFC activation in those with lower IPR. The current findings suggest that socioeconomic variation in reward processing is not simply a reflection of the salience of rewards and losses. The vmPFC plays complex roles in both decision-making (O'Doherty, 2011) and emotion regulation (e.g., Motzkin, Philippi, Wolf, Baskaya, & Koenigs, 2015). Given the importance of these processes for the development of well-being and human capital, future research should explore socioeconomic variation in vmPFC function in more detail.

Importantly, the vmPFC findings did not survive when age, sex, and race/ethnicity were included in statistical models, neither did the behavioral trend where greater IPR was associated with poorer accuracy. However, it is complicated to interpret these results, because, in this sample, and in the United States more generally, there are substantial racial and economic variations in wealth and income. These variations are not incidental, but a legacy of historical policies and practices (Williams, Priest, & Anderson, 2016). As a consequence, in a sample like this one, even the most elaborate covariance analyses cannot untangle the overlapping influences of SES, race, and ethnicity (for a statisical discussion, see the work of Miller & Chapman, 2001). Notably, most of the findings within attention regions did survive the inclusion of additional covariates, indicating they are independent of these characteristics.

Somewhat surprisingly, a significant effect of IPR in the striatum and caudate was not observed. The striatum, particularly the ventral striatum, is critically involved in reward processing (Schultz, 2006; O'Doherty, 2004), and, indeed, clear main effects of valence were observed in both the cue and feedback phases within the striatum/caudate.

Cognitive neuroscience models of reward processing implicate the ventral striatum in representing reward information and signaling prediction errors, whereas the vmPFC plays a more complex role in holding and manipulating reward information in a more abstract manner (O'Doherty, 2004, 2011). Theoretical models of the effects of poverty on cognition focus on how having fewer resources changes the meaningfulness of rewards in a given context (Mani et al., 2013). An individual with some savings is less threatened by a potential loss than someone with no savings. It is reasonable to suspect that this type of alternation of meaning in context would be represented in vmPFC, but not in striatum. Coupled with the subtle, and trend level, effect of IPR on task performance, it is possible that, at least during passive avoidance, the striatum, but not other reward-related brain regions, is functioning reasonably well under conditions of poverty. In contrast to this idea, a meta-analysis reported a relationship between low SES and striatal functioning (see the work of Yaple & Yu, 2020); however, several other studies have also failed to observe this pattern (e.g., Palacios-Barrios et al., 2021; Romens et al., 2015). The role of SES in striatum functioning requires further investigation.

The current study had a number of important strengths. This study involved a relatively large sample, particularly for an fMRI study with children. Moreover, the sample was diverse in terms of race and ethnicity and covered a large spectrum of incomes. Finally, the current study assessed SES contemporaneously with the imaging acquisition. As previously noted, many studies on childhood poverty focus on adults who had experienced poverty (e.g., Gonzalez et al., 2016; Gianaros et al., 2011). The question of the role of poverty on cognitive development is an important one, but it is distinct from understanding the role of poverty in actively influencing cognitive functioning in poor children.

The current study also has several limitations. First, despite using a very similar task, the current findings were different from the Palacio-Barrios et al. (2021) findings. Palacios-Barrios et al. utilized a computational neuroimaging approach that dramatically differed from the approach taken here, which may account for the differences in findings. Second, the current data are cross-sectional and therefore cannot address important developmental issues or questions regarding the permanence or mutability of neural changes associated with SES. Third, participants in the study did not receive a complete psychological assessment and, therefore, the roll of psychological disorders cannot be completely accounted for in the current data. Fourth, in order to retain a sufficient number of observations for the statistical analysis, we were unable to examine the neural impact of the magnitude of rewards and losses. Fifth, it is worth noting that at the population level, low SES tends to co-occur with other exposures, for example, air pollution, parental maltreatment, and health problems, that could be associated with alterations in reward processing (McCrory, Gerin, & Viding, 2017;

Raphael, 2011; Evans & Kantrowitz, 2002). Although it is important not to conflate low SES with these exposures, their cumulative and/or synergistic effects on reward processing should be considered in future work.

It has long been clear that SES is associated with variations in reward processing and decision-making, both behaviorally (Haushofer & Fehr, 2014; Mani et al., 2013) and neurally (Yaple & Yu, 2020). However, the specific neural mechanisms underlying these patterns are poorly understood. The current data suggest that both increased salience of reward and loss information and difficulty in distinguishing between reward and loss information may be critical factors in how poverty shapes behavior. Future work will need to include longitudinal work to examine the developmental implications of poverty, and work in conjunction with economic interventions (e.g., universal basic income projects) to understand the degree to which neural changes associated with poverty are malleable in a changed economic setting.

Data Availability Statement

These data will be archived consistent with NHLBI and NIH policies.

Author Contributions

Funding Information

Diversity in Citation Practices

A retrospective analysis of the citations in every article published in this journal from 2010 to 2020 has revealed a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .408, W(oman)/M = .335,

M/W = .108, and W/W = .149, the comparable proportions for the articles that these authorship teams cited were M/M = .579, W/M = .243, M/W = .102, and W/W = .076 (Fulvio et al., *JoCN*, 33:1, pp. 3–7). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

Note

1. A previous article has reported on the data from the current sample. Miller, White, Chen, and Nusslock (2021) examined the link between inflammation, SES, and BOLD activation within several regions-of-interest (ventral striatum and amygdala). The current article conducted a whole-brain analysis of the data and examined the neural mechanisms underpinning reward processing. Thus, the presented analyses are novel.

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