

## MIT Open Access Articles

*Striatal and Behavioral Responses to Reward Vary by Socioeconomic Status in Adolescents*

The MIT Faculty has made this article openly available. **Please share** how this access benefits you. Your story matters.

**Citation:** Alexandra L. Decker, Steven L. Meisler, Nicholas A. Hubbard, Clemens C.C. Bauer, Julia Leonard, Hannah Grotzinger, Melissa A. Giebler, Yesi Camacho Torres, Andrea Imhof, Rachel Romeo, John D. E. Gabrieli. *Journal of Neuroscience* 22 January 2024, e1633232023.

**As Published:** <https://doi.org/10.1523/JNEUROSCI.1633-23.2023>

**Persistent URL:** <https://hdl.handle.net/1721.1/153394>

**Version:** Author's final manuscript: final author's manuscript post peer review, without publisher's formatting or copy editing

**Terms of use:** Creative Commons Attribution-Noncommercial-Share Alike



1 **Striatal and Behavioral Responses to Reward Vary by Socioeconomic Status in**  
2 **Adolescents**

3 Abbreviated title: Reward Responses Vary By Adolescent Socioeconomic Status

4 Alexandra L. Decker<sup>1</sup>, Steven L. Meisler<sup>1,2,3</sup>, Nicholas A. Hubbard<sup>4</sup>, Clemens C.C.  
5 Bauer<sup>1,2,5</sup>, Julia Leonard<sup>6</sup>, Hannah Grotzinger<sup>7</sup>, Melissa A. Giebler<sup>8</sup>, Yesi Camacho  
6 Torres<sup>1</sup>, Andrea Imhof<sup>9</sup>, Rachel Romeo<sup>#10</sup>, and John D. E. Gabrieli<sup>#1,2</sup>

7 <sup>1</sup> McGovern Institute for Brain Research, Massachusetts Institute of Technology,  
8 Cambridge, MA

9 <sup>2</sup> Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology,  
10 Cambridge, MA

11 <sup>3</sup> Program in Speech and Hearing Bioscience and Technology, Harvard University,  
12 Cambridge, MA

13 <sup>4</sup> Department of Psychology, University of Nebraska, Lincoln, NE

14 <sup>5</sup> Department of Psychology, Northeastern University, Boston, MA

15 <sup>6</sup> Department of Psychology, Yale University, New Haven, CT

16 <sup>7</sup> Department of Psychological & Brain Sciences, University of California, Santa  
17 Barbara, CA

18 <sup>8</sup> Teachers College, Columbia University, New York, NY

19 <sup>9</sup> Department of Psychology, University of Oregon, Eugene, OR

20 <sup>10</sup> Departments of Human Development & Quantitative Methodology and Hearing &  
21 Speech Sciences, and Program in Neuroscience & Cognitive Science, University of  
22 Maryland College Park, Baltimore, MD

23 # co-senior authors

24 Corresponding author: Alexandra Decker; alexandrleerdecker@gmail.com

25 Number of Pages: 39

26 Number of Figures: 6; Number of Tables: 0

27 Conflict of interest statement: the authors declare no competing interests

28 Competing interest statement: The authors declare no competing interests.

29

30 Key Words: Socioeconomic Status, Adolescence, Reward, Striatum, Decision-Making,

31 Response Time

32

33

34

35

36

37

38

39

## Abstract

40  
41 Disparities in socioeconomic status (SES) lead to unequal access to financial and social  
42 support. These disparities are believed to influence reward sensitivity, which in turn, are  
43 hypothesized to shape how individuals respond to and pursue rewarding experiences.  
44 However, surprisingly little is known about how SES shapes reward sensitivity in  
45 adolescence. Here we investigated how SES influenced adolescent responses to  
46 reward, both in behavior and the striatum—a brain region that is highly sensitive to  
47 reward. We examined responses to both immediate reward (tracked by phasic  
48 dopamine) and average reward rate fluctuations (tracked by tonic dopamine) as these  
49 distinct signals independently shape learning and motivation. Adolescents (n=114; 12-  
50 14 years; 58 female) performed a gambling task during functional magnetic resonance  
51 imaging. We manipulated trial-by-trial reward and loss outcomes, leading to fluctuations  
52 between periods of reward scarcity and abundance. We found that a higher reward rate  
53 hastened behavioral responses, and increased guess switching, consistent with the  
54 idea that reward abundance increases response vigor and exploration. Moreover,  
55 immediate reward reinforced previously rewarding decisions (win-stay, lose-switch) and  
56 slowed responses (post-reward pausing), particularly when rewards were scarce.  
57 Notably, lower-SES adolescents slowed down less after rare rewards than higher-SES  
58 adolescents. In the brain, striatal activations covaried with the average reward rate  
59 across time, and showed greater activations during rewarding blocks. However, these  
60 striatal effects were diminished in lower-SES adolescents. These findings show that the  
61 striatum tracks reward rate fluctuations, which shape decisions and motivation.

62 Moreover, lower SES appears to attenuate reward-driven behavioral and brain  
63 responses.

64

65

66

67

68

69

70

71

72

73

74

75

76

77

78

79

80

81

82

83

84  
85  
86  
87  
88  
89  
90  
91  
92  
93  
94  
95  
96  
97  
98  
99  
100  
101  
102  
103  
104  
105

### **Significance statement**

Lower socioeconomic status (SES) is associated with reduced access to resources and opportunities. Such disparities may shape reward sensitivity, which in turn, could influence how individuals respond to and pursue rewarding experiences. Here, we show that lower-SES adolescents display reduced reward sensitivity in the brain and behavior. The striatum—a brain region that is highly sensitive to reward—showed greater activations during periods of high reward and tracked fluctuations between reward-rich and reward-scarce task phases. However, lower SES correlated with smaller reward-driven striatal responses, and reduced response slowing after rare rewards. These findings link lower SES to reduced reward responses, which could trigger a cycle of reduced reward pursuit, leading to fewer positive experiences, which could further diminish reward sensitivity.

106

## Introduction

107           Adolescents from lower socioeconomic status (SES) backgrounds have less  
108 access to enriching opportunities and resources than their higher-SES peers (Farah,  
109 2017). These disparities may influence reward sensitivity, which in turn, could shape  
110 how adolescents respond to or pursue rewarding experiences (Amir et al., 2018). Such  
111 a cycle could explain how SES—by modulating reward responses and related  
112 processes—is associated with many consequential developmental outcomes (Farah,  
113 2017). Here, we examined how SES relates to reward-driven responses in behavior and  
114 the brain in adolescents, focusing on the striatum because of its high sensitivity to  
115 reward (Schultz, 1993).

116           Rewards powerfully influence motivation, learning, and decision-making.  
117 Immediately rewarding outcomes, signaled by fast phasic striatal responses, are  
118 thought to serve as a learning signal to maximize rewards (Day et al., 2007). Rewarding  
119 outcomes strongly reinforce prior actions that led to rewards (Hamid et al., 2016) and  
120 induce “post-reward pausing” in behavior (Schlinger et al., 2008). Individuals are also  
121 sensitive to the overall amount of reward available in their environment. The average  
122 environmental reward rate (tracked by tonic dopamine and estimated from past reward  
123 history) influence moment-to-moment shifts in response time and exploration (Hamid et  
124 al., 2016; Niv et al., 2007; Wang et al., 2021). A high environmental reward rate boosts  
125 response speeding, in theory, by increasing the cost of time (slower responses forfeit  
126 more rewards) (Beierholm et al., 2013; Niv et al., 2006, 2007; Otto & Daw, 2019; Wang  
127 et al., 2013, 2021) and increases exploration, in theory, due to the high likelihood of

128 attaining rewards in the environment (Constantino & Daw, 2015; Niv et al., 2007;  
129 Sukumar et al., 2021). Interestingly, these distinct reward signals also interact: reward  
130 scarcity heightens sensitivity to immediate reward, amplifying both phasic dopamine  
131 firing following rewards (Bayer & Glimcher, 2005; Hamid et al., 2016) and behavioral  
132 pausing after rewarding outcomes (Schlinger et al., 2008).

133         How SES influences responses to these distinct reward signals in adolescents in  
134 the brain and behavior remains unclear. Previous research suggests that lower SES  
135 may increase sensitivity *to immediate* reward, as lower-SES individuals tend to choose  
136 small immediate rewards over larger, delayed ones (Oshri et al., 2019). This is  
137 hypothesized to adaptively enable individuals to quickly seize scarce reward  
138 opportunities to meet basic needs (Frankenhuis et al., 2016; Frankenhuis & Nettle,  
139 2020; Pepper & Nettle, 2017). Lower SES environments can also be less predictable  
140 (Evans, 2004), meaning past reward history may poorly predict future outcomes  
141 (Behrens et al., 2007; Ross & Hill, 2002). Based on this research, lower-SES  
142 adolescents may be highly responsive to *immediate* reward, but less responsive to past  
143 reward history, which could lead to contextually sub-optimal behavior.

144         This hypothesis, however, contrasts with two studies that found that lower SES in  
145 adolescents correlated with *reduced* responses to rewarding cues in the parietal (White  
146 et al., 2022) and frontal (Palacios-Barrios et al., 2021) cortices. Notably, however, both  
147 studies linked lower-SES to poorer behavioral learning of cue-reward associations  
148 (Palacios-Barrios et al., 2021; statistical trend White et al., 2022), which may have



149 altered expectations of reward when viewing reward-predicting cues. The present study  
150 therefore eliminated learning demands.

151 In the present study, we examined behavioral and striatal responses to reward and  
152 reward rate fluctuations in adolescents from diverse SES backgrounds. Adolescents  
153 performed a gambling task during functional magnetic resonance imaging in which they  
154 won or lost on each trial. Unbeknownst to participants, we manipulated trial outcomes,  
155 leading to alternating periods of reward scarcity and abundance. We examined how  
156 immediate reward and average reward rate fluctuations shaped vigor (response times  
157 or RTs) and choices differently by SES. We also examined SES-related differences in  
158 the influence of reward and average reward rate fluctuations on striatal responses. Our  
159 results support influential theories of decision that argue the striatum tracks average  
160 reward rate fluctuations, as well as theories that suggest that lower SES reduces  
161 behavioral and striatal reward sensitivity.

162

163

164

165

166

167

168

169

170

171  
172  
173  
174  
175  
176  
177  
178  
179  
180  
181  
182  
183  
184  
185  
186  
187  
188  
189  
190  
191

## Methods

### Participants

We recruited 127 adolescents from diverse SES backgrounds as part of a larger project examining the relationship between SES, brain development, and cognition. Eligible participants were in the 7th or 8th grade, proficient in English, had no MRI contraindications, were not diagnosed with autism or a neurological disability, and were not born premature (<34 weeks). Thirteen children did not complete the MRI, resulting in a sample of 114 adolescents (age range=12-14; mean (SD)=13.46 (0.68),  $n=56$  female). Five participants with excessive movement during scanning (average framewise displacement (FD) of more than 0.6 mm) were retained only for behavioral analyses, leaving 109 for the neuroimaging analysis (*correlation between FD and SES* among the included participants:  $\beta = 0.005$ ,  $SE = 0.01$ ,  $t(107) = 0.35$ ,  $p = .730$ ,  $r = 0.03$ ). Of note, the findings remained unchanged with a more conservative limit of movement (average FD of < 0.3mm). All children and their legal guardians provided assent and consent. The study was approved by the MIT Committee on the Use of Human Subjects. Participants received compensation for their time.

Before collecting data, we targeted a sample of at least 100 participants based on studies reporting medium-to-large effects (i.e., Cohen's  $d$  of 0.5-0.8) on the relationship between SES and cognitive performance (Finn et al., 2017; Leonard et al., 2019; Noble et al., 2007), brain structure (Decker, Duncan, et al., 2020; Romeo et al., 2018), and brain function (Finn et al., 2017). A sensitivity analysis revealed that our

192 sample size provided 80% power to detect medium effects (d of 0.53 or Pearson's *r* of  
193 0.25) in two-tailed between subject analyses.

194

### 195 **Measure of socioeconomic status (SES)**

196 Participants' caregivers reported their annual household income (*range*=\$2k-  
197 \$1.25m) and the number of years of schooling they had completed (*range*=7-20 years).

198 Our primary measure of SES incorporated both these variables. We averaged the z-  
199 scores of the maternal education, paternal education, and the z-score of the log-

200 transformed income measures (*Figure 1A depicts the SES distribution*). The log

201 transformation on income accounts for the greater impact that gains have for lower-SES

202 individuals. Two participants were missing one of the three measures, so their SES

203 index was the average of the two others.

204

### 205 **Experimental Design**

206 Participants performed a variant of Delgado et al.'s card guessing task (Delgado  
207 et al., 2000; Hubbard, Romeo, et al., 2020; Hubbard, Siless, et al., 2020); *Figure 1B*).

208 On each trial, adolescents guessed if an upcoming number, with a possible value from

209 1-9, would be larger or smaller than 5. They then received immediate feedback based

210 on the accuracy of their guess. Participants were told that accurate guesses would be

211 financially rewarded as wins, and inaccurate guesses would be financially punished as

212 losses, and that the sum of wins and losses would be calculated for an additional

213 payment. Unbeknownst to participants, trial-by-trial gains and losses were

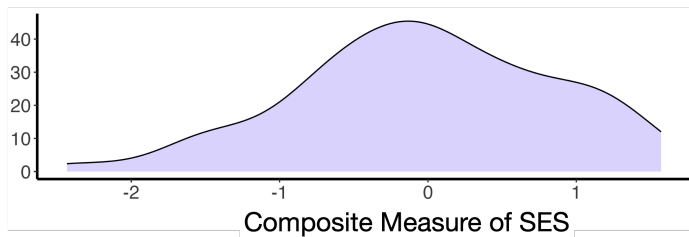
214 predetermined, and fixed across trials, with numbers generated to match the  
215 predetermined outcome for each trial. Outcomes were therefore unrelated to participant  
216 guesses, which equalized uncertainty across participants, and ensured everyone had  
217 the same experience of winning and losing.

218         Each trial began with a question mark, during which participants had 1.5 seconds  
219 to register a guess (smaller than 5=index finger; larger than 5=middle finger; Figure 1B).  
220 A number was then displayed for 500ms, followed by 500ms of feedback. Feedback  
221 indicated whether participants had won or lost money, or neither won nor lost money.  
222 Positive feedback, which followed correct guesses, consisted of a green arrow pointing  
223 up and the text “+\$1”; negative feedback, which followed incorrect guesses, consisted of  
224 a red arrow pointing down and text displaying “-\$0.5”; neutral feedback, which followed  
225 the number 5, consisted of a light green double-sided arrow. If participants did not  
226 register a guess, they received neutral feedback. This happened rarely (3.1 trials or  
227 4.5% of trials on average per participant; relationship between missed responses and  
228 SES:  $\beta = 0.27$ ,  $SE = 0.29$ ,  $t(114) = 0.95$ ,  $p = .35$ ). Participants viewed a fixation cross  
229 for 1 second before a new trial began.

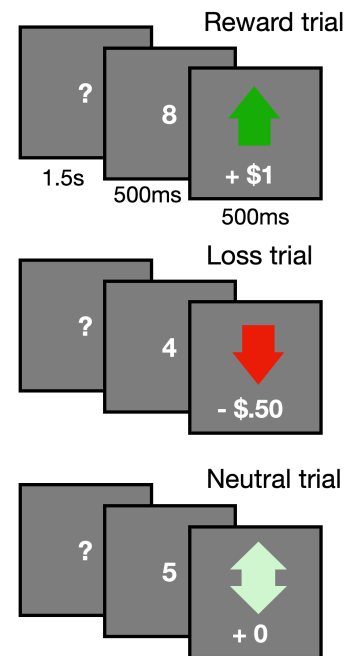
230         The task, in total, across both runs, consisted of 8 blocks of 8 trials each, with 4  
231 blocks of mostly positive outcomes ('reward blocks') and 4 blocks of mostly negative  
232 outcomes ('loss blocks'). Each of the 2 runs contained 2 reward and 2 loss blocks and  
233 each block was approximately 28 seconds. This block design maximized the ability to  
234 detect striatal responses to reward, while also leading to alternating periods of monetary  
235 reward scarcity and abundance, allowing us to examine the influence of fluctuations in

236 average reward rate across time (Figure 1D). To keep participants unaware of the fixed  
 237 outcomes, there was no delay between blocks, and blocks contained a few trials of the  
 238 opposite type (Figure 1C depicts trial outcomes in a representative reward and loss  
 239 block). Reward blocks included 6 reward trials interleaved with two of either loss or  
 240 neutral trials. Loss blocks included 6 loss trials interleaved with two of either reward or  
 241 neutral trials. All participants received \$10 in bonus money after the task.  
 242

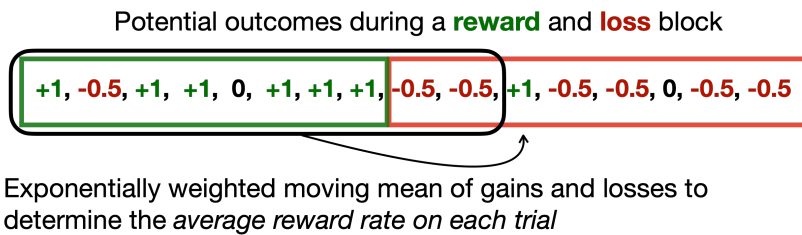
**A. Distribution of Socioeconomic Status**



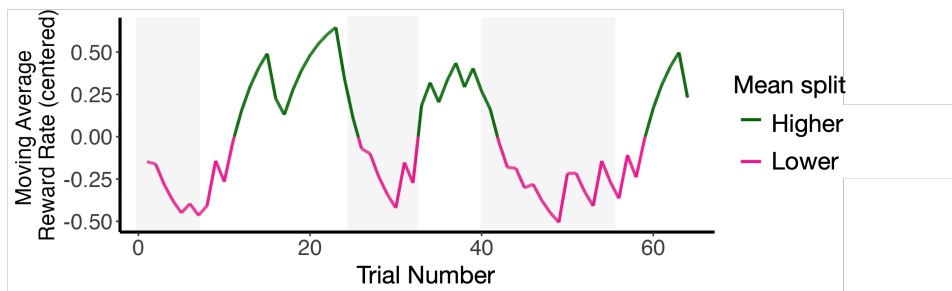
**B. Gambling task schematic**



**C. Calculating the moving average of reward**



**D. Reward rate fluctuations in a representative participant**



243

244 **Figure 1. SES score distribution, gambling task schematic, and trial-by-trial**  
 245 **moving average of rewards and losses.** (A) Distribution of SES composite scores:

246 SES was operationalized as the mean of the z-transformed maternal and paternal  
247 education variables (years of schooling completed), and z-scored log of annual  
248 household income. The distribution is displayed, with the y-axis representing sample  
249 proportions. (B) *Gambling task schematic*: Participants guessed whether a forthcoming  
250 number would be greater or less than 5. Next, the actual number was revealed, and  
251 participants received positive (top panel, green arrow), negative (middle panel, red  
252 arrow), or neutral feedback (if the number was 5; bottom panel, light green arrow)  
253 regarding their guess. A 1-second fixation cross (not depicted) preceded the next trial.  
254 (C) *Calculating the moving average of reward*: An exponentially weighted moving  
255 average of gains and losses quantified recent history of reward. This measure was used  
256 to examine whether distinct task phases associated with reward scarcity or abundance  
257 influenced trial-by-trial shifts in behavior (choices, RTs), and interacted with behavioral  
258 responses (choices, RTs) to immediate feedback. (D) Schematic of reward rate  
259 fluctuations in a representative participant. Grey shading represents loss blocks and  
260 non-grey areas represent reward blocks. Pink and green colors denote periods in which  
261 the moving average of reward is above or below the mean.  
262

## 263 **Image acquisition**

264 Participants practiced the gambling task and completed a mock scanning session  
265 to acclimate to the MRI environment, which improves compliance (de Bie et al., 2010;  
266 Gao et al., 2023). They then completed 2 runs of the gambling task inside the scanner  
267 and watched a movie while we acquired a T1-weighted (T1w) anatomical scan. Images  
268 were acquired using a 3T Siemens Prisma Fit scanner with a 32-channel head coil.  
269 Whole-brain functional BOLD images were acquired using an EPI sequence (TR=0.8s,  
270 TE=37s, Flip Angle=52°, voxel size=2mm isotropic, multi-band factor=8). The two runs  
271 were acquired with reversed phase encoding to support distortion correction. High  
272 resolution T1w images were acquired with an MP-RAGE sequence (TR=2.4s, T  
273 =2.18ms, Flip Angle=8°, voxel size=0.8mm isotropic).

274

## 275 **Image preprocessing**

276           Preprocessing of anatomical and functional data was performed using *fMRIPrep*  
277 version 22.1.1 (Esteban et al., 2019).

278

### 279 *Anatomical preprocessing*

280           The anatomical T1w image was corrected for intensity non-uniformity with  
281 N4BiasFieldCorrection (Tustison et al., 2010) distributed with ANTs 2.3.3 (Avants et al.,  
282 2008) and used as T1w-reference throughout the workflow. The T1w-reference was  
283 then skull-stripped using ANTs workflow with OASIS30ANTs as target template. Brain  
284 tissue segmentation of gray-matter, white-matter, and cerebrospinal fluid was performed  
285 on the brain-extracted T1w using fast (FSL 6.0.5.1:57b01774, RRID:SCR\_002823),  
286 (Zhang et al., 2001). Brain surfaces were reconstructed using recon-all from FreeSurfer  
287 version 7.2.0 (Dale et al., 1999)), and the brain mask estimated previously was refined  
288 with a custom variation of the method to reconcile ANTs-derived and FreeSurfer-derived  
289 segmentations of subcortical gray matter including striatal subregions (Fischl et al.,  
290 2002). Volume-based spatial normalization to one standard space was performed  
291 through nonlinear registration, using brain-extracted versions of both the T1w reference  
292 and T1w template. *FSL's MNI ICBM 152 non-linear 6th Generation Asymmetric*  
293 *Average Brain Stereotaxic Registration Model* (Evans et al., 2012), RRID:SCR\_002823;  
294 TemplateFlow ID: MNI152NLin6Asym] was selected for spatial normalization.

295

### 296 *Functional preprocessing*

297 A skull-stripped reference volume was generated using a custom methodology of  
298 *fMRIPrep*. Head-motion parameters were estimated using mcflirt (FSL  
299 6.0.5.1:57b01774, (Jenkinson et al., 2002). The estimated fieldmap was aligned with  
300 rigid-body registration to the target EPI reference run. Field coefficients were mapped  
301 onto the reference EPI using the rigid-body transform. BOLD runs were slice-time  
302 corrected using 3dTshift from *AFNI* (Cox & Hyde, 1997) RRID:SCR\_005927). The  
303 BOLD reference images were co-registered to the T1w reference using bbrregister  
304 (*FreeSurfer*, (Greve & Fischl, 2009), with six degrees of freedom. Noise regressors  
305 were estimated based on the preprocessed BOLD. Framewise displacement (FD) was  
306 computed using two formulations following Power (Power et al., 2014), and Jenkinson  
307 (Jenkinson et al., 2002). Physiological regressors were extracted from eroded  
308 cerebrospinal fluid and white-matter volumes for use in subsequent, component-based  
309 noise corrections (*CompCor*, Behzadi et al. 2007). The BOLD time-series were  
310 resampled into standard space in a single interpolation step by composing all the  
311 pertinent transformations (i.e., head-motion transform matrices, susceptibility distortion  
312 correction, and co-registrations to anatomical and output spaces). Volumetric  
313 resamplings were performed using ANTs, configured with Lanczos interpolation to  
314 minimize the smoothing effects of other kernels (Lanczos 1964).

315

## 316 **Statistical analyses**

317 Statistical analyses were conducted in R (version 4.2.2). Raw data, code, and  
318 extended analyses and supplementary tables are available at the following link:



319 <https://osf.io/pqtby/>. Unless stated otherwise, linear mixed effects regressions or general  
320 linear mixed effects regressions were employed for data that repeated within  
321 participants (e.g., single-trial RTs). Mixed effects models included random intercepts for  
322 each participant and random slopes for fixed effects that repeated within participants. In  
323 case of non-converging models, we followed recommendations in (Brown, 2021),  
324 iterating through the following until they converged: (1) using the "bobyqa" optimizer, (2)  
325 increasing the number of iterations, (3) forcing zero correlations among random effects,  
326 and (4) dropping random effects based on model comparison. RTs that fell 3 absolute  
327 deviations from an individual's median RT were excluded ( $n=2$  on average per  
328 participant). Measures were mean centered within or across participants or effect-coded  
329 prior to model fitting.

330

### 331 *Calculating trial-by-trial shifts in the moving average reward rate*

332 We computed an exponentially weighted moving average (EWMA) of rewards  
333 and losses across trials (\$1, \$0.5, or \$0; See *Figure 1C-D* for a schematic). Each trial  
334 was assigned a value based on the recent reward and loss history. High values  
335 indicated more gains than losses, whereas low values indicated more losses than gains.  
336 We used an exponentially weighted (rather than simple) moving average to emphasize  
337 recent time points, which have a larger impact on psychological state, while still  
338 incorporating data points from farther in the past (Awheda & Schwartz, 2016). We used  
339 the following update rule:

340

341 
$$EWMA_t = \alpha \times r_t + (1 - \alpha) \times EWMA_{t-1}$$

342

343 In this formula, the  $EWMA_t$  represents the EWMA at the current trial,  $t$ ,  $\alpha$  is the  
344 smoothing factor or learning rate parameter that determines the influence of the most  
345 recent observation on the moving average, and  $r$  represents the reward on the current  
346 trial,  $t$ . To prevent disproportionate initial weighting and to ensure the average reward  
347 rate stabilized, the first 3 trials were omitted from the EWMA measure. To balance  
348 recent and historical data,  $\alpha$  was based on an 8-period span, calculated as:  $\alpha = 2/(N+1)$ ,  
349 where  $N$  was set to 8 to match the number of trials in each fixed reward and loss block.  
350 However, we found that using EWMA's derived from smoothing factors of 5- and 10-  
351 period spans did not alter the pattern of results.

352 As an exploratory analysis, we also tested whether individual differences in  
353 optimal learning rates for the average reward rate variable differed by SES. To do so,  
354 we fit a model that estimated the learning rate as a free parameter for each participant  
355 using R's base *optim* function with the L-BFGS-B algorithm. The algorithm identified the  
356 learning rate per participant that minimized that residual sum of squares (RSS) in a  
357 model predicting subsequent RTs from the Exponentially Weighted Moving Average of  
358 Reward for each participant.

359 *Characterizing behavioral responses to rewards*

360 We examined how immediate feedback (win versus loss outcomes) and  
361 fluctuations in the average reward rate shaped RTs and guesses. We first fit a model

362 predicting RTs from the preceding trial's feedback (win, loss), the moving average of  
363 reward, and their interaction. We then re-fit this model after adding SES as a covariate  
364 and interaction term. We also examined the influence of immediate reward and average  
365 reward rate fluctuations on choices—specifically, how likely an individual was to repeat  
366 their prior guess or switch to a different guess (i.e., switched or stayed). Therefore, the  
367 dependent variable was whether an individual had repeated their prior choice (switched  
368 = 1; stayed = 0) and the independent variables were the preceding trial feedback (win,  
369 loss), the moving average of reward, and their interaction. We re-fit this model after  
370 adding SES as a covariate and interaction term. All models included trial number as a  
371 covariate to control for the general effects on time on task. Since there were only 8  
372 neutral trials per participant across the task, trials that followed neutral feedback were  
373 excluded from analysis.

374

### 375 **The relationship between SES and striatal volumes**

376 Three linear mixed effects models were fit to examine the association between  
377 SES and ROI volumes, separately for the caudate, putamen, and nucleus accumbens.  
378 Each model predicted volume from SES, hemisphere, and their interaction, to determine  
379 whether the influence of SES was stronger for one particular hemisphere. Age, sex, and  
380 intracranial volume were also included as covariates. ROIs with volumes that fell  $> 3$   
381 absolute deviations from the sample median were excluded (all regions for 1 participant,  
382 the caudate and right nucleus accumbens for another).

383

384 **Examining reward-driven striatal responses to reward and average reward rate**  
385 **fluctuations across time**

386 To ascertain if striatal activations during reward differed from loss blocks and to  
387 examine their covariance with average reward rate fluctuations, we conducted  
388 neuroimaging analyses with Nilearn. The scripts and data are publicly accessible  
389 (<https://osf.io/pqtbby/>). The approach involved two separate general linear models  
390 (GLMs) applied to participant data within MNI coordinate space. The first model had  
391 distinct regressors for reward and loss conditions. The second model incorporated a  
392 regressor for the exponentially weighted moving average of reward, resampled at the  
393 fMRI's TR. Both models were convolved with SPM's hemodynamic response function  
394 and controlled for head movement and noise components (3 translation and rotation  
395 parameters, plus top 5 principal AcompCor components (defined in a combined white  
396 matter and cerebrospinal fluid mask). This analysis yielded z-value effect size maps for  
397 each subject. The maps were entered into a group-level analysis to identify striatal  
398 voxels that were sensitive to the distinct reward versus loss blocks or to the average  
399 reward rate. Sensitivity was defined by voxel significance within the anatomical striatal  
400 mask from the Harvard-Oxford Atlas (FDR-corrected  $p < 0.05$ , minimum cluster size of  
401 10). For each analysis, we calculated the mean z value per participant across  
402 responsive voxels, separately for the caudate, putamen, and nucleus accumbens in  
403 each hemisphere. Participants therefore had 6 z values (1 per ROI) for each analysis.  
404 These values represented the average effect size for the differences in activations  
405 between reward and loss blocks and the relationship with the average reward rate.

406 To assess the degree to which these effect sizes deviated from zero, we fit 2  
407 intercept-only linear mixed-effects models, predicting mean z values per ROI, controlling  
408 for age and sex, with random intercepts per participant to account for repeated  
409 measures across hemispheres. We excluded outlier values that fell 3 absolute  
410 deviations from the sample's median (1 value for the left putamen and 1 for the left  
411 caudate). Including outliers did not change the pattern of results.

### 412 **Examining how reward-driven striatal responses differ by SES**

413 Finally, we tested how SES related to activation level differences between reward  
414 and loss blocks, as well as the degree to which striatal activations covaried with  
415 fluctuations in the average reward rate. To this end, we fit 2 linear mixed effects models.  
416 The dependent variables were z values reflecting, either, activation level differences for  
417 reward and loss blocks or the covariance between striatal activations and average  
418 reward rate fluctuations. Both models included SES, hemisphere, and their interaction  
419 as independent variables, and covariates for age and sex.

420

421

422

423

424

425

426

427

428

## Results

429

430

431

432

433

434

435

436

437

438

439

### **Average reward rate fluctuations influence RTs and post-reward pausing**

440

441

442

443

444

445

446

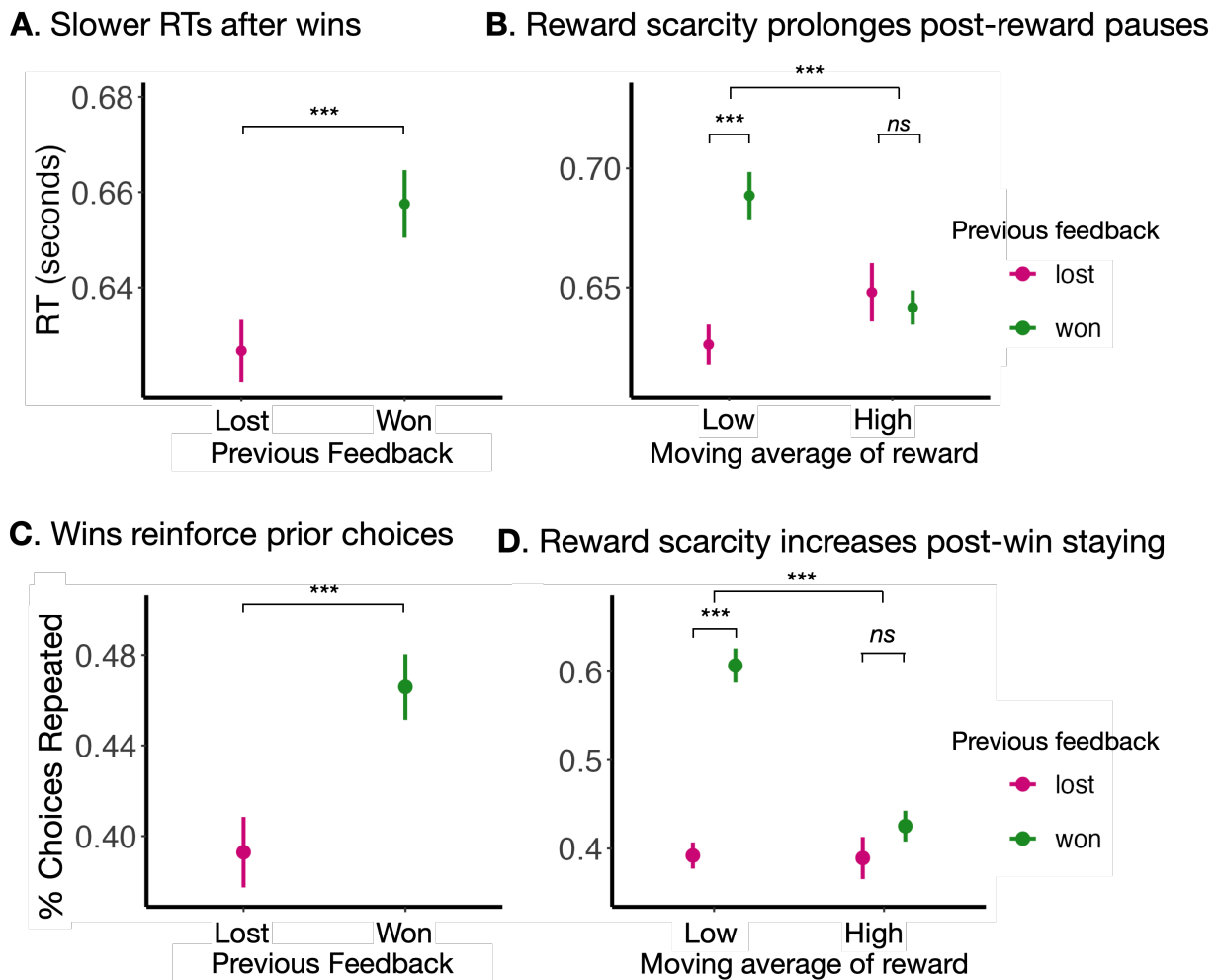
447

448

449

Adolescents responded more slowly after winning than losing (i.e., post-reward pausing:  $\beta = 0.02$ ,  $SE = 0.005$ ,  $t(262) = 4.68$ ,  $p < .001$ ; Figure 2A). Furthermore, trial-by-trial RTs covaried with fluctuations in the average reward rate, such that a higher average reward rate led to faster RTs ( $\beta = -0.04$ ,  $SE = 0.02$ ,  $t(98) = -2.32$ ,  $p = .022$ ). Fluctuations in the average reward rate also interacted with immediate feedback to shape RTs: periods of reward scarcity amplified post-reward pausing (*Reward Rate x Preceding feedback*:  $\beta = -0.05$ ,  $SE = 0.02$ ,  $t(104) = -3.53$ ,  $p < .001$ , Figure 2B), indicating responses to immediate reward were amplified by a history of low rewards. In fact, post-reward pausing was only observed when rewards were scarce but not when they were plentiful (*effect of preceding feedback when the reward rate is centered at -*

450 1SD below the mean:  $\beta = 0.04$ ,  $SE = 0.007$ ,  $t(100) = 6.23$ ,  $p < .001$ ; above the mean:  $\beta$   
 451  $= 0.003$ ,  $SE = 0.008$ ,  $t(104) = 0.43$ ,  $p = .665$ ). These findings show that adolescents  
 452 tracked fluctuations in the average reward rate, which shaped response times across  
 453 time and modulated sensitivity and responses to immediate reward.  
 454



455

456 **Figure 2. Immediate reward and the moving average reward rate shape RTs and**  
 457 **choices.** (A) Adolescents responded more slowly after a win than a loss ( $p < 0.001$ ). (B)  
 458 A lower average reward rate amplified post-reward slowing (*interaction*:  $p < 0.001$ )  
 459 indicating heightened behavioral responses to reward when rewards were scarce. (C)  
 460 Adolescents were most likely to repeat a guess when their guess had been rewarded on  
 461 the previous trial ( $p < 0.001$ ). (D) These “post-reward stay” effects were amplified by a  
 462 low average reward rate ( $p < 0.001$ ). In all figures, the mean and within-subject error  
 463 bars are plotted. The moving average reward rate was divided into low and high

464 average reward rate using a median split for ease of visualization. Note that we model  
465 the average reward rate continuously in all analyses.  
466

467

### 468 **Average reward rate fluctuations influence guess switching**

469 Immediate feedback reinforced decisions on subsequent trials: when adolescents  
470 won, they were more likely to repeat their prior guess on the subsequent trial than if  
471 they had lost ( $\beta = -0.31$ ,  $SE = 0.04$ ,  $z = -7.31$ ,  $p < .001$ ; Figure 2C). A lower average  
472 reward rate also increased the likelihood of repeating a previously rewarded guess (i.e.,  
473 increased win-stay, lose-switch effects (Reward Rate x Preceding Feedback:  $\beta = 0.57$ ,  
474  $SE = 0.12$ ,  $z = 4.73$ ,  $p < .001$ ; Figure 2D). Indeed, win-stay effects were most prominent  
475 when the average reward rate was low, indicating a history of low rewards increased the  
476 tendency to stick with a rare rewarding option (*main effect of immediate feedback on*  
477 *choices when the average reward rate is centered at -1SD below the mean:  $\beta = -0.51$ ,*  
478  *$SE = 0.05$ ,  $z = -9.64$ ,  $p < .001$ ; above the mean:  $\beta = -0.11$ ,  $SE = 0.06$ ,  $z = -1.75$ ,  $p =$*   
479 *.080*). In general, a history of high rewards (a higher average reward rate) also increased  
480 the likelihood of switching guesses across trials ( $\beta = 0.68$ ,  $SE = 0.15$ ,  $z = 4.46$ ,  $p <$   
481  $.001$ ), suggesting a greater tendency to make alternative exploratory decisions when  
482 rewards were abundant. These findings suggest that a history of low reward increases  
483 the tendency to stick with a previously rewarding option, and reduces the tendency to  
484 explore alternatives for reward.

485



486 **Reward rate fluctuations influence post-reward pausing more in higher-SES**  
487 **adolescents**

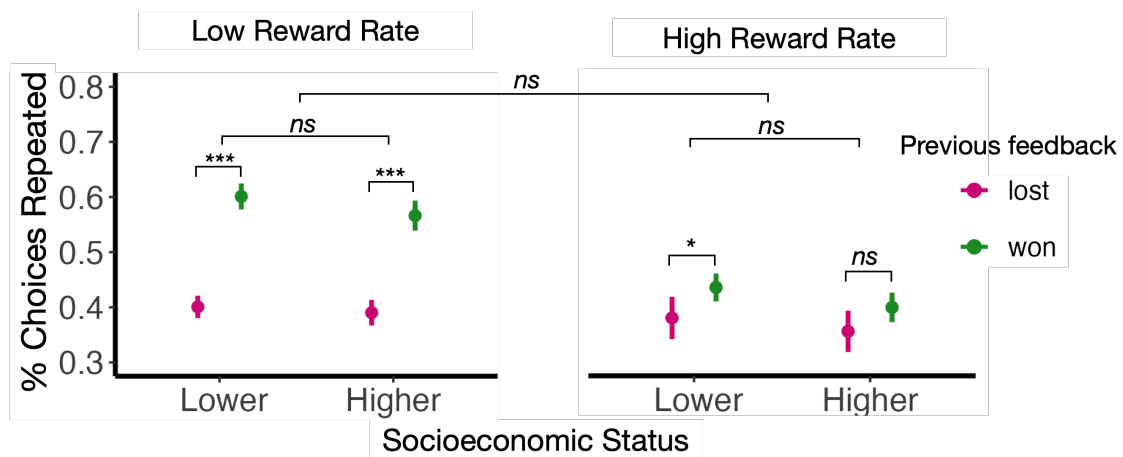
488 Immediate reward and average reward rate fluctuations influenced choices  
489 similarly regardless of SES (*SES x feedback*:  $\beta = 0.09$ ,  $SE = 0.05$ ,  $z = 1.73$ ,  $p = .084$ ;  
490 *SES x average reward rate*:  $\beta = -0.25$ ,  $SE = 0.18$ ,  $z = -1.40$ ,  $p = .161$ ; *SES x feedback*  
491 *type x moving average*:  $\beta = 0.18$ ,  $SE = 0.15$ ,  $z = 1.21$ ,  $p = .225$ ; *Figure 3A*). Additionally,  
492 these distinct temporal dimensions of reward influenced RTs similarly, regardless of  
493 SES (*SES x feedback*:  $\beta = -0.002$ ,  $SE = 0.005$ ,  $t(109) = -0.45$ ,  $p = .651$ ; *SES x average*  
494 *reward rate*:  $\beta = 0.02$ ,  $SE = 0.02$ ,  $t(100) = 1.04$ ,  $p = .301$ ; *Figure 3A*).

495 However, reward-rate fluctuations modulated post-reward pausing more in  
496 higher- than lower-SES adolescents (*SES x feedback type x moving average*:  $\beta =$   
497  $-0.04$ ,  $SE = 0.02$ ,  $t(105) = -2.54$ ,  $p = .013$ ; *Figure 3B*). That is, higher-SES adolescents  
498 slowed more following rare rewards (main effect of SES when the reward rate is  
499 *centered at -1SD below the mean to reflect reward scarcity*:  $\beta = 0.02$ ,  $SE = 0.007$ ,  $t(684)$   
500  $= 2.20$ ,  $p = .028$ ; *Figure 3B*). When rewards were plentiful, higher-SES adolescents  
501 slowed less following rewards than lower-SES adolescents (*centered at +1SD above*  
502 *the mean to reflect reward abundance*:  $\beta = -0.02$ ,  $SE = 0.008$ ,  $t(4949) = -2.05$ ,  $p =$   
503  $.041$ ; *Figure 3B*) though neither group showed significant evidence of post-reward  
504 pausing when rewards were plentiful ( $ps > 0.087$ ). Interestingly, SES was unrelated to  
505 individual differences in optimal learning rates ( $\beta = 0.06$ ,  $SE = 0.04$ ,  $t(114) = 1.32$ ,  $p =$   
506  $.189$ ), suggesting that heightened post-reward pausing was not driven by a greater  
507 tendency to update expectations in response to new information. These findings

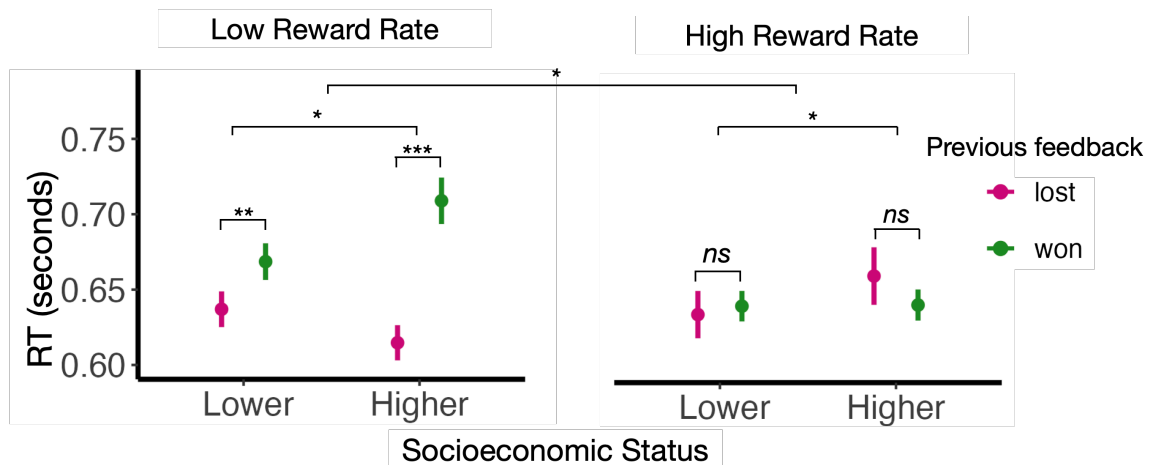
508 suggest that adolescents from lower-SES backgrounds were less likely to adapt  
 509 responses to immediate reward based on average reward rate fluctuations. Analyses  
 510 reported in our extended analyses on the Open Science Framework  
 511 (<https://osf.io/9vhtw>) demonstrate these results are robust when using education and  
 512 income to separately characterize SES.

513

**A. The influence of reward on choices does not differ by SES**



**B. Reward rate fluctuations shape post-reinforcement pausing differently by SES**



514

515 **Figure 3. Reward rate fluctuations modulate post-reward pausing more in higher-**  
 516 **SES adolescents.** (A) Reward rate fluctuations influenced choice switching following  
 517 immediate reward similarly by SES. (B) Reward rate fluctuations modulated post-reward

518 pausing more among higher- than lower-SES adolescents. This led to greater RT  
519 slowing following rewards when rewards were scarce among higher-SES adolescents.  
520 In all figures, we depict the mean and within-subject error bars. The moving average  
521 reward rate and socioeconomic status were divided into low and high bins using a  
522 median split for ease of visualization. Note that we model these variables continuously  
523 in the analyses reported in the paper.  
524

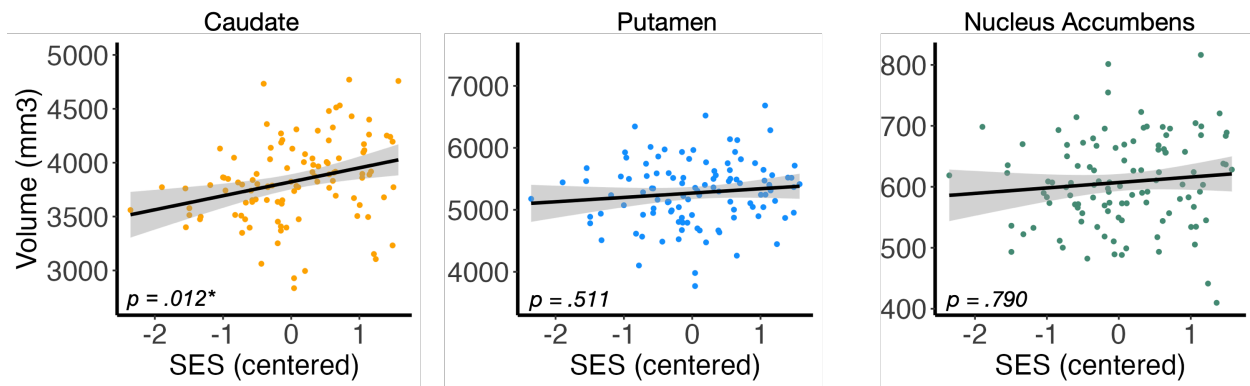
525

## 526 Lower SES correlates with smaller caudate volumes

527 Higher SES was associated with larger caudate volumes ( $\beta = 96.61$ ,  $SE = 37.65$ ,  
528  $t(103) = 2.57$ ,  $p = .012$ ; *Figure 4*). In contrast, there were no significant associations  
529 between SES and the volumes of the putamen ( $\beta = 32.78$ ,  $SE = 49.74$ ,  $t(103) = 0.66$ ,  $p$   
530  $= .511$ ) or nucleus accumbens ( $\beta = 1.94$ ,  $SE = 7.26$ ,  $t(104) = 0.27$ ,  $p = .790$ ). Moreover,  
531 there were no SES x hemisphere interactions in any ROI (*all ps* > 0.590), demonstrating  
532 that SES-related differences in volumes did not differ by hemisphere.

533

Lower SES correlates with smaller caudate volumes



534

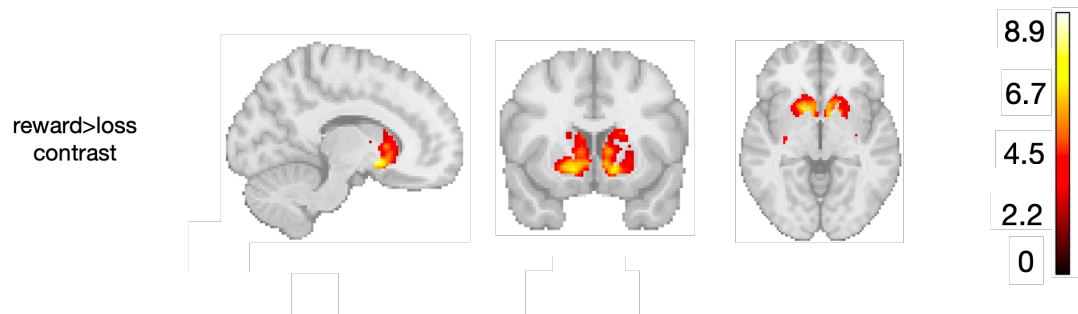
535 **Figure 4. SES and striatal volumes.** SES positively correlated with the volume of the  
536 caudate ( $p = 0.012$ ), but not the putamen or nucleus accumbens ( $ps > 0.510$ ). For ease  
537 of visualization, data points reflect the average volume of the left and right hemisphere,  
538 but the statistics reported in the text are from models that treat the left and right

539 hemisphere as repeated measures within participants. Individual data points represent  
540 participant level data, and the grey shading reflects the standard error of the mean.  
541

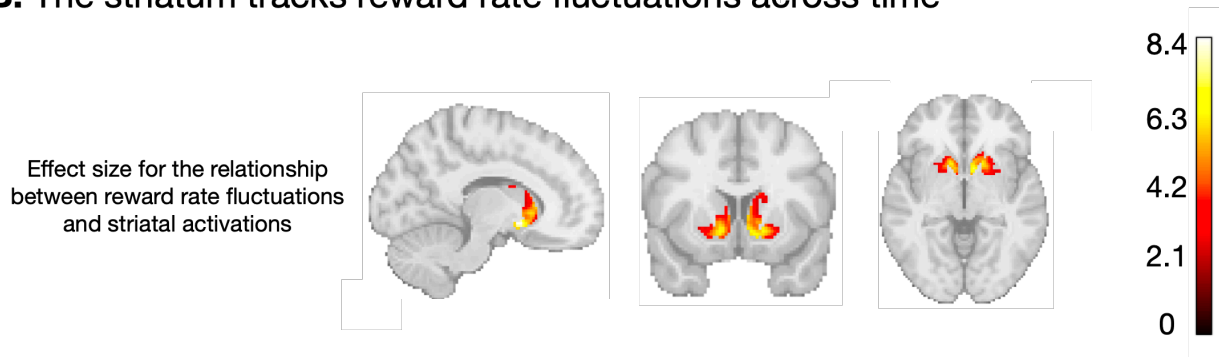
### 542 **The striatum tracks fluctuations in the average reward rate**

543 Across adolescents, mean activations were larger during reward than loss blocks in the  
544 caudate ( $\beta = 0.50$ ,  $SE = 0.07$ ,  $t(106) = 6.74$ ,  $p < .001$ ), putamen ( $\beta = 0.61$ ,  $SE = 0.08$ ,  
545  $t(106) = 7.83$ ,  $p < .001$ ), and nucleus accumbens ( $\beta = 0.77$ ,  $SE = 0.08$ ,  $t(107) = 9.87$ ,  $p$   
546  $< .001$ ; *Figure 5A*). Furthermore, striatal activations covaried with the average reward  
547 rate, such that a higher average reward rate led to greater activations in the caudate ( $\beta$   
548  $= 0.77$ ,  $SE = 0.08$ ,  $t(105) = 9.60$ ,  $p < .001$ ), putamen ( $\beta = 0.66$ ,  $SE = 0.07$ ,  $t(105) = 8.94$ ,  
549  $p < .001$ ), and nucleus accumbens ( $\beta = 1.32$ ,  $SE = 0.09$ ,  $t(103) = 14.07$ ,  $p < .001$ ; *Figure*  
550 *5B*). These findings show that the striatum not only responds more to reward than loss in  
551 general, but tracks moment-by-moment shifts in the average reward rate across time.  
552

## A. Higher striatal activations in reward than loss blocks



## B. The striatum tracks reward rate fluctuations across time



553

554 **Figure 5. Striatal activations covary with reward and loss blocks and reward rate**  
555 **fluctuations across time.** (A) Across the sample, activations in the striatum were  
556 greater during reward than loss blocks ( $ps < 0.001$ ). (B) Moreover, the striatum tracked  
557 average reward rate fluctuations across time, even after FDR correction for multiple  
558 comparisons across every voxel in the striatum ( $ps < 0.001$ ). In A and B, the color bar  
559 represents z-values and color intensity reflect the strength of the effect.

560

561

## 562 Lower SES correlates with reduced striatal responses to reward

563 Lower SES correlated with smaller activation level differences between reward

564 and loss blocks in the caudate ( $\beta = 0.22$ ,  $SE = 0.09$ ,  $t(105) = 2.54$ ,  $p = .013$ ) and

565 putamen ( $\beta = 0.25$ ,  $SE = 0.09$ ,  $t(104) = 2.73$ ,  $p = .007$ ) and marginally in the nucleus

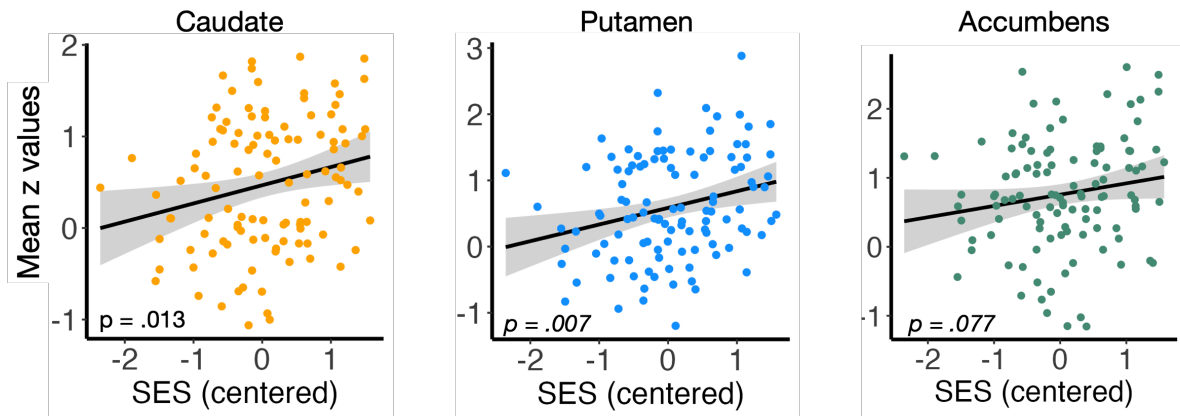
566 accumbens (marginal effect:  $\beta = 0.16$ ,  $SE = 0.09$ ,  $t(106) = 1.79$ ,  $p = .077$ ; Figure 6A).

567 None of these effects differed by hemisphere ( $SES \times hemisphere$ : all  $ps > 0.29$ ).

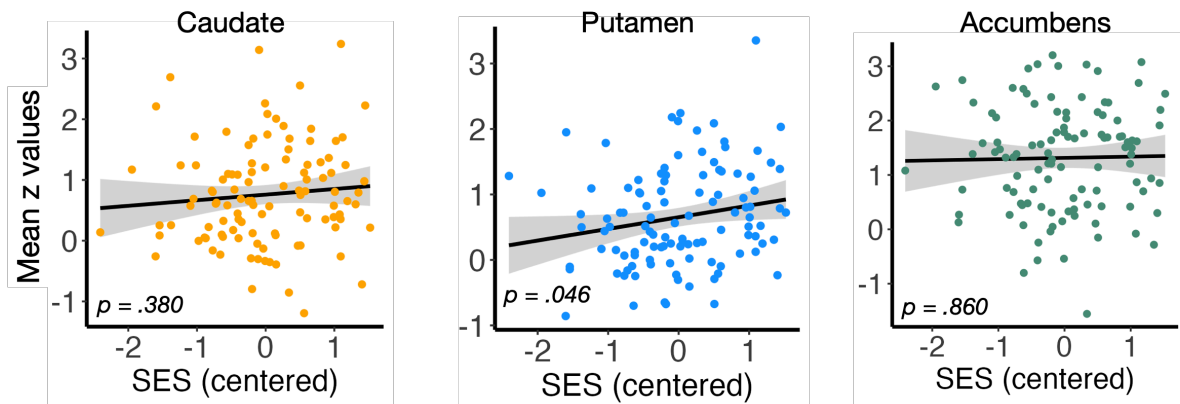
568 Furthermore, striatal activations covaried with average reward rate fluctuations more

569 strongly in higher-SES adolescents in the putamen ( $\beta = 0.17$ ,  $SE = 0.09$ ,  $t(104) = 2.02$ ,  
 570  $p = .046$ ; Figure 6B), but not the caudate ( $\beta = 0.08$ ,  $SE = 0.10$ ,  $t(104) = 0.88$ ,  $p = .380$ )  
 571 or nucleus accumbens ( $\beta = 0.02$ ,  $SE = 0.11$ ,  $t(101) = 0.18$ ,  $p = .860$ ). None of these  
 572 effects differed by hemisphere ( $SES \times hemisphere$ : all  $ps > 0.21$ ). Of note, the  
 573 relationship between SES and reward-driven activations also did not differ by striatal  
 574 subregion ( $SES \times subregion$  interaction: all  $ps > 0.10$ ).  
 575

**A. Lower SES correlates with smaller reward-driven activations**



**B. Putamen activations track reward rate fluctuations less in lower-SES adolescents**



576

577 **Figure 6. Lower SES correlates with reduced striatal activations to reward (A)**  
 578 Lower SES correlated with less activation differences between reward and loss blocks  
 579 in the caudate and putamen and marginally in the nucleus accumbens. (B) The

580 relationship between striatal activations and average reward rate fluctuations was  
581 stronger for higher- than lower-SES adolescents in the putamen ( $p=0.046$ ), but not in  
582 the caudate or nucleus accumbens ( $p>0.37$ ). For ease of visualization, individual data  
583 points reflect mean z values across the left and right hemisphere. Statistics reported in  
584 the text model the left and right hemisphere separately as repeated measures.  
585 Individual data points represent participant data, and the grey shading reflects the  
586 standard error of the mean.  
587

588

## 589 **Discussion**

590 We asked how socioeconomic status in adolescence was related to reward-  
591 driven responses in the brain and behavior. Drawing on influential models of decision-  
592 making (Constantino & Daw, 2015; Niv et al., 2006, 2007), we examined how choices,  
593 response times, and striatal activations were shaped by immediate reward outcomes  
594 and previous reward history (average reward rate fluctuations across time). We found  
595 that, behaviorally, participants were more likely to repeat a guess if it had led to a win  
596 (win-stay, lose-switch effects) and responded more slowly after receiving a reward  
597 (post-reward pausing). Fluctuations in the average reward rate also shaped behavior: a  
598 higher reward rate hastened RTs and increased guess switching. Moreover, a low  
599 reward rate increased behavioral sensitivity to immediately rewarding outcomes,  
600 augmenting win-stay, lose-switch effects and post-reward pausing. Notably, compared  
601 to higher-SES adolescents, lower-SES adolescents exhibited reduced post-reward  
602 pausing when rewards were scarce. We also observed that across participants, striatal  
603 activations were larger during reward than loss blocks, and covaried with fluctuations in  
604 the average reward rate across time. However, relative to higher-SES adolescents,  
605 lower-SES adolescents displayed reduced activations during reward relative to loss

606 blocks in the caudate and putamen, and marginally in the nucleus accumbens. And,  
607 putamen activations tracked average reward rate fluctuations less in lower-SES  
608 adolescents. These findings show that the striatum tracks average reward rate  
609 fluctuations, which shape choices and response times (Hamid et al., 2016; Niv et al.,  
610 2006, 2007; Wang et al., 2013, 2021). They also link lower SES in adolescence to  
611 reduced reward sensitivity, both in the brain and behavior.

612         We found that adolescents tracked fluctuations in the average reward rate across  
613 time, which influenced decisions and response times. When rewards were abundant,  
614 individuals were more likely to switch choices across trials. These findings align with  
615 studies in human adults (Constantino & Daw, 2015; Niv et al., 2007; Sukumar et al.,  
616 2021) and support theories of decision making (Constantino & Daw, 2015; Sukumar et  
617 al., 2021). These theories argue that when the average environmental reward rate is  
618 *lower* than an option's perceived value, it is rational to 'stay' with a rewarding option due  
619 to the limited prospects of finding rewards elsewhere. Conversely, when the  
620 environmental reward rate is *higher* than the perceived value of an option, it makes  
621 sense to switch to explore alternative sources of reward. It is possible, then, that  
622 adolescents used the average reward rate as a threshold for whether to switch or stay  
623 with a previous choice. Future research could examine how the tendency to track  
624 average reward rate fluctuations develops—and whether adolescents—given their  
625 heightened sensitivity to reward (Cohen et al., 2010; Davidow et al., 2016; Galvan,  
626 2010; Galvan et al., 2006) might be even more attuned to fluctuations in the average  
627 reward rate across time than adults.



628           A higher average reward rate also covaried with faster RTs. This finding is  
629 consistent with research in human adults (Beierholm et al., 2013; Otto & Daw, 2019)  
630 and supports theories arguing that fluctuations in the average reward rate shape the  
631 cost time (Niv et al., 2006, 2007). That is, when rewards are abundant, action delays  
632 are presumably more costly because one forfeits relatively more potential rewards,  
633 incentivizing faster responses. Interestingly, other researchers have theorized that  
634 rewards also govern the opportunity cost engaging effort and sustaining attention  
635 (Esterman et al., 2016; Esterman & Rothlein, 2019; Kurzban et al., 2013; Lin et al.,  
636 2022; Massar et al., 2016; Otto & Daw, 2019) raising the possibility that average reward  
637 rate fluctuations shape diverse aspects of cognition—such as fluctuations in attention  
638 (Decker et al., 2023, 2022; Decker & Duncan, 2020). Our findings therefore not only  
639 support theories linking reward rate fluctuations to motivation and decision-making and  
640 extend these ideas to human adolescents, but raise questions about the influence of  
641 reward rate fluctuations on other aspects of cognition.

642           Adolescents were also responsive to immediately rewarding outcomes, in line  
643 with previous research (Hamid et al., 2016; Reynolds et al., 2001): they were most likely  
644 to repeat a previous choice if it had led to a reward on the prior trial and responded  
645 more slowly after a reward outcome, a phenomenon known as “post-reward pausing”  
646 (Crossman, 1968; Felton & Lyon, 1966; McMillan, 1971; Schlinger et al., 2008; Wallace  
647 & Mulder, 1973; Williams et al., 2011). Notably, these effects were amplified by a lower  
648 average reward rate. Our finding adds to a growing body of research suggesting the  
649 background average reward rate modulates sensitivity to immediate reward. Indeed, in

650 animals and humans, post-reward pausing is prolonged when rewards are scarce  
651 (Schlinger et al., 2008). Furthermore, fewer recent rewards and lower tonic dopamine  
652 amplify phasic dopamine firing (Hamid et al., 2016)—a finding that potentially provides a  
653 neurobiological explanation for the increased rewards responsivity we observed here  
654 when reward were scarce. Slower responses after unexpected reward could also reflect  
655 surprise due to the infrequency of the event (Decker, Finn, et al., 2020) or heightened  
656 response caution that facilitated more deliberate decision-making (Schlinger et al.,  
657 2008, p. 50). Altogether, this finding shows that average reward rate fluctuations  
658 influenced responses to immediate outcomes, which shaped choices and RTs. When  
659 adolescents tune into the average environmental reward rate, they may make more  
660 adaptive decisions according to the overall rewards available in the environment.

661 We also observed that the extent of RT slowing after rare rewards varied by  
662 SES. Adolescents from higher-SES backgrounds showed greater post-reward pausing  
663 than lower-SES adolescents when rewards were scarce. This finding could reflect  
664 greater attunement to reward rate fluctuations among higher-SES adolescents, which  
665 would be expected to increase the saliency of receiving a rare reward when the reward  
666 rate was low. However, exploratory analyses showed that SES did not correlate with  
667 learning rates—the tendency to update the average reward rate in response to new  
668 outcomes. Thus, greater post-reward pausing may instead reflect a greater responsivity  
669 to rewards in reward-scarce contexts specifically, rather than a general tendency to  
670 more readily update the average reward rate.

671           Interestingly, reward rate fluctuations covaried with striatal activations in the  
672 caudate, putamen and nucleus accumbens, such that a higher reward rate led to  
673 greater activations in these regions. These findings are consistent with animals studies  
674 showing that tonic dopamine fluctuations in the striatum track the average reward rate  
675 and in doing so shapes motivational vigor and decision-making (Hamid et al., 2016;  
676 Wang et al., 2013, 2021), and, as far as we know, is the first human fMRI study  
677 demonstrating this relationship.

678           Our results extend prior findings linking lower SES to diminished reward  
679 sensitivity in *neocortical* regions like the anterior cingulate cortex (Palacios-Barrios et  
680 al., 2021) and parietal cortex (White et al., 2022). Indeed, we observed that the extent of  
681 reward-driven activations in the striatum differed by SES. Higher-SES adolescents  
682 showed greater reward-driven activations than lower-SES adolescents in the putamen,  
683 caudate, and marginally in the nucleus accumbens. Moreover, putamen activations  
684 tracked average reward rate fluctuations less in lower-SES adolescents. Notably, prior  
685 studies employed incremental learning tasks in which adolescents learned the value of  
686 cues in predicting outcomes over time. Our focus on a reward task that did *not* involve  
687 learnable cue-outcome contingencies broadens the literature by showing that reduced  
688 reward sensitivity is even observed when eliminating learning demands.

689           Our findings support proposals that lower SES environments reduce reward  
690 sensitivity (Seligman, 1972). Past literature suggests that chronic stress diminishes the  
691 belief that actions have consequences rendering individuals less motivated to pursue  
692 rewarding outcomes (Seligman, 1972). It is therefore possible that chronic stress and

693 reduced perceived control, which are more common among lower-SES individuals  
694 (Farah, 2018; Hackman et al., 2010; Hackman & Farah, 2009; McLaughlin et al., 2014)  
695 mediated the effects we observed here. Targeted research that employs direct measures  
696 of stress could directly test this mechanism.

697         The present findings offer insights into why cognitive performance (Noble et al.,  
698 2007) and emotional well-being (Reiss, 2013) are often reduced in lower SES  
699 adolescents. Reward sensitivity plays a vital role in many aspects of cognition,  
700 influencing everything from the ability to learn important associations (Davidow et al.,  
701 2016) to the ability to remain attentive to important events (Esterman & Rothlein, 2019;  
702 Shenhav et al., 2013). Rewards boost motivation (Frömer et al., 2021; Schultz, 1993;  
703 Westbrook et al., 2021; Westbrook & Braver, 2016), and support success in short and  
704 long-term endeavors, such as academic and workplace pursuits. Disparities in reward  
705 sensitivity, therefore, may contribute to disparities in learning, attentional performance,  
706 and motivation. Given the intimate link between reward sensitivity and emotional well-  
707 being, reduced reward sensitivity may contribute to the higher rates of depression  
708 (Auerbach et al., 2022; Reiss, 2013) and lower life satisfaction observed in lower-SES  
709 groups (Kahneman & Deaton, 2010). On a broader level, these insights stress the  
710 importance of socioeconomic policies (Farah, 2018) aimed at reducing the burdens of  
711 poverty to foster cognitive and emotional well-being in society.

712

713 **Data availability statement:** Code and data can be found at the following link:

714 <https://osf.io/pqtby/>

715  
716  
717  
718  
719  
720  
721  
722  
723  
724  
725  
726  
727  
728  
729  
730  
731  
732  
733  
734  
735  
736

**Author Contributions:** Conceptualization: A.D., N.A.H., R.R., C.C.C.B., J.L., J.D.E.G.;  
Data curation: A.D., S.L.M., A.I., M.A.G., H.G., Y.C.T, R.R; Formal analysis: A.D.;  
Funding Acquisition: J.D.E.G.; Investigation: Y.C.T., A.I., M.A.G., H.G., R.R.;  
Methodology: A.D., C.C.C.B.; Project Administration: N.A.H., A.I., M.A.G., H.G., Y.C.T.,  
R.R.; Resources: J.D.E.G.; Software: A.D., S.L.M, C.C.C.B.; Supervision: J.D.E.G.;  
Visualization: A.D.; Writing – Original Draft: A.D.; Writing – Review and Editing: all  
authors

**Acknowledgements:** We thank Hause Lin and Kenneth Harris for providing feedback  
on the neuroimaging analyses. This research was supported by the William and Flora  
Hewlett Foundation (#4429 [J. D. E. G.]) and a Natural Sciences and Engineering  
Research Council of Canada Postdoctoral Fellowship [A.L.D.]

737  
738  
739  
740  
741  
742  
743  
744  
745  
746  
747  
748  
749  
750  
751  
752  
753  
754  
755  
756  
757

## References

Amir, D., Jordan, M. R., & Rand, D. G. (2018). An uncertainty management perspective on long-run impacts of adversity: The influence of childhood socioeconomic status on risk, time, and social preferences. *Journal of Experimental Social Psychology, 79*, 217–226. <https://doi.org/10.1016/j.jesp.2018.07.014>

Auerbach, R. P., Pagliaccio, D., Hubbard, N. A., Frosch, I., Kremens, R., Cosby, E., Jones, R., Siless, V., Lo, N., Henin, A., Hofmann, S. G., Gabrieli, J. D. E., Yendiki, A., Whitfield-Gabrieli, S., & Pizzagalli, D. A. (2022). Reward-Related Neural Circuitry in Depressed and Anxious Adolescents: A Human Connectome Project. *Journal of the American Academy of Child & Adolescent Psychiatry, 61*(2), 308–320. <https://doi.org/10.1016/j.jaac.2021.04.014>

Avants, B. B., Epstein, C. L., Grossman, M., & Gee, J. C. (2008). Symmetric diffeomorphic image registration with cross-correlation: Evaluating automated labeling of elderly and neurodegenerative brain. *Medical Image Analysis, 12*(1), 26–41. <https://doi.org/10.1016/j.media.2007.06.004>

Awheda, M. D., & Schwartz, H. M. (2016). Exponential moving average based multiagent reinforcement learning algorithms. *Artificial Intelligence Review, 45*(3), 299–332. <https://doi.org/10.1007/s10462-015-9447-5>

Bayer, H. M., & Glimcher, P. W. (2005). Midbrain Dopamine Neurons Encode a Quantitative Reward Prediction Error Signal. *Neuron, 47*(1), 129–141. <https://doi.org/10.1016/j.neuron.2005.05.020>

758 Behrens, T. E. J., Woolrich, M. W., Walton, M. E., & Rushworth, M. F. S. (2007).  
759 Learning the value of information in an uncertain world. *Nature Neuroscience*,  
760 10(9), Article 9. <https://doi.org/10.1038/nn1954>

761 Beierholm, U., Guitart-Masip, M., Economides, M., Chowdhury, R., Düzcel, E., Dolan, R.,  
762 & Dayan, P. (2013). Dopamine Modulates Reward-Related Vigor.  
763 *Neuropsychopharmacology*, 38(8), 1495–1503.  
764 <https://doi.org/10.1038/npp.2013.48>

765 Brown, V. A. (2021). An Introduction to Linear Mixed-Effects Modeling in R. *Advances in*  
766 *Methods and Practices in Psychological Science*, 4(1), 2515245920960351.  
767 <https://doi.org/10.1177/2515245920960351>

768 Cohen, J. R., Asarnow, R. F., Sabb, F. W., Bilder, R. M., Bookheimer, S. Y., Knowlton,  
769 B. J., & Poldrack, R. A. (2010). A unique adolescent response to reward  
770 prediction errors. *Nature Neuroscience*, 13(6), 669–671.  
771 <https://doi.org/10.1038/nn.2558>

772 Constantino, S., & Daw, N. D. (2015). Learning the opportunity cost of time in a patch-  
773 foraging task. *Cognitive, Affective & Behavioral Neuroscience*, 15(4), 837–853.  
774 <https://doi.org/10.3758/s13415-015-0350-y>

775 Cox, R. W., & Hyde, J. S. (1997). Software tools for analysis and visualization of fMRI  
776 data. *NMR in Biomedicine*, 10(4–5), 171–178. [https://doi.org/10.1002/\(SICI\)1099-1492\(199706/08\)10:4/5<171::AID-NBM453>3.0.CO;2-L](https://doi.org/10.1002/(SICI)1099-1492(199706/08)10:4/5<171::AID-NBM453>3.0.CO;2-L)

778 Crossman, E. K. (1968). Pause relationships in multiple and chained fixed-ratio  
779 schedules. *Journal of the Experimental Analysis of Behavior*, 11(2), 117–126.  
780 <https://doi.org/10.1901/jeab.1968.11-117>

781 Dale, A. M., Fischl, B., & Sereno, M. I. (1999). Cortical surface-based analysis. I.  
782 Segmentation and surface reconstruction. *NeuroImage*, 9(2), 179–194.  
783 <https://doi.org/10.1006/nimg.1998.0395>

784 Davidow, J. Y., Foerde, K., Galván, A., & Shohamy, D. (2016). An Upside to Reward  
785 Sensitivity: The Hippocampus Supports Enhanced Reinforcement Learning in  
786 Adolescence. *Neuron*, 92(1), 93–99.  
787 <https://doi.org/10.1016/j.neuron.2016.08.031>

788 Day, J. J., Roitman, M. F., Wightman, R. M., & Carelli, R. M. (2007). Associative  
789 learning mediates dynamic shifts in dopamine signaling in the nucleus  
790 accumbens. *Nature Neuroscience*, 10(8), 1020–1028.  
791 <https://doi.org/10.1038/nn1923>

792 de Bie, H. M. A., Boersma, M., Wattjes, M. P., Adriaanse, S., Vermeulen, R. J.,  
793 Oostrom, K. J., Huisman, J., Veltman, D. J., & Delemarre-Van de Waal, H. A.  
794 (2010). Preparing children with a mock scanner training protocol results in high  
795 quality structural and functional MRI scans. *European Journal of Pediatrics*,  
796 169(9), 1079–1085. <https://doi.org/10.1007/s00431-010-1181-z>

797 Decker, A., Dubois, M., Duncan, K., & Finn, A. S. (2022). Pay attention and you might  
798 miss it: Greater learning during attentional lapses. *Psychonomic Bulletin &*  
799 *Review*. <https://doi.org/10.3758/s13423-022-02226-6>



800 Decker, A., & Duncan, K. (2020). Acetylcholine and the complex interdependence of  
801 memory and attention. *Current Opinion in Behavioral Sciences*, 32, 21–28.  
802 <https://doi.org/10.1016/j.cobeha.2020.01.013>

803 Decker, A., Finn, A., & Duncan, K. (2020). Errors lead to transient impairments in  
804 memory formation. *Cognition*, 204, 104338.  
805 <https://doi.org/10.1016/j.cognition.2020.104338>

806 Decker, Duncan, K., & Finn, A. S. (2023). Fluctuations in Sustained Attention Explain  
807 Moment-to-Moment Shifts in Children’s Memory Formation. *Psychological*  
808 *Science*. <https://doi.org/10.1177/09567976231206767>

809 Decker, Duncan, K., Finn, A. S., & Mabbott, D. J. (2020). Children’s family income is  
810 associated with cognitive function and volume of anterior not posterior  
811 hippocampus. *Nature Communications*, 11(1), Article 1.  
812 <https://doi.org/10.1038/s41467-020-17854-6>

813 Delgado, M. R., Nystrom, L. E., Fissell, C., Noll, D. C., & Fiez, J. A. (2000). Tracking the  
814 hemodynamic responses to reward and punishment in the striatum. *Journal of*  
815 *Neurophysiology*, 84(6), 3072–3077. <https://doi.org/10.1152/jn.2000.84.6.3072>

816 Esteban, O., Markiewicz, C. J., Blair, R. W., Moodie, C. A., Isik, A. I., Erramuzpe, A.,  
817 Kent, J. D., Goncalves, M., DuPre, E., Snyder, M., Oya, H., Ghosh, S. S., Wright,  
818 J., Durnez, J., Poldrack, R. A., & Gorgolewski, K. J. (2019). fMRIPrep: A robust  
819 preprocessing pipeline for functional MRI. *Nature Methods*, 16(1), 111–116.  
820 <https://doi.org/10.1038/s41592-018-0235-4>

821 Esterman, M., Grosso, M., Liu, G., Mitko, A., Morris, R., & DeGutis, J. (2016).  
822 Anticipation of Monetary Reward Can Attenuate the Vigilance Decrement. *PLoS*  
823 *One*, 11(7), e0159741. <https://doi.org/10.1371/journal.pone.0159741>

824 Esterman, M., & Rothlein, D. (2019). Models of sustained attention. *Current Opinion in*  
825 *Psychology*, 29, 174–180. <https://doi.org/10.1016/j.copsyc.2019.03.005>

826 Evans. (2004). The environment of childhood poverty. *The American Psychologist*,  
827 59(2), 77–92. <https://doi.org/10.1037/0003-066X.59.2.77>

828 Evans, Janke, Collins, & Baillet. (2012). Brain templates and atlases. *NeuroImage*,  
829 62(2), 911–922. <https://doi.org/10.1016/j.neuroimage.2012.01.024>

830 Farah, M. J. (2017). The Neuroscience of Socioeconomic Status: Correlates, Causes,  
831 and Consequences. *Neuron*, 96(1), 56–71.  
832 <https://doi.org/10.1016/j.neuron.2017.08.034>

833 Farah, M. J. (2018). Socioeconomic status and the brain: Prospects for neuroscience-  
834 informed policy. *Nature Reviews Neuroscience*, 19(7), 428.  
835 <https://doi.org/10.1038/s41583-018-0023-2>

836 Felton, M., & Lyon, D. O. (1966). The Post-Reinforcement Pause<sup>1</sup>. *Journal of the*  
837 *Experimental Analysis of Behavior*, 9(2), 131–134.  
838 <https://doi.org/10.1901/jeab.1966.9-131>

839 Finn, A. S., Minas, J. E., Leonard, J. A., Mackey, A. P., Salvatore, J., Goetz, C., West,  
840 M. R., Gabrieli, C. F. O., & Gabrieli, J. D. E. (2017). Functional brain organization  
841 of working memory in adolescents varies in relation to family income and

842 academic achievement. *Developmental Science*, 20(5), e12450.  
843 <https://doi.org/10.1111/desc.12450>

844 Fischl, B., Salat, D. H., Busa, E., Albert, M., Dieterich, M., Haselgrove, C., van der  
845 Kouwe, A., Killiany, R., Kennedy, D., Klaveness, S., Montillo, A., Makris, N.,  
846 Rosen, B., & Dale, A. M. (2002). Whole brain segmentation: Automated labeling  
847 of neuroanatomical structures in the human brain. *Neuron*, 33(3), 341–355.  
848 [https://doi.org/10.1016/s0896-6273\(02\)00569-x](https://doi.org/10.1016/s0896-6273(02)00569-x)

849 Frankenhuis, W. E., & Nettle, D. (2020). The Strengths of People in Poverty. *Current*  
850 *Directions in Psychological Science*, 29(1), 16–21.  
851 <https://doi.org/10.1177/0963721419881154>

852 Frankenhuis, W. E., Panchanathan, K., & Nettle, D. (2016). Cognition in harsh and  
853 unpredictable environments. *Current Opinion in Psychology*, 7, 76–80.  
854 <https://doi.org/10.1016/j.copsyc.2015.08.011>

855 Frömer, R., Lin, H., Dean Wolf, C. K., Inzlicht, M., & Shenhav, A. (2021). Expectations  
856 of reward and efficacy guide cognitive control allocation. *Nature*  
857 *Communications*, 12(1), 1030. <https://doi.org/10.1038/s41467-021-21315-z>

858 Galvan, A. (2010). Adolescent Development of the Reward System. *Frontiers in Human*  
859 *Neuroscience*, 4, 6. <https://doi.org/10.3389/neuro.09.006.2010>

860 Galvan, A., Hare, T. A., Parra, C. E., Penn, J., Voss, H., Glover, G., & Casey, B. J.  
861 (2006). Earlier Development of the Accumbens Relative to Orbitofrontal Cortex  
862 Might Underlie Risk-Taking Behavior in Adolescents. *Journal of Neuroscience*,  
863 26(25), 6885–6892. <https://doi.org/10.1523/JNEUROSCI.1062-06.2006>

864 Gao, P., Wang, Y.-S., Lu, Q.-Y., Rong, M.-J., Fan, X.-R., Holmes, A. J., Dong, H.-M., Li,  
865 H.-F., & Zuo, X.-N. (2023). Brief mock-scan training reduces head motion during  
866 real scanning for children: A growth curve study. *Developmental Cognitive*  
867 *Neuroscience*, 61, 101244. <https://doi.org/10.1016/j.dcn.2023.101244>

868 Greve, D. N., & Fischl, B. (2009). Accurate and robust brain image alignment using  
869 boundary-based registration. *NeuroImage*, 48(1), 63–72.  
870 <https://doi.org/10.1016/j.neuroimage.2009.06.060>

871 Hackman, D. A., & Farah, M. J. (2009). Socioeconomic status and the developing brain.  
872 *Trends in Cognitive Sciences*, 13(2), 65–73.  
873 <https://doi.org/10.1016/j.tics.2008.11.003>

874 Hackman, D. A., Farah, M. J., & Meaney, M. J. (2010). Socioeconomic status and the  
875 brain: Mechanistic insights from human and animal research. *Nature Reviews*.  
876 *Neuroscience*, 11(9), 651–659. <https://doi.org/10.1038/nrn2897>

877 Hamid, A. A., Pettibone, J. R., Mabrouk, O. S., Hetrick, V. L., Schmidt, R., Vander  
878 Weele, C. M., Kennedy, R. T., Aragona, B. J., & Berke, J. D. (2016). Mesolimbic  
879 dopamine signals the value of work. *Nature Neuroscience*, 19(1), Article 1.  
880 <https://doi.org/10.1038/nn.4173>

881 Hubbard, N. A., Romeo, R. R., Grotzinger, H., Giebler, M., Imhof, A., Bauer, C. C. C., &  
882 Gabrieli, J. D. E. (2020). Reward-Sensitive Basal Ganglia Stabilize the  
883 Maintenance of Goal-Relevant Neural Patterns in Adolescents. *Journal of*  
884 *Cognitive Neuroscience*, 32(8), 1508–1524.  
885 [https://doi.org/10.1162/jocn\\_a\\_01572](https://doi.org/10.1162/jocn_a_01572)

886 Hubbard, N. A., Siless, V., Frosch, I. R., Goncalves, M., Lo, N., Wang, J., Bauer, C. C.  
887 C., Conroy, K., Cosby, E., Hay, A., Jones, R., Pinaire, M., Vaz De Souza, F.,  
888 Vergara, G., Ghosh, S., Henin, A., Hirshfeld-Becker, D. R., Hofmann, S. G.,  
889 Rosso, I. M., ... Whitfield-Gabrieli, S. (2020). Brain function and clinical  
890 characterization in the Boston adolescent neuroimaging of depression and  
891 anxiety study. *NeuroImage: Clinical*, 27, 102240.  
892 <https://doi.org/10.1016/j.nicl.2020.102240>

893 Jenkinson, M., Bannister, P., Brady, M., & Smith, S. (2002). Improved Optimization for  
894 the Robust and Accurate Linear Registration and Motion Correction of Brain  
895 Images. *NeuroImage*, 17(2), 825–841. <https://doi.org/10.1006/nimg.2002.1132>

896 Kahneman, D., & Deaton, A. (2010). High income improves evaluation of life but not  
897 emotional well-being. *Proceedings of the National Academy of Sciences*,  
898 107(38), 16489–16493. <https://doi.org/10.1073/pnas.1011492107>

899 Kurzban, R., Duckworth, A., Kable, J. W., & Myers, J. (2013). An opportunity cost model  
900 of subjective effort and task performance. *The Behavioral and Brain Sciences*,  
901 36(6). <https://doi.org/10.1017/S0140525X12003196>

902 Leonard, J. A., Romeo, R. R., Park, A. T., Takada, M. E., Robinson, S. T., Grotzinger,  
903 H., Last, B. S., Finn, A. S., Gabrieli, J. D. E., & Mackey, A. P. (2019).  
904 Associations between cortical thickness and reasoning differ by socioeconomic  
905 status in development. *Developmental Cognitive Neuroscience*, 36, 100641.  
906 <https://doi.org/10.1016/j.dcn.2019.100641>

907 Lin, H., Ristic, J., Inzlicht, M., & Otto, A. R. (2022). The Average Reward Rate  
908 Modulates Behavioral and Neural Indices of Effortful Control Allocation. *Journal*  
909 *of Cognitive Neuroscience*, 34(11), 2113–2126.  
910 [https://doi.org/10.1162/jocn\\_a\\_01905](https://doi.org/10.1162/jocn_a_01905)

911 Massar, S. A. A., Lim, J., Sasmita, K., & Chee, M. W. L. (2016). Rewards boost  
912 sustained attention through higher effort: A value-based decision making  
913 approach. *Biological Psychology*, 120, 21–27.  
914 <https://doi.org/10.1016/j.biopsycho.2016.07.019>

915 McLaughlin, K. A., Sheridan, M. A., & Lambert, H. K. (2014). Childhood Adversity and  
916 Neural Development: Deprivation and Threat as Distinct Dimensions of Early  
917 Experience. *Neuroscience and Biobehavioral Reviews*, 47, 578–591.  
918 <https://doi.org/10.1016/j.neubiorev.2014.10.012>

919 McMillan, J. C. (1971). Percentage reinforcement of fixed-ratio and variable-interval  
920 performances. *Journal of the Experimental Analysis of Behavior*, 15(3), 297–302.  
921 <https://doi.org/10.1901/jeab.1971.15-297>

922 Niv, Y., Daw, N. D., Joel, D., & Dayan, P. (2007). Tonic dopamine: Opportunity costs  
923 and the control of response vigor. *Psychopharmacology*, 191(3), 507–520.  
924 <https://doi.org/10.1007/s00213-006-0502-4>

925 Niv, Y., Joel, D., & Dayan, P. (2006). A normative perspective on motivation. *Trends in*  
926 *Cognitive Sciences*, 10(8), 375–381. <https://doi.org/10.1016/j.tics.2006.06.010>

927 Noble, K. G., McCandliss, B. D., & Farah, M. J. (2007). Socioeconomic gradients predict  
928 individual differences in neurocognitive abilities. *Developmental Science*, *10*(4),  
929 464–480. <https://doi.org/10.1111/j.1467-7687.2007.00600.x>

930 Oshri, A., Hallowell, E., Liu, S., MacKillop, J., Galvan, A., Kogan, S. M., & Sweet, L. H.  
931 (2019). Socioeconomic hardship and delayed reward discounting: Associations  
932 with working memory and emotional reactivity. *Developmental Cognitive*  
933 *Neuroscience*, *37*. <https://doi.org/10.1016/j.dcn.2019.100642>

934 Otto, A. R., & Daw, N. D. (2019). The opportunity cost of time modulates cognitive  
935 effort. *Neuropsychologia*, *123*, 92–105.  
936 <https://doi.org/10.1016/j.neuropsychologia.2018.05.006>

937 Palacios-Barrios, E. E., Hanson, J. L., Barry, K. R., Albert, W. D., White, S. F., Skinner,  
938 A. T., Dodge, K. A., & Lansford, J. E. (2021). Lower neural value signaling in the  
939 prefrontal cortex is related to childhood family income and depressive  
940 symptomatology during adolescence. *Developmental Cognitive Neuroscience*,  
941 *48*, 100920. <https://doi.org/10.1016/j.dcn.2021.100920>

942 Pepper, G. V., & Nettle, D. (2017). The behavioural constellation of deprivation: Causes  
943 and consequences. *Behavioral and Brain Sciences*, *40*, e314.  
944 <https://doi.org/10.1017/S0140525X1600234X>

945 Power, J. D., Mitra, A., Laumann, T. O., Snyder, A. Z., Schlaggar, B. L., & Petersen, S.  
946 E. (2014). Methods to detect, characterize, and remove motion artifact in resting  
947 state fMRI. *NeuroImage*, *84*, 320–341.  
948 <https://doi.org/10.1016/j.neuroimage.2013.08.048>

949 Reiss, F. (2013). Socioeconomic inequalities and mental health problems in children  
950 and adolescents: A systematic review. *Social Science & Medicine*, *90*, 24–31.  
951 <https://doi.org/10.1016/j.socscimed.2013.04.026>

952 Reynolds, J. N., Hyland, B. I., & Wickens, J. R. (2001). A cellular mechanism of reward-  
953 related learning. *Nature*, *413*(6851), 67–70. <https://doi.org/10.1038/35092560>

954 Romeo, R. R., Christodoulou, J. A., Halverson, K. K., Murtagh, J., Cyr, A. B., Schimmel,  
955 C., Chang, P., Hook, P. E., & Gabrieli, J. D. E. (2018). Socioeconomic Status and  
956 Reading Disability: Neuroanatomy and Plasticity in Response to Intervention.  
957 *Cerebral Cortex*, *28*(7), 2297–2312. <https://doi.org/10.1093/cercor/bhx131>

958 Ross, L. T., & Hill, E. M. (2002). CHILDHOOD UNPREDICTABILITY, SCHEMAS FOR  
959 UNPREDICTABILITY, AND RISK TAKING. *Social Behavior and Personality: An*  
960 *International Journal*, *30*(5), 453–473. <https://doi.org/10.2224/sbp.2002.30.5.453>

961 Schlinger, H. D., Derenne, A., & Baron, A. (2008). What 50 Years of Research Tell Us  
962 About Pausing Under Ratio Schedules of Reinforcement. *The Behavior Analyst*,  
963 *31*(1). <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2395348/>

964 Schultz. (1993). Socioeconomic advantage and achievement motivation: Important  
965 mediators of academic performance in minority children in urban schools. *The*  
966 *Urban Review*, *25*(3), 221–232. <https://doi.org/10.1007/BF01112109>

967 Seligman, M. E. P. (1972). Learned Helplessness. *Annual Review of Medicine*, *23*(1),  
968 407–412. <https://doi.org/10.1146/annurev.me.23.020172.002203>



969 Shenhav, A., Botvinick, M. M., & Cohen, J. D. (2013). The Expected Value of Control:  
970 An Integrative Theory of Anterior Cingulate Cortex Function. *Neuron*, 79(2), 217–  
971 240. <https://doi.org/10.1016/j.neuron.2013.07.007>

972 Sukumar, S., Shadmehr, R., & Ahmed, A. A. (2021). *Effects of reward history on*  
973 *decision-making and movement vigor* [Preprint]. Neuroscience.  
974 <https://doi.org/10.1101/2021.07.22.453376>

975 Tustison, N. J., Avants, B. B., Cook, P. A., Zheng, Y., Egan, A., Yushkevich, P. A., &  
976 Gee, J. C. (2010). N4ITK: Improved N3 Bias Correction. *IEEE Transactions on*  
977 *Medical Imaging*, 29(6), 1310–1320. <https://doi.org/10.1109/TMI.2010.2046908>

978 Wallace, R. F., & Mulder, D. W. (1973). Fixed-ratio responding with human subjects.  
979 *Bulletin of the Psychonomic Society*, 1(5), 359–362.  
980 <https://doi.org/10.3758/BF03334372>

981 Wang, Miura, & Uchida. (2013). The dorsomedial striatum encodes net expected return,  
982 critical for energizing performance vigor. *Nature Neuroscience*, 16(5), Article 5.  
983 <https://doi.org/10.1038/nn.3377>

984 Wang, Toyoshima, Kunimatsu, J., Yamada, & Matsumoto. (2021). Tonic firing mode of  
985 midbrain dopamine neurons continuously tracks reward values changing  
986 moment-by-moment. *eLife*, 10, e63166. <https://doi.org/10.7554/eLife.63166>

987 Westbrook, A., & Braver, T. S. (2016). Dopamine Does Double Duty in Motivating  
988 Cognitive Effort. *Neuron*, 89(4), 695–710.  
989 <https://doi.org/10.1016/j.neuron.2015.12.029>

990 Westbrook, A., Frank, M. J., & Cools, R. (2021). A mosaic of cost-benefit control over  
991 cortico-striatal circuitry. *Trends in Cognitive Sciences*, 25(8), 710–721.  
992 <https://doi.org/10.1016/j.tics.2021.04.007>

993 White, S. F., Nusslock, R., & Miller, G. E. (2022). Low Socioeconomic Status Is  
994 Associated with a Greater Neural Response to Both Rewards and Losses.  
995 *Journal of Cognitive Neuroscience*, 34(10), 1939–1951.  
996 [https://doi.org/10.1162/jocn\\_a\\_01821](https://doi.org/10.1162/jocn_a_01821)

997 Williams, D. C., Saunders, K. J., & Perone, M. (2011). Extended Pausing by Humans on  
998 Multiple Fixed-Ratio Schedules with Varied Reinforcer Magnitude and Response  
999 Requirements. *Journal of the Experimental Analysis of Behavior*, 95(2), 203–220.  
1000 <https://doi.org/10.1901/jeab.2011.95-203>

1001 Zhang, Y., Brady, M., & Smith, S. (2001). Segmentation of brain MR images through a  
1002 hidden Markov random field model and the expectation-maximization algorithm.  
1003 *IEEE Transactions on Medical Imaging*, 20(1), 45–57.  
1004 <https://doi.org/10.1109/42.906424>

1005

1006