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

Massachusetts Institute of Technology

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

2   **Adolescents**

3   Abbreviated title: Reward Responses Vary By Adolescent Socioeconomic Status

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Abstract

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

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

63   responses.

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84 **Significance statement**

85 Lower socioeconomic status (SES) is associated with reduced access to resources and

86 opportunities. Such disparities may shape reward sensitivity, which in turn, could

87 influence how individuals respond to and pursue rewarding experiences. Here, we show

88 that lower-SES adolescents display reduced reward sensitivity in the brain and

89 behavior. The striatum–a brain region that is highly sensitive to reward–showed greater

90 activations during periods of high reward and tracked fluctuations between reward-rich

91 and reward-scarce task phases. However, lower SES correlated with smaller reward-

92 driven striatal responses, and reduced response slowing after rare rewards. These

93 findings link lower SES to reduced reward responses, which could trigger a cycle of

94 reduced reward pursuit, leading to fewer positive experiences, which could further

95 diminish reward sensitivity.

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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.

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Methods

172 **Participants**

173   We recruited 127 adolescents from diverse SES backgrounds as part of a larger

174 project examining the relationship between SES, brain development, and cognition.

175 Eligible participants were in the 7th or 8th grade, proficient in English, had no MRI

176 contraindications, were not diagnosed with autism or a neurological disability, and were

177 not born premature (<34 weeks). Thirteen children did not complete the MRI, resulting

178 in a sample of 114 adolescents (age range=12-14; mean (SD)=13.46 (0.68), n=56

179 female). Five participants with excessive movement during scanning (average

180 framewise displacement (FD) of more than 0.6 mm) were retained only for behavioral

181 analyses, leaving 109 for the neuroimaging analysis (*correlation between FD and SES*

182 among the included participants: β = 0.005, SE = 0.01, t(107) = 0.35, p = .730, r = 0.03).

183 Of note, the findings remained unchanged with a more conservative limit of movement

184 (average FD of < 0.3mm). All children and their legal guardians provided assent and

185 consent. The study was approved by the MIT Committee on the Use of Human

186 Subjects. Participants received compensation for their time.

187   Before collecting data, we targeted a sample of at least 100 participants based

188 on studies reporting medium-to-large effects (i.e., Cohen's *d* of 0.5-0.8) on the

189 relationship between SES and cognitive performance (Finn et al., 2017; Leonard et al.,

190 2019; Noble et al., 2007), brain structure (Decker, Duncan, et al., 2020; Romeo et al.,

191 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

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.

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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
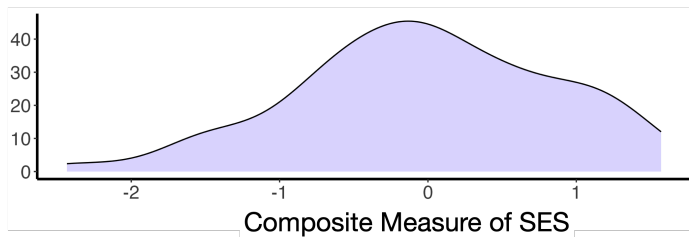
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214 predetermined, and fixed across trials, with numbers generated to match the

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

11

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

Potential outcomes during a **reward** and **loss** block

+1, -0.5, +1, +1, 0, +1, +1, +1, -0.5, -0.5, +1, -0.5, -0.5, 0, -0.5, -0.5

Exponentially weighted moving mean of gains and losses to determine the *average reward rate on each trial*
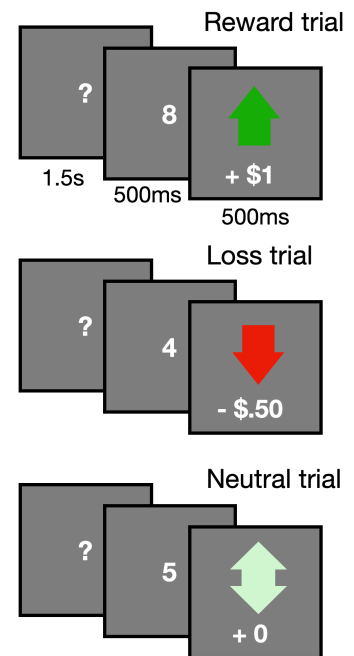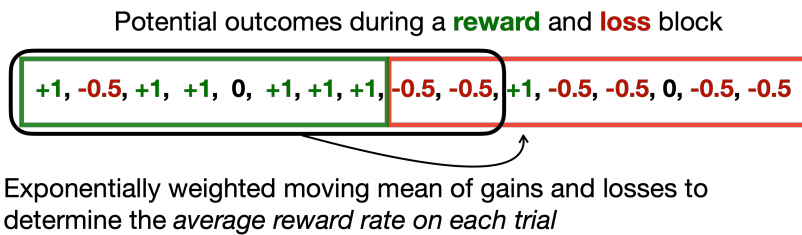
D. Reward rate fluctuations in a representative participant
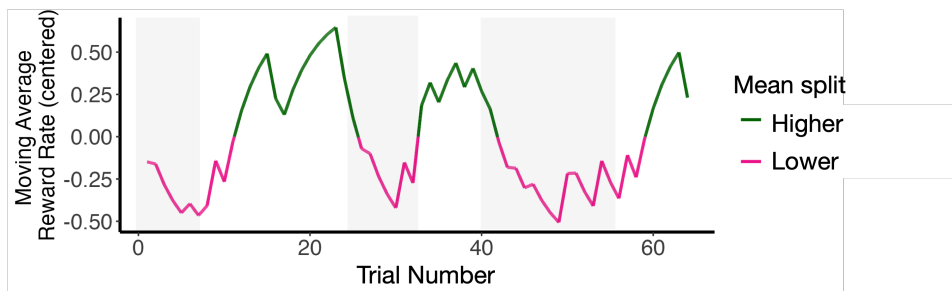
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244   *Figure 1. SES score distribution, gambling task schematic, and trial-by-trial*
245   *moving average of rewards and losses*. (A) *Distribution of SES composite scores*:

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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

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

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 bbregister

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              $$\text{EWMA}_t = α × r_t + (1 − α) × \text{EWMA}_{t\text{-}1}$$

342

343   In this formula, the EWMA_t represents the EWMA at the current trial, t, α 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, α was based on an 8-period span, calculated as: $α = 2/(N{+}1)$,

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 EWMAs 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

Examining reward-driven striatal responses to reward and average reward rate

fluctuations across time

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

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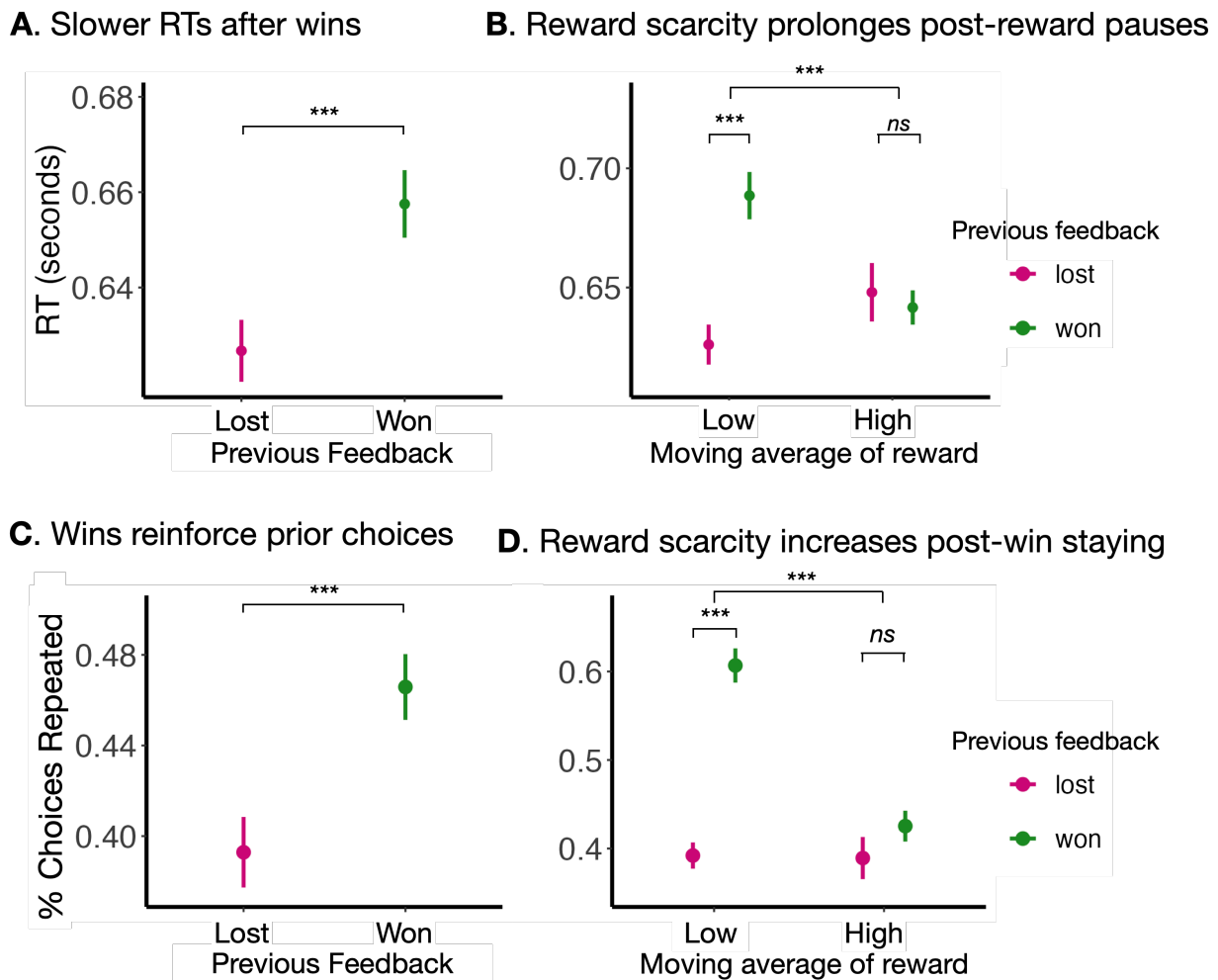426

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428   **Results**

429   We first describe how behavioral responses, specifically response times (RT)

430   and choices, are influenced by immediately rewarding outcomes, and covary with

431   fluctuations in the average reward rate across time. We then describe how these

432   behavioral responses differ by SES. Turning to the neuroimaging data, we then explore

433   the association between SES and the volume of the putamen, caudate, and nucleus

434   accumbens. Furthermore, we examine differences in striatal activations during reward

435   versus loss blocks, and examine how these activations covary with temporal

436   fluctuations in the average reward rate. Finally, we focus on disparities in striatal

437   responses across SES.

438

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

440   Adolescents responded more slowly after winning than losing (i.e., post-reward

441   pausing: $\beta = 0.02$, SE = 0.005, $t(262) = 4.68$, $p < .001$; Figure 2A). Furthermore, trial-by-

442   trial RTs covaried with fluctuations in the average reward rate, such that a higher

443   average reward rate led to faster RTs ($\beta = -0.04$, SE = 0.02, $t(98) = -2.32$, $p = .022$).

444   Fluctuations in the average reward rate also interacted with immediate feedback to

445   shape RTs: periods of reward scarcity amplified post-reward pausing *(Reward Rate x*

446   *Preceeding feedback: $\beta = -0.05$, SE = 0.02, $t(104) = -3.53$, $p < .001$, Figure 2B)*,

447   indicating responses to immediate reward were amplified by a history of low rewards. In

448   fact, post-reward pausing was only observed when rewards were scarce but not when

449   they were plentiful (*effect of preceding feedback when the reward rate is centered at -*

21

450   *1SD below the mean: β = 0.04, SE = 0.007, t(100) = 6.23, p < .001; above the mean: β*

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

A. Slower RTs after wins

B. Reward scarcity prolonges post-reward pauses

C. Wins reinforce prior choices

D. Reward scarcity increases post-win staying

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

22

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 Preceeding 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

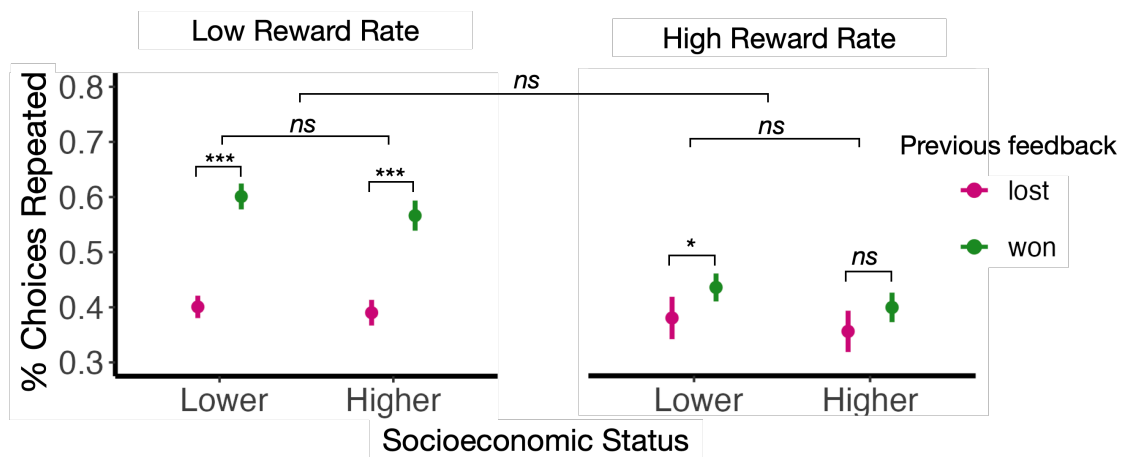**Reward rate fluctuations influence post-reward pausing more in higher-SES**

adolescents

Immediate reward and average reward rate fluctuations influenced choices

similarly regardless of SES (*SES x feedback*: *β = 0.09, SE = 0.05, z = 1.73, p = .084*;

SES x average reward rate: *β = –0.25, SE = 0.18, z = –1.40, p = .161; SES x feedback*

type x moving average: β = 0.18, SE = 0.15, z = 1.21, p = .225; Figure 3A). Additionally,

these distinct temporal dimensions of reward influenced RTs similarly, regardless of

SES (*SES x feedback*: *β = –0.002, SE = 0.005, t(109) = –0.45, p = .651; SES x average*

reward rate: *β = 0.02, SE = 0.02, t(100) = 1.04, p = .301; Figure 3A*).

However, reward-rate fluctuations modulated post-reward pausing more in

higher- than lower-SES adolescents (*SES x feedback type x moving average*: *β =*

–0.04, SE = 0.02, t(105) = –2.54, p = .013; Figure 3B). That is, higher-SES adolescents

slowed more following rare rewards (main effect of SES when the reward rate is

centered at -1SD below the mean to reflect reward scarcity: β = 0.02, SE = 0.007, t(684)

= 2.20, p = .028; Figure 3B). When rewards were plentiful, higher-SES adolescents

slowed less following rewards than lower-SES adolescents (*centered at +1SD above*

the mean to reflect reward abundance: β = –0.02, SE = 0.008, t(4949) = –2.05, p =

.041; *Figure 3B*) though neither group showed significant evience of post-reward

pausing when rewards were plentiful (*ps* > 0.087). Interestingly, SES was unrelated to

individual differences in optimal learning rates (β =0.06, SE = 0.04, t(114) = 1.32, p =

.189), suggesting that heightened post-reward pausing was not driven by a greater

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
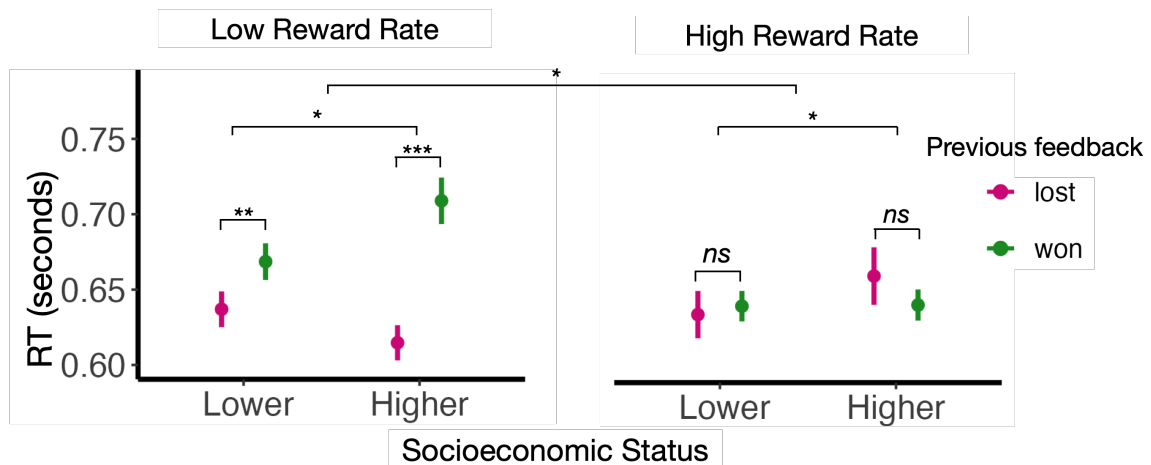
514

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 (β = 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 (β = 32.78, SE = 49.74, t(103) = 0.66, p

530 = .511) or nucleus accumbens (β = 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
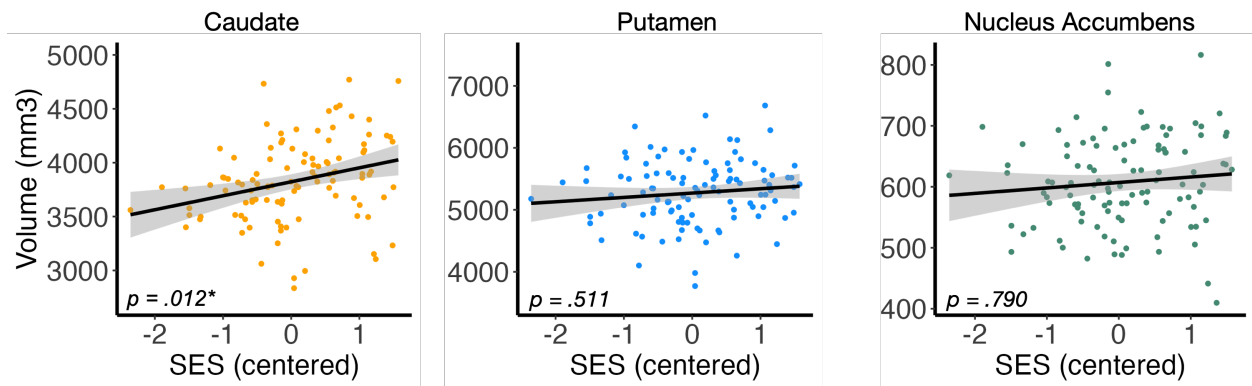
534

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.
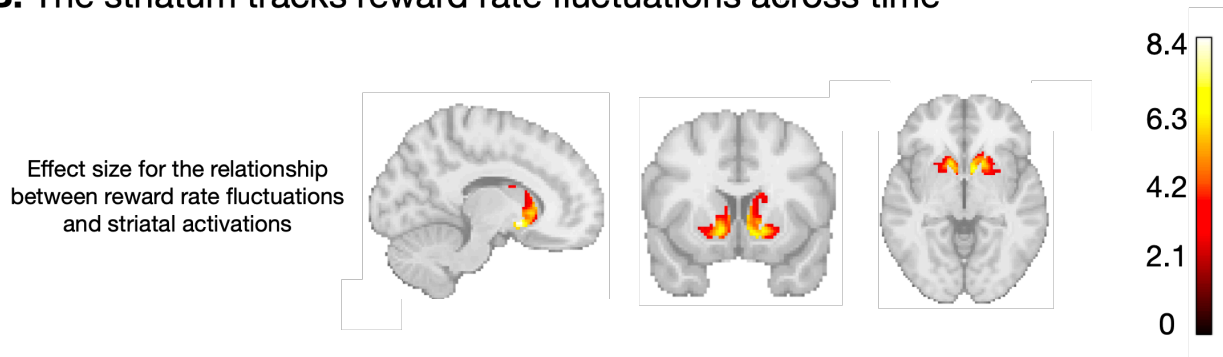541

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 (β = 0.50, SE = 0.07, t(106) = 6.74, p < .001), putamen (β = 0.61, SE = 0.08,

545 t(106) = 7.83, p < .001), and nucleus accumbens (β = 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 (β

548 *= 0.77, SE = 0.08, t(105) = 9.60, p < .001*), putamen (*β = 0.66, SE = 0.07, t(105) = 8.94,*

549 *p < .001*), and nucleus accumbens (*β = 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

reward>loss
contrast

8.9
6.7
4.5
2.2
0

B. The striatum tracks reward rate fluctuations across time

Effect size for the relationship
between reward rate fluctuations
and striatal activations

8.4
6.3
4.2
2.1
0

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 x hemisphere*: all *p*s > 0.29).

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

569 strongly in higher-SES adolescents in the putamen (β = 0.17, SE = 0.09, t(104) = 2.02,

570 p = .046; Figure 6B), but not the caudate (β = 0.08, SE = 0.10, t(104) = 0.88, p = .380)

571 or nucleus accumbens (β = 0.02, SE = 0.11, t(101) = 0.18, p = .860). None of these

572 effects differed by hemisphere (*SES x hemisphere*: all *p*s > 0.21). Of note, the

573 relationship between SES and reward-driven activations also did not differ by striatal

574 subregion (SES x subregion interaction: all ps > 0.10).

575

A. Lower SES correlates with smaller reward-driven activations
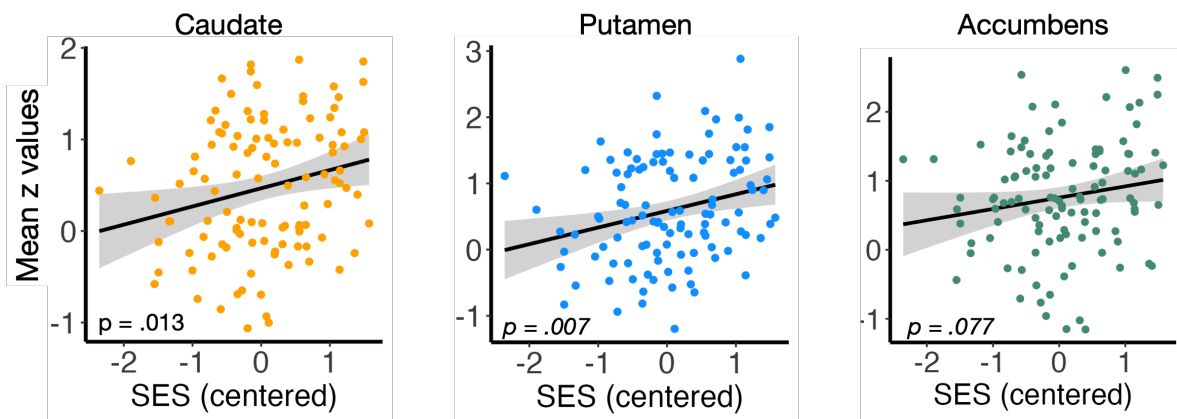
B. Putamen activations track reward rate fluctuations less in lower-SES adoelsecents
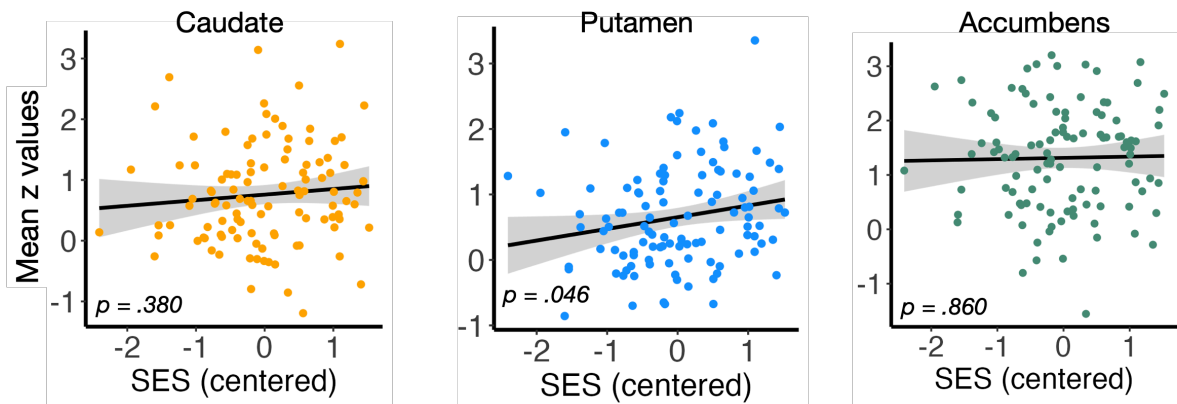
576

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 (*ps*>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 infuential 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* that 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/

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References

737 Amir, D., Jordan, M. R., & Rand, D. G. (2018). An uncertainty management perspective

738   on long-run impacts of adversity: The influence of childhood socioeconomic

739   status on risk, time, and social preferences. *Journal of Experimental Social*

740   *Psychology*, *79*, 217–226. https://doi.org/10.1016/j.jesp.2018.07.014

742 Auerbach, R. P., Pagliaccio, D., Hubbard, N. A., Frosch, I., Kremens, R., Cosby, E.,

743   Jones, R., Siless, V., Lo, N., Henin, A., Hofmann, S. G., Gabrieli, J. D. E.,

744   Yendiki, A., Whitfield-Gabrieli, S., & Pizzagalli, D. A. (2022). Reward-Related

745   Neural Circuitry in Depressed and Anxious Adolescents: A Human Connectome

746   Project. *Journal of the American Academy of Child & Adolescent Psychiatry*,

747   *61*(2), 308–320. https://doi.org/10.1016/j.jaac.2021.04.014

748 Avants, B. B., Epstein, C. L., Grossman, M., & Gee, J. C. (2008). Symmetric

749   diffeomorphic image registration with cross-correlation: Evaluating automated

750   labeling of elderly and neurodegenerative brain. *Medical Image Analysis*, *12*(1),

751   26–41. https://doi.org/10.1016/j.media.2007.06.004

752 Awheda, M. D., & Schwartz, H. M. (2016). Exponential moving average based

753   multiagent reinforcement learning algorithms. *Artificial Intelligence Review*, *45*(3),

754   299–332. https://doi.org/10.1007/s10462-015-9447-5

755 Bayer, H. M., & Glimcher, P. W. (2005). Midbrain Dopamine Neurons Encode a

756   Quantitative Reward Prediction Error Signal. *Neuron*, *47*(1), 129–141.

757   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., Düzel, 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-

777   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 Pause1. *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

academic achievement. *Developmental Science*, *20*(5), e12450.

https://doi.org/10.1111/desc.12450

Fischl, B., Salat, D. H., Busa, E., Albert, M., Dieterich, M., Haselgrove, C., van der

Kouwe, A., Killiany, R., Kennedy, D., Klaveness, S., Montillo, A., Makris, N.,

Rosen, B., & Dale, A. M. (2002). Whole brain segmentation: Automated labeling

of neuroanatomical structures in the human brain. *Neuron*, *33*(3), 341–355.

https://doi.org/10.1016/s0896-6273(02)00569-x

Frankenhuis, W. E., & Nettle, D. (2020). The Strengths of People in Poverty. *Current*

Directions in Psychological Science, *29*(1), 16–21.

https://doi.org/10.1177/0963721419881154

Frankenhuis, W. E., Panchanathan, K., & Nettle, D. (2016). Cognition in harsh and

unpredictable environments. *Current Opinion in Psychology*, *7*, 76–80.

https://doi.org/10.1016/j.copsyc.2015.08.011

Frömer, R., Lin, H., Dean Wolf, C. K., Inzlicht, M., & Shenhav, A. (2021). Expectations

of reward and efficacy guide cognitive control allocation. *Nature*

Communications, *12*(1), 1030. https://doi.org/10.1038/s41467-021-21315-z

Galvan, A. (2010). Adolescent Development of the Reward System. *Frontiers in Human*

Neuroscience, *4*, 6. https://doi.org/10.3389/neuro.09.006.2010

Galvan, A., Hare, T. A., Parra, C. E., Penn, J., Voss, H., Glover, G., & Casey, B. J.

(2006). Earlier Development of the Accumbens Relative to Orbitofrontal Cortex

Might Underlie Risk-Taking Behavior in Adolescents. *Journal of Neuroscience*,

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

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

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

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

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1006