



Examining the Association between Punishment and Reward Sensitivity and Response Inhibition to Previously-Incentivized Cues across Development

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Abstract

Processing and learning from affective cues to guide goal-directed behavior may be particularly important during adolescence; yet the factors that promote and/or disrupt the ability to integrate value in order to guide decision making across development remain unclear. The present study ($N = 1046$) assessed individual difference factors (self-reported punishment and reward sensitivity) related to whether previously-rewarded and previously-punished cues differentially impact goal-directed behavior (response inhibition) in a large developmental sample. Participants were between the ages of 8–21 years ($M_{\text{age}} = 14.29$, $SD = 3.97$, 50.38% female). Previously-rewarded cues improved response inhibition among participants age 14 and older. Further, punishment sensitivity predicted overall improved response inhibition among participants aged 10 to 18. The results highlight two main factors that are associated with improvements in the ability to integrate value to guide goal-directed behaviour – cues in the environment (e.g., reward-laden cues) and individual differences in punishment sensitivity. These findings have implications for both educational and social policies aimed at characterizing the ways in which youth integrate value to guide decision making.

Keywords Adolescence · Inhibitory control · Value · Punishment sensitivity · Reward sensitivity

Introduction

During adolescence cognitive and affective processes continue to mature to facilitate goal-directed behavior (Davidow et al., 2018; Somerville & Casey, 2010). Thus, the ability to process and learn from affective cues in the environment to guide subsequent behavior may be particularly important for decision-making and exploration during this phase of life. However, prior developmental work has been inconsistent in whether previously-incentivized cues improve or disrupt response inhibition during adolescence, focuses on cues with a history of *reward* (not punishment), and are typically based on relatively small developmental samples. Further, little work has investigated individual differences factors (e.g., punishment and reward sensitivity). This study addresses these gaps by assessing the association between punishment and reward

sensitivity and response inhibition to previously-incentivized cues across development in a large sample spanning from childhood to emerging adulthood. Ultimately, being able to distinguish the contexts that promote and/or disrupt the ability to integrate value to guide decision-making can have implications for both educational and social policies that promote the well-being of youth.

Cognitive control, selecting and executing the appropriate actions given one's environment and goals, supports a broad range of goal-directed behaviors (Miller & Cohen, 2001). One component of cognitive control is *response inhibition*, deliberately suppressing an inappropriate response. Previous research has shown that response inhibition to affectively neutral cues improves from childhood to early adulthood (e.g., Luna et al., 2004). Cues encountered in daily life, however, often are not affectively neutral and have acquired value based on *previous experience*, which may impact how individuals respond to these cues in the future. According to the Pavlovian Instrumental Transfer framework, there is an evolutionary bias to approach reward-related cues (which may disrupt response inhibition) and avoid punishment-related cues (which may facilitate

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response inhibition; J. A. Gray & McNaughton, 2000). For example, if you associate a car horn with traffic accidents, you may freeze when you hear that cue, anticipating a negative event (Raab & Hartley, 2020).

Yet, cues that were previously associated with value may impact response inhibition differently across development. Indeed, the ability to process and learn from affective cues to guide goal-directed behavior may be particularly important for decision-making and exploration during adolescence. At the same time, there are likely individual differences both within and across development that may impact the extent to which individuals use previously learned cues to guide their behavior. For example, an individual who has a strong emotional reaction to receiving punishment (henceforward referred to as punishment sensitivity to remain consistent with previous research; Carver & White, 1994), may have an even greater freezing response to a car horn than an individual who is less prone to being bothered by these types of cues. Trait differences in both reward and punishment sensitivity may increase the attentional salience of value cues (e.g., Heffer & Willoughby, 2021b; Hickey et al., 2010; Qi et al., 2013; Tull et al., 2012), and thus may subsequently impact the strength of the relationship between cues previously associated with value and response inhibition. A goal of the current study is to investigate whether punishment and reward sensitivity are associated with response inhibition to previously-incentivized cues across development.

A growing body of research has assessed how previously-incentivized cues impact response inhibition across development, with the majority of this work focusing on previously-rewarded cues (e.g., Davidow et al., 2019; Roper et al., 2014; Winter & Sheridan, 2014). Notably, there have been mixed findings in the literature as to the direction of this relationship. Some research has shown that adolescents, compared to individuals at other developmental phases, have *reduced* cognitive control in response to target cues that were previously rewarded yet are not currently incentivized (e.g., Davidow et al., 2019; Roper et al., 2014). In contrast, other work has found that previously rewarded cues *improved* response inhibition performance from childhood to early adolescence (e.g., Winter & Sheridan, 2014). For example, prior research shows that improved response inhibition accuracy for previously learned high magnitude gain (relative to low magnitude gain) cues emerged among older adolescents (Insel et al., 2019; see also Meyer et al., 2020). Thus, reward history associations may be particularly salient during adolescence; yet the nature of how reward history impacts response inhibition across development remains unclear.

There has been substantially less focus on how previously-punished cues impact response inhibition across development. In line with Pavlovian Instrumental Transfer,

better performance in response to previously-punished cues compared to previously-rewarded cues would be expected because response inhibition behavior (i.e., not acting) aligns with the punish-avoid association proposed by Pavlovian Instrumental Transfer. However, it is unclear whether this relationship will change across development. Research has shown that response inhibition accuracy for previously-punished cues improved from age 13 to 21, however, there were no differences in performance between high compared to low stakes punishment (Insel et al., 2019). In a sample of 61 participants between the ages of 8 and 25, prior work (Raab & Hartley, 2020) also found non-linear improvements in response inhibition to cues associated with punishment across development (although see Moutoussis et al., 2018 who found no age-related differences in response inhibition to previously-punished cues between adolescents and emerging adults). The current large-scale study seeks to clarify how cues that were previously associated with value impact response inhibition from childhood to early adulthood.

The mixed findings in the literature may reflect a need to assess factors that might moderate the relationship between age and response inhibition to previously-incentivized cues. It may be that punishment and reward sensitivity are important moderators to consider when assessing this relationship. Indeed, adolescence is a period of development where the evaluation of *rewards and punishments* is increasingly becoming salient (e.g., Foulkes & Blakemore, 2016; Hauser et al., 2015). Theories of adolescence propose that this phase of development is characterized by enhanced reactivity to emotionally-salient cues, relative to a still-developing capacity for cognitive control (Davidow et al., 2018; Somerville & Casey, 2010). Thus, during adolescence, there may be enhanced sensitivity to emotionally-provoking cues, which might exacerbate the expected relationship with Pavlovian Instrumental Transfer.

At the same time, there are likely important individual differences within this developmental period in their sensitivity to reward and punishment. For example, research has shown that although adolescents, compared to children and adults, had exaggerated neural activation in response to value cues, there also is a great deal of variability among adolescents (e.g., Hare et al., 2008). Additionally, prior work has identified distinct groups of adolescents who were characterized by differential levels of punishment sensitivity (Heffer et al., 2023; Heffer & Willoughby, 2021a). Notably, adolescents who were characterized by higher levels of punishment sensitivity had greater medial frontal theta, neural activation that is consistent with increased performance monitoring during response inhibition to neutral cues compared to adolescents who were characterized by lower levels of punishment sensitivity (Heffer et al., 2023). These findings suggest that not all adolescents are sensitive to

rewards and/or punishments to the same degree and, importantly, that individual differences may have implications for response inhibition. Yet, prior research has not examined whether individual differences in reward and punishment sensitivity relate to *previously*-incentivized cues across development. It may be that adolescents who do not have high sensitivity to rewards or punishments are less likely to attend to value cues in the environment, and thus the effect of Pavlovian Instrumental Transfer may be weaker for those adolescents.

Notably, risk for internalizing problems— that are associated with reward and punishment sensitivity (Naragon-Gainey et al., 2013; Sportel et al., 2013; Vervoort et al., 2010)— tend to rise during adolescence (e.g., depressive symptoms, anxiety; Kessler et al., 2007; McGrath et al., 2023). Adolescence susceptibility to internalizing problems may relate to a variety of cognitive and emotional processes (Davidow et al., 2018; Somerville & Casey, 2010). Thus, understanding factors, such as reward and punishment sensitivity, that could be associated with adolescents' ability to exert cognitive control in the context of emotionally-salient cues may help to elucidate which youth are most at risk for internalizing problems.

Current Study

Much of the past research assessing the relationship between response inhibition and previously-incentivized cues has shown inconsistent findings, focuses on cues with a history of reward, is based on small developmental samples, and often do not assess individual difference factors; thus the ways in which cues associated with value differentially impact goal-directed behavior across development remains unclear. The goal of the current study was to (1) assess age-related changes in response inhibition to previously-rewarded and previously-punished cues across a large developmental sample and (2) identify whether individual difference factors (punishment and reward sensitivity) are associated with response inhibition to previously-rewarded and previously-punished cues across development. Given that there is inconsistency in the literature as to whether previously-rewarded and punished cues improve or disrupt response inhibition and no studies investigating individual differences in reward/punishment sensitivity, the current study primarily was exploratory, although it is expected that heightened punishment sensitivity would strengthen any effect of previously-punished cues (compared to previously-rewarded cues) on response inhibition, while heightened reward sensitivity would strengthen any effect of previously-rewarded cues (compared to previously-punished cues) on response

inhibition. This study's sample inclusion criteria and analyses were preregistered online at OSF.

Method

Participants

Participants ($N = 1093$) included children, adolescents, and emerging adults between the ages of 8 and 21 years from the Human Connectome Project in Development (HCP-D), a large consortium study of youth brain development, behavior, and mental health (Harms et al., 2018; Somerville et al., 2018). HCP-D participants between the ages of 5 and 7 years were not included because they did not complete the self-report measures used in the current study. The participants were drawn from four different sites across the USA: Harvard University, University of California-Los Angeles, University of Minnesota, and Washington University in St Louis.

The exclusion criteria at recruitment for this sample were: premature birth; serious neurological condition (e.g. stroke, cerebral palsy); serious endocrine condition (e.g. precocious puberty, untreated growth hormone deficiency); long-term use of immunosuppressants or steroids; any history of serious head injury; hospitalization >2 days for certain physical or psychiatric conditions or substance use; treatment >12 months for psychiatric conditions; claustrophobia; or pregnancy.

Missing Data

Of the original sample, 28 participants did not have data from the behavioral task used in this study. Participants were excluded from the current study if they did not have at least one useable task run or they made no button presses during the task ($n = 5$). Two participants made no button press on their first run of the task and three participants made no button presses on their second run, these runs were excluded for these participants. There were 22 participants who only had one run of usable data, these participants were retained in the current study. The original exclusion criteria for this study also excluded participants who pressed the button on every trial, however, there were no participants who met this criteria. Thirteen participants did not complete the self-report measures and were excluded. The final sample included $N = 1046$ ($M_{\text{age}} = 14.29$, $SD = 3.97$, 50.38% female) distributed roughly equally across the age range (see Fig. 1).

Parent report of their child's race (and participants 18 and over's self-reported race), indicated that 0.2% of the sample identified as Native American/Alaska native, 6.8% as Asian, 12.1% as Black/African American, 0.2% as

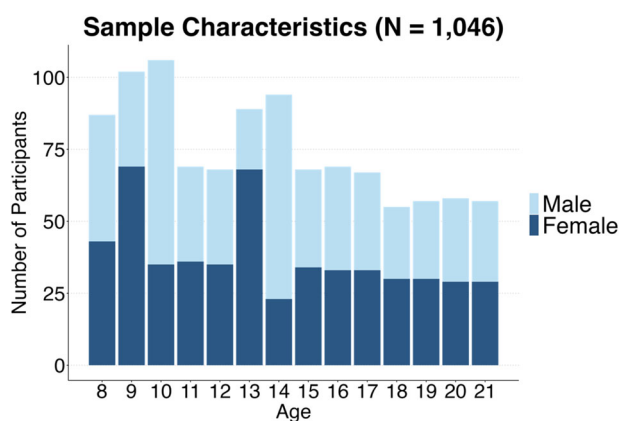


Fig. 1 Age/sex histogram of the sample ($N = 1046$). X-axis: Age (in years); Y-axis: number of participants. Sex was assessed as a binary measure indicating sex assigned at birth

Native Hawaiian/Pacific Islander, 62.5% as White, 15.6% as More than one race, and 2.6% as Unknown. The Institutional Review Board at Washington University in St Louis (IRB #201603135) approved this study and all participants provided written informed assent. Parents of participants under 18 years provided written informed consent.

Conditioned Appetitive Response Inhibition Task (CARIT)

The conditioned appetitive response inhibition task (CARIT; Davidow et al., 2019; Somerville et al., 2018; Winter & Sheridan, 2014) consisted of two phases. In the first phase, referred to as the conditioning phase (adapted from Delgado et al., 2011), two initially neutral shape cues are paired with win or loss monetary feedback. In the second phase, referred to as the inhibitory control phase, participants completed a response inhibition task where they were instructed to withhold their responses to the shape cues that had been paired with the receipt of wins and losses.

CARIT: Conditioning Phase

During the conditioned phase, participants win (reward feedback) or lose (punishment feedback) money of varying magnitudes. In each block, consisting of four trials, participants were informed whether subsequent trials were high stakes (\$1.00 for wins and -\$0.50 for losses) or low stakes (\$0.20 for wins and -\$0.10 for losses) trials (cue presented for 1.5 s). The losses are half as large as gains in accordance with prior work indicating that losses are over-weighted in human valuation processes (Tversky & Kahneman, 1991).

Next, participants viewed a guess cue (“?”) for 2 s, signaling for them to guess between two response options by pressing one of two buttons. After a jittered interstimulus

interval (ISI; 1.5, 2, or 2.5 s), participants received feedback about whether their guess was correct (resulting in monetary win) or incorrect (resulting in a monetary loss). Importantly, the visual display (presented for 1 s) for “win” feedback always included a square whereas the visual display for “loss” feedback always included a circle (irrespective of magnitude, and shape assignment was counterbalanced across participants). A fixation interblock interval (8 s) was presented at the end of each block of four trials. Across the task, participants had the opportunity to associate once-neutral shapes with either reward or punishment feedback. Circles and squares were subsequently carried forward to become stimuli in the inhibitory control phase.

Feedback during this conditioning phase was not tied to participants actual guesses and thus all participants received an equal number of feedback outcomes (50% wins, 50% losses). Participants aged 8–21 completed two runs of the task. Each run consisted of 24 trials across six blocks (half were high stakes and half were low-stakes blocks); thus, each run was composed of six high-win outcomes, six low-win outcomes, six high-loss outcomes, and six low-loss outcomes.

CARIT: Inhibitory Control Phase

The inhibitory control phase assessed the extent to which previous value associations (from the conditioned phase) impacts response inhibition. This phase of the task uses a version of a classic Go/NoGo task in which participants are instructed to rapidly push a button to frequent Go targets but to withhold responses to infrequent NoGo targets. The NoGo stimuli are circles and squares, which were previously paired with value during the immediately preceding conditioning phase, and the Go stimuli are six different shapes that had not been seen previously. There were no monetary gains or losses associated with performance during this phase of the task.

Participants completed two runs, consisting of 136 Go trials and 48 NoGo trials (24 previously rewarded, 24 previously punished). Stimuli were presented in pseudorandom order for 600 msec followed by a jittered fixation inter-stimulus interval ranging from 1.0 to 4.5 s. The window for recording correct responses was 800 msec from the onset of the stimulus. Response inhibition was measured using accuracy to NoGo conditions.

Punishment and Reward Sensitivity

The Behavioral Inhibition Scale and the Behavioral Activation Scale (BIS/BAS; Carver & White, 1994; Pagliaccio et al., 2016) assessed self-reported punishment and reward sensitivity, respectively. In line with Pagliaccio et al. (2016), two versions of the BIS/BAS scale were used in the

current study, an adult version was provided to participants 18 years and older and a youth version was provided to participants 8 to 17. There are slight variations in the questions used in these versions in order to make them developmentally appropriate. For example, youth were asked ‘I am very fearful compared to my friends’ whereas adults were asked ‘I have very few fears compared to my friends’. Given that children and adolescents have difficulty with negatively-phrased questions (e.g., Heffer et al., 2021), this developmental modification is important. Pagliaccio and colleagues (2016) conducted a rigorous validation and demonstrated that the two scale versions can be merged. Participants under the age of 18 years also had a parental-report version of these scales, which were not used in the current study given that older participants did not have this version. In both versions of the questionnaires, seven items were used to assess BIS (e.g., “I worry about making mistakes”; $\alpha = 0.79$) and thirteen items were used to assess BAS (e.g., “I crave excitement and new sensations”; $\alpha = 0.86$). In the adult version, response options ranged from 1 (*very true for me*) to 4 (*very false for me*). In the youth version, the response options for this scale ranged from 0 (*not true*) to 3 (*very true*). In order to combine the youth and adult versions of the BIS/BAS, the adult scale was recoded to a 0 to 3 scale and reverse scored so that higher scores reflect higher BIS/BAS. Possible scores ranged between 0 and 21 for BIS and 0 and 39 for BAS.

Plan of Analysis

Age-related differences in (1) punishment and reward sensitivity, (2) overall accuracy, and (3) accuracy to cues previously associated with value

Although the primary goal of this study was to assess the relationship between individual differences in punishment/reward sensitivity, age, and accuracy in the context of cues previously associated with value, several analyses to characterize age-related differences in (1) punishment/reward sensitivity, (2) overall response inhibition, and (3) response inhibition to cues previously associated with value are reported first.

Previous research has shown both self-reported sensitivity to punishment (J. D. Gray et al., 2016; Grisanzio et al., 2023; Pagliaccio et al., 2016; Vervoort et al., 2019) and reward (Pagliaccio et al., 2016; Urošević et al., 2012) tends to increase from childhood into adolescence. An aim of this analysis was to complement these findings by assessing non-linear trajectories of age and by using a large representative sample spanning a wide developmental age range. To model the age-related differences in punishment and reward sensitivity, generalized additive models (GAM) with thin-plate regression splines were implemented using

the “gam” function from the *mgcv* package (v 1.8.42; Wood, 2017, 2019) in R (v 4.3.1; R Core Team, 2019). This modeling technique uses cross-validation procedures and penalizes complex models to prevent overfitting (Wood, 2003), resulting in a stable, smooth, data-driven curve that is not constrained to linear or polynomial shapes. The effective degrees of freedom (EDF) of a smooth term approximates the degree of an equivalent polynomial shape. An EDF value of 1 is roughly equivalent to a linear model, while values of 2 and 3 are equivalent to quadratic and cubic shapes, respectively and more complex curves have higher EDF values (Wood, 2017). Two separate models were run at the subject-level. Punishment and reward sensitivity were entered as the dependent variables and modeled as conditionally normal distributions. For both models, the spline of age was the independent variable to assess non-linear patterns in the data.

To model age-related differences in accuracy, generalized additive mixed-effects models (GAMM) with thin-plate regression splines were implemented using the “gam” function from the *mgcv* package (v 1.8.42; Wood, 2017, 2019). Response inhibition accuracy (proportion of correct NoGo out of total NoGo trials) was the dependent variable in these models and was modeled as a conditionally binomial distribution. Behavioral performance was modeled at the subject level, separately for each condition (previously rewarded, previously punished). A random effect of participants was included in both models to account for dependency in the data. In the first model, the spline of age was the independent variable. In the second model, the spline of age and value condition, a factor (dummy coded as 0 and 1) indicating whether the NoGo target was previously punished or rewarded, were the independent variables. A factor-smooth interaction was used to assess whether age trajectory varied by condition. The “plot_diff” function from the *itsadug* package (v 2.4.1 van Rij et al., 2022) was used to isolate the difference between the GAMM curves for each condition. A simultaneous 95% CI (with a resolution of 100) was computed around the curve to allow us to visualize and interpret the age interaction.

Relationship between individual differences in punishment and reward sensitivity, age, and accuracy difference between previously rewarded and previously punished cues

The primary aim of the study was to assess whether individual differences in punishment sensitivity and reward sensitivity interact with age to predict behavioral differences in response inhibition accuracy to cues previously associated with value. To address this goal, two separate models were run to assess whether (1) punishment sensitivity or (2) reward sensitivity modulates age-related differences in

accuracy to cues previously associated with value. Given that an interest in the current study was to assess the accuracy to previously rewarded cues *compared* to previously punished cues, a difference score (proportion correct previously rewarded - proportion correct previously punished NoGo trials) was created. A generalized additive model (GAM) with thin-plate regression splines was implemented using the “gam” function from the *mgcv* package (v 1.8.42; Wood, 2017, 2019). The behavioral performance for these analyses was modeled at the subject level.

To characterize potential nonlinear patterns of the interaction between two continuous variables, a 3D heat map was used to visualize the nature of the interaction (i.e., smoothing tensor, which fits a 3D functional plane) using the *isadug* package (v 2.4.1; van Rij et al., 2022). The difference score for accuracy was used to compare condition differences directly. Finally, the above analysis was repeated using BAS to assess whether reward sensitivity and age interact to predict differences in accuracy conditions (proportion correct previously rewarded – proportion correct previously punished cues).

Exploratory analysis: Relationship between punishment and reward sensitivity, age, overall response inhibition

In a follow-up exploratory analysis, whether individual differences in punishment sensitivity and reward sensitivity interact with age to predict behavioral differences in overall response inhibition accuracy, controlling for value condition was assessed. Although creating a difference score (as done in the previous analysis) allows for investigation of whether individuals have better relative accuracy to reward or punishment, difference score measures omit baseline differences in performance. Thus, additional exploratory analyses were conducted to assess whether individual differences in punishment and reward sensitivity interact with age to predict behavioral differences in overall response inhibition accuracy, controlling for value condition.

Results

Descriptive statistics for all study variables are listed in Table 1.

Age-related Difference in Punishment and Reward Sensitivity

The results from the first GAM revealed that punishment sensitivity showed a non-linear increase across age ($edf = 4.894$, $ref.df = 5.977$, $F = 51.64$, $p < 0.001$; see Fig. 2). To further inspect the age-related differences in punishment sensitivity, a post hoc analysis was used to identify

Table 1 Descriptive Table for Study Variables

Variables	Mean (SD)	Range
Age	14.29 (3.97)	8.01–21.99
Punishment Sensitivity	10.24 (4.28)	0.00–21.00
Reward Sensitivity	23.65 (6.51)	2.00–39.00
Accuracy (nogo)	0.66 (0.18)	0.06–1.00

windows where the slope of age-related change in punishment sensitivity is significant (see Grisanzio et al., 2023 for further details and <https://osf.io/42gba/> for the code). Specifically, the “derivatives” function in R’s *gratia* package was used to simulate confidence intervals for the derivatives (Simpson, 2023). Confidence intervals that do not include zero are indicative of windows of accelerated change (Grisanzio et al., 2023; Ruppert et al., 2003). This investigation revealed significant increases in punishment sensitivity during the age window of 15.49 and 19.17 years (see Fig. 2A).

Reward sensitivity showed a non-linear increase across age ($edf = 4.968$, $ref.df = 6.06$, $F = 32.92$, $p < 0.001$). To further inspect the age-related differences in reward sensitivity, a post hoc analysis was used to identify windows where the slope of age-related change in reward sensitivity is significant (as done in the previous analysis). This revealed significant increases in reward sensitivity during the age window of 16.20 and 19.17 years (see Fig. 2B).

Age-related Difference in Overall Response Inhibition

Analysis of task performance revealed that overall response inhibition accuracy increased with age in a primarily linear trajectory ($edf = 1.009$, $ref.df = 1.01$, $Chi.Sq = 552.2$, $p < 0.001$). Given that this trajectory was primarily linear, follow up post hoc analysis to identify windows of accelerated change were not necessary.

Age-related Difference in Response Inhibition to Cues Previously Associated with Value

A significant main effect of value condition on accuracy was found ($OR = 1.05$, $se = .02$, $p = 0.014$). In contrast to the Pavlovian Instrumental Transfer framework, results revealed that the odds of accurately withholding a response to the NoGo cue is 1.05 times greater for previously rewarded targets compared to previously punished targets. The factor-smooth interaction was significant, with the effect of age evident in both value conditions (Previous loss condition: $edf = 1.005$, $ref.df = 1.009$, $Chi.Sq = 417.6$, $p < 0.001$; Previous reward condition: $edf = 1.005$, $ref.df = 1.010$, $Chi.Sq = 493.0$, $p < 0.001$). Figure 3 shows the age-



Fig. 2 Age-related differences in punishment (A) and reward (B) sensitivity. The solid black line represents the non-linear model fit. The shaded blue region (punishment sensitivity) and purple region (reward sensitivity) depict the 95% confidence interval (CI). The interval

captured inside the dashed lines shows the window of accelerated change in the GAM. Punishment/reward sensitivity are presented along the y-axis and continuous age (in years) is plotted along the x-axis. Raw scores are depicted in the background

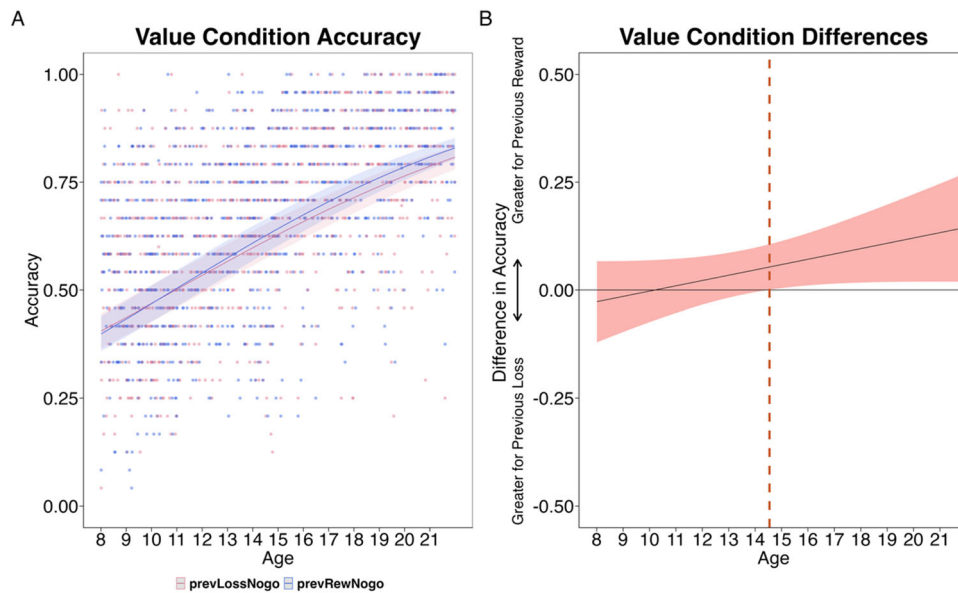


Fig. 3 A Age-related differences in response inhibition by condition. The solid lines represent the splines, plotted separately for each condition. The shaded regions depict the 95% confidence interval (CI). Accuracy is presented along the y-axis and continuous age (in years) is plotted along the x-axis. Raw scores are depicted in the background. prevLossNogo = NoGo targets that were previously associated with loss feedback; prevRewNogo = NoGo targets that were previously associated with reward feedback. B Age-related difference in response

inhibition to cues previously associated with value. The solid black line represents the condition differences in accuracy. The shaded red region depicts the 95% confidence interval around the difference. The dashed lines identify the age window where the 95% CI does not contain zero. Accuracy difference (previous reward – previous punished cues) is presented along the y-axis and continuous age (in years) is plotted along the x-axis

related trend in accuracy across the conditions and the difference between value conditions. The 95% CI around the accuracy difference was used to identify a significant difference in conditions for participants between the ages of 14.54 and 21.99. On average, participants within this age window were more accurate to previously rewarded compared to previously punished NoGo targets, an effect that grew with increasing age.

In order to further quantify the interaction, a follow-up analysis was conducted to assess how large the difference between conditions is at the youngest and oldest ages (8 and 21). The “predictions” command from the *marginaleffects* package (Arel-Bundock, 2023) was used to quantify the difference between the previous loss and previous win conditions across these age groups. Results from this analysis revealed that at age 8, the condition

difference in response inhibition was not significant ($M_{diff} = -0.006$, $SE = 0.009$, $p = 0.459$), whereas at age 21 the condition difference in response inhibition was significant, such that 21-year-olds were more accurate to previously rewarded than punished cues ($M_{diff} = 0.021$, $SE = 0.008$, $p = 0.007$). We next assessed whether the condition difference at age 21 was significantly different from the condition difference at age 8 (i.e., the difference of difference scores). The condition difference of accuracy between 21- and 8-year olds was significant ($M_{diff} = 0.028$, $SE = 0.014$, $p = 0.047$), whereby 21-year-olds had a significantly larger difference in accuracy between the conditions than 8-year-olds. Overall, the difference of differences scores on accuracy ($M_{diff} = 0.028$) is small.

Interaction with Punishment Sensitivity and Age to Predict Condition Differences in Response Inhibition

To examine whether individual differences in punishment sensitivity interact with age to predict differences in response inhibition accuracy to cues previously associated with value, a GAM was computed with accuracy difference (previous reward vs previous punishment) as the dependent variable and the interaction between age and punishment sensitivity, as well the main effect of age and the main effect of punishment sensitivity, were entered as predictors. None of the predictors in the model significantly predicted condition differences in accuracy: age ($edf = 1.000$, $ref.df = 1.000$, $F = 0.738$, $p = 0.390$), punishment sensitivity ($edf = 1.000$, $ref.df = 1.000$, $F = 0.662$, $p = 0.416$), the interaction between age and punishment sensitivity ($edf = 2.884$, $ref.df = 3.427$, $F = 1.315$, $p = 0.197$).

Interaction with Reward Sensitivity and Age to Predict Condition Differences in Response Inhibition

To examine whether individual differences in reward sensitivity interact with age to predict differences in response inhibition accuracy to cues previously associated with value, a GAM was computed with accuracy difference (previous reward vs previous punishment) as the dependent variable and the interaction between age and reward sensitivity, as well as the main effect of age and the main effect of reward sensitivity, were entered as predictors. None of the predictors in the model significantly predicted value condition differences in accuracy: age ($edf = 1.000$, $ref.df = 1.000$, $F = 0.662$, $p = 0.416$), reward sensitivity ($edf = 1.000$, $ref.df = 1.000$, $F = 1.302$, $p = 0.254$), interaction between age and reward sensitivity ($edf = 1.000$, $ref.df = 1.001$, $F = 0.014$, $p = 0.907$).

Exploratory Analysis: Interaction with Punishment Sensitivity and Age to Predict Overall Response Inhibition

To examine whether individual differences in punishment sensitivity interact with age to predict overall response inhibition accuracy, a GAMM was computed with accuracy as the dependent variable and the interaction between age and punishment sensitivity, as well as the main effects punishment sensitivity and age, were entered as predictors. Value condition was entered as a control variable and a random effect of participant was included in the model. Consistent with results reported above, value condition ($OR = 1.04$, $se = 0.02$, $p = 0.036$) and age ($edf = 1.001$, $ref.df = 1.001$, $Chi.Sq = 393.431$, $p < .001$) significantly predicted response inhibition. The overall effect of punishment sensitivity on accuracy was not significant ($edf = 1.431$, $ref.df = 1.501$, $Chi.Sq = 3.377$, $p = .198$). Findings revealed a significant punishment sensitivity-by-age interaction ($edf = 2.417$, $ref.df = 2.529$, $Chi.Sq = 8.458$, $p = 0.035$). A 3D heatmap was used to examine the interaction between these two nonlinear continuous variables (see Fig. 4). The heatmap shows that response inhibition accuracy improves across age, as reflected by the change from light to dark blue gradient across the x-axis. Accuracy is unrelated to punishment sensitivity in the oldest

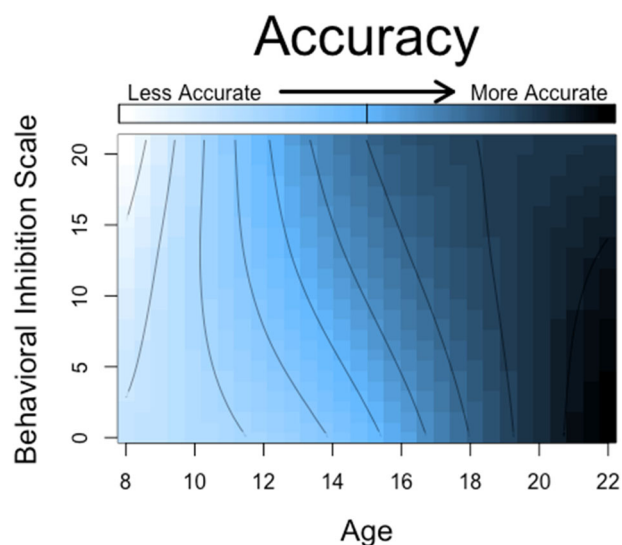


Fig. 4 Age-related effects of punishment sensitivity on overall response inhibition. The heatmap displays the fitted effects from the GAMM for both the main effects and interaction. Accuracy is represented by the color gradient, with lighter blue reflecting lower accuracy and darker blue reflecting higher accuracy. Age (in years) is represented on the x-axis and punishment sensitivity is along the y-axis. Participants are more accurate with increasing age, as reflected by the change from light to dark blue across the x-axis. During late childhood and adolescence, higher punishment sensitivity is associated with higher accuracy, as indicated by the change in color gradient from light to dark along the y-axis during this age period

individuals in the sample, as indicated by the homogeneity of color at all levels of punishment sensitivity on the right side of the heatmap. By contrast, during late childhood and adolescence, higher punishment sensitivity is associated with higher accuracy, as indicated by the change in color gradient from light to dark along the y-axis during this age period.

Although there appears to be a shift in the relationship between punishment sensitivity and accuracy across development— with young children high on punishment sensitivity being less accurate while emerging adults low on punishment sensitivity appearing more accurate— it is worth noting that this finding may be a product of the sparsity of data at the extreme ends of the heatmap. As shown above in Fig. 2, few children report extremely high levels of punishment sensitivity, while a few emerging adults report extremely low levels of punishment sensitivity. Thus, the apparent change in the relationship between punishment sensitivity and accuracy at the extreme ends of the age range in the heat map should be interpreted with caution, as this pattern of results may be more indicative of a developmental shift in punishment sensitivity (i.e., children are less likely to report high punishment sensitivity, but across age, higher levels of punishment sensitivity become more common). The interpretation of the heatmap in the current study is anchored on the assumption that those extreme points on the heatmap may be less reliable, given that they are based on few data points. Of note, with over 1000 participants, the current study does not lack statistical power; however, it would be beneficial for replication of this heatmap using a sample that targets more extreme scores on sensitivity to punishment to fill in the range of scores more completely.

Several additional analyses were run to investigate factors that might substantiate the finding that individual differences in punishment sensitivity interact with age to predict differences in overall response inhibition accuracy. One explanation for why punishment sensitivity may help facilitate response inhibition during adolescence is that higher punishment sensitivity is thought to be associated with more hypervigilant performance monitoring (i.e., increased alertness and cautious monitoring; J. A. Gray & McNaughton, 2000). To further probe this idea, the current study assessed whether other factors related to hypervigilance, such as slower more cautious reaction time and less impulsivity, also are associated with age-related differences in punishment sensitivity (see Supplemental materials). Of note, results revealed that age-related differences in punishment sensitivity were not associated with reaction time or impulsivity. Higher levels of punishment sensitivity, however, was associated with several dimensions of impulsivity, such as better planning ($edf = 2.097$, $ref.df = 2.662$, $F = 9.885$, $p < .001$) and perseverance ($edf = 3.314$,

$ref.df = 4.165$, $F = 3.895$, $p = 0.034$). See Supplemental Materials for full results.

Exploratory Analysis: Interaction with Reward Sensitivity and Age to Predict Overall Response Inhibition

To examine whether individual differences in reward sensitivity interact with age to predict overall response inhibition accuracy, a GAMM was computed with accuracy as the dependent variable and the interaction between age and reward sensitivity, as well as the main effects of reward sensitivity and age, were entered as predictors. Value condition was entered as a control variable and a random effect of participants was included in the model. Consistent with results reported above, value condition ($OR = 1.04$, $se = 0.02$, $p = 0.036$) and age ($edf = 2.254$, $ref.df = 2.380$, $Chi.Sq = 413.788$, $p < 0.001$) significantly predicted response inhibition. The overall effect of reward sensitivity ($edf = 1.170$, $ref.df = 1.200$, $Chi.Sq = 0.022$, $p = 0.935$) and the interaction between reward sensitivity and age were not significant ($edf = 3.802$, $ref.df = 4.094$, $Chi.Sq = 6.000$, $p = 0.248$).

Discussion

Research on the link between response inhibition to previously-incentivized cues across development has been both limited and mixed. Although the ability to process and learn from affective cues to guide goal-directed behavior may be particularly important at different stages of development (e.g., during adolescence), relatively little is known about the factors that promote and/or disrupt the ability to integrate value in order to guide decision making across age. The current study addressed this gap by investigating whether individual differences in punishment and reward sensitivity are differentially associated with response inhibition to cues that were previously associated with value across development. Participants completed the CARIT task, which is designed to assess how value-conditioned cues impact subsequent response inhibition. It was found that for adolescents and emerging adults, cues associated with a history of reward (compared to punishment) improved response inhibition— an effect that became stronger across age. Although self-reported sensitivity to punishment and reward were unrelated to differences in response inhibition to cues with value history (cues associated with reward – cues associated with punishment), the results revealed that punishment sensitivity predicted overall improved response inhibition accuracy between the ages of 10 and 18. Together, these findings provide novel insights into how the relationship between cognitive

control, value associations, and individual difference factors may change across development.

As a first step, this study examined age-related changes in self-reported punishment and reward sensitivity. Previous research has traditionally investigated linear relationships with these constructs across age (e.g., J. D. Gray et al., 2016; Urošević et al., 2012; Vervoort et al., 2019), showing that punishment and reward sensitivity tend to increase from childhood into adolescence. Notably, past research also has found that these constructs showed cubic relationships with age, characterized by rapid increases from childhood into adolescence until finally peaking in young adulthood (Pagliaccio et al., 2016). The current findings complement this research. Punishment and reward sensitivity were both characterized by non-linear trajectories that show a window of acceleration from mid-late adolescence. This pattern of results is consistent with research showing adolescence may be a period of development where the evaluation of *rewards and punishments* are increasingly becoming salient (e.g., Foulkes & Blakemore, 2016).

The current study found relatively linear age-related improvements in overall response inhibition. Although this is not a novel finding (Aïte et al., 2018; e.g., Luna et al., 2004; Wixted, 2018), it was important to verify that the task used in the current study was capturing expected age-related variability in cognitive control. Of interest, a significant, albeit small, improvement in response inhibition accuracy to previously rewarded compared to previously punished cues was identified, which started around 14 years old and grew increasingly with age. This rapid development of reward processing across adolescence is in line with other developmental work. For example, in a study assessing response inhibition to high and low rewards, across adolescence there was improved performance to high compared to low payouts, highlighting that improvements in the ability to use value to guide goal directed behavior improves throughout adolescence (Insel et al., 2017).

This finding also is in line with other work that has shown that *previously-rewarded* cues can improve response inhibition performance during adolescence (Insel et al., 2019). Although, another study (Winter & Sheridan, 2014) found that previously-rewarded cues improve response inhibition during adolescence, they also found this effect among children. This discrepancy may arise due to differences in tasks; Winter and Sheridan's task involved cartoon stimuli that may have been more rewarding to children than the shapes used in the current task, or the fractal stimuli used in the Insel and colleagues (2019) study. Collectively, these findings suggest that across adolescence cues associated with reward may be salient, and thus made detection and monitoring of this type of signal more readily available during response inhibition (Anderson & Yantis, 2013; Krebs et al., 2011). Results from prior work support this

notion, as research has shown enhanced recruitment in the visual cortex during the learning of previously high-rewarded cues (vs low-rewarded cues; Insel et al., 2019).

Although there is some support from previous literature that rewards may facilitate response inhibition, it is important to note that this past research has typically either compared (1) reward to neutral cues (e.g., Winter & Sheridan, 2014) or (2) high reward to low reward (e.g., Insel et al., 2019). Thus, it is not clear why cues associated with a history of reward improved response inhibition more strongly than cues with a history of punishment. In fact, according to the Pavlovian Instrumental Transfer framework, the opposite finding was expected—better performance in response to previously punished cues compared to previously rewarded cues because response inhibition behavior (i.e., not acting) aligns with the punish-avoid association. Therefore, adolescents and, to a greater extent, emerging adults seem to be overcoming the natural tendencies of Pavlovian Instrumental Transfer and performing better in the context of rewards compared to punishment.

There are a variety of different factors that might help explain the current results. First, it could be that cues with a history of punishment also are highly salient, but distracting. Indeed, many studies have found that distracting cues can impede goal-directed behavior (e.g., Anderson & Yantis, 2013; Cohen-Gilbert & Thomas, 2013; Padmala et al., 2011). An alternative explanation is that there may have been differences in how individuals originally encoded the conditioned neutral stimuli. Notably, during the conditioning phase, participants received feedback based on guesses that were not tied to behavioral skill. Thus, it could be that when participants were incorrect and received negative feedback, they were not overly concerned, given that the outcome is chance based and thus out of their control. Future research should assess whether reward and punishment processing during the conditioning phase relates to subsequent behavioral differences on the task.

Contrary to hypothesis, self-reported individual differences in punishment and reward sensitivity were not associated with differences in response inhibition to previously-incentivized cues. This analysis relied on a difference score, and thus it does not capture baseline differences in response inhibition (i.e., an individual who has high accuracy to both types of cues may have the same difference score as an individual who has low accuracy to both cue types). Further, the task used in the current study involved a subtle manipulation, whereby participants passively have the opportunity associate value with a once-neutral cue. It may be that this manipulation is not salient enough to be particularly concerning to individuals who have high reward/punishment sensitivity. Alternatively, it could be that both types of cues were salient to individuals with high punishment and reward sensitivity, and thus using a difference

score cancels out this effect. Future research would benefit from including neutral cue targets (in addition to the previously-rewarded and previously-punished cues) in the CARIT task to help tease apart these explanations.

Self-reported punishment sensitivity, however, was associated with *overall* improved response inhibition accuracy, specifically during late childhood and adolescence. This finding aligns with previous work showing that punishment sensitivity is associated with hypervigilant performance monitoring and overcontrolled behavior, factors that improve response inhibition accuracy (Heffer et al., 2023; Lamm et al., 2014; White et al., 2017). Punishment sensitivity may allow youth to rapidly detect cues in the environment to ensure safety (J. A. Gray & McNaughton, 2000), which may be particularly important during adolescence when exploration and learning from new contexts is critical.

Several additional analyses were run to investigate if other factors related to hypervigilance/ performance monitoring (e.g., reaction time and impulsivity) might be associated with punishment sensitivity across development. Reaction time was not found to be associated with age differences in punishment sensitivity. This is interesting, as it suggests that the pattern of results observed in the heat map are likely not due to youth with higher punishment sensitivity slowing down their responses. Impulsivity also did not interact with age to predict punishment sensitivity. Several dimensions of impulsivity, however, such as better planning and perseverance, were associated with higher levels of punishment sensitivity. Therefore, individuals who have higher punishment sensitivity may have some characteristics of lower impulsivity, which could help improve performance on a response inhibition task. Yet, this account does not explain the *age differences* in punishment sensitivity and response inhibition found in the current study. This finding might better be explained by an age-related shift in punishment sensitivity, with younger children rarely reporting high levels of punishment sensitivity, while emerging adults rarely reported low levels of punishment sensitivity. Thus, there may be less variability in punishment sensitivity during these age periods. Future research is needed to help substantiate this finding.

While there are several strengths of this study, including a large developmental sample, the experimental design, and the consideration of non-linear age-related differences in the key study variables, there are also limitations. First, this study is cross-sectional. Future research should leverage longitudinal designs in order to assess within-person change in how self-report measures of punishment and reward sensitivity are associated with the relationship between value history and response inhibition across development.

Second, the current study does not include a baseline condition where participants are asked to withhold their response to affectively neutral cues. Thus, the current study was unable to determine whether the history of value impacts performance *relative to baseline*. For example, it could be that both history of reward and punishment improve response inhibition relative to a neutral cue, but that cues with reward history did so to a greater extent.

The manipulation used in the current study is quite subtle by design. The current study focused on age differences in passive associations; thus, participants were not given any instructions to attend to the reward/punishment associations in the conditioning task, nor did the current study test whether participants learned the conditioned pairings. It was not feasible to include a test of learning in the already large battery of assessments included in the HCP-D study. Although previous research using the CARIT task has found that participants explicitly report learning these pairings (e.g., Davidow et al., 2019), the current study cannot confirm that the cues were learned explicitly, but rather the objective was to test the degree to which the availability of these passive associations impacted future behavior.

Of note, in the current study participants were not asked to self-report their subjective value of the feedback. Prior work, however, has not found age-related differences in subjective report of valence or arousal to monetary outcomes (Insel et al., 2017; Insel & Somerville, 2018). Additionally, in a separate study using the CARIT task, self-report ratings were collected to assess whether a conditioned high-reward shape has greater subjective importance than a conditioned no-reward shape across participants aged 8 to 25 (a wider sample than the current study; Davidow et al., 2019). Critically, this prior work found that participants rated the high-reward cue to be more valuable than the no-reward cue, and this effect did not differ across age. Thus, previous research suggests subjective assessment of monetary value is consistent from childhood into emerging adulthood.

Finally, given the subtlety of the manipulation used in the current study, it would be interesting for future research to manipulate the salience of the stimulus-value pairing during the conditioning phase. For example, adjusting the colour or thickness of the lines on the once-neutral cues would draw more attention to the cue. This would help tease apart whether attentional processes are important for understanding this relationship. Alternatively, the current study used monetary feedback during the conditioning phase; it would be interesting to assess how social feedback (e.g., happy and sad faces), which is thought to be particularly salient for adolescents, might differentially impact response inhibition.

Conclusion

Past research assessing the impact of previously-incentivized cues on response inhibition is inconsistent and often has not considered individual differences factors, which is necessary to gain a more comprehensive understanding of the ways in which cues associated with value differentially impact goal-directed behavior across development. The current study provides an important large-scale investigation of the link between previously-rewarded and punished cues, individual differences in punishment and reward sensitivity, and response inhibition across development. The current results highlight two main factors that are associated with improvements in response inhibition—cues in the environment (e.g., reward-laden cues) and individual differences in punishment sensitivity. The findings from this study offer a novel investigation linking individual differences in punishment sensitivity and passive value associations to age differences in goal-directed behavior. Given that adolescence is a time of intense learning and exploration, the ability to detect value and integrate it into future decision-making is fundamental for navigating this phase of development. Ultimately, distinguishing the contexts in which adolescents are able to navigate this skill successfully can have implications for both educational and social policies that promote the well-being of youth.

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Authors' Contributions TH conceived of the study, performed the statistical analysis, created visualizations, and drafted the manuscript; JF participated in data curation, methodology, statistical analyses, and helped draft the manuscript; GB participated in the statistical analysis, methodology, and helped draft the manuscript; LS coordinated, designed, and conceived the study, participated in data curation, statistical analyses, funding acquisition, study supervision and helped to draft the manuscript. All authors read and approved the final manuscript.

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Data Sharing Declaration HCP-D data are publicly available as part of the National Institute of Mental Health Data Archive: <https://nda.nih.gov/>. The analysis code can be found at <https://osf.io/42gba/>.

Compliance with ethical standards

Conflict of Interest The authors declare that they have no conflict of interest.

Ethical Approval The Institutional Review Board at Washington University in St Louis (IRB #201603135).

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