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Neurobiological responses in the adolescent striatum to being 'tested'

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Abstract

While emerging research implicates the striatum in adolescents' ability to learn from feedback, little is known about how motivational contexts, such as emphasizing the evaluative nature of learning tasks, modulate adolescents' striatal learning. We used functional magnetic resonance imaging during a feedback-based learning task, in conjunction with a within-subject evaluative threat manipulation, to determine whether evaluation threat influences behavioral and neural responses to feedback in adolescents. On average, adolescents were less sensitive than adults to the evaluation threat. In the adolescents, the effect of evaluation threat on performance was tracked with the striatal response to performance feedback during the evaluation threat condition, such that greater striatal sensitivity correlated with greater gains in learning performance. Our findings suggest that variability in how adolescents respond to a contextual threat of evaluation and associated striatal sensitivity can facilitate enhanced learning.

Key words: adolescents; learning; striatum; evaluation

Introduction

Learning is a major developmental task during adolescence, when youth must develop the knowledge and abilities they need to succeed in increasingly challenging academic domains. The ability to learn from informative feedback allows students to persist when their knowledge and study strategies are appropriate and to change course when they learn that they are wrong. Animal and human studies have established a prominent role for the striatum in learning from reinforcing outcomes (O'Doherty *et al.*, 2004; Niv, 2009), including informative feedback (e.g. Tricomi *et al.*, 2006; Satterthwaite *et al.*, 2012). Emerging evidence suggests that the striatum underlies feedback-based learning during adolescence (Peters and Crone, 2017), but how motivational contexts, such as the presentation of a task as a learning opportunity *vs* as an evaluation, modulate striatal learning remains unexplored.

Informative feedback about whether an individual choice was 'correct' or 'incorrect' elicits similar responses as rewards and punishments in the striatum (Tricomi *et al.*, 2006; Satterthwaite *et al.*, 2012). In adults, such responses can be modulated by individual differences in expectations and achievement goals, suggesting that the intrinsic value of learning outcomes may have reinforcing properties (DePasque Swanson and Tricomi, 2014; DePasque and Tricomi, 2015). During adolescence, striatal sensitivity to rewarding outcomes is heightened compared to childhood and adulthood, a developmental distinction that has been posited to underlie differences in adolescent decision-making (Galvan, 2013). Research further suggests that adolescents are more sensitive than adults to changing monetary value, taking greater risks in pursuit of increasingly valuable monetary outcomes (Barkley-Levenson and Galvan, 2014). However, it remains unclear whether they might show similarly heightened sensitivity to variations in the intrinsic value of non-monetary outcomes. In educational settings, it is often not possible to pair informative feedback with extrinsic reinforcers (i.e. money), and, moreover, it has

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been argued that extrinsic rewards can undermine intrinsic motivation for learning (Ryan and Deci, 2000). Although extrinsic incentives can also contribute to performance outcomes and do not always adversely affect intrinsic motivation, e.g. when the task at hand is not itself intrinsically enjoyable (Cerasoli et al., 2014), it is nonetheless important to understand how the affective salience of informative feedback might modulate adolescent learning systems in the absence of monetary incentives. In a learning context, the subjective value and learning efficacy of informative feedback might be modulated by the evaluative context in which learning takes place.

Because ongoing changes to corticostriatal circuitry influence adolescent sensitivity to emotionally heightened situations (Blakemore and Robbins, 2012; Crone and Dahl, 2012), it is possible that adolescents might evince developmentally distinct learning in situations with affectively charged outcomes; for instance, when participants are told that their performance is being evaluated and their abilities are being ranked compared to their peers. Prior research in adults suggests that striatal responses differentiate between positive and negative feedback when the evaluative aspect of negative feedback is emphasized and less so when it is perceived as merely informative (Lempert and Tricomi, 2016). If the threat of evaluation increases the affective salience of performance-related feedback, then adolescents might exhibit increased striatal sensitivity to positive *vs* negative feedback. For adolescents, threat of evaluation might modulate striatal sensitivity to feedback valence that could plausibly influence learning.

Striatal sensitivity to the informative value of feedback peaks during late adolescence (Peters and Crone, 2017), and striatal sensitivity to feedback valence peaks during mid-adolescence (Satterthwaite *et al.*, 2012). Furthermore, whereas children's and adolescents' learning depends primarily upon direct experience, in adulthood, task instructions can override the information provided by trial-and-error outcomes (Decker *et al.*, 2015). Together, the heightened reactivity of the adolescent striatum and behavioral observations of more experientially driven learning in youth suggests that learning may be more closely tied to striatal mechanisms in adolescents than in adults, for whom later-maturing cortical mechanisms facilitate the use of additional learning strategies and enhanced executive functioning (Luna *et al.*, 2004; Peters *et al.*, 2014). These findings support the hypothesis that the reinforcing properties of informative feedback might confer learning benefits during adolescence. However, more evidence is needed to establish whether striatal-based motivation drives learning to a greater extent in adolescents compared to adults.

The present study used functional magnetic resonance imaging (fMRI) to determine whether the affective context of evaluation threat influences behavioral and neural responses to feedback for early to mid-adolescents *vs* an adult comparison group. We used a feedback-based learning task that reliably engages the striatum in adults in an analogous manner to rewards and punishments, with positive feedback resulting in increased activation relative to negative feedback (Tricomi and Fiez, 2008; DePasque Swanson and Tricomi, 2014). In conjunction with the learning task, we also manipulated the affective salience of the feedback across blocks of trials by inducing the threat of evaluation during only some portions of the task. This approach has been shown to increase affective responses to negative feedback and interfere with learning in adult participants (Mangels *et al.*, 2011). We hypothesized that differences in striatal responses to evaluation would modulate learning to a greater extent in adolescents relative to adults.

Method

Participants. A total of 63 participants completed the fMRI study, including adolescents ages 11–16 (mean age, 14.37 years; $n = 32$; 17 female) and a comparison group of adults ages 23–30 (mean age, 26.19 years; $n = 31$; 17 female). Participants were recruited from the Los Angeles area via an existing database as well as advertisements in youth-friendly locations and online. All provided written consent and assent in accordance with the Declaration of Helsinki (1991; p. 1194) as approved by the university's institutional review board. To minimize motion, we implemented and established developmentally appropriate methods (Galván *et al.*, 2012), including acclimating participants to a mock scanner and breaking the scan into four short (~5 min) runs. We lost no data to excess motion (a max motion of <2.5 mm). A single fMRI run from one adult participant was unusable due to a software logging error, and one adult participant whose performance reached ceiling was excluded from contrasts involving negative feedback due to an absence of incorrect trials. Sample size was predetermined based on funding constraints and prior studies investigating feedback-based learning (Tricomi and Fiez, 2008; DePasque and Tricomi, 2015) and was similar to recent developmental studies comparing adolescents and adults on learning tasks (Somerville *et al.*, 2011; Davidow *et al.*, 2016; Insel *et al.*, 2017; Potter *et al.*, 2017).

Experimental task. Participants performed a word association learning task previously shown to engage the striatum in adults (Tricomi and Fiez, 2008; DePasque and Tricomi, 2015). On each trial, participants were instructed to associate a word with one of two options presented below it (Figure 1). Participants studied 170 distinct (non-repeating) word pairs, presented across 3 phases: a pre-scan Study Phase, in which the correct match for each target word was highlighted; a scanned Feedback Learning Phase, in which participants selected one option and received feedback about whether their choice was correct or incorrect; and an immediate post-scan Test Phase, in which participants again selected the match for each word. During each phase, the trials were randomized and the two options were randomly assigned to either the first or second position.

During the pre-scan Study Phase, participants observed the trials with correct answer highlighted, without making a response (4 s per trial). The 20 min Feedback Learning Phase was scanned using fMRI to observe brain responses to the feedback during learning. During the scanned Feedback Learning Phase, a subset of 112 trials was presented across 8 blocks of trials (14 trials/block). Participants had 4 s to select an answer using an MRI compatible button box.

Following the 4 s stimulus presentation, a brief jittered delay of 0–1.5 s preceded a 1.25 s feedback screen, which displayed a green checkmark for correct responses or a red X for incorrect responses. Between trials, a jittered inter-trial fixation cross of 2–4.5 s followed feedback presentation. This task had consistently elicited striatal responses to positive > negative feedback in prior studies of adult feedback processing and was pilot tested to ensure that it was comprehensible for youth. After the Feedback Learning Phase, participants exited the scanner and submitted their final answer for each pair during the Test Phase.

Evaluation threat 'testing' manipulation. Within subjects, we varied the threat of evaluation across blocks of trials by manipulating the instructions preceding each block (Mangels *et al.*, 2011). At the start of the task, a recorded introduction was played aloud, in which a male voice told participants that word association learning abilities are known to be important for school and

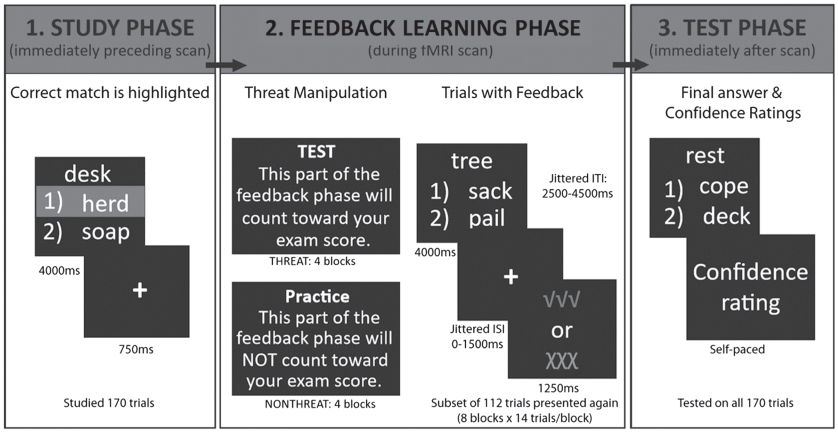

Fig. 1. Task schematic.

career success and that the purpose of the study is to examine brain processes that underlie these abilities to learn what makes some people better at word association learning compared to others. On half of the trials, we induced a threat of evaluation by instructing participants that some portions of the Feedback Learning Phase would count toward their exam score ('TEST'), while others would be unscored ('PRACTICE'). The test condition was designed to increase the affective salience of positive and negative performance feedback, while the practice condition encouraged participants to work on their learning strategies. To minimize differences in effort across conditions, participants were instructed not to begin each block until they felt prepared to 'concentrate and give a genuine effort' on the task. The scanned Feedback Learning Phase was divided into blocks of 14 trials, each starting with an instruction screen providing the test or practice context. Each participant experienced eight alternating test and practice blocks, presented in semi-random order such that one block from each condition would be completed in each scanning run.

Achievement test. During an intake visit conducted ∼1 week before the fMRI scan, participants completed the reading subscales of the Wide Range Achievement Test (WRAT-4; Wilkinson *et al.*, 2006), a brief but well-validated assessment. To control for differences in verbal proficiency that might influence word association task performance across participants, the standardized reading composite score was included as a covariate in analyses.

Intrinsic Motivation Inventory. To assess motivation, we administered two subscales of the Intrinsic Motivation Inventory (Ryan, 1982), a multidimensional measure of subjective experiences during a laboratory task. The subscales we used were interest/enjoyment (7 items, e.g. 'I enjoyed doing this activity very much') and effort/importance (5 items, e.g. 'I put a lot of effort into this'). Participants rated each item on a scale from 1 (not at all true) to 7 (very true), and average subscale scores were computed for each participant to investigate whether the effects of the test manipulation correlated with task motivation.

Data collection and analysis. Experiments were presented using E-prime (PST, Pittsburgh, PA). Task performance was defined as the percentage of correct responses during the learning and test phases, excluding non-responses. fMRI data acquired during the Feedback Learning Phase were preprocessed and analyzed using FSL (www.fmrib.ox.ac.uk/fsl), including brain extraction, MCFLIRT motion correction, spatial smoothing (5 mm, FWHM), high-pass temporal filtering and spatial normalization to Montreal Neurological Institute templates.

Scanning parameters. Scanning was conducted at UCLA's Staglin IMHRO Center for Cognitive Neuroscience on a 3-Tesla scanner. Some participants were scanned following a 'PrismaFit' upgrade of the Siemens Trio gradient hardware, but all scanning parameters were held constant and group-level analyses included scanner as a covariate of no interest. Parameters for functional image acquisition were as follows: TR, 2000 ms; TE, 30 ms; FoV, 192 mm; voxel size, 3.00 × 3.00 × 4.00 mm. For anatomical registration, we collected an MPRAGE structural scan: TR, 1900 ms; TE, 2.26 ms; FoV, 250 mm; slice thickness, 1 mm; 176 slices.

Whole-brain analysis. After preprocessing, fMRI data were analyzed using random effects general linear modeling (GLM), crossing test condition (TEST/PRACTICE) with feedback valence (positive/negative) for each age group (adults/adolescents). Analyses focused on activation at the time of feedback presentation in each of the task conditions, modeled as a stick function at the time of feedback onset and convolved with a double-gamma hemodynamic response function. Non-response trials, the period between trial onset and response, and six motion parameters and their derivatives were included in each model as predictors of no interest.

Separate GLM models probed the effects of (i) feedback valence (positive *vs* negative) and (ii) the interaction of test condition × valence (valence sensitivity under test compared to practice). At the group level, all analyses included scanner (pre- *vs* post-upgrade), WRAT reading scores and number of incorrect responses made during the scanned Feedback Learning Phase, mean centered, as covariates of no interest. WRAT scores were included as a measure of verbal proficiency to control the potential differences in ability to form word-pair associations, while the number of incorrect responses during the scan was included to control the frequency of negative feedback, since frequency of a particular outcome can affect striatal processing of outcome prediction error, as well as differences in ability to initially acquire the associations during the pre-scan Study Phase. These contrasts were compared across age groups, and additional analyses included age (in years) as a continuous covariate.

Regions of interest analyses. Due to our interest in affective modulation of learning in the striatum, we extracted parameter estimates from 4 mm spherical a priori regions of interest (ROIs) in the head of the caudate nucleus, which has been

Table 1. Task performance

Task performance	Age group	Mean, %	s.d., %	Between group comparison
Scanned Feedback Learning Phase	Adolescents	69.54	11.88	$t(61) = 1.86$, $P = 0.07$
	Adults	75.61	13.99	
Post-scan Test Phase (only feedback items)	Adolescents	78.26	12.33	$t(61) = 1.60$, $P = 0.115$
	Adults	83.17	12.05	
Post-scan Test Phase (no feedback)	Adolescents	69.77	13.66	$t(61) = 2.32$, $P = 0.024$*
	Adults	77.41	12.47	

*Significant at $P < 0.05$

previously implicated in feedback-based learning (e.g. Tricomi *et al.*, 2006), and the nucleus accumbens, which is often implicated in adolescent-specific changes in sensitivity to outcome value (Galvan, 2010). To avoid inflated correlations that arise when using ROIs defined based on a functional contrast of interest, we identified the peak coordinates associated with the anatomical terms 'caudate' (http://www.neurosynth.org/analyses/terms/caudate/; −8,10,8/12,10,12) and 'accumbens' in the Neurosynth meta-analytic database (http://www.neurosynth.org/analyses/terms/accumbens/; −10,10,−12/12,12,−10. Spheres centered on these peak coordinates were combined to form bilateral ROIs.

We used repeated-measures ANCOVAs to test whether parameter estimates from each bilateral ROI differed as a function of test condition or age group. As in the whole-brain analyses, ROI analyses controlled for scanner, WRAT reading scores and number of wrong answers during feedback learning. Furthermore, to probe the relation between striatal activation and learning on the task, we examined correlations between feedback learning score (percentage gain from Feedback Learning Phase to Test phase) under the test *vs* practice condition (TEST–PRACTICE) and ROI sensitivity to feedback valence (positive–negative feedback) under the test *vs* practice condition (TEST–PRACTICE valence sensitivity).

Results

Behavioral findings

Task performance. Task performance during the Feedback Learning Phase and post-scan Test Phase is summarized in Table 1. During the scanned Feedback Learning Phase, adults performed non-significantly better than the adolescents, $t(61) = 1.86$, $P = 0.068$. On the post-scan Test Phase, for items presented during both the study and feedback learning phases, performance was similar across the two groups, $t(61) = 1.60$, $P = 0.115$. However, adults outperformed adolescents on items that they had previously studied but which were not repeated during the scanned Feedback Learning Phase of the experiment, $t(61) = 2.32$, $P = 0.024$.

Learning from feedback. To quantify the amount learned from feedback, we calculated a learning score for each subject by subtracting the percent of items answered correctly during the scanned Feedback Learning Phase from the percent of items answered correctly on the post-scan Test Phase.

$$\text{Learning Score} = \text{Test Phase}\%\text{correct}^{*} - \text{Feedback Learning Phase}\%\text{Correct}$$

*Only items presented during Feedback Learning Phase (opportunity to learn from feedback)

Adolescents and adults exhibited similar learning from feedback, evidenced by similar learning scores [adolescents: mean (s.d.), 8.72 (5.90%); adults: mean (s.d.), 7.57 (5.81%); $t(61) = 0.78$; $P = 0.438$]. In other words, adolescents and adults learned equally from feedback, in spite of the slight, non-significant advantage adults initially exhibited after observing the word pairs in the pre-scan Study Phase.

Evaluation threat manipulation. Because the evaluation threat manipulation was not introduced until after the pre-scan Study Phase, we did not expect the manipulation to influence accuracy during the scanned Feedback Learning Phase. Consistent with this expectation, test condition did not affect task performance during the scanned Feedback Learning Phase, for either adolescents [TEST: mean (s.d.), 70.60 (12.42%); PRACTICE: mean (s.d.), 68.45 (12.59%); $t(31) = 1.55$; $P = 0.131$] or for adults [TEST: mean (s.d.), 75.62 (13.52%); PRACTICE: mean (s.d.), 75.61 (15.44%); $t(31) = 0.004$; $P = 0.997$].

Because the ability to learn from feedback might be affected by the threat of evaluation, we predicted that effects of test condition on performance would manifest in choice accuracy during the post-scan Test Phase, particularly with respect to items that had been answered incorrectly during the scan, since (i) threat of evaluation should particularly influence the subjective experience of negative feedback as evaluative and therefore punishing, rather than merely informative (Mangels *et al.*, 2011; Lempert and Tricomi, 2016); and (ii) it is negative feedback that signals the need to learn a new association, whereas positive feedback indicates that the correct word pair has already been selected. Both positive and negative feedback provide equivalent amounts of information (i.e. with only two choices present, either type of feedback allows the participant to know the correct response) and are therefore both equally 'useful'; nevertheless, a proportion of positive feedback trials likely represent word pairs for which participants confidently recalled the correct answer. Figure 2 illustrates Test Phase performance for items resulting in positive and negative feedback under the test *vs* practice conditions. For adolescents, error correction did not differ as a function of test condition, $t(31) = 1.29$, $P = 0.207$; for adults, error correction was significantly reduced under test compared to practice, $t(29) = 2.86$, $P = 0.008$. That is, for adults, the proportion of items corrected after receiving negative feedback was significantly lower under test (59.19%) *vs* practice (69.26%).

To directly test whether the effect of test condition on Test Phase performance differed by age group, we conducted a 2 × 2 × 2 repeated measures ANCOVA, with test condition (test *vs* practice) and feedback valence (positive *vs* negative) as within-subject variables and age group (adults *vs* adolescents) as a between-subjects variable, controlling for WRAT score and the number of items answered incorrectly during the scanned Feedback Learning Phase.

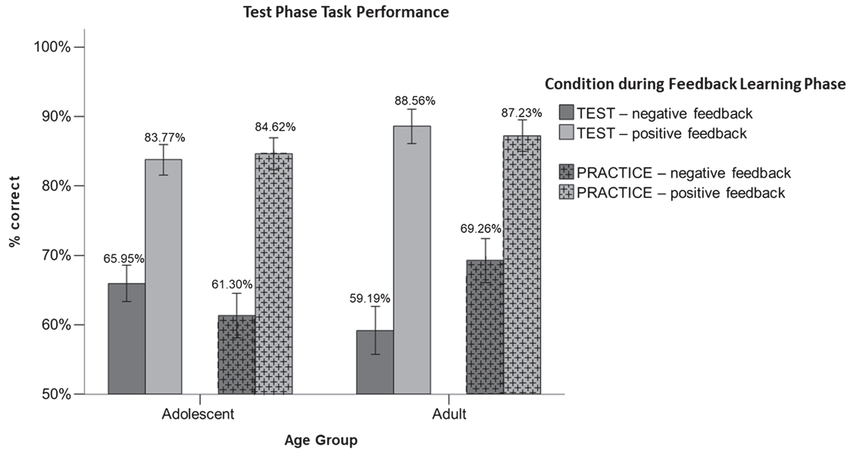

Fig. 2. Task performance (percentage of correct responses) during the post-scan Test Phase, for four learning conditions: items previously answered correctly *vs* incorrectly under the test *vs* practice conditions of the scanned Feedback Learning Phase.

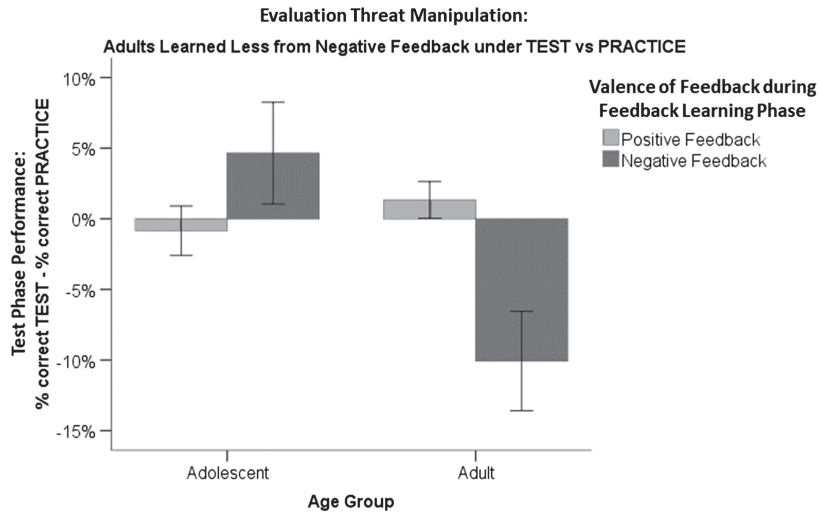

Fig. 3. Effect of test condition (TEST–PRACTICE) on task performance (% correct) during the post-scan Test Phase, for items initially answered correctly *vs* incorrectly.

The test condition × age group interaction was significant, $F(1,58) = 5.53$, $P = 0.022$, indicating that the effect of test condition on performance was greater in adults, as was the test condition × valence × group interaction, $F(1,58) = 13.21$, $P = 0.001$, such that, within the adult group, the test condition effect on performance was greater for items that had resulted in negative feedback during the scanned Feedback Learning Phase. In other words, adults learned less from negative feedback (incorrect responses) under TEST *vs* PRACTICE (Figure 3).

When the same ANCOVA was run with age as a continuous variable, rather than categorical, the test condition × age interaction was not significant, $F(1,58) = 3.73$, $P = 0.058$; however, the test condition × valence × age interaction was significant, $F(1,58) = 9.14$, $P = 0.004$, suggesting that age differences in the effects of threat are particularly evident in trials that resulted in negative feedback during the scanned Feedback Learning Phase.

Intrinsic motivation and test effect. Post-task motivation ratings correlated positively with the effect of the test manipulation on performance, such that participants who expressed (i) higher interest/enjoyment for the task and (ii) greater effort/importance of performing well performed better under the TEST than PRACTICE blocks [TEST: $r(61) = 0.26$, $P = 0.044$; PRACTICE: $r(58) = 0.335$, $P = 0.009$]. In other words, highly motivated participants showed performance gains under the TEST condition relative to PRACTICE.

Reaction time. The participants exhibited no differences in reaction time across the test *vs* practice conditions, $t(62) = -0.76$, $P = 0.449$, so there is no behavioral evidence that effort varied across conditions.

fMRI findings

Whole brain. Consistent with previous findings in adults (DePasque and Tricomi, 2015), whole-brain analyses revealed a network of regions that exhibited significantly greater activation during positive > negative feedback, including the dorsal and ventral striatum, medial prefrontal cortex, anterior and posterior cingulate cortex, precuneus, hippocampus and amygdala (Figure 4). Adolescents and adults engaged a highly similar network of brain regions during feedback processing, suggesting that despite adults' non-significantly better performance during the scanned Feedback Learning Phase, both groups engaged similarly with feedback during the task.

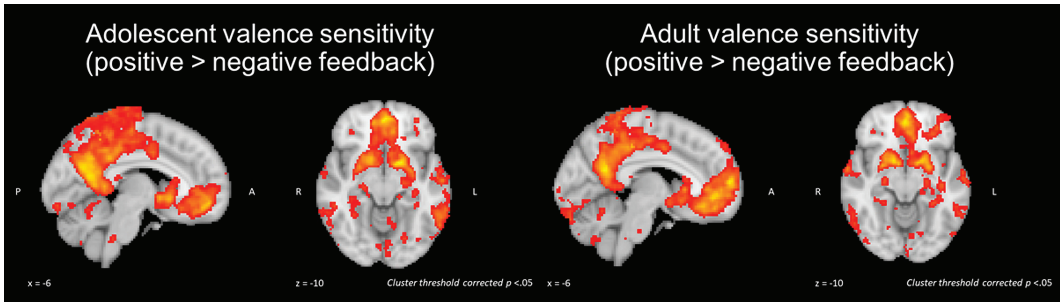

Fig. 4. Whole-brain results indicate that adults and adolescents show similar valence sensitivity across regions including the ventral striatum, caudate nucleus, medial prefrontal cortex, posterior cingulate, hippocampus and amygdala. Within each age group, analyses controlled for scanner, WRAT score and number of incorrect responses. Images were thresholded non-parametrically using clusters determined by $z > 3.1$ and a corrected cluster significance threshold of $P = 0.05$.

Direct comparisons of the adult *vs* adolescent participants revealed no regions in which activation to positive > negative feedback differed between groups. When age was entered as a continuous covariate, no regions showed significant modulation of positive > negative feedback activation by age.

Test condition. To determine whether test condition influenced sensitivity to feedback valence, we next conducted whole-brain analyses to identify regions where sensitivity to positive > negative feedback was greater under the TEST condition *vs* the PRACTICE condition. In this whole-brain analysis, the striatum did not exhibit significant effects of test condition on valence sensitivity. For effects of test condition that were identified outside of the striatum, see supplemental results.

Brain–behavior correlations. Across the whole sample, the effect of evaluation threat on valence sensitivity correlated positively with the effect of threat on learning scores in the dorsal anterior cingulate cortex and the postcentral gyrus (see supplemental results). Although no significant age differences in this brain–behavior correlation survived cluster threshold correction, an exploratory uncorrected analysis revealed stronger brain–behavior correlations in the adolescents compared to adults in the striatum, specifically the caudate nucleus and posterior putamen (Supplementary Figure S1).

ROI ANCOVA. We used ROI analyses to increase power for detecting relationships between task performance and activation in the striatal feedback learning system. To determine if the effects of age group and test condition that we observed on task performance were mirrored in striatal responses to feedback, we examined parameter estimates from a priori bilateral striatal ROIs in the caudate and nucleus accumbens (Figure 5). Controlling for scanner, WRAT scores and number of wrong answers, we found that the test condition (test *vs* practice) × age group (adolescent *vs* adult) interaction was significant in bilateral caudate, $F(1,57) = 4.57$, $P = 0.037$, and nucleus accumbens, $F(1,57) = 4.17$, $P = 0.046$. In both the caudate and nucleus accumbens, adults showed decreased activation under threat compared to non-threat. The test condition × age group × valence interaction was not significant in either caudate, $F(1,57) = 0.85$, $P = 0.362$, or nucleus accumbens, $F(1,57) = 0.001$, $P = 0.980$.

ROI correlations. On average, adolescents did not exhibit an overall effect of test condition on learning. However, individual differences in susceptibility to the manipulation correlated with individual differences in the effect of the manipulation on striatal feedback responses (Figure 6). Results are reported with one adult outlier winsorized, for whom the test effect on learning was more than three s.d.s below the mean. We controlled for scanner, WRAT scores and number of wrong answers using partial correlations. For adolescents, greater feedback sensitivity in bilateral caudate/nucleus accumbens under TEST > PRACTICE corresponded with greater learning scores under TEST > PRACTICE [$r(27) = 0.37$, $P = 0.046$/$r(27) = 0.41$, $P = 0.027$]. In other words, while test condition did not exert a uniform effect on performance or brain activity for adolescents as a group, adolescents whose learning was modulated by test condition exhibited corresponding effects of test condition on striatal sensitivity to feedback valence. These correlations did not approach significance in the adult age group, either for caudate, $r(25) = -0.15$, $P = 0.458$, or accumbens, $r(25) = 0.10$, $P = 0.617$.

Age differences in ROI correlations. A Fisher's r-to-z transformation was used to test whether the significant correlations in adolescents were significantly stronger than the null relationships observed in the adult age group. In the accumbens, correlations did not differ significantly between groups, $z = 1.25$, $P = 0.211$; however, in the caudate, the correlation between test effects on learning and test effects on feedback sensitivity was significantly stronger in adolescents compared to adults, $z = 2.03$, $P = 0.042$.

Discussion

Using feedback to guide performance is a crucial aspect of learning. In this study, we (i) reveal the neurocognitive mechanisms subserving the capacity to use feedback-based learning to improve performance in adolescents and (ii) demonstrate adolescent-unique individual differences in affective influences on striatal feedback responses, relating to the degree to which the threat of evaluation influenced learning. Whereas adults exhibited an overall decrease in ability to learn from negative feedback under the threat of evaluation, only the adolescent group exhibited a coupling between the effects of evaluation threat on striatal sensitivity to feedback and the ability to learn from feedback. Adolescents who showed greater striatal feedback engagement during test blocks learned more from those blocks than practice blocks, whereas the reverse pattern was seen for those who showed stronger striatal sensitivity during practice blocks. Our results support the hypothesis that adolescence may be a time when engagement of the striatal learning system via the reinforcing value of feedback can be leveraged into performance gains during learning.

Adolescents and adults learned similarly from feedback, a process that engaged a network of regions in both groups that has been previously implicated in feedback-based learning

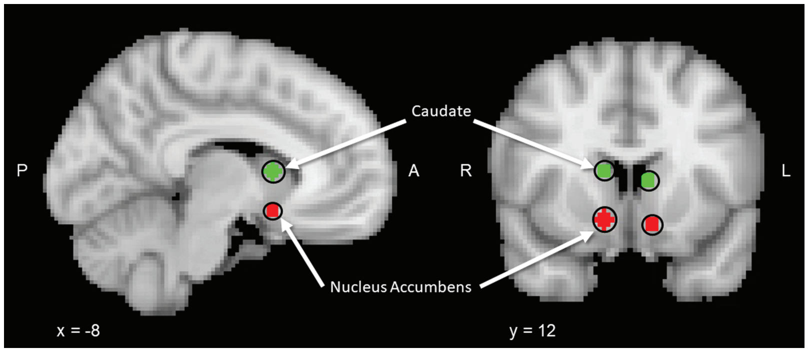

Fig. 5. ROI analyses examined activation within bilateral caudate nucleus and bilateral nucleus accumbens.

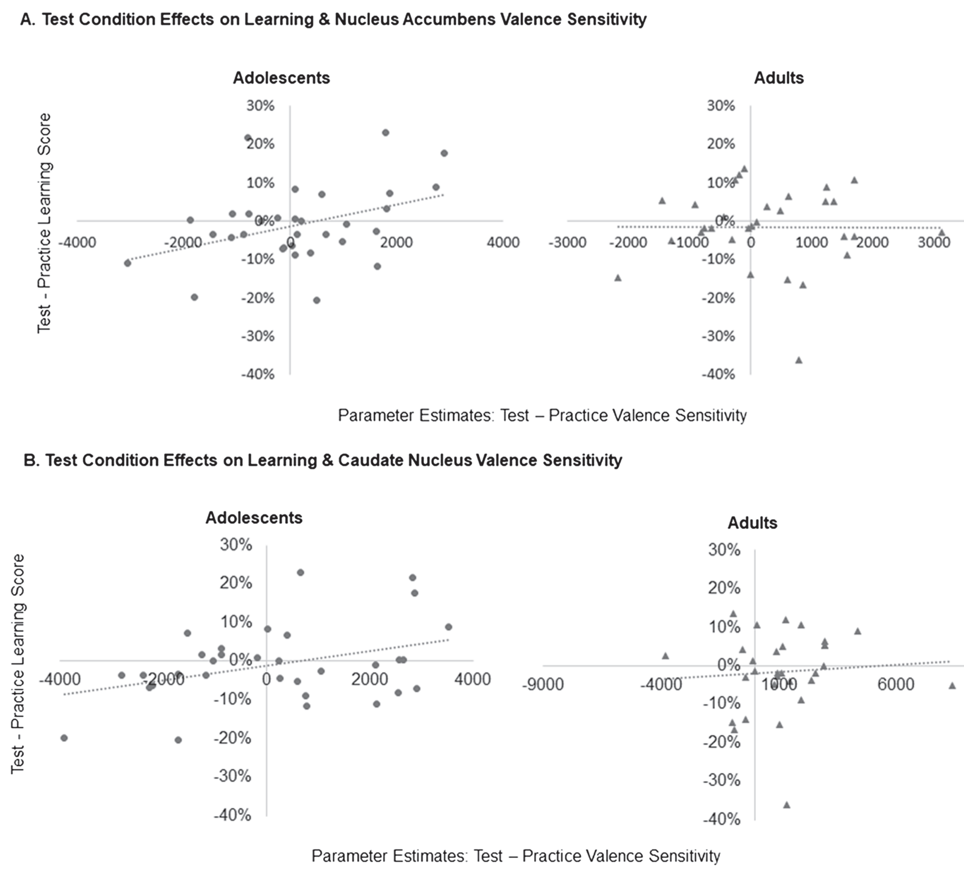

Fig. 6. Only adolescents exhibited significant correlations between testing effects on learning and testing effects on valence sensitivity in ventral striatum (A) and caudate nucleus (B).

(dorsal and ventral striatum, medial prefrontal cortex, anterior and posterior cingulate cortex, insula, hippocampus and amygdala). Unlike the adolescents, adults did not exhibit even a trending correspondence between the effects of evaluation threat on striatal responses and learning. Although prior research using the same task has reliably demonstrated striatal engagement during feedback in adults, their task performance was not significantly associated with that activation (Tricomi and Fiez, 2008; DePasque and Tricomi, 2015). Instead, activation associated with learning on this task was linked to activation in the left prefrontal cortex and left fusiform gyrus, regions that have been previously implicated in declarative memory (Tricomi and Fiez, 2008). This is unsurprising in light of the observation that adults can rely on a broader array of learning strategies, including the incorporation of explicit instructions and counterfactual information, compared with adolescents, who are more likely to rely upon straightforward, simple reinforcement learning (Decker *et al.*, 2015; Palminteri *et al.*, 2016). Thus, the significant link between striatal activation and task performance in adolescents may indicate that during adolescence, striatal engagement is important for adolescent learning. Adolescents, whose executive control processes may not yet be as reliably engaged as adults, may be more dependent on the functioning of the striatal system for learning on this task than adults. This may occur through increased striatal reinforcement of hippocampal memory processes during adolescence, as recent work has shown that superior probabilistic learning during adolescence is associated with enhanced functional associations between the striatum and hippocampus (Davidow *et al.*, 2016). Future work should examine this question in tasks that examine affective-based learning.

Contrary to our predictions, the key brain–behavior relationships significantly differed between the adolescents and adults in the caudate, but not in the ventral striatum. The lack of significant difference in correlation between the adolescents and adults was surprising not only because of the conceptual hypothesis that the adolescent striatum shows greater engagement in response to feedback learning (Peters and Crone, 2017), but also because the relation between nucleus accumbens valence sensitivity and learning score (Figure 6A) is virtually flat in adults while there is a clear positive relation in the adolescents. The greater variability in the relation between learning score and accumbens feedback in adults *vs* the relation between learning score and caudate feedback in adults may explain this finding.

Neurodevelopmental models propose that heightened engagement of affective processes during adolescence may motivate the engagement of cognitive resources needed to rapidly learn new skills (Crone and Dahl, 2012). Importantly, we found evidence that adolescents vary in their neural and behavioral responses to the threat of evaluation, suggesting that educators cannot simply apply a single fix to increase adolescent learning. This finding is consistent with prior developmental observations that adolescents often show greater response variation than adults (Goldenberg *et al.*, 2017). It will be important for future work to examine individual factors that could help to predict adolescents' susceptibility to efforts to enhance the affective salience of feedback. Effects of evaluation threat on learning have been previously associated with test anxiety: after being told of an impending test, more anxious students may experience diminished or distracted attention and withdraw from communications with their teachers, whereas less anxious students focus more, resist distraction and seek out feedback (Wine, 1979). In our study, some adolescents showed enhanced performance under the test condition, whereas others performed better in the practice condition. Further research should identify whether differences in personality variables, such as tendencies toward test anxiety, would predict which adolescents respond favorably to the different testing conditions.

The observation that adolescent task performance was less affected by the manipulation than adults may appear contrary to our hypothesis and theories that adolescent corticostriatal circuitry is more sensitive under emotionally heightened contexts (Crone and Dahl, 2012). However, it is consistent with a recent finding that cognitive performance is less influenced by 'high stakes' in adolescents compared to adults (Insel *et al.*, 2017). They report that behavior was only modulated by high-*vs*-low stakes when there was evidence of connectivity between the striatum and prefrontal cortex, which increased with age.

In our study, individual variability within the adolescent group suggests that those who did show enhancement of striatal feedback responses by test condition were able to modulate their learning. The significant relation between testing effects on brain responses and learning outcomes in adolescents is consistent with previous findings that adolescents who underperform in a neutral context compared to adults can benefit from the presence of incentives (Padmanabhan *et al.*, 2011). For those adolescents who showed greater feedback sensitivity during our test blocks, it is possible that the 'evaluation threat' served to incentivize good task performance, resulting in improved learning. This suggests that incentives need not only be extrinsic reinforcers (i.e. money) to be effective for adolescents and is consistent with the observed association between task motivation and performance enhancement under the TEST condition. We cannot rule out the possibility that increases in valence sensitivity and feedback-based learning under the threat of evaluation might be attributed to increases in effort due to a perception that these trials 'matter' more. The complexity of interpreting these findings speaks to the need to conduct further research with larger samples and built-in measures of effort and motivation, in order to further probe the precise nature of the motivational effects of testing conditions.

As a group, adolescents were not as consistently influenced as adults by the test manipulation. It is possible that, compared to adults, adolescents are less strategic in allocating their efforts, trying equally hard when they are being tested as when they are given an opportunity to learn. In the absence of a detailed self-report, we can only speculate about why this might be. Might adolescents experience the entire learning session as evaluative, even when they are instructed to practice their learning strategies? Are teens so accustomed to being tested that evaluation threat has no overall effect? Under the conditions we tested, adolescents who exhibited stronger patterns of neural feedback sensitivity under the threat of evaluation performed better under that condition, whereas others whose neural responses to feedback were greater in the practice condition performed better in the absence of evaluative threat. A prior work in adults has shown that the effects of evaluation threat on performance are moderated by a variety of personality variables, including membership in a stigmatized group and mindset about whether intelligence is a fixed or malleable trait (Good *et al.*, 2003; Mangels *et al.*, 2006); thus, it will be valuable for future research to explore the personality factors that influence adolescents' susceptibility to testing situations.

The finding that adolescents may be less susceptible on average to the affective influences of evaluative testing situations does not imply that the threat of evaluation is never problematic. In academic settings, as in other domains, tests can serve dual purposes. Testing that is primarily used to profile or compare performance, such as when test scores are used to rank and grade students, is known as a summative assessment. Educational research investigating downstream effects of high-stakes summative testing has found an increased test anxiety among grade school students for whom test results are used to incentivize or sanction educators, compared to regular classroom testing (Segool *et al.*, 2013). In contrast, formative assessment is a form of testing meant to guide decisions about further instruction (Harlen and James, 1997). Evidence from neuroscience suggests that adolescence is a time of great variability in how individuals might respond to these different forms of testing, so further work should probe the individual and contextual factors that interact with testing contexts to determine whether adolescents will respond adaptively or exhibit diminished performance. For those who are motivated by external evaluation, striatal engagement with feedback may be enhanced under such conditions and thereby facilitate better learning, whereas for others, striatal engagement with feedback might be enhanced when the threat of evaluation is removed.

Some limitations of the study should be noted. First, we do not have data demonstrating that the task increased affective salience for participants. Results from the Intrinsic Motivation Inventory suggest that this is the case given that participants who were more motivated exhibited greater gains in performance in the TEST blocks compared to the PRACTICE blocks but it remains an inferential assumption as based on the evaluative threat component of the study. Furthermore, this task has reliably elicited affective responses to negative feedback and interfered with learning in adult participants

(Mangels *et al.*, 2011). Second, the age range of the adolescents was broad. The selected age range for adolescents was based on previous empirical publications that examined feedback learning in adolescence and found the steepest upward slope in participants ages 11–16 years (Peters *et al.*, 2014; Peters and Crone, 2017; Potter *et al.*, 2017; Whitaker *et al.*, 2017).

Conclusions

Emerging evidence suggests that adolescence is a time of heightened reward-seeking and heightened learning. The present study has further demonstrated that, while adolescents can vary widely in how they perceive and respond to a contextual threat of evaluation, sensitivity to affective contexts in striatal circuitry can facilitate learning.

Supplementary data

Supplementary data are available at *SCAN* online.

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