



Striatum-medial prefrontal cortex connectivity predicts developmental changes in reinforcement learning

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Running Title: Development of Reinforcement Learning

**Striatum-medial prefrontal cortex connectivity predicts developmental changes
in reinforcement learning**

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Abstract

During development, children improve in learning from feedback to adapt their behavior. However, it is still unclear which neural mechanisms might underlie these developmental changes. In the current study we used a reinforcement learning model to investigate neurodevelopmental changes in the representation and processing of learning signals. Sixty-seven healthy volunteers between ages 8 and 22 (children: 8–11 years, adolescents: 13–16 years, and adults: 18–22 years) performed a probabilistic learning task while in a MRI scanner. The behavioral data demonstrated age differences in learning parameters with a stronger impact of negative feedback on expected value in children. Imaging data revealed that the neural representation of prediction errors was similar across age groups, but functional connectivity between the ventral striatum and the medial prefrontal cortex changed as a function of age. Furthermore, the connectivity strength predicted the tendency to alter expectations after receiving negative feedback. These findings suggest that the underlying mechanisms of developmental changes in learning are not related to differences in the neural representation of learning signals per se, but rather in how learning signals are used to guide behavior and expectations.

Keywords: functional connectivity, development, reinforcement learning, fMRI, brain maturation.

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3 The ability to learn contingencies between actions and positive or negative outcomes
4 in a dynamic environment forms the foundation of adaptive behavior (Rushworth &
5 Behrens, 2008). Learning from feedback in probabilistic environments is sensitive to
6 developmental changes, given the developmental improvements in learning from
7 positive and negative feedback which are observed until early adulthood (Crone & van
8 der Molen, 2004; Hooper et al., 2004; Huizinga et al., 2006). Intriguingly, prior
9 neuroimaging studies have demonstrated developmental differences in neural circuits
10 associated with learning from feedback in a fixed, static learning environment (van
11 Duijvenvoorde et al., 2008, Crone et al., 2008). These studies show that dorsolateral
12 prefrontal cortex and parietal cortex are increasingly engaged when receiving negative
13 feedback. However, in a probabilistic learning environment, learning takes place
14 gradually over trials and both positive and negative feedback informs future behavior.
15 Therefore, an important question concerns the neural mechanisms that underlie
16 developmental differences in probabilistic learning.
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36 A crucial aspect of adaptive learning is using feedback to estimate the
37 expected value of the available options. The first step in estimating the expected value
38 is the computation of prediction errors, that is, calculating the difference between
39 expected and experienced outcomes. Prediction errors can be positive, indicating that
40 outcomes are better than expected, or negative, indicating that outcomes are worse
41 than expected (Sutton & Barto, 1998). Next, these prediction errors are used to update
42 the expected value associated with the chosen option: the expected value increases
43 when the prediction error is positive and decreases when the prediction error is
44 negative.
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57 Prior neuroimaging studies have shown that activity in the ventral striatum, a
58 target area of dopaminergic midbrain neurons, correlates with positive and negative
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3 prediction errors (Knutson et al., 2000; Pagnoni et al., 2002; e.g. McClure et al., 2003;
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5 O'Doherty et al., 2003; McClure et al., 2004). The relation between prediction errors
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7 and subsequent learning is confirmed by studies demonstrating an association
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9 between the representation of prediction errors in the striatum and individual
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11 differences in performance on probabilistic learning tasks (Pessiglione et al., 2006;
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13 Schönberg et al., 2007). Furthermore, several studies have reported increased
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15 sensitivity of the striatum in adolescence after receiving monetary rewards or
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17 following other emotional stimuli (Galvan et al., 2006; McClure-Tone et al., 2008;
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19 Van Leijenhorst et al., 2009). This suggests that developmental differences in striatal
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21 sensitivity to rewards might contribute to the observed developmental differences in
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23 adaptive behavior. This hypothesis is supported by a recent developmental study that
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25 revealed heightened sensitivity in the striatum to positive prediction errors in
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27 adolescents relative to children and adults (Cohen et al., 2010).
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34 In contrast, there are also several studies using less salient rewards that have
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36 reported differences in adaptive behavior but suggest that there is a stable striatal
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38 activation pattern across adolescence (Casey et al., 2004; van Duijvenvoorde et al.,
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40 2008; Velanova et al., 2008). However, none of these developmental studies
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42 investigated the neural representation of prediction errors directly. Therefore, it is
43
44 possible that developmental differences in the representation of prediction errors are
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46 contributing to developmental changes in adaptive behavior.
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50 Several neuroimaging studies have shown that activity in the medial prefrontal
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52 cortex (mPFC) correlates with the expected value of stimuli or actions (for review see
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54 Rangel et al., 2008). Representations of expected values in the mPFC are thought to
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56 be updated by means of fronto-striatal connections, relating striatal prediction errors
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58 to medial prefrontal representations (Houk & Wise, 1995; Pasupathy & Miller, 2005;
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3 Frank & Claus, 2006; Camara et al., 2009). In support of this hypothesis, recent
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5 studies have shown increased functional connectivity between the ventral striatum and
6
7 mPFC during feedback processing (Camara et al., 2008; Munte et al., 2008).
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9 Furthermore, group differences in learning may be related to the connectivity strength
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11 between the striatum and the PFC during feedback processing. For example,
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13 substance-dependent individuals have an intact striatal representation of prediction
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15 errors, but are impaired in subsequently using these signals for learning (Park et al.,
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17 2010). This study showed that there is a positive relation between learning speed and
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19 the strength of functional connectivity between the striatum and PFC (see also Klein
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21 et al., 2007). Therefore, a second possible mechanism that may contribute to
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23 developmental changes in adaptive behavior is an increase in striatal-mPFC
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25 connectivity. Indeed, there are also still substantial changes in anatomical connectivity
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27 between subcortical structures and the prefrontal cortex during adolescence (Supekar
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29 et al., 2009; Schmithorst & Yuan, 2010).
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36 To test these two hypotheses, a computational reinforcement learning model
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38 was applied to investigate developmental differences in (a) the neural representation
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40 of prediction errors, and (b) changes in fronto-striatal connectivity. Participants of
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42 three age groups (children ages 8-11, adolescent sages 13-16 and young adults ages
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44 18-22) performed a probabilistic learning task (Frank et al., 2004) in an MRI scanner.
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46 We expect that with age, there is an improvement in learning from probabilistic
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48 feedback (Crone & van der Molen, 2004; van den Bos et al., 2009). In order to
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50 capture age-related changes in learning from positive and negative feedback
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52 separately, we use a reinforcement learning model with separate learning rates for
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54 positive and negative feedback (Kahnt et al., 2009). The individually estimated trial-
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56 by-trial prediction errors generated by this reinforcement model were subsequently
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used to test whether developmental differences in learning reflect functional differences in the representation of prediction errors and/or developmental changes in the propagation of prediction errors as measured by functional fronto-striatal connectivity (Park et al., 2010).

Material and Methods

Participants. Sixty-seven healthy right-handed paid volunteers ages 8-22 participated in the fMRI experiment. Age groups were based on adolescent development stage, resulting in three age groups: children (8- to 11-year-olds, $n=18$; 9 female), mid-adolescents (13- to 16-year-olds, $n=27$; 13 female) and young adults (18- to 22-year-olds, $n=22$; 13 female). A chi square analysis indicated that gender distribution did not differ between age groups, $X^2(2) = .79, p = .67$. All participants reported normal or corrected-to-normal vision and participants or their caregivers indicated an absence of neurological or psychiatric impairments. Participants gave informed consent for the study and all procedures were approved by the medical ethical committee of the Leiden University Medical Center.

Participants completed two subscales (similarities and block design) of either the Wechsler Adult Intelligence Scale (WAIS) or the Wechsler Intelligence Scale for Children (WISC) in order to obtain an estimate of their intelligence quotient (Wechsler, 1991, 1997). There were no significant differences in estimated IQ scores between the different age groups, $F(2, 66) = 1.63, p = .20$ (see Table 1).

Task Procedure. The procedure for the probabilistic learning task (PLT, Frank et al., 2004; van den Bos et al., 2009) was as follows: The task consisted of two stimulus pairs (called AB and CD). The stimulus pairs consisted of pictures of everyday

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3 objects (e.g., a chair and a clock). Each trial started with the presentation of one of the
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5 two stimulus pairs and subsequently the participant had to choose one (e.g., A or B).
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7 Stimuli were presented randomly on the left or the right side of the screen.
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9 Participants were instructed to choose either the left or the right stimulus by pressing a
10
11 button with the index or middle finger of the right hand. Responses had to be given
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13 within a 2500 ms window, which was followed by a 1000ms feedback display (see
14
15 Figure 1A). If no response was given within 2500ms, the text “too slow” was
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17 presented on the screen.
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22 Feedback was probabilistic; choosing stimulus A led to positive feedback on
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24 80% of AB trials, whereas choosing stimulus B led to positive feedback on 20% of
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26 these trials. The CD pair procedure was similar, but probability for reward was
27
28 different; choosing stimulus C led to positive feedback on 70% of CD trials, whereas
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30 choosing stimulus D led to positive feedback on 30% in these trials.
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34 Participants were instructed to earn as many points as possible (as indicated by
35
36 receiving a positive feedback signal), but were also informed that it was not possible
37
38 to receive positive feedback on every trial. After the instructions and before the
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40 scanning session, the participants played 40 practice rounds on a computer in a quiet
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42 laboratory to ensure they understood the task.
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46 In total, the task in the scanner consisted of two blocks of 100 trials each: 50
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48 AB trials and 50 CD trials per block. The first and the second block consisted of
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50 different sets of pictures and therefore, participants had to learn a new mapping in
51
52 both task blocks. The data from the last 60 trials of each block were also reported in
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54 another study using a rule-based analysis (van den Bos et al., 2009). The duration of
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56 each block was approximately 8.5 minutes. The stimuli were presented in pseudo-
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random order with a jittered interstimulus interval (min=1000 ms, max=6000 ms) optimized with OptSeq2 (Dale, 1999).

Reinforcement Learning Model. A standard reinforcement learning model (Sutton & Barto, 1998) was used to analyze behavioral and neural data (McClure et al., 2003; Cohen & Ranganath, 2005; Haruno & Kawato, 2006; Frank & Kong, 2008; Kahnt et al., 2009). The reinforcement learning model uses the prediction error (δ) to update the decisions weights (w) associated with each stimulus (in this case A, B, C or D). Thus, whenever feedback is better than expected, the model will generate a positive prediction error which is used to *increase* the decision weight of the chosen stimulus (e.g. stimulus A). However, when feedback is worse than expected, the model will generate a negative prediction error, which is used to *decrease* the decision weight of the chosen stimulus (e.g. stimulus B). The impact of the prediction error is usually scaled by the learning rate (α). We extended the standard reinforcement learning model by using separate learning rates for positive feedback (α_{pos}) and negative feedback (α_{neg}) (e.g. Kahnt et al., 2009). Thus, positive and negative feedback might have a different impact of the decisions weights. To model trial-by-trial choices, we used the soft-max mechanism to compute the probability (p) of choosing a high probability target (A or C) on trial t as the difference in the decision weights in each trial (w_t) associated with each stimulus, passed through a sigmoid function (Montague et al., 2004; Kahnt et al., 2009). For example, when stimulus pair AB is presented the probability of choosing A is determined by:

$$(1) \quad p(A)_t = \frac{1}{1 + e^{-\beta(w(A)_t - w(B)_t)}}$$

Where β is the inverse temperature accounting for the stochasticity of the choices.

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After each decision the prediction error (δ) is calculated as the difference between the outcome received ($r = 1$ for positive feedback and 0 for negative feedback) and the decision weight (w_t) for the chosen stimulus:

$$(2) \quad \delta_t = r_t - w(\text{chosen_stimulus})_t$$

Subsequently, the decision weights are updated according to:

$$(3) \quad w_{t+1} = w_t + \lambda \times \alpha(\text{outcome})_t \times \delta_t$$

Where λ is 1 for the chosen and 0 for the unchosen stimulus, $\alpha(\text{outcome})$ is a set of learning rates for positive (α_{pos}) and negative feedback (α_{neg}), which scale the effect of the prediction error on the future decision weights, and thus subsequent decisions. For example, a high learning rate for positive feedback but a low learning rate for negative feedback indicates that positive feedback has a high impact on future behavior, whereas negative feedback will hardly change future behavior. These two learning rates were individually estimated by fitting the model predictions ($p(\text{high probability stimulus})$) to participants' actual decisions. We used the multivariate constrained minimization function (`fmincon`) of the optimization toolbox implemented in MATLAB 6.5 for this fitting procedure. Initial values for learning rates were $\alpha_{\text{pos}} = \alpha_{\text{neg}} = 0.5$ and for action values, $w(\text{left}) = w(\text{right}) = 0$.

Finally, we performed behavioral analyses with an alternative model with just one-learning parameter in order to benchmark the performance of the two-learning parameter model. Model comparisons revealed that the two-parameter had a superior fit to the behavioral data, according to both the Bayesian and Akaike information criterion (BIC and AIC, see Supplementary Table 2). Because the two-learning rate model provides a better fit this is used in all subsequent analyses.

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Behavioral Analyses. To examine the correspondence between model predictions and participants' behavior, model predictions were compared with the actual behavior on a trial-by-trial basis. Model predictions based on estimated learning rates were regressed against the vector of participants' actual choices and individual regression coefficients were used to compare group differences in model fits. Only when there are no differences in model fit between groups one can confidently compare model parameters.

Next, we defined two dependent variables of behavioral performance to further investigate the relation between model parameters and choice behavior: $p(\text{lose/shift})$ and $p(\text{win/stay})$. 'Win-stay' was computed by calculating the proportion of choice repetitions following positive feedback and the total number of positive feedback events. Likewise, 'lose-shift' was computed by calculating the proportion of choice shifts following negative feedback and the total number of negative feedback events. To test whether the individually estimated learning rates $\alpha(\text{win})$ and $\alpha(\text{loss})$ predict different aspects of participants' behavior, both learning rates were simultaneously regressed against $p(\text{lose-shift})$ and $p(\text{win-stay})$, respectively, using multiple regression.

Data Acquisition. Participants were familiarized with the scanner environment on the day of the fMRI session through the use of a mock scanner, which simulated the sounds and environment of a real MRI scanner. Data were acquired using a 3.0T Philips Achieva scanner at the Leiden University Medical Center. Stimuli were projected onto a screen located at the head of the scanner bore and viewed by participants by means of a mirror mounted to the head coil assembly. First, a localizer scan was obtained for each participant. Subsequently, T2*-weighted Echo-Planar Images (EPI) (TR= 2.2 sec, TE= 30ms, 80 x 80 matrix, FOV = 220, 35 2.75mm

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3 transverse slices with 0.28mm gap) were obtained during 2 functional runs of 232
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5 volumes each. A high-resolution T1-weighted anatomical scan and a high-resolution
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7 T2-weighted matched-bandwidth anatomical scan, with the same slice prescription as
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9 the EPIs, were obtained from each participant after the functional runs. Stimulus
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11 presentation and the timing of all stimuli and response events were acquired using E-
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13 Prime software. Head motion was restricted by using a pillow and foam inserts that
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15 surrounded the head.
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21 *fMRI Data Analysis.* Data were preprocessed using SPM5 (Wellcome Department of
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23 CognitiveNeurology, London). The functional time series were realigned to
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25 compensate for small head movements. Translational movement parameters never
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27 exceeded 1 voxel (< 3 mm) in any direction for any subject or scan. There were no
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29 significant differences in movement parameters between age groups $F(2, 65) = .15, p$
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31 $= .85$, (see Table S1). Functional volumes were spatially normalized to EPI templates.
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33 The normalization algorithm used a 12 parameter affine transformation together with
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35 a nonlinear transformation involving cosine basis functions and resampled the
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37 volumes to 3 mm cubic voxels. Functional volumes were spatially smoothed using a
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39 8 mm full-width half-maximum Gaussian kernel. The MNI305 template was used for
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41 visualization and all results are reported in the MNI305 stereotaxic space (Cosoco,
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43 Kollokian, Kwan, & Evans, 1997)
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50 Statistical analyses were performed on individual participants' data using the
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52 general linear model in SPM5. The fMRI time series data were modeled by a series of
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54 events convolved with a canonical haemodynamic response function (HRF). The
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56 presentation of the feedback screen was modeled as 0-duration events. The stimuli
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58 and responses were not modeled separately as these occurred in one prior or
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60 overlapping EPI images as feedback presentation.

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4 To investigate the neural responses to feedback valence and prediction errors
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6 we set up a general linear model (GLM) with the onsets of each feedback type
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8 (positive and negative) as regressors. In this model, the stimulus functions for
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10 feedback were parametrically modulated by the trial-wise prediction errors derived
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12 from the reinforcement learning model. The modulated stick functions were
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14 convolved with the canonical HRF. These regressors were then orthogonalized with
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16 respect to the onset regressors of positive and negative feedback trials and regressed
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18 against the BOLD signal.
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23 Finally, to investigate linear and quadratic age trends we applied polynomial
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25 expansion analysis (Büchel et al., 1996) with age as continuous variable, using the
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27 forward model selection as described by Büchel and colleagues (1998). Thresholds
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29 were set to $p < .05$ FWE with an extend threshold of 10 continuous voxels for the
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31 whole group analyses. Analyses of age trends were set to $p < .001$ uncorrected with an
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33 extend threshold of 20 continuous voxels, reporting the SPM5 implemented small
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35 volume correction (SVC) FWE corrected p values, using the whole group PPI mPFC
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37 as a volume of interest (VOI).
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43 *Region-of-interest analyses.* We used the Marsbar toolbox for use with SPM5
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45 (<http://marsbar.sourceforge.net>, Brett et al. 2002) to perform Region of Interest (ROI)
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47 analyses to further characterize patterns of activation and estimate individual
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49 differences in connectivity measures.
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53 *Functional Connectivity Analyses.* To explore the interplay between the ventral
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55 striatum and other brain regions during reinforcement-guided decision making,
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57 functional connectivity was assessed using psychophysiological interaction (PPI)
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59 analysis (Friston, 1994; Cohen et al., 2005; Cohen et al., 2008). The functional whole
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3 brain mask, in which activity correlated significantly with prediction errors for the
4 whole group, was masked with an anatomical striatum ROI of the Marsbar toolbox
5 that included the bilateral caudate, putamen and nucleus accumbens, to create the seed
6 region of interest (ROI). The method used here relies on correlations in the observed
7 BOLD time-series data and makes no assumptions about the nature of the neural event
8 that contributed to the BOLD signal (Cohen et al., 2008). For each model, the entire
9 time series over the experiment was extracted from each subject in the clusters of the
10 (left and right) ventral striatum. Regressors were then created by multiplying the
11 normalized time series of each ROI with condition vectors that contained ones for
12 four TRs after positive or negative prediction errors and zeros otherwise (see also
13 Cohen & Ranganath, 2005; Kahnt et al., 2008; Park et al., 2010). Thus, the two
14 condition vectors of positive and negative prediction errors (containing ones and
15 zeros) were each multiplied with the time course of each ROI. These regressors were
16 then used as covariates in subsequent analyses.

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The time series between the left and right hemispheres for the ventral striatum were highly correlated ($r = .89$). Therefore, parameter estimates of left- and right structures were collapsed, and thus, represent the extent to which feedback-related activity in each voxel correlates with feedback-related activity in the bilateral ventral striatum.

Individual contrast images for positive vs. negative feedback were computed and entered into second-level one-sample t-tests. In order to find age related differences in the whole-brain analyses of functional connectivity with the ventral striatum, we performed a second-level regression analysis with a regressor for age.

Results

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Behavioral data*Reinforcement learning.*

First, we assessed how the model parameters differed between age groups. First of all, there was a good fit of the model to participants' behavior; the average regression coefficient was significantly above zero for all age groups (all p 's < .001. Figure 1B). Importantly, the model fit did not differ significantly between groups ($F_{(2,64)} = .96, p = .38$), reassuring that parameters estimations could be compared between groups. Importantly, we also found no significant relation between age and the value of the stochasticity parameter β ($r = .05, p = .74$). This indicates that behavioral differences are not due to age differences in choice stochasticity. Furthermore, previous behavioral analyses suggest that there are no significant difference in learning speed, and that participants of all ages reach a stable behavioral pattern after about 60 trials, showing matching behavior (see van den Bos et al., 2009).

Next, a two (learning parameters) x three (age groups) ANOVA tested for age differences in learning from positive and negative feedback. This analysis showed a significant group by parameter interaction ($F_{(2,64)} = 12.34, p < .001$, see Figure 1C), and post-hoc tests revealed that there was an age related decrease in α_{neg} , $F_{(2,67)} = 9.87, p < .001$, and a marginal age-related increase in α_{pos} , $F_{(2,67)} = 2.73, p = .06$.

Finally, to assess whether different learning rates captured different aspects of behavior, α_{win} and α_{loss} were simultaneously regressed against the two dependent variables of this study [$p(\text{win/stay})$ and $p(\text{lose/switch})$]. A multiple regression of both learning rates on $p(\text{win/stay})$ fitted significantly ($r = .51, F_{(2, 64)} = 11.05, p < .001$), but only α_{win} ($b_{\alpha(\text{win})} = .49, t_{(64)} = 4.46, p < .001$) and not α_{loss} ($b_{\alpha(\text{loss})} = -0.27, t_{(64)} = -2.04, p = .08$) contributed significantly to the regression. In contrast, in the regression against $p(\text{lose/switch})$ ($r = .33, F_{(2, 64)} = 6.85, p < .01$), α_{loss} ($b_{\alpha(\text{loss})} = .32, t_{(64)} = 2.55, p < .01$) but not α_{win} ($b_{\alpha(\text{win})} = -.218, t_{(64)} = -1.83, p = .08$) contributed significantly.

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3 Taken together, these results show that the learning rates captured different
4 behavioral aspects of reinforcement-guided decision-making. The results further show
5 that mainly the age related decrease in the influence of negative feedback on expected
6 values underlies developmental differences in adaptive behavior.
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fMRI results

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16 *Model-based fMRI.* Across all participants, individually generated trial-wise
17 prediction errors (positive and negative combined) correlated significantly with
18 BOLD responses in bilateral ventral striatum, mPFC and the right
19 parahippocampalgyrus (Figure 2A, and Table 1). Activity in the ventral striatum was
20 localized at an area comprising the ventral intersection between the putamen and the
21 head of the caudate. Tests for positive and negative prediction errors separately
22 revealed comparable results.
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33 Whole brain regression analyses for age differences revealed no linear or non-
34 linear age group differences (Figure 2B). This analysis was repeated for positive and
35 negative prediction errors separately and these analyses also revealed no linear or
36 non-linear age effects. These findings demonstrate that prediction errors (positive or
37 negative) are not represented differently between the three age groups.
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Functional Connectivity.

49 Functional connectivity between the striatum and other brain regions was assessed
50 during processing of negative and positive feedback using PPI. The contrast used for
51 testing functional connectivity was positive > negative feedback. Note that the vectors
52 for positive feedback events contain all positive prediction error events, and the
53 vectors for negative feedback events contain all negative prediction error events.
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60 Significantly enhanced functional connectivity was found during positive > negative

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3 feedback between the bilateral ventral striatum seed and the mPFC (Figure 3A). The
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5 opposite contrast (negative > positive feedback) did not reveal any significant changes
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7 in functional connectivity.
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10 Next, we examined age differences in ventral striatum connectivity by adding
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12 age as a regressor to the second-level PPI analysis. These analyses revealed age-
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14 related increases in functional connectivity of the ventral striatum seed with the mPFC
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16 (BA32/10) for positive > negative feedback (Figure 3B) at a an uncorrected threshold
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18 of $p < .001$ and $k > 20$ voxels (SVC: FWE, $p < .02$). No other areas were found when
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20 testing for non-linear age effects in functional connectivity.
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24 To further illustrate the age-related changes in fronto-striatal connectivity we
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26 extracted the strength of functional connectivity between ventral striatum and mPFC
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28 for each participant and plotted it against age as a continuous variable (Figure 3C).
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30 This plot reveals that the connectivity pattern shifts from a stronger connection after
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32 negative feedback for the youngest participants towards a stronger connection after
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34 positive prediction errors for the oldest participants.
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38 Finally, we performed ROI analyses to investigate whether striatum-mPFC
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40 connectivity was related to the individual learning parameters. The differential
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42 connectivity strength (positive > negative) between the ventral striatum and mPFC
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44 ROI was used to predict the individual differences in learning rates for positive and
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46 negative feedback. The relative connectivity measure correlated negatively with the
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48 learning rate for negative feedback ($r = -.41$, $p < .001$, Figure3D), and moderately
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50 positively with the learning rate for positive feedback ($r = .26$, $p = .06$). Thus, there
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52 was stronger striatum-mPFC coupling during negative > positive feedback in
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54 participants for whom negative feedback had a relatively large impact on future
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56 expected value, whereas the reverse was true (i.e., stronger coupling during positive >
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negative feedback) in participants for whom positive feedback had a relatively large impact on future expected value.

To summarize, increased functional connectivity between the ventral striatum and mPFC was observed during processing of positive feedback compared to negative feedback. Furthermore, this analysis revealed that the relative strength of the striatum-mPFC connectivity is correlated positively with age, but negatively with the learning rate for negative feedback.

Discussion

The goal of this study was to examine developmental changes in the neural mechanisms of probabilistic learning. The reinforcement model showed that with increasing age, negative feedback had decreasing effects on future expected values. Imaging analyses revealed that neural activation to prediction errors did not differ between age groups; however, age differences in the learning rates were associated with an age-related increase in functional connectivity between ventral striatum and the mPFC.

Developmental changes in learning rates

Using a reinforcement learning model we were able to disentangle differences in sensitivity to positive and negative feedback by estimating learning rates for positive and negative feedback separately. These estimated learning rates reflect the degree to which the future expected value of a stimulus will be changed after positive or negative prediction errors. Importantly, the model revealed that developmental differences in adaptive behavior were not related to differences in stochasticity in choice behavior. However, the analyses showed that with age there is a decrease in

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4 the learning rate for negative prediction errors (α_{neg}). This finding indicates that with
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6 increasing age particularly the impact of negative prediction errors on the future
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8 expected value decreases. Furthermore, as expected, the individual differences in
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10 learning rates were related to shifting behavior, showing a relation between updating
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12 of expected value and decision strategies. These results are consistent with
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14 developmental studies that have shown with increasing age participants are less
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16 influenced by irrelevant negative feedback (Crone et al., 2004, Eppinger et al., 2009).
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20 Taken together, the results show that an extended reinforcement model is (1)
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22 able to identify different computational processes involved in adaptive behavior, and
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24 (2) reveal an important (single) parameter underlying age-related changes in adaptive
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26 learning; the learning rate for negative learning signals. Additionally, given that the
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28 model fits the behavior of all ages equally well, it provides a solid basis for exploring
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30 the neurodevelopment changes in representing and the processing of learning signals.
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Neural Representation of prediction errors

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36 Consistent with previous studies, trial-by-trial prediction errors generated by the
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38 reinforcement learning model correlated with activity of a network of areas including
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40 the ventral striatum and the mPFC (Pagnoni et al., 2002; McClure et al., 2003;
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42 O'Doherty et al., 2003; Cohen & Ranganath, 2005). This result indicates that these
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44 areas are sensitive to differences in expected vs. received feedback; showing
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46 increased activation when feedback is better than expected and decreased activation
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48 when the feedback is worse than expected. Interestingly, our analyses did not reveal
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50 any (linear or non-linear) age related differences in (positive or negative) prediction
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52 error related activity in the striatum.
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These findings are consistent with prior studies using cognitive learning tasks, which have also reported stable striatal activation patterns across adolescence (Casey et al., 2004; van Duijvenvoorde et al., 2008; Velanova et al., 2008). However, the results of the current study provide different findings in comparison to affective decision-making paradigms. These studies have reported a peak in sensitivity of the striatum in adolescence after receiving monetary rewards or highly emotional stimuli (Galvan et al., 2006; McClure-Tone et al., 2008; Van Leijenhorst et al., 2009), which may be related to adolescent typical changes in the dopamine system (for a review see Galvan, 2010). Importantly, a recent developmental study of reward-based learning using a comparable reinforcement model with a single learning rate (for both negative and positive feedback), has also shown heightened sensitivity to positive prediction errors in adolescents compared to children and adults (Cohen et al., 2010)¹. Interestingly, Cohen et al. (2010) observed adolescent-specific increases in reaction times for large relative to small rewards. This suggests that particularly in the presence of salient rewards adolescents show increased striatal sensitivity, which in turn might bias decision-making processes. One possibility is that during adolescence, the presence of salient rewards increases the baseline level of striatal dopamine, which in turn increases sensitivity to positive prediction errors and may even decrease the sensitivity to negative prediction errors (Frank et al., 2004; Frank & Claus, 2006). In future studies, it will be important to further examine how the prediction error representation can be modulated by the use of specific reward magnitude manipulations, and how these manipulations affect decision-making parameters.

¹ It should be noted however, that Cohen and colleagues compared different age groups, as adolescence in this study was defined as the age range 14-19 years, and adulthood as 25-30 years. In this respect, the findings of the current study and the findings of Cohen et al. are not directly comparable.

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Developmental changes in striatum-mPFC connectivity

Connectivity analyses revealed that during feedback processing the seed region in the ventral striatum sensitive to prediction errors showed increased functional connectivity with the mPFC during positive compared to negative feedback. This pattern of connectivity is consistent with several studies that have shown feedback-related changes in functional connectivity of the striatum (for a review see Camara et al., 2009). In contrast to the neural representation of prediction errors, subsequent analyses revealed age-related changes in striatum–mPFC functional connectivity. The pattern shifted towards stronger connectivity after positive feedback with increasing age. Importantly, the striatum-mPFC connectivity strength was negatively correlated with the negative learning rate. Taken together these results suggest that the age related increase in striatum-mPFC connectivity underlies changes in adaptive behavior.. In other words, developmental changes in learning are not related to differences in the computation of learning signals per se, but rather to differences in how learning signals are used to update future expectations and subsequent behavior.

Given that during adolescent development there are still substantial changes in structural connectivity within the prefrontal cortex (Schmithorst & Yuan, 2010) it could be hypothesized that the developmental differences in striatum-mPFC functional connectivity are related to changes in structural connectivity between these two structures (Cohen et al., 2008). In future developmental studies, it will be of interest to combine measures of structural and functional connectivity in order to further explore this hypothesis.

A final question concerns how these results relate to previous developmental studies on feedback processing in deterministic environments (van Duijvenvoorde et al., 2008; Crone et al., 2008). Learning theories have suggested two separate learning

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3 strategies (Daw et al., 2005; Maia, 2009); a model-based strategy that operates on
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5 explicit task representations, such as rules describing the reward contingencies given
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7 the current state, and a model-free strategy that uses feedback directly to compute
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9 action values without any explicit model of the environment. Furthermore, research
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11 has suggested that the relative contribution of each learning strategy might be
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13 dependent on their respective certainties (Daw et al., 2005; Doya et al., 2002).
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18 Thus, given the deterministic or rule-based structure of previous experimental
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20 paradigms it is likely that reported developmental changes in the DLPFC-parietal
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22 network represent differences in the learning system that operates on task
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24 representations, whereas the current study shows developmental differences in neural
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26 systems that subserve the model-free computational strategy (see also Galvan et al.,
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28 2006; Cohen et al., 2010). This interpretation is supported by a recent study that
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30 showed that updating model-based task representations relies on the DLPFC-parietal
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32 network, whereas model-free feedback updating was associated with the striatal
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34 activity (Gläscher et al., 2010).
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39 The challenge for future developmental studies will be to disentangle the
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41 relative contributions of these learning strategies dependent on the learning context
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43 (Daw et al., 2005), and to understand how these two strategies, and related neural
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45 systems, contribute to developmental changes in feedback learning. An interesting
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47 hypothesis is that in a context where learning mainly relies on a model-based strategy,
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49 adolescents may be less susceptible to the presence of salient rewards than when
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51 learning is mainly based on a model-free strategy.
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58 *Conclusion*
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4 In the current study we used a reinforcement learning model to investigate
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6 neurodevelopmental changes in the representation and processing of learning signals
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8 in a probabilistic environment. The results of this study advance our understanding of
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10 the mechanisms underlying developmental changes related to learning in a
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12 probabilistic environment.
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15 First, behavioral analyses singled out a specific computational process,
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17 updating based on negative prediction errors, which showed developmental
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19 differences. Importantly, the age related differences in updating were also related to
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21 shifting behavior after negative feedback. Second, we provide evidence that
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23 developmental differences in adaptive learning may not be due to differences in the
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25 computation of learning signals, but rather to developmental differences in how
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27 learning signals are used to guide behavior and expectations. The imaging results
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29 suggest that the latter process is reflected in the strength of functional connectivity
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31 between the striatum and the mPFC.
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Table 1 :Brain Regions revealed by whole brain contrasts.

Anatomical region	L/R	BA	Z	MNI coordinates		
				x	y	z
Prediction Error						
Ventral Striatum	L/R		6.33	-19	13	-8
Right parahippocampalgyrus	R		5.61	37	-13	-37
Medial PFC	L/R	10/11	5.92	2	51	0
PPI (positive > negative)						
Medial Prefrontal Cortex	L/R	10	6.02	3	44	2
Ventral Striatum (caudate &putamen)	L/R		7.50	9	9	3
PPI (positive > negative) x Age						
Medial PFC	L	10	5.32	-9	49	-2

MNI coordinates, peak voxels reported.

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Figure 1

(A) Participants chose one stimulus by pressing the left or right button and received positive or negative feedback according to probabilistic rules. Two pairs of stimuli were presented to the participants: (1) the AB pair with 80% positive feedback for A and 20% for B and (2) the CD pair with 70% positive feedback for A and 30% for B where A 80%-20%. (B) Estimated learning rates for positive and negative feedback per age group. (C) Estimated model fits per age group. Error bars represent standard errors in all graphs.

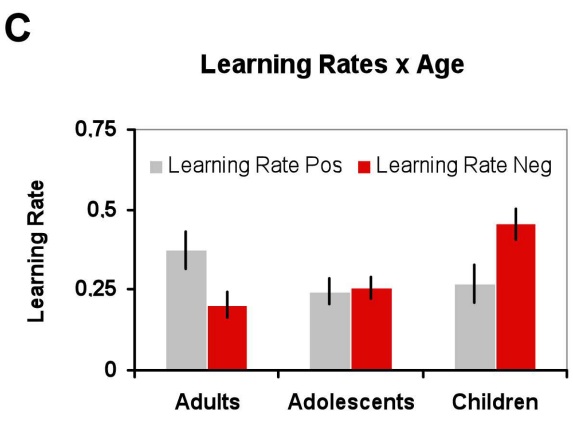
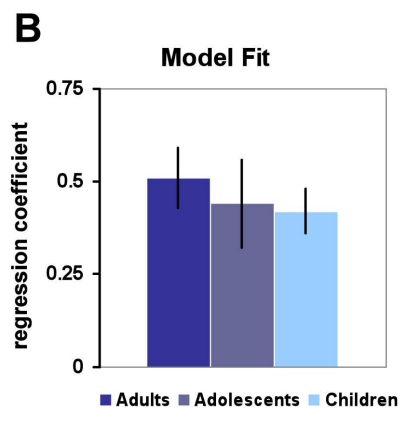
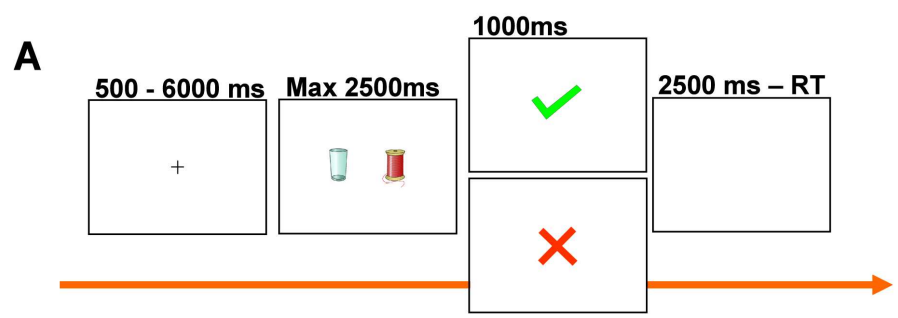
Figure 2

(A) Regions in the mPFC, ventral striatum and parahippocampal gyrus in which BOLD signal was significantly correlated with prediction errors. Thresholded at $p < .05$, FWE, $k > 10$ (B) Parameter estimates of the prediction errors per age group in the functionally defined ROIs for the mPFC, ventral striatum and parahippocampal gyrus.

Figure 3

(A) Regions which showed increased functional connectivity with the striatal seed region after positive compared to negative feedback. Thresholded at $p < .05$, FWE, $k > 10$ (B) Region in the mPFC that revealed age related changes in functional connectivity with the striatal seed region. Thresholded at $p < .001$, uncorrected, $k > 20$. (C) Scatterplot depicting the relationship between the functional connectivity measure of the striatum-mPFC (positive > negative feedback) and age. (D) Scatterplot depicting the relationship between the functional connectivity measure of the striatum-mPFC (positive > negative feedback) and learning rate (α_{neg}).

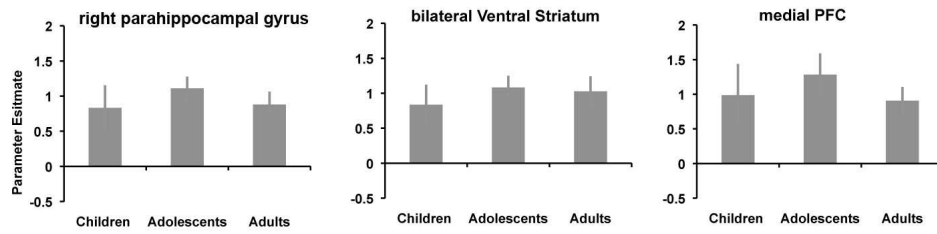
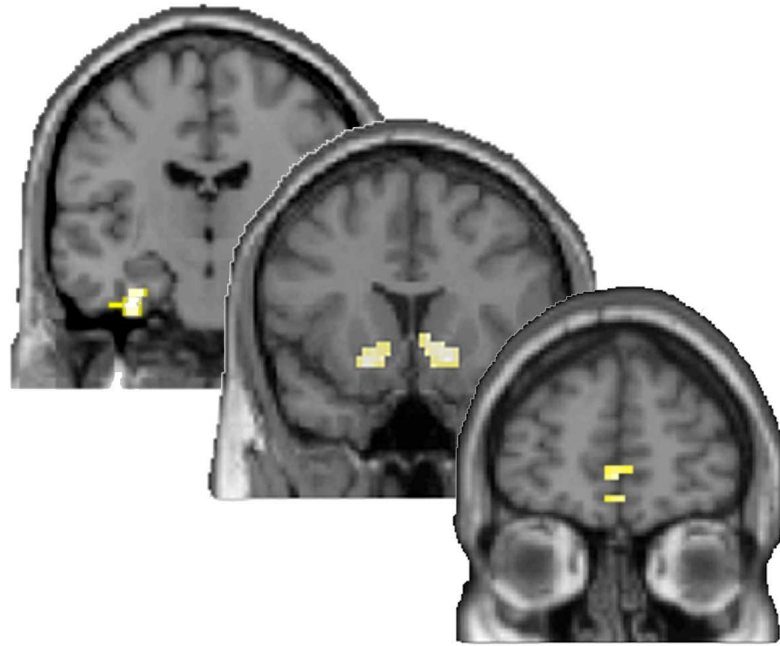
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Review

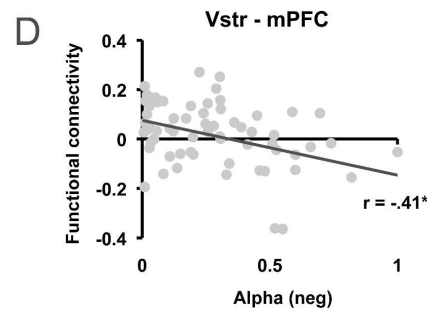
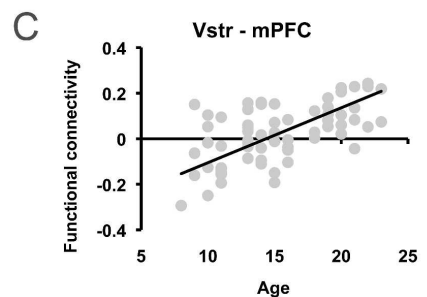
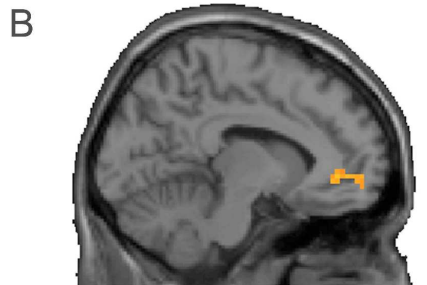
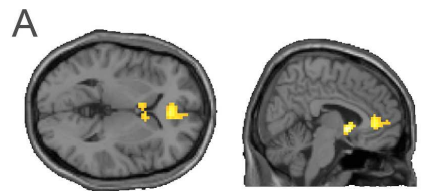
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146x400mm (300 x 300 DPI)

Supplement

Table S1

	IQ	reaction times (ms)	points	head motion		model fit	α_{pos}	α_{neg}
				avg (mm)	max(mm)			
Adults	107 (2.4)	811(44)	118(3)	.08(.01)	1.56	.51(.08)	.37(.05)	.20(.04)
Adolescents	108 (2.0)	773(39)	114(3)	.08(.01)	2.96	.44(.12)	.24(.03)	.24(.03)
Children	111 (2.6)	804(42)	107(6)	.09(.01)	2.85	.39(.06)	.23(.05)	.45(.05)

Table S2

	Two LR	One LR
Log Likelihood	-8961.7675	-9092.3823
AIC	179280	181870
BIC	179470	181970

Preprint Peer Review

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