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Modulation of meso-limbic reward processing by motivational tendencies in young adolescents and adults

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Abstract

Adolescence is a particularly vulnerable period for the onset of substance use disorders and other psychopathology. Individual variability in motivational tendencies and temperament and significant changes in functional brain organization during adolescence are important factors to consider in the development of substance use and dependence. Recent conceptualizations suggest that sensitivity to reward is heightened in adolescence and that this motivation tendency may precipitate subsequent substance abuse. The present study examined the role of personality traits in mesolimbic neurobehavioral response on a monetary incentive delay (MID) task in young adolescents (11–14 years) and emerging adults (18–25 years) using functional magnetic resonance imaging. As a group, adolescents were not more sensitive to gains than losses compared to adults during either anticipatory and feedback phases; instead, compared to adults they showed less sensitivity to incentive magnitude in mesolimbic circuitry during anticipation and feedback stages. However, personality modulated this response such that adolescents high in impulsivity or low in avoidance tendencies showed greater gain sensitivity and adolescents high in avoidance showed greater loss sensitivity during cue anticipation. In adults, mesolimbic response was modulated by the impulsivity construct such that high-impulsive adults showed reduced magnitude sensitivity during both anticipation and feedback compared to low impulsive adults. The present findings suggest that impulsive personality significantly modulates mesolimbic reward response during both adolescence and adulthood but avoidance and approach tendencies also modulate this response in adolescents. Moreover, personality modulated incentive valence in adolescents but incentive magnitude in adults. Collectively, these findings suggest that mesolimbic reward circuitry function is modulated by somewhat different parameters in adolescence than in adulthood.

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Conflict of interest

We have no conflicts of interest to declare

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1. Introduction

Individual differences in motivational tendencies and temperament are a major factor in risk for substance use and dependence. Individuals who exhibit strong approach motivation tendencies, like high sensation seeking, novelty seeking and reward dependence, or high impulsivity are more likely to experiment with drugs (Ball, Carroll, & Rounsaville, 1994; Donohew, Lorch, & Palmgreen, 1991), show greater sensitivity to the reinforcing or other behavioral effects of drugs and alcohol (Hutchison, Wood, & Swift, 1999; White, Lott, & de Wit, 2006), and escalate into substance dependence (Galizio & Stein, 1983; Wills, Vaccaro, & McNamara, 1994). Preclinical studies have also confirmed these patterns ((Bevins, Klebaur, & Bardo, 1997; Perry, Lawson, German, Madden, & Carroll, 2005). In some conceptual frameworks, adolescents are viewed as higher on approach tendencies and impulsivity than either younger children or adults (Chambers, Taylor, & Potenza, 2003). Approach- and impulsivity-related personality traits, together with measures of brain function or volume and early experimentation with alcohol, are strong predictors of future binge drinking during adolescence (Whelan, et al., 2014). Therefore, strong approach tendencies and impulsivity exhibited during adolescence can be a major risk factor for substance dependence.

One of the reasons proposed for high vulnerability to substance use during adolescence is that adolescents have drives similar to those of adults but they lack fully mature regulatory or behavioral inhibition system, as described in the dual-systems hypothesis of brain development (Chambers, et al., 2003). The imbalance between robust activation of motivational systems and weaker activation of inhibition systems increases the likelihood of engaging in risky and dangerous behaviors. Behavioral activation and approach behaviors have been strongly linked to mesolimbic dopamine circuitry (Depue & Collins, 1999). Consequently, adolescents might be expected to exhibit stronger mesolimbic activation or weaker prefrontal activation than adults on reward-processing tasks or other behaviors that are associated with motivation and behavioral activation.

One task that has been used very successfully to engage the mesolimbic system is the monetary incentive delay task [MID; (Knutson, Westdorp, Kaiser, & Hommer, 2000a)]. Numerous functional magnetic resonance imaging (fMRI) studies in adults show robust and replicable activation in ventral and dorsal striatum as well as the thalamus and cortical regions. Each trial of the MID task is typically composed of three separate phases (Figure 1): a cue or anticipation phase, a target or response phase, and a feedback or outcome phase. In the cue phase, a certain monetary amount is presented to the subject as an incentive to respond quickly to the target in the next phase. The monetary amount can be positive, negative or neutral (no consequences for responding fast enough or too slowly). Positive incentives mean that the subject earns the amount for correct (i.e., fast) responses or fails to earn that amount for incorrect (i.e., slow) responses during the target phase. Negative incentives mean that the subject avoids losing the amount for correct responses or incurs a loss for incorrect responses. The neutral condition has no consequences on earnings or losses.

Somewhat surprisingly, at least with respect to the dual systems hypothesis, adolescents do not necessarily show stronger MID activation than adults in mesolimbic circuitry. Although (Galvan, et al., 2006) reported greater mesolimbic response in 13–17 year olds compared to adults or younger children (7 to 11 years) in a MID-like task, several other studies have reported reduced mesolimbic activation in adolescents compared to adults, or no differences ((Bjork, et al., 2004b; Bjork, Smith, Chen, & Hommer, 2010; Cho, et al., 2013; Geier, Terwilliger, Teslovich, Velanova, & Luna, 2010; Lamm, et al., 2014; Vaidya, Knutson, O'Leary, Block, & Magnotta, 2013). In fact, a longitudinal study of MID response from mid- (16 years of age) to late adolescence (20 years of age) also reported reduced striatal response during mid-adolescence, especially for high incentive values, regardless of valence (Lamm, et al., 2014). However, another longitudinal fMRI study (Heitzeg, et al., 2014) reported that the nucleus accumbens response to rewards increased until mid-to-late adolescence, then declined after about age 20, but that study did not have a large sampling of the 16-to-20 year age range and the majority of the subjects were children of alcoholics. (Geier, et al., 2010) designed an anti-saccade MID task so that cue assessment could be analyzed separately from response preparation. In that task, adolescents showed reduced ventral striatal activation for cue assessment, but enhanced activation for response preparation, compared to adults. Consequently, adolescents show enhanced mesolimbic response compared to adults in some studies, but this may depend on the particular task phase that is sampled.

Another potential explanation for the mixed findings in adolescents on the MID task is that individual differences in genetic risk and personality or temperament may modulate mesolimbic response. For example, mesolimbic responses on the MID task are weaker in individuals who low in inhibition (Guyer, et al., 2006) or have a higher risk-taking bias (Schneider, et al., 2012). People who are high in impulsivity show less differentiation in mesolimbic fMRI among small incentive values (Vaidya, et al., 2013). In addition, youths and adults with ADHD (Hoogman, et al., 2011; Plichta & Scheres, 2014; Scheres, Milham, Knutson, & Castellanos, 2007), adolescent smokers (Peters, et al., 2011) and adolescent Met carriers (Nees, et al., 2015) also show reduced mesolimbic responses on the MID. On the other hand, greater mesolimbic MID response has been associated with higher approach motivation (Hahn, et al., 2009; Kennis, Rademaker, & Geuze, 2013; Simon, et al., 2010), trait positive affect (Wu, Samanez-Larkin, Katovich, & Knutson, 2014), higher sensation seeking (Abler, Walter, Erk, Kammerer, & Spitzer, 2006; Bjork, Knutson, & Hommer, 2008), and presence of or risk for externalizing disorders (Bjork, Chen, Smith, & Hommer, 2010; Bjork, Smith, Chen, & Hommer, 2011; Heitzeg, et al., 2014; Hoogman, et al., 2011; Yau, et al., 2012). In addition, high impulsivity shows a trend to be positively correlated with sensitivity to large versus small incentive values (Vaidya, et al., 2013). Together, the body of evidence thus far does not paint a clear picture as to whether approach motivation is associated with a stronger mesolimbic reward response as tapped by the MID task. This motivates the need for more studies of neurobehavioral incentive motivation response in adolescence.

One factor to consider regarding the discrepancy in the literature is that the majority of studies using the MID task in adolescence have focused on impulsivity and approach motivation (versus avoidance and inhibition; but see (Guyer, et al., 2006)), with good reason as these personality traits are risk factors in developing substance abuse, which in turn, is related to alterations in mesolimbic circuitry function. However, avoidance personality traits also contribute to substance abuse liability (Cheetham, et al., 2014; Marti, Stice, & Springer, 2010; Mellos, Liappas, & Paparrigopoulos, 2010). In addition, avoidance tendencies have been associated with an amygdala-centered emotional system (Kennis, et al., 2013) which may be hypersensitive to threat or hypo-sensitive to reward during adolescence (Ernst, 2014). Consequently, to address the possibility that different underlying personality dimensions can drive attenuation or amplification of mesolimbic reward response in adolescents and adults, the present study will further examine personality modulation of MID mesolimbic response using multiple personality measures that tap into approach, avoidance, and impulsivity constructs.

The MID paradigm captures many behaviors that are relevant for understanding incentivized motivation and the path to abuse or dependence. The cue phase is associated with *appetitive behavior*, or the wanting and craving of a stimulus, whereas the feedback phase is associated with *consummatory processing*, or the liking of a stimulus upon receipt. These two behaviors are often dissociated in addiction (Robinson & Berridge, 1993). In the present paper, we adopt the terms “expectation” (of reward) in place of “appetitive” processing and “reward receipt” in place of “consummatory” processing. Another aspect of the MID task that is important for substance dependence is the anticipation or receipt of potential rewards versus losses. This aspect of the task captures *incentive valence*, which is an important dimension of motivated behavior as it can tease apart reward (or gain) sensitivity versus loss sensitivity. MID tasks typically vary the amount of the incentives, thereby manipulating *incentive magnitude*. A normative response would reflect greater motivation for large incentives relative to small incentives. However, in some cases of incentive motivation using small and large doses of drugs, addicts or individuals at risk for drug abuse work as hard for small as for high doses (Lamb, et al., 1991; Stoops, et al., 2007).

Few prior studies that have used the MID task in adolescents have addressed expectation versus receipt of reward, small versus large incentives (incentive magnitude) and gains versus losses (incentive valence) all in the same study. In many cases, only gains and neutral conditions were included (Galvan, et al., 2006; Geier, et al., 2010; Heitzeg, et al., 2014; Nees, et al., 2012; Nees, et al., 2015; Peters, et al., 2011; Schneider, et al., 2012; Vaidya, et al., 2013); hence, a full appreciation of incentive valence is not possible without including losses. Also, some prior studies did not manipulate the magnitude of incentives (or did not convey the magnitude information to the subjects). Finally, many of the MID tasks in prior studies were not designed to separate out the different trial phases from each other to allow for deconvolving anticipation from outcome processing (e.g., (Galvan, et al., 2006; Lamm, et al., 2014)). Consequently, one goal of the present study was to more fully sample the parameter space of incentivized motivation using the MID task by addressing all of these facets of motivated behavior.

To accomplish this goal, the methodology described by (Joseph, et al., 2015) was used. Incentive magnitude was parametrically manipulated across 5 values (lose \$5, lose \$.5, neither win nor lose, win \$.5, win \$5) to isolate mesolimbic MID response. fMRI response across the 5 incentive values constitutes an fMRI incentive function. The incentive function can be described linearly or fit to a higher-order polynomial function. Fitting the incentive function to a 2nd order polynomial allows decomposing the function into linear and quadratic components (Figure 1b–c). The linear component of the MID incentive function reflects the slope. As shown in Figure 1b, if fMRI response does not vary across the 5 incentive levels, the slope is 0 and the particular brain region is not differentially sensitive to incentive valence. However, if the slope is positive, the region is more sensitive to reinforcement than avoidance contingencies during the cue phase (or gain than loss during the feedback phase); if the slope is negative, the region is more sensitive to avoidance than reinforcement during the cue phase (or loss than gain during the feedback phase). Consequently, the slope parameter of the MID incentive function reflects sensitivity to incentive valence. As shown in Figure 1c, the quadratic component reflects the degree of curvature of the incentive function. If this parameter is 0, then there is no curvature and the incentive function can be described linearly. Curvature of 0 reflects little sensitivity to incentive magnitude. Positive curvature reflects a function with a minimum vertex, yielding a concave function, which reflects a greater response to high magnitudes than to low magnitudes. Negative curvature reflects a function with a maximum vertex, yielding a convex function, which reflects a greater response to low magnitudes than to high magnitudes. In the present study, each individual's fMRI incentive response was fit to a 2nd order polynomial to yield two parameters of interest, slope (reflecting incentive valence) and curvature (reflecting incentive magnitude).

Another goal of the present study was to examine personality modulation of mesolimbic response by focusing on a non-clinical sample of adolescents and adults. In clinical samples, substance users or even subjects defined to be "at risk" for psychiatric disorders, the presence of certain behavioral tendencies may be a consequence of substance use, psychopathology or familial risk, rather than a trait that could predispose an individual to subsequent behavioral and mental health problems. Therefore, the present study aimed to better understand how personality modulates mesolimbic response apart from clinical symptomology by using healthy young / emerging adult (18–25 years of age) and young adolescent (11–14 years of age) subjects. In addition, a related goal was to sample a variety of different personality measures including the Urgency, Premeditation, Perseverance and Sensation Seeking Scale (Whiteside & Lynam, 2001), Big Five Inventory (John & Srivastava, 1999), Behavioral Inhibition System / Behavioral Activation System scales (Carver & White, 1994) and Sensitivity to Reward / Punishment scale (Torrubia, Avila, Molto, & Caseras, 2001). These scales not only include measures of impulsivity and approach-related traits but also measures of behavioral inhibition and neuroticism which are associated with the risk profile for substance use and dependence (Anderson, Tapert, Moadab, Crowley, & Brown, 2007; Kashdan, Vetter, & Collins, 2005; Magid & Colder, 2007) (Magid, Maclean, & Colder, 2007) (Stautz & Cooper, 2013). The primary hypothesis was that although adolescents, as a group, may not activate mesolimbic circuitry more strongly than adults on the MID, approach-related personality traits may be associated with a stronger MID response, especially to anticipation of or feedback about gains. The present experimental design will be able to tease apart whether this personality modulation is related most to expectation versus receipt of reward, incentive valence or incentive magnitude.

2. Materials and Methods

2.1 Participants

Fifty-one healthy young adults (18–25 years) and 27 adolescents (11–14 years) completed the Brief Sensation-Seeking Scale (Hoyle, Stephenson, Palmgreen, Lorch, & Donohew, 2002) online via RedCap (Harris, et al., 2009). Subjects were recruited from two different institutions (15 adult subjects were enrolled at the University of Kentucky and the remainder of the subjects were enrolled at the Medical University of South Carolina). Individuals with scores in the top and bottom quartiles of population-based norms or based on prior studies (Harrington, et al., 2003; Palmgreen, Donohew, Lorch, Hoyle, & Stephenson, 2001) were then contacted and invited to participate in the fMRI study. High sensation seekers (HSS) were defined as males or females with BSSS scores >31. Low sensation seekers (LSS) were defined as males with BSSS scores < 28, and females with BSSS scores < 26. fMRI data from 2 adults and 3 adolescents were excluded due to excessive head motion, leaving 49 adults, with 26 HSS (9 males) and 23 LSS (11 males), and 24 adolescents, with 16 HSS (7 males) and 8 LSS (3 males). Other exclusion criteria included the presence of metal in or on the body, pregnancy, a neurological or psychiatric diagnosis, learning disability, a history of substance abuse or smoking, current use of central nervous system medications, left-handedness (Oldfield, 1971), and poor vision that could not be corrected. Pregnancy and drug use were assessed prior to sessions via urinalysis. All individuals provided informed consent in accord with the University's Institutional Review Board and received financial compensation.

2.2 Design and Stimuli

The task was adapted from Knutson, et al., (2000b) and Bjork et al., (2004a) (Figure 1a). Participants could earn or lose money depending on response time to a white rectangle "target" stimulus. Each trial consisted of cue, target and feedback phases. The cue phase displayed the trial incentive condition (−\$5, −\$.5, 0, +\$.5, +\$5) for 1500 ms duration followed by a variable duration (1850 to 6150 ms). The target phase consisted of a white rectangle presented centrally for 250 msec initially. Participants were instructed to respond as quickly as possible when the rectangle appeared. If the response was made during the time that the target was displayed, the participant earned the positive incentive or avoided losing the negative incentive. If the response was delayed, the participant did not win the positive amount or incurred a loss of the negative amount. Responses during the \$0 incentive trials had no effect on losses or earnings. Responses were made using the index finger of the right or left hand, counterbalanced across participants. After the initial 2 trials, the duration of the target stimulus was adjusted in increments of +/−10 ms (up to a maximum of 360 ms) to keep average accuracy across trials at approximately 67%. Percentage of adjustments across participants ranged from 22% to 67%, (45% average). The feedback phase displayed a blue check mark to indicate timely (i.e., accurate) responses, and notification of gain on positive reinforcement trials, and no loss on avoidance trials, or a red

X to indicate delayed (i.e., inaccurate) responses, and notification of no gain on positive reinforcement trials and loss on avoidance trials, with the running total of earnings displayed simultaneously (for 2000 msec). Participants received the amount they earned during the MID task as a component of study compensation.

The three trial phases were separated by intervals of 2, 4 or 6 seconds to allow for deconvolution of the fMRI response associated with the different phases. Trial duration ranged from 9 to 21 sec. Nine repetitions of 5 incentive levels were presented across two runs (23 or 22 trials in a run) to provide a break for participants while in the scanner. The order of the 45 trials was determined using a randomization algorithm (http://surfer.nmr.mgh.harvard.edu/optseq), with 362 total brain volumes across both runs. The order of the trials was the same for every participant.

2.3 Procedure

Adults completed all procedures in a single visit and adolescents typically completed two visits (Visit 1 involved completing personality and cognitive measures, mock scanner training and anatomical scanning; Visit 2 involved fMRI testing). Participants completed two other tasks while in the scanner (emotional induction and viewing public service announcements), but results from these tasks are not reported here. Order of the three tasks in the scanner was counterbalanced across subjects. Participants also completed several personality assessments including UPPS (Whiteside & Lynam, 2001), Big Five Inventory (John & Srivastava, 1999), BIS/BAS scales (Carver & White, 1994) and sensitivity to reward / punishment scale (Torrubia, et al., 2001). Other measures included a Pubertal Developmental Scale (Martin, et al., 2002) (Peterson, Crockett, Richards, & Boxer, 1998), forward and backward digit span, Peabody Picture Vocabulary Test, Fourth Edition (PPVT, (Dunn & Dunn, 2007) and Ruff's 2 & 7 selective attention test (Ruff, Niemann, Allen, Farrow, & Wylie, 1992).

2.4 Data Acquisition

A 3-T Siemens Trio MRI system was used to collect echoplanar imaging data (repetition time = 2.0 s, echo time = 30 ms, flip angle = 81°; 36 axial slices: matrix = 64 × 64, 3.7-mm^3 resolution, collected in two separate scans including 184 and 178 volumes), a high-resolution T1-weighted MPRAGE anatomical volume (192 sagittal slices, matrix = 224 × 256, field of view = 224 × 256 mm^2, slice thickness = 1 mm, no gap, TE=2.56ms, TI=1100ms, TR=2100ms) and a fieldmap for geometric distortion correction. The only difference in acquisition parameters across the two data collection sites was that the MPRAGE had TE=2.38 ms at the Medical University of South Carolina site. Otherwise, scanning parameters were identical as was the version of the hardware (TrioTim) and software (Syngo MRB17). Stimuli were presented using a high-resolution rear-projection system (Avotec, Stuart, FL), and responses were recorded using a fiber-optic response pad (MRA Inc., Washington, PA). A computer running E-Prime (Version 1.1 SP3, Psychology Software Tools, Pittsburgh, PA) controlled stimulus presentation, which was synchronized with the collection of brain volumes via trigger pulses from the magnet.

2.5 fMRI Analysis

The images in each participant's time series were motion-corrected, geometric distortion corrected, spatially smoothed with a 3-D Gaussian kernel (full width at half maximum = 7 mm), and high-pass filtered with a cutoff period of 100s using FSL v. 4.1 (http://www.fmrib.ox.ac.uk/fsl). Customized waveforms for each event type (5 incentive levels × 3 task phases) were constructed then convolved with a gamma hemodynamic response function. A temporal derivative was also added for each event type. The statistical parametric maps were then registered via the subject's T1 anatomical scans to the MNI-2mm template. For the primary analysis, eight anatomical ROIs (aROIs) were defined according to Harvard-Oxford Subcortical Structural Atlas, including bilateral Thalamus, NAc, Putamen and Caudate. These regions were chosen based on the importance of mesolimbic circuitry in the MID task. fMRI signal (percent signal change) for each of the 15 experimental conditions for each subject was extracted using FSL's featquery tool.

For the secondary, exploratory analyses, statistical maps were generated for each subject for the contrasts of interest. We tested several trends at the group level: gain-sensitivity [−1, −0.1, 0, 0.1, 1], loss-sensitivity [1, 0.1, 0, −0.1, −1], positive magnitude sensitivity [0.56, −0.34, −0.44, −0.34, 0.56] and negative magnitude sensitivity [−0.56, 0.34, 0.44, 0.34, −0.56] for each of the two trial phases (cue and outcome). (Note that the weights used for the magnitude-sensitive contrasts are the demeaned versions of contrasts [1, 0.1, 0, .1, 1] and [−1, 0.1, 0, 0.1, −1]). In order to estimate these trends, for each contrast, the model included one EV for all adult effects, one EV for all adolescent effects, in addition to confound EVs which model each subjects' mean effect. Using FMRIB's Local Analysis of Mixed Effects module, group statistical parametric maps were obtained and thresholded at z=2.3, corrected cluster p=0.05. Statistical maps were generated for adults, adolescents and for the contrast of adults > adolescents.

2.6 Anatomical regions of interest (aROI) analysis

For the primary analysis, curve-fitting with a 2nd order polynomial was conducted for each subject to characterize the shape of the fMRI incentive function. Curve fitting yielded a slope (b1) and a curvature (b2) parameter for each task phase (cue, feedback), each subject and each aROI. The slope parameter reflects incentive valence and the curvature parameter reflects incentive magnitude. These parameters for each subject were then submitted to a 2 (age group) × 2 (SS group) ANOVA conducted separately for each parameter (b1 cue, b2 cue, b1 feedback, b2 feedback) and aROI. In each aROI and for each age group separately, the four parameters were also correlated with the three major personality constructs that resulted from dimension reduction (described below).

Another set of ANOVAs was conducted for each aROI, with percent signal change collapsed over incentive levels as the dependent measure, age group and SS group as between-subjects measures. Because this analysis is based on percent signal change, rather than slope and curvature parameters, it allows a somewhat more direct comparison to other MID studies that have typically analyzed percent signal change.

2.7 Dimension reduction for personality variables

Given that we had collected a rich set of personality measures, some of which were highly intercorrelated, we conducted a dimension reduction of the personality measures using principal components analysis (PCA; IBM SPSS Statistics, Chicago, IL) with varimax rotation. The PCA revealed four components with eigenvalues > 1 that explained 65.3% of the variance. These components were used for subsequent analyses. The component loadings (Table 1) indicated that the first dimension (22.3 % explained variance) included high sensation seeking, sensitivity to reward and the three behavioral activation subscales (reward, drive and fun). We termed this dimension “approach.” The second dimension (16.0 % explained variance) included high neuroticism, sensitivity to punishment, behavioral inhibition and low extraversion. We termed this dimension “avoidance.” The third dimension (14.5 % explained variance) included high lack of premeditation and lack of perseverance and low conscientiousness. We termed this dimension “impulsivity.” The fourth dimension (12.5 % explained variance) included high agreeableness and openness and low urgency. We termed this dimension “Openness.” Scores on each of these dimensions were then used in the correlations with slope and curvature parameters in each aROI.

3. Results

3.1 MID Behavioral Response

Overall accuracy was 64.2% for adults and 61.9% for adolescents. Inspection of individual-subject performance (average accuracy across all experimental conditions) revealed that 11 subjects (4 adolescents and 7 adults) had accuracy less than 60%. Because poor performance on this task directly reflects earnings and the feedback provided to the subjects, poor accuracy could lead to greater frustration or negative affect, compared to average performance. For this reason, these 11 subjects were omitted from subsequent analyses.

A 3-way repeated measures mixed ANOVA with age group (adults, adolescents) and SS group (HSS, LSS) as between subjects factors and incentive value (−\$5, −\$.5, \$0, \$.5, \$5) as a repeated measure revealed only a main effect of incentive value on accuracy, $F(4, 232) = 18.3$, $p = .0001$. Although incentive functions appear to be slightly different by age group or SS group (Figure 2a–b), no interactions were significant. However, the main effect of age was significant, $F(1, 58) = 5.8$, $p = .019$, with adults slightly more accurate than adolescents (66.4% v. 64.1%, respectively). For the analysis of speed on correct trials (i.e., trials in which subjects responded while the target was still on the screen), The main effect of incentive was significant, $F(4, 224) = 5.2$, $p = .001$, and the SS × Age Group interaction was marginally significant, $F(4, 224) = 2.3$, $p = .066$. As shown in Figure 2c, adolescents tended to be less magnitude-sensitive than adults. Neither the Incentive × SS interaction nor main effects were significant (Figure 2d).

3.2 Age × SS ANOVAs in aROIs

Before conducting the primary analyses, we examined average percent signal change in each of the 8 aROIs as a function of test site in adults using a one-way ANOVA to determine whether site had an effect on overall fMRI signal. No significant differences emerged in any of the 8 aROIs (.47 < p < .97), indicating that fMRI signal intensity was, on average, the same across the two test sites. Therefore, subsequent analyses of fMRI data collapsed data across site.

For the primary analysis, the 2-way ANOVAs revealed no significant main effects or interactions for cue-valence or feedback--valence. However, the main effect of age was significant in all of the 8 aROIs for cue-magnitude (Table 2). Adults showed greater magnitude sensitivity than adolescents, indicating greater sensitivity to large incentives than small incentives (Figure 3). Neither the main effect of SS nor the Age × SS interaction was significant in these ROIs for cue-valence.

For feedback-magnitude, the main effect of age was significant in the bilateral caudate and bilateral putamen (Table 3; Figure 4). Adults were more magnitude-sensitive in the bilateral caudate and exhibited negative curvature. Adolescents showed greater magnitude-sensitivity and positive curvature in the bilateral putamen. Although the age differences in magnitude sensitivity look pronounced in the bilateral NAc, the age effects were not significant. Neither the main effect of SS nor the Age × SS interaction was significant in any of these ROIs, except for a significant effect of SS in the left NAc. In this case LSS showed more negative curvature than HSS.

For the 3-way ANOVAs conducted on percent signal change in each aROI, the effect of phase was significant in the left, $F(1, 58) = 19.5$, $p = .0001$, and right caudate, $F(1, 58) = 19.5$, $p = .0001$, and left, $F(1, 58) = 24.3$, $p = .0001$, and right NAc, $F(1, 58) = 25.8$, $p = .0001$. The phase effect in the bilateral caudate and left NAc was driven by positive fMRI signal in the cue phase and negative fMRI signal (deactivation) in the feedback phase. In the right NAc, the difference was driven by a greater fMRI signal in the cue phase than in the feedback phase (although both signals were positive). The main effect of age was only significant in the left, $F(1, 58) = 10.7$, $p = .002$, and right putamen, $F(1, 69) = 6.5$, $p = .013$ in which adults showed a greater signal than adolescents. No other main effects or interactions were significant in any of the aROIs.

3.3 Personality modulation of MID fMRI response

Tables 4 and 5 summarize the correlations between fMRI incentive parameters in the 8 aROIs and personality constructs for adults and adolescents, respectively. Individual variability in MID fMRI response in adults was associated primarily with the impulsivity construct whereas individual variability in adolescents was associated most strongly with the impulsivity construct, but there were also some correlations with avoidance and approach constructs. Another difference by age group was that individual variation in MID response in adults was associated with both the cue and feedback stages, but individual variation in MID response in adolescents was primarily associated with the cue stage. Finally, individual variation in adults was linked to incentive magnitude whereas individual variation in adolescents was linked mostly to incentive valence.

To better illustrate these individual differences in fMRI incentive functions, Figure 5 shows fMRI response as a function of incentive level for adults high or low in impulsivity in regions where correlations between the impulsivity construct and the curvature parameter were significant. Impulsivity and curvature were significantly correlated in the cue phase in adults in the bilateral putamen and left thalamus. Adults high in impulsivity showed reduced sensitivity to high incentive magnitude compared to adults low in impulsivity (Figure 5a). Impulsivity and curvature were also significantly correlated in the feedback stage in adults in the bilateral caudate, bilateral putamen and left thalamus (Figure 5b, left thalamus not shown). Adults high in impulsivity showed less magnitude sensitivity overall, but greater sensitivity to high incentives in the putamen and thalamus, compared to adults low in impulsivity. In the caudate, however, adults high in impulsivity show reduced sensitivity to low incentives compared to adults low in impulsivity.

For adolescents, the personality construct that was significantly correlated with mesolimbic neurobehavioral incentive functions was impulsivity, but marginally significant correlations emerged for the avoidance and approach constructs. Impulsivity and avoidance modulated cue phase responses whereas the approach personality construct modulated feedback phase responses. Most of these modulations were in terms of the incentive valence parameter, some of which are shown in Figure 6. For the marginal avoidance correlations, subjects low in avoidance showed greater gain sensitivity than subjects high in avoidance in the cue phase. For the approach construct, subjects high in approach tendencies showed greater gain-sensitivity than subjects low in approach tendencies during the feedback stage. The overall pattern for impulsivity was that adolescents high in impulsivity showed greater sensitivity to potential gains whereas adolescents low in impulsivity showed greater sensitivity to potential losses.

3.4 fMRI activation in the cue phase

Both adolescents and adults showed activation for gain-sensitivity (Figure 7a), but adults (yellow) show more extensive activation than adolescents (pink). In adults, the activation spans frontal, opercular and occipital cortex as well as the expected striatal activation. Adolescents show activation in occipital and anterior temporal cortex and some striatal activation (putamen and thalamus) but not the expected ventral striatum / nucleus accumbens activation and no activation in frontal cortex. Despite these seemingly large differences by age group, the contrast of adults versus adolescents yielded no significant clusters.

Both adolescents and adults showed activation for the magnitude-sensitive contrast in the cue phase (Figure 7b), with adults activating large expanses of lateral occipital, frontal, opercular and striatal regions. Adolescents showed some activation in the ventral striatum, but the direct contrast of adults versus adolescents yielded differences primarily in the striatum (nucleus accumbens and thalamus).

Table 6 lists all of the activation maxima for the cue phase contrasts. No clusters of activation survived for the loss-sensitive and negative-magnitude sensitive contrasts.

3.5 fMRI activation in the feedback phase

For the gain-sensitive contrast in the feedback phase (Figure 7c), adults show extensive striatal and occipital activation, whereas no activation survived threshold in adolescents. The direct contrast of adults versus adolescents (green) yielded activation primarily in the ventral striatum. For the magnitude-sensitive contrast in the feedback phase (Figure 7d), adults show strong focal activation in the anterior cingulate whereas adolescents show strong activation in the putamen, thalamus and insula. For the negative magnitude-sensitive contrast in the feedback phase (Figure 7e), adults show strong activation in the ventral and dorsal striatum (caudate nucleus) whereas no activation emerged in adolescents. The direct contrast of adults versus adolescents revealed activation that overlapped with the magnitude-sensitive activation for adolescents (Figure 7d, pink) which was not surprising since the negative magnitude-sensitive contrast is simply the inverse of the magnitude-sensitive contrast. However, because the negative magnitude-sensitive activation revealed by the adults versus adolescents contrast did not overlap extensively with the activation for adults alone, this reflects deactivation, which we do not presently interpret. Table 7 lists all of the activation maxima for the feedback phase contrasts.

4. Discussion

The present study examined neurobehavioral response in incentive motivation in healthy adolescents and adults. Given that prior literature findings are mixed as to whether adolescents hyper-activate or hypo-activate mesolimbic circuitry compared to adults, the present study examined age group differences across different aspects of incentive motivation: different motivation states (expectation versus receipt of reward), incentive valence and incentive magnitude. In addition, the present study examined modulation of neurobehavioral MID response by four personality constructs derived from multiple personality scales: approach, avoidance, impulsivity and openness. Overall, the present findings show clear differences between adolescents and adults in the recruitment of mesolimbic reward circuitry. Adolescents are less magnitude-sensitive than adults, but are sensitive to valence in some components of the mesolimbic reward system. However, this valence sensitivity was modulated by impulsivity, avoidance and approach personality constructs in adolescents. High-impulsive and low-avoidant adolescents showed gain sensitivity during expectation of reward whereas adolescents high in approach tendencies showed gain sensitivity during receipt of reward. Adolescents high in avoidance showed greater mesolimbic response to losses. Adult mesolimbic responses were also modulated by personality, but this modulation was primarily by impulsivity.

4.1 Adolescent versus adult mesolimbic response differences in signal magnitude

The analysis of fMRI signal magnitude within anatomical ROIs did not reveal many age differences. The only exception was that adults showed overall greater activation of the bilateral putamen than adolescents, but this was the case across incentive values and motivational states. (Cho, et al., 2013) also reported that, during cue anticipation, adults activated the right putamen more strongly than adolescents (for both gains and losses). Activation in the putamen is very often reported in fMRI MID studies but its specific role in incentive motivation is rarely discussed. However, recent studies have implicated the putamen in risk for substance dependence. (Joseph, et al., 2015) reported that reduced MID magnitude sensitivity in the left putamen was related to problem drinking in a non-clinical young adult sample. Although it was not the only region involved in this association it had one of the strongest correlations. Also, (Nees, et al., 2015) reported that adolescent Met carriers with high levels of current alcohol use showed reduced MID anticipatory activation in the left putamen compared to Met carriers with low current use. In addition, low left putamen response on MID outcomes predicted likelihood of drinking 2 years later. Although a more precise role of the putamen has yet to be determined for incentive motivation tasks, these recent findings together with the present one suggest that a reduced putamen response is associated with a more immature neurobehavioral profile and that this profile is also associated with risk for alcohol problems.

The secondary analysis of whole-brain activation using voxel-wise general linear modeling (GLM) revealed more age differences than the ROI analysis. There were no conditions in which adolescents showed more activation than adults, but there were several conditions in which adults showed greater activation than adolescents (Figure 7, green activation): cue magnitude-sensitivity, feedback gain-sensitivity and feedback negative magnitude-sensitivity. These age differences were largely in mesolimbic circuitry (see Tables 6 and 7) but gain-sensitivity during feedback implicated greater frontal cortex recruitment in adults. Given delayed frontal cortex maturation, it is not surprising that adolescents would show less frontal recruitment. However, it is possible that some aspects of the GLM reduced signal amplitude in adolescents. Calhoun et al. (Calhoun, Stevens, Pearlson, & Kiehl, 2004) reported that the use of temporal derivatives in GLM can reduce signal amplitude if hemodynamic delays are long. Hence, if adolescents show a greater hemodynamic delay, then the GLM analysis would underestimate signal amplitude in adolescents. This is an important point to consider when comparing age groups through voxel-wise GLM. The same concern could apply to the GLM analysis in the present study, but that analysis was secondary to the anatomical ROI-based analysis. The ROI analysis, which was the primary analysis in the present study, used percent signal change extracted from the parameter estimate maps for each condition versus baseline. Hence, the ROI analysis was not subject to the effects of temporal derivatives, as these are only applied when GLM is used. We note, though, that the age differences revealed with the ROI analysis (i.e., greater magnitude sensitivity in adults during cue and curvature differences during feedback) are largely supported by the GLM analysis (see Figure 7).

4.2 Adolescent versus adult mesolimbic response to incentive valence

An influential proposal about adolescent brain development is that adolescents are more reward-sensitive than adults, owing to the somewhat earlier maturation of mesolimbic dopamine circuitry relative to the more protracted development of frontal cortical regions involved in top-down behavioral regulation (Chambers, et al., 2003; Steinberg, 2008). This view has garnered support from a number of different cognitive and affective neurobehavioral findings, but with respect to the MID task, findings have been mixed. In the present study, adolescents as a whole were not more gain-sensitive than adults because age effects on incentive valence did not emerge. However, incentive valence was modulated by personality in adolescents but not adults. As discussed more in Section 4.5, adolescents who exhibited higher impulsivity, greater approach tendencies, or lower avoidance tendencies do show greater gain-sensitivity than adolescents low in impulsivity and approach tendencies or high in avoidance tendencies.

4.3 Adolescent versus adult mesolimbic response to incentive magnitude

The most robust finding concerning age groups was that adolescents were clearly less sensitive to incentive magnitude than adults in most mesolimbic regions during the cue phase and in the caudate nucleus in the feedback phase. As illustrated in Figure 3, the fMRI incentive functions for the cue phase in adolescents were flat in these regions, indicating small differences in signal magnitude or very non-systematic fMRI signal differences as a function of incentive magnitude. Other studies have similarly reported that adolescents are less sensitive than adults to incentive magnitude or that their mesolimbic incentive functions are more variable than adults (Bjork, et al., 2004b; Vaidya, et al., 2013). For example, (Vaidya, et al., 2013) showed that right ventral striatal response in adolescents did not reflect the absolute value of a reward, whereas in adults the higher the absolute value the greater the fMRI signal. In addition, that same study showed that when a given incentive value ($1) was the greater or lesser of incentive values (e.g., $1 v. $.20 or $1 v. $5) right ventral striatal response was the same for both conditions in adolescents but not in adults. In other words, adolescents were not sensitive to the relative value of incentives in the right ventral striatum. As (Vaidya, et al., 2013) argue, this insensitivity to relative value may reflect a failure to contextualize reward values, which in turn, may be due to immature frontal circuitry associated with valuation. We do note, however, that adolescents were more magnitude-sensitive than adults in the bilateral putamen during feedback, even though overall they showed a reduced signal (as discussed in Section 4.1). Adolescents showed clear positive curvature indicating sensitivity to large incentives. Hence, even though adolescents were less magnitude-sensitive than adults, the response in the putamen is an exception. As mentioned above, the role of the putamen in monetary incentive delay tasks is not well understood, so future studies are needed to better elucidate its function.

4.4 Adolescent versus adult mesolimbic response for different motivational states

Age differences were apparent for both expectation (cue) and receipt of reward (feedback). Prior studies more often reported age differences for the cue phase than other phases (Bjork, et al., 2004b; Bjork, Smith, et al., 2010; Geier, et al., 2010; Lamm, et al., 2014), and like the present study, there is reduced activation or sensitivity to magnitude in adolescents during cue. However, unlike prior studies, the present study found age differences in the feedback stage as well. The lack of age differences in the feedback stage in other studies may be partly due to the fact that either the feedback phase was not analyzed separately or the task was not designed to allow for the cue and feedback phases to be analyzed separately. However, those studies that did analyze the feedback phase separately reported no differences between adults and adolescents in receipt of reward (Bjork, et al., 2004b; Bjork, Smith, et al., 2010; Vaidya, et al., 2013). We suspect that one reason for the age effects in the present study was the separation of the fMRI incentive functions into valence (slope) and magnitude (curvature) parameters. As shown in Figure 4 there are very clear age differences in curvature. However, if fMRI signal were simply contrasted between gain and loss conditions (as in prior studies) the age differences would be much less pronounced.

4.5 Adolescent versus adult mesolimbic modulation by personality

Among both adults and adolescents, the impulsivity construct explained more variability in mesolimbic MID response than any other personality dimension. Impulsivity in the present study was largely characterized by more cognitively oriented behaviors such as failing to think through consequences (lack of premeditation) and not maintaining focus to see tasks to completion (lack of perseverance and low conscientiousness). Some prior studies reported that subjects who are high in impulsivity (Vaidya, et al., 2013) or low in inhibition (Guyer, et al., 2006) have weaker mesolimbic responses on the MID task. In fact, the impulsivity measure used by (Vaidya, et al., 2013) also included elements of conscientiousness, similar to the present impulsivity measure. In line with these prior reports, the overall activation levels of high-impulsive adults were lower than those of low-impulsive adults, at least in the cue phase. Yet other reports have described hyperactivation with high impulsivity in the typical population (Plichta & Scheres, 2014). We suspect that some of this discrepancy can be attributed to the various contrasts of conditions that have been used to assess hyper- versus hypoactivation. Adopting the present approach of decomposing the MID response into valence and magnitude parameters has shed additional light on this issue.

Specifically, the neurobehavioral profile of adults high in impulsivity was marked by weakened sensitivity to incentive magnitude during both the cue and feedback stages. However, in the cue stage (Figure 5a), high-impulsive adults showed a reduced response to potential loss compared to potential gain (whereas low impulsive adults showed about the same fMRI response to gains and losses). Similarly, the neurobehavioral profile of adolescents high in impulsivity was marked by greater gain sensitivity during cue anticipation (Figure 6c). The greater gain sensitivity (or reduced loss sensitivity) profiles may reflect an aspect of impulsivity related to valuation of potential outcomes in that negative consequences are not weighed as heavily. In the feedback stage (Figure 5b), high impulsive adults showed little variation in magnitude of fMRI signal as a function of incentive value in the bilateral putamen and thalamus. Adolescent MID responses were not modulated by impulsivity during feedback. Given that the feedback phase is a period of processing outcomes and consequences of behavior, it is a potential opportunity to learn from behaviors and appropriately adjust future actions. High impulsive adults show reduced sensitivity to or evaluation of outcomes of different magnitudes. This could reflect less involvement of frontal circuitry, which is compromised in high-impulsive adults (Matsuo, et al., 2009). In fact, both youth and adults with ADHD show weaker mesolimbic MID responses compared to controls (Edel, et al., 2013; Plichta & Scheres, 2014; Scheres, et al., 2007).

In addition to impulsivity, other personality traits modulated neurobehavioral MID response in adolescents (albeit marginally), but not in adults. One hypothesis of the present study was that approach-related personality traits would be associated with greater gain-sensitivity, as evidenced in several prior studies of both adolescents and adults (Bjork, et al., 2008; Hahn, et al., 2009; Simon, et al., 2010; Weiland, et al., 2013; Wu, et al., 2014). In support of this, the approach construct was correlated with neurobehavioral MID response in adolescents during reward receipt, with high approach tendencies associated with greater gain sensitivity. Because the approach construct included aspects of positive affect such as reward, fun, and sensation seeking, the greater gain sensitivity during feedback in high approach subjects may reflect the reinforcing effects of positive outcomes which may guide future behaviors and tendencies to seek out rewarding experiences. In contrast, the avoidance construct, which included elements of negative affect, neuroticism and inhibition, modulated neurobehavioral MID response during reward expectation: adolescents low in avoidance tendencies showed greater gain-sensitivity than adolescents high in avoidance, or conversely, adolescents high in avoidance showed greater sensitivity to loss during the anticipation stage. Consequently, the avoidance construct, may be more relevant for modulating incentive context during expectation.

4.6 Limitations

One potential limitation of the present study was the relatively small sample size (especially for the adolescent group), which could limit conclusions about individual differences in personality. Although the present sample was small, some of the traits identified in this study are consistently implicated in risk for substance use in larger scale studies. As an example, (Whelan, et al., 2014) examined the role of a range of personality, genetic, history, brain imaging / cognitive measures in classifying adolescent binge drinkers (14 years of age) and predicting future binge drinking (at age 16) in a very large sample (n = 692). Not only was personality strongly related to current binging and predicted future binging, but the strongest associations were with respect to low conscientious or aspects of high novelty seeking. Therefore, modulation of mesolimbic reward response by impulsivity as defined in the present study has not only been reported by others (Vaidya, et al., 2013), but also is implicated in risk for substance abuse.

The use of delays between all trial phases was necessary in order to deconvolve the hemodynamic response related to the different phases. However, these delays could be as long as 6 seconds in some cases. Such delays might induce negative affective states (impatience or frustration) or inattention, particularly in high impulsive subjects. In turn, these negative affective states might invoke patterns of activation that would not be present during incentive processing without such delays. We acknowledge that this is a possibility in the present study. Future analyses could address this by modeling the delay period itself. In addition, other designs are available in which long delays are not needed to disentangle reward expectation from reward receipt (Geier, et al., 2010).

The present finding that mesolimbic response was modulated by an avoidance dimension in young adolescents has not been reported before, to our knowledge. However, the majority of fMRI MID studies in adolescents have focused on more approach-related dimensions like sensation seeking and many prior studies included older adolescents (up to age 17) compared to the present study. Therefore, the present finding that (low) avoidance tendencies are related to neurobehavioral MID response may not necessarily be due to the small sample size. Nevertheless, this finding would need to be replicated with a larger sample.

5. Conclusions

We view this study as a preliminary examination of a wide range of personality variables coupled with a comprehensive exploration of the parameter space of incentive processing (valence, magnitude and motivational state). Few prior studies of incentive motivation have examined this range of personality constructs in combination with a MID task design that enables teasing apart different aspects of reward processing. The ultimate application of this work is to understand personality and neurobehavioral risk for substance use and dependence as well as other psychopathology. Even in young adolescents, neurobehavioral response during incentive motivation is modulated by personality and the traits that modulate the response in adolescence (avoidance, approach) are somewhat different and more varied compared to the traits that modulate the response in adults (only impulsivity). Therefore, future studies of adolescent risk for substance use should consider a range of personality constructs that include both approach and avoidance tendencies, in addition to impulsivity, rather than focus only on those traits that have been implicated in adulthood.

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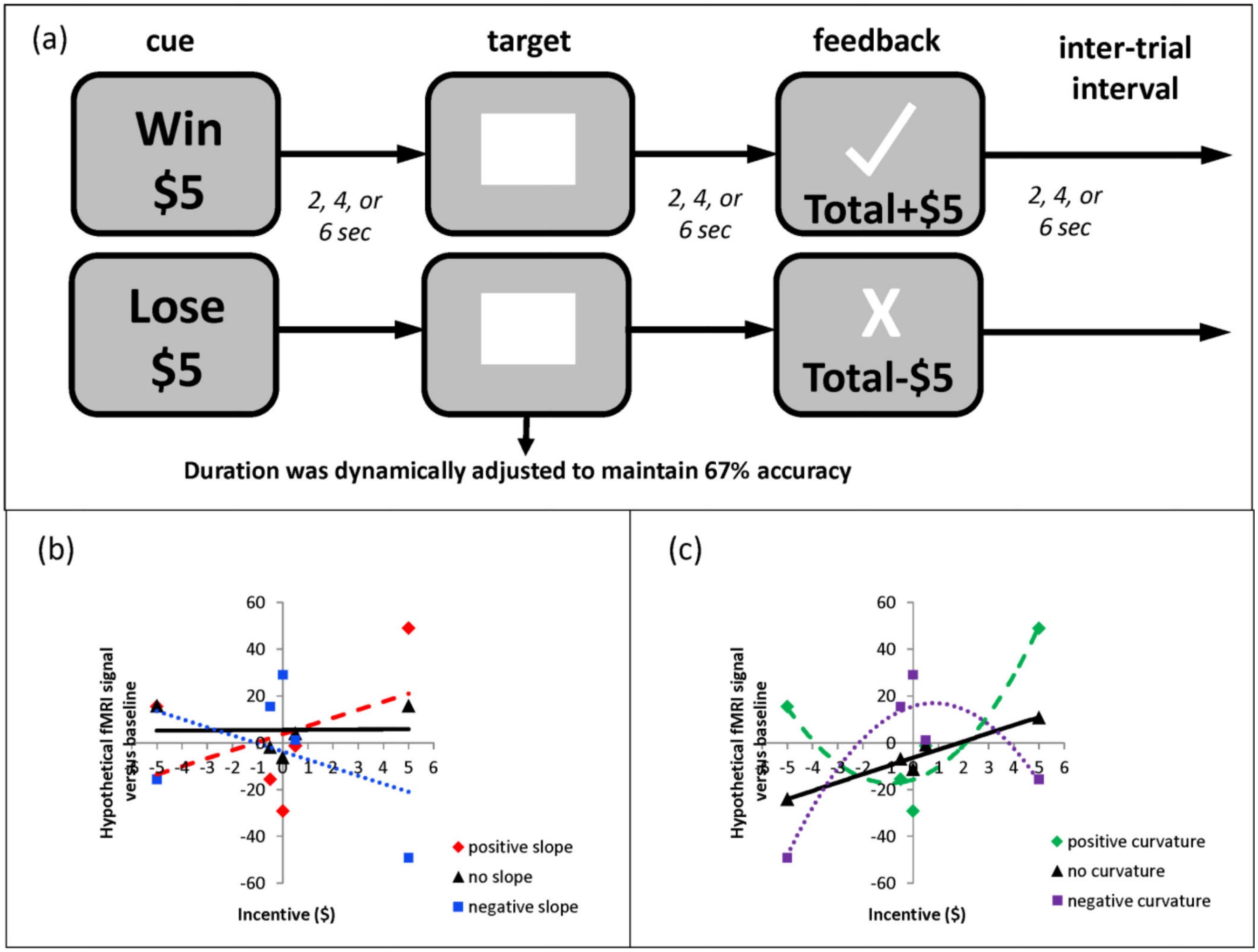

Figure 1.

(a) Monetary Incentive Delay task used in the present study. Participants could earn or lose money depending on speed of responding to a target stimulus (white rectangle). Each trial consisted of cue, target and feedback phases. The cue phase displayed a monetary value that could be won or lost. The target phase consisted of a simple stimulus presented briefly, and participants were instructed to respond within the duration of the target display (on the order of 250 ms). If the response time was less than the target duration a checkmark appeared on the feedback screen and the participant earned or avoided losing money. If the response time exceeded the target duration, an X appeared on the feedback screen and the participant did not win or incurred a loss of money. Across trials, the target display duration was adjusted to maintain trial accuracy at 67%. (b) The slope parameter indicates the slope of the linear component of a quadratic function fit to the fMRI signal in the different incentive conditions. A positive slope indicates greater fMRI response to positive incentive values and a negative slope indicates greater fMRI response to negative incentive values. (c) The curvature parameter indicates the degree of curvature of the quadratic function. A curvature value of 0 indicates no curvature; a positive curvature value indicates greater concavity and a negative curvature value indicates greater convexity. In other words, a more concave

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function would reflect greater fMRI signal for the extreme compared to small incentive values but a more convex function would reflect a greater fMRI signal for small values.

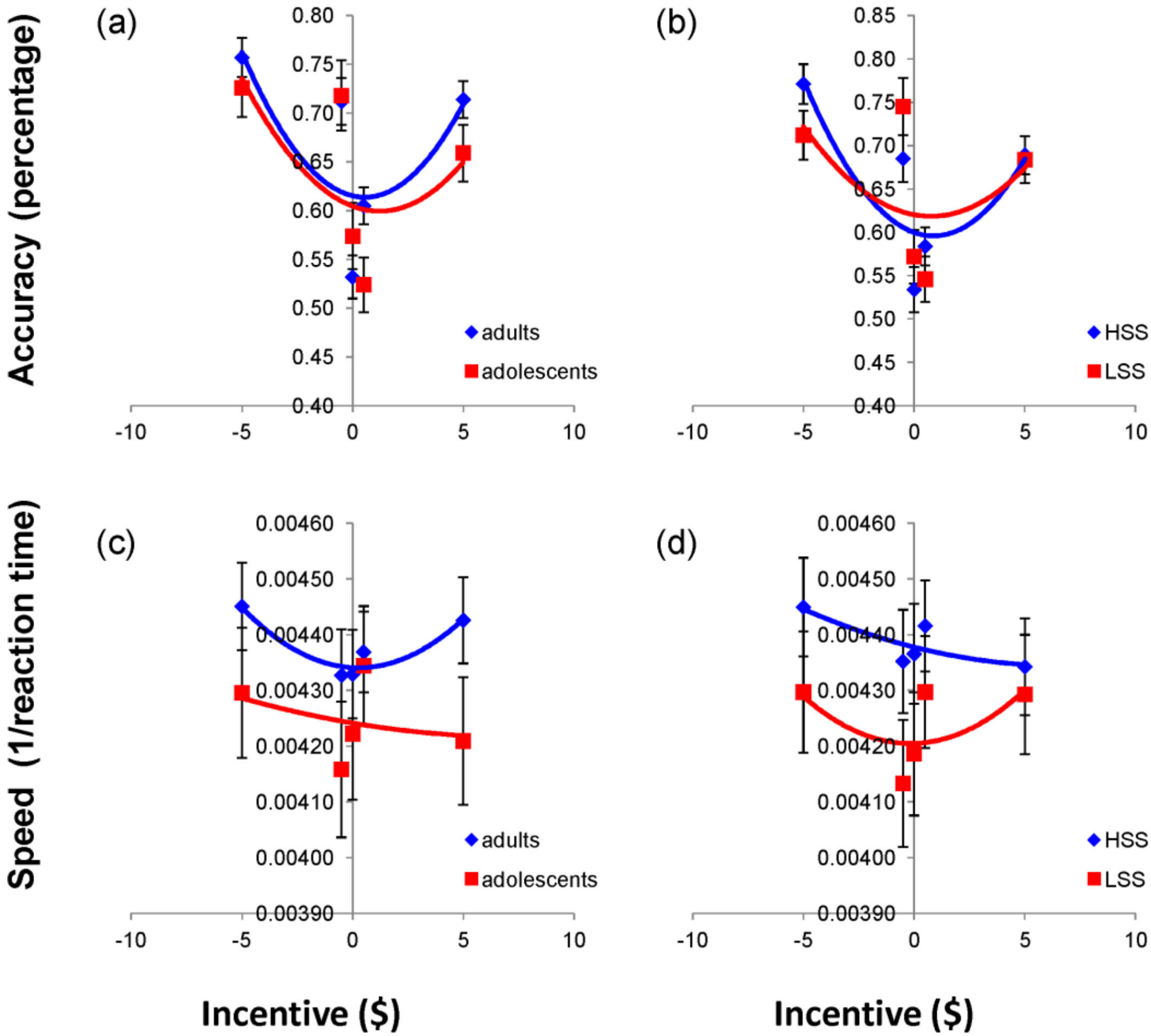

Figure 2.

Behavioral results. (a) accuracy as a function of incentive value and age group. (b) Accuracy as a function of incentive value and sensation seeking group. (c) Speed of responding as a function of incentive value and age group. (d) Speed of responding as a function of incentive value and sensation seeking group. The trend line represents the curvature parameter based on the group mean (but note that the analyses calculated curvature and slope separately for each subject). HSS = high sensation seekers; LSS = low sensation seekers. Error bars are standard error of the mean.

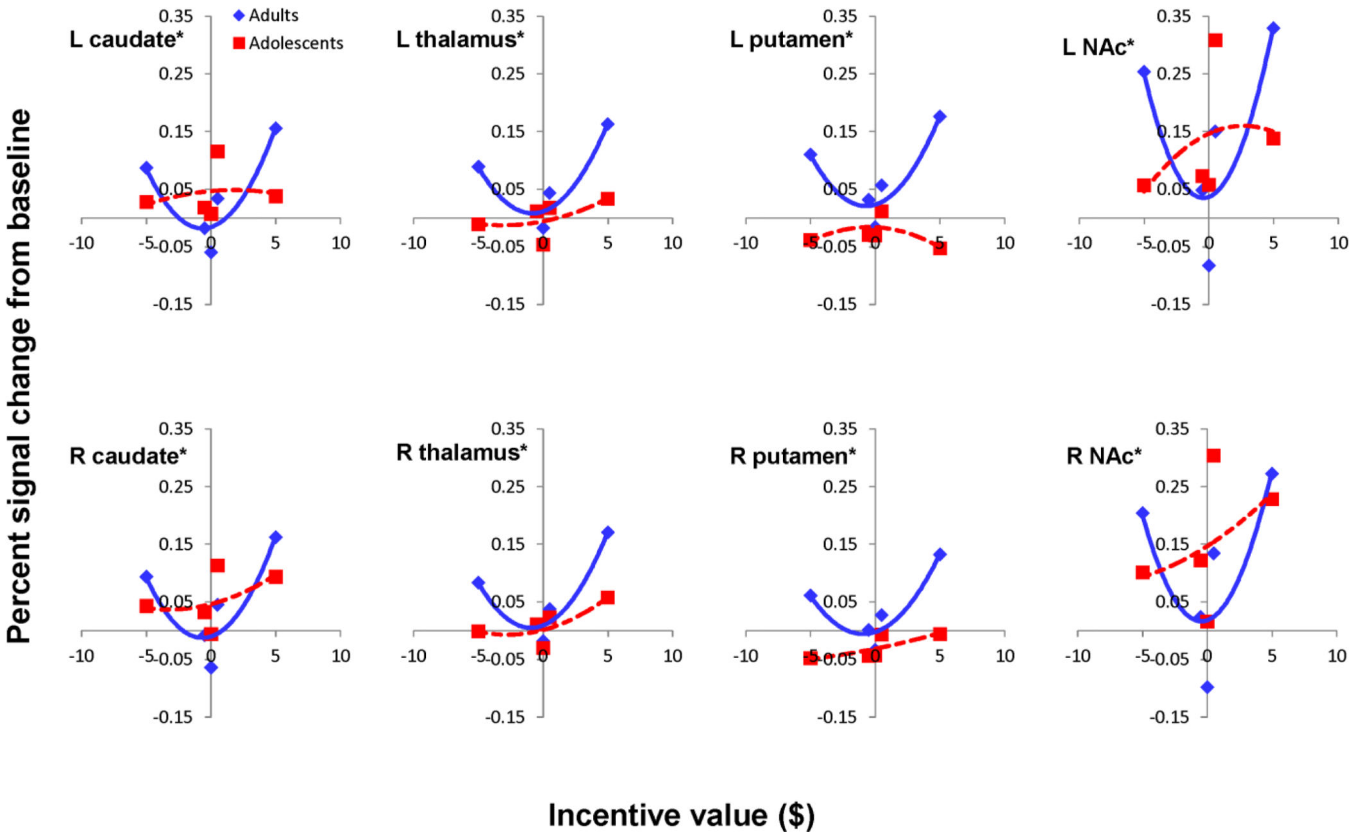

Figure 3.

fMRI incentive functions in the 8 regions-of-interest for the cue phase. Regions indicated with * had a significant effect of age on the curvature of the fMRI incentive function. The trend line represents the curvature parameter based on the group mean (but note that the analyses calculated curvature and slope separately for each subject).

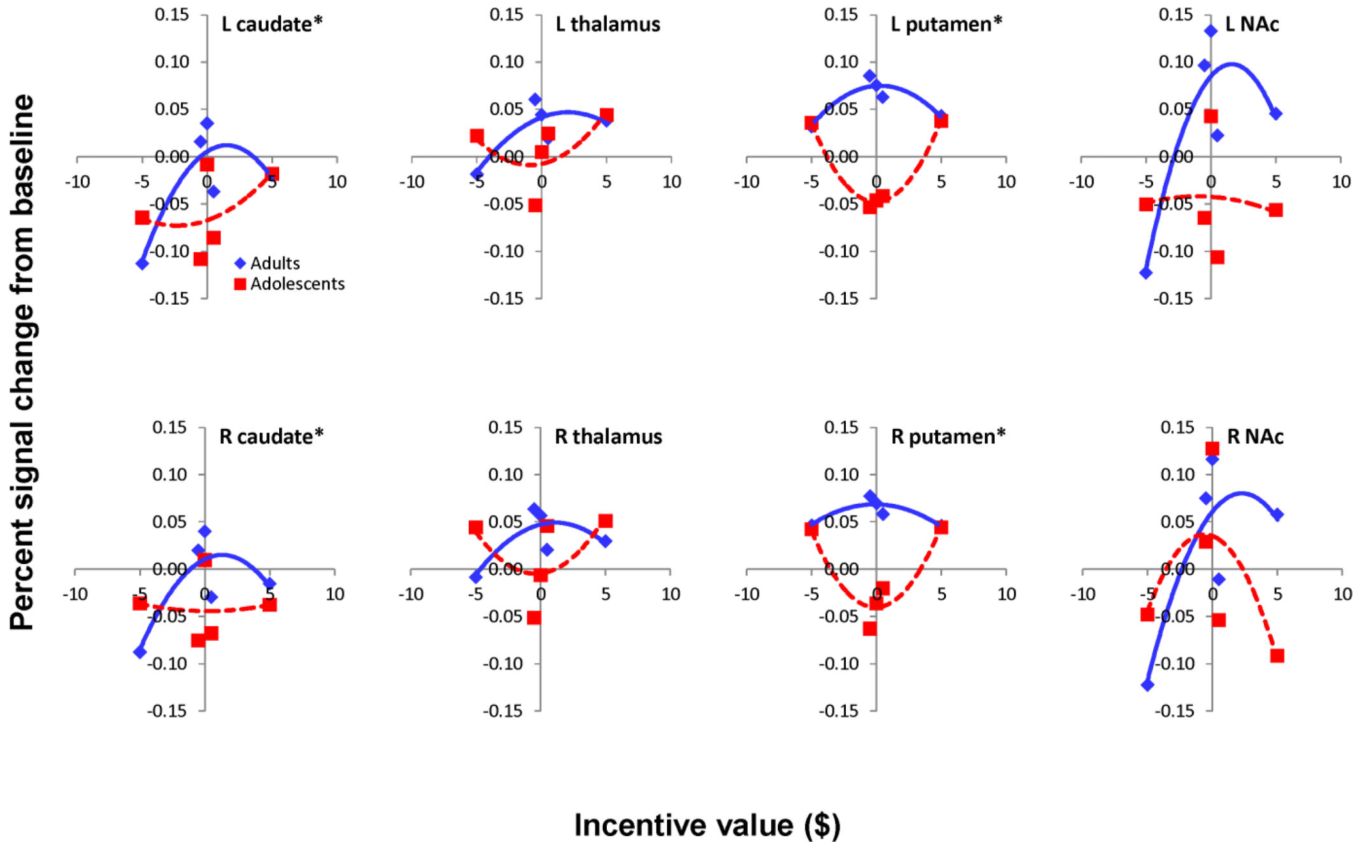

Figure 4.

fMRI incentive functions in the 8 regions-of-interest for the feedback phase. Regions indicated with * had a significant effect of age on the magnitude of the fMRI incentive function. The trend line represents the cruvature parameter based on the group mean (but note that the analyses calculated curvature and slope separately for each subject).

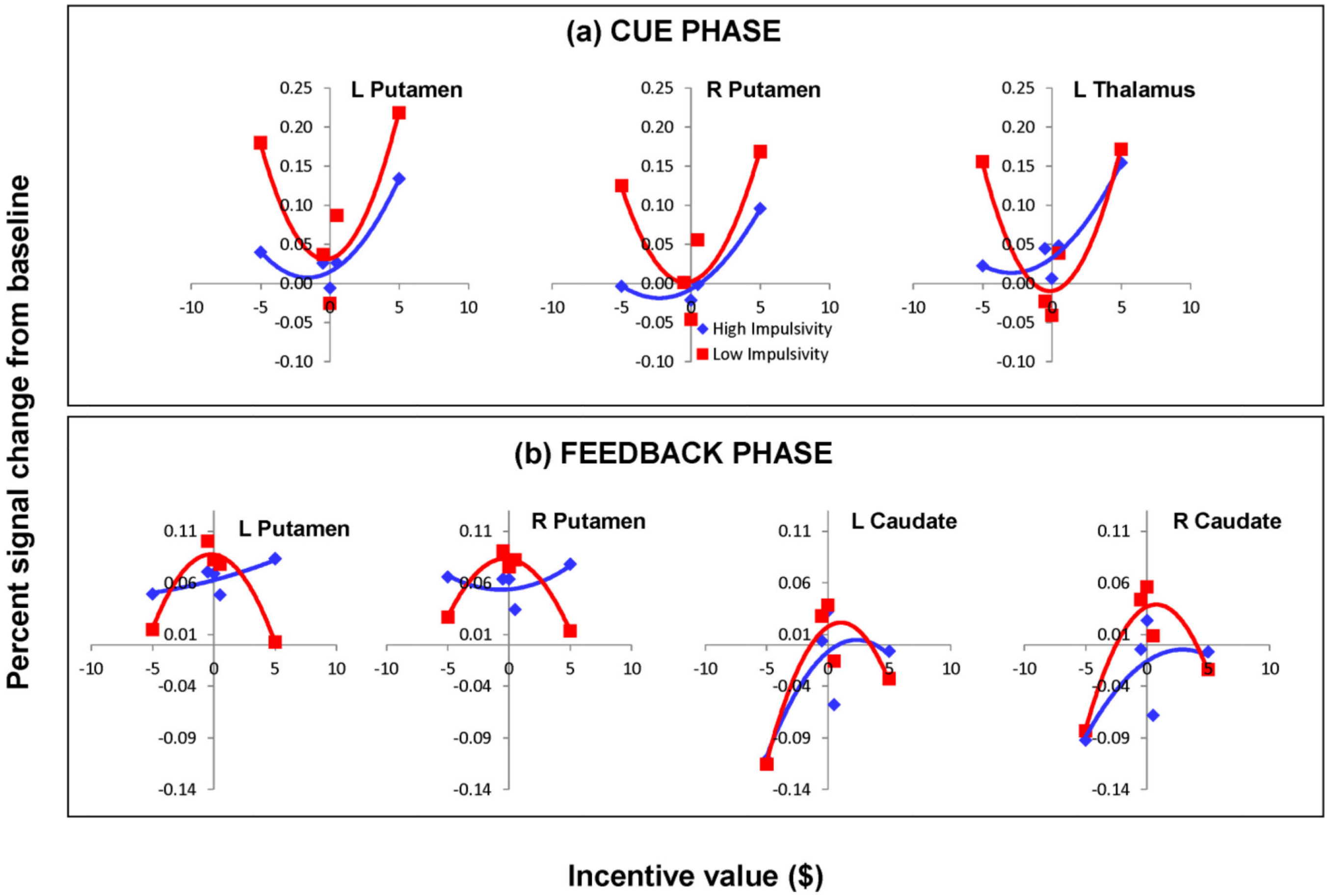

Figure 5.

Modulation of fMRI incentive function magnitude parameter by impulsivity in adults. (a) regions modulated by impulsivity in the cue phase. (b) regions modulated by impulsivity in the feedback phase. Although the graphs depict the fMRI incentive functions by high (blue) and low (red) impulsivity groups, the primary analysis was a correlation between the curvature parameter of the incentive function (cue-magnitude variable or feedback-magnitude variable) and the impulsivity factor score. The correlation between the impulsivity personality dimension and the curvature parameter was significant in each of these regions. The trend line represents the curvature parameter based on the high or low group means (but note that the analyses calculated curvature and slope separately for each subject).

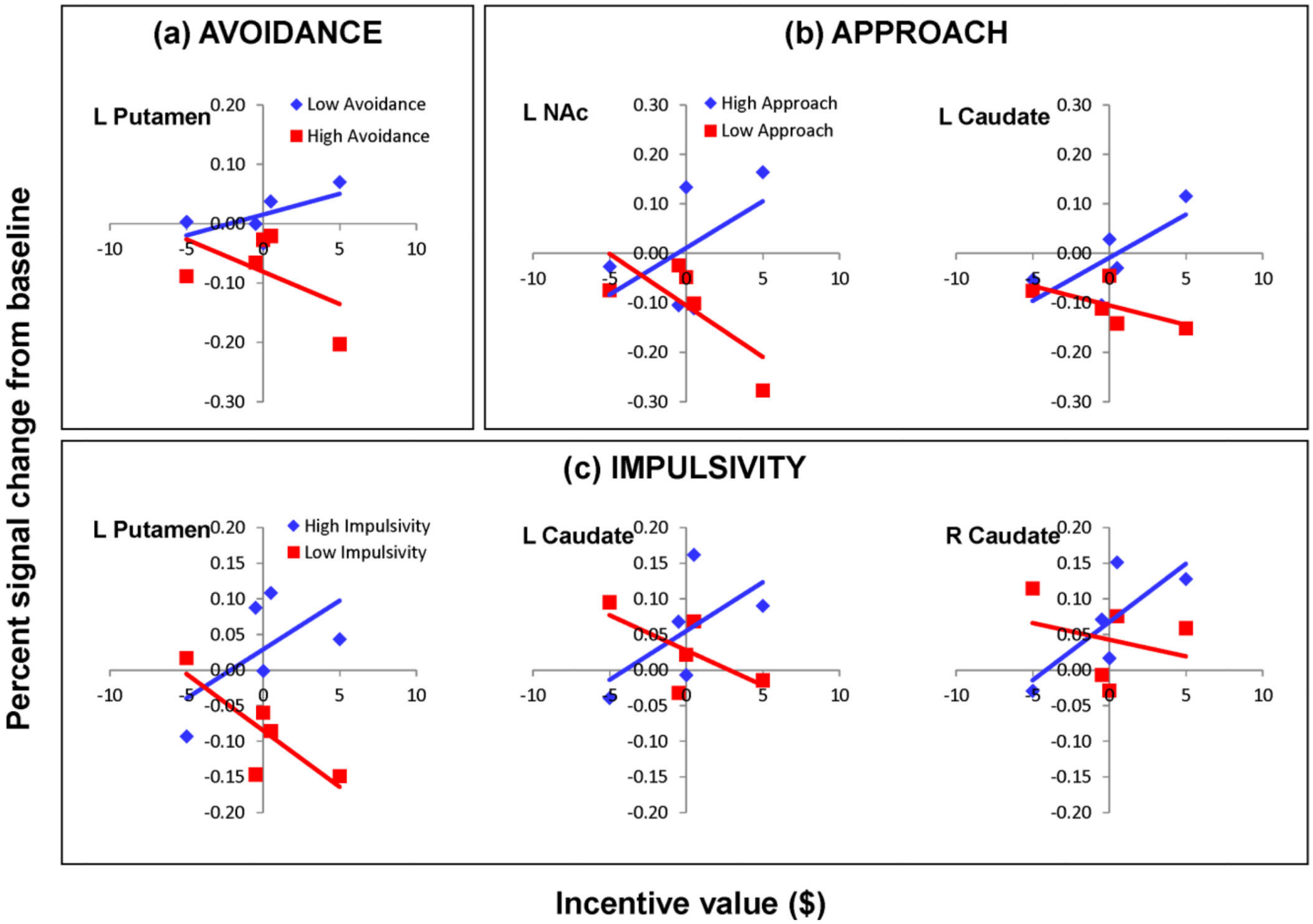

Figure 6.
Modulation of fMRI incentive function valence parameter by (a) avoidance, (b) approach and (c) impulsivity personality constructs in adolescents. Although the graphs depict the fMRI incentive functions by high and low groups for each construct, the primary analysis was a correlation between the slope parameter of the incentive function (cue-valence variable) and the personality construct factor score. The trend line represents the slope parameter based on the high or low group means (but note that the analyses calculated curvature and slope separately for each subject).

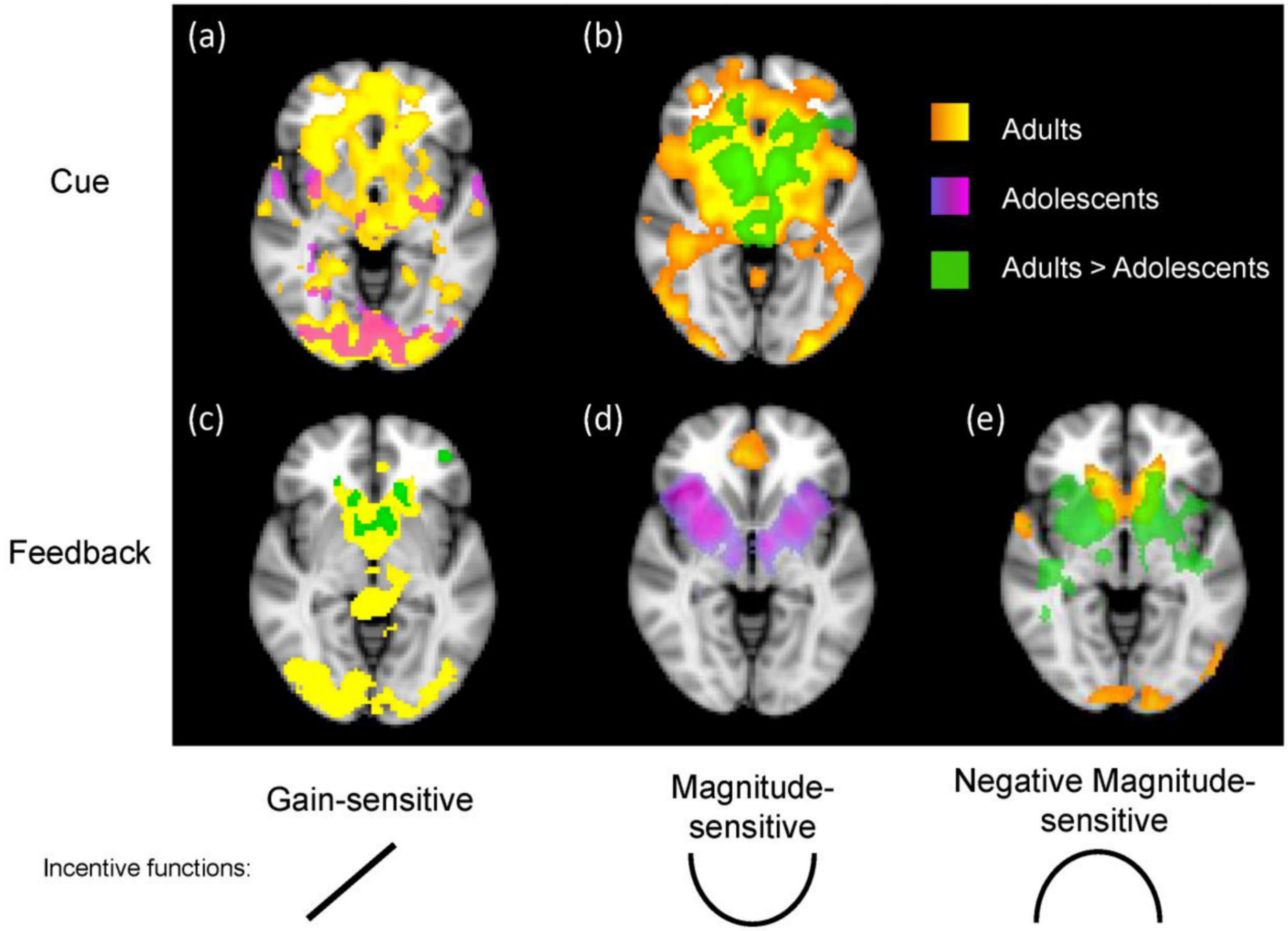

Figure 7.

Results of the voxel-wise analyses for the gain-sensitive, magnitude-sensitive and negative magnitude-sensitivity contrasts. Activation for adults is depicted in red-yellow; activation for adolescents is depicted in purple; activation for Adults > Adolescents is depicted in green. All activations are significant at $p < .05$, cluster corrected. (a) Cue phase gain sensitivity. (b) Cue phase magnitude sensitivity. (c) Feedback phase gain sensitivity. (d) Feedback phase magnitude sensitivity. (e) Feedback phase negative magnitude-sensitivity.

Table 1

Principal components analysis loadings for data reduction of the personality measures

Dimension	Explained Variance[a]	Measure	Loading
Approach	22.3%	UPPS-Sensation Seeking	.79
		Sensitivity to Reward	.75
		BAS-Reward	.68
		BAS-Approach	.70
		BAS-Fun	.76
Avoidance	16.0%	BFI-Extraversion	−.52
		BFI-Neuroticism	.75
		Sensitivity to Punishment	.80
		BIS	.69
Impulsivity	14.5%	UPPS-Lack of Premeditation	.59
		UPPS-Lack of Perseverance	.91
		BFI-Conscientiousness	−.85
Openness	12.5%	UPPS-Urgency	−.63
		BFI-Agreeableness	.74
		BFI-Openness	.69

[a]Rotation Sums of Squared Loadings

Table 2

Sensation Seeking × Age Group Analysis of Variance results for each of the anatomical regions of interest for cue magnitude

Region	Main Effect of Age F(1, 58) =	Main Effect of SS F(1, 58) =	Interaction of Age and SS F(1, 58) =
L n. accumbens	15.9 [a]	ns	ns
R n. accumbens	8.7 [a]	ns	ns
L putamen	10.6 [a]	ns	ns
R putamen	5.2 [a]	ns	ns
L thalamus	5.2 [a]	ns	ns
R thalamus	5.2 [a]	ns	ns
L caudate nucleus	12.2 [a]	ns	ns
R caudate nucleus	8.2 [a]	ns	ns

[a] $p < .05$

SS, sensation seeking

Table 3

Sensation Seeking × Age Group Analysis of Variance results for each of the anatomical regions of interest for feedback magnitude

Region	Main Effect of Age F(1, 58) =	Main Effect of SS F(1, 58) =	Interaction of Age and SS F(1, 58) =
L n. accumbens	ns	5.3 [a]	ns
R n. accumbens	ns	ns	ns
L putamen	7.8 [a]	ns	ns
R putamen	7.1 [a]	ns	ns
L thalamus	ns	ns	ns
R thalamus	ns	ns	ns
L caudate nucleus	7.0 [a]	ns	ns
R caudate nucleus	4.0 [a]	ns	ns

[a] $p < .05$

SS, sensation seeking

Table 4

Personality modulation of incentive magnitude or valence in anatomical regions of interest for adults indicated by Spearman rank correlations (rho values are shown)

Region	Personality Component	Cue		Feedback	
		Valence	Magnitude	Valence	Magnitude
L n. accumbens	Openness	ns	−.39 [a]	ns	.35 [a]
R n. accumbens	None	ns	ns	ns	ns
L putamen	Impulsivity	ns	−.45 [a]	ns	.35 [a]
R putamen	Impulsivity	ns	−.43 [a]	ns	.36 [a]
L thalamus	Impulsivity	ns	−.38 [a]	ns	.30
R thalamus	None	ns	ns	ns	ns
L caudate nucleus	Impulsivity	ns	ns	ns	.37 [a]
R caudate nucleus	Impulsivity	ns	ns	ns	.38 [a]

[a] $p <= .05$

ns, not significant

Table 5

Personality modulation of incentive magnitude or valence in anatomical regions of interest for adolescents indicated by Spearman rank correlations (rho values are shown)

Region	Personality Component	Cue		Feedback	
		Valence	Magnitude	Valence	Magnitude
L n. accumbens	Approach	ns	ns	.47[a]	ns
R n. accumbens	None	ns	ns	ns	ns
L putamen	Avoidance	−.44 [b]	ns	ns	ns
	Impulsivity	.54[a]	ns	ns	ns
R putamen	Impulsivity	.44[b]	ns	ns	ns
L thalamus	Avoidance	−.42[b]	ns	ns	ns
R thalamus	Impulsivity	.41[b]	ns	ns	ns
L caudate nucleus	Avoidance	−.42[b]	ns	ns	ns
	Impulsivity	.45[a]	ns	ns	ns
	Approach	ns	ns	.42[b]	.41[b]
R caudate nucleus	Avoidance	−.40[b]	ns	ns	ns
	Impulsivity	.42[b]	ns	ns	ns

[a] $p <= .05$

[b] $.05 < p <= .08$

ns, not significant

Table 6

Local Maxima of different trends in cue phase using a cluster corrected threshold of z=2.3 and p = .05

Trend	Age Group / Contrast	Region	Max z	Coordinates		
				x	y	z
Magnitude-sensitive	Adult	Right putamen	9.60	10	10	0
		Left putamen	9.35	−10	6	−4
		Left posterior cingulate	7.97	−2	−2	50
		Left thalamus	8.04	−10	−16	−2
		Right thalamus	7.10	8	−24	−10
		Left precentral	6.53	−30	−12	60
		Right precentral	6.25	48	−4	44
		Right inferior frontal	5.79	60	6	20
		Right anterior cingulate	6.63	10	32	24
		Left occipital pole	5.91	−28	−94	−8
		Left postcentral	5.89	−44	−24	52
		Right superior parietal	5.28	10	−64	54
		Left inferior frontal	5.45	−54	4	10
		Right supramarginal	5.44	60	−36	28
		Right occipital pole	4.85	30	−94	−6
		Left supramarginal	4.50	−56	−26	22
		Right postcentral	3.47	40	−32	42
	Adolescent	Right postcentral	4.65	40	−26	34
		Right posterior cingulate	4.08	18	−28	34
		Right precuneus	3.63	24	−44	28
		Right mid-cingulate	3.94	10	2	34
		Right posterior cingulate	3.60	16	−30	36
		Left superior frontal	3.40	−18	−2	50
	Adult > Adolescent	Right cerebellum	3.71	16	−44	−20
		Left nucleus accumbens	4.75	−10	6	−4
		Right nucleus accumbens	4.52	10	6	−4

Trend	Age Group / Contrast	Region	Max z	Coordinates x	y	z
		Right brainstem	3.75	8	−28	−6
		Right caudate	4.02	18	6	6
Negative Magnitude-Sensitive	Adult	None				
	Adolescent	None				
	Adult > Adolescent	None				
Gain-sensitive	Adult	Right occipital pole	5.13	10	−92	−4
		Left lateral occipital	4.90	−28	−92	6
		Left precentral	5.09	−42	−8	32
		Left inferior frontal	4.89	−30	22	20
		Left caudate	5.10	−6	16	6
		Right inferior frontal	4.89	48	10	26
		Right thalamus	4.83	12	−20	10
		Left fusiform	4.40	−34	−52	−16
		Right postcentral	4.76	36	−24	48
		Right insula	4.67	32	16	−4
		Right caudate	4.57	6	16	6
		Left thalamus	4.31	−16	−12	−4
		Right anterior cingulate	4.22	10	44	−6
		Left anterior cingulate	4.37	−8	46	−8
	Adolescent	Right precentral	4.94	12	−10	58
		Left precentral	4.51	−12	−12	60
		Right superior frontal	4.44	30	−12	42
		Right superior parietal	4.52	20	−48	58
		Left Posterior cingulate	4.32	−4	−14	44
		Right thalamus	4.22	6	−20	16
		Left occipital pole	3.38	−12	−88	4
		Left thalamus	3.22	−8	−14	12
		Right occipital pole	3.19	20	−84	−6

Trend	Age Group / Contrast	Region	Max z	Coordinates		
				x	y	z
	Adult > Adolescent	Right anterior cingulate	3.72	8	42	26
		Right superior frontal	3.17	10	42	46
Loss-sensitive	Adult	None				
	Adolescent	None				
	Adult > Adolescent	None				

Table 7

Local Maxima of different trends in feedback phase using a cluster corrected threshold of $z = 2.3$ and $p = 0.05$

Trend	Age Group / Contrast	Region	Max z	coordinate x	coordinate y	coordinate z
Magnitude-sensitive	Adult	Right anterior cingulate	5.36	4	42	16
		Right anterior / paracingulate	4.54	6	34	32
		Right superior frontal	4.73	24	32	42
	Adolescent	Right insula	5.03	34	24	−6
		Right striatum	4.84	24	2	−4
		Right anterior / paracingulate	4.50	8	22	34
		Left thalamus	4.12	−10	−6	0
		Right anterior cingulate	4.61	6	30	22
		Left insula	3.94	−32	18	−8
	Adult > Adolescent	None				
Negative magnitude-sensitive	Adult	Left temporal pole	6.45	−32	0	−34
		Left orbito-frontal	6.13	−14	30	−10
		Left nucleus accumbens	5.14	−10	10	−10
		Right caudate	5.11	12	26	−2
		Right nucleus accumbens	4.82	10	12	−6
		Right inferior frontal	4.45	62	0	8
		Left Caudate(body)	4.16	−22	−16	26
		Right caudate(body)	4.14	20	−6	22
		Left amygdala	3.85	−18	−4	−24
		Right hippocampus	3.67	38	−16	−22
	Adolescent	None				
	Adult > Adolescent	Right Caudate (body)	4.45	20	−6	20
		Right pallidum	4.30	18	2	−4
		Left caudate	4.29	−18	18	0
		Right thalamus	4.18	18	−16	14

Trend	Age Group / Contrast	Region	Max z	coordinate		
				x	y	z
		Left pallidum	4.12	−18	4	−6
		Right superior temporal	3.60	44	−22	−6
		Right insula	3.69	36	4	−2
		Right amygdala	3.44	16	−8	−16
		Left amygdala	3.31	−18	−14	−16
		Right inferior temporal	3.23	44	−46	−10
		Left fusiform	3.26	−34	−52	−14
		Left insula	3.33	−42	12	0
Gain-sensitive	Adult	Fornix	4.96	0	2	0
		Left lateral occipital	4.45	−26	−92	24
		Right fusiform	4.33	36	−72	−18
		Right lateral occipital	4.62	36	−86	6
		Right occipital pole	4.54	18	−98	2
		Left thalamus	4.15	−18	−24	14
		Right precentral	3.55	24	−16	66
		Left inferior temporal	3.86	−46	−14	−24
		Left orbito-frontal	3.78	−20	12	−22
		Left fusiform	3.81	−44	−66	−24
		Posterior cingulate	3.11	0	−12	34
		Left caudate	3.58	−16	20	10
		Right caudate	2.89	22	16	14
	Adolescent	None				
	Adult > Adolescent	Left orbito-frontal	3.92	−20	42	−12
		Right frontal pole	3.33	30	58	20
		Right paracingulate / Premotor	2.62	4	26	56
		Left caudate	3.12	−4	14	0
Loss-sensitive	Adult	None				
	Adolescent	None				

Trend	Age Group / Contrast	Region	Max z	coordinate		
				x	y	z
	Adult > Adolescent	None				