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Neurobiological sensitivity to social rewards and punishments moderates relationship between

peer norms and adolescent risk taking

Eva H. Telzer, Nathan A. Jorgensen, Mitchell J. Prinstein, & Kristen A. Lindquist

University of North Carolina at Chapel Hill

Correspondence: ehtelzer@unc.edu

Abstract

Though peer influence is a strong predictor of adolescents' risk-taking behaviors, not all adolescents are susceptible to their peer group. 136 adolescents (M_{age}=12.79 years) completed an fMRI scan, measures of perceived peer group norms and engagement in risky behavior. Ventral striatum sensitivity when anticipating social rewards and avoiding social punishments significantly moderated the association between negative perceived peer norms and adolescents' own risk behaviors. Negative perceived peer norms were associated with increased risky behavior only for those with high ventral striatum sensitivity; adolescents with low ventral striatum sensitivity were resilient to negative peer norms, showing low risk taking regardless of peer context. Findings provide a novel contribution to the study of peer influence susceptibility.

Keywords: adolescence, influence, peers, risk taking, fMRI

Adolescence is a time of heightened vulnerability for risk-taking behavior that gives rise to later substance abuse, substance dependence, related health risk behaviors, and has critical implications for morbidity and mortality throughout the lifespan (see Telzer et al., 2017). Perceptions of peers' risk behavior strongly predicts adolescents' initiation and escalation of risk-taking behaviors (Brechwald & Prinstein, 2011; Prentice, 2008). Yet, substantial work suggests notable variability in adolescents' peer influence susceptibility; for some, perceptions of peers' engagement in substance use is a strong predictor of adolescents' own substance use trajectories, while other adolescents are remarkably resilient to peer socialization pressures (Brechwald & Prinstein, 2011). However, it remains unclear which underlying processes make some adolescents more susceptible to peer influence. Unfortunately, individuals, and perhaps especially adolescents, are remarkably unaware of, and unable to report the implicit processes that contribute to conformity (Nisbett & Wilson, 1977). Self-reported measures of susceptibility may thus be limited. Therefore, for effective prospective identification of at-risk youth we need a process-based understanding of peer influence that does not rely solely on self-report. The psychological processes underlying individual differences in susceptibility may be best understood through the examination of neural processes.

Peer Influence Susceptibility in Adolescence

Peer influences, whether prosocial or deviant, may be especially salient during adolescence, when a reorientation from parental to peer contexts occurs (Blakemore & Mills, 2014; Nelson, Jarcho, & Guyer., 2016). Increased time spent with peers, as well as a greater emphasis on gaining peer acceptance, may place adolescents at risk for conforming to the norms and behaviors of their peer group in an effort to enhance their social belonging (i.e., "fitting in"; Do, Prinstein, & Telzer, in press). Perceptions of negative peer norms (e.g., peers who encourage

deviant, risky, behaviors) can influence adolescents' attitudes regarding the acceptability of such behaviors, thereby encouraging engagement in health risk behaviors. As such, adolescence is generally a time of heightened susceptibility to peer influence. For instance, experimental studies have shown that compared to children and adults, adolescents engage in more risk taking in the presence of peers versus alone (e.g., Gardner & Steinberg, 2005) and tend to conform to the attitudes of their peers about risky behaviors (Cohen & Prinstein, 2005; Knoll, Magis-Weinberg, Speekenbrink, & Blakemore, 2015). Moreover, many prospective longitudinal studies have demonstrated that in addition to adolescents' tendency to befriend peers who engage in similar levels of risk taking (i.e., selection effects), adolescents' perception that peers are engaging in health risk behaviors significantly predicts adolescents' later engagement in health risk behaviors via socialization effects (Brechwald & Prinstein, 2011). Taken together, a large body of research shows that adolescents are generally susceptible to negative peer influence.

However, while some adolescents are indeed likely to emulate peers' risk-taking behaviors, others are resilient to conformity pressures (Brechwald & Prinstein, 2011; Steinberg & Monahan, 2007). For instance, research using both self-reported and performance-based approaches to study peer influence susceptibility have shown that susceptibility is a normally distributed construct (Prinstein, Brechwald, & Cohen, 2011; Widman et al., 2016), suggesting approximately equal proportions of youth who are extremely high or low in susceptibility. This variability in adolescents' susceptibility prospectively predicts peer influence effects. For adolescents who are high in susceptibility (i.e., greater changes in behavior following exposure to experimentally manipulated peer norms), perceptions of friends' risky behavior are associated with adolescents' risky behavior. In contrast, adolescents who are low in susceptibility do not show peer-related changes in risky behavior over time (Prinstein et al., 2011; Teunissen et al.,

2016). Moreover, late adolescents who self-report high susceptibility show a stronger link between perceived peer norms and their own drinking behavior compared to their low susceptibility peers (DiGuiseppi et al., 2018). Taken together, the perceived norms of peers can play a powerful role in predicting adolescents' risky behavior, but only for those who are highly susceptible.

Sensitivity to Social Rewards and Punishments

The *Social Reward/Social Punishment Framework* (Falk, Way, & Jasinka, 2012) suggests two pathways by which susceptibility to normative social influence occurs. One pathway occurs via the drive to pursue social rewards conferred by conforming, and the second pathway occurs via the avoidance of social punishment, including social exclusion. Individual differences in adolescents' propensity to seek social rewards (e.g., approval by others) and avoid social punishment (e.g., disapproval by others) may be one factor that differentiates adolescents who are susceptible to peer influence and adolescents who are not. A stronger drive to gain social rewards and avoid social punishments may increase conformity to peer group norms, such that youth engage in the behaviors that they think are encouraged by the peer group as a means to attain peer approval and avoid peer rejection (Do, Prinstein, & Telzer, in press). Importantly, social rewards and punishments need not be directly experienced but only anticipated to elicit social conformity (Falk, Way, & Jasinka, 2012). Indeed, the mere threat of peer rejection is enough to limit group deviance, and increase adherence to social norms (Juvonen & Gross, 2005). Thus, approaching rewards and avoiding punishments are key motivational drivers and are reinforced via approval/acceptance and disapproval/rejection from peers. Peer influence susceptibility is therefore likely driven both by the motivation to affiliate, be accepted, and

maintain a positive self-concept as well to avoid exclusion and negative self-concept in the peer group (Falk, Way, & Jasinka, 2012).

Given the limited efficacy of self-reports for understanding implicit processes of conformity (Nisbett & Wilson, 1977), examining neurobiological sensitivity may be a promising avenue for probing individual differences in susceptibility to peer influence. The ventral striatum (VS) is a key brain region central to incentive-based, motivated behaviors (Smith et al., 2011) and is implicated in encoding both appetitive (i.e., rewarding, approach-related) and aversive (i.e., punishing, avoidance-related) social cues in the environment (Kohls et al., 2013). Across rodents, non-human primates, and humans, increases in dopamine signaling peak during adolescence (Wahlstrom et al., 2010), influencing motivated behaviors that are altered in adolescence (Padmanabhan & Luna, 2014). For instance, adolescents exhibit greater ventral striatum activation than children and adults when receiving primary (e.g., sweet liquid; Galván & McGlennen, 2013) and secondary rewards (e.g., money; Galván et al., 2006; Van Leijenhorst et al., 2010; Schreuders et al., 2018), as well as when anticipating social rewards and avoiding social punishments (e.g., social acceptance or rejection from peers; Chein, Albert, O'Brien, Uckert, & Steinberg, 2011; Guyer, McClure-Tone, Shiffrin, Pine, & Nelson, 2009; Somerville, Hare, & Casey, 2011; 32 33). Thus, conformity to peers may be driven, in part, by a desire to attain social rewards and avoid social punishments, which may be substantiated via alterations in ventral striatum sensitivity.

Preliminary evidence suggests that individual differences in ventral striatum activation interact with the social context to predict adolescent behavior. While traditionally viewed as a vulnerability biomarker, heightened ventral striatum activation can also promote resilience depending on the social context (see Telzer, 2016). Indeed, the ventral striatum processes the

motivational salience of both positive and negative contexts (Levita et al., 2009; Lindquist et al., 2016), including anticipated positive outcomes like rewards as well as avoidance of negative and aversive outcomes such as punishments (Kohls et al., 2013). For instance, heightened ventral striatum activation in a risky context, particularly in the presence of peers or social rewards, is associated with compromised cognitive control and increases in risk taking (Chein et al., 2011; Galván, Hare, Voss, Glover, & Casey, 2007; Qu et al., 2015; Perino, Miernicki, & Telzer, 2016; Telzer, Fuligni, Lieberman, & Galván, 2013). However, heightened ventral striatum activation in positive, prosocial contexts is associated with decreases in risk taking (Telzer et al., 2013), underscoring that individual differences in ventral striatum sensitivity interact with the social context to promote or impede adolescent adjustment.

Current Study

We examined how variability in VS activation when anticipating the receipt of social rewards and the avoidance of social punishments moderates the link between deviant peer group norms and adolescent risk taking. This approach diverges from prior research that has either examined the neural correlates of social influence itself (e.g., Cascio, O'Donnell, Bayer, Tinney, & Falk, 2015; Nook & Zaki, 2015; Welborn et al., 2016) or tested how VS activation predicts concurrent or future risk taking and peer conformity effects (e.g., Cascio, Carp, et al., 2015; Qu et al., 215), which assumes that neurobiological sensitivity applies equally to all adolescents and fails to consider that the environment may determine if, and how, neurobiological sensitivity influences developmental outcomes. Thus, considering neurobiological sensitivity as a moderator of social context is a promising avenue for identification of the most susceptible and at-risk youth (Schriber & Guyer, 2016).

In the current study, adolescents completed the Social Incentive Delay (SID) task during an fMRI scan to measure VS sensitivity when anticipating the receipt of social rewards and avoidance of social punishments, as well as measures of perceived peer group norms and self-reported risk-taking behaviors. Adolescents rated the extent to which the peer norms they encountered in daily life encouraged prosocial activities (e.g., try hard in school, volunteer for a good cause) and deviant activities (e.g., drink alcohol, lie to adults). We focused on adolescents' perceptions of peers' behaviors since perceptions of friends' risk behaviors are a stronger predictor of adolescents' own risk behavior compared to actual peer behavior (Iannotti & Bush, 1992; Slagt, Dubas, Deković, Haselager, & van Aken, 2015; DiGuiseppi et al., 2018). Although prior research has measured both adolescents' perceptions of their friends' behavior, as well as friends' own reported behavior (Prinstein & Giletta, 2016), the extent literature suggests that peer norms need only be perceived to influence adolescents' behavior.

We hypothesized that adolescents who perceive more deviant relative to prosocial peer norms would show heightened risk taking, but this would be moderated by neurobiological sensitivity to social rewards and punishments. In particular, we predicted that adolescents who perceived that their peers were engaging in relatively more risky behaviors (e.g., deviant peer norms) than positive behaviors (e.g., prosocial peer norms) would be particularly vulnerable to risk taking, but only if those adolescents had heightened VS activation when anticipating receiving social rewards and avoiding social punishments. For these same neurobiologically sensitive youth, we hypothesized that when they perceived that their peers engaged in relatively more positive than deviant behaviors, they would be buffered from risk taking. We additionally predicted that adolescents with low VS activation would be resilient to peer influence effects, insofar as those adolescents would not be motivated to adhere to peer norms, whatever peer

context they found themselves in. By measuring VS activation when anticipating social rewards and punishments, we were able to test whether peer influence susceptibility is characterized by a drive to obtain social rewards, a heightened motivation to avoid social punishments, or both.

In addition to examining neurobiological sensitivity as a moderator of peer norms on adolescent risk taking, we examined whether self-reported susceptibility (assessed with the Resistance to Peer Influence (RPI) scale; Steinberg & Monahan, 2007) moderates this link. Self-report instruments, such as the RPI, allow adolescents an opportunity to reflect on their own tendencies to resist pressures from peers, with reported changes in youths' responses across development (Steinberg & Monahan, 2007). However, self-reported susceptibility may be less predictive of adolescents' behaviors, as youth are often unaware of, unable to, or unwilling to report on their conformity tendencies (Nisbett & Wilson, 1977; Prinstein et al., 2011; Prinstein & Giletta, 2016). Indeed, prior neuroimaging work has begun to reveal how neural activation predicts risk-taking behavior even more powerfully than adolescents' own self-reports (Falk et al., 2014; Telzer et al., 2013). Thus, we hypothesized that neurobiological susceptibility would moderate the link between peer group norms and adolescent risk taking, above and beyond self-reported susceptibility.

Methods

Participants

Participants were recruited from three rural public middle schools in the southeast United States. Between 66.7-72.1% of students in these schools were classified as economically disadvantaged (NCDPI, 2017), and 69.5% of students in the district were eligible for free or reduced-price lunch based on district reports. Of the 148 participants who completed the fMRI session, three were excluded from analyses due to not completing the scan, two for excessive

motion (>2mm in any direction), one for technical errors, one for an MRI artifact, and five for

missing data on the peer group norms questions, leading to a total sample of 136 adolescents (70

female) ages 11-14 (M_{age} = 12.79, SD = .59). We focus on early adolescents (ages 11-14) given

that this developmental period is marked by increased behavioral (i.e., conformity) and neural

(i.e., ventral striatum activation) sensitivity to peers. For instance, early adolescents show greater

peer influence effects in both prosocial (van Hoorn et al., 2016; Foulkes et al., 2018) and deviant

(Knoll et al., 2017) peer contexts, and report lower resistance to peer influence (Steinberg &

Monahan, 2007) relative to older adolescents.

Adolescents were from diverse racial/ethnic backgrounds (47 Hispanic/Latinx, 40 White,

31 Black/African-American, 12 multi-racial, 6 other). Overall, the sample was from low to

middle socioeconomic status in terms of parental reported household income (31% less than

$30,000, 34% $30-$60,000, 35% over $60,000), parental education (25% less than high school,

16% high school diploma, 30% some college, 29% associate's degree or higher), and census-

based area deprivation index (percentiles compared to national average with higher scores

meaning greater deprivation: Range = 22-97; M = 68.0, SD = 17.8; University of Wisconsin,

2018). Adolescents and parents gave written assent/consent in accordance with the university's

Institutional Review Board.

Procedures

Participants were recruited from a larger study of 873 students in 6th and 7th grade.

Participants from the larger study provided interest in being contacted for a future fMRI study.

Interested participants were then called and screened on the phone for eligibility (i.e., MRI

contraindications) and recruited for the fMRI study within the same academic year as the larger

study. We screened 284 families, of whom 91 were ineligible due to learning disabilities, braces,

head trauma or other MRI contraindications, and 45 were eligible but did not participate due to

scheduling difficulties or no longer interested in participating, resulting in a final sample of 148

adolescents. Thus, of those contacted and eligible, 77.5% participated.

For the current study, adolescents and their primary caregiver attended the fMRI session,

during which consent and assent were obtained. Participants completed an fMRI scan that lasted

approximately 1.5 hours, during which they completed the SID task (described below), as well as

four other tasks that are not the focus of the current manuscript. Following the scan, participants

completed several self-report measures using computer-assisted software in a private room,

including perceived peer group norms and risk-taking behaviors, as well as other measures which

are not the focus of this manuscript. Adolescents were compensated with a monetary

remuneration of $90, small prizes for completing the full scan and staying still (e.g., headphones,

candy; worth $20), snacks during the visit, and a meal. Parents were compensated with a

monetary remuneration of $50, as well as a meal, compensation for gas, and parking.

Questionnaire Measures

Perceived peer group norms. Participants completed a revised version of the Perception

of Peer Group Norms Questionnaire (Marshall-Denton, Véronneau, & Dishion, 2016).

Participants indicated how many of their close friends participate in 16 behaviors on a 1- (*none*)

to 6- (*almost all*) point scale, including eight negative (e.g., "may have tried or use tobacco"; "lie

to adults"; "fight or bully others") and eight positive (e.g., "try to set goals for school success";

"volunteer for a good cause"; "resist peer activities involving tobacco, drugs, and alcohol use")

behaviors. All positive statements were reverse coded and a total mean score was calculated so

that higher scores indicate perceptions of relatively more negative peer group norms, and lower

numbers indicate perceptions of relatively more positive peer group norms. The scale

demonstrated good reliability (α = .827).

Risk-taking behaviors. Participants completed a modified version of the Adolescent

Risk-taking Scale (Alexander et al., 1990). Adolescents reported on their frequency of engaging

in 14 risky behaviors on a 4-point scale (0=*never, 1=once or twice, 2=several times, 3=many*

times). The scale included questions about rule breaking (e.g., "I have snuck out of my house

without my parents knowing"), sexual activity (e.g., "I have had sex with someone I just met"),

substance use (e.g., "I have gotten drunk or high at a party"), and dangerous behavior (e.g., "I did

something risky or dangerous on a dare"). A total mean score for all items was calculated (α =

.769).

Resistance to peer influence. To examine self-reported peer susceptibility, we utilized

the Resistance to Peer Influence Scale (Steinberg & Monahan, 2007) that included 10 items (e.g.,

"I go along with my friends just to keep my friends happy."). The original scale uses a two-

question tree-structure for each item to derive final scores on a 4-point Likert scale. In order to

simplify readability for participants, items used in this study were condensed into one question

each on a 1- (really true) to 4- (not at all true) point scale, with higher scores representing higher

resistance to peer influence and lower scores representing greater peer susceptibility.

Additionally, all items were modified to be 'I' statements rather than "Some people" statements.

The scale demonstrated good internal consistency (α = .858).

Social Incentive Delay Task

Participants completed the Social Incentive Delay Task while undergoing fMRI to

measure neural responses when anticipating receiving social rewards and avoiding social

punishments. The SID is modified from the widely used Monetary Incentive Delay Task

(Knutson, Westdorp, Kaiser, & Hommer, 2000), and reliably engages the VS (Cremers, Veer,

Spinhoven, Rombouts, & Roelofs, 2015; Kohls et al., 2013). For instance, anticipation of both

social and monetary rewards recruits the VS (Spreckelmeyer et al., 2009), and the anticipation of

avoidable social punishments recruits the VS similarly to VS activation during the anticipation of

social reward gain (Kohls et al., 2013).

Each trial of the SID began with a cue that signaled whether the anticipated feedback

would be a reward, punishment, or neutral (500 ms; see Figure 1). The cue was a different shape

for each condition. The cue was followed by a jittered crosshair (between .48 and 3.9 seconds, M

= 2.0 seconds), which was followed by the target (a white square; 300 ms), at which point

participants were instructed to press a button as quickly as possible. The display of social

feedback (1450 ms) was dependent on the trial type and participants' reaction time. In the reward

condition, a hit (i.e., fast enough response) earned the feedback of a happy face (i.e., social

reward feedback), and a miss (i.e., too slow response) earned a blurred face (i.e., neutral

feedback). During the punishment condition, a hit earned a blurred face (i.e., neutral feedback)

and a miss earned an angry face (i.e., social punishment feedback). Both hits and misses were

followed by a blurred face in the neutral condition. After the feedback, another jittered crosshair

(between .51 and 4.2 seconds, M = 2.3 seconds) was presented before the next trial began. Trials

were presented in an event-related design, with reward, punishment, and neutral conditions

randomly ordered. Participants completed two rounds of the task, totaling 116 trials (48 reward,

48 punishment, 20 neutral).

To prevent a ceiling or floor performance effect and ensure participants performed

roughly at 50% accuracy so that they received relatively equal amount of positive and negative

feedback, the time required for a successful hit was adaptive, starting at .30 seconds for the first

trial and adding or subtracting .02 seconds after a miss or hit, respectively, with an upper bound

of .50 seconds and a lower bound of .16 seconds. In order to make the task motivationally

salient, age-matched adolescent faces posing emotional facial expressions were utilized as

rewards and punishments. The faces were photographs of ethnically diverse male and female

adolescents (24 faces, 12 female) taken from the National Institute of Mental Health Child

Emotional Faces Picture Set (NIMH-ChEFS). Participants were trained on the meaning of each

cue and completed 12 practice trials prior to entering the scanner. Three participants only had

one round of usable fMRI data from the task (due to early exit from scanner or technical issues),

but were included in analyses because they met a priori requirements for the number of trials

needed per condition (8 hits, or above a 15% hit rate).

fMRI Data Acquisition and Preprocessing

Imaging data were collected using a 3 Tesla Siemens Prisma MRI scanner. The SID was

presented on a computer screen and projected through a mirror. A high-resolution structural T2*-

weighted echo-planar imaging (EPI) volume (TR = 2000ms; TE = 25ms; matrix = 92 x 92; FOV

= 230mm; 37 slices; slice thickness = 3mm; voxel size 2.5 x 2.5 x 3 mm3) was acquired coplanar

with a T2*-weighted structural matched-bandwidth (MBW), high-resolution, anatomical scan

(TR = 5700ms; TE = 65ms; matrix = 192 x 192; FOV = 230mm; 38 slices; slice thickness =

3mm). In addition, a T1* magnetization-prepared rapid-acquisition gradient echo (MPRAGE;

TR = 2400ms; TE = 2.22ms; matrix = 256 x 256; FOV = 256mm; sagittal plane; slice thickness

= 0.8mm; 208 slices) was acquired. The orientation for the EPI and MBW scans was oblique

axial to maximize brain coverage and to reduce noise. Preprocessing was conducted using FSL

(FMRIB's Software Library, version 6.0; www.fmrib.ox.ac.uk/fsl) and included the following

steps: Skull stripping using BET (Smith, 2002); motion correction with MCFLIRT (Jenkinson,

Bannister, Brady, & Smith, 2002); spatial smoothing with Gaussian kernel of full width at half

maximum (FWHM) 6 mm; high-pass temporal filtering with a filter width of 128 s (Gaussian-

weighted least-squares straight line fitting, with sigma=64.0s); grand-mean intensity

normalization of the entire 4D dataset by a single multiplicative factor; and individual level ICA

denoising for motion and physiological noise using MELODIC (version 3.15; Beckmann &

Smith, 2004), combined with an automated signal classifier (Tohka et al., 2008; Neyman-

Pearson threshold = .03). For the spatial normalization, the EPI data were registered to the T1

image with a linear transformation, followed by a white-matter boundary based transformation

(BBR; Greve & Fischl, 2009) using FLIRT, linear and non-linear transformations to standard

Montreal Neurological Institute (MNI) 2-mm brain were performed using Advanced

Neuroimaging Tools (ANTs; Avants et al, 2011), and then spatial normalization of the EPI

image to the MNI.

fMRI Data Analysis

Individual level, fixed-effects analyses were estimated using the general linear model

convolved with a canonical hemodynamic response function in SPM8. The task was modeled as

event-related with eight conditions, including three anticipation conditions (reward, punishment,

neutral), two outcome conditions for both reward (hit, miss) and punishment (hit, miss), and one

outcome condition for neutral. Anticipation conditions were modeled as the onset of the cue and

the duration of the cue and jitter prior to the target, and outcome conditions were modeled at the

onset of and for the full duration of the feedback. Six motion parameters were modeled as

regressors of no interest. Using the parameter estimates from the GLM, linear contrast images

comparing each of the conditions of interest were calculated for each individual. The primary

contrasts of interest for this study was reward anticipation vs. neutral anticipation and punishment anticipation vs. neutral anticipation.

Individual subject contrasts were then submitted to random effects, group-level analyses using GLMFlex (McLaren, Schultz, Locascio, Sperling, & Atri, 2011), which corrects for variance–covariance inequality, removes outliers and sudden activation changes in the brain, partitions error terms, and analyzes all voxels containing data (http://mrtools.mgh.harvard.edu/index.php/GLM_Flex). Exploratory, whole-brain analyses for each contrast are presented in Supporting Information Table 1 and are available on Neurovault (Gorgolewski et al., 2015: https://neurovault.org/collections/LXPKHSIX/). Notably, the ventral striatum was activated more to anticipating social rewards and social punishments than to neutral. Our primary, confirmatory analyses employed a region-of-interest (ROI) approach with the bilateral ventral striatum using a mask based on Neurosynth by searching "ventral striatum" (http://neurosynth.org/analyses/terms/ventral%20striatum/). The resulting automated meta-analytic image was based on 415 studies, and was thresholded at $Z = 14$ (see Supporting Information, Figure 1). Using this mask, we extracted parameter estimates of signal intensity from the primary contrasts of interest (reward anticipation vs. neutral anticipation and punishment anticipation vs. neutral anticipation). Parameter estimates from each of these contrasts therefore represent neural activation in the ventral striatum when anticipating social rewards and social punishments, each controlling for anticipation to neutral. Parameter estimates from the ventral striatum ROI were used as a moderator in subsequent analyses to test our primary hypotheses.

Analysis Plan

Moderation analyses were conducted in SPSS (version 25, IBM) using the PROCESS macro (Hayes, 2013). This is a path-analysis approach to moderation that simultaneously models multiple conditional effects using ordinary least squares regression for continuous outcomes. Bootstrap bias-corrected confidence intervals (95%) are estimated, where nonzero overlapping confidence intervals indicate a significant effect. Moderation was conducted by standardizing the predictor and moderator variables prior to analysis. Adolescent risk taking served as the dependent variable, and age was entered as a covariate. We first tested whether self-reported susceptibility (i.e., RPI) moderates the link between peer group norms and adolescent risk taking. We then tested whether ventral striatum activation to anticipating social rewards and punishments moderates the link between peer group norms and adolescent risk taking. We further included RPI as a covariate to ensure ventral striatum activation serves as a moderator above and beyond self-reported peer influence susceptibility. For probing the significant moderation effects, we used the Johnson-Neyman technique and marginal-effects plots in conjunction with visual depictions of simple slope using small multiples (created with the R-based interActive data visualization tool; McCabe, Kim & King, 2018).

Results

Descriptive Statistics

Table 1 presents correlations among all study variables. Adolescents who perceived relatively more negative than positive peer group norms reported greater risk taking. Ventral striatum activation when anticipating social rewards or punishments was not associated with peer group norms or risk taking. Age was positively correlated with risk taking, and marginally related to more negative peer group norms. Males and females did not differ on any of the study variables (ps > .16). We therefore controlled for age but not sex in our primary analyses.

Moderation of Link between Peer Norms and Adolescent Risk Taking

Self-reported resistance to peer influence did not moderate the association between perceived peer group norms and adolescent risk taking (B=.024, SE=.019, p=.22, 95% CI [-.014, .061]). In contrast, ventral striatum activation when anticipating receiving social rewards and avoiding social punishments each moderated the association between peer group norms and risk taking, above and beyond self-reported RPI (Table 2).

We probed this interaction by using the Johnson–Neyman technique (Bauer & Curran, 2005; Hayes & Matthes, 2009), which mathematically derives the "regions of significance", where the conditional effect of the predictor variable transitions between not statistically significant to statistically significant. The simple slope of perceived peer group norms on adolescent risk taking is no longer significant at .95 standard deviations below the mean on ventral striatum activation to social rewards (78.65% of observations are within the region of significance) and .90 standard deviations below the mean on ventral striatum activation to social punishments (66.85% of observations are within the region of significance).

For visualization purposes, we used small multiples to plot a broad range of simple slope effects, which displays the observed data that is most representative of each simple slope (McCabe et al., 2018). As shown in Figure 2, for adolescents with relatively higher ventral striatum activation (.5SD below the mean and higher), peer group norms were significantly associated with adolescent risk taking, such that those perceiving relatively more deviant peer norms showed heightened risk taking, whereas those perceiving relatively more prosocial peer norms were buffered from heightened risk taking. In contrast adolescents with relatively lower ventral striatum activation were resilient to peer norms, such that prosocial and deviant peer norms were not associated with risk taking. As shown in Figure 2, the crossover point (small

diamond on each line) captures where the groups (i.e., high and low neurobiologically sensitive youth) are no longer significantly different from one another. The crossover point occurs when youth report relatively more prosocial peer group norms, suggesting that high and low neurobiologically sensitive youth only differ in their risk-taking behaviors when they are in more deviant peer contexts.

Discussion

Adolescence is marked by increases in susceptibility to peers, heightened risk taking, and rapid changes in ventral striatum activation. The current study examined how variability in ventral striatum sensitivity to social rewards and punishments moderates individual differences in susceptibility to peers. We found that heightened ventral striatum activation when anticipating social rewards and avoiding social punishments moderated the association between perceived peer norms and risk taking, suggesting that the ventral striatum is signaling the motivational relevance of anticipating social feedback, regardless of valence, placing youth at risk when they are in negative peer contexts but buffering them in positive peer contexts.

While prior research has examined the neural correlates of peer conformity (e.g., Cascio, O'Donnell, Bayer, Tinney, & Falk, 2015; Nook & Zaki, 2015; Welborn et al., 2016), or how heightened striatal activation predicts concurrent or future peer influence and conformity effects (e.g., Cascio, Carp, et al., 2015), the current study provides a novel contribution by examining how variability in ventral striatum sensitivity to social rewards and punishments moderates the link between social context and risk taking. In particular, we found that perceptions of more deviant peer norms were associated with increased risk-taking behavior but only for adolescents with high ventral striatum activation when anticipating both social rewards and punishments.

Adolescents with high ventral striatum sensitivity who perceived more prosocial peer norms engaged in less risk taking. In contrast, adolescents with low ventral striatum activation were resilient in the face of negative peer norms, showing low risk taking regardless of peer context. Together, these findings suggest that ventral striatum sensitivity to social rewards and punishments does not serve as a monolithic negative susceptibility marker, but instead may tune adolescents to the social norms of their peer context, amplifying peer influence effects in both positive and negative ways. These effects persisted above and beyond self-reported peer influence susceptibility, suggesting that neurobiological sensitivity to social rewards and punishments may be a more sensitive index of heightened susceptibility to peer influence, and may capture more implicit aspects of susceptibility that are not accessible to or reported by individuals.

This method of using the brain as a moderator of social context diverges from prior research emphasizing that neurobiological sensitivity applies equally to all adolescents. This perspective offers two important advantages which may be especially relevant for prevention efforts. First, this perspective underscores that not all adolescents are vulnerable to peer influence effects, and that adolescents with low neurobiological sensitivity (i.e., low ventral striatum activation) will be resilient to conformity pressures, as they may not be motivated to adhere to peer norms, no matter the peer context they find themselves in. Second, this perspective underscores that high ventral striatum sensitivity does not equally place all youth at risk; only for adolescents in negative peer contexts (e.g., deviant peer norms) is heightened ventral striatum activation linked to adolescents' own risk behaviors. Adolescents with high ventral striatum activation who are in positive peer environments (e.g., prosocial peer norms) are buffered from engaging in risk taking. Importantly, our results may not only identify adolescents

most at risk, but also perhaps those who may be the most open to positive socializing influences

from prosocial peers. Future research should examine the extent to which sensitivity to social

rewards and punishments moderates the links between prosocial norms and prosocial behaviors.

Heightened VS activation reinforces the rewarding nature of engaging in motivated

appetitive behaviors and avoiding aversive behaviors (Kohls et al., 2013). Although speculative,

individuals with heightened VS activation to both anticipated social reward gain and social

punishment avoidance may experience greater motivation to adhere to peers' behavior, perhaps

out of a purported desire to gain peer acceptance, increase social connection, and avoid peer

disapproval and rejection (Falk et al., 2012). As such, those with heightened VS activation in

negative peer contexts (e.g., perceived deviant peers) may adhere to those norms and engage in

more risk taking, whereas those with heightened VS activation in positive peer contexts (e.g.,

perceived prosocial peers) may adhere to those norms and avoid risk taking, engaging in levels

similar to their peers with low VS sensitivity. Collectively, these findings implicate high VS

activation to both anticipated social reward gain and social punishment avoidance as a potential

biomarker that modulates the perceived value associated with peer influence.

These findings have implications for interventions seeking to decrease adolescent risk

taking. While some youth will be impervious to interventions, those who are neurobiologically

sensitive (i.e., have heightened VS activation to social rewards and punishments) will be more

likely to benefit from interventions that focus on changing adolescents' social context and the

perceived norms of their peers. Indeed, prior work suggests that peer influence may be driven by

misperceptions of norms and overestimations of risk attitudes among peers (i.e., pluralistic

ignorance) (Prentice & Miller, 1993; Prinstein & Wang, 2005). Thus, among youth who are

neurobiologically sensitive (i.e., heightened VS activation), interventions that focus on helping

adolescents seek alternate socially rewarding stimuli (e.g., engagement with prosocial peers) may have the largest impact. These findings suggest social contextual processes that might be most relevant to target in psychosocial preventive approaches, and greater awareness of the biologically reinforcing properties of peer conformity.

Limitations and Future Directions

Although the adolescent transition represents a key period of heightened susceptibility to peers (Brechwald & Prinstein, 2011; Prentice, 2008) in both deviant and prosocial contexts (Foulkes et al., 2018; Knoll et al., 2017; van Hoorn et al., 2016), remarkably little prospective longitudinal work has been conducted, especially examining the developmental psychobiological precursors of peer influence susceptibility. Because our study was cross-sectional, we are unable to examine how peer influence and neurobiological susceptibility unfold over time. Specifically, we cannot test the direction of effects, and it is possible that adolescents engaging in risk taking seek out peers who endorse the same behaviors (i.e., selection effects). Given substantial reorganization of the adolescent brain (Nelson, Jarcho, & Guyer., 2016), including significant changes in ventral striatum activation across adolescence (Telzer, 2016), it is possible that there are sensitive periods during which heightened ventral striatum activation is a particularly salient susceptibility marker. Longitudinal research will be key to unpack whether early striatal sensitivity, sensitivity at particular developmental periods, and/or longitudinal increases in ventral striatum sensitivity similarly serve as particular risk factors. A developmental longitudinal investigation of peer influence susceptibility will allow us to examine how changes in psychobiological processes might be associated with changes in peer influence susceptibility and correspondingly, prospective risk-taking behaviors.

In addition, peer influence susceptibility likely is the product of complex and interacting networks throughout the brain. While this study examined regional brain activity within the ventral striatum, this research reflects the assumption that brain regions operate in isolation. Compared to work on adults (e.g., O'Donnell et al., 2017; Wasylyshyn et al., 2018), more research is needed among youth using a network neuroscience approach. For instance, greater connectivity between regions involved in executive control (e.g., dorsolateral prefrontal cortex) and motivational relevance (e.g., ventral striatum) may be associated with less peer influence susceptibility, as heightened connectivity may signal effective top-down cognitive control. In contrast, greater connectivity between regions involved in affective salience (e.g., amygdala) and motivational relevance (e.g., ventral striatum) may be associated with greater peer influence susceptibility, as heightened connectivity may signal greater attention to socio-affective stimuli and a motivation to seek social rewards. Focus on connectivity within and between these networks will allow us to begin to identify the psychobiological processes associated with peer influence susceptibility across development.

Finally, future research would benefit from the use of peers' self-reported norms and behaviors, which would reduce concerns about methods variance. Nonetheless, the use of adolescents' perceived peer norms offers an advantage in examining a more proximal predictor of risk behavior, since prior work shows that adolescents' perceptions of their peers' behavior mediates the association between peers' actual reported behavior and adolescents' own behavior (Fromme & Ruela, 1994; Prinsteim & Wang, 2005).

Conclusions

Adolescents vary considerably in peer influence susceptibility (Brechwald & Prinstein, 2011), however remarkably little work has adequately operationalized, measured, or examined

the predictive validity of peer susceptibility markers. This work revealed that ventral striatum

sensitivity to both anticipated social reward gain and social punishment avoidance significantly

moderates the association between exposure to perceived peer norms and adolescents' own risk

behaviors. These findings provide a novel and innovative contribution to the study of peer

influence susceptibility, and to work revealing how individual differences in neural responses

may be associated with developmental adaptation.

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Table 1

Descriptives and Correlations Among Study Variables

| Variable	1.	2.	3.	4.	5.	6.
1. Peer Group Norms	1	-.03	-.09	-.16	.44***	.14[+]
2. VS Reward-Neutral		1	.72***	.07	.11	-.04
3. VS Punish-Neutral			1	.10	.02	.08
4. Resistance to Peer Influence				1	-.10	.06
5. Risk Taking					1	.24**
6. Age						1
M (SE)	2.16 (.06)	.11 (.02)	.06 (.02)	3.33(.05)	.24 (.02)	
range	1.0–4.13	-.61–.76	-.89–.88	1.0–4.0	0–1.43	

Note. *** $p < .001$; ** $p < .005$; [+] $p < .10$

Table 2

Ventral Striatum Sensitivity to Social Rewards and Social Punishments Moderates Link Between

Perceived Peer Group Norms and Adolescent Risk Taking

	ΔR^2	B (SE)	p	95% CI
Reward - Neutral				
Step 1, Covariates	.072		.007	
RPI		-.108 (.080)	.177	[-.266, .050]
Age		.243 (.081)	.003	[.082, .403]
Step 2, Main Effects	.176		.000	
Peer Group Norms (PGN)		.394 (.075)	.000	[.246, .542]
VS Reward-Neutral		.130 (.072)	.074	[-.013, .273]
Step 3, Interaction	.027		.030	
PGN * VS		.161 (.073)	.030	[.016, .306]
Total R^2	.275			
Punishment - Neutral				
Step 1, Covariates	.072		.007	
RPI		-.108 (.080)	.177	[-.266, .050]
Age		.243 (.081)	.003	[.082, .403]
Step 2, Main Effects	.160		.000	
Peer Group Norms (PGN)		.396 (.076)	.000	[.246, .546]
VS Punish-Neutral		.048 (.078)	.537	[-.105, .201]
Step 3, Interaction	.050		.003	
PGN * VS		.229 (.076)	.003	[.078, .380]
Total R^2	.282			

Note. PGN=peer group norms; VS= ventral striatum activation; RPI=resistance to peer influence
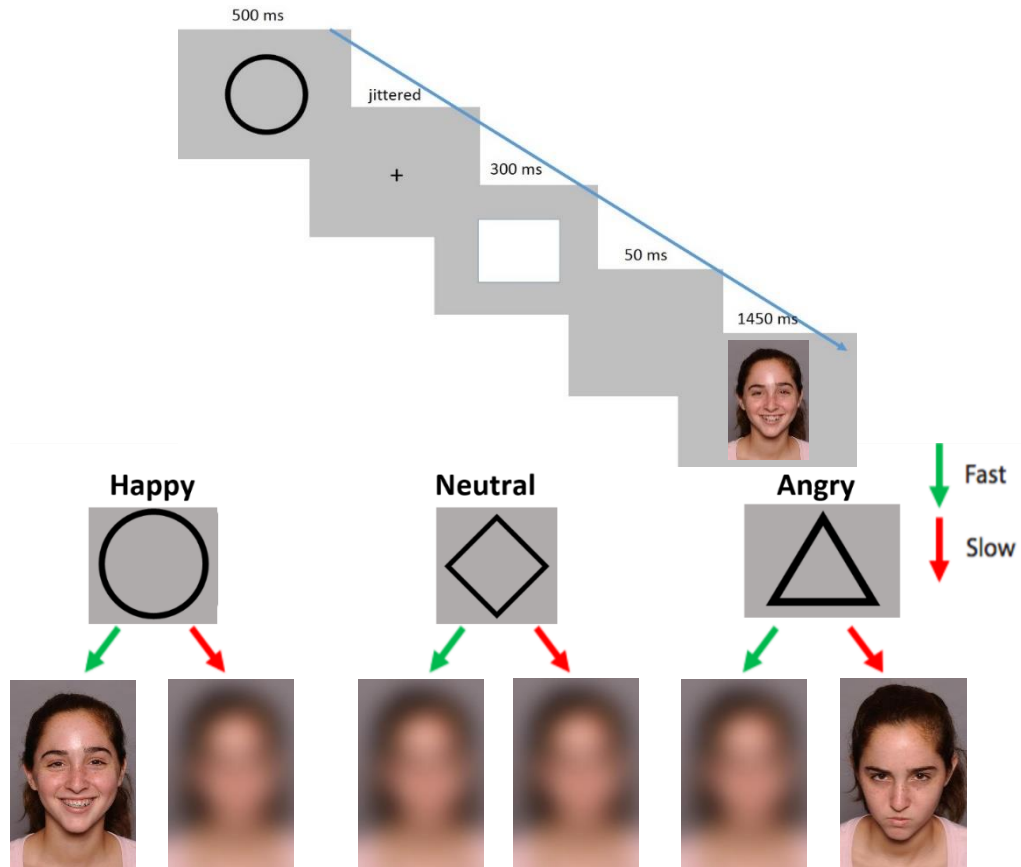
Figure 1. Social Incentive Delay Task. Each trial consists of a cue (circle, diamond, or triangle), a jittered crosshair delay, a target (white square) signaling participants to press a button, and feedback (e.g., happy face). Each cue and corresponding feedback depicted in lower panel of figure.
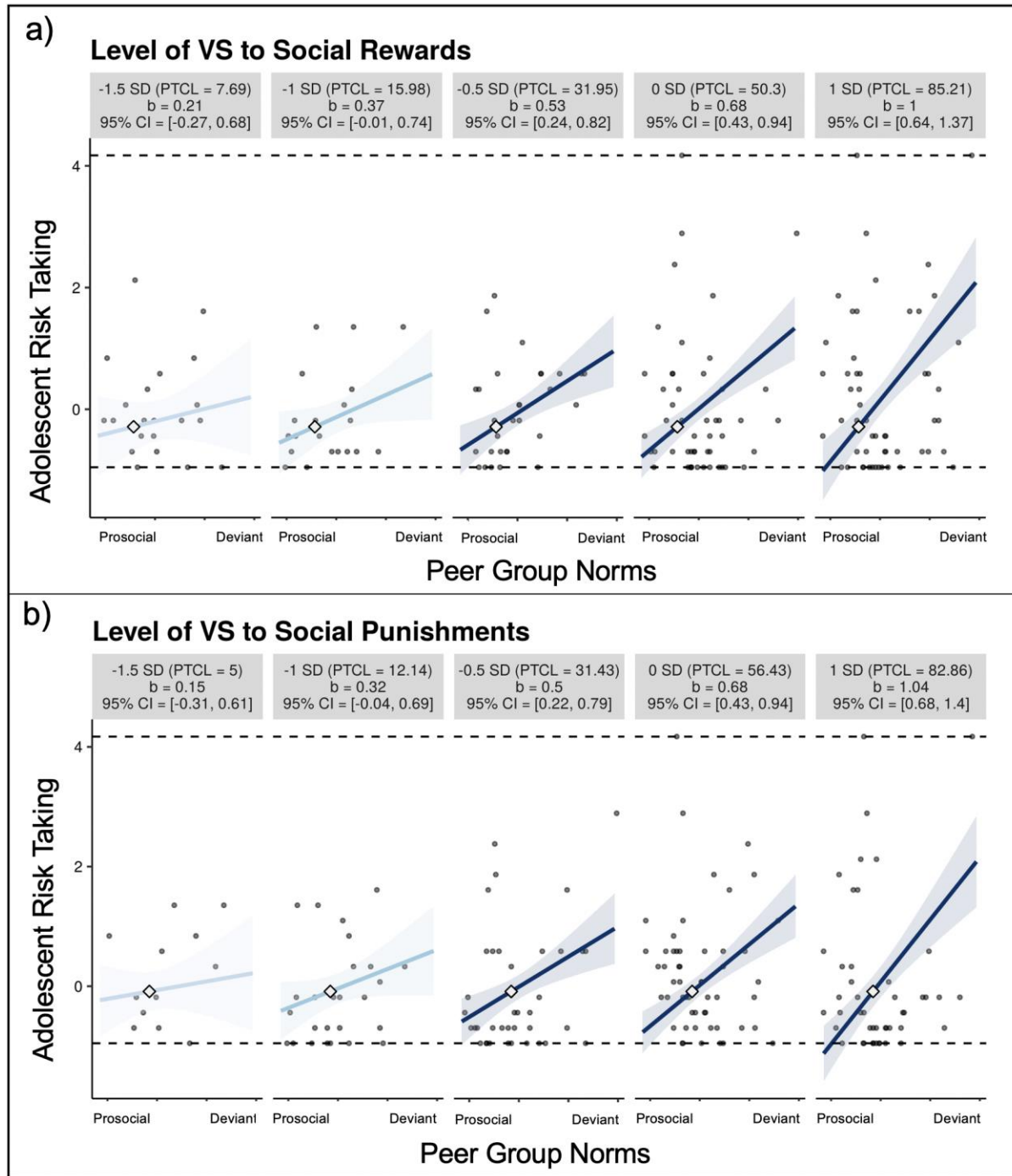
Figure 2. Small-multiples depictions of the interaction effect of perceived peer group norms and ventral striatum activation on adolescent risk taking. The small multiples illustrate the interaction across the range from 1.5 SD below to 1 SD above the mean in VS activation to (a) social rewards and (b) social punishments. Each graphic shows the computed 95% confidence region (shaded area), the observed data (gray circles), the maximum and minimum values of the outcome (dashed horizontal lines), and the crossover point (diamond). CI = confidence interval; PTCL = percentile. We z-transformed risk taking,

such that negative scores represent below average risk taking, whereas positive scores represent above average risk taking.

Supporting Information

Table 1

Whole Brain, Main Effect Analysis for Contrasts of Interest

Region Label	k	t	MNI Coordinates x	y	z
Reward>Neutral Anticipation					
R Ventral Striatum[c]	2847	6.312	10	8	-8
L Ventral Striatum[c]		5.218	-12	4	-10
L Linual Gyrus[a]	2271	13.379	-18	-94	-6
L Fusiform Gyrus[a]		4.638	-34	-68	-12
R Linual Gyrus[b]	2560	12.644	20	-88	-6
R Fusiform Gyrus[b]		5.868	40	-36	-20
Cerebellum	476	5.979	0	-54	-32
L Fusiform Gyrus	266	5.645	-38	-46	-18
R Middle Temporal Gyrus	173	5.296	52	-6	-16
R Insula Lobe	291	4.624	40	-8	-2
Neutral>Reward Anticipation					
Supplementary Motor Area	234	3.042	-4	-10	74
R Inferior Temporal Gyrus	1481	2.972	62	-42	-10
L Linual Gyrus	14792	7.164	-10	-82	6
L Middle Frontal Gyrus	9481	5.201	-44	2-	42
L Superior Medial Gyrus	9481	6.105	-6	26	40
R Middle Frontal Gyrus	9481	5.852	34	20	48
R Inferior Temporal Gyrus	1481	6.220	66	-36	-14
L Superior Orbital Gyrus	169	3.887	-22	66	8
L Middle Occipital Gyrus	140	3.886	-36	-80	10
R Rolandic Operculum	168	3.679	62	-2	14
Punish>Neutral Anticipation					
R Ventral Striatum[f]	1496	3.246	4	8	-8
L Ventral Striatum[f]		3.495	-8	6	-8
R Linual Gyrus[d]	3087	13.020	20	-92	-6
R Fusiform Gyrus[d]		6.746	40	-44	-18
R Middle Temporal Gyrus[d]		5.630	52	-6	-16
L Linual Gyrus[e]	2566	12.510	-18	-92	-8

	k	t	x	y	z
L Fusiform Gyrus[e]		5.913	-40	-44	-18
Neutral>Punish Anticipation					
Cerebellum	150	5.011	0	-54	-32
R Inferior Temporal Gyrus	151	4.288	30	0	-38
L Angular Gyrus[f]	10410	2.738	-34	-66	46
L Linual Gyrus[f]		7.138	-8	-80	4
R Superior Temporal Gyrus	586	5.300	64	-18	0
R Middle Frontal Gyrus[g]	1208	4.524	28	14	54
R Superior Frontal Gyrus[g]		3.585	18	32	58
L Middle Temporal Gyrus	160	4.379	-60	-24	0
R Inferior Temporal Gyrus	338	4.232	62	-32	-14
L Inferior Temporal Gyrus	638	4.224	-52	-38	-16
L Inferior Frontal Gyrus	360	4.193	-36	44	-12
R Inferior Frontal Gyrus	185	4.143	42	42	-12
L Superior Frontal Gyrus[h]	897	4.062	-22	18	62
L Middle Frontal Gyrus[h]		3.835	-46	10	46
R Putamen	248	3.889	30	-4	4

Note. L and R refer to left and right hemispheres; k refers to the number of contiguous voxels in each significant cluster; t refers to peak activation level in each cluster. Clusters that share the same superscript are part of the same contiguous cluster. All results are threshold at $p<.005$, with a cluster extent threshold based on 3dClustSim in the AFNI software package (updated version April 2017; Ward, 2000), corresponding to $p<.05$ FWE corrected (cluster extent of 124 voxels for reward vs. neutral anticipation and 135 voxels for punishment vs. neutral anticipation).
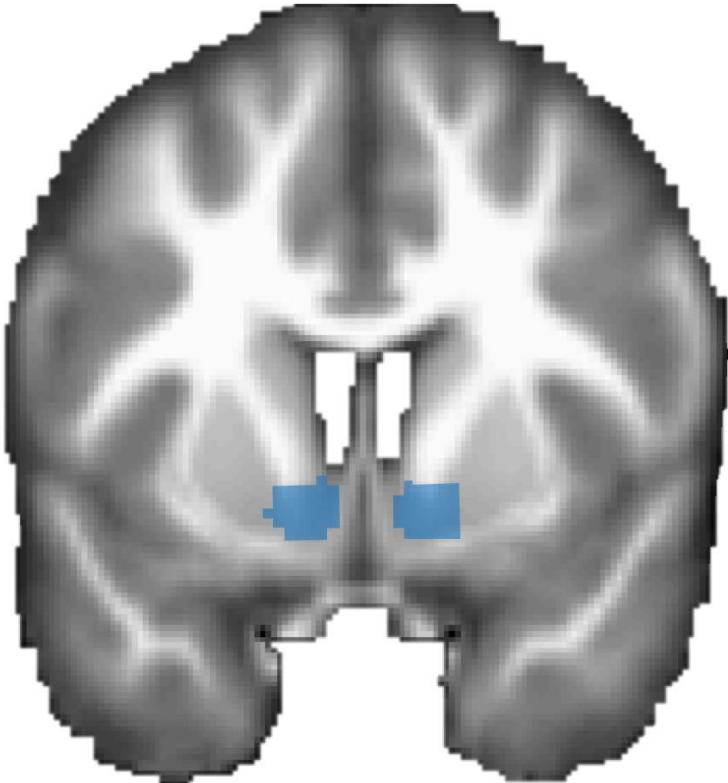
Figure 1. Ventral striatum ROI from Neurosynth.