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The effect of social rank feedback on risk taking and associated reward processes in adolescent girls

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Abstract

The onset of adolescence is associated with an increased tendency to engage in risky behaviors and a developmental shift toward peers that contributes to increased prioritization for learning about and achieving social status. There is relatively little understanding about the specific links between these adolescent-typical phenomena, particularly regarding their neural underpinnings. Based on existing models that suggest the role of puberty in promoting adolescent status-seeking and risk-taking tendencies, we investigated the relation of pubertal hormones with behavioral and neural responses to status-relevant social information in the context of risk taking. We used a probabilistic decision task in which 11- to 13-year-old girls chose to take a risk, or not, while receiving either social rank or monetary performance feedback. While feedback type did not differentially influence risk-taking behavior, whole-brain imaging results showed that activation in the anterior insula was increased for risk taking in the social rank feedback condition compared to the monetary feedback condition. This heightened activation was more pronounced in girls with higher estradiol levels. These findings suggest that brain processes involved in adolescent risky decisions may be influenced by the desire for social-status enhancement and provide preliminary evidence for the role of pubertal hormones in enhancing this adolescent-typical social sensitivity.

Key words: fMRI; puberty; social status; insula; estradiol

Introduction

Adolescence is a developmental period characterized by a ‘social reorientation’ (Nelson *et al.*, 2005, 2016). That is, adolescents become more focused on their peers and start to behave in accordance with social goals, such as the achievement of higher social status with respect to their peers. Social status, or rank, refers to one’s relative standing compared with others within a social hierarchy, which can be inferred from one’s own subjective experience (e.g. dominance), the subjective experience of others (e.g. popularity or reputation), or from an objective measure that enables direct comparison with others (e.g. task performance) (Koski *et al.*, 2015). The adult neuroimaging literature has shown that processing of status-related cues involves

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activation of reward-related brain regions, such as the ventral striatum (Ly *et al.*, 2011; Zerubavel *et al.*, 2015). These findings suggest that social status may have a relatively direct influence upon the neural mechanisms that evaluate reward. According to the social-information processing network model (Nelson *et al.*, 2005, 2016), earlier development of reward-related brain regions compared to cognitive-regulatory brain regions gives rise, in adolescence, to the increased emotional salience of social information (e.g. one's social status among peers) and the motivation to learn about and act upon these socio-emotional experiences by engaging in behaviors highly valued by one's peers (i.e. status-seeking behavior).

One example of status-seeking behavior is the engagement in risk taking. According to a dual-systems model (Steinberg, 2008; Shulman *et al.*, 2016), the tendency to take risks increases across adolescence, particularly in the presence of peers, due to heightened activation in reward-related brain regions combined with suboptimal levels of activation in brain regions that regulate these reward-related processes. As a result, adolescents become more motivated to engage in socially rewarding behaviors, despite the potential negative consequences associated with risk taking. Evidence supporting this model comes from studies that focused on risk taking in the presence of peers. These studies showed that adolescents, as opposed to children and adults, make more risky decisions in the presence of peers compared to when alone (Gardner and Steinberg, 2005; Chein *et al.*, 2011; Smith *et al.* 2014a). Furthermore, adolescents, but neither children or adults, who engaged in more risk taking showed increased reward-related activation—in both ventral striatum and orbitofrontal cortex—in the presence of peers compared to when alone (Chein *et al.*, 2011). Together, these findings support the notion that adolescence is a unique time in development during which individuals are particularly sensitive to social influences from their peers (Blakemore and Mills, 2014; Knoll *et al.*, 2015) and highlight the importance of reward-related processes for peer influences on risk taking.

Another perspective, based on the belief that adolescents are engaging in goal-directed behavior, is that adolescents become more attuned to socio-emotional information and learn to regulate their behavior to accomplish social goals that are adaptive (Nelson and Guyer, 2011; Crone and Dahl, 2012). In other words, adolescents might engage in risk taking to impress peers and achieve or maintain higher social status, instead of risk taking resulting from a lack in the ability to regulate their socially induced emotional tendencies. Indeed, the importance of social status, relative to other domains, peaks during early adolescence (LaFontana and Cillessen, 2010). Furthermore, results of a longitudinal study among high school students showed that engaging in smoking behavior in tenth grade led to increased social status over time (Mayeux *et al.*, 2008). Together, these findings suggest that adolescence is a time in development during which individuals engage in risk taking as a form of status-seeking behavior. Moreover, a common (neural) mechanism may underlie the motivation to achieve higher social status and to engage in risk taking (Bhanji and Delgado, 2014).

One model for understanding the possible links between status-seeking and risk-taking tendencies in adolescence focuses on pubertal changes in social and affective valuation (Nelson *et al.*, 2005; Forbes and Dahl, 2010; Crone and Dahl, 2012). Specifically, hormonal changes might promote adaptive tendencies for youth to explore ways to enhance status (i.e. to find a niche that provides admiration). Indeed, the rise in testosterone and estradiol during puberty is thought to reorganize the adolescent brain (Sisk and Zehr, 2005; Schulz *et al.*, 2009) and impact social behaviors (Schulz and Sisk, 2006; Forbes and Dahl, 2010) as well as risk taking (Peper and Dahl, 2013). Previous studies in adults have shown that testosterone is involved in the attainment and maintenance of social status (Eisenegger *et al.*, 2011; Terburg and Van Honk, 2013). For example, a study using a multi-player auction task in young adult men showed that higher levels of testosterone corresponded with a willingness to incur monetary losses by overbidding, for the sake of winning the auction (Van den Bos *et al.*, 2013). Less is known about the role of estradiol in status-seeking behavior, although existing findings in female adults suggest that estradiol leads to behaviors that augment social status, particularly in women who are competing with other women (Knight and Mehta, 2014). Together, these findings suggest that the rise in testosterone and estradiol during puberty may play a role in enhancing status-relevant information, which in turn may increase status-seeking behaviors, such as risk taking, across adolescence.

In this study, we set out to investigate the role of pubertal hormones (testosterone and estradiol) in social influences on adolescent risky decisions and associated reward-related brain processes. To maximize the variance of our pubertal measures while keeping age relatively constant, we recruited participants around the onset of puberty. In this early adolescent sample, we tested whether information about one's social status in the form of social rank performance feedback compared to monetary performance feedback differentially influenced risk taking and/or reward processing. In keeping with current understandings of the neural networks involved in social cognition in adolescence (reviewed in Blakemore, 2008), multiple brain regions might differentiate these feedback conditions. In particular, sensitivity to the presence of social hierarchies engages the dorsal anterior cingulate and insular cortices (reviewed in Chiao, 2010), which, along with the ventrolateral prefrontal cortex and striatum, can also be more active during the experience of social conformity (Izuma, 2013) or social exclusion (Pfeifer and Peake, 2012). However, given the potentially important relationship between social influences and rewards, we focused on a region that subserves a more general function relevant to social behavior (i.e. reward processing) and is engaged during risk taking: the nucleus accumbens (NAc) and medial prefrontal cortex (mPFC) (Haber and Knutson, 2010; Bhanji and Delgado, 2014).

Based on prior research, we predicted that adolescents would show increased risk taking in the context of receiving social rank feedback compared to monetary feedback about their task performance (e.g. Chein *et al.*, 2011). Furthermore, we predicted that adolescents with higher testosterone and/or estradiol levels would be more biased toward risky decisions in the social rank compared to monetary feedback context (e.g. Van den Bos *et al.*, 2013). Finally, we predicted that reward-related brain activation (in NAc and mPFC) associated with risky decisions would be enhanced in the social rank compared to monetary feedback context (Chein *et al.*, 2011; Engelmann and Hein, 2013; Bhanji and Delgado, 2014), and that this effect would be moderated by the level of pubertal hormones (according to a model proposed by Crone and Dahl, 2012).

Methods and materials

Participants

The results presented here are based on 58 participants: 23 11-year-olds, 19 12-year-olds, and 16 13-year-olds (*M* age = 12.4, SD = 0.92). Participants were recruited within a narrow age range around the onset of puberty to capture the developmental window during which individual differences in pubertal stage are the largest while keeping age relatively constant. Among the included participants 46.6% were Caucasian, 10.3% Asian, 5.2% Hispanic/Latin, 3.4% African-American, 24.1% were multiracial and 10.4% did not provide information about their race or ethnicity. All participants scored within the normal range on the Child Behavior Checklist (Achenbach, 1991), based on their total score. Furthermore, there were no age-related differences in cognitive functioning, as measured by their performance on the matrix-reasoning subtest of the Wechsler Abbreviated Scale of Intelligence (Wechsler, 1999). See Supplementary Table S1 for the means, SD and ranges for each age group.

Before entering the study, written informed consent was obtained from the parent or legal guardian of the participant, and assent was obtained from the participant. All participants received $130 in gift cards at the end of the study, which included compensation for their travel time, the time spent in the lab, and additional task winnings. See Supplementary Materials for a detailed description of the recruitment and study procedures. The University of California Berkeley Institutional Review Board approved all procedures.

Pubertal measures

In this study, we collected multiple measures of pubertal stage. Self-reported pubertal stage was assessed using the Pubertal Development Scale (PDS; Petersen *et al.*, 1988). Testosterone and estradiol levels were measured based on two saliva samples from each participant, collected at home across two mornings. Furthermore, we calculated body mass index (BMI) to index physical size. See Supplementary Materials for a detailed description of these developmental measures as well as the sample means of, and correlations between, these measures.

Jackpot task with feedback about performance

For this study, we used a modified version of the Jackpot task (based on Op de Macks *et al.*, 2011), which included *feedback* phases during which participants were presented with their cumulative performance. The feedback phases were presented after every six trials. Participants were instructed that their performance was calculated based on the number of points accumulated during preceding trials and expressed either as the amount of money earned (monetary feedback), or as the participant's rank compared with other, same-aged girls who had also played the task (social rank feedback). Participants were told that they had $5 in play money, which they could increase up to $30 if they chose to play. Participants were also told that they would be paid according to their final score—in points—which was translated into a monetary amount at the end of the experiment.

To increase the credibility of the social rank manipulation, a picture was taken of each participant's side profile during the first lab visit. This picture was converted into a black-and-white silhouette that was incorporated into the Jackpot task that they played during the second lab visit, while undergoing MRI. During the feedback phases of the task, participants would see their silhouette depicted on an upward pointing arrow at one of seven levels, depending on their cumulative task performance (Figure 1A). More specifically, during the monetary feedback phases, participants would see their silhouette depicted on an arrow next to seven 'heads' of coins. During the social rank feedback phases, participants would see their silhouette depicted on an arrow next to seven silhouettes of other participants who were ranked according to their performance. In actuality, these other silhouettes were based on pictures of researchers and participants of our pilot study (after obtaining written permission). The order of these silhouettes was consistent across participants, so that visual experience of feedback presentation was equal across participants (except for their own silhouette). Although we did not explicitly ask participants whether they believed that they were being ranked against peers, we did have participants report on their subjective experience of the task using a questionnaire that was administered immediately after the MRI scan. Participants tended to report being more nervous during the social rank than monetary feedback conditions, especially when they were older, indicating that they differentiated between the two feedback contexts (see Supplementary Materials for a more detailed report of these results).

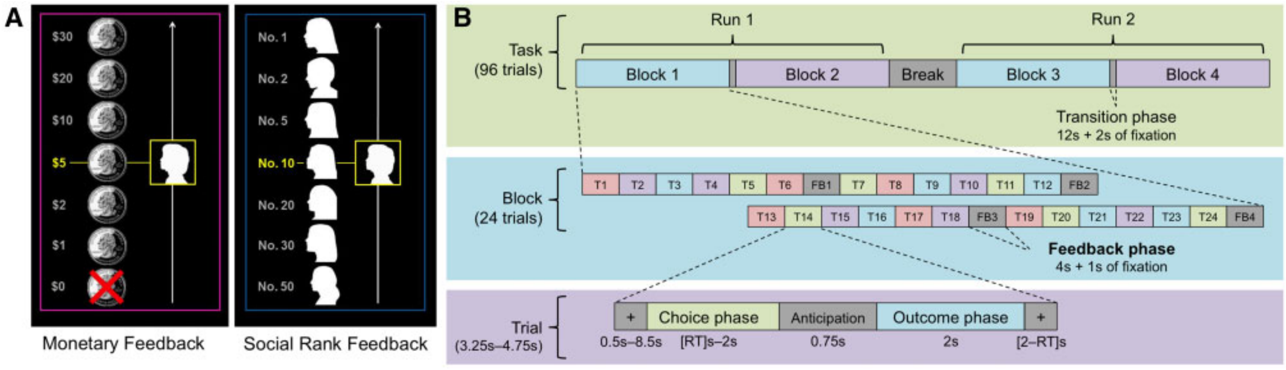

Fig. 1. The Jackpot task with feedback phases. **(A)** During the feedback phases, participants were shown their cumulative performance expressed as the amount of money earned (monetary feedback), or as the participant's rank compared with other, same-aged girls who had also played the task (social rank feedback). **(B)** Upper panel: The task was administered across two runs of scans with a self-paced break in between. Before each run, participants were told which feedback type would be presented first; in between blocks (within the same run) they were visually prompted about the transition in feedback type (i.e. transition phase). A fixation cross was also presented at the start of every run for 2 s and after each feedback phase (1 s) and transition phase (2 s). Throughout each block, feedback type (Social rank or Money) was held constant and the order was counterbalanced between participants (MSMS or SMSM), within each age group. Middle panel: Each block consisted of 24 trials, 6 trials of each condition, presented in random order. Feedback phases occurred after every 6 trials (i.e. four times in each block). Bottom panel: Trials consisted of a choice phase, in which participants chose to play or pass based on information about risk level (33 *vs* 67%) and stakes (1 *vs* 3 pts), and an outcome phase, during which participants were shown whether they won or lost (upon the choice to play), or that nothing changed (upon the choice to pass). Each trial started with a 500 ms fixation cross, which was jittered for an additional 0–8 s at 2 s increments.

The type of feedback (social rank or monetary) presented during the feedback phases was held constant within a block of 24 trials. In total, there were four blocks (96 trials), administered across 2 runs of scans with a self-paced break in between runs. As such, there were two blocks—a total of eight feedback phases—for each feedback type. The type of feedback alternated between blocks and the order was counterbalanced across participants, within each age group. Before each run, participants were instructed verbally (via the intercom) about which feedback type they would start with. They received a written prompt that announced the switch of feedback type in between blocks (i.e. ‘transition phases’). See Figure 1B for an overview of the task design.

On each trial, participants decided to ‘play’ or ‘pass’ based on information about the risk level (33 or 67% chance to win) and stakes (1 or 3 points) involved with the decision to play, which was presented to them simultaneously during the ‘choice phase’ (Figure 1C). The resulting trial types—low-risk/low-stakes (LR-1pt), low-risk/high-stakes (LR-3pts), high-risk/low-stakes (HR-1pt), and high-risk/high-stakes (HR-3pts)—were presented in random order across the task. Here, we collapsed across the different trial types to investigate whether feedback type (social rank *vs* money) influenced decision-making and/or associated reward processes. Results of the effects of trial-level manipulations (risk level and stakes), collapsed across feedback type, on risk taking and reward-related brain processes are reported elsewhere (Op de Macks *et al.*, in press).

Upon a button press—with the right index finger for ‘play’ and the right middle finger for ‘pass’—participants were presented with the outcome of their choice (‘outcome phase’). Although outcomes of play choices could be gains or losses, outcomes of pass choices and misses were always the same: neutral (no gains or losses) and losses (of 1 pt), respectively. Net gains (in points) across six trials would lead to the participant moving up the arrow during the feedback phase, whereas net losses would lead to the participant moving down the arrow (Figure 1A).

To investigate whether the type of feedback differentially influenced risk taking and associated brain processes, we looked at choice behavior and brain responses during the trials and contrasted them between the social rank and monetary feedback blocks. We did not analyze the feedback phases themselves, since there was no choice behavior during those phases and there were not enough instances of feedback presentation (i.e. eight feedback phases for each feedback type) to reliably calculate and compare the brain responses during feedback presentation. More importantly, we were interested in the influence of social ‘context’ on decisions and reward processes during risk taking, not the influence of feedback *per se*.

Resistance to peer influence

Participants also completed the resistance to peer influence (RPI) scale (Steinberg and Monahan, 2007). This questionnaire consists of ten pairs of opposing statements; e.g. ‘Some people go along with their friends just to keep their friends happy BUT other people refuse to go along with what their friends want to do, even though they know it will make their friends unhappy’. Participants were instructed to choose one statement and to report whether the chosen statement was ‘really true’ or ‘sort of true’ for them. Item scores ranged from 1 to 4 and the average across all ten items provides an index of RPI score, with higher scores indicating more self-reported resistance to peer influence. RPI scores for the 11-year olds ($n = 23$) ranged from 2.3 to 3.6 ($M = 3.0 \pm 0.32$), for the 12-year olds ($n = 19$) scores ranged from 1.8 to 3.8 ($M = 3.1 \pm 0.45$), and for the 13-year olds ($n = 16$) scores ranged from 2.2 to 3.8 ($M = 2.9 \pm 0.45$). There were no differences between age groups, $F(2, 55) = 0.38$, $P = 0.69$. Furthermore, RPI score did not correlate with any of the other developmental measures (Table 1), indicating that individual differences in resistance to peer influence did not correspond with differences in pubertal maturation.

fMRI analyses

See Supplementary Materials for a detailed description of the image acquisition and preprocessing steps. Statistical analyses were performed on individual subjects’ data using the general linear model (GLM) in SPM8 (http://www.fil.ion.ucl.ac.uk). Trials were modeled as separate zero-duration events starting at the onset of stimulus presentation. Note that while each trial consisted of a stimulus, anticipation, and outcome phase, these phases were not modeled separately due to the absence of jittered periods in between the different phases within each trial. Feedback phases were also modeled as zero-duration events starting at the onset of feedback presentation. Transition phases were modeled as 12-s events starting at the onset of the transition screen presentation. Here, we report the results of analyses collapsed across the different trial types (LR-1pt, LR-3pts, HR-1pt, HR-3pts).

We created two separate subject-specific design matrices to look at risk taking (choice model) and reward processing (outcome model), separately for the social rank and monetary feedback conditions. The choice model included four regressors of

Table 1. Correlations between the developmental measures, self-reported resistance to peer influence, and the relative measures of risk taking and RT (in percentages)

	Developmental measures				
	Age	PDS	Testosterone	Estradiol	BMI
RPI score	($n = 58$) $r = -0.03$ $P = 0.85$	($n = 58$) $r = -0.02$ $p = 0.87$	($n = 57$) $r = -0.02$ $P = 0.88$	($n = 56$) $r = 0.15$ $P = 0.29$	($n = 56$) $r = -0.11$ $P = 0.43$
Risk taking (relative %)	($n = 58$) $R = 0.01$ $P = 0.92$	($n = 58$) $r = 0.07$ $P = 0.62$	($n = 57$) $r = -0.03$ $P = 0.84$	($n = 56$) $r = 0.11$ $P = 0.43$	($n = 56$) $r = 0.12$ $P = 0.38$
RT (relative %)	$r = -0.19$ $P = 0.15$	$r = .03$ $P = 0.85$	$r = .14$ $P = 0.29$	$r = -0.01$ $P = 0.94$	$r = 0.12$ $P = 0.40$

RPI, resistance to peer influence; RT, response time; PDS, pubertal development stage; BMI, body-mass index.

interest that modeled the trials based on the choices participants made, separately for each feedback type: Social Play, Monetary Play, Social Pass, and Monetary Pass. The outcome model included six regressors of interest that modeled the trials based on the outcomes participants experienced, separately for each feedback type: Social Gain, Monetary Gain, Social Loss, and Monetary Loss (for Play trials); Social Pass and Monetary Pass (for Pass trials). Note that the only difference between these two models is the further categorization of Play trials (in the choice model) into (i) play choices that resulted in gains, and (ii) play choices that resulted in losses (in the outcome model), which allowed for the comparison of Gain and Loss outcomes following the choice to play (separately for each feedback type). For each of these first-level statistical models, misses (trials on which participants failed to make a response within the allotted time) were modeled as a separate regressor of no interest. Additional regressors of no interest were included for (i) feedback phases, (ii) transition phases, and (iii–viii) the movement parameters (roll, pitch, yaw and displacement in superior, left and posterior directions). The feedback phases themselves were not analysed, since there were only eight instances of monetary and social rank feedback. More importantly, as noted earlier, we were interested in the influence of social 'context' on decisions and associated reward processes, not the influence of feedback *per se*.

To examine group-level differences between the feedback types in risk taking-related brain activation, we conducted second-level statistical analyses to test the contrasts of Social *vs* Monetary Play and Social *vs* Monetary Pass. To examine group-level differences in reward-related brain activation associated with risk taking, we tested the contrasts of Social *vs* Monetary Gain and Social *vs* Monetary Loss (following the choice to play). Task-related responses were considered significant if they exceeded a family-wise error (FWE) corrected threshold of $P < 0.05$.

To examine individual differences in choice and reward-related brain activation, we applied the MarsBar toolbox for use with SPM8 (Brett *et al.*, 2002) to extract parameter estimates from specific regions of interest (ROIs). The NAc ROI was created by drawing 4 mm-radius spheres around the coordinates for bilateral NAc ($x = \pm 10$, $y = 12$, $z = -3$), as reported in Haber and Knutson (2010). The mPFC ROI was defined by taking the entire functional cluster located in the mPFC that resulted from the Gain > Loss contrast calculated across the group (reported in Op de Macks *et al.*, in press). To ensure the inspection of brain functioning within anatomical boundaries, additional masked ROIs were each created by taking the overlapping region of (i) the entire cluster of activation that resulted from the whole-brain results for the contrast of Social > Monetary Play trials (i.e. the functional ROI) and (ii) the anatomical ROI, available through the MarsBar anatomical automatic labeling (AAL) toolbox.

To test whether differences in brain and behavior as a function of feedback type were related to differences in pubertal hormones, we correlated the parameter estimates extracted for each participant with individual (averaged) levels of testosterone and estradiol. We also looked at the relation of brain and behavior with other measures of development (age, pubertal stage and BMI) and self-reported resistance to peer influence.

Results

Effects of feedback context on decision-making

Risk taking was measured as the percentage of play choices; response time (RT) was measured as the time between stimulus onset and the button press to indicate the participant's choice (in milliseconds). At the group level, there was no main effect of feedback type on risk taking, $F(1, 57) = 0.05$, $P = 0.82$ (Figure 2A) nor on RT, $F(1, 57) = 0.01$, $P = 0.91$. However, there were *individual differences*—in both risk taking and RT—across the two feedback contexts. While some girls chose to play more often in the social rank feedback context, other girls chose to play more often in the monetary feedback context (Figure 2B). To index these individual differences, we calculated the relative difference (in percentages) between a) risk taking in the social rank feedback context and b) risk taking in the monetary feedback context (i.e. [a – b]/b * 100); the same was done to calculate the relative difference for RTs. Thus, positive percentages represented more risk taking (or longer RTs) in the social rank feedback context, whereas negative percentages represented more risk taking (or longer RTs) in the monetary feedback context.

None of the developmental measures were associated with the relative measures of risk taking or RT (Table 1), indicating that differences in testosterone level, estradiol level, age, pubertal stage or BMI did not explain the task-related behavioral differences between the feedback contexts. Furthermore, we

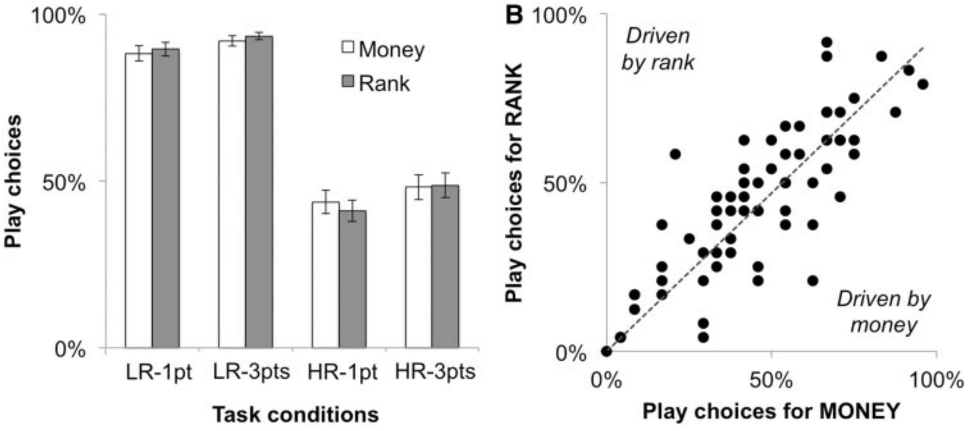

Fig. 2. Effects of feedback type on risk taking. **(A)** Group averages for risk taking in the four task conditions, plotted separately for the social rank (Rank) and monetary (Money) feedback contexts. Error bars represent the standard errors. **(B)** Individual differences in risk taking in the monetary feedback context plotted against risk taking in the social rank feedback context. Participants with greater perpendicular distance to the dotted line were more biased toward risk taking in a particular feedback context. Note that the dotted line represents the identity line ($y = x$), not the regression line.

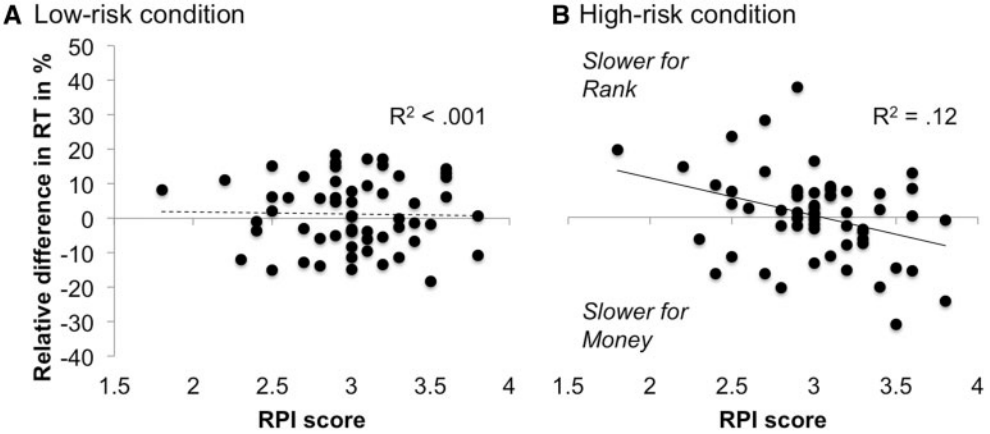

Fig. 3. Scatterplots of the relations between self-reported resistance to peer influence (i.e. RPI scores, which can range from 1 to 4) and the relative difference in RTs between the social *vs* monetary feedback context, plotted separately for decisions in the low-risk **(A)** and high-risk **(B)** conditions.

explored the relation between self-reported resistance to peer influence and task behavior. Although there were no associations between RPI score and the relative difference in RT ($r = -0.20$, $P = 0.14$), or risk taking ($r = -0.06$, $P = 0.67$), there was a negative association between RPI score and the relative differences in RT in the HR condition ($r = -0.35$, $P = 0.008$), but not the LR condition ($r = -0.02$, $P = 0.86$) (see Figure 3). These correlations were significantly different from one another (Steiger's $Z = 2.3$, $P = 0.020$; Steiger, 1980). These findings indicate that girls who reported being *less* resistant to peer influence were relatively slower decision-makers in the social rank feedback context, but only when the chance to win was relatively small. In other words, girls who were more concerned with their social environment took longer to decide—for riskier decisions only—whether they wanted to play or pass when they were going to be ranked against peers relative to receiving monetary feedback. No association was found between RPI score and the relative differences in risk taking for each of the conditions (LR: $r = 0.001$, $P = 0.99$; HR: $r = -0.09$, $P = 0.50$, $n = 57$).

Imaging results: main effects

To test whether feedback type modulated activation in regions associated with reward processing during risk taking, we examined individual differences in activation of NAc (based on Haber and Knutson, 2010) and mPFC (based on Op de Macks *et al.*, in press). Results of the ROI analyses showed that, across participants, there was no main effect of feedback type on either NAc or mPFC activation (Supplementary Figure S1). To examine whether other brain regions showed a main effect of feedback type, we conducted whole-brain analyses for brain activation during risk taking and reward processing separately.

Risk taking-related brain activation. Results of the whole-brain analysis across participants ($n = 58$) for the contrast of Social > Monetary Play revealed clusters of activation in bilateral anterior insula (AI), with the left peak at: $x = -38$, $y = 17$, $z = -8$ (cluster-level FWE corrected $P = 0.004$), and the right peak at: $x = 46$, $y = 22$, $z = -5$ (cluster-level FWE corrected $P = 0.002$) (Figure 4A). These results indicate that bilateral AI was more active during trials on which participants chose to play in the social rank feedback context compared to trials on which participants chose to play in the monetary feedback context. Further examination of the patterns of brain activation in bilateral AI showed that activation in this region was increased for Play choices—regardless of whether they resulted in Gain or Loss—compared with Pass choices in the social rank feedback context [Gain > Pass: $t(57) = 2.9$, $P = 0.005$; Loss > Pass: $t(57) = 2.5$, $P = 0.015$], but not in the monetary feedback context (Gain > Pass: $t(56) = 0.22$, $P = 0.83$; Loss > Pass: $t(56) = 0.78$, $p = 0.44$) (Figure 5A). These findings indicate that bilateral AI distinguished between risky and safe choices when playing for rank, but not when playing for money. Additional clusters of activation were found in left fusiform (peak at: $x = -30$, $y = -52$, $z = -14$, cluster-level FWE corrected $P < 0.001$) and lingual gyrus (peak at: $x = -12$, $y = -85$, $z = -3$, cluster-level FWE corrected $P = 0.003$). No regions of activation survived correction for multiple comparisons (at either peak- or cluster-level) for the opposite contrast of Monetary > Social Play, nor for the contrasts of Social > Monetary Pass and Monetary > Social Pass.

Reward-related brain activation. Results of the whole-brain analysis across participants for the contrast of Social > Monetary Gain revealed clusters of activation in left fusiform gyrus (peak at: $x = -32$, $y = -69$, $z = -11$, cluster-level FWE corrected $P < .001$), and in right AI (peak at: $x = 36$, $y = 16$, $z = -6$, cluster-level FWE corrected $P < 0.001$) (Figure 4B). No regions of activation survived correction for multiple comparisons (at either peak- or cluster-level) for the opposite contrast of Monetary > Social Gain, nor for the contrasts of Social > Monetary Loss and Monetary > Social Loss. However, at a lowered threshold of $P < 0.001$ uncorrected with $k \geq 10$ voxels, we found a cluster of activation in left AI (peak at: $x = -38$, $y = 17$, $z = -9$) for Social > Monetary Loss (Figure 4C). These results indicate that AI (and fusiform gyrus) was more strongly activated when playing for rank resulted in gains than when playing for money resulted in gains. See Supplementary Figure S2 for the BOLD time-courses of the left and right AI, plotted separately for gain, loss, and pass trials in both the social rank and monetary feedback conditions.

Individual differences in AI activation

To test whether pubertal hormones moderated the neural response to social context, we correlated individual differences in AI activation with our developmental measures. Results showed a significant positive association between estradiol level and AI activation for Social > Monetary Play ($r = 0.27$, $P = 0.048$, $n = 56$), indicating that girls with higher levels of estradiol tended to show increased activation of bilateral AI for risk taking in the

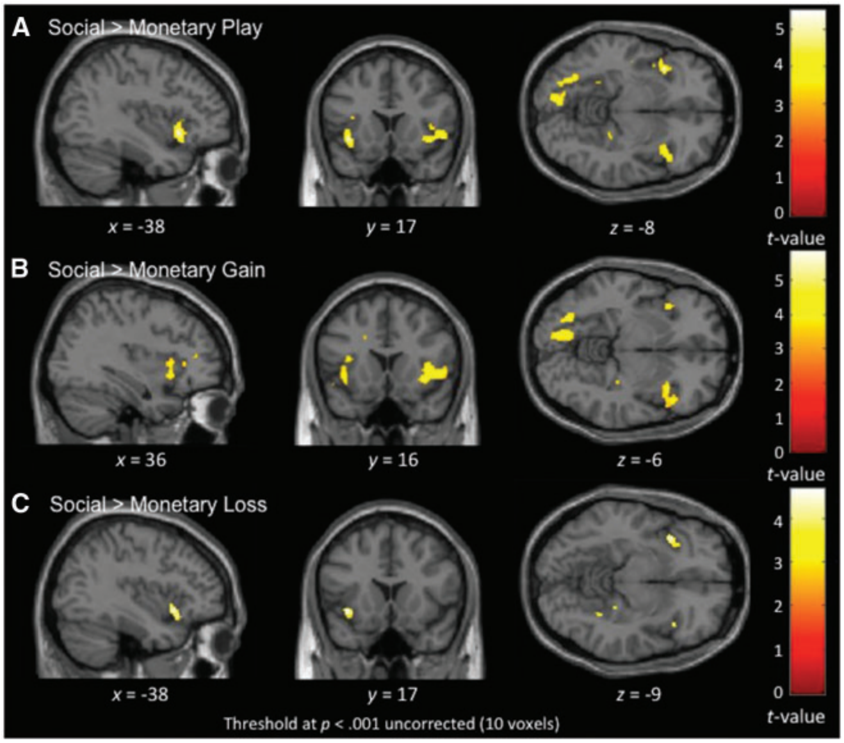

Fig. 4. Regions of activation when comparing social rank with monetary feedback contexts for **(A)** risk taking (i.e. Social > Monetary Play), and for **(B)** positive outcomes (i.e. Social > Monetary Gain) as well as **(C)** negative outcomes (i.e. Social > Monetary Loss) upon the choice to play, presented at $P < 0.001$ uncorrected, $k \geq 10$ voxels.

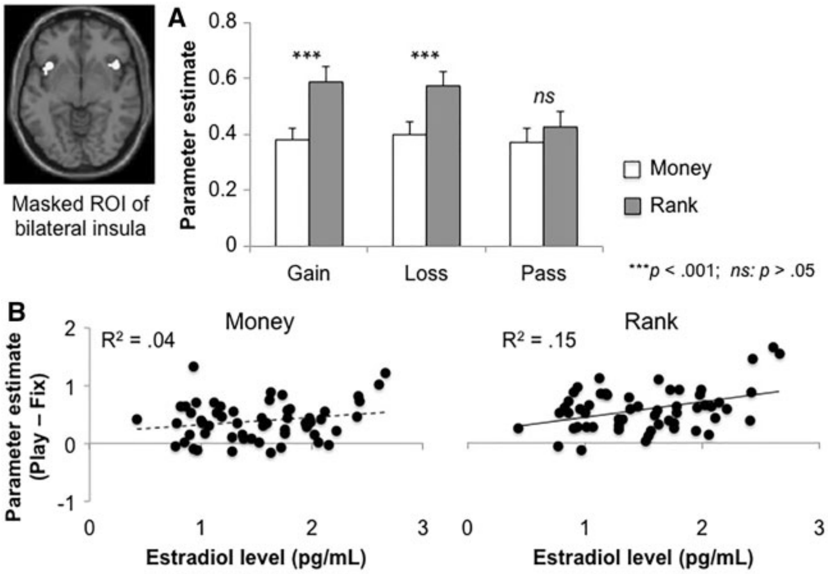

Fig. 5. **(A)** Average activation, across the group, in bilateral AI for trials on which participants chose to play—plotted separately for gain and loss outcomes—and for trials on which participants chose to pass, plotted separately for the monetary (white bars) and social rank feedback context (gray bars). Error bars represent standard errors. **(B)** Scatterplots of estradiol level plotted against risk taking-related (i.e. Play–fixation) insula activation in the monetary feedback context (left) and social rank feedback context (right).

social rank compared to monetary feedback context. Specifically, higher estradiol levels corresponded with increased AI activation for risk taking (compared to fixation) in the social rank feedback context ($r = 0.39$, $P = 0.003$), but not in the monetary feedback context ($r = 0.21$, $P = 0.12$); these correlations were marginally different from one another (Steiger's $Z = 1.8$, $P = 0.073$; Figure 5B).

Results of a linear regression analysis in which AI activation during risk taking in the social rank feedback context was predicted by estradiol level while controlling for age, showed that estradiol level ($\beta = 0.34$, $P = 0.017$) but not age ($\beta = 0.11$, $P = 0.44$) accounted for 16% of the variance in AI activation, $F(2, 53) = 5.2$, $P = 0.009$. Results of a regression analysis with AI activation during risk taking in the monetary feedback context as the dependent variable showed that neither estradiol level ($\beta = 0.18$, $P = 0.24$), nor age ($\beta = 0.07$, $P = 0.63$) accounted for the individual differences AI activation, $F(2, 53) = 1.3$, $P = 0.27$. Together, these findings suggest that girls with higher estradiol levels—independent of age—are more likely to engage bilateral AI for risky decisions in the social rank feedback context, but not in the monetary feedback context. None of the other developmental measures were associated with differences in AI activation between the feedback contexts (testosterone level: $r = 0.17$, $P = 0.20$, $n = 57$; pubertal stage: $r = 0.06$, $P = 0.66$, $n = 58$; BMI: $r = 0.09$, $P = 0.53$, $n = 56$). See Supplementary Materials for correlations of individual differences in AI activation with differences in RPI, subjective task experience and task behavior.

Discussion

In this study, we examined whether social rank performance feedback increased risk taking and associated reward processing compared to monetary performance feedback. Although we predicted enhanced risk taking and reward processing in the social rank *vs* monetary feedback condition (e.g. Chein *et al.*, 2011), results showed that across participants the type of feedback did not differentially influence risk taking or reward processing (i.e. NAc and mPFC activation). Instead, we found increased AI activation during risk taking in the social rank feedback compared to the monetary feedback condition. Furthermore, we predicted that individual differences in both behavioral and neural responses to feedback type would be related to pubertal hormones (e.g. Crone and Dahl, 2012; Van den Bos *et al.*, 2013). However, results showed that only differences in the *neural* response to feedback type (i.e. insula activation) correlated with individual differences in estradiol level.

Social comparison vs peer presence

Previous studies have shown that among adolescents the presence of peers enhances risk taking and reward processes associated with risky decisions (Gardner and Steinberg, 2005; Chein *et al.*, 2011; Smith *et al.*, 2014a). In this study, we did not find evidence for an enhancing effect of social context on risk taking or reward processing. A possible explanation is that although both the presence of peers and the presentation of status-relevant social information (i.e. social rank) provide a social context, the psychological processes triggered by these two types of social contexts are expected to differ. For example, the presence of peers is more likely to induce brain processes associated with social evaluation. Previous research has shown that adolescents who believed that peers were watching them through a video camera showed a peak in mPFC activation compared with children and adults, as well as greater functional coupling between mPFC and striatum (including NAc) (Somerville *et al.*, 2013). These findings indicate that the thought or experience of being evaluated (or simply being watched) by peers influences reward processing and suggest that being ranked against peers, or social comparison, may not trigger the same social-evaluative processes that influence reward processing in the (simulated) presence of peers. Future studies are needed to identify which psychological processes triggered by the presence of peers impact risk taking.

Another possible explanation for the absence of an enhancing effect of social context on risk taking or reward processing during the Jackpot task is that the current manipulation—in which the girls were depicted alongside ‘heads’ of coins or silhouettes of anonymous peers—may have been too subtle for consistently inducing status-seeking behavior (i.e. increased risk taking) and/or changes in reward-related brain processes across the group. Our goal with the current design of the task was to control for the visual experience during the feedback phases, which may have resulted also in a more similar emotional experience across the two types of feedback. In future studies, the motivation to increase social status as opposed to winning money could be differentiated more by ranking the participants against friends as opposed to disliked peers (Braams *et al.*, 2014), or against peers whom they meet virtually or in person (Peake *et al.*, 2013) rather than anonymous peers.

The potential role of AI

Although risk taking during social rank *vs* monetary feedback blocks did not differentially activate NAc and mPFC, we did find differential activation in bilateral AI. Specifically, activation in AI during risk taking was increased when the girls received social rank feedback, but not when they received monetary feedback. Given its connections with both affective and cognitive-regulatory brain regions, AI has been hypothesized to function as a ‘hub’ for the integration of affective and cognitive information necessary to guide (decision) behavior (Menon and Uddin, 2010; Chang *et al.*, 2013; Smith *et al.*, 2014b). Specifically, AI activation has been associated with the detection of salient events (Menon and Uddin, 2010), such as errors (Ullsperger *et al.*, 2010), and recruitment of additional attentional resources (e.g. working memory) needed for task set maintenance (Nelson *et al.*, 2010). In the context of risky decision-making, AI activation has been thought to reflect “deliberative processes, including harm avoidance” that continue to mature during adolescence, as indicated by increased AI activation with age (Smith *et al.*, 2014b: page 205).

Alternatively, AI is thought to represent emotional states of self (and others) and to integrate this internal information with external cues (from the social environment) to form a “subjective feeling state” that in turn guides behavior (Lamm and Singer, 2010: page 586). For example, insula activation has been hypothesized to reflect the ‘urge’ to engage in behavior change, which was supported by a study in young adults who were given the opportunity to adjust their decisions based on prior outcomes of their risky decisions that showed that participants were more likely to take risks after playing it safe, a tendency that was mediated by AI activation (Xue *et al.*, 2010). Yet, another study that used a probabilistic reversal-learning paradigm found that adolescents learned at a faster rate and showed increased AI activation in response to negative prediction errors compared to adults, which was interpreted as reflective of stronger emotional weighting of negative feedback associated with greater cognitive flexibility during adolescence (Hauser *et al.*, 2015).

Taken together, these findings suggest that playing for social rank may have been more (emotionally) salient compared to playing for money for the girls in our sample, thereby potentially placing higher demands on task set maintenance, eliciting increased deliberation and/or facilitating learning during the social feedback blocks compared to the monetary feedback blocks. Thus, heightened AI activation during risk taking in the social rank feedback condition might reflect an increased allocation of attentional resources. This interpretation is not only supported by our finding of additional activation in left fusiform gyrus—a region involved in visual attention (Lim *et al.*, 2013)—during risk taking in social rank *vs* monetary feedback blocks, but is also in line with the hypothesis that adolescence is a time of increased social learning (Blakemore and Mills, 2014) and heightened motivation to achieve social status (Crone and Dahl, 2012). Future research that involves the administration of the Jackpot task in an adult sample would provide insight into whether this heightened insula (and fusiform) response in the social rank feedback condition is unique to adolescence.

Individual differences in sensitivity to context

Instead of an overall enhancing effect of social rank feedback on risk taking and reward processing, we found individual differences in the behavioral and neural responses to feedback type, suggesting that at least some girls appeared sensitive to the feedback manipulation. Behavioral differences in sensitivity to feedback type could not be explained by differences in developmental stage (as measured by age, hormone level, pubertal stage, or BMI). However, exploratory analyses revealed that individual differences in relative decision speed corresponded with differences in resistance to peer influence (RPI) for decisions that involved a small chance of winning (i.e. high-risk decisions). Although these findings suggest that differences in the behavioral sensitivity to feedback type might be related to differences in traits rather than developmental stage, this exploratory finding calls for replication. Furthermore, we cannot rule out the role of development, especially since RPI increases with age (Steinberg and Monahan, 2007). Future longitudinal research is needed to confirm whether the behavioral sensitivity to feedback type may be more reflective of trait-like, as opposed to developmental factors.

In contrast, individual differences in brain processes associated with risk taking were associated with pubertal maturation. Specifically, girls with higher levels of estradiol (but not testosterone) activated AI more strongly for risk taking in the social rank, but not the monetary feedback condition. Given that differences in estradiol level, relative to testosterone level, are more reflective of differences in pubertal maturation among girls (Biro *et al.*, 2014), this finding suggests that social context moderates the relation between pubertal maturation and insula activation (in the context of risk taking). This idea is consistent with studies that reported increased AI involvement in adolescence (Smith *et al.*, 2014b) and provides additional insight into the potential underlying mechanism (i.e. puberty-related changes) and context (i.e. social) in which these developmental processes are most salient. Although a longitudinal follow-up is needed to confirm whether changes in estradiol (reflective of pubertal maturation in girls) are indeed associated with increases in insula activation over time, this finding suggests that biological and social influences on brain processes associated with adolescent risk taking interact.

Conclusion

This study demonstrated that adolescent girls differ in their relative motivations to engage in risk taking—some girls took more risks when they were playing for money, whereas others took more risks when they were being ranked against peers. Although the current feedback manipulation did not elicit differences in reward-related brain processes, AI activation was found to be enhanced for risky decisions in the social rank *vs* monetary feedback context, especially in girls with higher estradiol levels. These cross-sectional findings provide preliminary evidence for an interaction between pubertal and social influences on risk taking, and emphasize the need for interdisciplinary and longitudinal research to understand adolescent behavior.

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Supplementary data

Supplementary data are available at *SCAN* online.

Conflict of interest. None declared.

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