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Gambling for self, friends, and antagonists: Differential contributions of affective and social brain regions on adolescent reward processing

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ABSTRACT

Adolescence is a time of increasing emotional arousal, sensation-seeking and risk-taking, especially in the context of peers. Recent neuroscientific studies have pinpointed to the role of the ventral striatum as a brain region which is particularly sensitive to reward, and to 'social brain' regions, such as the medial prefrontal cortex (mPFC), the precuneus, and the temporal parietal junction, as being particularly responsive to social contexts. However, no study to date has examined adolescents' sensitivity to reward across different social contexts. In this study we examined 249 participants between the ages 8 and 25, on a monetary reward-processing task. Participants could win or lose money for themselves, their best friend and a disliked peer. Winning for self resulted in a mid- to late adolescent specific peak in neural activation in the ventral striatum, whereas winning for a disliked peer resulted in a mid- to late adolescent specific peak in the mPFC. Our findings reveal that ventral striatum and mPFC hypersensitivity in adolescence is dependent on social context. Taken together, these results suggest that increased risk-taking and sensation seeking observed in adolescence might not be purely related to hyperactivity of the ventral striatum, but that these behaviors are probably strongly related to the social context in which they occur.

Adolescence is a period of increased risk-taking and sensation-seeking, especially in the presence of peers (Steinberg, 2004). Excessive risk-taking can have adverse effects, such as injury due to risky driving or excessive alcohol use. An important component of risk-taking involves anticipation and processing of rewards. It is well known that reward processing is associated with activation in the ventral striatum (VS) (Delgado, 2007; Sescousse et al., 2013). Prior developmental studies have further shown that activity in the VS is elevated in adolescence (Ernst et al., 2005; Galvan et al., 2006; Van Leijenhorst et al., 2010a). However, these studies reported mixed results with respect to the specificity of the VS response to rewards, possibly due to different task demands and differences in selection of age groups (Richards et al., 2013). Especially the VS response to anticipation of rewards has yielded mixed findings. Although some studies have found elevated VS responses in adolescence in response to anticipation of gains (Galvan et al., 2006; Van Leijenhorst et al., 2010a), other studies have reported an under activation of the VS in response to anticipation of rewards (Bjork et al., 2004, 2010; Geier et al., 2010).

Adolescence is also a period of re-orientation towards the peer group, coupled with an increasing importance of friendships (Rubin et al., 2008). Despite the pronounced changes in this social orientation towards peers, less is known about how similar reward processing for self and others is. Telzer et al. (2010) previously showed that gaining money for family results in increased activation in the ventral striatum. This activity was stronger for those adolescents who derived greater fulfillment from helping their family. Thus, there seems to be a link between gaining for relevant others and activity in the VS. Also, Varnum et al. (2014) showed that when adult participants were primed for an interdependent self-construal, winning for friends resulted in as much striatum activation as when participants won for themselves. These findings led to the hypothesis that receiving rewards for friends would also result in VS activity and we tested whether this response was stronger in mid adolescence relative to childhood and adulthood.

Several previous studies have suggested that processing of rewards and thinking about friends depend on separate but interacting brain networks in adults (Braams et al., 2013; Fareri et al., 2012). Specifically, processing of rewards is associated with VS activation, whereas thinking about friends or significant others results in activation in a set of cortical midline structures (medial prefrontal cortex and precuneus) as well as the temporal–parietal junction (Güroğlu et al., 2008), regions also referred to as the 'social brain network' (Blakemore, 2008; Van Overwalle, 2009; Young et al., 2010). In a neuroimaging study with adult participants, we found that the social brain areas were more active when playing a simple heads-or-tail gambling game for another person relative to playing the game for yourself, independent of the outcome of the game (reward or loss). In contrast, VS activity was dependent on the beneficiary, such that VS activity was higher when winning for self and

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friends, but not when winning for disliked others (Braams et al., 2013). Self-report ratings of how much participants liked to win and lose for the two other players exhibited the same pattern, with highest ratings for winning for friend, followed by losing and winning for the disliked other and lowest ratings for losing for the friend. Similarly, a study by Fareri et al. (2012) showed that sharing with a friend resulted in more VS activation compared to sharing with a confederate or a computer, suggesting that VS activation is dependent on social context. In this study, mPFC activation was also higher when sharing with a friend compared to the other two players.

Developmental studies have reported differences in recruitment of the social brain areas in adolescence compared to adulthood. Adolescents appear to recruit the more anterior regions, such as mPFC, more than adults, whereas adults recruit more posterior regions, such as temporal regions, more than adolescents (Blakemore, 2008). Elevated activation in the mPFC has been found in mid-adolescence, in response to socially demanding contexts, such as thinking about others' intentions or distinguishing between social and basic emotions (Blakemore, 2008; Burnett et al., 2009; Goddings et al., 2012). However, it is not yet known whether mPFC activity decreases from childhood to adulthood or whether mPFC shows peak sensitivity in mid-adolescence.

Based on developmental studies pointing out an elevated response in the striatum (Galvan et al., 2006; Van Leijenhorst et al., 2010a) and social sensitivity in adolescents (Chein et al., 2011), and findings from neuroimaging studies in adults pointing out the context sensitivity of the VS activity (Braams et al., 2013; Fareri et al., 2012), we examined adolescent specific differences in the VS when participants received rewards for themselves, their friend, and a disliked other (i.e. antagonist). First, we predicted that adolescents would show elevated VS responses to rewards when playing a gambling game in comparison to children and adults (replicating Galvan et al., 2006; Van Leijenhorst et al., 2010a). Second, we investigated the role of social factors on reward processing in the VS and how this changes during adolescence, by having the participants perform a gambling game for themselves, as well as for their best friend and an antagonist. Based on the prior neuroimaging study in adults showing higher VS activity when playing for self and friends relative to antagonists (Braams et al., 2013), we predicted a similar pattern for the younger age groups. Furthermore, we expected self-report ratings indicating how much participants liked to win and lose for the different players to correspond with the VS activity. Given the importance of friendships in adolescence (Rubin et al., 2008), the current study had a special focus on the role of friendship quality on VS activity. Therefore, we examined the relation between self-reported friendship quality and VS responses to winning for friends. We predicted a stronger VS response to playing for a friend for participants who reported a better friendship quality. Finally, we tested whether the social brain network, which was previously found to be most active when playing for friends and antagonists in adults (Braams et al., 2013), would show hypersensitivity in adolescence.

Materials and methods

Participants

Final inclusion consisted of 249 participants between the ages of 8 and 25 who were members of the general public, recruited through schools and local advertisements. An additional 14 participants were excluded for not finishing the task or technical problems during data collection, and an additional 36 participants were excluded for excessive head motion (more than 3 mm in any direction) which is common in developmental neuroimaging studies (approximately 12%) (Galvan et al., 2012; Poldrack et al., 2002). When only participants who moved less than 1/2 voxel were included in the analysis, the results were comparable (see the supplemental material for a description of these results). Descriptives of the age and division of gender of the final sample can be found in Supplemental Table 1. For some of the analyses, indicated where appropriate, the total sample was divided into 9 age groups, such that each group represented participants of the same age in years. The 8- and 9-year-olds were grouped together because of the relatively smaller sample size of these age groups. Results of the adult group (ages 18–25) have been reported separately in an earlier study (Braams et al., 2013).

An approximation of IQ was determined by two subscales, similarities and block design, of the Wechsler Intelligence Scale for Adults (WAIS-III) or the Wechsler Intelligence Scale for Children (WISC-III) (Wechsler, 1997). Estimated IQ for all participants fell within the normal range ($M = 109$, $SD = 10$). Informed consent from adult participants and from the parents of under aged participants was obtained before the start of the study. Participants were screened for MRI contra indications and were free of neurological and psychiatric disorders. All procedures were reviewed and approved by the university medical ethical committee. Participants received an endowment (€60 for adults, €25 for participants aged 12–17 and €20 for participants younger than 12) for their participation in a larger scale study.

Experimental design

Gambling task

Participants performed a gambling task in which they could choose heads or tails and win (or lose) money when the computer selected the chosen (or not chosen) side of the coin. Therefore, probability of winning or losing was 50% on each trial. The number of coins that could be won or lost on each trial was varied. Three variations were included: trials in which five coins could be won or two coins could be lost, trials on which three coins could be won or three coins could be lost and trials on which two coins could be won or five coins could be lost. The reason for presenting three variations was to keep the participants engaged in the task (see also Braams et al., 2013). To maximize statistical power we collapsed across these variations.

Before the start of the experiment, the participants were told that they would play the gambling task for themselves, for their same-sex best friend and for another participant from the study. The participant's best friend and the other participant were not present at the time of the experiment. Participants were explained that one of the three players (self, friend or other) would be paid the money that was earned for that person during the task. Care was taken that the participants understood that the money won during the game was not hypothetical. We asked the participants to fill out a Friendship Quality Questionnaire about their best friend, prior to the experiment, and the name of the best friend was used in the best friend condition during the game. To manipulate the liking of the other participant that they would play the gambling game for, a cover story was used. This cover story was as follows: "*You will play a game with another participant in the study, who will participate after you. You can divide 10 euros between yourself and the next participant. You can split the amount as you like, but the next participant will decide whether the division is accepted or not. If the division is not accepted, you will both receive nothing.* [Participant makes offer]. *You will now receive the offer from a prior participant and you can decide whether you want to accept the division or not.* [Participant receives unfair division of 9 coins for the proposer and 1 coin for the participant, and makes a choice to accept or reject]. *We will now practice the gambling game that you will play in the scanner. You will play this game for yourself, for* [name of participant who made unfair offer] *and for* [name of best friend]." The average offer made by the participants in the division (also known as an Ultimatum Game) was 4.7 euros out of 10 euros ($SD = .08$). The average rejection rate of the 9–1 offer made by the antagonist was 73%. One-way ANOVAs with age group as independent variable showed no significant differences between age groups, neither for the height of the offer nor for the rejection rate (all p's > .05). This cover story with an unfair ultimatum game offer allowed us to create an antagonist as the third player (Braams et al., 2013; Sanfey et al., 2003; Singer et al., 2006). To validate that the participants liked the