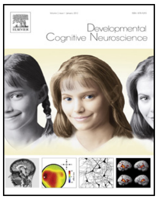
Developmental Cognitive Neuroscience 6 (2013) 113–124

Contents lists available at ScienceDirect

Developmental Cognitive Neuroscience

journal homepage: http://www.elsevier.com/locate/dcn



Different developmental trajectories for anticipation and receipt of reward during adolescence

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ARTICLE INFO

Article history:
Received 22 May 2013
Received in revised form 24 July 2013
Accepted 26 August 2013

Keywords:
Adolescence
Development
fMRI
Nucleus accumbens
Reward
Striatum

ABSTRACT

Typical adolescent behaviour such as increased risk-taking and novelty-seeking is probably related to developmental changes in the brain reward system. This functional MRI study investigated how brain activation related to two components of reward processing (Reward Anticipation and Reward Outcome) changes with age in a sample of 39 children, adolescents and young adults aged 10–25. Our data revealed age-related changes in brain activity during both components of reward processing. Activation related to Reward Anticipation increased with age, while activation related to Reward Outcome decreased in various regions of the reward network. This shift from outcome to anticipation was confirmed by subsequent analyses showing positive correlations between age and the difference in activation between Reward Anticipation and Reward Outcome. The shift was predominantly present in striatal regions and was accompanied by a significant effect of age on behaviour, with older participants showing more response speeding on potentially rewarding trials than younger participants. This study provides evidence for functional changes in the reward system which may underlie typical adolescent behaviour.

1. Introduction

Increased risk-taking and novelty-seeking are characteristics of adolescent behaviour (Casey et al., 2008a; Crone and Dahl, 2012; Ernst and Mueller, 2008; Spear, 2000; Steinberg, 2007). It has been suggested that these tendencies may be adaptive because they trigger adolescents to explore the world and become independent individuals (Crone and Dahl, 2012; Strang et al., 2013), but they could also lead to a substantial increase in morbidity related to dangerous behaviour (Casey et al., 2010a; Casey and Caudle, 2013) and an enhanced vulnerability for addiction (Gladwin et al., 2011; Schneider et al., 2012). The brain reward system is an important contributor to motivated behaviour (Somerville and Casey, 2010) and changes in the functioning of this circuit during adolescence are thought to underlie this typical adolescent behaviour. In fact, it has been suggested that the dopaminergic reward network, in particular the ventral striatum, is overactive in adolescents, making them hypersensitive to reward and leading to a greater motivational drive for novel, risky experiences (Chambers et al., 2003).

Indeed, *increased* ventral striatum activation is reported in adolescents in response to the actual receipt of reward (Ernst et al., 2005; Galvan et al., 2006; Van Leijenhorst et al., 2010a,b), during an unexpected positive outcome

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http://dx.doi.org/10.1016/j.dcn.2013.08.004

(Cohen et al., 2010) and during rewarded trials in an incentive motivated antisaccade task (Padmanabhan et al., 2011). Other studies, however, have shown *decreased* ventral striatum activation during the anticipation of reward (Bjork et al., 2010, 2004) and the assessment of a reward cue (Geier et al., 2010) in adolescents relative to adults.

These results indicate that the adolescent reward system is not simply hyper- or hypoactive compared to that of adults. Indeed, functional differences between the adult and adolescent reward system may depend on the component of reward processing that is considered (Bjork et al., 2010; Cohen et al., 2010; Geier and Luna, 2009; Geier et al., 2010; Van Leijenhorst et al., 2010b): the anticipation of a potential reward or the actual outcome, i.e. the receipt or omission of a reward (Knutson et al., 2001b).

Earlier studies in primates (Schultz et al., 2000) and humans (Knutson et al., 2001b) have shown that these different components of reward processing elicit dissociable brain responses in the reward system (see Haber and Knutson, 2010, for a review). In line with these results, previous work has suggested that the adolescent reward system may be characterized by different developmental trajectories for these two components of reward processing (Bjork et al., 2010; Geier and Luna, 2009; Geier et al., 2010). In fact, the hypothesis has been put forward that adolescents have an *enhanced* reactivity to the receipt of reward while displaying a *decreased* sensitivity to the anticipatorycues predicting reward (for reviews see Galván, 2010a; Spear, 2011).

However, direct evidence for this hypothesis is lacking: there are, to the best of our knowledge, no studies demonstrating age-related activation differences during *both* components of reward processing (i.e. during the anticipation and the actual outcome of reward). Moreover, combining the results of the available studies to substantiate the hypothesis is complicated because these studies used different tasks and included different age groups.

Here, we investigated age-related changes in reward-related brain activity in a sample of children, adolescents and adults aged 10–25 during anticipation and outcome of reward. We applied a modified version of the Monetary Incentive Delay task (Knutson et al., 2001a) which was optimized to analyse changes in brain activity related to the anticipation and outcome of reward separately (Figee et al., 2011; Van Hell et al., 2010). In addition, we used age as a continuous variable, in order to avoid confounds related to defining age groups (Luna et al., 2010) and enabling us to investigate both linear and non-linear effects of age (Casey, 2013). Activation changes were investigated in six predefined anatomical Regions of Interest (ROIs) which are all involved in the processing of reward (Knutson et al., 2001b): the bilateral ventral striatum, dorsal caudate, putamen, insula, cingulate cortex, and orbitofrontal cortex.

2. Materials and methods

2.1. Participants

Forty-two right-handed healthy volunteers aged 10–25 years (mean age 16.7 y, SD 4.8 y; 22 males) participated in the study. The study was approved by the Medical Ethics Committee of the University Medical Center Utrecht and all participants (and their parents in the case of minors) gave written informed consent. Data from three participants (1 male aged 14.9 y; 2 females aged 13.8 y and 23.8 y) were excluded from the analyses because they were outliers, with performance more than two standard deviations away from the group mean. This resulted in a sample of 39 participants.

Subjects received monetary compensation for participation: a fixed amount for participation and a flexible additional amount based on performance in the Reward Task.

Before scanning, participants who were scanner-naïve (except two adult participants, 1 male age 22.4 y, 1 female age 18.2 y) were familiarized with the scanning-procedure using a mock scanner in order to reduce scanner-related anxiety (Galván, 2010b).

2.2. Reward Task

Participants performed a Reward Task (Fig. 1) based on the Monetary Incentive Delay task (Knutson et al., 2001a). Trials were potentially rewarding (30 trials) or neutral (30 trials), as indicated by a cue at the start of the trial. Following this cue and a fixation star, the target was presented. Participants were instructed to respond as fast as possible to this target by pressing a button, irrespective of cue type. Subsequent feedback notified participants of their performance, indicating if they had earned money, as well as their cumulative total at that moment. We told participants that they would receive the cumulative total amount of reward of the actual experiment in addition to the standard compensation for participation.

Target duration was individually adjusted to ensure that each participant could succeed in 50% of the trials. This adjustment was based on twenty practice trials, presented prior to the start of the experiment. From these practice data, the shortest reaction time to the target was used to determine the individual time limit for responses to the target. In 50% of the trials, the target was presented for the duration of the individual time limit plus 200 ms, enabling participants to be successful in these trials. In the other trials, the time limit was decreased with 150 ms, to make sure that participants could not respond in time.

The task was designed in such a way that maximum statistical power concerning the fMRI analyses could be reached in a relatively short time period: only one level of reward was used and no loss trials were included. Collinearity between the factors coding for anticipation (i.e. time between presentation of the cue and presentation of the target) and feedback was minimized by varying the duration of the anticipation time randomly (mean duration 3286 ms, range 779–6729 ms) and the inter-trial interval (mean duration 3535 ms, range 1029–6979 ms). This way, the blood-oxygen level-dependent (BOLD) signal in response to Reward Anticipation could be modelled independently from that to Reward Outcome (Figee et al., 2011; Van Hell et al., 2010). The actual task consisted of 60 trials with a mean duration of 9571 ms (range 4946–16107 ms), resulting in a total task duration of 9 min 35 s.