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Anna C. K. Van Duijvenvoorde and Eveline A. Crone
Leiden University, Leiden Institute for Brain and Cognition, and University of Amsterdam

Abstract
Recent neuroscientific studies have pinpointed a relative imbalance between the development of subcortical-affective and prefrontal-control brain networks that creates specific sensitivities during adolescence. Despite these advances in understanding adolescent brain development, there is a strong need for a more mechanistic understanding of the way these limbic and frontal-cortical areas interact and contribute to adolescents' risky and social decision-making. We discuss a neuroeconomic approach that has the potential to significantly forward the understanding of decision making in adolescence.

Keywords
risky decision making, social decision making, neuroeconomics, adolescence, learning

Adolescence spans the developmental phase between childhood and adulthood; it starts with puberty (around approximately 9–10 years of age), during which numerous hormonal changes influence the body and brain (Spear, 2011), and extends into the early 20s, when adolescents learn to take adult roles and responsibilities (Dahl & Gunnar, 2009). In adolescence, there are pronounced changes in social-affective engagement, including increases in motivation, sensation seeking, and risk taking, as well as emerging sensitivities to social context and peer status (Steinberg, 2008). The increase in social-affective engagement provides several important advantages; for example, it provides adolescents with the motivational drive to actively explore their environment and pursue long-term goals. Yet it also comes with some challenges and potential health risks, such as when explorative risk taking or extreme sensitivities to social context lead to problems such as drug abuse, depression, or social withdrawal (Dahl, 2004).

Recently, several novel lines of research have explored the neurobiological mechanisms that contribute to adolescents' sensitivity to social-affective contexts. One of the prevailing models, based on functional-neuroimaging studies, states that adolescent brain development is associated with a relatively fast development of limbic brain regions that respond to immediate social-affective states, such as the presence of rewards or other emotional stimuli, and a relatively slow development of frontal-parietal brain regions that allow for the regulation of emotions (Ernst & Fudge, 2009; Somerville, Jones, & Casey, 2010). Some studies have suggested that adolescence is associated with a peak in dopamine availability (Luciana, Wahlstrom, Porter, & Collins, 2012), which may lead to stronger social-affective responses. One of the key questions in moving this model forward is how the intensification of social-affective engagement is related to the interactions between these prefrontal-control and subcortical-affective networks (Crone & Dahl, 2012; Pfeifer & Allen, 2012).

In this review, we argue that a neuroeconomic approach has many advantages when aiming to understand the specific sensitivities in adolescents' decision making. Neuroeconomics brings together fields of psychology, economy, neuroscience, and computational science to investigate how people make decisions (Sharp, Monterosso, & Montague, 2012). This interdisciplinary field uses a model-based approach to specify processes of decision making in a set of estimable parameters that can be linked to underlying neurobiology. That is to say, distinct parameters may be characterized for components of decision making (see also Rangel, Camerer, & Montague, 2008). Here, we dissociate the following components of adolescent decision making: (a) risky choice, (b) sensitivity to gains and losses, and (c) social perspective taking.

Risky Choice

One way in which developmental changes in decision making have been studied is by presenting children, adolescents, and

Corresponding author:
Eveline A. Crone, Institute of Psychology, Leiden University, Wassenaarseweg 52, 2333 AK Leiden, The Netherlands
E-mail: ecrone@fsw.leidenuniv.nl

adults with choices that can lead to rewarding outcomes with a known probability. This type of decision making is referred to as risky choice. Meta-analyses have demonstrated that in adults, a wide network of cortical areas is engaged during risky choice, including the ventral striatum, the posterior cingulate cortex, and the ventral-medial prefrontal cortex (PFC; Krain, Wilson, Arbuckle, Castellanos, & Milham, 2006; Levy, Snell, Nelson, Rustichini, & Glimcher, 2010; Mohr, Biele, & Heekeren, 2010).

One of the studies that focused on risky choice in a developmental sample (Van Leijenhorst, Gunther Moor, et al., 2010) used an economic-choice paradigm with participants from four age groups (ages 8–10, 12–14, 15–17, and 19–25). Participants were presented with choices between options with a high probability of a small reward (*low-risk/low-reward*) and options with a low probability of a large reward (*high-risk/high-reward*). Results showed that on trials in which expected value of high- and low-risk options was equal, 8- to 10-year-olds chose mostly the high-risk/high-reward options, whereas adults chose mostly the low-risk/low-reward options; adolescents showed an intermediate pattern. These results seem to indicate a developmental decrease in taste for risk (i.e., increasing risk averseness). Neural results indicated, however, elevated ventral-medial PFC activity in adolescents, compared with children and adults, when choosing the high-risk/high-reward options.

From this heightened neural activity it is not yet clear which component of the high-risk/high-reward choice drives this specific sensitivity in adolescence. That is to say, because options that carry greater risks typically also carry greater rewards, it is difficult to estimate how these factors independently drive risky decision making across development. Therefore, the use of refined tasks together with a computational-model approach present a starting point for decomposing these influences on adolescents' decision making. One example is the *risk-return model*, which describes an individual's risk-taking behavior as a result of a trade-off between the expected return and the perceived risk of a choice (Weber, Blais, & Betz, 2002). Greater expected return makes an option more attractive, whereas greater perceived risk makes it less attractive. This model allows for estimation of both parameters in individuals' choice behaviors, and although it originated in finance (using objective values as expected value and variance in returns as risks, respectively), it is applicable to a range of decision-making domains (see also Figner & Weber, 2011; Paulsen, Platt, Huettel, & Brannon, 2011).

Whereas in a *risky* choice the probabilities of outcomes are known, an *ambiguous* choice carries unknown information on the probability of a gain or loss. A recent study estimated individuals' risk aversion and ambiguity aversion from choice behavior (Tymula et al., 2012). Results showed that adolescents, compared with adults, did not differ in their risk aversion but were more tolerant toward ambiguity—that is, adolescents showed a greater tendency to gamble when probabilities were not known. Together, these examples illustrate that a modeling approach has the potential to advance insights into the building blocks of adolescents' risky decision making.

Sensitivity to Gains and Losses

A second component of adolescent decision making involves sensitivity to decision outcomes such as gains and losses. As a type of reward, gains are linked to dopamine innervations, which lead to a robust signal in the ventral striatum (Haber & Knutson, 2010). Several studies have reported that this ventral-striatum response to gains is elevated in adolescents compared with children and adults (Galvan, 2010; Van Leijenhorst, Gunther Moor, et al., 2010; Van Leijenhorst, Zanolie, et al., 2010) and that in "hot" (i.e., affective) contexts, specifically, adolescents are more prone to risky choices (Figner, Mackinlay, Wilkening, & Weber, 2009) and show less advantageous choice behavior (Van Duijvenvoorde, Jansen, Visser, & Huizenga, 2010). These findings have led to the hypothesis that rewards are particularly meaningful or arousing for adolescents (but see also Bjork, Smith, Chen, & Hommer, 2010, for a discussion on task-context sensitivity).

A more detailed analysis of sensitivity to gains and losses can be made by examining outcomes in relation to prior expectations. When decision outcomes (i.e., gains or losses) do not match expectations formed on the basis of previous trials, they trigger a learning signal that is referred to as a *prediction error*. A prediction error signals a mismatch between expected and obtained outcomes, and is therefore positive if outcomes are better than expected and negative if outcomes are worse than expected. One study showed that in probabilistic learning, adolescents (ages 13–19) show an elevated positive prediction error in the striatum compared with children (ages 8–12) and adults (ages 25–30; Cohen et al., 2010; see Fig. 1), which was thought to reflect adolescents' increased motivation to obtain positive outcomes. In a comparable study using slightly different age groups, the prediction error itself was not different between children (ages 8–11), adolescents (ages 13–16), and late adolescents/young adults (ages 18–22), but the connectivity between the striatum and the medial frontal cortex changed with age, such that, following positive outcomes, it strengthened more among older participants than younger ones (Van den Bos, Cohen, Kahnt, & Crone, 2012). Thus, the way the ventral striatum responds to learning signals may be associated with the way individuals engage the frontal-parietal network.

Responses to gains and losses have also been studied in choice tasks involving gains and probabilistic losses, in which participants need to learn to maximize their outcomes. A developmental comparison showed that children and young adolescents, in contrast to adults, continued to be more

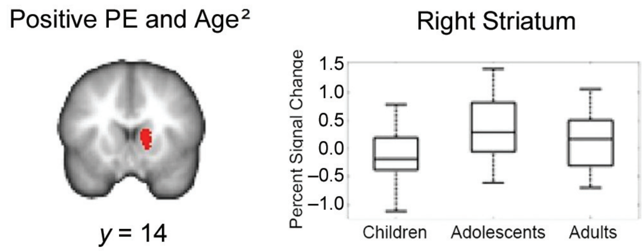

Fig. 1. Elevated striatum response to prediction errors (PEs) in adolescents in Cohen et al. (2010). Striatal regions were negatively correlated with age squared (a) because the mean age squared was subtracted from each value prior to squaring and age squared was lowest for adolescents; thus, the negative correlation reflects greater signals for adolescents. The *y* coordinate (in mm) refers to standard Montreal Neurological Institute (MNI) space. The graph (b) presents the lower-quartile, median, and upper-quartile values of the striatal activation for each age group. Whiskers show the extent of the remaining data. Reprinted from "A Unique Adolescent Response to Reward Prediction Errors," by J. R. Cohen et al., 2010, *Nature Neuroscience, 13*, p. 670. Reprinted with permission.

reactive, that is, their choice behavior was driven more by occasional outcomes (Van Duijvenvoorde, Jansen, Bredman, & Huizenga, 2012). That is, they continued to change behavior after an occasional loss throughout the task, which resulted in lower overall outcomes. The ability to control choice behavior in response to gains and losses may depend specifically on the prefrontal cortex and its connections.

Together, these studies indicate that prediction-error signals from the striatum recruit a relatively flexible and goal-dependent activation of the frontal-parietal network that drives subsequent behavioral adjustments—that is, learning. The interaction between these networks may be specifically flexible in adolescents, which in some contexts might result in great steps in learning (e.g., when individuals are motivated to learn new complex music repertoires), but in other contexts may diminish learning (e.g., when individuals are distracted by conversations with peers during a boring lecture). Future challenges lie in investigating how different decision-making contexts or levels of motivation drive differences in learning.

Social Perspective Taking

One of the great challenges for adolescents is to learn how to navigate a complex social world and adjust to changes in social environments. A crucial component of navigating a social world is *mentalizing*, which is the ability to infer mental states of others, such as their intentions, beliefs, and desires. Two important component processes of mentalizing are perspective taking, or thinking about the intentions of others and consequences for others (Saxe & Kanwisher, 2003), and self-referential processing, which involves comparing consequences for oneself with consequences for others (Rilling & Sanfey, 2011). Several meta-analyses have demonstrated that in adults, perspective-taking is associated with activity in the temporal-parietal junction (TPJ), superior temporal sulcus, and the dorsal regions of the medial PFC (Denny, Kober, Wager, & Ochsner, 2012; Van Overwalle, 2009), whereas self-referential processing is associated with activity in the ventral medial PFC (Amodio & Frith, 2006; Denny et al., 2012). Activation in these regions, which together are sometimes referred to as the *social brain*, has been shown to change remarkably across adolescence and may influence adolescents' perspective-taking ability in decision making (Blakemore, 2008).

A game-theoretical paradigm that has been useful for researching perspective taking is the Trust Game (Berg, Dickhaut, & McCabe, 1995). In the Trust Game, there are two players and a certain stake of money involved. The first player can decide either to divide the money independently or to trust the second player with the money, after which it is tripled. However, the second player now has the power to divide all of the money as he or she wishes. The second player can thus reciprocate the trust given (by dividing the money relatively fairly between him- or herself and the first player) or defect and keep the profit (giving none or only a small amount of the money back to the first player). Though there are many variations to the game, it usually involves a single transaction with an unknown other to avoid reputation effects.

In a developmental comparison of four age groups (ages 9–10, 12–14, 15–17, and 18–22), it was found that older participants, as second players, were more responsive to the perspective of the first player (Van den Bos, Westenberg, Van Dijk, & Crone, 2010). This was investigated by varying the amount of risk (i.e., the amount of money that could be lost) that the first player took by trusting the second player. Results showed that on high-risk trials, older adolescents and young adults were more likely to reciprocate trust than younger adolescents were. Results from a subsequent neuroimaging study revealed that, when receiving trust as second player, activation in the TPJ increased across adolescence. This neural response to being trusted correlated with a behavioral measure of perspective taking in the Trust Game, reinforcing the notion that the TPJ is important for perspective taking and that this ability increases with age (Van den Bos, Van Dijk, Westenberg, Rombouts, & Crone, 2011).

In addition, during the decision to defect trust—compared with the decision to reciprocate—medial PFC was more active in older adolescents and young adults than in younger adolescents. However, in younger adolescents, compared with a no-trust (baseline) decision, medial PFC was active for both reciprocate and defect trials (Van den Bos et al., 2011; see Fig. 2). These results are consistent with the notion that the ventral medial PFC is activated during self-referential processing (Denny et al., 2012; Rilling & Sanfey, 2011), which may be overly present in social decision making in early adolescence (Pfeifer, Lieberman, & Dapretto, 2007).

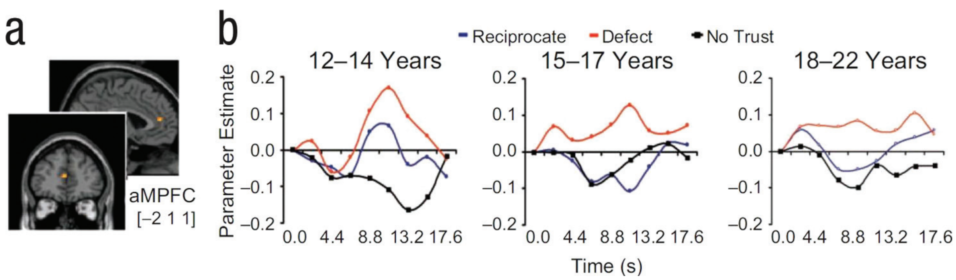

Fig. 2. Asynchronous development of the social-brain network in adolescents playing the Trust Game in Van den Bos, Van Dijk, Westenberg, Rombouts, and Crone (2011). Asynchronous development is revealed by age differences in activity in the anterior medial prefrontal cortex (aMPFC) associated with decisions to defect versus reciprocate. In the functional MRI images (a), yellow clusters indicate an early age-related increase (tested with a between-age group contrast: −2 1 1) in the difference between activation in defect and reciprocate conditions. The graphs (b) show parameter estimates in the aMPFC for the defect, reciprocate, and no-trust conditions as a function of time for each age group. On the *x*-axis of each graph, 0 indicates either the onset of the first player's choice (trust) or the outcome of the experiment (no trust). Reprinted from "Changing Brains, Changing Perspectives: The Neurocognitive Development of Reciprocity," by W. Van den Bos, E. Van Dijk, M. Westenberg, S. A. Rombouts, and E. A. Crone, 2011, *Psychological Science, 22*, p. 67. Copyright 2011 by Sage. Reprinted with permission.

The question remains which signal biases adolescents toward a decision to reciprocate or defect trust. Adult studies have reported that in economic exchange tasks, larger striatum activity is linked to future cooperation and correlated with individuals' prosocial tendencies (Rilling & Sanfey, 2011; Van den Bos, Van Dijk, Westenberg, Rombouts, & Crone, 2009). Currently, it is not well understood how the ventral-striatum response contributes to collaboration in adolescence, but the role of the ventral striatum in reward processing (Galvan, 2010) and prediction errors (Cohen et al., 2010) raises some compelling questions. For example, a heightened ventral-striatum response to outcomes of mutual cooperation (i.e., trust and reciprocation) in adolescents may correlate with a greater need for social acceptance during the formation of friendships and when striving for peer acceptance and admiration (Güroğlu et al., 2008). Future studies will benefit from using such economic paradigms to answer these important questions about social influences on adolescents' behavior.

Conclusion

Adolescence is a period of marked changes in social-affective engagement. In this review, we have explored how the intensification of social-affective processing may influence adolescents' decision making. Accordingly, we have discussed adolescents' risky choice, sensitivity to gains and losses, and perspective taking as key components of decision making. We propose that a neuroeconomic approach, combining behavioral modeling and economic paradigms with brain-based measures, leads to new insights into the behavioral and neural mechanisms underlying adolescent decision making across a range of domains.

From this review, it is apparent that specific challenges remain, such as decomposing risky choice, investigating the influence of gains and losses on subsequent choices, and pinpointing the influence of social perspective taking in decision making. In all of these domains, a specific focus may be on the flexible interactions between subcortical and prefrontal-parietal regions that are thought to drive adolescent-specific sensitivities in decision making.

Although adolescence is often described as a period of heightened risk taking, the flexible nature of adolescence can also have several advantages for rapid learning and adjustment to changing social contexts. For example, it was found that midadolescents have certain benefits when it comes to creative problem solving (Kleibeuker, De Dreu, & Crone, 2013). Specific increases in motivation may also, for example, lead to quick learning of the use of multiple forms of social media. A better conceptualization of adolescents' sensitivities will be an important step toward understanding the mechanisms underlying adolescent advantages, as well as specific dangerous behaviors.

Recommended Reading

Cohen, J. R., Asarnow, R. F., Sabb, F. W., Bilder, R. M., Bookheimer, S. Y., Knowlton, B. J., & Poldrack, R. A. (2010). (See References). An exciting study that investigates the development of the prediction error in adolescents and describes how this may underlie developmental changes in risk taking in adolescence.

Figner, B., & Weber, E. (2011). (See References). An innovative review that discusses individual and contextual effects on risk-taking behavior to better understand its underlying mechanisms.

Sharp, C., Monterosso, J., & Montague, P. R. (2012). (See References). An innovative review that explores applications of neuroeconomics to neuroimaging data and specifically discusses translational research in the field of psychiatry.

Somerville, L., Jones, R., & Casey, B. (2010). (See References). A compelling review that discusses the neurobiological interactions between affective-motivational and cognitive-control systems in explaining adolescents' specific sensitivities.

Van den Bos, W., Van Dijk, E., Westenberg, M., Rombouts, S. A., & Crone, E. A. (2011). (See References). A functional MRI study using a neuroeconomics approach to investigate changes across adolescence in the neural mechanisms of social decision making, such as mentalizing, and decisions to reciprocate and defect.

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The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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