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The neuroscience of adolescent decision-making

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Abstract

Adolescence is a phase of lifespan associated with greater independence, and thus greater demands to make self-guided decisions in the face of risks, uncertainty, and varying proximal and distal outcomes. A new wave of developmental research takes a neuroeconomic approach to specify what decision processes are changing during adolescence, along what trajectory they are changing, and what neurodevelopmental processes support these changes. Evidence is mounting to suggest that multiple decision processes are tuned differently in adolescents and adults including reward reactivity, uncertainty-tolerance, delay discounting, and experiential assessments of value and risk. Unique interactions between prefrontal cortical, striatal, and salience processing systems during adolescence both constrain and amplify various component processes of mature decision-making.

The phase of the lifespan known as adolescence begins around the time of physical puberty and ends with the assumption of adult-like levels of autonomy. Relative to childhood, adolescents are faced with more frequent and complex demands on independent decision-making. Though adolescence is typically a phase of robust physical health, adolescents in many western societies face prominent health risks that stem, at least in part, from their own choices. Adolescents spend more time unmonitored by guardians and have growing access to risky and ambiguous situations that involve potential negative outcomes such as access to illegal substances, opportunities to take physical and sexual risks, and complex peer-related decisions that could impact their social status. Understanding what is unique about adolescent decision-making has come under the spotlight of applied research aimed at promoting adolescent health.

Adolescent decision-making is also coming under the spotlight from another direction: neuroscience. Here, we evaluate the complex ways in which trajectories of brain development shape adolescent decision processes. A recent wave of developmental research has drawn on neuroeconomic experimental approaches that allow complex decisions to be decomposed into component processes.

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Neuroeconomic approaches employ formal mathematical models to estimate parameters that modulate individual choice behavior and make quantitative predictions about the neural signals underlying idiosyncratic decision computations. Thus, neuroeconomic approaches permit precise characterization of the underlying aspects of complex decisions that are (or are not) changing with age. This review highlights recent work that links understanding of *a)* what decision processes are changing during adolescence and along what trajectory they are changing, and *b)* neurodevelopmental features of well-characterized neural circuits that have been implicated in different facets of adult decision-making.

To isolate developmental shifts in decision processes, empirical studies typically compare adolescent-aged participants with a reference group or groups of older and/or younger participants. However, the field lacks consensus on which age ranges should be compared and the boundaries between age groups (see Box 1 for further discussion on this point). Thus, by necessity this review reflects diverse operationalizations of ‘developmental change’.

Further, development is often assumed to represent progressive, linear patterns of change over time. However, many features of adolescent development are nonlinear, and this review demonstrates that some decision processes are “tuned” uniquely during adolescence when compared to both earlier and later stages of development. Whereas studies with narrow age ranges lack the age span to target nonlinear changes, studies that incorporate both preand post-adolescent comparison groups allow for detection of both linear and complex patterns of change.

Trajectories of adolescent neurodevelopment of neurocircuitry important for decision computations

Although the overall size and gross organization of the brain is similar in adolescents and adults, dynamic changes in brain structure, function, and features of neuromodulatory systems are occurring throughout adolescence. Structural magnetic resonance imaging (MRI) studies have revealed developmentally normative reductions in the volume of gray matter across adolescence [1,2] that are thought to reflect experience-dependent pruning processes. Lagged structural development of the prefrontal cortex, particularly dorsolateral regions, has been linked to a number of functional outcomes during adolescence, including continued improvement in impulse control [3], working memory [4], and complex reasoning [5]. As such, late development of the prefrontal cortex could constrain components of decision-making that rely heavily on deliberation or integrating complex sources of information.

By contrast, certain properties of dopaminergic signaling exhibit adolescent-specific peaks. Structurally, there is a proliferation of D1 and D2 receptors in various targets within the mesolimbic dopamine system, which prune 50% or more from the transition of adolescence to adulthood [6] paired with a peaking tissue concentration of dopamine [7]. Corresponding studies in humans using functional MRI have demonstrated an adolescent-specific exaggeration of response to various forms of reward [8,9**] and stronger parametric tracking of expected value [10] in the ventral striatum, a key target of dopaminergic signaling.

The observed developmental asymmetries in prefrontal and striatal signaling and connectivity have informed theoretical frameworks describing adolescent behavior as reflecting staggered trajectories of neurodevelopment [11-13]. Whereas the adolescent striatum exhibits exaggerated response properties in many studies, the function of prefrontal systems, which can modulate dopaminergic signals [14], is thought to be developmentally constrained. Additional findings suggest that neural signals that reflect attributions of salience or elicited arousal similarly exhibit adolescent-specific shifts in activity. Such a developmentally normative functional neurocircuitry could manifest behaviorally in robust incentive motivation [15*], reward reactivity [16], and sensation seeking [17] paired with still-developing executive control. In the remaining sections, we highlight themes emerging from our nascent understanding of how these staggered neurodevelopmental trajectories influence multiple component processes of decision-making.

Value-based learning

By taking actions in the world and observing their positive and negative consequences, one can learn through experience how to make beneficial choices. Dopaminergic reward prediction errors, which reflect the discrepancy between an expected outcome and what actually occurs, carry critical information that enables this learning process. Prediction error signals typically correlate with activity of the ventral striatum in adults [18]. Such signals have also been observed in children and adolescents [19*-21], consistent with evidence of successful feedback-based learning across development [19*,22,23]. Increased magnitude of both positive [24*] and negative [25] prediction error signals have been observed during adolescence, consistent with reports of heightened adolescent responses to both reward [8,26] and punishment [27]. However, such age differences in prediction error signals have not been consistently observed [19-21].

The extent to which a reward prediction error alters subsequent expected values depends on one's learning rate. High learning rates give a heavy weighting to a recent outcome, whereas lower learning rates integrate over a longer feedback history, with recent outcomes yielding only a small value adjustment. Several studies have observed valence-dependent developmental differences in the integration of feedback [19,25,28,29]. These studies suggest that children weigh recent negative feedback heavily in their updated values, and that this tendency decreases with age, a change that is associated with increased connectivity between the ventromedial prefrontal cortex (vmPFC) and the ventral striatum [19]. A developmental decline in the influence of negative outcomes might foster adaptive responding in decision contexts in which reward is probabilistic, and one should persist with a response despite occasional negative feedback.

In contrast, the weighting of recent rewarding outcomes has been found to increase from childhood into adulthood [19,28]. Adolescents, lying at the intersection of these opposing linear trajectories, exhibit variable weighting of positive and negative prediction errors across different tasks [19,25,28,29]. This sensitivity to task demands is to be expected, as distinct asymmetric weightings of positive and negative feedback can optimize performance given different reinforcement structures. However, as higher learning rates for positive versus negative outcomes, independent of performance demands, can promote risk-seeking behavior [30], future studies might examine whether such a reward bias in value-based learning might contribute to adolescent risk-taking. Learning elicited through reward and punishment is mediated by D1 and D2 receptor activity, respectively [31]. The marked changes in the expression and pruning of striatal D1:D2 receptors during the transition into and out of adolescence likely play a critical mediating role in these valence-dependent alterations in value-based learning [6].

Studies in adults have highlighted a distinction between two forms of value-based learning [32]. A “model-free” process, relying upon the striatal error-driven updating mechanism described above, evaluates an action based solely upon previous experienced feedback. In contrast, “model-based” evaluations, recruiting additional contributions from prefrontal and hippocampal regions, also take into account the structure of the decision environment and specific potential outcomes. Burgeoning evidence suggests that whereas model-free learning is employed from childhood onwards, reliance on model-based learning only emerges during adolescence, and continues to increase into adulthood [33]. This finding suggests that the normal developmental changes occurring in the brain across adolescence confer an expansion in the repertoire of evaluative processes that are available to inform one's decisions.

Risk

In economics, a “risky” choice is typically defined as a decision with multiple potential outcomes, which have probabilities that are known or can be estimated. Early accounts asserted that adolescents make risky choices because they either did not understand the potential negative consequences associated with particular actions, or perceived themselves as invulnerable to those consequences. However, several studies have refuted these assertions by demonstrating that adolescents know the potential negative consequences of risks, overestimate the probability of rare negative outcomes, as adults do, and perceive themselves as *more* vulnerable to those outcomes [34]. Consequently, Reyna and Farley [35*] have argued that adolescents have achieved a cognitive threshold for comprehending probabilistic outcomes [36] and for reasoning about complex decisions.

Studies have therefore turned to identifying biases in risk computations and information processing that might account for developmental differences in risky decision-making. Adolescents have been reported to exhibit similar, if not more, risk aversion relative to adults when risk attitudes are assessed via choices between statistically described gambles [37,38*]. However, a recent meta-analysis by Defoe and colleagues [39*] compiled dozens of studies using a variety of experimental tasks including the Iowa Gambling Task [40], the Balloon Analog Risk Task [41], and the Columbia Card Task (CCT; [42]) and observed reliably heightened rates of risky choices in adolescents compared to adults, with a medium effect size. Analyses of moderating effects showed that tasks in which risk is assessed experientially through immediate gain and loss feedback show the greatest uptick in risky choice in adolescents compared to adults [9,29,42,43]. Additional work has demonstrated that adolescents exhibit increased risk-taking (relative to adults) in situations where risk must be learned through trial and error [29] and in dynamic choice contexts that involve incremental risk-taking (relative to both children and adults) [9,42]. This difference in adolescent risk attitudes across decision contexts echoes the noted discrepancy in adulthood between risky choices made on the basis of personal experience versus formal description [43].

Direct comparison of children and adolescents revealed equivalent overall levels of risky choice. However, whether adolescents or children exhibited greater risk-taking varied substantially across tasks, and the distinctions between tasks underlying such differences were not readily apparent. As these preliminary findings are based on the small number of studies that included children within their sample, a more precise characterization of differences in risk-taking in children and adolescents awaits converging findings from additional studies.

In adults, evaluation of risk in decisions has been associated with activity of the lateral prefrontal cortex [44] and insular cortex [45,46]. Few developmental studies to date have decoupled risk from other decision parameters such as subjective value. Van Duijvenvoode and colleagues [47*] conducted an fMRI study using the CCT, a card-based choice task optimized for isolating the influence of trial-by-trial varying risk (i.e., outcome variability) and return (i.e., expected value) on decisions. Both aversion to risk and sensitivity to return increased from childhood to adulthood. Activation in the insular cortex and prefrontal cortex tracking trial-by-trial variation in risk was exaggerated in adolescents relative to children and adults, with adolescents who exhibited greater activation in these regions showing more avoidance of risk. Further work isolating risk from other decision components is needed to clarify how neurodevelopmental shifts in risk tracking relate to adolescents' orientation toward risk, as well as how the manner in which risk is evaluated alters choice.

Uncertainty

A related decision-making construct is uncertainty, or a dearth of information regarding potential outcomes or their probabilities when making decisions. Decisions in daily life are fraught with uncertainty, and the level of uncertainty for complex decisions might be particularly high for adolescents, whose information stems from a more impoverished repertoire of past experiences than adults. A study by Tymula and colleagues [38*] contrasted decision-making under risk and under ambiguity (i.e. uncertainty regarding outcome probabilities) by parametrically obscuring a proportion of the information depicting odds of winning in a monetary choice task. They found that adolescents showed a greater tolerance for these ambiguous decisions than adults, whereas risk tolerance for gambles with explicit probabilities did not differ. Many real-world decisions (as well as experimental choice tasks) that are characterized as “risky” do not involve known outcome probabilities. Thus, the use of experimental approaches that deconfound ambiguity from related decision parameters holds promise in uncovering the role ambiguity tolerance plays in unique adolescent decisions. Convergent work has extended the concept of adolescent uncertainty tolerance to the temporal domain. Using a simple task probing the degree to which simple behavioral responses are slowed by temporally unpredictable stimulus presentations, recent work has demonstrated that adolescents are less slowed by uncertainty than both children and adults [48].

Both human adolescents and other mammalian models of adolescence demonstrate a precipitous rise in novelty seeking and exploratory behavior [49*,50]. A willingness to explore novel environments inherently requires tolerance of uncertain outcomes. Prominent theoretical views have considered adolescent exploratory tendencies to be highly adaptive [15*,51], given that a primary challenge of adolescence is to seek resources, mates, information about the world, and self-directed learning opportunities. This adaptive function of exploration is consistent with a recent proposal that developmental shifts from high to low exploration (akin to changes in search “temperature” in computational “simulated annealing” algorithms) may reflect a developmentally optimized search process that promotes broad investigation of potential behaviors before focusing more narrowly on those that have proven most beneficial [52]. Tolerance for ambiguity might represent a mechanism facilitating adolescent-specific exploratory tendencies.

Time

Many of the everyday choices adolescents face carry consequences that unfold over time. While going to a party on Friday night might be fun, studying for Monday's exam may bring more valuable long-term benefits. Economic models propose that when making choices between proximal rewards and more substantial but deferred reinforcement, one decreases or “discounts” the subjective value of a delayed outcome as a function of the amount of time one must wait to receive it. Intertemporal choice in the lab has been found to have striking ecological validity, predicting an array of real world decisions that reflect prioritization of future rewards [53]. Convergent findings across numerous developmental studies of intertemporal choice suggest that discount rates decline throughout adolescence and asymptote in early adulthood [54-58]. Collectively, these studies suggest that throughout adolescent maturation, delayed rewards become more highly valued.

This developmental increase in preference for delayed rewards has been associated with both structural and functional changes in the brain [55,57-59]. Consistent with abundant evidence for the roles of both the vmPFC and the ventral striatum in the computation of subjective value [60], functional connectivity between these regions during intertemporal choice has been shown to increase linearly from childhood into adulthood, predicting a corresponding decrease in discount rates [57]. Both structural and functional connectivity between the ventral striatum and more lateral prefrontal regions has also been associated with age-related increases in patient intertemporal choice [58]. Gradual maturation of corticostriatal connectivity throughout adolescence has been proposed to underlie the development of self-regulatory ability [61] and reductions in impulsivity [62], cognitive processes that are commonly associated with decreases in discounting. This interpretation is supported by evidence in developmental samples that steeper discount rates predict alternative forms of impulsivity, such as poor response inhibition [59,63] but see [58].

Greater recruitment of prospective future-oriented cognition might also contribute to decreases in discount rates with age. Burgeoning evidence suggests that the episodic simulation of the future during intertemporal choice promotes more patient choices [53,64]. While the capacity for episodic mental simulation is evident from childhood [65], the recruitment of future-oriented cognitive processes such planning, or anticipating consequences prior to action continues to increase throughout adolescence [56]. In adults, the influence of mental simulation on intertemporal choice has been shown to depend upon functional connectivity between the PFC and the hippocampus [53]. Although few studies neuroimaging studies have examined the development of PFC-hippocampal connectivity, the white matter tracts connecting these regions undergo continued myelination during adolescence [66], suggesting protracted maturation of related cognitive processes. Age-related increases in foresight during choice might be facilitated by the accumulation of experience with decisions that have temporally extended consequences.

Context dependency of adolescent decisions

People who interact with adolescents often are frustrated by the mercurial qualities of their decisions. Having the flexibility to make different decisions in different contexts has been described as an adaptive consequence of continuing neurodevelopment [51,67]. Research has begun to explore the context-dependency of adolescent decisions in two domains in which adolescents might display particularly robust sensitivity: contexts of heightened arousal or excitement, and contexts involving peers.

Inspired by dual process theories, the modulation of adolescent decision-making in arousing or “hot”, compared to deliberative or “cold” situations has been examined using the Columbia Card Task (CCT; [42]). In the CCT, participants select a number of cards from a deck of mixed gain and loss cards on each trial, which terminates when a loss is encountered. In the “cold” condition, participants are encouraged to use deliberation and to weigh the available odds information to determine how many cards to select. In this condition, adolescents and adults selected an equivalent number of cards. However, despite explicit knowledge of risk information, adolescents drew more cards than adults in a “hot” condition where each choice to draw a card was made one at a time, inducing physiological arousal and encouraging the feeling of a “hot hand” via incremental win feedback. This contextual increase in adolescents' risk-taking reflects a diminished influence of information about odds and outcomes in the “hot” condition. This work suggests that in arousing or exciting situations where outcomes are directly experienced, adolescents are less influenced by their explicit knowledge of the probabilities of potential negative outcomes, and are more willing to take risks to obtain potential rewards.

The presence of peers is another uniquely powerful context that shapes adolescents' decisions [68]. Inspired by statistics showing that peer-aged passengers predict a precipitous rise in traffic fatalities among adolescent drivers [69], controlled laboratory studies using driving simulation games have found that adolescents choose to speed through a yellow light, rather than stop, more often when a peer observes their driving, whereas adults are unaffected by peer monitoring [70,71]. Similarly, adolescents show exaggerated delay discounting in the presence of peers [72], and peripubertal but not adult rodents demonstrate an age-unique increase in time spent consuming alcohol in the presence of peer-aged

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conspecifics [73], suggesting that peers may influence impulsive or risky decision-making across multiple domains.

Social modulation of risky behavior is perhaps unsurprising given the intensive social reorientation that characterizes adolescence [51,74]. Dramatic changes in peer relationships yield a greater importance assigned to peers, which could manifest as a greater reliance on peers' attitudes as a factor in decision value computations (e.g., [75]). Indeed, reward-related signals in the ventral striatum are intensified when adolescents choose to run a yellow light while a friend is monitoring risky decisions, compared to those of adults as well as to when they are alone [70]. However, adolescent attunement to the social environment is perhaps even more subtle than originally thought – merely being looked at by a peer is sufficient to induce uniquely high levels of physiological arousal in adolescents and modulation of corticostriatal valuation systems [76,77]. While peers are clearly influential during adolescence behavior, peers do not uniformly influence adolescents' reward valuation processes [78]. As the majority of tasks in which peer modulation of risky decision-making has been observed do not permit identification of the underlying decision computations that are affected, further research is warranted to clarify precisely how adolescent decision-making is shaped by social context.

Conclusions

Independent decision-making is a burgeoning challenge for adolescents, who are often stereotyped as making poor choices in everyday life. Scientific evidence is emerging to suggest that adolescents' decision-making is indeed unique, and that their patterns of uniqueness can be partially attributed to normative maturational changes in brain function.

Although adolescents appear to have full access to many of the cognitive foundations of decision-making, several aspects of decision-making such as intertemporal choice, prospective evaluation, and integration of positive and negative feedback are not yet tuned to typical adult levels. Still other processes that inform decision-making are uniquely amplified during adolescence: learning from direct experience, reward reactivity, tolerance of ambiguity, and context-dependent orientation toward risk in exciting or peer-laden situations.

Greater insight into adolescent decision processes can be gained by considering the putative neurodevelopmental changes that contribute to biased decision computations. Based on the adult literature, the amplified components of decisions are largely signaled by neural systems that assign reward or salience value to information in the environment such as the striatum. This observation is broadly consistent with the nonlinear functional developmental trajectories for these regions. Conversely, those aspects of decisions that require reliance on abstract goals, distal outcomes, and complex cost-benefit calculation are thought to be mediated by interactions between subcortical and cortical systems, including a prominent role for the lateral prefrontal cortex. Therefore, the late development of the prefrontal cortex, and continued development of corticostriatal connectivity, could constrain the utilization of such strategic aspects of decision-making in adolescence.

Although adolescents' decision-making is not adult-like, it is developmentally normative. Thus, adolescents' unique decision computations may be optimized for the fulfillment of the specific goals of this developmental phase. Adolescents are tasked with attaining independence despite limited amounts of direct experience. Therefore, it might be advantageous for the adolescent brain to be attuned to more proximal outcomes, to be tolerant of uncertainty, and to benefit from robust learning signals that can entrain a richer experience base to scaffold the transition to independence.

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Box 1

Where to go from here?: Conceptual challenges in the study of adolescent decision-making

Applying quantitative, neuroeconomics-based analyses has proven to be highly useful in delineating precise mechanisms underlying developmental shifts in complex choice behavior. Here we specify challenges and future directions in hopes of stimulating progress in these domains:

- **Who is an adolescent?** There is presently wide variability across studies with regard to operationalizing 'adolescence'. As adolescence is a culturally defined concept without straightforwardly observable starting and ending points, it is perhaps not surprising that consensus is lacking. Even pubertal onset, a relatively agreed upon trigger for the onset of adolescence, varies widely across sexes and across individuals, and begins centrally well before secondary sex characteristics are observed. However, such variability frequently muddies clear-cut comparison of research findings across studies.

  We encourage researchers to incorporate as wide of an age range as is feasible to capture linear and nonlinear changes, to allow for continuous analyses of age that circumvent issues related to arbitrary delineations between age "groups", and with consideration of the samples in existing studies to which one wishes to compare their findings.

- **Applying 'adult' quantitative models of decision-making to developmental populations.** Formal models of decision-making rely on mathematical assumptions that define the latent structure of decision processes. It is important to acknowledge that these latent models have largely been developed with an adult decision-maker in mind. Applying such models to the study of developmental populations enables discovery of quantitative changes in decision processes, but this approach is relatively insensitive to qualitative differences in decision-making that might be best described by alternative models.

  As 'adult' models are utilized, careful examination of unexplained variance in decision-making could open doors to characterization of qualitative shifts in decision making that occur across development.

- **Ecological validity of assessments of adolescent decision-making.** Many tasks employed in neuroeconomic studies fail to capture key qualitative features of naturalistic choice contexts, which may diminish their validity for understanding real-world decision-making. While preserving the precision of neuroeconomics-based tasks, new tasks should be developed that also evoke the anticipatory and feedback-driven affective responses that typically accompany motivated decision-making. In addition, adolescent decision-making typically occurs within rich environments that often involve complex motivations. Prominent motivations at this age, which can compete and conflict with one another, include maintaining status with peers, achieving goals in academic, athletic, or other arenas, finding independence, and maintaining harmony within the family. Future work should attempt to strike balance between experimental precision and ecological validity.

Studies employing techniques that index choices in the real world and their specific motivational contexts (e.g. ecological momentary assessment) may offer unique insights into adolescents' naturalistic decision-making.

Highlights

- We examine how trajectories of brain development shape adolescent decision processes.
- Prolonged prefrontal development may constrain multiple component processes of choice.
- Adolescent-specific peaks in incentive processing uniquely alter decision-computations.
- Adolescent decision-making may be optimized for attaining specific developmental goals.