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Developmental neurobiology of cognitive control and motivational systems

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One form of cognitive control is the ability to resist temptation in favor of long-term goal-oriented behavior. Historically, the development of cognitive control capacity has been described by a linear function from infancy to adulthood. However, the context in which control is required impacts behavioral regulation abilities, such that emotionally charged or rewarding contexts can diminish control. More recently, studies have begun to examine the development of cognitive control in contexts that vary in motivation. These studies suggest specific windows of development in which cognitive control capacity is more vulnerable to incentive-based modulation. In this review we highlight the most recent work on neurobiological changes supporting motivational and cognitive development, underscoring the importance of functional organization and development of the underlying circuitry implicated in these processes, and provide a theoretical perspective that moves away from discussing singular functional regions toward considering functional circuitry.

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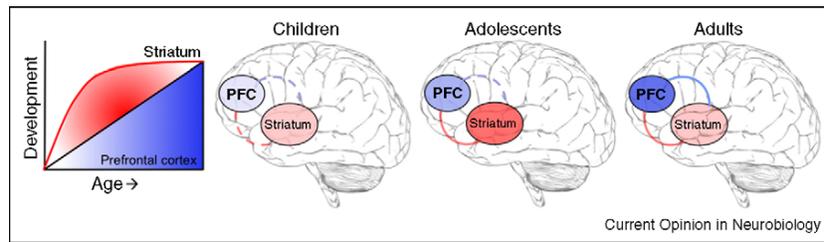
Resistance to temptation or delay of immediate gratification has been studied in the context of social, developmental and cognitive psychology. Developmentally, this ability has been measured by assessing how long a toddler can resist an immediate reward (e.g. a cookie) in favor of a larger reward later (e.g. two cookies) [1]. Although we each vary in this ability even as adults, developmental studies suggest windows of development when we are particularly susceptible to temptations. This ability has been described as a form of cognitive control [2] and is operationally defined as the ability to accomplish goal-directed behavior in the face of salient, competing inputs and actions.

Developmental studies have shown a steady improvement in cognitive control capacity from infancy to adulthood [3] using experimental paradigms in controlled laboratory settings. Yet, in less controlled settings within the real world that involve emotionally charged interactions, we often see diminished cognitive control. This reduced control is especially evident during the period of adolescence, when rates of risky sexual and drug-related behaviors peak [4–6,7]. These observations imply that developmental trajectories of cognitive control are complex and can be modulated by heated or emotionally charged contexts, in which cognitive control demands interact with motivational drives or processes.

In the last few years, there has been an explosion of studies examining the developmental neurobiology of adolescence. These studies have focused predominantly on evaluating the hypothesis that during adolescence, unique patterns of brain activity arise that predict stereotypical aspects of adolescent behavior including risk-taking and suboptimal decision-making in the face of incentives [8,9]. This work challenges the more traditional view that adolescent risky behavior is due to immature cognitive control capacities and their underlying neural substrates (e.g. prefrontal cortex) [10]. According to the recent studies, adolescents show a unique sensitivity to motivational cues that challenges the less mature cognitive control system, resulting in an imbalance between these systems and ultimately patterns of behavior that are unique to adolescents.

Inflections in adolescent behavior, distinct from child and adult behavior represent dynamic maturation of brain circuitry underlying motivational and cognitive processes [11,12]. Two key regions implicated in cognitive and motivational behavior are the prefrontal cortex known to be important for cognitive control [13], and the striatum critical in detecting and learning about novel and rewarding cues in the environment [14]. This review highlights the most recent work on neurobiological changes supporting these motivational and cognitive systems across development. We underscore the importance of examining circuitry rather than regional change, especially within frontostriatal circuits that underlie different forms of goal-oriented behavior. This theoretical perspective moves the field away from characterizing how each region matures in isolation toward how they may interact in the context of interconnected circuits.

Figure 1



Cartoon model of striatal and prefrontal interactions across development. Deeper color indicates greater regional signaling. Line represents functional connectivity, with solid line indicating mature connection and dotted line indicating immaturity.

Motivational modulation of cognitive control across development

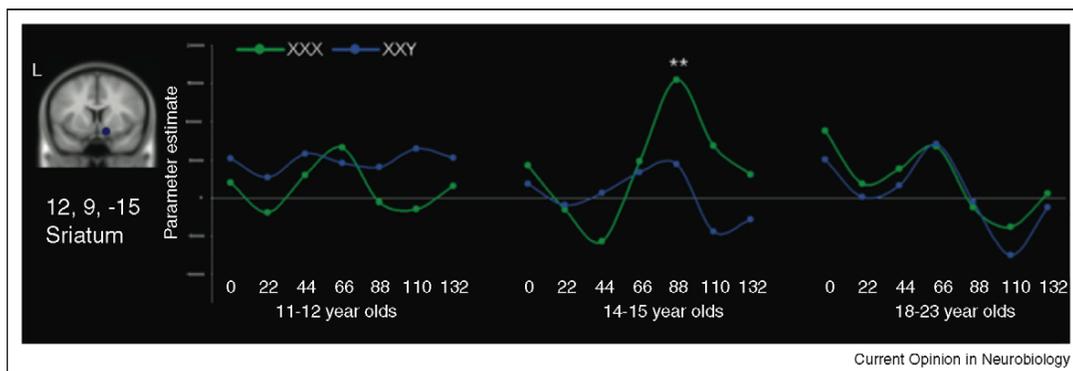
Incentives can modulate cognitive control in numerous ways. Being rewarded for performance on a given task may make people work harder and ultimately perform better than when not rewarded. Alternatively, the capacity to exert control is challenged when required to suppress thoughts and actions toward appetitive cues. Recent studies of adolescent development have begun to compare cognitive control capacity in relatively neutral versus motivational contexts. These studies suggest a change in sensitivity to environmental cues, especially reward-based cues (see [8,15] for discussion of sensitivity to aversive cues), at different points in development, and suggest a unique influence of motivation on cognition during the adolescent years.

In general, cognitive control capacities improve in a linear function from childhood to adulthood. This observation is supported by a wealth of behavioral evidence from tasks including the Go–NoGo, Simon task, and task-switching paradigms requiring participants to override a prepotent response in order to achieve a correct one [3]. However,

when it is advantageous to suppress a response to incentive-related cues, adolescents’ cognitive control suffers.

Recent studies provide elegant demonstrations of how adolescent behavior is differentially biased in motivational contexts. Using a gambling task in which reward feedback was provided during decision-making (‘hot’ trials which heightened task-elicited arousal) or held until after the decision (‘cold’ trials), Figner *et al.* [16*] showed that adolescents made disproportionately more risky gambles compared to adults but only in the emotionally charged ‘hot’ condition. Steinberg and colleagues, using a similar gambling task [17] and a delay discounting task [18**], have shown that sensitivity to rewards and incentives peaks during adolescence, with a steady increase from late childhood to adolescence and subsequent decline from late adolescence to adulthood. These findings illustrate a \cap -shaped function, peaking between 14 and 16, and then declining. Taken together, these studies suggest that during adolescence, motivational cues of potential reward are particularly salient and can lead to riskier or suboptimal choices that diminish effective goal-oriented behavior.

Figure 2



Adolescents show enhanced striatal sensitivity to the receipt of a monetary reward relative to children or adults. XXX = reward, XXY = no reward. Adapted with permission from [40**].

Developmental neurobiology of corticosubcortical control

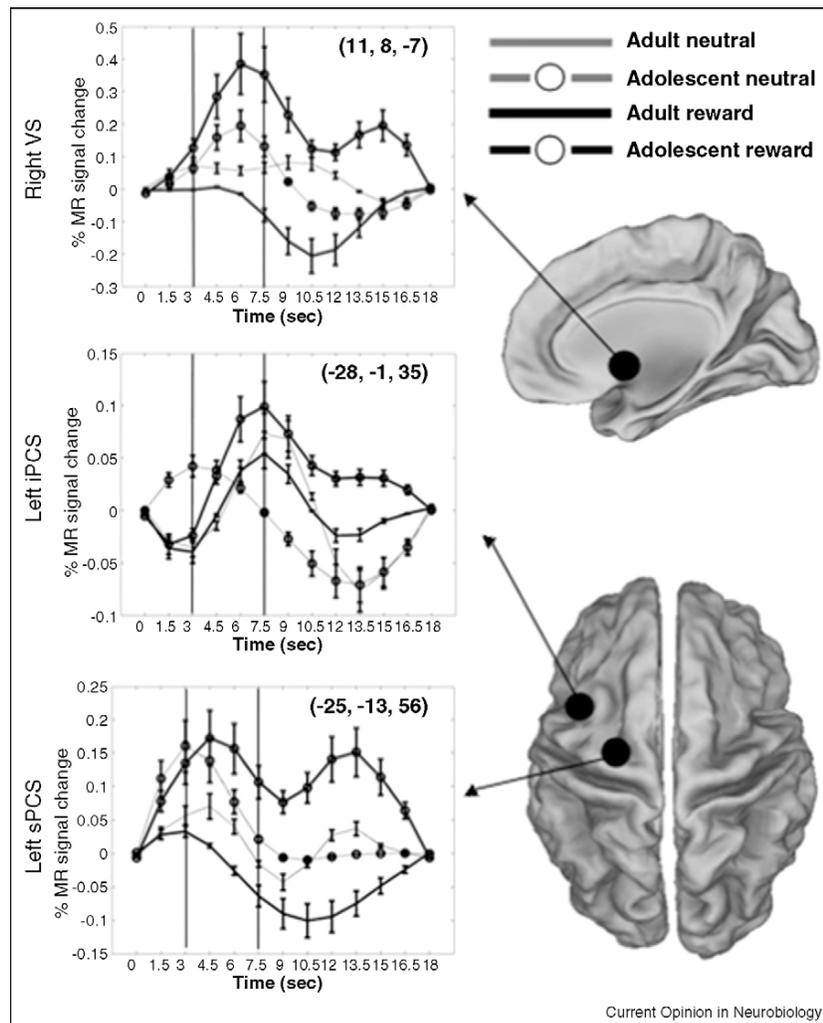
We have recently proposed a simple and testable neurobiological model of cognitive and motivational processes ([7^{*}], see Figure 1) to account for real-world behavior of adolescents that is supported by recent laboratory evidence. This model suggests linear development of top down prefrontal regions relative to a U-shaped function for the development of bottom-up striatal regions involved in detecting salient cues in the environment.

Evidence in support of this model comes from animal and human studies of frontostriatal function and development [19–21]. Seminal work has shown how striatal and prefrontal cortical regions shape goal-directed behavior. Using single-unit recordings in monkeys, Pasupathy

and Miller [22] demonstrated that when flexibly learning a set of reward contingencies, very early activity in the dorsal striatum lays down reward-based associations, whereas later, more deliberative prefrontal mechanisms are engaged to maintain the behavioral outputs that optimize the greatest gains. A role for the striatum in early temporal coding of reward contingencies before the onset of prefrontal regions has also been demonstrated in humans [23]. These findings suggest that understanding the interactions between regions (along with their component functions) — particularly within frontostriatal circuitry — is critical for developing a model of cognitive and motivational control.

Recent human imaging studies provide further support for the importance of examining connections between

Figure 3



Striatal and prefrontal responses are upregulated in adolescents while preparing for rewarded versus nonreward trials. Adapted with permission from [37^{**}].

frontostriatal regions in establishing circuit-specific function across development. Using diffusion tensor imaging (DTI) and functional magnetic resonance imaging (fMRI), Casey and colleagues have linked connection strength between these regions with the capacity to effectively engage cognitive control in typically and atypically developing individuals [24,25]. These studies illustrate the importance of signaling within corticostriatal circuitry in supporting the capacity to effectively engage in cognitive control.

In the last few years much attention has been given how subcortical systems like the striatum and the prefrontal cortex interact to give rise to aberrant behavior observed in adolescents. Developmentally, cortical association areas including the prefrontal and parietal cortex thought to subservise age-related improvement in cognitive control [26–30] undergo delayed maturation [31–33]. These studies provide insights into the role of these regions in cognitive control processes across development, though the delineation of circuit-level development has been less clear. Using network modeling techniques, Fair *et al.* recently mapped the developmental trajectory of cognitive control networks using small-world network modeling [34]. From childhood to adulthood, the functional interactions between regions within a frontoparietal network and cingulate-lateral prefrontal network show lessening of short-range functional connections with neighboring regions and strengthening long-distance connections between distal regions. These novel network-level findings bolster the claim that cognitive maturation occurs not in unitary structures but in the connectivity and interactions between structures (e.g. [35]).

Recent studies have mapped developmental modulation of motivational systems such as the striatum in salient and motivational contexts. Seminal work by Ernst, Galvan, Luna and Crone and others supports the notion that adolescents show an enhanced sensitivity to incentives relative to children and adults within areas of the dorsal and ventral striatum [36,37,38,39]. For example, a recent study by van Leijenhorst *et al.* [40] observed exaggerated ventral striatal responses in adolescents during the anticipation and receipt of a monetary reward (Figure 2). The magnitude of ventral striatum response to reward cues has been linked to real-world behavior, with greater ventral striatal activity to rewards being predictive of real-life risk-taking tendencies [41]. These studies together suggest that striatal responses show an inverted U function across development in response to incentives.

A scientific area that has received less attention is determining how cognitive control and motivational systems interact over the course of development. Very recent work has suggested that adolescents possess an enhanced ability to flexibly upregulate cognitive performance if an incentive is at stake. The work by Ernst and colleagues

[42,43] used an antisaccade task to measure cognitive control behavior and promised a financial reward for accurate performance on some trials but not others. Results showed that promise of a reward facilitated adolescent cognitive control behavior more than for adults, a finding that has recently been extended to social rewards (e.g. happy faces) as well [44].

Geier *et al.* [37] identified the neural substrates of this cognitive upregulation using a variant of an antisaccade task during functional brain imaging. In adolescents and adults, trials for which money was at stake speeded performance and facilitated accuracy, but this effect was larger in adolescents. Following a cue that the next trial would be rewarded, adolescents showed exaggerated activation in the ventral striatum while preparing for and subsequently executing the antisaccade (Figure 3). An exaggerated response was also observed in adolescents

Box 1 Issues for developmental neurobiology of cognitive and motivational processes

Measuring neurobiological change across development poses several unique challenges and current areas of debate, outlined below.

- (1) *What constitutes 'maturation' in fMRI signal?* Conflicting arguments have been made with regard to what pattern of functional activity represents functional maturity. Some studies report higher magnitude activity as immature, reflecting neural inefficiency or increased effort. Other studies interpret higher magnitude activity as more mature, reflecting greater capacity to utilize the functionality of the region. Others have asserted that maturation is reflected in the refinement of activation extent, shifting from larger, diffuse activations to more focal activations with increasing age [45]. For a more extensive discussion of this complex issue, see [26].
- (2) *How can age and performance-related activity be deconfounded?* Cognitive task performance often co-varies with age. Some studies assess functional recruitment in performance-matched samples [46] whereas others use differential behavioral performance as a variable of interest [15]. A final approach is to separately characterize the variance accounted for by age and performance [47], though this requires a larger sample than is typically acquired.
- (3) *How can nonlinear developmental changes best be detected?* In this report we describe nonlinear aspects of cognitive development. These patterns are overlooked in many studies using exclusively linear models to assess changes across age and when testing small samples and relatively small discrete age ranges (e.g. comparing 12–13 year olds with 21 year olds). A gold standard in developmental neuroscience is to examine developmental trajectories as individuals transition into and out of developmental periods of interest.
- (4) *How do developmental differences in representation of motivation bias findings?* In experiments involving reward and affect, the assumption is often made that the potency of an experimental manipulation or stimulus is equivalent across ages. For example, is a \$1 gain equally 'rewarding' to a child, an adolescent, and an adult? Preliminary evidence suggests this is not the case [36]. Future work will need to equate the rewarding and aversive properties of experimental stimuli and manipulations across development.

within prefrontal regions important for controlling eye movements, suggesting a reward-related upregulation in control regions as well. Together, these studies suggest incentive modulation of frontostriatal circuits at the level of the striatum and are consistent with our proposed neurobiological model of striatal and prefrontal interactions across development.

Conclusions

This is an exciting time in developmental neurobiology research of cognitive and motivational processes, with a surge in studies focused on the development of these processes in adolescence. Recent findings suggest that an enhanced sensitivity to motivational cues in adolescents, represented at the level of the striatum, modulates cognitive control-related processes differently from children and adults. As such, adolescent cognitive control capacity can be enhanced or impaired, depending on whether task demands require suppression of or attention to these motivational cues. More research is needed to understand the interplay between how subcortical and cortical regions interact to accomplish these dynamic cognitive control processes across development and how motivational cues may vary in salience across development (see Box 1).

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