Journal of Adolescent Health 52 (2013) S7–S13

JOURNAL OF
ADOLESCENT
HEALTH

www.jahonline.org

Review article

Adolescent Neurodevelopment

Linda Patia Spear, Ph.D.*

Department of Psychology, Center for Development and Behavioral Neuroscience, Binghamton University, Binghamton, New York

Article history: Received January 22, 2012; Accepted May 23, 2012
Keywords: Adolescence; Brain; Neurodevelopment; Brain imaging; Cognitive control; Reward sensitivity; Aversive stimuli; Emotions; Risk taking; Public policy

A B S T R A C T

Purpose: The purpose of this article is to outline notable alterations occurring in the adolescent brain, and to consider potential ramifications of these developmental transformations for public policy and programs involving adolescents.
Methods: Developmental changes in the adolescent brain obtained from human imaging work are reviewed, along with results of basic science studies.
Results: Adolescent brain transformations include both progressive and regressive changes that are regionally specific and serve to refine brain functional connectivity. Along with still-maturing inhibitory control systems that can be overcome under emotional circumstances, the adolescent brain is associated with sometimes elevated activation of reward-relevant brain regions, whereas sensitivity to aversive stimuli may be attenuated. At this time, the developmental shift from greater brain plasticity early in life to the relative stability of the mature brain is still tilted more toward plasticity than seen in adulthood, perhaps providing an opportunity for some experience-influenced sculpting of the adolescent brain.
Conclusions: Normal developmental transformations in brain reward/aversive systems, areas critical for inhibitory control, and regions activated by emotional, exciting, and stressful stimuli may promote some normative degree of adolescent risk taking. These findings have a number of potential implications for public policies and programs focused on adolescent health and well-being.

Development of the brain is far from complete at the time of birth, with maturation continuing through childhood and adolescence, and even some age-related changes in brain organization and function (including the generation of modest numbers of brain cells) into adult life [1]. Studies conducted over the past several decades have revealed adolescence as a time of particularly notable morphological and functional transformations in the brain that, along with increasing hormone levels and other biological changes, interact with cultural, economic, and psychosocial forces to shape how adolescents think, feel, and behave [2]. The purpose of this article is to outline some of the more notable alterations occurring in the adolescent brain, and briefly consider some potential ramifications of these normal developmental transformations for public policies and programs involving adolescents.

Understanding of adolescent brain development continues to escalate rapidly, aided considerably by increasingly informative insight into normal developing human brains provided by continued improvements in imaging technologies. Magnetic resonance imaging (MRI) and other imaging technologies have proved valuable for detailing the size of [3,4] and connectivity across [5,6] brain regions at different ages, as well as for indexing relative changes in regional activation patterns during performance of target risk taking, decision making, or other tasks [7]. However, space and movement constraints limit task-related responses possible within scanners, making it a challenge to relate these findings to the social and emotionally arousing situations in which adolescents often engage in risky behavior. Dissecting causal relationships and the precise morphological and molecular underpinnings of observed age differences typically requires approaches and levels of analyses largely unavailable

* Address correspondence to: Linda Spear, Ph.D., Department of Psychology, Box 6000, Binghamton University, Binghamton, NY 13902-6000.
E-mail address: lspear@binghamton.edu (L.P. Spear).

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http://dx.doi.org/10.1016/j.jadohealth.2012.05.006

with imaging, but more amenable to study using animal models of adolescence. Although the human brain and the behavior it supports are far more complex than those of other species, relevance of research using simple mammalian models of adolescence is aided by considerable across-species similarities in behavior and biology seen between humans and other mammalian species. The basics of brain structure and function arose millions of years ago, and the relative timing of regional brain development has been evolutionarily conserved as well [8]. Common behavioral proclivities seen in human adolescents and their counterparts in other species include elevations in peer-directed social interactions along with occasional increases in fighting with parents [9–11], increases in novelty seeking, sensation seeking, and risk taking [12–15], and greater per-occasion alcohol use [16,17]. These across-species similarities support the suggestion that certain neurobehavioral characteristics of adolescence may be tethered in part by biological roots embedded in the evolutionary past [18].

Recent Advances in Understanding of Adolescent Brain Development

Synaptic pruning and myelination

Brain development is a mix of expansion and regression. Many more brain cells specialized for processing and transmitting information (neurons) and their synaptic connections are produced than will ultimately be retained [19,20]. This overproduction and pruning are thought to ensure that appropriate connectivity is established, with neurons and synapses that fail to make appropriate connections being lost [21]. Although such regressive processes are most prevalent during early brain development, they continue to some extent throughout life, with synaptic pruning, in particular, being a hallmark of the brain transformations of adolescence. Pruning during adolescence is highly specific and can be pronounced, resulting in a loss of approximately 50% of the synaptic connections in some regions, but with little decline in others [21]. Pruning has been speculated to help with the "rewiring" of brain connections into adult-typical patterns, and could potentially represent relatively late opportunities for brain plasticity, as discussed later in the text. Synapses are energetically costly, and declines in their numbers likely contribute to the increases in brain efficiency seen during adolescence, reflected by the declines in brain energy use seen through adolescence in humans and other species [22,23].

Not all brain changes during adolescence are regressive, with some neurons continuing to grow processes and establish new synaptic connections [1]. There are also major shifts in the speed and timing of information flow across the brain that influence functional connectivity across brain regions during adolescence [24]. Speed and efficiency of information flow across relatively distant regions are accelerated during adolescence because neuronal axons interconnecting certain brain areas become insulated with a white, fat-enriched substance called myelin, thereby markedly increasing the speed of electrical transmission along axons and at the same time reducing the energy needed to maintain this process. Although myelination begins early in life and continues into adulthood, its production escalates notably during adolescence [25], thereby speeding information flow across distant regions and magnifying its impact [26].

These processes of myelination and synaptic pruning help to reconfigure brain connectivity into the adult form and are thought to contribute to the developmental "thinning" that occurs in the neocortex, that is, the decline in thickness of outer layers of the brain that are most evolutionarily advanced in humans and are thought to play particularly important roles in higher levels of information processing and orchestrating actions. The thinning of cortical "gray matter" regions enriched in neurons, synapses, and support cells with maturation may be related not only to declines in the number of synaptic processes but also to increases in myelinated "white matter" tracts that pass underneath cortical gray matter, decreasing relative gray matter to white matter volume [27].

Regional specificity, changes in connectivity, and refinement of networks

Cortical development generally proceeds in "waves," with the timing of gray matter thinning occurring well before adolescence in cortical regions involved in basic sensory and motor function, whereas thinning continues throughout adolescence in prefrontal cortex (PFC) and other frontal cortical regions implicated in advanced cognitive functions. Development in noncortical areas is also thought to contribute to adolescent-characteristic behaviors. Subcortical regions receiving notable attention, which will be reviewed later in the text, include areas modulating social, aversive, and emotional stimuli, such as the amygdala, and regions implicated in the processing of rewarding stimuli, as exemplified later by neurons releasing the neurotransmitter dopamine (DA) and regions receiving this input, such as the ventral striatum. Developmental changes in these areas will be considered in conjunction with cognitive and behavioral data to support the suggestion that enhanced proclivities for risk taking, sensation seeking, and alcohol/drug use often seen during adolescence are influenced in part by immature cognitive control capacities, which can be overwhelmed by enhanced reactivity (and perhaps cross-reactivity) to social and emotional stimuli and to rewards under certain circumstances, along with sometimes attenuated reactivity to aversive stimuli/consequences.

However, development of the brain is not simply a chronology of developmental immaturities, with different areas coming online at different times. Rather, contemporary views of brain maturation consider it to be a dynamic process by which separate networks of functionally related regions become more strongly linked over time [24,28,29] via weakening connections between different networks while intensifying within-network connections, particularly those linking more distant network regions [30]—the latter presumably aided by the preferential myelination of longer axonal tracts as discussed previously. Such increases in network cohesion may contribute to developmental changes in patterns of brain activation, with activation in task-relevant regions often becoming less diffuse and more focal (distinct) with development [31].

Prefrontal areas and development of cognitive control

Theories of adolescent brain development generally concur on the importance of delayed maturation of the PFC and other frontal regions for developmental immaturities in cognitive control, attentional regulation, response inhibition, and other relatively advanced cognitive functions [7]. Although youth can perform well on tasks tapping these cognitive functions under certain conditions, performance impairments often emerge with increases in task demands, or under conditions of heightened