



Who are those “risk-taking adolescents”? Individual differences in developmental neuroimaging research

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ABSTRACT

Functional magnetic resonance imaging (fMRI) has illuminated the development of human brain function. Some of this work in typically-developing youth has ostensibly captured neural underpinnings of adolescent behavior which is characterized by risk-seeking propensity, according to psychometric questionnaires and a wealth of anecdote. Notably, cross-sectional comparisons have revealed age-dependent differences between adolescents and other age groups in regional brain responsiveness to prospective or experienced rewards (usually greater in adolescents) or penalties (usually diminished in adolescents). These differences have been interpreted as reflecting an imbalance between motivational drive and behavioral control mechanisms, especially in mid-adolescence, thus promoting greater risk-taking. While intriguing, we caution here that researchers should be more circumspect in attributing clinically significant adolescent risky behavior to age-group differences in task-elicited fMRI responses from neurotypical subjects. This is because actual mortality and morbidity from behavioral causes (e.g. substance abuse, violence) by mid-adolescence is heavily concentrated in individuals who are not neurotypical, who rather have shown a lifelong history of behavioral disinhibition that frequently meets criteria for a disruptive behavior disorder, such as conduct disorder, oppositional-defiant disorder, or attention-deficit hyperactivity disorder. These young people are at extreme risk of poor psychosocial outcomes, and should be a focus of future neurodevelopmental research.

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“Everybody’s youth is a dream, a form of chemical madness.”- F. Scott Fitzgerald

1. Introduction

Understanding the neural underpinnings of adolescent behavior is of increasing interest, and is enabled by functional magnetic resonance imaging (fMRI) technology for non-invasive probes of human brain function. This research has led to an influential theory that attributes

behavior-related mortality and morbidity in adolescents to overactive incentive-motivational circuitry relative to underactive frontocortical behavior control neurocircuitry. In this review, we present a case that in light of epidemiological and longitudinal data, this brain functioning imbalance is likely specific to a subset of youth with disruptive behavior disorders (DBD), and is not especially pronounced or significant in neurotypical youth. We first briefly describe the neuroanatomy of reward-related decision-making, and the fMRI studies of these brain regions that give rise to these opponent-process theories. We then discuss how longitudinal studies, laboratory behavioral studies, and fMRI studies of youth with DBD indicate that these individuals, who are at extreme risk

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of substance use disorder (SUD) are likely the youth who would show an aberrant opponent-process. We conclude with some directions for future research.

2. Neurodevelopmental models of adolescent risk-taking

Adolescents are renowned for risky behavior, from skateboard stunts to binge drinking and unprotected sex. Reports of adolescents committing violent crime grab headlines. Empirical assessments with psychometric questionnaires and laboratory tasks have also supported a peak in venturesomeness or risk-seeking in mid-adolescence (reviewed in (Steinberg, 2004)). While age-comparison findings with laboratory decision tasks are somewhat inconsistent, the results generally support either a linear decline in risky-choice from adolescence to adulthood (Deakin et al., 2004; Overman et al., 2004), or a developmental peak in pursuit of risky choices in mid-adolescence relative to younger children and adults (Steinberg, 2005; Figner et al., 2009; Burnett et al., 2010). The advent of fMRI has sparked intense interest in whether trajectories of brain maturation contribute to adolescent risk-taking, where developmental differences in structure and function of brain regions involved in incentive processing and behavioral control are touted (and funded) as having a potential public health impact.

Where in the brain do we look? Portions of ventral striatum (VS); including nucleus accumbens (NAcc) have been extensively linked with motivational processing (reviewed in (Knutson et al., 2009)). Notably, adolescents show greater ambiguity tolerance (willingness to take risks when odds are not known) compared to adults, but not greater explicit risk tolerance (Tymula et al., 2012). When the probability of reward in a goal-directed task is uncertain, a wide variety of rewarding stimuli activate cortico-basal ganglia system that includes the orbitofrontal cortex (OFC), anterior cingulate cortex (ACC), insula, thalamus, and dorsal and ventral striatum (Delgado, 2007; Dolan, 2007; Seymour et al., 2007). In these tasks, punishment (i.e., the loss of money) often recruits a similar set of neural circuits, albeit areas in the VS often show less pronounced or even negative activation relative to baseline (e.g. (Delgado et al., 2000; Tom et al., 2007)). Inhibiting approach to potential rewards that may also result in a penalty involves frontal cortex structures, which have been extensively linked to cognitive control in both lesion studies (Bechara et al., 2001; Bechara and Van Der Linden, 2005) and in functional imaging studies (Durston et al., 2002; Ridderinkhof et al., 2004b). For example, in healthy adolescents and adults, cognitive control tasks activate a neural network that includes the dorsolateral and inferior prefrontal regions, ACC, and inferior parietal cortex (Rubia et al., 2001; Aron et al., 2004; Luna and Sweeney, 2004; Buchsbaum et al., 2005).

Initial developmental surveys using magnetic resonance imaging (MRI) documented morphological brain differences from childhood to adulthood in several brain regions. For example, frontocortical gray matter volume follows an inverted-U pattern, peaking around age 12, while temporal lobe gray matter volume increases nearly

linearly throughout adolescence (Giedd et al., 1999; Sowell et al., 1999; Sowell et al., 2001). Meanwhile, frontocortical white matter volume as a proportion of total frontocortical volume increases from childhood to adulthood (reviewed in (Marsh et al., 2008)). Finally, developmental diffusion tensor imaging (DTI) studies indicate that organization of this increased frontocortical white matter is composed of increasingly orderly fiber tracts, in that fractional anisotropy of white matter water flow increases from childhood to adulthood (Barnea-Goraly et al., 2005; Imperati et al., 2011; Jernigan et al., 2011).

Two cross-sectional surveys of resting-state functional connectivity (RSFC) (Fox and Raichle, 2007) during fMRI indicated that from childhood to mid-adulthood, the strength of long-range connections between brain regions tends to increase with age while the strength of short-range connections tends to get weaker with age (Supekar et al., 2009; Dosenbach et al., 2010), and these relative connection strengths can predict an omnibus developmental “age” of the brain (Dosenbach et al., 2010). Whether inter-regional brain connectivity is directly assessed (structurally) by DTI measures of white matter or whether connectivity is inferred from synchronized brain activity between regions during a resting-state, indices of frontocortical network maturation may have clinical or behavioral significance in that decision-making requires extensive cortical integration for the representations of incentive values, potential penalties, future self with the respective outcomes, as well as for formulation of action-plans.

Particularly compelling, however, are findings of developmental (age-group) differences in brain responsiveness to risk and rewards when children, adolescents, and adults perform incentive-laden tasks during functional fMRI. Most experiments indicate that adolescents show greater responsiveness of the VS to rewards than younger children or adults. First, adolescents showed greater left VS activation by notification of money won in a “Wheel of Fortune” gambling task compared to adults (Ernst et al., 2005). Later Galvan et al. (2006) reported that once associations between cartoon cues and rewarding outcomes had become learned, adolescents showed greater VS activation during delivery of unspecified monetary reward compared to activation in adults or younger children. Similarly, Van Leijenhorst et al. (2010a) found that mid-adolescents showed greater VS activation by risky gains than younger children or young adults. A decision-making task also indicated that the adolescent striatum is more sensitive to the delivery of unexpected rewards during cue-reward association learning (Cohen et al., 2010). Moreover, in a slot machine simulation, mid-adolescents also showed more VS activation by reward-predictive slot results than younger children and young adults (Van Leijenhorst et al., 2010b). If one assumes that visual stimuli of happy faces is rewarding, Somerville et al. (2011) reported that compared to younger children and young adults, adolescents emitted more commission errors to (and had greater VS recruitment by) photographs of happy faces assigned as non-target stimuli in a go–nogo task. Finally, in a seminal investigation on the effects of social context on reward processing, Chein et al. (2011) demonstrated that running virtual yellow lights in

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