Neuroscience and Biobehavioral Reviews 70 (2016) 334–338

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Commentary on the special issue on the adolescent brain
A tribute to the adolescent brain

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ARTICLE INFO

Article history:
Received 3 May 2016
Accepted 15 June 2016
Available online 17 June 2016

Keywords:
Intrinsic functional connectivity
Resting state networks
Social processes
Plasticity
Organizational and sensitive window
Puberty
Neural systems model
Dual attention system
Learning

1. Introduction

This series of invited reviews vividly illustrates the way in which the explosion of research on the adolescent brain was able to awaken and catalyze novel research in multiple domains of neuroscience (e.g., functional brain organization, primacy of social processes, dynamic processes interfering with brain plasticity, among others). This commentary is an attempt to reflect on provocative ideas as well as potential shifts in neurodevelopment research, using a few themes covered in this series.

2. Why adolescence?

The recognition of adolescence as a unique period of *neural* development is relatively new, and coincides, to a certain extent, with the advent of neuroimaging technology. Indeed, while neurodevelopmental research has a long history, the focus on the adolescent period is recent, principally for two reasons. First, whereas interest in *human* adolescence started more than a century ago (Hall, 1904) (see review Steinberg and Lerner, 2004), research on the neural underpinnings of the typical behavioral changes in adolescence emerged only in the 90′s with the advent of neuroimaging tools. Indeed, these tools, particularly magnetic resonance imaging (MRI), turn out to be quite suitable to study adolescents, but not as easy to use with children, making adolescence a prime topic of investigation and propelling research on adolescence to a new level. Second, animal neurobehavioral work requires extensive amount of time to train animals on behavioral paradigms that can be used to query brain-behavior relationships. Adolescence in animals is relatively short, which limits the ability to comprehensively assess adolescent phenotypes (e.g., fitting both training and testing within the limited time-span of adolescence). However, renewed effort has been deployed to study adolescence, in tandem with the rise of the adolescence neurodevelopmental field in humans.

Finally, although often considered in this series, findings about sex differences in the [development of the] adolescent brain seem to be generally weak, and segregated to discrete findings across a variety of domains (e.g., structural brain changes, effects of neurosteroids on social behavior). This area of research deserves a concerted effort, from both basic and human research, to provide a landscape of the fundamental aspects of brain neurophysiology that differ between males and females across development into adulthood. Because of the corpus of data on sex differences is too parcellated, this commentary will not address sex differences;

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http://dx.doi.org/10.1016/j.neubiorev.2016.06.017
0149-7634/Published by Elsevier Ltd.

although we believe it is a critical area of research that should be expanded.

3. Time for a paradigm shift

Almost every review of this series addresses the neural systems models (see review, (Shulman et al., 2016)), originally developed to account for the adolescents' propensity for risk-taking behavior, and, later, generalized to motivated behaviors at large. These heuristic models are based on two or three functionally distinct neural systems that integrate cognitive, emotional and motivational information to guide behavior (for review, (Shulman et al., 2016)). The basic premise is that the behavioral output of these 2- or 3-pronged models depends on the qualitative (e.g., positive valence bias) and quantitative (e.g., efficiency) level of function of each system. Critically, the function of these systems depends on their respective maturational level, and, ultimately, the generated behavior may be more or less determined by the emotional, motivational or cognitive responses of these systems. This being said, a key message that emerged from the consideration of these models is that it is time to go beyond such broad formulation, while integrating the new forays in neurobehavioral research.

New considerations have arisen in the past decade from multiple sources, such as progress made in neuroimaging methodology (e.g., resting state connectivity), upsurge in new research areas (e.g., social processes), new theoretical models from adolescence animal research (e.g., lock-in theory), or translation of neural mechanisms from the adult into the adolescence human literature (e.g., dual attention model). The present commentary will touch on a few of these directions, with the hope to spark potential new directions in adolescence research.

4. Research methodology: intrinsic functional connectivity

The review by Stevens (this issue) on functional connectivity covers this topic beautifully. The functional significance of resting state functional connectivity (rsFC) is fairly recent, first acknowledged in 2003 by Greicius et al. (Greicius et al., 2003). One of the foremost contributions of rsFC has been to provide a modeling of the overall organization of cerebral function across the whole brain. Notwithstanding the many processing and analytical issues still in need of resolution (see Stevens of this issue; (Poldrack, 2012), the ontogeny of brain organization stands out as a critical contributor of this global brain modeling. Naturally, the addition of a temporal developmental dimension to the mapping of how neural function is organized, together with knowledge on how emotion/cognition evolves with age, provides powerful insights into theoretical models of brain function.

For example, on a broad level, neurodevelopmental rsFC studies across adolescence suggest that maturational changes reflect, on the one hand, a strengthening and refinement of modular organization, through local networks becoming more restricted and specialized, and, on the other hand, an increased efficiency of integrative organization, through strengthening of long-range connections (see review (Ernst et al., 2015)). These two lines of maturational evolution tend to support a synergistic integration of the two broad views (modular and non-modular) of brain organization. The modular view proposes that the brain operates via a collection of autonomous parts, each holding a specific function that is content- and domain-specific (e.g., (Fodor, 1983)). The non-modular view (e.g., connectionism, (Gasser, 1990), holds the notion that the brain output is the global result of interactions among networks. The modular view is considered to be hard-wired, while the connectionist view leaves more room for experience-related, developmental influences. Neurodevelopmental findings, so far, argue for a model that integrates both views.

A more specific example concerns findings about neural networks, particularly those involved in the aforementioned neural systems models. Regarding the reward-related system, whose main node is centered on the striatum, preliminary findings suggest distinct maturational trajectories among striatal subregions (e.g., (Porter et al., 2015)). Regarding the ventral striatum, which is associated with motivation coding, a quadratic pattern was reported, describing a selective peak of iFC connectivity strength during adolescence. Regarding the dorsal striatum, preferentially associated with automatic motor responses, a steady curvilinear increase of iFC connectivity was associated with age. These trajectory patterns were interpreted as the emergence of a powerful, ready to use, network to code motivation in adolescence, in contrast to a progressive increase in automatic responses to the environment. This would fit well with the strong emotional drives that characterize adolescence, and the growing prominence of automatic responses. Automatic responses, which engage limited computing resources, allow more of these resources to be available for more complex or numerous tasks. Indeed, adult life is marked by the multiplication of tasks bearing financial, familial, occupational and societal responsibilities, whose performance is made possible by the increase in automatic processes.

Finally, a last significant advantage of rsFC is how it lends itself to big data approaches for large-scale fMRI. New large-scale studies are currently being launched to study longitudinally brain development and concomitant behavioral changes (e.g, Adolescent Brain Cognitive Development (ABCD) Study, http://www.addictionresearch.nih.gov/abcd-study). Big data are critical to understand individual differences in behavior and brain function, particularly across development. In the next 10 years, considerable strides in knowledge are expected, were the promises of big data approach to be fulfilled.

5. Upsurge in new research areas: social processes

Fostered by the ability to examine the neural correlates of behavior with the advent of fMRI technology, research in the biology of social behavior has exploded. The scale of the growth in this research area is well illustrated by the creation of the new discipline of social neuroscience, and the concomitant emergence in 2006 of the Journal of Social Neuroscience and the Journal of Social Cognitive and Affective Neuroscience. A major force in this new discipline has been the investigation of how the "social brain" unfolds with age. Here again, the added dimension of developmental changes to the study of the neural processes underlying social behavior could permit predicting causal relationships and building mechanistic models of brain-behavior translations.

The rise of social neuroscience has contributed to bring stronger awareness to the fundamental social metamorphoses that take place during adolescence (see Guyer and Blakemore of this series). These changes, well described in social psychology, have only recently made their way into the neuroscience inquiry (Blakemore, 2008; Nelson et al., 2005). The novel perspective of mapping social behavior to neural function raises loudly the notion of the biological determinism of these changes, which are shown to be well-preserved across species (Spear, this issue). Of course, environment and experience contribute to the shaping of the "social brain" during adolescence. However, the key features of social reorientation from family to peers, enhanced sensitivity to social stimuli, and romantic involvement might largely be anchored in both hormonal-dependent and hormonal-independent neural changes. Given that social influence permeates the direction and motivation of much of human goal-directed behavior, a key ques-