Developmental Review xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Developmental Review

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

Review

Rapid infant prefrontal cortex development and sensitivity to early environmental experience

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ARTICLE INFO

Keywords:
Prefrontal cortex
Brain development
Early experience
Infancy

ABSTRACT

Over the last fifteen years, the emerging field of developmental cognitive neuroscience has described the relatively late development of prefrontal cortex in children and the relation between gradual structural changes and children's protracted development of prefrontal-dependent skills. Widespread recognition by the broader scientific community of the extended development of prefrontal cortex has led to the overwhelming perception of prefrontal cortex as a "late developing" region of the brain. However, despite its supposedly protracted development, multiple lines of research have converged to suggest that prefrontal cortex development may be particularly susceptible to individual differences in children's early environments. Recent studies demonstrate that the impacts of early adverse environments on prefrontal cortex are present very early in development: within the first year of life. This review provides a comprehensive overview of new neuroimaging evidence demonstrating that prefrontal cortex should be characterized as a "rapidly developing" region of the brain, discusses the converging impacts of early adversity on prefrontal circuits, and presents potential mechanisms via which adverse environments shape both concurrent and long-term measures of prefrontal cortex development. Given that environmentally-induced disparities are present in prefrontal cortex development within the first year of life, translational work in intervention and/or prevention science should focus on intervening early in development to take advantages of this early period of rapid prefrontal development and heightened plasticity.

Introduction

Human brain development is not a linear process. Widespread recognition of the extended development of prefrontal cortex in human children has led to the overwhelming perception of prefrontal cortex as a "late developing" region of the brain. Mapping the protracted trajectory of prefrontal cortex development has been central to explanations of age-related changes in children's cognitive development. Rapid improvements in children's ability to regulate their behavior and emotions in a goal-directed fashion, commonly referred to as executive function (EF) skills (Fuster, 2002), rely on the development of prefrontal cortex (e.g. see Best & Miller, 2010). Slow refinement of prefrontal circuits necessary for decision-making and cognitive control is presumed to underlie the vulnerability of adolescents to making risky choices (Casey et al., 2011). Early individual differences in prefrontal-dependent behaviors also show predictive power over the lifespan; EF skills at preschool-age are predictive of long-term measures of well-being, including academic achievement, social competence, stress resilience, externalizing disorders, divorce rates, and adult body mass index (Ayduk et al., 2000; Casey et al., 2011; Eigsti et al., 2006; Mischel, Shoda, & Peake, 1988; Mischel, Shoda, & Rodriguez, 1989; Schlam, Wilson,

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https://doi.org/10.1016/j.dr.2018.02.003
Received 26 July 2017; Received in revised form 16 December 2017

Shoda, Mischel, & Ayduk, 2013; Shoda, Mischel, & Peake, 1990).

The characterization of frontal lobe as late developing has been useful in conveying to the general public one reason why children and adolescents think and behave differently from adults, and has even generated important dialogue regarding the application of developmental science to the field of law (Steinberg, 2009). It has also resulted in an unintended and unfortunate cost: a perception of prefrontal cortex as structurally and functionally undeveloped in young infants and toddlers. Neuroimaging techniques have advanced remarkably over the last 10 years and prefrontal cortex development can now be investigated in extremely young infants. These new studies purport that prefrontal cortex development advances most rapidly within the first two years of life, and that frontal lobe regions organize and direct cortical development in intriguing ways.

If prefrontal cortex development is uniquely precocious during early infancy, this has important implications for how children's early environments shape the development of frontal circuits important for complex cognitive skills. Animal models and human studies suggest that development of frontal lobe structure, function, and behaviors are permanently shaped by, and may be uniquely susceptible to, early adverse experiences. Fortunately, there is growing awareness across the scientific community, government organizations, private corporations, and the general public that children are not 'just resilient': adverse early experiences can lead to a myriad of harmful outcomes at both the individual and societal level. The extensive media coverage of the ACE (Adverse Childhood Experiences) Study has been particularly instrumental in demonstrating the importance of early experiences for health-related outcomes in adulthood (e.g. Anda et al., 2006). Vulnerable young children are exposed to adverse environments in high numbers; even in highly industrialized countries like the United States, one in five children live in poverty (Jiang, Ekono, & Skinner, 2016). Understanding the mechanisms via which experiences shape the development of prefrontal cortex is critical to the design of intervention programs that effectively ameliorate the impact of adversity early in life when the brain remains most malleable. Unfortunately, because the rapid development of infant prefrontal cortex has been underappreciated, our field lacks a comprehensive understanding of how experiences impact prefrontal development during the earliest years of life.

Aims and structure of review

The overarching goal of this review is to provide an integrated evidence base for considering how and why the rapidly developing infant prefrontal cortex is highly susceptible to variations in early life experience. "Early" prefrontal cortex development is conceptualized as approximately the first two years of life, as postmortem studies suggest that basic brain structure and connectivity is present by this age (e.g. Huttenlocher & Dabholkar, 1997) and deviations in brain development associated with developmental disorders can already be detected (e.g. Hazlett et al., 2011). In doing so, this review has three unified aims to advance our understanding of the impact of early adversity on prefrontal cortex development from a biopsychosocial perspective that are briefly summarized below.

Normative development of prefrontal cortex dependent behaviors has been well-described in children and adolescents (Best & Miller, 2010; Zelazo & Müller, 2002). However, the role of infant prefrontal cortex in guiding complex behaviors has only been recently summarized (Grossmann, 2013a, 2015; Hendry, Jones, & Charman, 2016) and has not been discussed in tandem with new neuroimaging research. As such, the first aim of this review is to provide a comprehensive summary of unique temporal and organizational features of prenatal and infant prefrontal cortex development, across neurobiological processes and metrics of structural brain development. In sum, the evidence presented suggests that prefrontal cortex shows particularly precocious development in the first years of life.

A rich legacy exists in our field of conceptualizing the child's environment (Bronfenbrenner, 1999) and considering its influence on brain development (Greenough, Black, & Wallace, 1987). In fact, multiple lines of research have already convincingly demonstrated the negative impacts of adversity on childhood or adult prefrontal cortex development, yet this work is not unified across risk factors. The second aim of this review is to provide a novel integration of research in three previously separate domains (maltreatment, poverty, and preterm birth) to illustrate that disparate types of early adversity result in a similar neural and behavioral phenotype of impaired prefrontal cortex development – and that these negative impacts can be observed even in the first years of life.

An understanding of the mechanisms via which early experience shapes prefrontal cortex development bolsters effective translation of this work. However, it is unlikely that one mechanism specifically explains how early experiences are biologically instantiated in later frontal lobe development. The third aim of this review is to identify candidate processes by which prefrontal cortex development may be impacted by the early environment. In doing so this review highlights gaps in our abilities to measure and quantify experience and its impacts on prefrontal cortex development and closes with a discussion of future directions and challenges.

Frontal lobe contributions to infant cognition

Commonalities in behavior of adult prefrontal lesion patients and young infants and toddlers are often used as evidence of the relative immaturity or "functional silence" of prefrontal cortex early in life (see Zelazo & Müller, 2002 for review of this argument). However, one of the first developmental neuroimaging studies demonstrated that metabolic activity in frontal lobe changes dramatically over the first year of life (Chugani & Phelps, 1986). To date, there has been a dramatic convergence of evidence from behavioral studies and the application of neuroimaging techniques to the study of cognition in young infants and toddlers to suggest that frontal lobe functioning is actively changing, even early in infancy. This section briefly highlights examples of diverse infant cognitive and socioemotional processes supported by early prefrontal cortex development to make the argument that even in the first year of life, infant prefrontal cortex is already implicated in a diverse set of cognitive behaviors. For more comprehensive recent reviews of prefrontal-dependent behaviors across the infancy and toddler years, please see Grossmann (2015) or Hendry et al. (2016).