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Stress and prefrontal cortical plasticity in the developing brain

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ABSTRACT

There is a large literature showing that stress in adulthood induces the production of stress hormones leading to a modulation of brain function, which is accomplished, in part, by changing the structure of neurons, especially in the hippocampus and prefrontal cortex, and these changes are correlated with behavioral change. Here we review the effects of preconception, gestational, and bystander gestational stress, as well as maternal separation on prefrontal cortex and behavioral development, largely in animal models. The general conclusion is that developmental stressors modify the organization of the prefrontal cortex in adulthood with results varying according to age at stress and region measured. It is likely that all of these stress effects are mediated by (re)programming of later gene activity in the brains of the offspring.

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1. Introduction

The modern idea that stress changes the body, including the brain, can be traced to Hans Selye in the 1930s. Selye, a physician, noticed that all of his patients, regardless of what they were hospitalized with, looked sick. He inferred that they must all be under physical stress that resulted in the release of stress hormones. This observation led him to search for a stress-processing mechanism, eventually leading to the concept of the hypothalamic-pituitary-adrenal system (HPA axis) (e.g., Harris, 1970; Selye, 1950, 1978). Although Selye's focus was on physiological stressors it became clear that psychological factors could also stimulate the HPA axis to affect the body and brain. Further, over the past 60 years it has become evident that the effects of stress are not only dependent upon the HPA axis but involves a two-way communication between the brain and the cardiovascular, immune, and other systems via neural and endocrine mechanisms (McEwen, 2006).

One of the effects of stress hormones is a modulation of brain function, which is accomplished, in part, by changing the structure of neurons, especially in the hippocampus (CA3 and the dentate gyrus), amygdala, and prefrontal cortex (Chattarji, Tomar, Suvrathan, Ghosh, & Mohammed, 2015). This review provides an overview of the effects of stress on the developing prefrontal cortex, with an emphasis on the effects in laboratory rats, which is the most-studied model to date. Understanding the effects of stress on the PFC has become increasingly interesting owing to its vulnerability to stress and the realization that the PFC has a significant role in many neuropsychiatric disorders (McEwen & Morrison, 2013).

1.1. Organization of the prefrontal cortex of rodents

In the 1960s the prefrontal cortex (PFC), which was often called the frontal granular cortex, was defined by both the frontal granular cell layer and the connections it made with the dorsomedial nucleus of the thalamus (MD) (Warren & Akert, 1964). Although these two definitions define a large region of overlap, the MD-projection cortex extends well beyond the frontal granular cortex of primates (Wise, 2008). Rodents do not have a frontal granular cortex but they do have an MD-projection area that was first described by Leonard (1969). This region does not include the frontal pole but rather includes regions along the anterior medial wall of the cerebral hemispheres as well as the ventral and lateral regions bordering the rhinal fissure (See Fig. 1). Later definitions of the rodent PFC expanded to include the connections with the amygdala and ventral tegmentum (Reep, 1984; Schoenbaum & Setlow, 2002) as well as the basal ganglia (Uylings, Groenewegen, & Kolb, 2003).

The degree to which the rat and primate "prefrontal" regions are homologous has been controversial (e.g., Wise, 2008), but there are clearly areas of the rat PFC that sub-serve functions similar to those in the primate (Brown & Bowman, 2002; Kolb, 1984). For our purposes we will assume that the medial prefrontal cortex of the rat (mPFC), including anterior cingulate (AC), prelimbic (PL), and infralimbic (IL) cortices house many functions similar to the medial or dorsolateral regions of the primate, whereas the orbitofrontal region (OFC) including the ventral, ventral lateral, lateral orbital regions (VO, VLO, LO) and the ventral and dorsal and agranular insular regions (AID) house functions similar to the orbital region of the primate (Uylings et al., 2003). Although an extensive discussion of the behavioral functions associated with the PFC is beyond the scope of this review, it will be useful to describe the general functions of the prefrontal regions (see also Wise, 2008). At a general level the dorsolateral region of primates plays an important role in working memory, particularly as it relates to certain executive processes such as the monitoring, sequencing, and planning of behaviors, as well as directed attention to

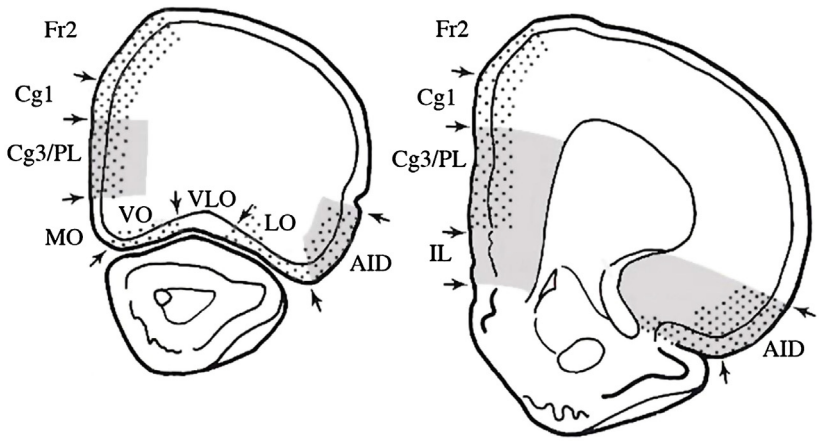

Fig. 1. The prefrontal cortex of the rat. Serial sections through a rat brain showing different cytoarchitectonic regions (Zilles, 1985, nomenclature). Dotted areas receive projections from MD; gray areas receive projections from the amygdala. Abbreviations: Cg1, cingulate area 1; Cg3, cingulate area 3; Fr2, frontal area 2 IL, infralimbic; AID, agranular insular; MO, medial orbital; PL, prelimbic; VLO, ventral lateral orbital; VO, ventral orbital, LO, lateral orbital. (Modified and adapted from Reep, 1984).

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