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REVIEW

Fetal programming by maternal stress: Insights from a conflict perspective

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Summary Maternal stress during pregnancy has pervasive effects on the offspring's physiology and behavior, including the development of anxious, reactive temperament and increased stress responsivity. These outcomes can be seen as the result of adaptive developmental plasticity: maternal stress hormones carry useful information about the state of the external world, which can be used by the developing fetus to match its phenotype to the predicted environment. This account, however, neglects the inherent conflict of interest between mother and fetus about the outcomes of fetal programming. The aim of this paper is to extend the adaptive model of prenatal stress by framing mother-fetus interactions in an evolutionary conflict perspective. In the paper, I show how a conflict perspective provides many new insights in the functions and mechanisms of fetal programming, with particular emphasis on human pregnancy. I then take advantage of those insights to make sense of some puzzling features of maternal and fetal physiology and generate novel empirical predictions.

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1. Introduction

From conception to delivery, mammalian fetuses are exposed to a continual stream of chemical signals carried by maternal blood. Among these signals, a prominent role is played by the hormones associated with the stress response. A growing amount of evidence from human and nonhuman studies shows that maternal stress during pregnancy exerts pervasive, long-lasting effects on the development of the fetal nervous system — and, ultimately, on the offspring's physiology and behavior. In psychology and medicine, the classic approach to maternal stress has been to treat it as a disruptive influence on fetal development and a net risk factor for future pathology (e.g., Van den Bergh et al., 2005; Weinstock, 2005; Mennes et al., 2006). In marked contrast with this view, the last decade has witnessed the emergence and consolidation of an alternative model, based on evolutionary biology, in which fetal programming by maternal stress is seen as an evolved adaptive process (e.g., Matthews, 2002; Kaiser and Sachser, 2005, 2009; Kapoor et al., 2006; Talge et al., 2007; Glover, 2011; Pluess and Belsky, 2011; Sandman et al., 2012).

At the core of the adaptive model is the idea that maternal stress hormones carry useful *information* about the state of the external world — for example its safety and predictability, the presence of threats, and so forth — that is otherwise inaccessible to the fetus. The developing fetus can use this information as a "forecast" of the environmental conditions it will eventually face after birth, and start adjusting its physiological and behavioral profile to match the requirements of the world it will probably encounter. In this perspective, fetal programming is an instance of adaptive developmental plasticity (West-Eberhard, 2003). More specifically, it can be considered a *predictive adaptive response*, as the fetus makes use of present cues to entrain the development of alternative phenotypes that will become adaptive in the future (Hinde, 1986; Belsky et al., 1991; Bateson et al., 2004; Gluckman and Hanson, 2004; Gluckman et al., 2005).

The adaptive model of prenatal stress is a powerful application of evolutionary theory to early development. By uncovering the ultimate logic of physiological processes, it helps make sense of a broad array of empirical findings. Nevertheless, a crucial piece is still missing from the puzzle: the inherent *conflict of interest* between mother and fetus about the outcomes of fetal programming. The aim of this paper is to extend the adaptive model by framing mother-fetus interactions in an evolutionary conflict perspective. In the remainder of this section I will briefly review the behavioral and neurobiological outcomes of prenatal stress, introduce the theory of parent-offspring conflict, and discuss some conflictual aspects of mother-fetus interactions. In Sections 2 and 3, I will show how a conflict perspective provides many new insights in the functions and mechanisms of fetal programming. I will then take advantage of those insights to make sense of some puzzling features of maternal and fetal physiology, and generate novel empirical predictions.

1.1. Behavioral outcomes of prenatal stress as adaptive responses

A general pattern, observed in rats and nonhuman primates alike, is that the offspring of prenatally stressed mothers tend to show increased anxiety-like behaviors and reduced attentional span. They also show higher basal activity of the hypothalamic-pituitary-adrenal (HPA) axis, as well as potentiated and prolonged HPA responses to stressors (reviewed in Van den Bergh et al., 2005; Talge et al., 2007; Cirulli et al., 2009; Flinn et al., 2011). While the behavioral effects of prenatal stress may vary across species and between males and females, the big picture shows a consistent tendency toward hyper-responsivity. As an example of a more complex pattern, the offspring of guinea pigs exposed to social stressors during pregnancy show female masculinization and male infantilization (i.e., display of behavioral patterns typical of very young males). These behavioral outcomes can be adaptive because of the different implications of social instability for the males and females of this species (Kaiser and Sachser, 2005, 2009).

These disparate findings can be usefully integrated within the framework of life history theory (e.g., Kaiser and Sachser, 2005). In this perspective, information about key parameters of the environment (safety, predictability, resource availability, social competition, and so forth) can be used to inform the organism's reproductive strategy, for example by altering the trade-off between reproduction and survival, current and future reproduction, quality and quantity of offspring, or mating and parenting effort (see Belsky