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Review

Reproductive experiential regulation of cognitive and emotional resilience

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ABSTRACT

Adaptation virtually defines survival. For mammals, arguably, no other developmental milestone is exemplified by – nor more reliant on – the sudden and dramatic behavioral alterations observed in the maternal female, which rapidly must undergo change in order to express a large suite of proper and effective maternal behaviors. As pregnancy progresses, as well as during lactation, when pup cues are rich and rampant, the female is literally transformed from an organism that actively avoided offspring-related signals, to one highly motivated by those same cues to build nests, be attracted to pups and to retrieve, group, groom, crouch-over, care for, and protect, the young. Ancillary responses such as reference memory, spatial learning, foraging (including predation), and boldness improve in mothers compared to virgins. Such modifications arise early and are persistent, with neural benefits that last well into senescence. Evolutionarily, such enhancements have likely reduced the maternal burdens associated with sheltering and feeding the vulnerable young; collectively, this strengthens the mother's/parent's reproductive fitness and that of the pups in which all this effort is invested. Of the many behaviors that change as a function of pending or concurrent maternity, therefore, what is the role of modifications to resilience, the ability to withstand the numerous, unpredictable, and threatening environmental events that the mother/parent must daily, indeed, multiply daily, face and thwart in order to bring the offspring from pups to fully functioning adults. We explore these questions, and their connections, here in a multi-disciplinary manner focused on the constellation of change that summates to fundamentally alter the female for the rest of her life. Behavior, brain, neurochemistry and genes are fundamentally changed as the substrate for reproduction unfolds and expresses its inherent plasticity.

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1. Maternal brain-induced resiliency

In the current manuscript we will argue for, and present evidence strongly suggesting, that mothers are made, not born. Further, it is apparent that there is a lot of building going on. For the maternal mammal, the construction site includes the central nervous system, which is acted upon by a relentless cascade of pregnancy-induced hormonal stimuli. Such actions render the sensitive neural substrate both motivated toward, and responsive to, the offspring, whose own stimuli may maintain what the hormones began (Kinsley et al., 1999; Lambert et al., 2005). The new mother experiences a most significant and transformative event during this conversion from virgin to mother, nulliparity to primiparity, self- versus other-directed. Along with the creation of a litter bearing half of her genes, the episode graphically demonstrates the inherent plasticity of the female brain, a neural flexibility that is expressed only following the onset of pregnancy. Given the enormity of the changes occurring, we believe that this period represents a developmental epoch every bit as significant as sexual differentiation and puberty, which precede it. “M” may be “for the many things a mother does,” but it is the “M”odifications in her neural substrate that lead to significant augmentations in her survivability, the attention devoted to her pups, and hence, their survival.

1.1. Nature gives moms a “boost,” which likely translates into behavioral economies

For any new mother, the adjustment from nulliparous to parous requires a throng of modifications, especially in mammals. For the female rat, provisioning her nest and its new inhabitants takes precedence, where finding and acquiring food or subduing prey is integral to everyone surviving another day; but the process of reproduction begins almost immediately after menarche. The obstacles arrayed against successful reproduction, however, are formidable and many. They range from properly functioning physiology; the discovery and acquisition of a suitable mate; actual mating; a healthy, event-free pregnancy; development of the embryos/fetuses; full and effective parturition, itself freighted with multiple dangers, and the healthy delivery of the infants. Then, should the offspring be born successfully, the mother’s work only just begins. It appears, though, based on a raft of converging data, that evolution has bestowed on the mother some incremental advantages that help her adapt to the short-term but intractable obstacles arrayed before her.

For example, in order to manage a likely vulnerability-laden nest (it is a nest, after all, not a fortress) and a group of insistent young, the new mother forges a Faustian bargain, a balance of costs and benefits: does she stay or does she go? Hazards/predators await both her young and her should she leave the relative safety of the nest and her helpless offspring to forage for food and resources. Equally hazardous, she could remain ensconced in her nest, safe, protected, but guaranteed a slow, mutual, and costly fate for pup and mother alike. Enter maternal nervous system adaptation – and the many accompanying behavioral solutions which ensue, leading to greater survivability. Her decision is aided by positive modifications to behavioral economies, that is, tiny savings in time, effort, resources, etc., that accrue and contribute to the survival of mother and young. Maternal plasticity, therefore, is insurance against genetic oblivion.

Most researchers have looked at maternal behavior per se, as a unidirectional phenomenon, ignoring the reverse events. That is, the mother certainly cares for young, and the benefits accrue to offspring alone through the labors of the mother. We, however, have taken a different tack as we examine the maternal–infant interaction. We realized that the offspring could be viewed as a form of enriched environment, providing the mother’s brain with a flood of rich stimuli. For example, beginning with the pregnancy, the levels and length of exposure to the powerful hormonal events are themselves capable of significant anatomical alteration. Elevated levels of estradiol, progesterone, prolactin, relaxin, and other hormones are released for extended periods, acting on a malleable brain and nervous system very sensitive to them, an event that recalls a heavy rain falling on a fertile plain. Add to this mix a complicated cascade of neuropeptide events including oxytocin, neuropeptide-Y, substance-P, cholecystokinin, galanin, etc. (Josefsson et al., 2010), likewise indicate a volatile neurochemical landscape absorbing and responding to these ligand signals. Thus, many of the neuroanatomical changes reported during pregnancy (Keyser et al., 2001; Kinsley et al., 2006, etc.) are assuredly due to the endocrine and related events of pregnancy literally making their mark.

The many hormonal and other actions that accompany pregnancy exert multi-level changes and thrust plasticity upon the female’s brain, which in turn, enhances learning and memory. It is a complicated story, however, that begins with the normal plastic changes that mark the female’s estrus cycle, and which presage the even greater modifications that occur with pregnancy and beyond. A brief description of these effects is illustrative of the greater ones to follow. For example, Berry et al. (1997) examined learning related to hormonal status in the female rat. These subjects’ spatial navigation was assessed at particular points in the estrus cycle that corresponded to low (viz., during estrus) and high (proestrus) circulating estrogen levels. Following water-maze training, the rats were taught the location of an escape platform in the maze in a single session of eight training trials. Estrus and proestrus rats were indistinguishable on all behavioral measures, irrespective of their hormonal status during the task. The authors conclude that rapid learning and retention for spatial information over a relatively short interval may be reserved independent of the morphological alterations in hippocampal dendritic spine density that normally occur over the span of the estrus cycle. There have been reports of estrus-cycle/hormonal effects on other, more molecular/functional aspects of learning. For instance, Woolley et al. (1990a,b) recorded electrophysiological alterations in neuronal activities that paralleled stage of the estrus cycle, with proestrus having the greatest degree of change. Warren et al. (1995) reported that long term potentiation (LTP), a purported mediator of learning and memory (Kandel et al., 1991), varied across the estrous cycle in rats. The greatest degree of potentiation occurred during the afternoon of proestrus, also a time that others had reported as having the highest degree of dendritic spine and synapse number