

Editorial overview: Development and behavior

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Frances A Champagne is an associate professor of Psychology at Columbia University and member of the Columbia University Center for Integrative Animal Behavior. She is also a Sackler Scientist in the Columbia Sackler Institute for Developmental Psychobiology and a faculty member in the Columbia Population Research Center. She received her PhD in neuroscience from McGill University in 2004 and was a post-doctoral fellow at the Sub-Department of Animal Behavior at the University of Cambridge from 2004 to 2006. Professor Champagne is an internationally recognized expert in the field of behavioral epigenetics through her research on the developmental impact of prenatal and postnatal environmental exposures on neurobiological and behavioral outcomes. This research has highlighted the epigenetic plasticity of the developing brain. Importantly, Professor Champagne's research has also illustrated that there are transgenerational consequences of early life experiences. This work has contributed to an expanded notion of the mechanisms of inheritance. Though primarily based in laboratory animal models, Professor Champagne's research is increasingly integrating studies in human populations. In 2007, Professor Champagne was awarded the National Institutes of Health Director's New Innovator Award, and her research is funded by the National Institutes of Environmental Health and the National Institutes of Mental Health.

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Early life experiences can have a profound impact on developmental trajectories, with implications for later life biobehavioral outcomes. This phenomenon is highly conserved across species and occurs in response to a broad range of environmental signals. The papers in this issue highlight the influence of experiences occurring during sensitive periods in early development, including prenatal, postnatal and adolescence, on behavioral development, with a focus on mechanisms, theoretical frameworks, and implications for health, welfare, and fitness.

Organisms are highly sensitive to stress and adversity in their environments and this sensitivity allows an individual to react and coordinate physiological and neuroendocrine systems to promote survival. However, the adverse effects of early life exposure to stress observed in both natural populations and in the laboratory suggest that these physiological adaptations come at a significant cost when experienced developmentally. In *Bell et al.*, the impact of maternal and paternal stress exposure is considered within the three-spined stickleback (*Gasterosteus aculeatus*). Pre-fertilization maternal exposure to predator stress results in altered predator response and learning behaviors in offspring, likely mediated through maternal cortisol levels in eggs. In male sticklebacks, predator stress impacts post-fertilization paternal care of offspring, resulting in poorer growth and reduced activity levels. *Bell et al.* discuss the potential of maternal–paternal interplay in this model system and consider the adaptiveness of the effects of parental stress. The role of stress is also explored in mammals using rat and mouse models. *Cartier et al.* examine the consequences of pre-natal exposure to stress, whereas *Brydges* focuses on post-natal developmental time-points, specifically pre-pubertal periods of stress. Both explore the possible role of epigenetic changes at key genetic loci as mediators of the consequences of stress at these critical time-points. Additionally, both these papers also explore the ramifications for human mental health in later years, with *Cartier et al.* discussing the use of synthetic glucocorticoids as a possible preventative treatment.

During prenatal development, hormones play a critical role in shaping the developing organism. In their paper, *Rodenburg and de Haas* explore how maternal hormones in the egg of laying hens shapes the developing chick's later behavior. In particular, *Rodenburg and de Haas* examine the interplay with genetics and how the action of these hormones can result in inter-generational effects. In the paper by *Berenbaum and Beltz*, the association between prenatal androgen levels and the emergence of sex differences in behavior is discussed. Studies in humans suggest that over-production or insensitivity to androgens is predictive of cognition, behavior, and neural

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responses and Berenbaum and Beltz suggest the importance of considering both prenatal androgens and postnatal socialization in understanding the origins of sexual differentiation. This process of sexual differentiation and emergence of sexual dimorphism is also highlighted by [Palanza *et al.*](#) who discuss evidence for the disruption of these processes by prenatal and postnatal exposure to the endocrine disruptor bisphenol A (BPA). Focused primarily on studies in rodents, the findings suggesting long-term behavioral and neurobiological consequences of BPA have implications for human development and similar to Berenbaum and Beltz, this paper suggests the importance of considering the interplay between direct exposure to BPA and variation in the social environment.

The importance of nutrition in gestation for the developing brain is well documented, and here [Overeem *et al.*](#) examine the specific role played by vitamin D. As they highlight, vitamin D deficiency has been linked to a number of neurological and psychiatric disorders in humans. Using both rat and mouse models, Overeem *et al.* show that the timing of vitamin D deficiency is critical, with different outcomes for developmental and adult deficiency.

The quality of social interactions occurring postnatally can have a profound developmental influence. In this issue, [Hane and Fox](#) describe the neuro-behavioral consequences of variation in the quality of the early care environment (ECE), consisting primarily of the quality and quantity of mother-infant interactions. Low quality of the ECE, observed in newborns placed in neonatal intensive care units (NICU) or institutionalized infants, can have epigenetic consequences and result in heightened stress reactivity. In their paper, Hane and Fox describe these outcomes from the perspective of *phenotypic plasticity* — the ability to adapt to the demands of the environment — and *context-dependent reactivation* — the enhanced reactivity (e.g. stress responsivity) observed in individuals who have experienced low ECE and are later re-exposed to adversity. This paper illustrates the value of integrating an ecological and neurodevelopmental perspective when considering the impact of early life environments. While Hane and Fox focus primarily on social adversity in rodent models and in humans, the impact on non-human primates is reviewed by [French and Carp](#). In this paper the impact of early-life social adversity (ELSA) on macaques (*Macaca* spp.), squirrel monkeys (*Saimiri sciureus*), and marmosets (*Callithrix* spp.) is described and illustrates the effect of disrupted social environments of affective and social behavior, cognition, and neurobiological outcomes. This research also highlights the notions of programming and phenotypic plasticity discussed by Hane and Fox.

The impact of early rearing experiences is further explored in the paper by [Richardson *et al.*](#), which describes how exposure to maternal separation impacts the development of fear memory systems. This paper discusses the neurobiological mechanisms that may account for the effects of these early life experiences and treatment strategies that focus on brain–gut interplay. Richardson *et al.* illustrate the acceleration of developing fear memory systems in response to early life adversity, a theme further explored by [Callaghan and Tottenham](#) who discuss emerging evidence for acceleration in the development of the neural circuits regulating emotion regulation and learning in response to early life deprivation of parental care. This research indicates that the maturation of connectivity between the amygdala and medial prefrontal cortex may be accelerated in pace (becoming adult-like sooner) when individuals are exposed to early life social deprivation — an adaptation that increases risk of psychopathology in later life. [Grindstaff](#)

explores how immune activation during this early social period is important for adult behavioral outcomes in a number of bird models. Immune challenges, caused by ectoparasites, such as mites, and/or viruses and other infections, can result in the development of different patterns of a wide-range of behaviors including dispersal, song, and learning. Grindstaff finishes by discussing if these behavioral changes are simply consequences of the pathological process, or whether they are adaptive modifications.

The sensory experiences occurring during development serve to refine and shape subsequent sensitivity and perception of auditory, visual, and somatosensory stimulation. The impact of light exposure during development is reviewed by [Fonken and Nelson](#). Light exposure at night occurring at any age can disrupt circadian rhythms with physiological and behavioral consequences. However, when this exposure occurs during development, the maturation of the suprachiasmatic nuclei (SCN) within the hypothalamus is altered and studies in rodents suggest there may be lifelong effects on sleep–wake rhythms, metabolism and mood. These lifelong effects of early life sensory experiences are likewise observed in response to neonatal exposure to pain described in [Victoria and Murphy](#). This developmental experience is characteristic of the early life environment in preterm infants, and

Victoria and Murphy discuss evidence from laboratory studies in rodents and longitudinal studies in humans for the sensory, cognitive, emotional, and neuroendocrine outcomes associated with pain exposure and suggest that the short-term adaptations that occur in response to painful stimuli in development may lead to maladaptive behavioral and neurobiological outcomes.

Sensory experiences are also addressed by [Ljubičić *et al.*](#) who surveys the development of vocal communication in a range of species, including humans, but with a focus on songbirds. The review explores the recent methodological advances that have allowed the tracking of specific social influences on vocal learning. As [Ljubičić *et al.*](#) discuss, this has expanded our understanding of the variety of social influences on song development. Finally these ideas are expanded upon by [Boawitz and Shafiq](#), who provide an overview of computational models of social influences on development and learning in children.

Overall, the papers in this issue elegantly demonstrate the broad range of experiences and species in which the effects of early life environments have been explored — giving insight into the biological mechanisms that account for the lasting impact of the environment and the theoretical frameworks that may help us to better predict the adaptiveness of this plasticity.