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# Myron Hofer's synthesis of evolution and development: A commentary

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# Myron Hofer's synthesis of evolution and development: A commentary

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Myron Hofer's integration of research and theory into a synthesized view of evolution and development is a powerful and elegant achievement. He argues that the epigenetic revolution provides a way to integrate evolution and development, which were considered separate processes for most of the twentieth century. Moreover, Hofer argues that our understanding of the effects of early experience gleaned through animal models provides a new, rich biological underpinning to the psychoanalytic theory of the effects of early experience – a way to re-integrate biology and psychoanalysis. I comment on several topics which directly relate to my own work on mother-infant communication: the role of ethology; Hofer's "hidden maternal regulators" in attachment, and how they can be translated into my work on the origins of attachment; Hofer's use of animal models to conceptualize early human mental development and a similar argument for the origins of human infant procedural representations in the work of Daniel Stern, and in my work with Stern and Lachmann.

**Keywords:** animal models of mother-infant interaction; attachment; epigenetics; evolution and development

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In this important paper, Myron Hofer tells us the story of his own intellectual development. He takes us with him on the road to his discoveries, sharing his own questions, uncertainties, and evolving understanding. He leads us carefully through his personal narrative of theory and research, his own and that of others.

Hofer shows us how the animal models of the effects of early experience can inform and enrich psychoanalysis. He argues that research on the psychobiology of mother-infant interaction reconfirms, as well as powerfully elaborates on, the basic psychoanalytic premise that early experience has long-lasting effects in development. But Hofer does even more in this essay: he offers us a new view of development, one that is inextricably intertwined with evolution.

## Twentieth-century history of biology

The history of biology in the twentieth century is an essential backdrop to Hofer's story. In Freud's era at the end of the nineteenth century, biology still considered early experience to be a major force in development. But in the early twentieth century, a paradigm shift occurred: genes were thought to pass over unchanged to the next generation. There was no basis for interactions with the environment to affect development. Hofer argues that this paradigm shift conceptually disengaged development from evolution.

Remarkably, it is only in the last two decades that research on epigenetics has shown the interacting roles of genes and environment in the processes of development. This research shows that early experience affects development into the next generation and beyond. Explicating this research, Hofer shows how development and evolution have become re-integrated.

## Importance of ethology

Early in the twentieth century, Hofer argues, developmental psychology and psychoanalytic developmental theory operated without substantial links to evolutionary or developmental biology. Hofer credits ethology, which burgeoned mid-century, with the important role of holding open an interest in the development of mind and behavior from a biological perspective. John Bowlby's (1969) work on attachment is a key example of this perspective.

Hofer describes many influences on his intellectual development. As a psychoanalytically oriented psychiatrist, he was influenced by a psychodynamic understanding of the long-term effects of early experience and the importance of the parent-child relationship. He was also influenced by a cellular theory of learning and emotional behavior, and by Harry Harlow's work on the effects of maternal deprivation in rhesus monkeys. But he gives the most credit to Ethel Tobach and the field of ethology which he studied at the American Museum of Natural History in the Department of Animal Behavior. Hofer was drawn to animal models in his search for a better

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understanding of the biological basis for the effects of early experience.

In my own area of research, mother-infant face-to-face communication, ethology was a critical intellectual influence. This research emerged around 1970 spearheaded by Stern (1971), Brazelton (Brazelton, Kozlowski, & Main, 1974), and Trevarthen (1977). Ethology's method of the careful description of behavior in the animal's natural habitat inspired methods of second-by-second microanalysis of film and videotape of mother-infant interaction. This research tradition viewed early development from the point of view of behavior: the coordination of mother and infant behaviors in many complex forms. Because many of the key researchers were also psychoanalysts (for example, Beebe & Stern, 1977; Lyons-Ruth, 1999; Sander, 1977; Stern, 1971, 1985), this research did inform a psychoanalytic theory of early development. Thus, from the 1970s on, psychoanalysis was not completely divorced from a theory of development based on careful observation of mother-infant behavior. However, only recently has this area of research forged strong links to developmental biology (see, for example, Atzil, Hendler, & Feldman, 2011; Geva & Feldman, 2008; Ham & Tronick, 2006, 2009; Kaplan, Evans, & Monk, 2008; Schechter et al., 2004; Schechter et al., 2012). Note that Hofer is a co-author on both Schechter et al. (2004) and Schechter et al. (2012).

## Hofer's hidden regulators

Hofer's work in developmental psychobiology since the 1970s laid a foundation for the more recent epigenetic revolution. Hofer became interested in processes of attachment and separation in animal models of mother-infant interaction. His discovery of "hidden maternal regulators" in the mother-infant interaction provided a developmental mechanism that could mediate the long-term effects of early experience (Hofer, 1994, 2006).

Hofer studied the effects of maternal separation in two-week-old rats and broke the process down into its component sub-processes. For example, an infant rat's response to separation from the mother is based on many subcomponents, such as nutrients, warmth, odor, tactile stimulation, and the timing or rhythm with which these occur, all of which have different functions in the system. Hofer described these subcomponents as regulatory processes "hidden" within the mother-infant interaction.

Hofer came to question the concept that the separation response of the infant pup is a response to the disruption of an emotional "bond." Instead, he came to view it as the result of the removal of a number of different behavioral and biological interactions with the mother. He argues that the concept of attachment is a general one, referring to a cluster of behavioral and physiological sub-processes that maintain and regulate sustained social relationships.

Hofer's work underscores the importance of carefully examining the details of how the more general concept of attachment might operate. This is the focus of my work as well, examining the origins of 12-month infant attachment in 4-month videotaped mother-infant interaction (Beebe et al., 2010). We code mother and infant behaviors separately, on a 1s time-base. A remarkable complexity and differentiation were documented in the 4-month interaction patterns which were precursors of infant attachment classifications at 12 months. The subcomponents of the communication system that we analyzed were (1) partner (mother behavior/infant behavior), (2) type of measure (behavioral frequency/behavioral contingency measured by time-series approaches), (3) type of contingency (self/interactive), and (4) modality of communication (attention, emotion, spatial orientation, and touch). The prediction of attachment required a careful consideration of all these subcomponents. Our results can be seen as examples of Hofer's concept of hidden regulators, various forms of behavioral regulation in different subcomponents of the system.

Hofer proposed that hidden regulators within the mother-infant relationship might constitute a developmental mechanism that could mediate the long-term effects of early experience. In the mid-1970s, a fascinating set of experiments with Sig Ackerman on early weaning showed that early experience could extend to the next generation. Early weaning withdrew all "maternal regulators" at once and increased the susceptibility of the rats as adults to gastric ulcers. They understood the result as the premature loss of all maternal regulators at once, which affected a number of the offspring's physiological and behavioral systems. Then Neil Skolnick, a clinical psychology intern (and now a practicing psychoanalyst), proposed that the early weaned rats might be less effective mothers, producing a vulnerability to ulcers in their pups, even if the pups were normally weaned. He was right.

But then a "cross-fostering" experiment showed something even more complex. The offspring of early-weaned mothers were cross-fostered and raised by normally weaned mothers. These cross-fostered offspring still developed the vulnerability to ulcers and stress (Skolnick, Ackerman, Hofer, & Weiner, 1980). Thus, the vulnerability to ulcers in the offspring could not be due to a change in the early-weaned mothers' behavior. The researchers speculated that the vulnerability might have been transmitted during the affected offspring's embryonic and fetal development. But, in retrospect, I speculate that it was an epigenetic effect.

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## The epigenetics revolution

With epigenetics, the interaction between organism and environment re-enters as central. In response to varying environmental conditions, Hofer explains, "when cells divide, some genes in the daughter cells become silenced whereas other genes become activated" (Hofer, 2014, this issue). This regulation of gene activity by messenger molecules results from minute local changes on chromatin.

Michael Meaney and his colleagues have played a central role in the epigenetics revolution. They showed that high- versus low-licking and grooming rat dams produce long-term changes in anxiety and corticosterone in the adult offspring and even the grand pups. Different maternal levels of licking and grooming alter the chromatin marks on specific genes, silencing some genes and activating others. These effects occur even when the pup is cross-fostered by another mother.

Champagne and Meaney (2006) subjected pregnant female rats to stressful conditions. These mothers licked and groomed their newborn pups less. These pups were thereby pre-adapted to harsh conditions. As adults they were more aggressive, less anxious, and less likely to show extreme responses to stress, a survival advantage. This epigenetic process retains changes that equip the offspring in advance for predictable environmental threats.

However, as Suomi (1999) noted, not all transgenerational effects are genetic or epigenetic.

## An evolutionary developmental process

The epigenetics research provides a mechanism for transgenerational effects of early maternal experience, which can be shown to alter maternal behavior in the grand pups of the original mothers. Hofer describes this as an *evolutionary developmental process*.

Hofer concludes in this essay,

> The mother-infant relationship is thus in a position to function as a matrix and template to guide and shape developmental patterns in her offspring. And the adaptations of immature animals to the early environments created by their parents are *evolutionarily-shaped functions of development* [italics added] …. changes in the biological substrates of maternal behavior that are induced in the mother by stresses in her life may become 'targets' for evolutionary selection … Such developmental variations are potentially heritable through altered maternal behavior being passed on to the next generation. (Hofer. 2014, this issue)

Hofer argues that, until the epigenetics revolution, evolution and development were considered separate processes. Now we are beginning to understand that epigenetic mechanisms are one source of variation generated by evolution. Genetic potentials interact with specific environments, activating and silencing specific genes. These epigenetic mechanisms affect the ways that the environment influences development. As Hofer argues, "development and its capacity to generate variation is seen as a major participant and even a cause of evolution" (Hofer, 2014, this issue). Because of epigenetics, we now have a different understanding of evolution, of development, and how they interrelate.

## Animal models and early human mental development

Hofer describes the process of his own thinking:

> We could not easily imagine a level of biological processes that could mediate what seemed to be 'innately human' behavior … humans operated at the level of affect, memory, and inner experience … whereas lower mammals … were driven by instincts, reflexes, and … 'fixed action patterns'. (Hofer, 2014, this issue)

But now Hofer thinks of human mental life as having emerged from the behavioral and physiological processes he observed in his research. The same biological/behavioral processes he observed in laboratory animals continue to underlie infant mental development as well as the psychological processes in psychoanalysis.

Hofer argues that the infant rat's attachment bond,

> consists of a set of memories and associated feeling states, laid down through specific interactions with its mother. These can be viewed as constituting a simple mental representation of the sensations, contingencies, physiological/emotional states, and actions previously experienced. Thus, it is highly likely that a human baby, and even a fetus learning to recognize its own mother's voice … also starts to form internal object representations very early, and in a roughly similar way: through associative learning processes. (Hofer, 2014, this issue)

A similar argument for the origins of infant procedural representations was made in an early paper by Beebe and Stern in 1977:

> … a spectrum of interpersonal object experiences along the dimensions of engagement-disengagement will be examined. By 'object experiences' we mean the infant sensorimotor experience of modulating or regulating his own behavior in relation to the behavior of an interpersonal object…. It will be proposed that the behaviors constituting the gradations of the engagement-disengagement spectrum … are the early building blocks for later internal representations. (Beebe & Stern, 1977, p. 36)

> The hypothesis is that the dominant modes of the ongoing relationship, based on detailed analysis of behavioral organization and mutual regulation, will prevail in the internalized representation of the relationship… what is initially internalized is not an object per se, but an 'object-relation': actions of self with reference to actions of object. (Beebe & Stern, 1977, p. 52)

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Stern went on to elaborate this argument for the origins of early infant procedural representations in a series of elegant articles and books, of which the best-known is *The Interpersonal World of the Infant* (Stern, 1985). Stern and Hofer were lifelong colleagues and friends. Beebe and Lachmann also went on to elaborate this argument in a series of articles and books (for example, Beebe & Lachmann, 1988, 1994, 2002, 2013). Infant learning of *contingencies* between his behavior and that of the mother, or contingencies within his own behavior and within the mother's behavior, have figured prominently in our empirical work on infant procedural representations and the origins of attachment (Beebe et al., 2010). This body of empirical work has influenced psychoanalysis over the past several decades.

However, Hofer emphasizes that, once formed, these infant mental representations may act as superordinate regulators of biological systems. In this way, Hofer links the human work on the origins of infant procedural representations to the animal work. Along the lines that Hofer suggests, recent research links mother-infant interaction patterns with biological processes, such as physiological measures of stress, genetic processes, and hormones (see, for example, Atzil et al., 2011; Ham & Tronick, 2006; Schechter et al., 2004). This work is just beginning.

## From animal to human

Hofer argues that animal models of the effects of early experience have huge relevance for human development. Are there any limits to this argument? Suomi (1999), for example, suggests that this argument may be easier to make in the simpler animals. It is difficult to create human studies that parallel the animal models, such as cross-generational effects from documented early experiences of a mother to effects on her child, not to mention grandchild. Nevertheless, new developments in this arena are very likely on the horizon.

Currently there is human research that parallels in more limited ways the animal models that Hofer discusses. As one example, Hane and Fox (2006), inspired by the work of Meaney, showed that ordinary variations in maternal caregiving behavior predicted biobehavioral markers of infant stress reactivity. They conclude that their findings offer evidence to suggest that the quality of the early caregiving environment yields phenotypic changes in the systems involved in regulation of stress, and that these effects closely parallel the rodent epigenetic models.

A large body of human research documents the effects of early experience on infant attachment outcomes (see Cassidy & Shaver, 2008 and De Wolff & Van Ijzendoorn, 1997, for reviews). A cross-generation transmission model shows that maternal representations of attachment assessed in the last trimester of pregnancy predict subsequent infant-mother attachment patterns at one year (Fonagy, Steele, & Steele, 1991). A remarkable series of longitudinal studies in the last decade show that infant attachment status sets a trajectory in development that predicts young adult outcomes (for example, Dutra, Bureau, Holmes, Lyubchik, & Lyons-Ruth, 2009; Fraley, 2002; Grossmann, Grossmann, Winter, & Zimmermann, 2002; Lyons-Ruth & Jacobvitz, 2008; Shi, Bureau, Easterbrooks, Zhao, & Lyons-Ruth, 2012; Sroufe, Egeland, Carlson, & Collins, 2005; Waters, Merrick, Treboux, Crowell, & Albersheim, 2000). Our own work shows that the degree of vocal rhythm coordination in infancy predicts 1-year, 4-year, and 21-year attachment outcomes (Beebe et al., 2013; Jaffe, Beebe, Fedstein, Crown, & Jasnow, 2001; Markese, Beebe, Jaffe, & Feldstein, 2008). None of these studies, however, use a documented pattern of early experience in one generation to predict a behavioral assessment of the offspring in the following generation.

Many of Hofer's suggestions for psychoanalysis have begun. Moving forward, we need to understand how the mother-infant relationship regulates physiology (see Geva & Feldman, 2008; Ham & Tronick, 2009; Peña, Monk, & Champagne, 2012; Schecter et al., 2004, as examples). We need to specify the long-term effects of early experience (see studies above predicting adult outcomes from infant attachment). We need to understand the transmission of early effects across generations; this will be harder. We are just at the beginning of understanding the implications of the epigenetics revolution for human development.

## Conclusion

Myron Hofer argues that our understanding of the effects of early experience gleaned through animal models provides a new, rich biological underpinning to the psychoanalytic theory of the effects of early experience. He urges psychoanalysts to integrate this new information for research and practice. Hofer's own integration of a massive amount of research and theory into a synthesized theory of evolution and development makes this possible. It is a powerful and elegant achievement.

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