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DEVELOPMENTAL PSYCHOLOGY

REVISITING

THE CLASSIC STUDIES

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1

Attachment and Early Social Deprivation

Revisiting Harlow's Monkey Studies

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BACKGROUND TO THE CLASSIC STUDY

In his 1958 presidential address to the American Psychological Association, "The Nature of Love," Harlow suggested that the psychologists, "at least those who write textbooks, not only show no interest in the origin and development of love or affection, but they seem to be unaware of its very existence." Furthermore, he noted that the failure of experimental psychologists to consider love or affection stood in sharp contrast to "the attitude taken by many famous and normal people" (Harlow, 1958). For Harlow, it was an "obvious fact" that the human infant's affection for the mother provided a basis for later close relationships and the development of subsequent affectional bonds (Harlow & Zimmerman, 1958). By the time "Social Deprivation in Monkeys" was published in *Scientific American* (Harlow & Harlow, 1962), Harlow's experiments with rhesus monkeys had clearly established that affectional bonds could be the subject of scientific investigation. This initial work laid the foundation for examining the effects of early social experience on later personality development.

Harlow's experiments during the 1950s had challenged prevailing learning and psychoanalytic explanations of the infant-mother relationship. Learning theorists viewed the reinforcement that infants associated with feeding as the primary factor accounting for the formation of the mother-infant bond. In this view, the mother-infant relationship was a secondary byproduct of the reduction of the primary drives that included hunger, thirst, and pain. Psychoanalytic models converged with learning theories by focusing on oral needs for nurturance as the primary motivational system during the infant stage of development. Harlow noted that one problem with the learning or drive reduction model was that it failed to account for the lifelong, unrelenting persistence of the bond following extinction trials when the mother ceases to be associated with feeding. Instead he started with the idea that infants were predisposed to forming an affectional bond with the mother, a predisposition that was independent of their need for food.

The "surrogate" mother studies provided a critical test of Harlow's notion that infant monkeys were motivated by a primary need for affection or "contact comfort." He had observed that young monkeys became "attached" to soft cloth pads and showed distress when they were separated from them (Harlow & Zimmerman, 1959). The contact comfort derived from the terry cloth was a variable that could be clearly distinguished from feeding as a factor influencing the formation of the infant-mother affectional bond. By creating "surrogate" wire and cloth mothers, the preferences of infants for different surrogates could be measured and variables that were critical to the mother-infant bond could be evaluated. In a series of studies using the surrogate preference paradigm, Harlow demonstrated that infant monkeys showed large and consistent preferences for cloth surrogates that provided contact comfort over wire surrogates that provided food.

Beyond accounting for the factors that led to the formation of the affectional bond, Harlow's studies also demonstrated the function of the bond in reducing fear and promoting exploratory activity. Harlow set up laboratory situations that not only gave the infant monkey access to the mother surrogate, but also tested how monkeys responded to fear situations such as the "open field test" and exploratory situations evoked by novel objects. In fear situations, infants sought contact with the cloth surrogate, and the contact resulted in comfort and reduced fear. After a period of contact, monkeys were able to use the cloth surrogate as a base for gradually approaching novel stimuli. These exploratory bouts were balanced with contact seeking toward the surrogate, suggesting that monkeys were using the cloth surrogate as a secure base for exploration. The interplay between the attachment, fear, and exploratory systems that Harlow observed in his laboratory monkeys suggested an alternative view of motivation that was consistent with the views of ethologists that motivational systems could be understood as serving biological functions in promoting species survival.

DESCRIPTION OF THE CLASSIC STUDY:
THE EFFECTS OF EARLY SOCIAL DEPRIVATION
ON LATER DEVELOPMENT

After establishing the significance of the infant-mother bond, Harlow conducted a series of studies on the effects of early social deprivation on subsequent adaptation (Harlow & Harlow, 1962). René Spitz's studies of children raised in institutions had called attention to potential problems resulting from early maternal deprivation. In the 1940s, Spitz had identified a syndrome which he termed "hospitalism" that suggested institutionalized children were subject to severe depressive symptoms and possible long-term damage to their adult personality (Horst & Veer, 2008). By systematically exposing infant monkeys to varying degrees of social deprivation, Harlow addressed a series of questions about early social experience that had clear implications for the treatment of young children. His prospective designs could not

only control exposures to early social adversity, but also map their effects on subsequent adaptation.

The largest sample reported in the 1962 paper consisted of 56 monkeys that had been raised in conditions of "partial social isolation." These monkeys had been housed in cages where they could see and hear other monkeys but not interact or make physical contact with them during their first year of life. At ages ranging from five to eight years, a period that is equivalent to adulthood in humans, Harlow noted that this group showed a range of abnormalities compared to monkeys who had been born in the wild and brought to the lab as preadolescents or adolescents. Compared to monkeys born in the wild, who were subsequently housed in cages, the laboratory-born monkeys "stare fixedly into space, circle their cages in a repetitive stereotyped manner and rock for long periods of time." Many of the lab-raised monkeys showed obsessive behaviors such as repetitively picking at skin. In some cases, these obsessive patterns became more extreme or "self-punitive" including behaviors such as chewing or tearing at a body part until it bled. The laboratory-raised monkeys also showed difficulty in interacting with others. At the approach of another person, lab-raised monkeys would show "a complete breakdown and reversal of normal defensive behaviors," resorting to withdrawn and self-aggressive behaviors.

A series of pilot experiments followed. The first study sought to replicate the initial findings. Six monkeys that had been cage-raised for their first two years, or under conditions of partial social isolation, were compared to six matched monkeys who had been raised in the wild for the first year and subsequently housed in cages during their second year. At two years of age, none of the lab-raised monkeys showed normal sexual behavior with peers. These monkeys displayed sexual approach but did not orient themselves correctly and did not succeed in mating. As these monkeys grew older, they tended to pay less attention to animals in neighboring cages and no heterosexual behavior was observed between male and female cagemates, even between those that had lived together for as long as seven years.

Harlow also compared the cage-raised monkeys to monkeys who were provided with the cloth surrogates that had been used in his early studies. These infant monkeys formed a clear "attachment" to the cloth surrogates and this attachment persisted even following two years of separation from the surrogate. However, as the 60 cloth-surrogate monkeys matured into adolescence and adulthood at three to five years of age, their behavior was as socially and sexually aberrant as that of the monkeys who had been raised under conditions of partial social isolation in bare wire cages. When exposed to adolescent and adult monkeys raised in the breeding colony, not one of the males and only one of the females showed normal mating behavior. By comparison, all of the monkeys born in the wild and captured during their first year, and then housed together in captivity, displayed normal sexual behavior. They had learned to live with others in a stable hierarchy of dominance, fought less, and engaged in social grooming.

Another study tested the extent to which early social deprivation could be reversed by later experience. Harlow moved 19 lab-raised monkeys to the

municipal zoo where they had to contend with new survival challenges more in line with those experienced by monkeys living in the wild. In this new environment, the lab-raised monkeys had to drink from a trough, compete for food, and learn to live together in a group. Although three of the monkeys died or showed severe stress in making the transition, the remaining monkeys were able to establish a dominance hierarchy that reduced fighting, formed friendship pairs, and displayed some sexual behavior. However, the sexual behavior was infantile in form and did not result in any females becoming pregnant. When returned to the laboratory, the monkeys ceased to groom and returned to more frequent fighting and aggressive behavior. Harlow viewed this attempt at rehabilitation largely as a failure.

Yet another set of studies tested the differential effects of both the duration and degree of early social isolation on later outcomes. Monkeys were exposed to total social isolation, a condition in which they were individually housed in a cubicle with solid walls that eliminated all visual and auditory contact with other monkeys. Human experimenters interacted with the monkeys via oneway vision screens and remote control. The monkeys who spent two years in what Harlow described as "the pit of despair" showed severe social deficits. They froze or fled on interaction with other monkeys and made no effort to defend themselves from aggressive assaults. Even prolonged subsequent exposure to more normal monkeys failed to reverse these social deficits. In the next study, monkeys were isolated for only their first six months. After exposure to other monkeys, these monkeys eventually showed physical movement but remained almost totally devoid of normal social behavior. By comparison, monkeys who were exposed to only 80 days of total social isolation made rapid gains when the first 80-day period was followed by eight months of play with normal monkeys. These monkeys approached normal play and defense behaviors by two years of age. Harlow concluded that total social isolation for the first six months of life was a critical period that created irreversible effects on subsequent social adaptation. He indicated that this six-month period in the rhesus monkey was equivalent to the first two to three years of life for the human infant.

A final set of experiments attempted to disentangle the effects of maternal deprivation from the effects of isolation from age-mates. Harlow noted that "little attention has been given, in fact, to child-to-child relations in the study of early personality development." To address this question, he tested four groups of monkeys. The most privileged were two groups of four monkeys, each of whom was raised with their mother from birth and given regular access to playing with age-mates. A third group was raised with age-mates in their cage but without their mothers and only with the terrycloth surrogates used in the earlier experiments. After 20–30 days, the two groups were allowed to leave their home cages. During the following two years, the mothered monkeys showed more complex play patterns. However, by two years of age, the monkeys raised solely with age-mates were indistinguishable in their play, defense, and sexual behavior from those raised with their mothers. Finally, a fourth group consisted of four monkeys born to "motherless" mothers. When these monkeys had offspring, Harlow described their maternal behavior as completely abnormal, "ranging from indifference to

outright abuse." This group was exposed to peers in a playpen group and approached normal play behaviors with the peers. However, as they matured, the group showed more precocious sexual activity and aggressive behavior than the other three groups of monkeys.

The Harlows concluded that contact with age-mates could largely compensate for the effects of maternal deprivation on subsequent play, defense, and sexual behavior in the juvenile period. Yet, they were more cautious about the degree to which agemates could compensate for deficits in later maternal behaviour of the monkeys toward their offspring. The monkeys who had experienced early partial social isolation showed severely abnormal maternal behavior ranging from indifference to outright abuse toward their offspring. Further, young monkeys who were exposed to this deviant caregiving behavior developed poorly in spite of their opportunity to have contact with age-mates. Although infant-infant contact was effective in compensating for the effects of maternal deprivation on play, defense, and sexual behaviors with peers, it was not clear that opportunities to interact with peers could compensate for intergenerational effects on maternal behavior or adult social adjustment.

IMPACT OF THE CLASSIC PAPER

An earlier generation of childcare experts had focused on providing children raised in institutions with the conditions necessary to promote physical growth and protection from disease. Surprisingly, in spite of substantial anecdotal evidence from institutions, most professionals at the time remained skeptical that early and prolonged separations of infants and young children from their mothers or an alternative adult caregiver would have lasting emotional consequences. Harlow's paper provided critical experimental evidence about the importance of early social experience to later adaptive outcomes ranging from sexual and repro-ductive to caregiving behavior. He also began the important task of differentiating between types of social deprivation that are primarily influenced by relationships with peers or age-mates and those that are largely dependent on the attachment bond between the infant and the caregiver.

Harlow's paper had an immediate impact on the ongoing debate about the importance of the mother-infant bond in child psychiatry. During the 1950s, John Bowlby, a British psychiatrist, had published a monograph (1951) on the effects of maternal deprivation on children's development. In his visits to Harlow's lab in the 1950s, Bowlby may have been responsible for pointing out to Harlow that his cage-raised monkey colony created conditions that were equivalent to partial social isolation (Suomi, Horst, & Veer, 2008). Harlow's 1962 paper, in turn, lent support to Bowlby's efforts to convince psychiatrists and other healthcare professionals that young children could be adversely affected by prolonged or inexplicable separations from their mothers (Horst & Veer, 2008).

Harlow's paper also directed attention toward measuring outcomes that had clear implications for overall adaptation and inclusive fitness. He called attention to

motivational systems that served biological functions. In his view, the infant-caregiver bond served not only as a source of protection when confronted with danger, but also as a context in which the child acquired the capacity to form subsequent affectional bonds with peers, sexual partners, and offspring. This approach was influenced by European ethologists, particularly Robert Hinde, and by Harlow's sensitivity to the effects of different rearing environments ranging from his lab, to the local zoo, to monkeys born and raised in the wild. Harlow's creativity in designing laboratory environments that elicit attachment, fear, exploratory, and affiliative behavior showed a unique understanding of the importance of context in assessing how early social experience could influence subsequent development. He actively designed environments that tested the interplay between attachment, fear, and exploration. Peer and play environments provided contexts to assess the development of defensive and sexual behavior. The importance of context in observing and assessing behavior greatly expanded approaches to behavioral assessment and motivational systems.

Bowlby (1969) formalized Harlow's work into a theory of control systems that were activated and terminated by environmental conditions. Bowlby's theory emphasized contextual factors that both activated and terminated behavioral systems. In infancy, he viewed the attachment, fear, and exploratory systems as each having set goals that needed to be maintained based on ongoing monitoring of and feedback from the environment. Control systems theory in turn guided systematic observations of human infants in the village and home environment (Ainsworth, 1967). It also led to the development of a laboratory paradigm that tested the abilities of infants to use their caregiver as a source of safety and base for exploration (Ainsworth, Blehar, Waters, & Wall 1978). The development of Ainsworth's Strange Situation paradigm (see Chapter 2) – in which the responses of infants to separation from, and subsequent reunion with, their mother, and their reactions to an unfamiliar woman were recorded – in turn became a paradigm for assessing individual differences in the security of the relationships of infants with their primary caregiver.

The notion of affectional systems provided a foundation for a broader lifespan theory of close relationships. Although the mother-infant bond was a primary focus of his initial studies, Harlow viewed the mother-infant bond as a possible prototype for subsequent affectional bonds formed in later developmental stages. Attachment theorists further elaborated the notion of affectional bond by emphasizing the role of emotions in bond formation and maintenance. Bowlby (1979) and Ainsworth (1989) noted that affectional bonds are defined by distress resulting from inexplicable separations, joy upon reunion, and grief at the loss of a relationship partner. Ainsworth (1989) emphasized that affectional bonds differed on the basis of the behavioral system that motivated bond formation. Whereas children's bonds with caregivers were motivated by the attachment system, the adult's bond to the child was motivated by the caregiving system. Bonds to a peer may be motivated by either affiliation in the case of friends or sexual and reproductive systems in the case of adult pair bonds.

Finally, the prospective design of Harlow's study provided a model for the emerging field of developmental psychopathology (Rutter & Sroufe, 2000). Only with prospective designs could the effects of early adversity on later outcomes be tested. In a single set of studies, Harlow illustrated how questions of timing of exposure to adversity could be addressed, allowing for consideration of whether there were particular windows or critical periods in development. Harlow also considered how later experiences could modify or remediate the effects of early adversity. His work further showed how measures of adaptation needed to be adapted to particular developmental stages. He used developmentally salient issues that served clear biological functions as a guide to his observational assessments. This approach resulted in measures of early attachment behavior in infancy, observations of play, defensive, and sexual behaviors of the juvenile period, and assessments of sexual and caregiving outcomes in the adolescent and adult periods.

CRITIQUE OF THE CLASSIC STUDY

The finding that rearing with age-mates could compensate for the effects of maternal deprivation on developing peer relationships was the most controversial and tentative finding in the 1962 paper. Working with small numbers of monkeys, Harlow observed few differences between mother-raised and peer-raised monkeys on play, defensive, or sexual behavior with peers during the juvenile period of development. In fact, when compared to the mother-raised monkeys who were not exposed to peers early in their development, the peer-raised monkeys showed better outcomes. This finding led Harlow to conclude that play with agemates was "more necessary than mothering to the development of effective social relations" (Harlow & Harlow, 1962, p. 495). However, Harlow remained tentative about his conclusions noting that they were limited to outcomes only up to two years of age. As a result, the notion that peer rearing could compensate for maternal deprivation was limited to juvenile play, defensive, and sexual behavior (Harlow & Harlow, 1962). The intergenerational effects of peer-rearing on maternal behavior and adult adjustment were yet to be tested.

Follow-up studies of peer-reared monkeys by Harlow's former graduate student, Steve Suomi, suggested a less sanguine view of peer-raised monkeys even during the juvenile period of development (Suomi, Horst, & Veer, 2008). Although young monkeys formed affectional bonds with peers and became very distressed at being separated, these bonds did not serve the same functions of reducing fear in the face of novelty or supporting exploratory or learning activities as was the case with monkeys raised by their mothers or by another adult. The restricted exploratory activity of the peer-raised monkeys was also evident in terms of more shyness and withdrawal when they came in contact with unfamiliar peers (Suomi, 2016). When these peer-raised monkeys were grouped with mother-raised monkeys,

they dropped to the bottom of the peer dominance hierarchies (Bastian, Sponberg, Suomi, & Higley, 2002).

HOW THE STUDY ADVANCED THINKING, AND HOW THINKING HAS SUBSEQUENTLY ADVANCED

"Social Deprivation in Monkeys" framed a series of questions about the effects of early social experience that have guided both human and animal studies for nearly five decades. Research has advanced from the social deprivation paradigms in several respects. First, researchers have examined more subtle variations in early caregiving environments by considering the effects of temporary separations from caregivers as well as variations in the quality of maternal care provided to offspring (Suomi & Levine, 1998). Second, researchers have begun to examine individual differences in the susceptibility of offspring to environmental influences (Bakermans-Kranenburg & van IJzendoorn, 2015). Finally, efforts to understand individual differences in children's susceptibility to caregiving environments have been advanced by investigations of the genetic, neural, and physiological mechanisms through which early experience affects later outcomes (Gee et al., 2013). Both animal and human models of early experience have made major contributions to our understanding of the neural and physiological mechanisms through which early experience influences or "programs" developmental outcomes. Many of these findings remain to be translated into prospective longitudinal designs for modeling the effects of early experience in studies of humans.

ENVIRONMENTAL MANIPULATIONS

Harlow's manipulations of early social experience were extreme by comparison to most subsequent animal and human studies. Initial efforts to consider less extreme forms of early adversity focused on separations between infants and their mothers. In studies of human infants and young children, Bowlby had called attention to a phasic response to prolonged separations. Children responding to prolonged or inexplicable separations, such as a mother having to be hospitalized for a period of weeks, showed a pattern of initial protest characterized by overt distress and anger, followed by despair, sadness, and withdrawal, which was eventually replaced by what Bowlby described as detachment. This later phase was viewed as a defense that protected the child from painful feelings associated with the separation. Upon reuniting with the parent, this detachment only gradually gave way to more active approach and engagement with the parent. Working with a social worker, James Robertson, Bowlby filmed children's reactions to separations that illustrated the phasic response and demonstrated the emotional significance of the young child's attachment bond to a primary caregiver.

Studies of early experience in rodents further qualified the nature of separations that can have enduring negative effects. Daily separations are a normal part of the developing attachment bond in humans and the young child's ability to re-establish

contact with the caregiver following separation is critical for the maintenance of the bond. This point was illustrated by Seymour Levine's work with rodents. He developed an "early handling" paradigm in which it was discovered that rat pups who experienced brief 15-minute separations from their mothers performed better as adults in an avoidance learning paradigm than pups who had not been separated from their mothers (Suomi & Levine, 1998). This finding showed how exposure to normally occurring or "intermittent stressors" early in development results in the development of effective coping strategies later in life. Levine's early handling paradigm and the effects of intermittent stressors have consistently been replicated in both rodent and monkey models (Lyons, Parker, & Schatzberg, 2010).

A major advance in both human and animal models of early social experience was the recognition that there was naturally occurring variability in maternal caregiving behavior. In her observations of mothers and their infants in the home environment, Mary Ainsworth developed codes for discriminating between sensitive and insensitive caregiving behavior (Ainsworth et al., 1978). Infants who experienced sensitive caregiving were subsequently classified as secure in laboratory tests using the Strange Situation paradigm at 12 and 18 months. Security of infants in the Strange Situation, in turn, has predicted aspects of subsequent child adaptation in preschool, childhood, and adolescence (Sroufe, Carlson, Egeland, & Collins, 2005). The notion that individual differences in the quality of care received from the mother can have long-term effects on psychosocial outcomes has generally been supported in several major longitudinal studies (Groh, Fearon, van IJzendoorn, Bakermans-Kranenburg, & Roisman, 2017).

A rodent model for studying early maternal care uses naturally occurring variations in maternal behavior over the first eight days after birth (Champagne & Meaney, 2007). Direct observation of mother–pup interactions in normally-reared animals identified two forms of maternal behavior – those involving licking/grooming of pups (LG) and another characterized by arched-back nursing (ABN) in which a mother nurses her pups with her back conspicuously arched. Because the two types of maternal behavior tend to co-occur, mothers could be classified as either High or Low LG–ABN. The consequences for offspring of differential mothering were established by the intergenerational stability of maternal behavior, with mothers who were high on LB-ABN showing similar maternal behavior to their offspring when they subsequently became mothers, and increased explora-tory activity of the offspring and decreased startle responses as adults (Cameron, Champagne, & Parent, 2005). Cross-fostering of high LG mothers to rat pups served to rule out the genetic transmission of intergenerational effects. Offspring of low LG mothers matched to high LG foster mothers showed high LG maternal behaviors. Early exposure to high LG mothers has also produced effects on the subsequent sexual and reproductive behavior of female offspring (Cameron et al., 2005; Curley, Champagne, & Bateson, 2008).

Variations in maternal caregiving are also subject to changes in the physical envi-ronment, such as material and food supply. In a series of studies of bonnet macaque infants and their mothers, Rosenblum and his colleagues developed a paradigm that exposed mothers to resource-rich environments that created Low Foraging

Demand (LFD), or impoverished environments that created High Foraging Demand (HFD) in which the mother had to spend several hours each day to obtain adequate nutrition for herself and her offspring (Andrews & Rosenblum, 1991). A third condition varied the LFD and HFD environments every two weeks creating a Variable Foraging Demand (VFD) condition. Mothers in the VFD condition showed substantially reduced investment in their offspring compared to mothers in either the LFD or HFD conditions. Under these conditions, mothers interacted less with their infants and their offspring showed less ability to use the mother to explore the environment (Andrews & Rosenblum, 1991). During their juvenile period, monkeys raised in VFD conditions were less gregarious, less capable of responding to fear stimuli, and demonstrated a different profile of neuroendocrine activity in response to stressors (Rosenblum, Forger, & Noland, 2001).

In sum, studies of both animals and humans suggest that variation in the quality of the early caregiving environment can have lasting effects on subsequent adaptation. Furthermore, the effects of early experience have been demonstrated with less extreme forms of social deprivation than those used in Harlow's early investigations. Yet, some of the forms of deviant caregiving that Harlow reported in his motherless monkeys bear striking parallels to the more deviant forms of human caregiving found in maltreating families that have documented physical abuse and neglect of offspring. Further, the quality of care that infants and young offspring receive is itself shaped by the caregivers' social ecology and access to the resources necessary to nurture offspring.

Transactional models—child effects

As researchers have examined more subtle variation in early caregiving environments, new attention has been directed toward the substantial variability in how children respond to their environments. Many children raised under adverse conditions, ranging from institutions to neglectful or abusive parenting, have shown remarkable recovery in their later emotional and cognitive functioning. Child characteristics that contribute to "resilience" have been investigated in a wide range of human and animal studies (Sameroff, 2010). These "child effects" have been conceptualized and measured at the genetic, physiological, and behavioral levels of analysis (Obradović & Boyce, 2009). Molecular analyses have centered primarily on identifying genetic polymorphisms that increase or reduce the child's vulnerability to adverse environments. Physiological measures have focused on autonomic or neuroendocrine measures of reactivity to stressful events, while behavioral measures have focused on individual differences in temperament conceived in terms of shy/inhibited or impulsive/aggressive dimensions (Suomi, 2006). Not surprisingly, children with increased genetic vulnerabilities, physiological stress reactivity, or with more extreme aspects of temperament are more vulnerable or less resilient in the face of early social adversity.

The ability to measure variability in both the caregiving environment and in children's susceptibility to environmental exposures has fostered new research on the mechanisms through which early experience affects later adaptation

(Meaney, 2010). This dynamic transaction between the child and the caregiving environment is evident in studies of gene/environment interactions associated with psychiatric disorders (Bakermans-Kranenburg & van IJzendoorn, 2015). Work in rodents has identified how early experience can influence gene expression and produce stable epigenetic modifications that alter individual phenotypes across the lifespan (Roth & Sweatt, 2011). The effects of early experience on gene expression are also being investigated as a putative mechanism of intergenerational effects on maternal behavior (Curley et al., 2008). Studies on the effects of early psychosocial deprivation on children's developing brain structure and function have advanced understanding of how adversity is carried forward to future psychological and behavioral impairments (Nelson, Zeanah, & Fox, 2019). Specific exposure to deprivation in the form of neglect or threat in the context of abuse has shown differential effects on children's neural processing of threat and reward stimuli (McLaughlin, Sheridan, & Lambert, 2014).

CONCLUSION

Harlow's paper on early social deprivation called attention to an aspect of early experience that had been largely neglected by the experimental psychology of his day. The notion that early social relationships could play a significant role in the survival and reproduction of a species was remarkably controversial at the time. By experimentally testing this notion, Harlow opened up decades of research on the effects of early social experience in both humans and animals that has remained a major focus for subsequent developmental investigations. Recent research has begun to advance our understanding of the mechanisms through which early social experience influences subsequent adaptation. Putative mechanisms that operate at the genetic, neural, physiological, and behavioral levels of analysis have been examined. Much remains to be learned and the questions that Harlow addressed in his 1962 paper are likely to endure in the decades to come.

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