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Neural Foundations of Variability in Attachment

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Abstract

Neuroscience offers insight into processes that support the development of the social brain within the cultural contexts that permit attachment relationships to form. Both human and nonhuman animal studies are critical to inform theory development and hypothesis testing via descriptive and experimental studies. A scientifically valid evolutionary theory is necessary to account for the remarkable diversity of parenting systems across human and many nonhuman animals. This chapter examines the neural foundations of attachment and poses critical questions that relate to the initiation of this relationship: How does attachment interface with brain development? What is the interplay between attachment and brain development (including elements of bidirectionality)? Are there negative consequences associated with variation in attachment, and are they reversible? Rather than conceptualizing attachment in terms of a single type of relationship, or a rigid developmental channel, this chapter proposes that an expanded consideration of variation is necessary to understand the neural foundations of infant-caregiver relationships, and the role of those relationships in developing competence across the life span. This approach will permit identification of common neurobiological elements of attachment as well as the remarkable plasticity and diversity within and across individuals, cultures, and species.

Group photos (top left to bottom right) Allyson Bennett, William Hopkins, Margaret Sheridan, Ruth Feldman, Michael Lamb, Jay Giedd, Valeria Gazzola, Stephen Suomi, Nim Tottenham, Akemi Tomoda, Margaret Sheridan, Dirk Scheele, Michael Lamb, Allyson Bennett, Jay Giedd, Nim Tottenham, Valeria Gazzola and Dirk Scheele, Akemi Tomoda, Ruth Feldman, Stephen Suomi, William Hopkins

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Introduction

Neuroscience offers insight into processes that support the development of the social brain within the cultural contexts that permit attachment relationships to form. Both human and nonhuman animal studies are critical to inform theory development and hypothesis testing via descriptive and experimental studies. Understanding the neural foundations of attachment relationships can extend insights beyond the human case. In turn, identifying core cross-species similarities in the neural processes involved in the initiation and maintenance of attachment relationships provides the foundation to better understand individual, cultural, and species variability, both in the development and the outcome of attachment relationships. A scientifically valid evolutionary theory is necessary to account for the remarkable diversity of parenting systems across human and many nonhuman animals. Neuroscience can enrich our understanding of the biological mechanisms that support plasticity in attachment formation and outcomes.

A number of guiding questions shaped our consideration of the neural foundations of attachment. How attachment interfaces with brain development was a primary focus, in part because the infant-caregiver(s) relationship occurs at a period in which neural systems undergo major maturational changes. At the same time, the interplay between attachment and brain development (including elements of bidirectionality) is necessary to frame other research questions and to form testable hypotheses and theory. For instance, uncovering shared and unique neural systems across species and cultures is productively informed by identifying how neural development supports, and is affected by, attachment relationships. This information is requisite to address another major question of relevance to healthy development: If there are negative consequences associated with variation in attachment, are they reversible? Finally, understanding the degree to which the neural circuitry underlying infant-caregiver attachment is the same or different from the neural circuitry underlying other relationships (e.g., pair bonds) is important for a number of reasons. Better understanding of the similarities and differences in neural circuitry involved in different types of relationships is needed to identify the neural processes involved in relationships across an individual's life span, across cultures, and across species. This is particularly true given the differences in infant-caregiver arrangements across the nonhuman animal species that provide important avenues for experimental research aimed at identifying neural foundations of attachment.

We begin with a discussion of attachment in the context of studying neural development. The themes selected highlight both advances in understanding of attachment as well as ongoing challenges related to the range of neural plasticity that supports diverse systems for infant caregiving. We briefly highlight what is known and what remains unknown with respect to the neural processes involved in infant-caregiver relationships, and propose a conceptual

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framework to guide further consideration of how current evidence provides a foundation for new avenues of research.

Attachment: Neural Development across Cultures and Species

Social relationships occur in diverse configurations across human cultures and different species: no single definitive type of social relationship exists in human and nonhuman animals (see Hawkes et al. and Morelli et al., this volume). While these relationships may emerge from, and indeed depend on, some of the same neurodevelopmental processes and neural circuitry, early relationships between infants and their caregivers vary in a number of key aspects. Our primary focus is on attachment; however information specific to attachment is not always available. Thus, studies of social relationships, considered more broadly, play a key role in developing our knowledge about the neural contributors to attachment.

With respect to differentiating attachment relationships from others, the features that are most readily apparent are primacy and dependency. From the perspective of considering the neural foundations of attachment, the primacy of the relationship differentiates it from other relationships in a number of critically important ways. As a result of developmental timing (i.e., it occurs during a period of rapid neural maturation and integration of neural, behavioral, physiological, and other systems), attachment is fundamentally tied to survival and early competencies during infancy as well as to competence in subsequent life periods. In other words, given the time course of neural development, relationships during infancy are uniquely positioned to affect developmental trajectories for perceptual, motor, emotional, social, and cognitive health.

Asymmetrically dependent social relationships (i.e., those between the infant and the caregiver) occur for infants of many species. For some, the infant-caregiver(s) relationships are characterized in a specific way as attachments. We interpret this to mean that there is a degree of specificity to these relationships: each individual has a relationship with a *particular* other—or *particular* individuals—and the relationship is reciprocated by the other (or others). Whereas this distinction and definition of reciprocity may not be equivalent across human cultures, it is one that can productively organize comparative analyses and considerations of the usefulness of nonhuman animal models. Figure 10.1 illustrates our views of attachment as found across animals, highlighting differences between species both in terms of reciprocity and specificity. As illustrated, in some rodents, reciprocated specificity is not evident, such that the participants are, for example, specifically rewarded by the other's presence (as opposed to that of any other) and are not specifically concerned about the other's absence. By contrast, relationships in chimpanzees and in

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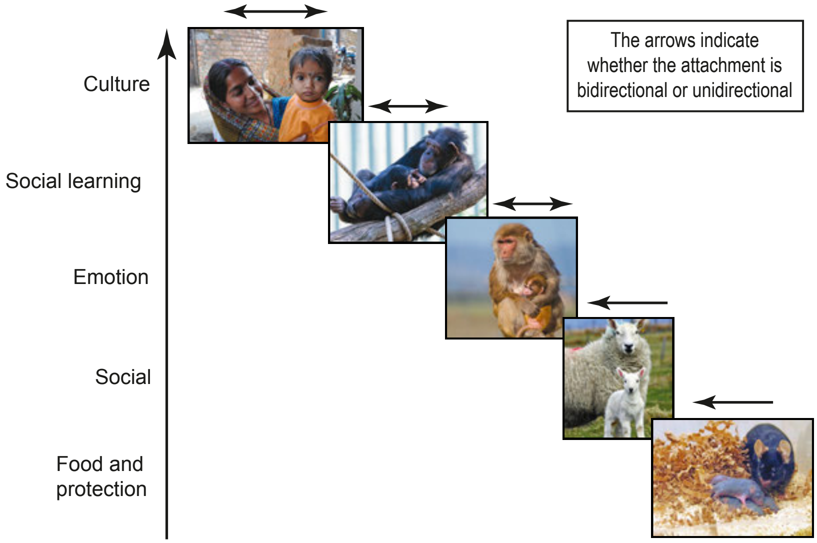

Figure 10.1 Illustration of the bidirectionality of attachment relationships across different model species that are often compared in neurobiological studies relevant to attachment. Complexity of functions and domains involved in the infant-caregiver(s) relationship is shown as increasing across phyla. Photo credits: culture, Nandita Chaudhary; social learning, Magnus Johansson; emotion, ©Kathy West Studios; social, Donald Macleod; food and protection, Indiana University.

humans can—but may not always—be characterized by both bidirectionality and specificity.

Figure 10.1 also highlights the increasing complexity of functions that play a role in, or may be crucial to, such relationships. At the most basic level, this includes the provision of food and protection and extends, with increasing complexity, to incorporate socioemotional, cognitive (social learning), and cultural domains. Infant-caregiver relationships—particularly for the infant—may exhibit common features (including common neural foundations) across different species. Social relationships, including attachments, have multiple components that include perceptual, behavioral, emotional, cognitive, and higher-order representational features that are subject to variation at the level of the individual, culture, and species. Attachment in nonhuman primates, for example, may have a high degree of overlap with humans in terms of many behavioral and emotional processes, but differ in aspects of cognitive representation. In addition, infant-caregiver relationships among mammals may share behavioral features and underlying neural processes, but differ in emotional and cognitive components compared with primates. The core similarities provide the critical foundation for studies aimed at better understanding the neural foundations of attachment, as well as the variation in attachment that occurs across individuals, cultures, and species. As we aim for this, however, we must remember that these differences exist and are of central importance.

Conceptual Framework: Variation and Neural Development

To facilitate better understanding of the neural processes involved in attachment and identify how variation in attachment affects neural development, we put forth the following conceptual framework. As illustrated in Figure 10.2, attachment relationships are initiated over the course of early development as infant-caregiver(s) relationship(s) develop. The initiation is conceptualized as a process separable from the maintenance of the relationship(s) that unfolds over time, across the entire life span. The time course of development is represented across the horizontal area of the figure, on to which the range in variation of outcomes is overlaid. Outcomes are represented as a spectrum related to behavioral, social, emotional, and cognitive "competence" and the associated degree of functionality of the neural systems that support those processes. As illustrated, the model conceptualizes a wide range of variability in which competent functioning may occur, with an optimal level that is defined within the context of the individual's environment and culture (e.g., Keller and Chaudhary, this volume).

The model also illustrates a lower zone in which competence and outcomes are compromised, again within the context of the individual's environment and culture. Finally, the model explicitly includes recognition of plasticity (as

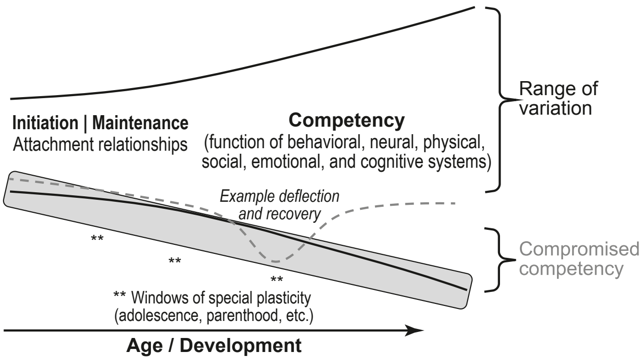

Figure 10.2 Conceptual framework showing the relationship between early attachment and development of competence in a range of systems critical to individual functioning. Variation in outcomes and development is shown as a vertical range; the lower limit represents compromised competency, which significantly impedes the individual. Plasticity across development and following the early attachment relationships is depicted as a dotted line to show deflection and recovery. This underscores an anti-determinist perspective and acknowledges that development of competence can follow suboptimal attachment relationships. Finally, the model incorporates windows of special plasticity (**) throughout development (e.g., adolescence and parenthood).

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opposed to determinism). Thus, there is potential for variability in development, across the life span, even following relative similarity in the early attachment network. Moreover, there are "windows of special plasticity," corresponding to developmental points in time, in which neural plasticity is high (e.g., during infancy, adolescence, parenthood).

The development of competence is not specified in terms of specific outcomes or systems; these could include neural, behavioral, emotional, physical, and cognitive outcomes as well as the interplay between them. Our framework does, however, emphasize the area under the threshold: whereas there can be a great deal of variation in competence that remains in the functional range, there is both a relatively smaller range and significant concern for outcomes that have substantial and persistent adverse effects on individual's ability to function competently (including their survival). An individual's trajectory may vary, however, as a function of unstable, disrupted, or absent infant-caregiver relationships, with the predicted trajectory represented in terms of higher likelihood of challenge to attain competency.

For an individual organism, the developmental trajectory is influenced by (a) previous developmental outcomes, (b) environmental and experiential events and conditions, (c) genetic factors, and (d) resulting interactions (Gottlieb 2007). An interaction occurs because an individual's own state, development, and previous experiences all play a role in shaping an individual's experience with a subsequent environment or experience: two individuals can experience the same event and/or environment differently. Plasticity is represented in this model as potential for deflection from a developmental trajectory. In the case of risk, deflection is a movement away from competence. In the case of recovery or resilience, movement is toward greater competence and includes recovery from pathology or compromised function.

A core principle of our framework is the idea that the central functions of different developmental phases—reflected in behavioral, reproductive, affective, and cognitive changes—have a neural basis and can bidirectionally affect their neural substrates. From the neural perspective, therefore, it is particularly important that the developmental trajectory contains "windows of potential" for especially high plasticity (e.g., Dahl 2004). These windows may, for example, be transition periods that correspond to developmental stages known to show high levels of change: infancy, adolescence, and perhaps parenthood.

The framework is inclusive of variation across cultures, populations, and species with respect to typical maturational timelines and parameters for well-being. What is constant is the initiation of the attachment relationship(s), or the infant-caregiver relationship(s), during infancy and the maintenance of that relationship network during the critical infant and juvenile developmental period. Moreover, the framework allows for variation in the configuration of infant-caregiver relationships. This variation is critical as it provides a way to encompass the range of infant caregiving practices for humans and is also inclusive of the range of infant care practices across the many species that may be studied to inform attachment research.

"Flexible Glue" Model

The "flexible glue" model offers a way to describe the initial process of attachment (initiation) and the subsequent maintenance of the relationship. Here, attachment is conceptualized as a flexible glue or bond between an infant and caregiver(s). The glue is strengthened, or becomes more stable over time, but the glue need not be permanent and is subject to change across the life span. This glue, or the bond that initiates attachment, is essential to infant survival. It forms during a period of neural development which involves multiple systems central to social relationships, including regulation of affect and behavior. Then, over the course of child and adult development, attachment grows and it can change, for example, in response to disruptions.

Attachment describes the special relationship between caregiver(s) and a child. Although the unit of analysis most often used to identify an attachment relationship is the child, it is important to stress that the attachment process—that is, the linking of a child and caregiver(s)—can be observed and evaluated in both the child's and caregiver's brain. In addition, the attachment relationship impacts on the child's brain. Thus, for the purposes of considering the "*neurobiology of attachment*," we must consider: (a) the neurobiology (or core processes) within the parental brain that results in an attachment to a child; (b) the neurobiology within the child brain that results in an attachment to a caregiver or group of caregivers; and (c) the impact of that attachment relationship on neural structure and function. The latter is related to the maintenance of the attachment relationship, not the initiation of this relationship. In this way, the neurobiology of attachment is likely to be quite different as a function of which member of the attachment relationship and which stage of attachment (initiation vs. maintenance) is being discussed. Some systems will be shared across these individuals and stages whereas some systems will not.

Three sets of questions organized around the "flexible glue" model can guide enquiry into the neural foundations of attachment. The first centers on the effect of variation in caregiver(s)-infant arrangements. Here, the goal is to understand how the initiation and maintenance of relationships are affected by variation in caregiver(s)-infant arrangements and how these are represented at a neural level. This line of enquiry seeks to identify the neural foundations of the process (including what systems and substrates are required and involved in initiating and maintaining attachment relationships) and the neural outcomes which specify, for instance, the neural consequences and pathways affected by the relationships.

The second set of questions looks at neural foundations of attachment across species. For both the dependent infant and the caregiver(s), the initiation of an

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attachment relationship relies on reward and salience systems. Reward systems include the dopamine-modulated ventral striatal and prefrontal areas of the brain; salience systems involve the amygdala and striatum. Evidence for this has been obtained in the adult caretaker (Feldman 2015, 2017), but evidence in infants is limited to the salience network and is largely incomplete. Most research has been conducted during the maintenance phase, where impact was on function and structure of the salience and reward networks, as well as higher-order cognitive/emotional processing regions (e.g., prefrontal cortex and potentially association cortex, more generally; see Sheridan and Bard, this volume).

The third set of questions addresses the range of variation in competence and developmental change. Decades of evidence from both human and nonhuman animal studies demonstrate deleterious, wide-ranging, and persistent health outcomes associated with severe impairment (or even absence) of infant and childhood caregiver(s) attachment relationships (Felitti et al. 1998; De Bellis et al. 1999; Machado and Bachevalier 2003; Teicher et al. 2003; Gilbert et al. 2009; Tottenham and Sheridan 2010; Nelson et al. 2011; Callaghan and Tottenham 2016a). These extreme cases include maltreated and neglected children, children raised in severely impoverished orphanages, and nonhuman animal models in which offspring are reared without parental attachment which include seminal studies in rhesus monkeys (e.g., Harlow 1958; Harlow and Harlow 1965; Sackett 1965). Focus on extreme cases offers an important opportunity to address a significant human health challenge; it also can deepen our understanding of how neural and other systems are impacted when development is affected by early attachment relationships. Just as lesion studies have played a role in isolating the specific neural substrates of behavioral and cognitive functions, studies of the outcomes following absence of early attachment relationships have yielded critical insight into pathways and neural substrates involved in healthy development. To identify core systems, one approach is to analyze how widely variable relationships (within and across species) are supported by common neural systems, and whether there are some that depend upon unique neural foundations.

Less well studied is the association between early attachment relationships and the range of variation in development of competence that occupies the center of the range above pathological or deleterious and into optimal states. Pathological states have been of central interest from the perspective of high relevance to minimizing adverse outcomes and challenges to human health. By contrast, the broad swath of variability within the central range has remained relatively underexplored. This is the case both in the context of neurobiologically informed studies of outcomes from particular infant-caregiver(s) attachment arrangements, as well those within a broader cross-cultural or cross-species perspective.

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State of Current Knowledge

Neural Foundations of the Attachment System

One of the benefits of neurobiology is that it can be used to identify sensitive periods to assess the impact of experience. In general, data which pinpoint the impact of deficits in the presence or quality of the attachment relationship reveal that early deficits in attachment are always more detrimental to neurobiological outcomes than later deficits. This is consistent with the fact that earlier in development a child's brain is more plastic, and therefore more vulnerable than later in life. Beyond this general principal, we lack ample evidence about when certain kinds of attachment disruptions are most detrimental. This area requires increased investigation. Here we highlight current knowledge about the neurobiology of attachment itself (i.e., the glue).

To facilitate integration of current neurobiological knowledge across both humans and nonhuman animals that serve as model systems, attachment can be represented as a multidimensional system with neural, perceptual, behavioral, and other components which can—and do—overlap with those used for other social bonds. In other words, components of the systems and circuits involved in infant-caregiver networks also subserve other social relationships, including peer, romantic, or sexual relationships. At the same time, components or processes evident in less cognitively complex species may serve as basic common modules that are elaborated upon with increases in neural, behavioral, or cognitive complexity.

We divided our consideration to the following examples of knowledge about neurobiological systems. First we considered sensory modality and oxytocin as they play roles in early bonding, or pre-attachment. Second, we considered lines of neural and physiological evidence about the initiation and maintenance of the bond that can develop into attachment relationships. Understanding early bonding is relevant to illustrate some of the likely foundations upon which initiation of attachment—the initial glue in our model—depends. It also provides a translational bridge to model systems in which infant-caregiver bonds occur but do not develop into attachment, the sustained relationships similar to those found in humans.

Sensory Modality

Research on human attachment has primarily focused on visual and auditory modalities, but the glue that binds individuals is multimodal. For instance, evidence for the importance of tactile stimulation comes from studies documenting the beneficial effects of early skin-to-skin contact between a mother and infant, particularly on increasing cardio-respiratory stability and decreasing infant crying (Moore et al. 2012). In fact, the practice of skin-to-skin contact, early suckling, or both during the first two hours after birth can positively

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influence mother-infant interaction one year later (Bystrova et al. 2009). Skin-to-skin contact between a mother or father and their preterm infant induces the release of oxytocin, which in turn may mediate the positive anti-stress effects and stimulate the reinforcement system (Uvnas-Moberg et al. 2014; Cong et al. 2015). Further, this contact appears to have long-term effects, as demonstrated in a randomized study which showed that skin-to-skin contact improved the mother-infant relationship and the infant's neurobiological system (respiratory sinus arrhythmia, stress response, sleep, executive functions) for up to ten years (Feldman et al. 2014). Interestingly, people spontaneously stroke their partners and their baby with velocities that are effective in stimulating C tactile fibers in the stroked recipient (Croy et al. 2016); this supports the notion of overlapping affection systems. It is important to note, however, the caveat that much of the evidence is from Western middle-class families in which the mother is the main caretaker. Thus, we do not know, for example, about oxytocin release in babies who are passed from arm to arm after birth, as in multiple caregiving among the Beng (Gottlieb 2014).

While olfaction may not be as important for parent-infant bonding in humans as in other macrosomatic mammals (Levy et al. 2004), chemosensory signals have been found to modulate very early interactions between mother and infant. For instance, natural breast odors are sufficient to attract and guide neonates to the odor source (Varendi and Porter 2001), and the presence of pleasant familiar odors increases infants' attention and reduces crying and mouthing, but increases smiling (Coffield et al. 2014). Furthermore, mothers can use odor cues to identify their infant as early as 2–6 days postpartum (Porter et al. 1983), and it has been observed that the mother's odor can elicit automatic imitation effects in children with autism (Parma et al. 2013).

Neurohormones

The neuropeptide oxytocin (OXT) has been implicated in mediating numerous prosocial effects, ranging from approach/avoidance behavior (Scheele et al. 2013) to interpersonal trust (Kosfeld et al. 2005). Importantly, accumulating evidence from animal and human studies suggest that OXT is a key factor for both mother-infant bonding and pair bonding (Feldman 2012b, 2016; Feldman et al. 2010; Gordon et al. 2010; Weisman et al. 2012). Intracerebroventricular infusions of OXT induce maternal behavior in hormone-primed rats (Pedersen et al. 1982) and sheep (Kendrick et al. 1987). Furthermore, central OXT receptor distribution has been linked to naturally occurring variations in maternal behavior in the rat (Champagne et al. 2001), and it has been shown that OXT in female mice enables pup retrieval behavior by enhancing auditory cortical pup call responses (Marlin et al. 2015). However, OXT not only shapes maternal behavior, it also influences the social behavior of the infant. For instance, OXT increased affiliative affective facial expressions in newborn macaques toward the caregiver and decreased salivary cortisol (Simpson et al. 2014).

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Interestingly, the neurobiological mechanisms underlying the long-term persistence of mother-infant bonds in rats and pair bonds in monogamous prairie voles are remarkably similar (Numan and Young 2015). Both bonds are based on OXT and dopamine (DA) action within the nucleus accumbens, which promotes the synaptic plasticity required to make the infant or the mating partner rewarding (Atzil et al. 2011; Feldman 2017).

In humans, viewing the face of the romantic partner produces activity in striatal regions (Bartels and Zeki 2000; Acevedo et al. 2012), and an overlapping set of areas is activated when mothers are confronted with photographs of their children (Bartels and Zeki 2004). New lovers have higher OXT plasma concentrations than people not in a relationship (Schneiderman et al. 2012), and OXT administration significantly increased positive communication behavior during an instructed couple conflict discussion (Ditzen et al. 2009). By using functional magnetic resonance imaging (fMRI), it was shown that OXT may also enhance the bond between romantic partners. Specifically, the intranasal administration of OXT augmented neural responses to the romantic partner compared to a familiar person in the ventral tegmental area and nucleus accumbens in men (Scheele et al. 2013) and women (Scheele et al. 2016). Notably, this OXT effect was evident only in women who did not use hormonal contraception, indicating that bonding-related OXT effects are also influenced by gonadal steroids. To date, however, there is no direct evidence from human studies that these social effects of OXT are mediated by DA. The existence of OXT DA D2 receptor heteromers in the ventral and dorsal striatum have been documented (Romero-Fernandez et al. 2012), but so far the only positron emission tomography (PET) study to use the D2 receptor radioligand [11C] raclopride did not find altered endogenous DA release in the striatum or pallidum following OXT administration (Striepens et al. 2014). In this PET study, highly attractive but unfamiliar faces were presented to the participants, and the absence of bonding-specific stimuli (e.g. the participant's romantic partner or own child) could account for this null finding. Still, it is conceivable that non-dopaminergic actions are more important. In mice, the rewarding properties of social interaction require the coordinated activity of OXT and serotonin in the nucleus accumbens (Dolen et al. 2013), and another human PET study observed a modulatory impact of OXT on serotonin signaling (Mottolese et al. 2014).

Further fMRI studies have revealed that OXT also influences how mothers and fathers respond to photographs of children. Mascaro et al. (2014) reported that fathers have higher plasma OXT concentrations than nonfathers, whereas Wittfoth-Schardt et al. (2012) found that OXT increased activity in the caudate body in fathers in response to photographs of their own child compared to an unfamiliar child. Interestingly, Wittfoth-Schardt et al. also observed a diminished response in the globus pallidus to their own child or an unfamiliar child compared to a familiar child. In postpartum and nulliparous women, OXT enhanced activity in the ventral tegmental area to photographs of unfamiliar crying infants (Gregory et al. 2015). The presentation of an infant crying (Riem et al. 2011) and laughing sounds (Riem et al. 2012) produced activations in the amygdala which were reduced under OXT, thus suggesting that OXT also improves responsiveness to infant cues within parents in WEIRD (Western, educated, industrialized, rich and democratic) populations.

Notably, early life experiences appear to have a long-lasting effect on the OXT system. Current information in WEIRD contexts suggests that OXT interacts with attachment representations in adults' responses to infants. The OXT effect on amygdala reactivity in response to infant crying is particularly pronounced in individuals with insecure attachment representations (Riem et al. 2016). Likewise, the peripheral OXT response to infant contact at seven months is significantly higher in secure mothers compared to insecure/dismissive mothers, and positively correlated with greater activation in the ventral striatum when mothers with a secure attachment viewed their own infant's smiling and crying faces (Strathearn et al. 2009). Moreover, harsh parenting experiences moderate the OXT effect on the use of excessive force while listening to infant cry sounds (Bakermans-Kranenburg et al. 2012). Intriguingly, the exogenous administration of OXT also augments attachment representations later in life. Less anxiously attached individuals remembered their mother as being more caring and close after OXT, but more anxiously attached individuals remembered their mother as being less caring and close after OXT administration (Bartz et al. 2010; see also Buchheim et al. 2009). Thus, current concepts of social OXT effects emphasize the moderating role of interindividual and contextual factors (Olff et al. 2013; Hurlemann and Scheele 2015). For instance, OXT increases the perceived pleasantness of interpersonal touch and its associated neural response in insula, precuneus, orbitofrontal, and pregenual anterior cingulate cortex only when the touch is framed in a positive manner (Scheele et al. 2014). Along these lines, it seems likely that OXT also moderates the pleasant experience of interpersonal touch between parents and infants, as well as romantic partners. Collectively, OXT may contribute to human social bonding by modulating activity in a broad neurocircuitry involving reward-associated brain areas, such as the nucleus accumbens and ventral tegmental area and the amygdala (see also Sheridan and Bard, this volume). Clearly, future studies are warranted to elucidate how the multifaceted social effects of OXT result from the interplay between OXT and other neurotransmitter/hormonal systems.

Parental-Offspring Behavioral and Physiological Synchrony

Synchrony is one process that has been studied in some forms of attachment, albeit primarily in WEIRD populations. We note that synchrony is a general term that can refer to overlapping or joint action, as well as to contingent action—the latter defined as turn-taking and stimulus-response types of activity. Contingent actions are much more common in WEIRD mother-infant

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interactions, whereas overlapping or joint behaviors are more prevalent in relationally oriented cultures (Gratier 2003; Otto 2014; Morelli et al., this volume). Synchrony unfolds in different ways in more Western and more collectivistic societies (see Feldman et al. 2006). Although it remains for ongoing study to fully identify how synchrony unfolds and the specific aspects of similarity and difference across populations, current knowledge suggests that it is one core process in particular types of attachment relationships.

Early attachment relationships can provide a unique opportunity for "biobehavioral synchrony" or attunement between parent and child's physiological processes (Feldman 2012a). Biobehavioral synchrony is defined as the coordination between a parent and child's physiological (e.g., autonomic, hypothalamic-pituitary axis, alpha band activation in temporoparietal areas, OXT release) and behavioral states. Behavioral synchrony occurs via nonverbal patterns in the gaze, affective expression, co-vocalization, and touch-and-contact modalities. Of note, there is cultural variation with respect to the modalities that are emphasized. Thus, differences may appear in terms of norms for continuous contact or gaze synchrony, predominant in WEIRD cultures, whereas physical contact and movement synchrony may predominate in rural, relationally oriented cultures (Keller 2007; Morelli et al., this volume). Overall, synchrony can occur via any nonverbal modality and it likely shapes culture-specific neural pathways toward species-typical outcomes. For instance, we have behavioral evidence that Western parents express more facial synchrony whereas in other cultures, caregivers express more contact synchrony. In each culture, however, synchrony can predict a child's adaptation to the social group in later childhood and can also relate to a reduction of aggression toward peers.

In Western populations, synchronous interactions (in which behaviors are matched between parents and child) occur in somewhat different ways when the partner is the mother or the father. The maternal and paternal forms of synchrony—with more mutual gazing, affectionate contact, co-vocalization in the mother, and more matching of high positive arousal, exploratory behavior, and stimulatory touch in the father—can predict biological processes, such as OXT response or cortisol modulation. Parent-infant synchrony may play an important role in the three main functions of early relationships. These include the management of stress-regulation-homeostasis of physiological processes. In some cultures, the early relationship also serves to amplify positive arousal. For instance, young infants may experience positive affect primarily in social contexts, and less often when they are alone. Parent-infant synchrony may also function as a mechanism by which infants learn culture-specific rules of social behavior. Such learning may generally include whether, when, and how much expression of affect or emotion is appropriate in social contexts. More specifically, infants may learn how much arousal is appropriate to express, how much gaze to elders is permitted, and to what extent expression of negative affect is appropriate in social contexts.

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Links between infant-parent synchrony and a range of outcomes in later life have been found in longitudinal studies from the newborn to late adolescence (18 years of age) (Feldman 2007a, 2012a). These studies show that the experience of synchrony (mother or father) predicts a host of social-emotional outcomes across childhood and adolescence, such as greater empathy, emotion regulation, and socialization in multiple contexts (e.g., with close friends, social group, parents, or siblings). By contrast, disruption of synchrony can occur in ways that are unique to specific conditions that interfere with parent-infant bonding, such as prematurity, postpartum depression, or high contextual stress. Each of these may disrupt different aspects of synchrony. For example, in maternal depression, there is a major reduction in typical maternal behavior. By contrast, in conditions of high anxiety or stress, mothers often overstimulate and thus overload the infant, whereas mothers with substance abuse disorders often oscillate unpredictably between "too much" and "too little" mothering. Of key importance from the perspective of plasticity, it appears that each of these deflections may be repaired by synchrony-focused interventions (Bernard et al. 2013).

The evidence provided here is largely specific to one type of attachment relationship and derives from studies of a limited number of populations. Synchrony is a core process in some forms of attachment, especially between infants and caregivers, but we do not know in the same amount of detail, the forms and roles of synchrony in contexts with other caregiving arrangements. It seems possible that because synchrony requires familiarity with the behavioral pattern of the partners, the number of caregivers with whom an infant might establish synchrony is limited, not infinite. Thus, broadening the study of synchrony to include populations with other forms of infant-caregiver relationship networks remains important in order to identify the extent of similarity in terms of contributing to the development of competence and underlying neural processes.

The Parent/Caregiver Brain

Processes such as synchrony provide one example of how joint consideration of both the infant and the caregiver can illuminate the neural foundations of attachment. The role of the parental, or caregiver, brain is also of inherent interest in understanding how attachment relationships unfold. What we know about the parental brain is largely derived from work in rodents, including that of Fleming et al. (2009). They describe a subcortical system that includes the medial preoptic area, primed by hormones of pregnancy (OXT, prolactin), that projects to both ventral tegmental area (increasing maternal reward from pup stimuli) and amygdala (increasing maternal vigilance). This charts a subcortical system underpinning "motherhood."

Human studies have shown that these structures, particularly striatal and amygdala, are also activated in humans in response to their infants' cues. In humans, these subcortical structures are connected via multiple ascending and descending projections to several cortical systems, particularly those involved in "mentalizing" (temporoparietal junction, superior temporal sulcus), "mirroring" (inferior frontal gyrus, supplementary motor area), "affect sharing or empathy" (anterior cingulate cortex, anterior insula), and "emotion regulation" (medial prefrontal cortex, orbitofrontal cortex) to enable parents to share infant affect, infer intention from action, and plan long-term goals. The maternal and paternal brains chart somewhat different pathways. However, when fathers are primary caregivers, there are mechanisms by which the "paternal" pathway recruits the "maternal" pathways and no differences are found between them.

In Western human contexts, there is evidence that both the mother and father "synchronize" their brain response to their infant cues in real time in mentalizing and mirroring networks (supplementary motor area, temporoparietal junction, superior temporal sulcus, anterior insula). Whether similar rapid online brain-to-brain synchronization may occur or be required to support caregiving in arrangements in which multiple individuals care for the same infant is not yet known. What is known is that disruptions to the parent-infant bonding process (e.g., in situations of abuse, depression, or premature birth) also disrupt the parental brain in multiple ways. As with behavioral synchrony (discussed above), preliminary evidence shows that the parental brain is plastic and that some changes can occur after intervention.

Neural Outcomes of Disrupted Attachment and the Development of Competence

Much of our current knowledge about the neural processes and outcomes associated with attachment is derived from studies of individuals with significant disruption early in life, including children placed in orphanages, those abused as children, and those with diagnosed attachment disorders. Experimental studies of nonhuman animals have also focused on disruption models to identify neural consequences of infant-caregiver relationships. Although these studies do not directly identify the neural processes involved in the initiation and maintenance of infant-caregiver(s) attachments, they have been extremely valuable in identifying neural circuits and processes, brain regions, and functions that are likely involved in attachment.

The consequences of absent and adverse offspring-caregiver relationships are robust, apparent in many neurobehavioral systems, and show some consistency across species. For instance, a relatively old and large body of literature demonstrates that the hypothalamic-pituitary-adrenal (HPA) axis system is profoundly affected by disruption of infant care in multiple species, including humans, monkeys, and rodents (Gunnar et al. 2015a, b). Nonhuman animal studies are critically important to address questions that cannot be answered with human studies. Therefore the convergences between the results of human studies of disrupted early care and those of animal models provide key

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foundational data for hypothesis-driven experimental studies. Below we highlight, as examples, several areas in which both human and nonhuman animal studies provide such convergent evidence of neurobiological outcomes associated with absent or adverse offspring-caregiver relationships. The biological evidence gained from experimental studies in animal models has reliably underscored the persistent effects of early childhood experiences and their significance for health across the life span. It is important, however, to note the probabilistic nature of the relevant processes. Even the harshest conditions, which can be devastating for most people, can be associated with successful "adaptation" in some cases. This speaks to the multiple pathways to success and the incredible resilience of human development.

Oxytocin

Long-term consequences of negative child-caregiver relationships are found in neuropeptides that are centrally involved in social relationships. For example, lower than normal levels of OXT in cerebrospinal fluid occur in adult women with a history of childhood trauma and abuse (Heim et al. 2009), whereas lower than normal levels of OXT are found in the urine of socially deprived children when they interact with their mothers (Wismer Fries et al. 2005). Oxytocin diurnal secretions are presumably hyperregulated for coping with the environment in order for maltreated children to survive and thrive. Hormonal dysregulation was found by measuring salivary cortisol/OXT diurnal patterns; differences were found in maltreated children living in "settled" environments and "unsettled" environments (Mizushima et al. 2015).

Brain Morphology and Neurofunction

A growing body of evidence demonstrates associations between childhood maltreatment and aspects of brain morphology and function. The volume of some brain structures are reduced in individuals with childhood maltreatment: in the superior temporal gyrus (De Bellis et al. 2002), cerebellum (De Bellis and Kuchibhatla 2006), corpus callosum, and hippocampus (for a review, see Teicher et al. 2003). In children with reactive attachment disorder (RAD), a range of alterations in brain morphology and function are observed. In comparison with children with secure attachment relationships, children with RAD have a decreased volume of gray matter in the visual cortex and ventral striatum (Shimada et al. 2015). Neural circuits involved in fearfulness are affected by maternal care in rodents (Caldji et al. 1998) #and by maltreatment in human children (Gee et al. 2013; Fareri and Tottenham 2016; for a review, see VanTieghem and Tottenham 2017). In humans, maltreatment is associated with deficits in emotion regulation and with difficulties in activating the ventral medial prefrontal cortex in the context of negative affect. In addition,

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maltreatment is associated with deficits in behavioral and neural responses to rewarding stimuli.

In U.S. study populations, other forms of childhood adversity, such as poverty, are associated with difficulties in higher-order functions, particularly language and executive function. These behavioral differences are likely related to differences in prefrontal cortex function and structure, which are observed in children from lower socioeconomic status (SES) parents compared to higher SES parents (Hackman and Farah 2009; Noble et al. 2012; Sheridan et al. 2012b). In addition, poverty is associated with differences in hippocampal function and structure (Hanson et al. 2011). Whereas the deficits in higher-order cognition may be related to the quantity and quality of parent-child interactions, the differences in hippocampal function and structure are likely the result of chronic stress exposure associated with poverty (Hair et al. 2015). Although consistent with a long tradition of work on the behavioral and educational outcomes of poverty, these claims have yet to be substantiated with experimental studies.

Neurocognitive Development

In humans, there is also robust evidence of the influence of institutional care on child attachment and neurocognitive development. For institutionalized children, the lack of an attachment relationship is associated with risk for dysfunction in neurocognitive deficits: reduction in IQ, cognitive deficits, impulsivity, and attention as well as decreases in cortical volume and function (see Sheridan and Bard, this volume).

Childhood maltreatment also increases the risk for psychiatric disorders throughout childhood and into adulthood (Edwards et al. 2003; Gilbert et al. 2009). Maltreatment encompasses a spectrum of abusive actions (sexual, physical, emotional abuse) or lack of actions (physical, emotional neglect) by the parent or other caregivers. Associated with early life abuse and neglect, RAD is a psychiatric disorder that is characterized by a child's wary, watchful, and emotionally withdrawn behavior (APA 2013). Given the emotional dampening that occurs in RAD, the disorder closely resembles internalizing disorders with depressive and anxiety symptoms. In populations of maltreated children in foster care, 19–40% had signs of RAD based on DSM-IV criteria (Zeanah et al. 2004; Lehmann et al. 2013), in which RAD (inhibited type) and disinhibited social engagement disorder (disinhibited type) were not completely independent. Within a general population, RAD (as defined by DSM-5 criteria) has been reported in 1.4% of children (Minnis et al. 2013; Pritchett et al. 2014).

Despite its high prevalence and clinical importance, there have been very few investigations on the possible neurobiological consequences of RAD except for recent publications by Tomodo and her colleagues (Mizuno et al. 2015; Shimada et al. 2015; Takiguchi et al. 2015). Children with RAD have reduced activity in caudate and nucleus accumbens relative to typical-developing

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children. Overall, dopaminergic system alterations appear to be associated with RAD, in a manner that provides convergent evidence that attachment disruption is associated with persistent effects on the neural circuitry involved in both salience and reward (Tomoda 2016).

Nonhuman Primates

Decades of research with nonhuman primates have evaluated the neural consequences of variation in maternal care and infant rearing. A long-standing literature demonstrates that experimental manipulations, which include alternation of maternal behavior as a result of variable foraging demands and nursery-rearing in absence of the mother, produce wide-ranging and persistent effects. In these comparisons, individuals who are reared by their mothers are contrasted with individuals reared in a nursery, which parallels institutionalized children in terms of lack of primary attachment relationship (van IJzendoorn et al. 2009). In rhesus monkeys, a range of adverse early social experiences (e.g., maternal deprivation, maternal neglect, chronic low maternal status during the infant's first 6–7 months of life) is associated with both short- and long-term disruption of normal peer relationships (low play, excessive aggression), altered HPA reactivity, chronically low central serotonin metabolism, higher C-reactive protein levels, as well as differences in brain structure and function (Suomi 1987; Kraemer and Bachevalier 1998; Machado and Bachevalier 2003; Lyons et al. 2009; Nelson and Winslow 2009; Bennett and Pierre 2010). Consistent with findings from human studies (see above), monkeys with disrupted attachment exhibit alternations in responding to both rewarding and aversive stimuli (Nelson et al. 2009).

Studies that have addressed neurobiological differences between mother- and nursery-reared macaque monkeys have consistently (with the exception of Ginsberg et al. 1993) demonstrated significant effects of early differential rearing on various measures of brain morphology and composition, including differences in the caudate-putamen (Martin et al. 1991; Ichise et al. 2006), hippocampus (Siegel et al. 1993), cerebellar vermis, dorsomedial prefrontal cortex, dorsal anterior cingulate cortex (Spinelli et al. 2009), and corpus callosum (Sanchez et al. 1998; cf. Spinelli et al. 2009). The pattern of early-rearing group differences in these monkeys parallels the findings from neuroimaging studies of human populations with histories of early stress and trauma. However, some differences in brain morphology, such as hippocampal volume, that are associated with low SES in humans (see above) do not seem to be apparent in nursery-reared monkeys (Spinelli et al. 2009). The divergence in findings suggests that the experimental control possible in nonhuman primate studies (including group equivalence in adequate nutrition, environment, and clinical care) allows for a disentangling of the effects of the infant-caregiver relationship from other factors that can be confounded in human studies.

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In chimpanzees, we know that nursery-reared individuals have lower gray matter volumes than mother-reared individuals; however, no difference in white matter volume, total gyrification, or overall gray matter thickness has been found (Bogart et al. 2014). We also know that early-rearing experiences have a significant impact on the heritability of personality and dimensions of psychopathy, including meanness, boldness, and disinhibition. These traits are significantly heritable in mother-reared but not nursery-reared chimpanzees (Latzman et al. 2015). In rhesus monkeys, nursery rearing results in major changes in genome-wide patterns of mRNA expression (Cole et al. 2012) and DNA methylation (in lymphocytes and in prefrontal cortex; Provencal et al. 2012; Massart et al. 2014). As is true in other neurobiological systems associated with attachment, these patterns appear to be at least partially reversible with subsequent targeted interventions (Dettmer and Suomi 2014).

Genes, Epigenetics, and Plasticity

Evidence of plasticity, as well as knowledge about the biological mechanistic pathways that underlie plasticity, continues to emerge, as noted in many of the findings discussed above. There is a remarkable range of outcomes associated with variation in early experiences, including the nature of infant-caregiver relationships and, potentially, the diversity of relationship networks. The findings underscore a critical cautionary note: there is not a *single* structure, system, or gene responsible for overall outcomes with respect to the development of competence. Likewise, we should not expect that a *single* variable will account for an overwhelming proportion of variance in development. Such a cautionary note may appear obvious and simple. It is worth remembering, however, that as scientific findings are conveyed to the public and policy-makers, interpretative errors may convey a determinism that is not warranted (see Chapters 13 and 14, this volume) Both the exaggeration of the magnitude of effects as well as implications that a *particular* effect or mechanism is the *only* possibility can give the impression of determinism that is neither consistent with the multiple, redundant, developmental pathways, nor with our current knowledge of plasticity and epigenetic change.

Caveats and Limitations

In reviewing what is currently known, it is important to note that relatively narrow definitions of attachment have been employed to date, and that the majority of findings on the neural bases of attachment have been derived from research that has been conducted on a narrow range of model species. These limitations have most likely hindered the identification of universal core processes, which together permit variation and adaptation in offspring-caregiver relationships. That progress has relied on studies from relatively few species is not surprising, since laboratory studies in biological psychology, neuroscience,

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and other fields which contribute to this research focus primarily on a few model species. Arguably, this very focus may have enabled the detailed knowledge that we currently have. Nonetheless, because the diversity of offspring-caregiver relationships among other species is great (Hawkes et al., this volume), research should expand to include more diverse species. This is needed to uncover both similarity and variation in neural systems that contribute to attachment relationships.

It is critical to note that constraints involving the range of species used in neurobiological studies do not result from a narrowness in scientific inquiry, but rather from practical, political, economic, and sociocultural factors imposed on science. These constraints may occur across different types of study and pose unique challenges to research that is geared toward understanding the neural foundations of attachment: some assessments are noninvasive (e.g., OXT administration, cortisol from saliva), but detailed mechanistic experimental studies require different protocols. Much of what we know at the molecular level is from invasive research, terminal, and large N studies conducted with rodents (e.g., mice, rats, voles). This type of mechanistic work has been largely conducted in rodents not only because they are common laboratory model species, but also because their designation as such reflects particular societal views and practical considerations.

There is a wide range of nonhuman animals that are more similar to humans than rodents, in terms of neurobiology, behavior, or offspring-caregiver relationships—features which would enable comparative studies and increase our understanding of the neural foundations of attachment. Such animals include primates (particularly apes), dogs, cats, dolphins, and elephants. However, due to societal and practical considerations, it is highly unlikely that new (or continuing) experimental or invasive studies will occur using these animals. Thus, while it is crucial to include a greater range of species that can represent a greater variation in infant-caregiver relationships, there is also a great need for sensitivity to the broader sociopolitical reality in which the work occurs. In parallel, there is a corresponding need for thoughtful consideration of how sociopolitical reality affects the scope of scientific questions, the probability of advances in understanding causal mechanisms and the neural foundations of behavior, and in turn, the implications and consequences of those effects on both human and nonhuman animals (Bennett and Panicker 2016).

Open Questions

Many questions about the neural foundations of attachment remain as challenges. Some of these require attention from researchers working at points of intersection with basic neurobiological research and often involve nonhuman animal studies. Increased understanding of how culture impacts attachment

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would be beneficial, since a more specific understanding of the diversity of infant-caregiver(s) relationship networks is needed to inform the basic assumptions and definitions which underlie the selection of questions, animal models, specific hypotheses, and design of studies in attachment neuroscience research. Here we provide a summary of several sets of open questions that we believe are essential to advancing knowledge about the neural foundations of attachment.

Generalization, Cross-Cultural, and Cross-Species Considerations

Basic descriptive information about the processes and time course of different infant-caregiver arrangements is needed to generate hypotheses and design studies that can illuminate variation in neurobiological foundations related to attachment. For instance, all things being equal, does attachment manifest in the same way in monomatric and other forms of child-rearing? If one were to measure HPA axis in one-year-old children in different child-rearing cultures, would both the stress response and time course to return to baseline be the same across cultures?

A parallel set of open questions surrounds cross-species comparisons. Similar to the cross-cultural consideration, questions about the neurobiology of attachment could be informed by comparative analyses of species that vary in infant-caregiver arrangements. For instance, do the infants of mothers from primate species with and without alloparenting differ in HPA axis in response to separation? Do they differ in response to presentation of a stranger? To take another example, some prosimian species "park" their infants while the parent forages. What is the experience for the offspring during these times? Do they show any stress response over repeated separations?

When thinking about variation across species as well as across cultures, it is helpful to pay close attention to the ecology—broadly conceived (e.g., Keller 2007)—and other species characteristics, because this will help us define the challenges faced by both infants and parents. For example, the challenge for sheep (group-living mammals who deliver precocial young) is for mother and lamb to identify one another and learn to recognize each other very quickly; otherwise they will become separated, thus threatening the survival of the lamb. For primates, there is wide variation across species with respect to where they live, what they eat, whether or not they have multiple births, and group composition (size, stability, and structure). For humans, we tend to pay too little attention to these issues, because all human babies are born immature and are highly dependent for a long period of time. Nonetheless, ecology and subsistence patterns obviously play a role in determining childcare patterns. For example, within hunter-gatherer groups, there are differences between forest-dwelling, desert-living, savannah, and fishing-oriented groups in terms of what adults need to do to care for children (Hewlett and Lamb 2005). Do these environmental differences have implications or correlates at the neural

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level? If so, are these correlates differentially associated with the development of competency, with risk, or with plasticity?

Individual Differences, Stability over Time/ Development, Range of Variation in Competency

As discussed above, much of what we know about the neural bases involved in infant-caregiver(s) relationships derives from studies focused on disruption and aimed at understanding the effects of adversity and compromised outcomes. As a result, many open questions remain about individual differences in behavioral, emotional, and cognitive development; biological functioning; brain development; and patterns of gene expression or methylation. Additional questions exist concerning how these individual differences and child-rearing circumstances interact within different cultures, given the diversity of infant-caregiver(s) relationships. From the perspective of developmental systems theory, the need for basic knowledge about individual variation encompasses an appreciation of complex multidirectional processes, with interplay between culture, environment, behavior, brain, and genes, that unfolds across the life span. Better understanding of the range of variation within the spectrum of competency and underlying neural functioning is needed to guide the identification of core processes that are basic and common across the diversity of infant-caregiver(s) arrangements. How variation in developmental trajectories is associated with infant experiences and how experiences influence individuals during periods of special plasticity (i.e., adolescence, parenthood) also remain open. At the same time, they are questions that can be guided by integration of rapidly increasing knowledge about neural development during those life stages.

Evaluation of Domain-Specific Sensory Systems

It is clear that both the initiation and the maintenance of the infant-caregiver(s) relationship involve multiple and interacting systems. What is currently unclear, however, is whether evidence from one system can inform knowledge about others. For instance, to what extent can the neurobiological substrates of visual and auditory attachment cues be extrapolated to tactile and olfactory stimuli? Further research is needed to evaluate both the generalizability and the specificity of the role of different systems and domains in the development and maintenance of attachment.

Animal Models

Studies of nonhuman animals as model species are crucial to progress in understanding the neural foundations of attachment. Identifying the molecular mechanisms for plasticity, for instance, would most likely depend on experimental study, including invasive research, that is prohibited in humans. As a result, open questions surrounding what aspects of attachment can and cannot be modeled in other animals remain as large and ongoing challenges. A key differentiation here is in identifying what we know (and do not know) about behavioral, social, emotional, cognitive, and higher-order representational processes of diverse species. In turn, open questions about the implication of these similarities and differences for processes relevant to attachment and infant-caregiver(s) relationships must also be addressed to advance hypotheses about underlying neural systems.

Possible Research Avenues

We have identified a broad range of gaps in knowledge about the neural foundations of attachment, particularly as concerns variance across cultures, species, and infant-caregiver arrangements. The number of avenues for possible research is extensive and diverse. Still, we believe that core areas for research have the potential to advance our understanding of neural contributions to attachment and may thus provide a more robust platform for identifying similarities and differences across culture, species, and types of infant-caregiver relationships. Here we outline several of those areas.

Neural Bases of Initiation and Maintenance of Attachment

With respect to the flexible glue model proposed above, several foundational questions need to be addressed. Identifying the core processes involved in both the initiation and the maintenance of attachment—and doing so at the level of neural, behavioral, and hormonal processes—is important. Mirror neurons, OXT, and amygdala-prefrontal cortex connectivity are potential areas to target: they have been identified in studies of disrupted relationships and in social neuroscience, and provide good examples for hypothesis generation and testing. It is of critical importance, however, for hypothesis-driven study to evaluate explicitly whether—and how—these core processes are unique to infant-caregiver attachment relationships. Fully identifying the neural and molecular elements of these processes will likely depend on experimental research with nonhuman animals.

In terms of the initiation phase specified in the flexible glue model, we believe that it will be difficult to pull apart the specific attachment pathway from other systems, particularly early in life. It may, however, be feasible in the future to demonstrate individual variations in attachment through longitudinal studies. At the same time, continued studies that focus on disruption of the developing attachment system are anticipated to contribute important data, particularly when the form or type of "adverse" experience is increasingly specified or constrained (e.g., Sheridan and McLaughlin 2014).

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Regarding the maintenance phase, there is a need to focus on the neural basis of children's attachment during this phase. There is a good amount of knowledge about how parents (mostly the mother or father in WEIRD populations) respond when they see pictures of their own versus other children. Less is known, however, about other modalities, the neural activity in children, and the range of variation. Studies directed toward understanding caregivers' response to hearing their own versus another child crying or to a response to an infant's body pheromones would, for example, be of interest.

Variability across Individuals, Culture, and Species

Future research needs to address variation in attachment across individuals, cultures, and species. Identifying species similarity and differences is crucial if we are to understand the neural systems involved in attachment and connect neural systems with different aspects of the infant-caregiver relationship. Identifying variations is also central to theory refinement and hypothesis testing. In addition, investigating the neural correlates of cultural variation in infant-caregiver(s) attachment networks is needed. Neuroscientific enquiry, however, must depend on, and be informed by, basic research on cultural variation in attachment. For example, research to identify the range of variation in the development of competency across cultures and how attachments are related to cultural variation is the necessary foundation to identify the underlying neural correlates of core processes, as well as variation. Thus, neurobiological research will continue to be dependent on research from other disciplines which assess variations in the quality of care, attachment, and outcomes in other countries. Absent that knowledge, neuroscientific studies will remain in jeopardy of applying inappropriate lenses.

Consequences of Adversity across Cultures and Generations

Despite substantial knowledge about the neural consequences of childhood adversity and disrupted attachment relationships, large gaps remain that need to be informed by cross-cultural study. Avenues for future research include identifying the neural consequences of adverse experiences that occur across cultures (e.g., infant and child abuse). Does cultural context modulate neural outcome? If so, how does this occur? It is critical to note that research must begin with a determination of the basic phenomena under investigation, as this is necessary to ensure comparability of data.

Alongside cross-cultural evaluation of the neural consequences of adversity, attachment across generations should also be examined. Research is needed, for instance, to illuminate how parenting and the underlying neural processes or "parent brain" may differ in individuals whose own early attachment was disrupted. There is good evidence that there is often cross-generational

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continuity. There is also good evidence that this is not even remotely *inevitable*. Thus, while making the case that an individual's own early experiences affects how they engage in infant-caregiver relationships, it is important to emphasize that, in many cases, adverse early-life experiences do not result in compromised competency. It is critically important to communicate this nuance and to avoid conveying an element of early-experience determinism. Evaluation of the neural consequences of variation in infant-caregiver(s) experiences, integrated with consideration of multiple systems which play a role in competency and the full range of outcomes, provides a path away from determinism and toward a more eclectic understanding.

Integration: Identifying Core Processes to Further Understanding

An important yet still unanswered area of enquiry concerns the need to identify and delineate better those systems and processes that facilitate the initiation of the attachment system, as well as those which contribute to its maintenance. Over the past decades, areas of the brain used to act upon, feel, and sense the environment have been observed to reactivate when these actions are observed in other individuals. This reactivation of the motor, emotional, and sensory systems has been named "shared circuits." The association between attachment and shared circuits is likely to be bi- or multidirectional. Shared circuits may help initiate and maintain attachment, and attachment may help wire up shared circuits.

Attachment may contribute to the development of shared circuits. Although we still know little about how shared circuits develop in infants, an influential theory suggests that congruence between (a) infants' motor programs, sensations, and emotions and (b) the sight and sound of these, as perceived by sensory systems, is key for the brain to connect neurons in sensory systems selectively with matching representations in the motor, somatosensory, and emotional systems, respectively (Keysers and Gazzola 2014). In some cases, such Hebbian learning does not rely on social interactions. For instance, when a child learns to grasp objects, we know that the child will look intensely at his/her own hand. This means that the child will simultaneously activate neurons encoding motor programs to perform these actions and neurons encoding the sight of the action that the child now sees him/herself perform.

These simultaneous activations mean that synaptic plasticity will reinforce the connections between neurons responding to the sight of grasping with those responsible for the motor program for grasping. After this training, the sight of grasping will trigger activity in neurons responsible for performing the action. When a child sees someone else perform this action, the same connections will trigger the child's own motor program: a shared circuit has been wired. However, for other actions where we know shared circuits exist, the child cannot see him/herself perform the action. When a child is happy, for instance,

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the child will smile, but the child cannot see the smile. In Western societies, child-parent dyads show patterns of behavior in which the parent will avidly imitate the facial expressions of the baby. A happy baby will thus see the parent return a smile. The better this interpersonal synchrony, the more the brain will be able, according to Hebbian learning theories, to connect neurons involved in smiling and being happy with neurons representing the sight and sound of a smile and giggle. After repeated synchronized imitative interactions, the baby's brain will activate his/her own smile and happiness when witnessing happiness in others. A shared circuit now emerges from the synchronized social interactions which characterize parents generating healthy attachment styles in Western contexts.

To test whether attachment really favors the development of shared circuits via interpersonal synchrony, a promising research line might involve comparing societies in which parents imitate the facial expressions of their young babies with societies in which parents do not. With this type of study, we could explore whether an experience of imitation of facial expressions would lead to systematic differences in levels of motor and limbic activations in children when witnessing the facial expressions of others.

The visual-motor association described above could also be complemented and/or replaced by other sensory modalities-motor association. For instance, a happy state could be associated with an increase in vocalization, which would then allow the recognition of other's emotional states primarily through the auditory domain. Cultural and species differences in the preferred modality, therefore, would not necessarily impair the development of shared circuits or their relationship with attachment.

In addition to attachment being the basis for the development of shared circuits, shared circuits might be the basis for the development of attachment. This could take two forms. First, individual differences in shared circuits have been associated with differences in reported empathy (Singer et al. 2004; Jabbi et al. 2007), as well as with levels of prosocial motivation (Hein et al. 2010). Individuals who demonstrate stronger activations in shared circuits for emotions have been found to show higher levels of empathy for others and greater willingness to help. Accordingly, shared circuits in the parent may be a motivator for engaging in the type of interactions with the child that are the basis for the generation of healthy attachment. Second, shared circuits have been associated with the ability to engage in interpersonal synchrony—the ability to generate congruent actions in real time, in response to the actions of others (Kokal et al. 2009). As has been shown, Western parents who synchronize their actions to those of the child have children with more secure attachments; shared circuits in the parents may thus be critical in establishing and maintaining attachment. Finally, because they develop in part via attachment (see above), shared circuits enable the child to share the emotions of the caregiver and attune his/her own actions to those of the parent. Accordingly, the synchrony that is so critical for strong attachments is then no longer entirely the burden

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of the parent, but increasingly becomes the result of fine-tuned bidirectional synchronization via shared circuits in the child.

Although this approach would allow a certain degree of variability in the amount of synchronization required and the agent offering such synchronization, the presence of at least another agent and a certain degree of synchronization seem to be necessary conditions. Investigating shared circuits across different cultural settings or other species will expand understanding of the impact that the amount or type of synchronization and the number of agents might have on the relationship between shared circuits and attachment. Studying those cases in which shared circuits are impaired would then further facilitate understanding of the causality between shared circuits and attachment. Cases of poor or absent attachment could be used to investigate whether alterations in attachment cause a reduction in shared activity.

Conclusion

In this chapter, we have summarized important aspects of what is known about the neurobiology of attachment and posed critical questions that surround understanding of how attachment relationships are initiated. Much of what is known about the neural foundations of attachment derive from research that has been conducted on a limited range of species, within limited cultural contexts, and has focused on limited types of infant-caregiver relationships. Increased biological evidence about specific neural components of infant-caregiver relationships has, however, produced a fertile platform for hypothesis-driven and descriptive research, and can advance understanding of how brain development interacts with experiences from a diversity of caregiving relationships. Furthermore, it has become increasingly apparent that plasticity (and thus, resilience) constitutes a common theme in neurobiological, epigenetic, and behavioral findings. Observed plasticity illuminates what we believe to be a centrally important point in contextualizing attachment for neuroscientific study. Rather than conceptualize attachment in terms of a single type of relationship, or a rigid developmental channel, an expanded consideration of variation is needed to understand the neural foundations of infant-caregiver relationships and the role these relationships play in developing competence across the life span. This approach should enable the identification of common neurobiological elements of attachment, as well as the remarkable plasticity and diversity within and across individuals, cultures, and species.

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