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TOWARD A NEUROSCIENCE OF ATTACHMENT

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Toward a Neuroscience of Attachment

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Neurobiological studies of attachment are either abundant or scarce, depending on one's research tradition and scientific understanding of the term "attachment." On the one hand, the past two decades have seen a great deal of nonhuman animal work detailing the various neural manifestations of social bonding, familiarity, affiliation, caregiving, and other behaviors that can (and often do) fall under the general rubric of "attachment." On the other hand, neuroscientific investigations of normative attachment in humans have been limited and slow to develop, and similar investigations of the neural circuits supporting, or even associated with, individual differences in attachment (e.g., secure, anxious, avoidant, in the social psychology tradition; autonomous, preoccupied, and dismissing, in the clinical and developmental tradition; see Crowell & Fraley, Chapter 26, this volume) are exceedingly rare. These facts (and a cursory glance at the table of contents for this volume) underscore the complexity of attachment as a domain of inquiry, and suggest that, at present, any neuroscience of attachment is likely to strike some as limited in both empirical foundation and theoretical scope.

Nevertheless, it is important to make a beginning somewhere, and a neuroscience of attachment has much to gain from the integration of multiple research perspectives. Following Bowlby (1969/1982) and Ainsworth (1989), attachment bonds are considered in the present chapter to be those characterized by a high frequency of close proximity to the putative "attachment figure," especially during times of emotional stress. Moreover, attachment relationships are considered in this chapter to serve regulatory functions, often in relation to basic

physiological needs, but also with respect to many forms of emotional responding. These regulatory functions are social insofar as they result from interaction with conspecifics (other members of the same species). Some of the regulatory functions of attachment relationships are obvious and fundamental. For example, human infants literally cannot survive without the assistance of an adult caregiver. In later childhood, however, and in adult attachment relationships, emotion becomes the primary target of social regulation (Mikulincer & Shaver, Chapter 23, this volume). A major source of interest here is that the likely mechanism underlying the well-known link between social contact and health is the social regulation of emotion, particularly the social regulation of threat responding. The social regulation of threat responding is itself a major feature of attachment (Carter & DeVries, 1999; Edens, Larkin, & Abel, 1992; Hofer, 1995).

A large literature now suggests that a range of interactive social behaviors target physiological systems, temperamental dispositions, and overt behaviors associated with the stress response (Berscheid, 2003; Diamond, 2001; Sapolsky, 1998; Uchino, Cacioppo, & Kiecolt-Glaser, 1996). For example, supportive social behaviors are known to attenuate stress-related activity in the autonomic nervous system (ANS) and the hypothalamic-pituitary-adrenal (HPA) axis (Boccia, Reite, & Laudenslager, 1989; Flinn & England, 1997; Lewis & Ramsay, 1999; Weiss, 1990; Wiedenmayer, Magarinos, McEwen, & Barr, 2003). Maternal grooming behaviors affect glucocorticoid receptor gene expression underlying hippocampal and HPA-axis stress reactivity in rat pups (Weaver et al., 2004). In the context of a novel, mildly stressful new environment, rats in the company of a familiar companion engage in more exploration and play-soliciting behavior compared to rats in the company of an unfamiliar companion (Terranova, Cirulli, & Laviola, 1999).

Theorists have long argued that social bonding serves security-provision and distress-alleviation regulatory functions with respect to negative affect and arousal (Bowlby, 1973; Mikulincer, Shaver, & Pereg, 2003). Prominent evolutionary theorists dating to Darwin have even argued that because mammalian emotional responding evolved in a social context, emotional behavior is virtually inextricable from social behavior (Brewer & Caporeal, 1990; Buss & Kenrick, 1998; Darwin, 1872/1998). These diverse perspectives and literatures suggest that any robust conception of attachment will include multiple, distributed subsystems including (but probably not limited to) those devoted to emotion, motivation, emotion regulation, and social affiliation.

The promise of the emerging field of what we can here consider to be "attachment neuroscience" is at once to provide critical information about how the brain supports attachment behaviors and to forge links between research traditions as diverse as the basic neurosciences, behavioral ecology, and various subdomains of psychology such as developmental, social, and clinical, as well as affective science. In this chapter, the neural systems supporting emotion, motivation, emotion regulation, and social behavior are first reviewed. Following this, the social regulation of emotion and individual difference in attachment behavior will be considered from the perspective of behavioral neuroscience. Based on these reviews, the social baseline model of social affect regulation will be proposed. The social baseline model uses a neuroscientific framework to integrate models of attachment with a neuroscientific principle, economy of action, in the management of metabolic resources devoted to emotional and social behavior. Finally, recommendations are made for the development of a robust future neuroscience of attachment.

Attachment as a Neural Construct

Although attachment bonds are widely believed to result from a universal, innate "attachment behavioral system," attempts to locate a single, dedicated attachment circuit are likely to be, to paraphrase Wittgenstein, a bit like trying to find the real artichoke by peeling away all its leaves. Almost any interpretation of the attachment behavioral system reveals it to be a higher order construct comprised of constituent behaviors about which a great deal is known, even at the neural level (Fox & Hane, Chapter 10, this volume; Polan & Hofer, Chapter 7, this volume). For example, many studies have addressed the neurobiology of social behaviors such as recognition and familiarity, proximity seeking, separation distress, soothing behaviors, and maternal caregiving. Thus, one of the goals of this chapter is to introduce the neuroscientific study of attachment from the perspective of what is currently known about its social and emotional *constituents*.

A corollary goal is to move toward bridging two broad, rigorous, productive, and unfortunately disparate literatures. One is a thriving animal literature dedicated to what is variously termed "social bonding," "pair bonding," and "attachment bonding." The other contains a vast body of research on human attachment behavior, including studies of individual differences in internal working models of attachment (reviewed in Mikulincer & Shaver, 2007, and in J. Feeney, Chapter 21, this volume). Traditionally, these two worlds have had little to say to each other—a reflection of their starkly different research strategies as much as their different subject populations. Animal models, partly by virtue of what is ethically permissible with the population, often emphasize the study of social processes in terms of specific causal neural structures, circuits, neurotransmitters, neuropeptides, pheromones, or hormones. Attachment relationships are defined observationally, by the presence of separation distress or physiological soothing as a function of close proximity, or both. By contrast, social, clinical, and developmental psychologists often focus their efforts on "behavioral systems," seeking to understand how humans behave in and, importantly, what they have to say about, relational contexts.

This is not to say that research on attachment in humans has not utilized physiological measurement. On the contrary, psychologists have used measures of autonomic physiology, electroencephalography (EEG), glucocorticoid levels, and, more recently, functional magnetic resonance imaging (fMRI). These measures have provided valuable insights into human social behavior, but they are rarely capable of identifying causal brain- behavior relationships (Norris, Coan, & Johnstone, 2007), and their frequent dependence on self-report measures (including coded interviews) may result in neurobiological correlates that are quite distinct from those of behaviorally defined animal models (cf. Williamson, 2006).

Yet another difficulty presents itself in bridging these literatures. Even if the definitions of attachment were perfectly matched and each neural measure applied to humans and non- human animals were identical, the neural processes associated with attachment behaviors in non-human animals may not generalize perfectly to those in humans. Work on the social communication value of pheromones provides an excellent example of this point. Pheromones are chemical substances that convey information between members of the same species (Insel & Fernald, 2004). It is certain that nearly all animals, including humans, show at least some evidence of two distinct olfactory systems. The primary olfactory system is dedicated to the detection of odors that convey information about food or the presence or predators, and this system is most commonly associated with the sense of smell. By contrast, the accessory

olfactory system is, in many species, dedicated to the detection of specific pheromonal information. This accessory olfactory system consists of the vomeronasal organ (VNO) and the accessory olfactory bulb (AOB). Pheromones make contact with the VNO, exciting pheromone-specific sensory neurons projecting to the AOB.

In a wide variety of species, this system is capable of providing rapid and powerful information about sex, reproductive capacity, mate location, territorial boundaries, and even social status (Insel & Fernald, 2004). Nevertheless, the strongest of these findings derive exclusively from studies of animal populations, and after a great deal of initial excitement about the possibility of a human pheromone system, enthusiasm has waned significantly amid evidence that, although there does appear to be a human VNO, (a) there is no obvious pheromone-specific sensory neuron associated with it; (b) vomeronasal receptor genes present in the human genome appear to be pseudogenes (genes that have lost their protein-coding ability); and (c) the AOB does not appear to exist at all in the brains of adult humans (Meredith, 2001). In other words, the VNO—the primary and best-understood mechanism of socially critical pheromonal communication in animals—appears to be vestigial in humans.

Interestingly, evidence does suggest that chemical communication between humans can occur (e.g., Jacob & McClintock, 2000). However, unlike so many social species, the extent to which such effects are pheromonal, and whether they have anything whatever to do with the VNO, is uncertain at best. It is more likely that odors can moderate social information in humans, and that they do so through a distinct mechanism that is as yet poorly defined and understood (Meredith, 2001).

Despite all of these cautions, it is clear that research on animals has yielded invaluable information about the neurobiology of attachment, without which any understanding of human attachment would, at the neural level, be severely impoverished. Moreover, advanced neuroimaging techniques such as high density EEG, positron emission tomography (PET), transcranial magnetic stimulation (TMS), and functional magnetic resonance imaging (fMRI) promise access to human neural processes at a level of detail undreamed of until the very end of the 20th century. Hence the potential for building bridges between the animal and human attachment literatures is higher than it has ever been. FMRI studies in particular are, by virtue of their rapid proliferation and relative lack of invasiveness, beginning to supply pieces of the human social bonding puzzle that will compliment anatomical and molecular work in animals. Such advances promise the formation of a more comprehensive neuroscience of attachment.

The Neural Constituents of Attachment

Neural systems supporting attachment are likely to include, at a minimum, those underlying incentive motivation, certain forms of emotional responding, emotion regulation, and discrete social behaviors such as the establishment of familiarity and preference, proximity seeking, separation distress, and social affect regulation. This chapter is not intended to provide an exhaustive treatment of all possible constituent systems underlying attachment. In truth, because so many neural structures are involved one way or another in attachment behavior, it is possible to think of the entire human brain as a neural attachment system. Auditory, olfactory, and visual sensory systems are heavily implicated for obvious reasons. Memory processes involving, for example, long-term memory consolidation and retrieval in the hippocampus, underlie familiarity, recognition, and the maintenance of shared histories. A wide variety of

regulatory needs affected by attachment relationships are likely to be related to activity in the hypothalamus. Conflict monitoring demands will be made on the anterior cingulate cortex (ACC). Each of these systems and more contribute to attachment in a variety of ways. In this chapter, however, a smaller number of putatively basic elements will be reviewed.

Behavioral versus neural systems. I should first distinguish between what ethologists have long referred to as "behavioral systems" and what neuroscientists refer to as "neural systems." In ethology, a behavioral system is a set of behaviors associated with a common causal antecedent and resulting, once activated, in a common consequent, which in turn deactivates the system. Drawing on an ethological approach, Bowlby (1969/1982) described several behavioral systems associated with attachment. When discussing behavioral systems such as these, there is a great temptation to view the behavioral system as having a one-to-one relationship with some underlying neural system. But such tidy correspondences are rare. The term "neural system" describes coordinated neural inputs and signaling targets among a population of neurons that form a circuit. Neural systems can be tightly organized in close physical proximity or distributed throughout the brain. Highly similar or even identical behaviors may, across individuals, result from different combinations of activity in dissimilar neural systems. Moreover, similar neural activations can result in quite distinct behaviors. Thus, the search for specific neural circuits associated with time-honored, observationally defined behavioral systems is fraught with theoretical and empirical difficulty.

Bottom-up versus top-down processing. Although the terms "bottom-up" and "top-down" processing are frequently used in the cognitive neurosciences (and throughout the remainder of this chapter), their meanings may not be immediately obvious. Bottom- up processes are thought to begin, more or less, with sensory information, or with more evolutionarily "primitive" brain structures, working "up" to more integrative and evolutionarily modern areas such as the cortex. The process of receiving sensory inputs from the environment and converting those inputs into neural pulses that are relayed to cortical structures as consciously perceived information about one's surroundings would be an example of this. Top-down processes are essentially the opposite. In this case, integrative and evolutionarily "new" structures pass neural information "down" to more sensory-oriented and evolutionarily old structures, often to suit some regulatory purpose. One example of a top-down process might be the brain's tendency to impute information from memory and experience into stimuli in the periphery of the visual field, thereby imposing "best guesses" on visual information that is ambiguous.

Emotional and Motivational Elements

Incentive motivation, reward, and the dopamine system. Incentive motivation involves the acquisition of rewarding stimuli. The intensity of incentive motivation varies as a function of the state of the individual and the magnitude of the reward. For example, if a typical Westerner is mildly hungry and is offered a kind of food that is normally undesirable to him or her—uni (raw sea urchin), for example—there will be little incentive motivation to eat the food. If the individual is extremely hungry, however, the incentive motivation to eat the uni will be high. Similarly, if the same individual is again only mildly hungry, but is given a food item that is highly desirable—say a piece of chocolate cake—the incentive motivation to eat the cake will be high.

Incentive motivation plays a key role in a number of attachment-related processes (e.g., proximity seeking) and is tightly linked to the dopamine projection system of the ventral teg-

mental area (VTA). Dopamine is produced in the VTA and substantia nigra and projected to as many as 30 distinct networks (Le Moal & Simon, 1991). It has long been held that dopaminergic activity represents a neural substrate for the facilitation of goal- directed behavior (Berridge, 2007; Depue & Collins, 1999). Strongly implicated in this function is the nucleus accumbens, which is a major terminal area of dopaminergic projections from the VTA (Tzschentke & Schmidt, 2000). Dopaminergic activity within the VTA and nucleus accumbens has been repeatedly associated with reinforcing stimuli and the experience of pleasure. For example, rats capable of directly stimulating these circuits with a lever press will repeatedly do so, even in lieu of access to food, water, and sex. This preference for lever pressing over food and water will continue even to the point of death (Bozarth & Wise, 1996).

Dopaminergic cells in the VTA are also highly responsive to conditioning (Depue & Collins, 1999), especially to cues that predict the receipt of reward (Schultz, Dayan, & Montague, 1997). Importantly, the VTA is also responsive to stimuli that are unconditioned. Unconditioned stimuli are those that naturally, automatically, and unconditionally trigger a response in an organism. Positive unconditioned stimuli act as reinforcers, and include certain flavors, water, sleep, touch, and the presence of a variety of social cues. Negative unconditioned stimuli act as punishers or negative reinforcers, and include pain, social deprivation, and putrefying odors (Rolls, 2007a). With repeated exposure to unconditionally reinforcing stimuli, dopaminergic neurons in the VTA become sensitive to cues associated with those stimuli. In this way, the VTA begins to activate the nucleus accumbens earlier and earlier in a "chain of cues" that increase the probability of coming into contact with the original unconditioned reinforcer (e.g., an attractive potential mate). Put another way, conditioned associations between cues related to desirable unconditioned stimuli and dopaminergic activity in the VTA increase the predictability of those unconditioned stimuli, and, hence, the opportunities for obtaining them (Depue & Collins, 1999).

The amygdala and hippocampus in affect and memory. The amygdala is now one of the most widely recognized brain structures associated with emotion (Phelps & LeDoux, 2005). Far from a unitary structure, the amygdala contains many sub-nuclei, accounting for its involvement in a vast array of emotional responses. A large body of research now supports the notion that the amygdala is sensitive to both conditioned and unconditioned signs of threat. Moreover, at least two pathways to amygdala activation associated with visual stimuli exist, both of which can mediate fear learning. One is a very rapid and direct route through the thalamus (the thalamo-amygdala pathway) that processes obvious or highly specific sensory information (e.g., the shape of a snake, Le Doux, 2000; Öhman, 2005). Another pathway processes slower and more complex information in the visual cortex before activating the amygdala. When paired with unconditioned aversive stimuli (e.g., a loud noise, pain), otherwise meaningless stimuli quickly come to be associated with the presence of a threat, and this conditioning appears to be dependent to a large degree on amygdala functioning in humans as well as animals. Importantly, although it at first appears as if threat responding in the amygdala is an entirely bottom-up phenomenon, there is evidence that amygdala activity is modulated by top-down processes related to attention (Pessoa, Kastnerb, & Ungerleider, 2002).

Interestingly, the amygdala is exquisitely sensitive to social signals expressed on the face (Benuzzi et al., 2007; Rolls, 2007b). Human patients with impaired amygdala functioning have difficulty processing emotional facial expressions, especially those communicating social emotions (Adolphs, Baron-Cohen, & Tranel,

2002; Adolphs & Tranel, 2003; Adolphs, Tranel, & Damasio, 1998). Fearful faces in particular reliably activate amygdala in normal human subjects (Thomas et al., 2001; Whalen, in press), even when the presentation of faces is so rapid that subjects have no conscious memory of them (Whalen et al., 1998), or when the faces are reduced to "essential elements," such as when no cue but the raised upper eyelid is shown (Whalen et al., 2004).

Bearing all of this in mind, it is noteworthy that the amygdala also plays a major role in the consolidation of both positive and negative long-term memories. Amygdala activity during memory encoding is associated with the recall of emotionally salient information even weeks after testing (Hamann, Ely, Grafton, & Kilts, 1999). Beta-adrenergic blockade of amygdala function appears to impair these effects (Cahill, Prins, Weber, & McGaugh, 1994). These findings suggest that the amygdala "tags" sensory experiences as significant or salient and that this tagging is prominently represented in long-term memory consolidation. Importantly, the hippocampus appears to support the formation, storage, and consolidation of associations between internal states and spatial or contextual environmental stimuli (Brasted, Bussey, Murray, & Wise, 2003; Kennedy & Shapiro, 2004).

Ultimately, both the amygdala and the hippocampus are likely to underlie the identification and consolidation of significant interactions between attachment figures and emotionally salient situations. The amygdala will tag emotionally salient stimuli and participate, along with the hippocampus, in the consolidation of contextual cues associated with those stimuli in long-term memory. Among those contextual cues will be the behavior of attachment figures.

Threat responding, social soothing, and the hypothalamus. The hypothalamus regulates a variety of metabolic and autonomic processes, as well as linking the central nervous system to the endocrine system, most famously in the case of cortisol release via the hypothalamic-pituitary-adrenal (HPA) axis (Kemeny, 2003). The hypothalamus receives inputs from a wide variety of structures implicated in social behavior, emotion, stress, and attachment, including the amygdala, prefrontal cortex, and hippocampus (McEwan, 2007). The periventricular nucleus of the hypothalamus is capable of synthesizing corticotrophin-releasing hormone (CRH; Gainer & Wray, 1994). In threat responding, CRH released by the hypothalamus stimulates the release of adrenocorticotropic hormone (ACTH) in the pituitary gland. ACTH causes increased production of cortisol and catecholamines (e.g., epinephrine and norepinephrine) in the adrenal cortex. This cortisol is circulated throughout the body, including the brain. Critically, circulating cortisol in the brain is capable of activating glucocorticoid receptors in the hippocampus that feed back to inhibit the HPA- axis (Kemeny, 2003).

Importantly, the hypothalamus is one of the key structures implicated in the regulatory effects of social soothing on neural threat responding, including interactions with attachment figures (Carter, 2003; Coan, Schaefer, & Davidson, 2006b). The precise mechanisms by which social soothing down-regulates HPA-axis activity are currently unknown (Coan et al., 2006b), but the hypothalamus is known to coordinate the activity of many behavioral and physiological systems, including those involved in maternal behavior and pair bonding. Moreover, maternal and pair bonding behaviors are strongly associated with oxytocin and vasopressin, neuropeptides (reviewed below) that the hypothalamus is capable of synthesizing in abundance (Carter, 2003; Gainer & Wray, 1994).

The prefrontal cortex (PFC), emotion, and emotion regulation. Many regions of the PFC are implicated in emotion, motivation, and emotion regulation (Coan & Allen, 2004; Coan, Allen, &

McKnight, 2006a). Indeed, portions of the PFC are strongly connected to the dopaminergic projection system (e.g., nucleus accumbens and VTA), and the PFC shares numerous connections with the amygdala, hippocampus, and hypothalamus. For example, the orbitofrontal region of the PFC assists the amygdala and hippocampus in linking the emotional value of secondary sensory information (e.g., place cues) to primary reinforcers such as food, water, and social contact (Rolls, 2007a).

One of the major functions of the PFC is the regulation of emotion. Prefrontal regions may bias brain circuits responsible for appraising the emotional content of sensory stimuli and instantiating behavior directed toward approach- or avoidance- related goals (e.g., via amygdala or nucleus accumbens; Davidson & Irwin, 1999). Different portions of the PFC underlie different emotion-regulation strategies (see Ochsner & Gross, 2005, for a review). These can include "automatic" forms of emotion-regulation and effortful forms related to the cognitive control of attention or stimulus appraisal (Ellenbogen, Schwartzman, Stewart, & Walker, 2006). Automatic forms of emotion regulation include conditioning and extinction learning, including instrumental avoidance. These rapid and automatic regulatory functions (especially extinction learning) have been associated with the ventromedial and medial orbital PFC (Milad et al., 2005; Quirk & Beer, 2006; Sierra-Mercado, Corcoran, Lebrón-Milad, & Quirk, 2006). More "effortful" forms of regulation require attention, working memory, and other cognitive operations (Ochsner, Bunge, Gross, & Gabrieli, 2002). For example, cognitive reappraisals have been used to alter the meaning of a stimulus, and attentional practices (e.g., meditation) have been used to alter attentional foci associated with affective stimuli. These processes have been associated with more lateral, especially dorsolateral, portions of the PFC—regions also known to support working memory, language, and action planning operations (Ochsner et al., 2002).

Thus, the PFC may be associated with attachment processes in at least two ways. First, over time, medial orbital circuits may encode conditioned or "automatic" responses to attachment figures related to excitatory or inhibitory responses to threat cues. Second, dorsolateral circuits may modulate cognitive operations associated with attachment figures in reflective, working memory. In truth, these distinctions are not likely to be as discrete as the above formulation suggests, but the distinction between medial orbital and dorsolateral circuits of the PFC offers a useful neural heuristic for thinking about the regulatory influences of attachment figures in automatic versus explicit terms, respectively.

Emotional constituents in combination. Because all of the constituent systems described above are linked, it is possible for them to coordinate in important ways. For example, dopaminergic neurons in the VTA share connections with many regions other than the nucleus accumbens, including the amygdala (in various nuclei as well as the extended amygdala), the hippocampus, the hypothalamus, and the PFC (Depue & Collins, 1999). In this way, these structures form their own distributed networks of often reciprocal influence. To understand how such a network may function, consider the distribution of activity following an encounter with an unconditionally rewarding stimulus. Dopamine is released from the VTA, which stimulates dopaminergic activity in the nucleus accumbens associated with pleasure. The amygdala "tags" sensory properties of the stimulus as affectively salient or significant, placing special emphasis on those properties during the process of long-term memory consolidation via the hippocampus, which also encodes contextual information as part of the consolidation process. The PFC uses this information to effect action plans and regulate

subsequent behavior—both automatic and effortful—relevant to the stimulus. As experience with the rewarding stimulus increases in frequency (partly as a function of successful regulation and action planning activity in the PFC), the affective "tagging" of cues associated with it proceeds down a "chain of cues," increasing the probability that the rewarding stimulus will be accessed (or avoided in the case of unconditionally negative reinforcers).

For a more concrete example, consider an encounter with an attractive potential mate. In many species, including humans, such an encounter is unconditionally reinforcing. The encounter initially elicits pleasurable feelings and an increase in incentive motivation associated with the partner. Amygdala tags sensory features of the encounter as salient during the process of memory consolidation in cooperation with the hippocampus, and the VTA becomes conditioned to cues associated with (and predictive of) the potential mate, thereby activating incentive motivation circuits early in the "chain of cues" that will increase the likelihood of encountering the potential mate again. With repeated exposures, and perhaps a bit of luck, the potential mate may even respond in kind. With this, the foundation of pair-bond attachment has been set, and the complex process of attachment bonding has begun (see Zeifman & Hazan, Chapter 20, this volume). During the attachment bonding process, the PFC utilizes information about the potential mate to adjust its emotion-regulatory activities, opting, in many cases, to cede some level of regulatory effort to the potential mate, as discussed below.

Social Elements

Familiarity and preference. One of the bedrock features of any species deemed social (as well as any conception of attachment) is the ability to distinguish individuals who are familiar from those who are not—an ability that in turn is yoked to a preference for the familiar. Indeed, the establishment and maintenance of preferences for familiar others (caregivers, peers, one's mate, etc.) form the first necessary condition of attachment bonds. Through evolutionary time, familiarity was likely a matter of survival, and so it remains in the case of infants and their caregivers. One of the striking things about humans (and many other mammals) is how well designed we are for affiliation (Depue & Morrone-Strupinsky, 2005). Many stereotyped behaviors, including facial expressions, vocalization, bodily gestures, etc., are calibrated to signal social closeness and/or discomfort. These signals are readily recognized by most humans, and may in many cases be innate (Laird & Strout, 2007; Rolls, 2007a).

More than half a century ago, Bowlby (1969/1982) suggested that infant-mother bonds, characterized by both the ability to distinguish the caregiver from others and a strong preference for the caregiver, formed very rapidly, and this appears to be true in many species. Most researchers who study infants agree that the development of attachment bonds is critical, because infants often must survive long periods of early development totally dependent upon their caregivers, even when those caregivers are neglectful or abusive (Simpson & Belsky, Chapter 6, this volume). The formation of such bonds appears mainly among birds and mammals, and is thought to have been present in their common ancestor, the therapsids (Insel & Winslow, 1998).

Among social species, the most common manifestation of the attachment bond—indeed its commonest exemplar—is, as Bowlby suggested, the bond between a human infant and its mother (Insel & Fernald, 2004). Human infants have the capacity to distinguish their mother from others within hours after birth (DeCasper & Fifer, 1980). Most researchers agree, however, that in many species attachment bonding represents a more generalized capacity—one that is only very frequently ap-

plied to the actual mother. Indeed, many birds become bonded within hours to the first moving object they encounter. Interestingly, Lorenz (1935) discovered that geese reared by him not only bonded to him (and followed him) as if he was the parent, but also that they "courted" him upon reaching sexual maturity, preferring him to other geese. These observations raise important questions for a neuroscience of attachment, concerning the degree to which early sensory objects associated with a caregiver are rapidly and permanently "etched" into the developing brain, how such a thing can occur, and whether a critical period of bonding formation exists in early development.

Filial bonding, the locus coeruleus, and the amygdala. Filial affiliations are those concerning an offspring relating to a parent. In humans, strong attachment to the caregiver usually develops at six months of age, but filial bonds resembling this process appear from birth. Filial bonds may, however, differ from adult affiliation behaviors in important ways due to the dependent nature of the offspring-parent relationship. Many offspring of social species are totally dependent upon a caregiver for survival, and attachments are imperative regardless of the quality of the care (Hofer & Sullivan, 2001). Indeed, nonhuman primates have been observed to exhibit strong attachments to their mothers even when the mothers are abusive, and this pattern extends to human children (Moriceau & Sullivan, 2005). Rat pups have been observed to form preferences even to stimuli paired with electric shock, a seemingly paradoxical effect thought to have developed as a means of preventing pups from aversion learning while being handled roughly by the mother (Hofer, 2006), an unfortunate predicament but generally not as unfavorable as being abandoned. Ultimately, filial bonds need to be understood in the context of this high level of dependence, at least early in development.

It is largely for this reason that at least some of the neural circuitry associated with attachment in infants is likely to be different from that in adults. This may explain why filial bonds occur so rapidly and unconditionally by comparison with attachment formation in adulthood. In fact, filial bonding may precede birth, where learning about the mother's voice and odor may occur. In many species, odor is thought to play a significant role in the identification of the primary caregiver soon after birth and thereafter, even among human infants (Insel & Fernald, 2002). For example, maternal odor has been observed to elicit orienting responses in infants, as well as having soothing effects on human infant crying (Marlier & Schaal, 2005; Schaal, Marlier, & Soussignan, 1998).

Filial bonding also occurs in a context of significant neural development. The human brain grows exponentially during the first year of life and continues to develop rapidly into the second year (Franceschini et al., 2007). Glucose metabolism rises gradually until about the 4th year, and on average the level of brain glucose metabolism is more than double that of adults until about age 10 (Chugani, 1998). The production of neurotrophins— proteins that aid in neuron survival—are dependent upon neuronal activity and, by extension, environmental stimuli (Berardi & Maffei, 1999; Cancedda et al., 2004). Within the first two years of development in humans, the brain's production of axons, dendrites, and synapses far exceeds its needs. Synaptic connections are then "pruned" throughout childhood due to lack of use; that is, synaptic connections that go unused are discarded (Reichardt, 2006). In this way, the environment exerts its influence on the otherwise genetically determined neural development of the brain. At a systems level, neural organization tends to follow functioning— repetitive and patterned activation—during development (Hebb, 1949; Posner & Rothbart, 2007).

Throughout the earliest stages of this process, at least two brain structures, the locus coeruleus and the amygdala, interact to facilitate the familiarity and reinforcement associated with the caregiver in filial bonding. Although in adults, norepinephrine (NE) moderates memory consolidation and learning (Cahill et al., 1994), NE from the locus coeruleus appears to be both necessary and sufficient for learning in human and animal neonates (Sullivan, 2003). And the neonate locus coeruleus releases large amounts of NE early in development (Nakamura & Sakaguchi, 1990). When combined with sensory information such as the look, sound, and smell of a caregiver, that sensory information is likely to be learned rapidly. Importantly, this learning is occurring alongside a neonatal amygdala that is not yet fully functional, making it difficult or impossible for aversive conditioning to occur (Sullivan, 2003). In other words, the amygdala, being immature during early neonatal development, may not be capable of associating aversive stimuli with alarm or avoidance behavior, leaving virtually all stimuli to be simply encoded as "familiar," which is, for many intents and purposes at this stage, unconditionally reinforcing.

During this developmental period, neural pathways linking amygdala to hippocampus are similarly underdeveloped, as are many regions within the PFC (Herschkowitz, 2000). This suggests that learning in neonates may not involve the PFC, or may do so only in limited ways. In either case, these systems begin to develop rapidly in infancy, leading many to refer to this developmental time as a "critical" or "sensitive" period for neural development. Sensitive periods have been studied extensively in terms of the brain's sensory systems. For example, Hubel and Wiesel (1970) observed that a temporary blockage of visual input to one eye in cats during early development caused irreversible impairment in the visual cortex. Similarly, children born deaf have been observed to cease vocalizations in late infancy, likely due to a lack of auditory stimuli (Schauwers et al., 2004). Interestingly, research on the social complexity of rearing environments in rats suggests that environments rich in social and cognitive complexity are associated with significantly more synapses per neuron throughout the visual cortex compared to simple socially paired housing and individual housing (Briones, Klintsova, & Greenough, 2004). These effects remained even after later environments were changed or reversed, suggesting that plastic changes associated with early experiences are persistent.

In combination, these findings suggest that filial bonding occurs rapidly and unconditionally. Moreover, the filial bond develops in a context of rapid neural development, during what appears to be a sensitive period of learning. As will be discussed in greater detail below, this process, especially to the extent that it involves developing links between the PFC and affective structures like the amygdala and nucleus accumbens, may result in the development of different reflexive "assumptions" about the nature of the social world, including that world as it will be encountered in the future. This may set the stage for different broad strategies for engaging (or avoiding) social stimuli, perhaps especially during emotional situations. Indeed, conditions under which the filial bond forms and develops may constitute a kind of rudimentary "pre-working model" of interdependence and affect regulation—of attachment—that is either altered or reinforced during the course of development throughout childhood.

Adult affiliation, nucleus accumbens, and the social neuropeptides. Of course, attachment bonds characterized by interdependence and affect regulation extend far beyond the prototypic mother/infant relationship. Adult attachments occur in the context of romantic relationships—especially monogamous ones—but

adult attachment is probably not restricted to this. Indeed, relationships that meet attachment criteria have by now been documented between pairs of individuals as diverse as adult romantic partners (Fraley & Shaver, 2000); captive chimpanzee cage mates (Bard, 1983; Miller, Bard, Juno, & Nadler, 1986); chimpanzees and their human caretakers (Miller, Bard, Juno, & Nadler, 1990); and even between domesticated dogs and their owners (Topal, Miklosi, Csanyi, & Doka, 1998). Aspects of attachment seem to occur even between organization members and their leaders (Davidovitz, Mikulincer, Shaver, Ijzak, & Popper, 2007).

Of interest here are neural circuits that support the establishment and maintenance of attachment bonds in later childhood and adulthood. How does the brain facilitate movement from close proximity, to familiarity, to attachment? To start, positive, possibly unconditioned, social affiliation behaviors (e.g., eye gaze, soothing vocalizations, non-threatening facial and bodily behaviors) increase proximity between conspecifics, setting the stage for motivated attachment bonding. It is clear that some social cues are unconditionally capable of activating neural structures supporting incentive or reward motivation, especially the nucleus accumbens and the VTA (Allen et al., 2003). For example, passively viewed images of female faces have been observed to activate the VTA and nucleus accumbens unconditionally in heterosexual men (Aharon et al., 2001). In rats, maternal females show an increase in dopamine release in the nucleus accumbens when exposed to pups (Hansen, Bergvall, & Nyiredi, 1993). Depletion of dopamine in the VTA and nucleus accumbens via lesions or dopamine antagonists virtually eliminates rat maternal behavior (Hansen, Harthon, Wallin, Löfberg, & Svensson, 1991). Interestingly, maternal behaviors not directly associated with caregiving, such as nest building, passive nursing, and aggression, are virtually unaffected by these manipulations. Other studies have linked dopamine release in the nucleus accumbens and VTA to the spontaneous establishment of partner preferences (Aragona et al., 2006).

Mating behavior in the absence of partner preference is also associated with dopamine in the nucleus accumbens (Balfour, Yu, & Coolen, 2004; Pfaus, Kippin, & Centeno, 2001), however, suggesting that dopaminergic activity in the nucleus accumbens is insufficient for the establishment of partner preferences. This raises the question of how the establishment of partner preferences is "linked up" to the dopaminergic incentive motivation system. Here, the neuropeptides oxytocin and vasopressin appear to play major roles (Depue & Morrone-Strupinsky, 2005; Young & Wang, 2004). Both have been associated with the formation of partner preferences regardless of mating behavior, and both, but especially oxytocin, are elicited by positive social behaviors (Uvnaes-Moberg, 1998).

Perhaps the most celebrated example of the function of these neuropeptides derives from work on pair bonding within monogamous prairie voles (Borman-Spurrell, Allen, Hauser, Carter, & Cole-Detke, 1995; Carter, 2003; Insel & Fernald, 2004; Young & Wang, 2004). When these animals forge a pair bond, they mate, share nests and territory, cooperate in care of young, and forcefully reject intruders of either sex (Borman-Spurrell et al., 1995). Unlike nonmonogamous animals—including other variants of vole—the nucleus accumbens of these animals is rich in oxytocin receptors. Moreover, structures like the ventral tegmentum and ventral palladium are rich in receptors for vasopressin (Lim, Hammock, & Young, 2004; Lim & Young, 2006).

Findings such as these provide clues as to how social cues activate incentive motives associated with dopaminergic activity and in turn the formation of partner preferences and proximity-

seeking behavior. Socially sensitive oxytocin and vasopressin circuits in the VTA, nucleus accumbens, and ventral palladium probably stimulate dopaminergic activity linked to incentive motivation. Because activation of this dopaminergic system is frequently associated with positive affect and reward, it may be that the degree of oxytocin and vasopressin activity determines the degree to which a social experience is rewarding, by virtue of the dopaminergic cascade that follows it.

Proximity seeking, the dopamine system, and endogenous opiates. One of the natural consequences of familiarity, preference, and bonding is proximity seeking, a characteristic of social behavior strongly associated with attachment. Proximity seeking is likely an extension of motivational circuits associated with reward and partner preference. Of course, individuals can seek close proximity as a function of positive affect and reward or in response to cues of punishment where the goal is the provision of safety (Depue & Morrone-Strupinsky, 2005). In the case of positive affect, proximity is sought because the attachment figure has become associated with rewarding feelings of pleasure, and close proximity increases the frequency or intensity of these feelings. In the case of negative affect, the attachment figure may serve as a safety cue, eliciting approach behaviors oriented toward the acquisition of security. In this way, proximity seeking can involve both reward-related approach behaviors and approach behaviors associated with active avoidance.

Behaviorally, these motivations may appear to be identical, but they are likely to involve both shared and distinct neural circuits. Moreover, although attachment theory emphasizes the emotion-regulatory function of proximity-seeking due to the need for security, it may be counterproductive to downplay the role of proximity-seeking due to reward processes. It may be the case, for example, that at the neural level reward-related proximity conditioning is tightly bound to the provision of security by the attachment figure in other contexts. From the perspective of the VTA and nucleus accumbens, there may be little difference, because they become in either case sensitized to the presence of the attachment figure as a positive outcome.

In addition to the reinforcing nature of dopaminergic activation, consummatory pleasure may play a role in rewarding social interaction. After all, positive social experiences are characterized in everything from semi-structured scientific interviews to ancient literature as involving feelings of warmth, closeness, love, affection, and pleasure. Depue and Morrone- Strupinsky (2005) have argued that feelings of consummatory pleasure promote the development of contextual associative memory networks that help both to establish and to maintain social bonds and that are ultimately responsible for many of the regulatory effects associated with the soothing and security provided by attachment relationships. The critical substrate for these feelings, and perhaps for the socioaffective regulatory effects that accompany them, may be the release of opiates that often follow activation of oxytocin receptors, also in structures like the nucleus accumbens and VTA.

There is abundant evidence for the role of endogenous opiates in a wide variety of social behaviors. In humans and other animals, these opiates are released during childbirth, nursing, maternal caregiving, sexual activity, and many modes of tactile stimulation, including grooming and play behavior (Carter & Keverne, 2002; Keverne, Martensz, & Tuite, 1989. This release may mediate the reward associations that are forged between infants and mothers, as well as between romantic partners, and even platonic friends. For example, morphine, an opiate receptor agonist, increases the reinforcing effects of a host of maternal behaviors, mother-infant bonding, time spent by juveniles (rats) with

their mothers after a brief separation, grooming, and juvenile play behavior (Agmo, Barreau, & Lemaire, 1997; Niesink, Vanderschuren, & van Ree, 1996; Nocjar & Panksepp, 2007; Panksepp, Nelson, & Siviy, 1994). By contrast, opiate receptor antagonists such as naltrexone reduce reward conditioning effects associated with each of these forms of social contact (Graves, Wallen, & Maestripieri, 2002; Holloway, Cornil, & Balthazart, 2004). In humans, the administration of the opiate antagonist naltrexone was associated with increased voluntary isolation from friends, as well as decreased levels of enjoyment in the company of others (Jamner & Leigh, 1999).

Importantly, tactile stimulation appears to play a particularly powerful role in the activation of affiliative reward conditioning (Burgdorf & Panksepp, 2001; Melo et al., 2006). In some animals, the affiliative conditioning associated with maternal behavior is attenuated in the absence of tactile stimulation (Melo et al., 2006).

Attachment and the Social Regulation of Emotion

Many evolutionary accounts of the reproductive advantages of infant-caregiver bonds have been proposed, but similar accounts of adult attachment bonds are relatively recent (Simpson & Belsky, Chapter 6, this volume; Zeifman & Hazan, Chapter 20, this volume). Fraley and Shaver proposed that adult attachments represent homologies of the infant-caregiver bond co-opted by natural selection to facilitate pair bonding (Fraley & Shaver, 2000). By this account, adult and infant-caregiver attachment systems entail similar goals (the survival of offspring) and operate according to similar conditions of activation (e.g., presence of a threat) and termination (e.g., regulation of threat responding by the attachment figure). Evolutionary perspectives like these address ultimate function, in the sense of explaining why attachment bonds and capabilities persist among so many species.

Function can be considered in a more proximal, ontogenetic sense as well, and it is at this level that the regulation of affect may take center stage. Proximal functions of the attachment system are, following basic survival during infancy (Hofer, 2006), primarily concerned with the social regulation of emotional responding. Bowlby (1969/1982), following along with Ainsworth and her colleagues (e.g., Ainsworth, Blehar, Waters, & Wall, 1978), argued that a critical function of attachment figures was the provision of a secure base from which infants could explore their worlds relatively free of anxiety, and a safe haven to which the infant could return when distressed. It was proposed, for example, that the base from which an infant could explore its world was secure to the extent that the caregiver was responsive to the infant's distress. Many have since proposed that the quality of the caregiver-infant attachment bond—especially of the caregiver's status as a secure base—holds consequences for child and adult emotional functioning, including styles of interpersonal relating and emotion-regulation capabilities. A very large behavioral database now supports this notion with respect to both childhood and adulthood (for reviews, see Thompson, Chapter 16, and Mikulincer & Shaver, Chapter 23, both in this volume).

Throughout childhood, and certainly by adulthood, the regulatory effects of attachment relationships are likely to be felt in two broad ways. The first is immediate, as when the attachment figure is present and regulating emotional responding "on line." An example of this may be when a caregiver holds her child's hand during a blood draw at the doctor's office, thus actively soothing the child's anxiety as it occurs. The second is generalized, where the attachment figure is present only in the form of a mental representation. These representations may in theory manifest either as "internal working

models" based on procedural and semantic memory, or as declarative, explicitly recalled mental images. Indeed, on-line regulation experiences likely condition mental representations in both implicit and declarative memory. In the sections that follow, immediate, "on line" regulation is considered in contrast to "mental representations" of the attachment figure, often referred to as "internal working models," that may serve to preempt the level of distress an individual experiences in the face of a potential threat.

The "On-Line" Social Regulation of Emotion

Many researchers have observed the stress-buffering effects of social contact on behaviors and physiological systems related to emotional responding. This social buffering occurs at all levels (e.g., group, caregiver, familiar conspecific), but familiarity and attachment are associated with the strength of social regulation effects. Even in rats, the presence of familiar conspecifics ("buddy" rats) increases exploration and attenuates HPA-axis activity under conditions of threat (Kiyokawa, Kikusui, Takeuchi, & Mori, 2004; Ruis et al., 1999; Terranova et al., 1999). Familiar conspecifics attenuate emotional stress responding in non-human primates during new social group formation and social conflict (Gust, Gordon, Brodie, & McClure, 1996; Weaver & de Waal, 2003). As reviewed above, these effects are widely believed to derive from social cues that activate the release of oxytocin and vasopressin in the VTA, ventral palladium, and nucleus accumbens (Carter & DeVries, 1999; Heinrichs et al., 2001; Izzo et al., 1999; Uvnaes-Moberg, 1998; Windle, Shanks, Lightman, & Ingram, 1997). This in turn is thought to activate dopaminergic and endogenous opiate activity associated with consummatory pleasure and physiological soothing.

In humans, very little work to date has actually sought to identify how neural circuits associated with social affiliation and emotion function in a context that combines social interaction with externally generated emotional stress. Recently, Coan and colleagues (Coan et al., 2006b) collected functional brain images from 16 married women as they were subjected to the threat of mild electric shock while either holding their husband's hand, holding the hand of an anonymous male experimenter, or holding no hand at all. Their results suggest that physical contact from both attachment figures and strangers attenuates threat responsive neural activity in affect-related action and bodily arousal circuits (e.g., in the ventral anterior cingulate cortex), but also that down regulation of structures such as the nucleus accumbens, dorsolateral prefrontal cortex, and superior colliculus was achieved only via hand holding with the attachment figure. Moreover, Coan et al. (2006b) observed that some of the regulatory effects of soothing physical contact varied as a function of relationship quality, with higher quality predicting yet greater attenuation of threat-related neural activation in the right anterior insula, superior frontal gyrus, and hypothalamus during spousal, but not stranger, hand holding. These findings suggest that social proximity in general, and the presence of an attachment figure in particular, exerts bottom-up regulatory influences on the perception of threat in the brain. Moreover, the fact that stranger hand holding conferred regulatory benefits at all suggests that the human brain is unconditionally soothed to some extent by social proximity, which may lay the groundwork for the additional regulatory benefits associated with attachment figures.

Internal Working Models and Individual Differences

Thus far, we have primarily considered basic systems supporting "normative" manifestations

of attachment behavior, as well as a concrete example of the emotion-regulation functions of the attachment system occurring "on line" in real time. However, the emotion-regulatory effects of caregiving experiences such as those between infants and caregivers, or even between romantic partners, are likely to extend far beyond online moments of soothing and security provision. Bowlby (1979) considered many facets of early attachment experiences to hold implications for interpersonal and emotional functioning "from the cradle to the grave" (p. 129), and in the past several decades many researchers have adopted this idea as one way to understand adult interpersonal functioning and emotion-regulation capabilities.

Unfortunately, a large portion of what is known about links between early social experience, neural development, and subsequent emotional behavior derive from studies of abuse and neglect. For example, neglect and abuse (both physical and verbal aggression) are associated with risk for heightened stress reactivity, anxiety, depression, and social deviance that extend well into adulthood (Teicher, Samson, Polcari, & McGreenery, 2006). In one recent study, children who had experienced social deprivation and neglect in Romanian orphanages were observed to have lower overall levels of vasopressin, as well as blunted oxytocin responses to physical contact with their caregivers, relative to normally family-reared children (Wismer-Fries, Ziegler, Kurian, Jacoris, & Pollak, 2005). This is consistent with findings regarding social isolation as a well-known risk factor for a number of neurodevelopmental and psychosocial problems, ranging from anxiety and depression to increased risk of suicide, family problems, and even stress-related dwarfism (Barber, Eccles, & Stone, 2001; Kawachi, 2001; Newcomb & Bentler, 1988; Skuse, Albanese, Stanhope, Gilmour, & Voss, 1996). In nonhuman primates, frequent or prolonged separation of offspring from caregivers (primarily mothers) can result in socially deviant behavior and physiology later in life (Mineka & Suomi, 1978). Among brown capuchins monkeys, patterns of mother/offspring behavior partially determine the post-conflict reconciliation styles of offspring during later interactions with nonfamilial conspecifics (Weaver & de Waal, 2003).

Neural mechanisms linking early parental care to trait-like individual differences in threat responding over the life span have been expertly described by Meaney and colleagues (Weaver et al., 2004). This work suggests that in rats, grooming behavior by the mother "sets" or "programs" the degree to which her offspring react to threat cues throughout their lives. This modulation of threat reactivity has been observed both in behavior and in HPA- axis activity. Moreover, associations between maternal grooming and offspring threat reactivity have been linked to the expression of specific genes that moderate HPA-axis functioning. As reviewed above, the HPA-axis has its own built-in regulatory mechanism in the hippocampus, whereby circulating cortisol activates hippocampal glucocorticoid receptors, which in turn down-regulate the production of corticotrophin-releasing hormone in the hypothalamus. Grooming induces the expression of genes that encode for glucocorticoid receptors in the hippocampus, thus making the hippocampus more sensitive to circulating cortisol and, hence, more susceptible to down-regulation during stress. Cross- fostering studies by Meaney and colleagues strongly suggest that lifelong stress reactivity, and even the subsequent maternal behavior of female rat pups, is largely attributable the degree of post-natal maternal grooming and not to genetic inheritance (Weaver et al., 2004).

Attachment and internal working models. According to attachment theory (Bowlby, 1969/1982, 1973; Mikulincer & Shaver, 2007; Mikulincer &Shaver, Chapter 23, this volume), threat de-

tection capabilities evolved in part to activate the attachment behavioral system, thus increasing the likelihood that humans, beginning in infancy, would seek out and maintain proximity to attachment figures. Moderating the degree to which proximity to attachment figures is sought out in the context of a threat is attachment security, which is itself the product of many attachment-related experiences involving both threats and attachment figures. These experiences shape "internal working models" of attachment that guide emotion-regulation throughout life (see Bretherton & Munholland, Chapter 5, this volume). According to Bowlby (1969/1982), internal working models are mental representations of the availability and practical utility of attachment figures when threats arise, and of the self in relationship with these figures.

Recently, Hofer (2006) described a process by which very early developmental experiences in interactions with a caregiver may plausibly proceed from the on-line regulation of fundamental neural systems supporting sensory-motor, thermal, and nutrient functions to the shaping of internal working models of attachment security. In this model, access to primary reinforcers (e.g., food, water, warmth, touch) is dependent in early development on (a) caregiver support and (b) affective brain circuitry used to solicit caregiver support via expressed affect. Over the course of development, what begins as the regulation of physiological needs via affect becomes the regulation of affect per se (Hofer, 2006). Throughout this process, the regulatory behavior of the attachment figure (e.g., the provision of security, the alleviation of distress) is likely to set expectations about the availability of attachment figures during times of stress—the "internal working models" reflecting attachment security.

Thus, internal working models likely reflect conditioned associations between proximity to attachment figures and both internal needs and external signs of threat, mediated through the amygdala, nucleus accumbens and hippocampus, as well as portions of the prefrontal cortex. These conditioned associations may remain stable for long periods of time, especially to the extent that they continue to be reinforced by internal feelings of security, prevailing social contingencies, or both.

This process likely allows individuals to adapt themselves to a variety of environmental conditions (e.g., security restoring or enhancing experiences with attachment figures, frequent or lengthy absence of the caregiver, abuse by the caregiver, excessive caregiving). Such adaptations are referred to, in various research traditions, as attachment patterns, attachment styles, or attachment states of mind (e.g., secure, anxious, avoidant, preoccupied). These adaptations are thought to be relatively stable when the individual remains in a stable environment, and can be measured by observations, self-report questionnaires, and structured interviews (e.g., Crowell & Fraley, Chapter 26, Kerns, Chapter 17, and Solomon & George, Chapter 18, all this volume).

Behavioral research on the effects of different adult attachment styles suggests the presence of two relatively independent axes regarding attachment insecurity—anxiety and avoidance—along which individuals can vary (J. Feeney, Chapter 21, this volume; Mikulincer & Shaver, 2007). Moreover, different combinations of scores along these dimensions can result in particular styles of relating interpersonally. For example, individuals low in attachment anxiety and low in attachment avoidance would be considered generally secure in their attachments to others. Individuals high in both avoidance and anxiety are thought to avoid attachment relationships out of fear, while those high in avoidance but low in anxiety are thought to be "dismissing" of attachments, compulsively self-reliant, and unlikely to seek proximity to attachment figures under stress

(Bartholomew & Horowitz, 1991; Brennan, Clark, & Shaver, 1998). Finally, individuals low on avoidance but high on anxiety are thought to be preoccupied with attachment relationships.

Few studies to date have investigated individual differences in attachment styles using measures of neural activity, and some of the work that has been done serves only as an approximation. Indeed, attachment styles may, at a neural level, manifest as little more than individual differences in response capabilities among neural circuits supporting emotion, emotion-regulation, and social behavior. Interestingly, Dawson and colleagues (Dawson et al., 2001) observed that insecurely attached infants of depressed mothers were more likely to show PFC asymmetries lateralized to the right. By this metric, asymmetries in EEG activity in the alpha (8-13Hz) range (Coan & Allen, 2003; Coan & Allen, 2004) correspond with emotion regulation capabilities (Coan et al., 2006a), with relatively greater left PFC activity indexing an increased probability of approach behavior (e.g., anger, joy), and relatively greater right PFC activity indexing an increased probability of withdrawal behavior (e.g., sadness, fear). Thus, according to Dawson, insecurely attached infants of depressed mothers have a trait-like propensity to engage in withdrawal behavior (Dawson et al., 2001).

A very small number of studies have begun to associate adult attachment styles with brain function using functional neuroimaging technology. Recently, Coan and colleagues (2005) reported a variety of interaction effects between self-reported attachment scores and hand holding condition (spouse, stranger, alone) on threat-related neural activity throughout the brain. For example, under threat of mild electric shock, secure attachment scores were negatively associated with activity in the ventral anterior cingulate cortex (vACC) during spouse hand holding, and positively correlated with activity in the same region when holding the hand of a stranger. The vACC is implicated in the modulation of affect-related arousal. Avoidance scores corresponded with increased activation during spouse hand holding, and decreased activation during stranger handholding, in the right ventromedial PFC, a region commonly associated with the regulation of negative affect.

In another recent fMRI study, 20 women were asked to think about—and then to stop thinking about—various relationship scenarios (Gillath, Bunge, Shaver, Wendelken, & Mikulincer, 2005). Attachment anxiety was positively associated with activity in the dorsal anterior cingulate cortex, and anxiety scores were positively correlated with brain activity in the temporal pole, but negatively with brain activity in the orbitofrontal cortex, during thoughts about negative relationship scenarios. This suggests that attachment-anxious individuals are not engaging neural systems that would help to regulate their emotional responses during negative relationship thoughts.

More recently, Bucheim and colleagues (Buchheim et al., 2006) collected functional images of the brain while adults told "attachment stories" in response to images from the Adult Attachment Projective (Lorberbaum et al., 1999) intended to activate the attachment behavioral system. Attachment stories from the AAP were used to classify individuals as either "organized" or "disorganized." Individuals classified as disorganized were more likely to show amygdala and hippocampal activation when shown pictures portraying traumatic as opposed to neutral attachment situations.

Although findings from each of the studies described above should be considered preliminary, they do contribute to our understanding of how attachment styles and internal working models may moderate neural processes associated with the regulation of emotion. They are

the initial steps in what is likely to be an increasing effort to use brain imaging techniques to study the neural correlates and underpinnings of processes studied previously only through verbal and behavioral reactions to laboratory procedures.

The Social Baseline Model

Social influences on the regulation of affect are sufficiently powerful and unconditioned to suggest that the brain's first and most powerful approach to affect regulation is via social proximity and interaction. This is most obvious in infancy, where very basic physiological needs are regulated first via affect expression, leading to a dynamic of regulating affect per se, where caregivers become the primary agent through which infants regulate affective responding (Hofer, 2006). For the infant, this is occurring in a context of rapid and expansive neural development—possibly a "critical period" during which a number of expectations about the nature of the infant's future environment are being formed. A great deal of this development is occurring in the prefrontal cortex, a region of the brain powerfully implicated in self-regulation of affect. Because the prefrontal cortex is underdeveloped in infancy, the caregiver effectively serves as a kind of surrogate prefrontal cortex, a function that attachment figures likely continue to serve for each other to varying degrees throughout life.

What I will call the social baseline model suggests that social affect regulation was long ago adopted as an efficient and cost- effective means of regulating affect. It draws on the principle of economy of action, which states that organisms must, over time, consume more energy than they expend if they are to survive to reproduce (Proffitt, 2006). Because all bodily activities—including

neural activities—expend energy, energy expenditure must be managed. Proffitt (2006) has proposed that one of the ways in which the brain manages energy expenditure is via alterations in sensory perception that aid in decision-making about the deployment of an organism's resources. For example, Proffitt (2006) has observed that donning a heavy backpack causes hills to appear steeper and objects to appear farther away, thus discouraging individuals from using their resources to climb those hills or approach those objects. In this way, the brain can be thought of as a "Bayesian machine," making "bets" at any given time about what resources to deploy, and at what level of effort (Addis, Wong, & Schacter, 2007; Bar, 2007).

The social baseline model proposes that social species are hard-wired to assume relatively close proximity to conspecifics, because they have adopted social proximity and interaction as a strategy for reducing energy expenditure relative to energy consumption. This implies that the absence of conspecifics, in defying this baseline assumption, functionally adds to the perceived cost of interacting with the environment—especially in threatening contexts (an implication discussed explicitly by Bowlby, 1969/1982). In other words, the social baseline model proposes that social isolation is, for a social organism, akin to donning a heavy backpack, altering the real and perceived demands associated with its environment. There are at least two ways in which the presence of conspecifics may reduce, for social organisms, the actual and perceived cost of engagement with the environment. I will call these strategies risk distribution and load sharing.

Risk distribution. The first way in which social species, including humans, benefit from close social proximity is via the simple distribution of risk in the environment. Many species benefit from living in groups, and simple risk distribution strategies are likely to be plesiomorphic, or relatively ancient in evolutionary terms. Although group living comes at a cost at the level of resource consumption, the benefits may

outweigh those costs sufficiently to create conditions under which group cohesion ultimately promotes the survival of each individual in the group. Risk distribution speaks to the amount of risk a given individual carries as a function of the degree to which he or she is alone, and it can manifest in many ways (Krebs & Davies, 1993). For example, the larger the group, the more individuals there are to scan for possible signs of danger. Similarly, a given individual is at substantially reduced risk of personal danger (e.g., predation) when group size increases. A similar example among warm-blooded species may be the thermal advantage of huddling together. Some social species utilize group size to maximize their performance as predators, and this, too, can be a form of risk distribution, for if predation (especially of large target animals) is maximized in groups of predators, the risk that any one predator will perish from starvation is minimized.

From the perspective of the social baseline model, it is important that the brains of social species appear to be capable of assessing the distribution of risk and making Bayesian decisions about the cost-effectiveness of affective behavior at any given time. Practically speaking, the presence or absence of conspecifics provides, at the lowest level of social proximity, a heuristic for deploying potentially costly resources. For example, in the presence of others, individuals may work less hard at being vigilant for—or even fleeing—predators. These activities, which may be yoked to perceived bodily resources (Proffitt, 2006), are deployed only as needed. The resources that are saved by close social proximity are either simply conserved or used for other valuable purposes.

Load sharing. Risk distribution processes are not likely to have strong effects on processing at the cortical level, especially in the prefrontal regions supporting attention, working memory, and the self-regulation of affect. Interestingly, such prefrontally mediated activities are thought to be particularly costly to deploy (Galliot & Baumeister, 2007). Evidence for this derives from studies of cognitive depletion as a consequence of effortful attention and self-control. In this work, individuals who are asked to engage in tasks requiring self-regulation are subsequently less capable of similar tasks. Moreover, engaging in these tasks has been observed to result in temporary depletions in blood glucose concentration (Galliot & Baumeister, 2007).

The social baseline model predicts that the prefrontal cortex, and many of the regulatory processes it supports, may be particularly affected by the presence of an attachment figure, especially in the context of a threat. Here, the advantage of close proximity extends far beyond simple models of risk distribution: Over and above the dilution of risk via large numbers, a trusted and interdependent associate can be counted on to engage in a number of health- and safety-enhancing behaviors on one's behalf. Such behaviors may include the identification and acquisition of resources, vigilance for environmental threats, caring for one's needs, and nurturing of one's offspring. These allegiances—these attachments—serve to distribute the cost of many of life's metabolically expensive activities, not least being the regulation of one's own negative affect. Simply put, affect regulation is possible, but more difficult, in isolation. I refer to this second level of social regulation as load sharing, and I believe it is an essential component of attachment relationships throughout the life span. Load sharing is likely to be apomorphic, or relatively advanced in evolutionary terms, having arisen as a strategy relatively recently. Human brains are highly sensitive to the load sharing significance of close attachment bonds, and adjust their efforts accordingly. For example, individuals in close, trusted relationships will invest less effort in down-regulating their negative affect, leaving them less responsive to threat cues and other

signs of possible harm (Coan et al., 2006b; Edens et al., 1992; Mikulincer & Florian, 1998; Robles & Kiecolt-Glaser, 2003). Thus, the social brain is designed in part to distribute affect regulation activities to attachment figures. As with the metabolic benefits of risk distribution, this should produce major metabolic resource savings.

Unlike risk distribution strategies, which are primarily sensitive to numbers alone, load sharing, especially in adult attachment relationships, likely develops as the brains of individuals in a relationship become conditioned to one another, especially in the context of coping with threats. Over time, individuals in attachment relationships literally become part of each other's emotion regulation strategy. This is not metaphorical, but literal, even at the neural level. For example, an individual who has been alone for a long period of time may have learned to exercise his prefrontal cortex in the service of regulating his threat responses. The social baseline model predicts that upon establishing an attachment relationship, the individual's perception of the degree to which his environment is threatening or dangerous will change, decreasing the frequency with which he exercises his prefrontal cortex in the service of emotion regulation. Note that this is because his brain assumes a decrease in the need for emotion regulation. With sufficient experience in the relationship, the level of interdependence associated with emotion-regulation needs can become strong. Indeed, a grim reminder of this occurs when one or the other member of an attached pair is suddenly absent due to death or divorce, leaving the partner severely dysregulated (Bowlby, 1980; Sbarra, 2006); see Fraley & Shaver, Chapter 3, this volume).

An example of this dynamic of increasing need for self- regulation as a function of distance from an attachment figure can be found in the previously mentioned study by Coan et al. (2006b), in which married women in an MRI scanner were confronted with the threat of a mild electric shock under each of three conditions: while alone, while holding a stranger's hand, and while holding their spouse's hand. Women in the highest quality relationships showed the lowest degree of threat-related brain activation, limiting their response to relatively automatic regulation of threat perception via structures such as the ventromedial PFC. When the marital relationship was of relatively poor quality, however, the

number of problems confronting the woman's brain under threat increased to include attention to bodily sensory afferents, presumably related to the threat of shock (right anterior insula), task salience (superior frontal gyrus), and release of regulatory stress hormones (hypothalamus).

Presumably, the regulatory benefits associated with attachment figures in both the higher and lower quality relationships reflected the load sharing function of attachment relationships. As the nature of the hand-holding partner switched from attachment figure to stranger, however, yet more problems presented themselves, with additional threat-related brain activations triggered to solve them. For example, threat-related vigilance increased (e.g., via the superior colliculus), effortful emotion-regulation strategies were employed (e.g., via right dorsolateral PFC), and areas were recruited that indicated increased threat-related avoidance motivation (e.g., caudate/nucleus accumbens).

Still, the brain was less active while holding the hand of a stranger than while alone, presumably reflecting the effects of risk distribution via fairly minimal social proximity. While alone, the brain appears to get busy solving yet more perceived problems, adding to those already enumerated somatic preparations for threat responding, increasing bodily arousal (e.g., through the ventral ACC) and coordinating vis-

ceral and musculoskeletal responses (e.g., posterior cingulate, supramarginal gyrus, postcentral gyrus).

It is important to emphasize that social affect regulation appears to be a relatively bottom-up process, as opposed to one's solo affect regulation, which is more top down. When engaging in self-regulation, a person is likely to need to engage in costly, effortful cognitive and attentional strategies in the service of inhibiting either somatic responses or structures supporting the identification of threat cues. This effortful regulation of affect relies to a great degree the prefrontal cortex. In this way, self- regulation frequently occurs in the context of an affective response that has already occurred. By contrast, social affect regulation may often affect the perception of threat in the first place, thereby decreasing the need for threat responding and leaving the prefrontal cortex with relatively little or nothing to regulate. Thus, social affect regulation could be said to be more efficient, or less costly, than self-regulation strategies, such as the suppression of emotional responses, the cognitive reappraisal of threatening situations, and even popular strategies such as meditation. The extent to which this is true awaits further investigation.

Attachment styles as Bayesian priors. Of course, the preceding discussion offers only a simplified, idealized model of social affect regulation, and one highly dependent on situational contingencies. It is likely that superimposed on all of the processes described above are trait-like assumptions about the function and metabolic cost of social factors in regulating the perception of threat cues and, hence, of affect. Accordingly, one way to conceptualize attachment styles and internal working models is as prior probabilities in a Bayesian decision-making process, where the goal is to predict the regulatory cost-effectiveness of attachment figures. In this way, attachment styles come to represent strategies, based on prior experience, for making decisions about how to utilize one's own neural resources in the presence or absence of strangers and attachment figures. A secure attachment style presumably disposes a person to make bets closely in accordance with the idealized picture described above. By contrast, avoidant and anxious strategies may encourage individuals to make greater use of their own resources, even in the presence of social support, or to place themselves outside the reach of social support in the hopes of avoiding additional costs (e.g., having to regulate others as well as self), thus again requiring one to rely on one's own emotion-regulation strategies.

At present, the social baseline model, as well as this Bayesian conceptualization of attachment style, is predominantly a matter of conjecture. As I stated at the outset, however, we have to begin somewhere in the move from evolutionary, behavioral, observational, self-report, and interview-based analyses of attachment processes to analyses based on the methods provided by rapidly developing neuroscience. I expect that future neuroscientific studies of attachment will provide additional clues as to the nature of social affect regulation in the brain.

Recommendations and Conclusions

In this chapter I have sought to synthesize a broad array of studies in the service of introducing the reader to the current state of the neurosciences as they pertain to research on attachment, and to propose a plausible model of how what is known about the social brain and affect regulation may eventually be combined with attachment theory. This effort necessarily included discussions of the neural constituents of attachment, from neural systems supporting emotion and motivation to those supporting emotion- regulation, filial bonding, familiarity, proximity seeking, and individual differences in attachment style. What follows is a partial list of recommendations for research-

ers excited about pursuing the neuroscience of attachment. (Other models and suggestions can be found in other chapters in the present volume, especially those by Simpson & Belsky; Fox & Hane; and Polan & Hofer.)

Use designs that combine social contact with emotional provocations. Studies of the neural systems underlying attachment should combine the presence or absence of attachment cues (e.g., proximity to attachment figures) with laboratory situations that elicit emotional responses, including threats to either the participant's attachment system or to the participant directly. Many theorists have proposed that the attachment behavioral system is activated during threats to the individual or to the individual's attachment bond, but few studies of attachment processes at the neural level have actually designed studies with this in mind. Moreover, no work to date has sought to identify how social contact influences neural responses to positive affect elicitations.

Be sensitive to sex differences. Little is known about how the sex of an individual under study affects activity in the attachment behavioral system, or the neural constituents of attachment. Self- reported sex differences have been noted in behavioral studies, however. For example, women are more likely to endorse items indicating a preoccupied attachment strategy (characterized by worry that the partner will leave them), whereas men are more likely to endorse a dismissive-avoidant strategy (characterized by discomfort with interpersonal closeness) (Bartholomew & Horowitz, 1991). And many studies have found that women are most bothered by their male partners' avoidance, whereas men are most bothered by their female partners' anxiety (Mikulincer & Shaver, 2007). Others have reported sex differences in relationship stability as a function of attachment styles, suggesting that attachment styles may interact in important ways with gender roles (Kirkpatrick & Davis, 1994). Our own work on the normative regulation of affect via social channels was done only with women, and it may not generalize to men.

Pursue animal models of attachment style. To date, virtually no studies exist of attachment styles in non-human animals, despite growing evidence that other personality dimensions are evident in non-human animals (Gosling & John, 1999). For example, King and Figueredo (1997) provided strong evidence that the "big five" personality structure and distribution is very similar in humans and chimpanzees, and the anxiety and avoidance dimensions of attachment style are somewhat related to the big-five traits of neuroticism and agreeableness, respectively (Noftle & Shaver, 2006). Other personality traits shared to one degree or another with humans have been observed in species as diverse as gorillas, hyenas, domesticated dogs, cats, donkeys, pigs, rats, octopi, and even guppies (Gosling & John, 1999). Attempts to study attachment styles in non-human animals would constitute a badly needed step toward bridging the gaps between the human and animal literatures addressing attachment behavior.

Allow for systemic effects in research designs. Most attachment style research identifies effects of a given participant's attachment style on that person's own attachment behavior. One question of great interest is the degree to which the attachment style of one member of a dyad affects the behavior of the other member. (See J. Feeney, Chapter 21, this volume for examples.) For instance, Coan et al. (2005) presented evidence that the husband's preoccupation score corresponded with increased neural threat reactivity throughout the wife's brain if she was holding the hand of a stranger (while her possibly jealous husband looked on). These sorts of effects are likely to be numerous and are of great interest to any neuroscience of attachment. (Such findings also suggest that the effects of context are likely to be profound.)

Seek to understand contextual and situational influences. Nearly a half-century of research makes clear that personality is most stable within classes of situations as opposed to across situations (Mischel, Shoda, & Mendoza-Denton, 2002). The question can reasonably be asked: Is a given individual secure in her relationship with her spouse to the same degree as she is in her relationship with her best friend mother, or sister? Moreover, does her attachment style manifest in the same way to a threat to her relationship as it does to her personal sense of bodily harm? Would she have endorsed the same level of security during her last relationship as she does in her current one? Some studies suggest that within-person variation in attachment style across different relationships is substantial (La Guardia, Ryan, Couchman, & Deci, 2000). This is likely to be especially true at the neural level, where measures can be very sensitive to small changes in context.

Implement longitudinal designs. One extremely important problem for the neuroscience of attachment is delineating the process by which two individuals progress from not being attached to being attached (see Zeifman & Hazan, Chapter 20, this volume for a discussion of this issue). What is the rate at which this typically occurs? How is this affected by attachment style? With special relevance to the present chapter, which neural structures associated with emotional responding, motivation, and emotion regulation are particularly sensitive to this process? For example, at what point, or with what kinds of interpersonal experiences, does a stranger who regulates the brain's autonomic and musculoskeletal response to threat become a partner who regulates additional neural processes related to effortful affect regulation and threat vigilance? Longitudinal studies may also address questions of within-subject variation in attachment style over both time and relationships.

Pursue clinical implications. As reviewed briefly above, and by scores of other scholars in recent decades (Cacioppo et al., 2002; Coyne et al., 2001; Flinn & England, 1997; Harrison, Williams, Berbaum, Stem, & Leeper, 2000; House, Landis, & Umberson, 1988; Kawachi, 2001; Kim & McKenry, 2002; Robles & Kiecolt-Glaser, 2003; Uchino et al., 1996; Uvnaes-Moberg, 1998), social relationships hold major implications for health and well-being. As the neural mechanisms supporting these effects become better known, it may be possible to implement clinical interventions that not only emphasize the forging and maintenance of close relationships, but that also focus on the use of social affect regulation for clinical purposes.

For example, it may be possible to use certain relationship interventions (see Johnson, Chapter 33, this volume) to transform couples that do not show a strong social regulation effect on neural threat responding into those that do. Johnson (2002) has already used attachment-related marital interventions to help with the treatment of post-traumatic stress disorder.

It warrants emphasis here that most stress-reduction techniques involve highly individualized activities (e.g., cognitive behavioral therapy, mindfulness meditation) that may be less efficient or more costly than using social networks or attachment relationships in the implementation of affect-regulation strategies. Few or no interventions are designed with this specifically in mind, and even those that are rarely if ever offer training in how to allow oneself to be soothed by another person.

Finally, the careful delineation of neural systems underlying attachment stands to expand our basic understanding of a wide variety of disorders that implicate social processes. The potential exists for this work to inform research on disorders ranging from autism to fragile X syndrome, Williams syndrome, depression, so-

cial anxiety, schizophrenia, and virtually all of the personality disorders (most or all of which are more or less defined in terms of social behaviors).

Differentiate behavioral from neural systems. A major challenge to future neuroscientists interested in the study of attachment will be the temptation to think of the attachment behavioral system as a unitary neural construct, which it almost certainly is not. A host of neural processes, each with its own unique problems to solve, contribute to what we have come to call the attachment behavioral system, and the attachment behavioral system may indeed be little more than a convenient rubric for describing the collective social activities of social bonding and social affect regulation. On the other hand, the attachment behavioral system may represent an emergent property of its constituent neural components that is, under some conditions and in some situations, relatively irreducible.

Collaborate. The neuroscience of attachment represents uncommonly fertile ground for a wide variety of researchers, from neuroscientists to psychologists, biologists, physicians, epidemiologists, and others. Individuals from diverse scientific traditions stand to contribute many essential pieces to this fundamentally important puzzle. Because this area is so necessarily multidisciplinary, researchers interested in these and related questions will do well to explore contacts in related disciplines as their particular research questions call for it (Cacioppo et al., 2007). It is for precisely this reason that collaborations are increasingly the norm among the social, cognitive, and affective neurosciences. Such collaborations enrich the science, and often richly reward the scientists who take part. When such efforts are focused on a question as fundamentally important as the neuroscience of attachment, it is expected that collaborative efforts will be embraced with great enthusiasm.

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