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ARTICLE *in* PSYCHOLOGICAL REVIEW · AUGUST 2000

Impact Factor: 7.97 · DOI: 10.1037/0033-295X.107.3.411 · Source: PubMed

Psychological Review
2000, Vol. 107, No. 3, 411-429

www.apa.org/journals/rev.html

Biobehavioral Responses to Stress in Females: Tend-and-Befriend, not Fight-or-Flight

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The human stress response has been characterized, both physiologically and behaviorally, as "fight-or-flight." Although fight-or-flight may characterize the primary physiological responses to stress for both males and females, we propose that, behaviorally, females' responses to stress are more marked by a pattern of "tend and befriend." Tending involves nurturant activities designed to protect the self and offspring that promote safety and reduce distress; befriending is the creation and maintenance of social networks that may aid in this process. The biobehavioral mechanism that underlies the tend and befriend pattern appears to draw heavily on the attachment/caregiving system, and considerable neuroendocrine evidence from animal and human studies suggests that oxytocin, in conjunction with female reproductive hormones and endogenous opioid peptide mechanisms, may be at its core. This previously unexplored stress regulatory system has manifold implications for the study of stress.

Survival depends upon the ability to mount a successful response to threat. The human stress response has been characterized as fight-or-flight (Cannon, 1932), and has been represented as an essential mechanism in the survival process. We propose that human female responses to stress (as well as those of some animal species) are not well characterized by fight-or-flight, as research has implicitly assumed, but rather are more typically characterized by a pattern we term "tend and befriend." Specifically, we will suggest that, by virtue of differential parental investment, female stress responses have selectively evolved to maximize the survival of self and offspring. We suggest that females respond to stress by nurturing offspring, behaviors that protect them from harm and reduce neuroendocrine responses that may compromise offspring health (the tending pattern); and by befriending, namely affiliating with social groups to reduce risk. We hypothesize and consider evidence from humans and other species to suggest that females create, maintain, and utilize these social groups, especially relations with other females, to manage stressful conditions. We suggest that female responses to stress may build on attachment/caregiving processes that downregulate sympathetic and hypothalamic-pituitary-adrenocortical (HPA) responses to stress. In support of this biobehavioral theory, we consider a large animal and human literature on neuroendocrine responses to stress, suggesting that the tend and befriend pattern may be oxytocin-mediated and moderated by sex hormones and endogenous opioid peptide mechanisms.

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Support for preparation of this article was provided by National Science Foundation Grant SBR 9905157, National Institute of Mental Health Grant MH 056880, and the MacArthur Foundation's SES and Health Network. All of the authors except the first were supported by a National Institute of Mental Health Training Grant in MH 15750 in health psychology at various points throughout the preparation of this article. We are grateful to Nancy Adler, David A. Armor, Lisa Aspinwall, John Cacioppo, Elissa Epel, Alan Fiske, Gregg Gold, Melissa Hines, Margaret Kemeny, Jennifer Lerner, Sonja Lyubomirsky, Karen Matthews, Bruce McEwen, L. Anne Peplau, Lien Pham, Inna Rivkin, Joan Silk, Robert Trivers, and Rosemary Veniegas for their comments on previous versions of this article.

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Background

The fight-or-flight response is generally regarded as the prototypic human response to stress. First described by Walter Cannon in 1932, the fight-or-flight response is characterized physiologically by sympathetic nervous system activation that innervates the adrenal medulla, producing a hormonal cascade that results in the secretion of catecholamines, especially norepinephrine and epinephrine, into the bloodstream. In addition to its physiological concomitants, fight-or-flight has been adopted as a metaphor for human behavioral responses to stress, and whether a human (or animal) fights or flees in response to sympathetic arousal is thought to depend on the nature of the stressor. If the organism sizes up a threat or predator and determines that it has a realistic chance of overcoming it, then attack is likely. In circumstances in which the threat is perceived to be more formidable, flight is more probable.

A coordinated biobehavioral stress response is believed to be at the core of reactions to threats of all kinds, including attacks by predators, assaults by members of the same species, dangerous conditions such as fire, earthquake, tornado, or flooding, and other threatening events. As such, an appropriate and modulated stress response is at the core of survival. Through principles of natural

selection, an organism whose response to stress was successful would likely pass that response on to subsequent generations, and the fight-or-flight response is thought to be such an evolved response.

A little-known fact about the fight-or-flight response is that the preponderance of research exploring its parameters has been conducted on males, especially on male rats. Until recently, the human literature was little better. Prior to 1995, women constituted about 17% of participants in laboratory studies of physiological and neuroendocrine responses to stress. In the last five years, the gender balance has been somewhat redressed. We identified 200 studies of physiological and neuroendocrine responses to an acute experimental stressor conducted between 1985 and the present, utilizing 14,548 participants, 66% of whom were male, and 34% of whom were female. Despite movement toward parity, the inclusion of women in human stress studies remains heavily dependent on the specific topic under investigation. For example, women are overrepresented in studies of affiliative responses to stress, and men are overrepresented in studies of neuroendocrine responses to physical and mental challenges (Gruenewald, Taylor, Klein, & Seeman, 1999).

Why have stress studies been so heavily based on males? The justification for this bias is similar to the rationale for the exclusion, until recently, of females from many clinical trials of drugs, from research on treatments for major chronic diseases, and from animal research on illness vulnerabilities. The rationale has been that, because females have greater cyclical variation in neuroendocrine responses (due to the reproductive cycle), their data present a confusing and often uninterpretable pattern of results. The fight-or-flight response may also be affected by female cycling, and, as a result, evidence concerning a fight-or-flight response in females has been inconsistent. But what if the equivocal nature of the female data is not due solely to neuroendocrine variation, but also to the fact that the female stress response is not exclusively, nor even predominantly, fight-or-flight?

Theoretical Model

An empirical gap such as the identified gender bias in stress studies provides a striking opportunity to build theory. From a metatheoretical perspective, we reasoned that a viable theoretical framework for understanding female responses to stress may be derived by making a few conservative evolutionary assumptions and then building parallel and mutually constraining biological and behavioral models.

We propose, first, that successful responses to stress have been passed on to subsequent generations through principles of natural selection: Those without successful responses to threat are disproportionately unlikely to reach an age when reproduction is possible. In the case of females, an additional assumption is that, because females have typically borne a greater role in the care of young offspring, responses to threat that were successfully passed on would have been those that protected offspring as well as the self. The female of the species makes a greater investment initially in pregnancy and nursing, and typically plays the primary role in activities designed to bring the offspring to maturity. High maternal investment should lead to selection for female stress responses that do not jeopardize the health of the female and her offspring and that maximize the likelihood that they will survive.[1] "Tending", that is, quieting and caring for offspring and blending into the environment may be effective for addressing a broad array of threats. In contrast, fight responses on the part of females may put themselves and their offspring in jeopardy, and flight behavior on the part of females may be compromised by pregnancy and/or the need to care for immature offspring. Thus, alternative behavioral responses are likely to have evolved in females.

The protection of self and offspring is a complex and difficult task in many threatening circumstances, and those who made effective use of the social group would have been more successful against many threats than those who did not. This assumption leads to the prediction that females may selectively affiliate in response to stress, which maximizes the likelihood that multiple group members will protect both them and their offspring. Accordingly, we suggest that the female stress response of tending to offspring and affiliating with a social group is facilitated by the process of "befriending," which is the creation of networks of associations that provide resources and protection for the female and her offspring under conditions of stress.

We propose that the biobehavorial mechanism underlying the tend-and-befriend pattern is the attachment/caregiving system, a stress-related system that has been previously explored largely for its role in maternal bonding and child development. In certain respects, the female tending response under stressful conditions may represent the counterpart of the infant attachment mechanism that appears to be so critical for the development of normal biological regulatory systems in offspring (Hofer, 1995). Numerous investigations have explored the effects of the mother-infant bond on infants' emotional, social, and biological development, but less literature has explored the counterpart maternal mechanism, that is, what evokes tending behavior in the mother. We will attempt to redress that oversight here. In addition, we will suggest that the "befriending" pattern may have piggy-backed onto the attachment/caregiving system and thus may be at least partially regulated by the same biobehavioral systems

that regulate tending. From this analysis, it follows that neuroendocrine mechanisms would have evolved to regulate these response to stress, much as sympathetic activation is thought to provide the physiological basis for the fight-or-flight response. We propose that the neurobiological underpinnings of the attachment/caregiving system (e.g. Pankesepp, 1998) provide a foundation for this stress regulatory system; specifically, oxytocin and endogenous opioid mechanisms may be at the core of the tend-and-befriend response.

In essence, then, we are proposing the existence of an endogenous stress regulatory system that has heretofore been largely ignored in the biological and behavioral literatures on stress, especially in humans. Accordingly, the empirical evaluation of the viability of this theoretical position requires us to address several questions: Is there neuroendocrine and behavioral evidence for our contention that fight-or-flight is less characteristic of female than male responses to stress? Is there a neuroendocrinological basis for and behavioral evidence for

[1] We note here that the term, "parental investment," is a technical term from evolutionary theory, referring to time and effort devoted to offspring, and not a judgmental evaluation suggesting that women care more about children than men do, or a proscriptive term suggesting that women are or must be the only parent who can take appropriate care of offspring.

"tending" under stress in females, that is, nurturance and caring for offspring under conditions of threat? Is there evidence of differential affiliation by females under stress and a neuroendocrine mechanism that may underlie it?

To evaluate these hypotheses, we draw on several sources of scientific evidence. We begin with evidence for gender divergences in biological and behavioral responses to stress and examine substantial neuroendocrine data from animal studies that may account for these divergences. We use the animal literature not to draw direct connections to human behavior, but because animal studies enable researchers to test neuroendocrine mechanisms directly, whereas such evidence is typically more indirect in human studies. We then consider whether there are neuroendocrine and behavioral parallels in the literature on human and non-human primate responses to stress. Clearly, there are risks in combining evidence from multiple sources that include behavioral studies with humans and non-human primates and neuroendocrine research from animal studies. However, any effort to understand stress responses that ignores one or more of these lines of evidence is potentially risky, because a comprehensive biobehavioral account of stress response requires integration across multiple sources of evidence. We will suggest appropriate caveats in generalizing from one line of work to another when they are warranted.

Females and the Fight-or-Flight Response

The basic neuroendocrine core of stress responses does not seem to vary substantially between human males and females.[2] Both sexes experience a cascade of hormonal responses to threat that appears to begin with the rapid release of oxytocin, vasopressin, CRF (corticotropin-releasing factor), and possibly other hormones produced in the paraventricular nucleus of the hypothalamus.[3] Direct neural activation of the adrenal medulla triggers release of the catecholamines, norepinephrine and epinephrine, and concomitant sympathetic responses, as noted. Hypothalamic release of CRF and other hormones stimulate the release of adrenocorticotropin hormone (ACTH) from the anterior pituitary, which, in turn, stimulates the adrenal cortex to release corticosteroids, especially cortisol or corticosterone, depending upon the species (Jezova, Skultetyova, Tokarev, Bakos, & Vigas, 1995; Sapolsky, 1992a). As such, both males and females are mobilized to meet the short-term demands presented by stress.

As already noted, however, a stress response geared toward aggressing or fleeing may be somewhat adaptive for males, but it may not address the different challenges faced by females, especially those that arise from maternal investment in offspring. The demands of pregnancy, nursing, and infant care render females extremely vulnerable to external threats. Should a threat present itself during this time, attacking a predator or fleeing by the mother could render offspring fatally unprotected. Instead, behaviors that involve getting offspring out of the way, retrieving them from threatening circumstances, calming them down and quieting them, protecting them from further threat, and anticipating protective measures for stressors that are imminent may increase the likelihood of survival of offspring. Given the adaptiveness of such behaviors for females, neuroendocrine mechanisms may have evolved to facilitate these behaviors and inhibit behavioral tendencies to fight or flee.

Neuroendocrine Perspective on Fight

Consistent with the above analysis, neuroendocrine differences between the sexes suggest that females are unlikely to show a physical "fight" response to threat. Females largely lack androgens and, in many species, androgens act to develop the male brain for aggression either prenatally or post-natally, and then activate aggressive behavior in specific threatening contexts (such as responses to territorial establishment and defense).[4] In humans, gonadal hormones appear to influence the development of both rough-and-tumble play and tendencies toward aggression, both of which show moderate to large sex differences (Collaer & Hines, 1995).

Although the exact role of testosterone in male attack behaviors remains controversial, testosterone has been associated with hostility and aggressive behavior in both human (e.g., Bergman & Brismar, 1994; Olweus, Mattson, Schalling, & Low, 1980) and animal studies (Lumia, Thorner, & McGinnis, 1994). In humans, testosterone has been shown to increase with acute stress, including high-intensity exercise (e.g., Cumming, Brunsting, Strich, Ries, & Rebar, 1986; Mathur, Toriola, & Dada, 1986;

Wheeler et al., 1994) and psychological stress (although the effects vary by the nature of the stressor and by individual differences) (Christensen, Knussmann, & Couwenbergs, 1985; Hellhammer, Hubert, & Schurmeyer, 1985; Williams et al., 1982). Girdler, Jamner, and Shapiro (1997) found that, in men, testosterone increased significantly with acute stress, and testosterone reactivity to acute stressors was significantly associated with level of hostility. Although human male aggression is generally regarded as being under greater cortical control than is true for lower order animals, a small but consistently positive relation between self-reported hostility and testosterone has been found in meta-analyses of aggression, as has a consistent relationship between testosterone levels and assessments of aggression made by others (Archer, 1990). Studies of captive human male populations, including incarcerated felons and psychiatric patients, also show positive relations between testosterone and ratings of aggressive behavior (Benton, 1992). Thus, testosterone may be a link by which sympathetic arousal is channeled into hostility and interpersonal attack behavior among males.

The androgens, especially testosterone, are also implicated in

[2] Both sexes show sympathetic arousal in response to the perception of threat, with men showing somewhat stronger vascular responses, and women somewhat stronger heart rate responses (Allen, Stoney, Owens, & Matthews, 1993; Matthews & Stoney, 1988; Stoney, Davis, & Matthews, 1987; Stoney, Matthews, McDonald, & Johnson, 1988).

[3] Different combinations of these hormones may be released in response to different types of stressors. Vasopressin secretion, for example, is not stimulated by a variety of stressors, although oxytocin release appears to be a more consistent, though not universal, component of the neuroendocrine response to stress (Jezova et al., 1995; Kalin et al., 1985).

[4] The exact role that testosterone plays in aggression varies by species, particularly whether it has organizational effects, activational effects, or both (Archer, 1990; Beatty, 1984). In rodent species, for example, aggression is organized perinatally by testosterone and requires androgren for the activation of aggression in adulthood. Aggression in primates is thought to be organized by testosterone prenatally, but is not necessarily dependent upon androgens for later activation.

the development of rough-and-tumble play (Beatty, 1984; Collaer & Hines, 1995). From an early age, one male acts as an evocative stimulus for another male, inducing aggressive behavior (Maccoby & Jacklin, 1974). In the human male, rough-and-tumble play is believed to be organized prenatally by testosterone and androgens, but because it occurs before puberty, it may not be dependent upon testosterone for activation (see Beatty, 1984; Collaer & Hines, 1995, for reviews).

Human female aggressive responses are not organized by testosterone or androgens either prenatally or post-natally, and the typical low levels of those hormones in juvenile and adult females means that predominantly male hormones are unlikely to be the organizing factors that evoke a female fight response as they do in males. The presence of either another male or another female does not typically act as an evocative stimulus for human female attack behavior, and human females do not engage in rough-and-tumble play at the levels observed in males (Maccoby & Jacklin, 1974).[5] In human males, there appears to be a link between sympathetic reactivity and hostility, whereas women's hostility is not reliably linked to sympathetic arousal, suggesting that it is not a necessary component of a fight-or-flight response (Girdler et al., 1997).

Female aggression is well-documented, of course. Our argument is not that female aggression fails to occur, but that it is not mediated by the sympathetic arousal-testosterone links that appear to be implicated in fight responses for men. Extensive reviews of the human aggression literature suggest that males may not be inherently more aggressive than females, but that the patterns of aggression between males and females differ (Bjorkqvist & Niemela, 1992, for a review). Males are more likely to use physical aggression in struggles for power within a hierarchy or to defend territory against external enemies. Females reliably show less physical aggression than males, but as much or more indirect aggression (Holmstrom, 1992), that is, aggression in the form of gossip, rumor-spreading, and enlisting the cooperation of a third party in undermining an acquaintance. However, human females still show lower levels of verbal aggression than males, although this sex difference is smaller than that for physical aggression (Eagly and Steffen, 1986). Overall, female aggressive responses appear to be tied less to sympathetic arousal than male aggression, being instead more cerebral in nature. For example, female aggressive behavior may be more moderated by social norms and learning, and by cultural, situational, and individual differences (Bjorkqvist & Niemela, 1992; Eagly & Steffen, 1986).

The physical fight response is the most robust area of aggression that shows higher levels for males than females, and these differences are found in rodents, primates, and humans (Archer, 1990; Eagly & Steffen, 1986; Hyde, 1984). When female attack behavior if observed, it appears to be confined to particular circumstances. For example, female adult rats are aggressive toward intruder (i.e., unfamiliar) males and females, primarily when they are pregnant or nursing, behaviors which fall off rapidly as pups mature (Adams, 1992). In addition, maternal attack behavior toward potential predators that threaten offspring has been well-documented (Adams, 1992; Brain, Haug, & Parmigiani, 1992; Sandnabba, 1992). In summary, female physical aggression appears to be confined to situations requiring defense, rather than to the broader array of threats that is found in males.[6]

Neuroendocrine Perspective on Flight

Although flight might appear to be the more probable first line of defense of females to stressful events or threatening circumstances, this response, too, may not be dominant in the hierarchy of stress responses of females. Females who are pregnant, nursing, or otherwise responsible for offspring may be unable to flee without jeopardizing the health and safety of their offspring. Although flight behavior among females is well-documented in species whose offspring have the capability to flee within hours after birth (e.g., ungulates such as deer or antelope), in species where offspring remain immature for long periods of time, flight by the female can require abandonment of offspring. Females of most species spend a substantial proportion of their fertile lives either pregnant, nursing, or raising young children, and until recently, this was largely true of human females as well. Given the very central role that these activities play in the perpetuation of the species, stress responses that enabled the female to simultaneously protect herself and her offspring are likely to have resulted in more surviving offspring.

If flight behavior in response to stress is indeed inhibited in females, might there be a neuroendocrine basis for this inhibition? McCarthy (1995) alludes to such a mechanism in her animal studies of the behavioral effects of oxytocin and its modulation by estrogen. In particular, she argues that animals in the natural environment face a constant barrage of stress, and a continuous stress response can have deleterious physiological effects. Consequently, reactions that control stress responses have physiological advantages. Oxytocin release may be such a reaction. Oxytocin is a posterior pituitary hormone that is released to a broad array of stressors by both males and females. It is associated with parasympathetic (vagal) functioning, suggesting a counterregulatory role in fear responses to stress (Dreifuss, Dubois-Dauphin, Widmer, & Raggenbass, 1992; Sawchenko & Swanson, 1982; Swanson & Sawchenko, 1980). In experimental studies of the effects of exogenously-administered oxytocin with rodents, oxytocin has been found to enhance sedation and relaxation, reduce fearfulness, and decrease sympathetic activity, patterns of responses that are antithetical to the fight-or-flight response (Uvnas-Moberg, 1997). These effects appear to be substantially more pronounced in female rats than in males for several reasons. First, oxytocin release in response to stress appears to be greater in females than in males (Jezova, Jurankova, Mosnarova, Kriska, & Skultetyova, 1996). Second, androgens have been shown to inhibit oxytocin release under conditions of

[5] Female rhesus monkeys exposed to testosterone in utero show intermediate levels of rough-and-tumble play (greater than normal females and less than males), underscoring the organizational effect that testosterone appears to play prenatally for physical aggression at least some primates (Goy, 1966, 1978; Phoenix, 1974a, 1974b, 1974c; Phoenix, Goy, & Resko, 1968). There is also some evidence that aggression in extremely aggressive women is associated with testosterone (Benton, 1992).

[6] When female attack behavior is documented in rats, primates, or human females, it is much more likely to be female-female aggression than female-to-male aggression (Burbank, 1987; Fry, 1992) (except when threats to offspring are involved); this female-to-female aggression appears to be directed primarily against outsiders, such as intruder females in the rat, and females outside one's immediate social grouping in primates and humans.

stress (Jezova et al., 1996); and, third, the effects of oxytocin are strongly modulated by estrogen (McCarthy, 1995).

The estrogen-enhanced anxiolytic properties of oxytocin (e.g., Windle, Shanks, Lightman, & Ingram, 1997) may explain the consistent sex differences found in stress-related behavior among rats. For example, in response to acute stress, female laboratory rats show fewer behavioral indications of fear (e.g., freezing) than males (e.g., Klein, Popke, & Grunberg, 1998), slower withdrawal latencies to heat and mechanical stimuli, a longer tail-flick response (Uvnas-Moberg, 1997), higher ambulation scores in open-field tests, faster time to emerge from familiar into novel territory, and a greater amount of exploration of novel territory (Gray, 1971a, 1971b, as cited in Gray & Lalljee, 1974). The exogenous administration of oxytocin in rats results in decreased blood pressure (effects that last longer in females), decreased pain sensitivity, and decreased corticosteroid levels, among other findings also suggestive of a reduced stress response (Uvnas-Moberg, 1997). Oxytocin is also known to promote maternal and other forms of affiliative behavior which, McCarthy (1995) argues, may be functional under stress, representing more adaptive responses than extreme fear. Although McCarthy's oxytocin-based argument does not address flight behavior per se, its emphasis on fear reduction for moderating the typical behavioral responses to fear suggests that oxytocin may be implicated in the processes by which fear in the rat is reduced, flight is avoided, and maternal and other forms of affiliative behavior are increased under conditions of threat (see McCarthy, 1995). These effects may be conditional upon the development of a maternal bond between mother and infant: Among mother-infant pairs where attachment bonds have been formed, abandonment of infants under stress is rarely, if ever, found (Keverne, Nevison, & Martel, 1999; Mendoza & Mason, 1999).

Whether and exactly how McCarthy's argument can be applied to the human situation remains to be seen. For example, although female rats show fewer behavioral signs of anxiety than males, that pattern may be reversed in non-human primates and humans, although the data are ambiguous (Gray, 1971a, 1971b, as cited in Gray & Lalljee, 1974).[7] Nonetheless, as will shortly be described, oxytocin in human females has been found to have similar effects on anxiety, affiliation, and maternal behavior (e.g., Uvnas-Moberg, 1997), and estrogen is associated with reduced anxiety in human females (Gray, 1971a). In humans, oxytocin inhibits the release of glucocorticoids, also suggesting an anxiolytic effect (Chiodera et al., 1991). Consequently, the role of oxytocin in the inhibition of "flight" responses merits continued cross-species investigations.

In summary, we suggest that the flight response to stress may be inhibited in females, and that such inhibition favors the survival of the female and her offspring under conditions of stress. The neuroendocrine underpinnings of this response may be oxytocin-mediated.

Tending under Stress

Tending

As previously stated, the basic neuroendocrine core of stress responses does not seem to vary substantially between human males and females. In both sexes, threat triggers sympathetic-adrenal-medullary (SAM) and hypothalamic-pituitary-adrenal (HPA) activation, as well as the release of other neuroendocrine responses that operate to prepare the organism to respond to the stressor. How would a female responding to stress with sympathetic arousal nonetheless quiet and calm down offspring? We propose that the biobehavioral mechanism for the tending process builds on the attachment/caregiving system. We explore the hypothesis that the neuroendocrine mechanisms which may act to modulate sympathetic arousal and HPA activation also act to encourage tending to offspring under conditions of threat.

Attachment was originally conceived as a stress-related biobehavioral system that is the mainstay of maternal bonding and of child socialization (Bowlby, 1988). This largely innate caregiving system is thought to be especially activated in response to threat and to signs of offspring distress (such as "distress vocalization"). The caregiving system has been heavily explored through animal studies, with parallels in human developmental investigations. A paradigm frequently adopted for empirical investigations of mother-infant attachment/caregiving processes involves separation, and under these circumstances, in a number of species, both mothers and offspring show distress at separation. For example, in a study of squirrel monkeys, a 30- to 60-minute separation of mother and infant led to signs of distress and increased plasma cortisol in both mothers and infants (Coe, Mendoza, Smotherman, & Levine, 1978); upon being reunited, the stress responses of both mother and infant declined (Mendoza, Coe, Smotherman, Kaplan, & Levine, 1980). Meaney and colleagues (e.g. Liu et al, 1997; Liu et al, in press; Frances, Diorio, Liu, and Meaney, 1999) explicitly link tending responses to stress and demonstrate consequent effects on the development of stress regulatory systems. In one of their paradigms, infant rats are removed from the nest, handled by a human experimenter, and then returned to the nest. The immediate response of the mother is intense licking and grooming and arched-back nursing which provides the pup with immediate stimulation that nurtures and soothes it; over the long-term, this maternal behavior results in better regulation of somatic growth and neural development, especially enhancing hippocampal synaptic development and consequent spatial learning and memory in offspring. In certain respects, the female tending response under stressful conditions may represent the counterpart of the infant attachment and separation distress signaling system (Hofer, 1995). Although considerable research has explored the effects of the mother-infant bond on infants' development, less literature has explored the counterpart mechanism in the mother. We here attempt to outline the rudiments of what that response might be.

Oxytocin and endogenous opioid mechanisms may be at the core of the tending response (Panksepp, Nelson, & Bekkedal, 1999). Evidence from a broad array of animal studies involving rats, prairie voles, monkeys, and sheep show that central administration of oxytocin reduces anxiety and has mildly sedative properties in both males and females (e.g., Carter, Williams, Witt, & Insel, 1992; Drago, Pederson, Caldwell, & Prange, 1986; Fahrbach, Morrell, & Pfaff, 1985; McCarthy & Goldman, 1994; McCarthy, Chung, Ogawa, Kow, & Pfaff, 1991; Uvnas-Moberg,

[7] Women report more psychological distress in response to stressful events than do men, but these self-reports do not necessarily parallel physiological processes (e.g., Collins & Frankenhaeuser, 1978; Frankenhaeuser, Dunne, & Lundberg, 1976).

1997; Witt, Carter, & Walton, 1990). As noted, this response appears to be stronger in females than in males, and oxytocin may play two roles with regard to the female stress response. It may serve to both calm the female who is physiologically aroused by a stressor and also to promote affiliative behaviors, including maternal behavior toward offspring. For example, studies of ewes have found that intracerebroventricular administration of oxytocin stimulates maternal behavior (Kendrick, Keverne, & Baldwin, 1987; see also Kendrick et al., 1997). The resulting grooming and touching that occurs in mother-infant contact may help quiet infants. These effects appear to be bidirectional, inasmuch as oxytocin enhances affiliative and affectionate contact which, in turn, enhances the flow of oxytocin (Uvnas-Moberg, 1999).[8] As noted above, endogenous opioid mechanisms are also implicated in maternal attachment processes. In rhesus monkeys, administration of naloxone (an opioid antagonist) is associated with less caregiving and protective behavior toward infants (Martel, Nevison, Rayment, Simpson, & Keverne, 1993). Similarly, administration of naltrexone, another opioid antagonist, inhibits maternal behavior in sheep under experimental conditions (Kendrick & Keverne, 1989). In rat studies, administration of oxytocin antagonists diminishes the attractive qualities of conditioned maternal cues and blocks behavioral indices of infant-mother attachment (Panksepp et al., 1999).

A large number of animal studies suggest that this maternal contact under stressful conditions has a wide array of immediate benefits for offspring. Maternal touching among rats reduces hypothalamic-pituitary-adrenal (HPA) alterations indicative of a stress response in pups (i.e., corticotrophin-releasing factor) (Liu et al., 1997; Pihoker, Owens, Kuhn, Schanberg, & Nemeroff, 1993; Wang, Bartolome, & Schanberg, 1996). Separation from the mother increases corticosterone secretion in rat pups, which is reduced when the mother returns (Kuhn, Pauk, & Schanberg, 1990; Stanton, Gutierrez, & Levine, 1988). Studies of rhesus monkeys have found that ventral contact between offspring and mother following a threatening event promotes rapid decreases in HPA activity and in sympathetic nervous system arousal (Gunnar, Gonzalez, Goodlin, & Levine, 1981; Mendoza, Smotherman, Miner, Kaplan, & Levine, 1978; Reite, Short, Seiler, & Pauley, 1981).

The estrogen-enhanced oxytocin responses documented in rats and now explored in humans appear to be very strong. McCarthy (1995), for example, refers to the effects of estrogen on oxytocin as among the strongest known effects of estrogen. Uvnas-Moberg (1997) found that, in rats, oxytocin-induced calming may last for several weeks, suggesting that it is not continuously maintained by oxytocin flow but, instead, is maintained by secondary changes induced by the peptide. Moreover, these effects are not easily blocked by oxytocin antagonists. The surprisingly robust, long duration of these oxytocin-mediated effects suggests that they may be exerted at the level of the genome (Uvnas-Moberg, 1997). Thus, the oxytocin effect in females is potent, long-lasting, and maintained by secondary changes, suggesting centrality and importance, at least in animal studies.

Although studies with humans are less able to provide evidence of underlying mechanisms, mother-infant attachment processes have been found to have much the same benefits on human infants, and as has been true in animal studies, oxytocin and endogenous opioid mechanisms are thought to be at their core. Some of the human evidence on the behavioral concomitants of oxytocin has involved studies of nursing mothers, because oxytocin levels are known to be high at this time. As in animal studies, nursing is soothing to both mothers and infants. Blass (1997) reported that consuming milk significantly reduced crying in human infants, and sucking on a nipple is known to have a physiologically calming effects in infants and can also reduce crying (Field & Goldson, 1984). Lower levels of sympathetic arousal have also been found in lactating versus non-lactating women (Wiesenfeld, Malatesta, Whitman, Grannose, & Vile, 1985). Women who are breastfeeding are calmer and more social than matched-age women who are not breastfeeding or pregnant, as determined by personality inventories (Uvnas-Moberg, 1996); moreover, the levels of oxytocin in these breastfeeding women correlated strongly with the level of calm reported, and oxytocin pulsatility was significantly correlated with self-reported sociability (Uvnas-Moberg, 1996). Similar findings are reported by Adler, Cook, Davidson, West, and Bancroft (1986). Altemus, Deuster, Galliven, Carter, & Gold (1995) found that lactating women showed suppressed hypothalamic-pituitary-adrenocortical responses to stress, consistent with the animal literature showing reduced HPA activity in response to oxytocin (see also Chiodera et al., 1991; Lightman & Young, 1989). Dunn and Richards (1977) also reported higher levels of maternal behavior among lactating versus non-lactating mothers.

Until recently, it was difficult to examine the relation of oxytocin to human social behavior except during lactation, in part because of ethical issues involved with manipulating oxytocin levels, and in part because there were no commercially-available assays to measure oxytocin at the levels suspected to be implicated in stress responses. Emerging evidence suggests that oxytocin is associated with relaxation and interpersonal outcomes in non-lactating women as well. For example, in a sample of nulliparous women, Turner, Altemus, Enos, Cooper, and McGuinness (1999) found that oxytocin levels increased in response to relaxation massage, and decreased in response to sad emotions. Women who reported fewer interpersonal problems of intrusiveness showed greater increases in oxytocin in response to these sources of stimulation. Maintaining oxytocin levels during sadness was associated with lower anxiety in close relationships, and high basal levels of oxytocin were associated with greater interpersonal distress. In an experimental study with older women, Taylor, Klein, Greendale, and Seeman (1999) found that higher levels of oxytocin were associated with reduced cortisol responses to stress and with faster HPA recovery following an acute stress laboratory challenge.

As is true in animal studies, human studies show that nurturing behaviors under conditions of stress benefit both mother and offspring. Field and colleagues have shown that touching an infant and carrying an infant close to the mother's chest can soothe and calm the infant (Field, Malphurs, Carraway, & Pelaez-Nogueras, 1996; Field, Schanberg, Davalos, & Malphurs, 1996). High levels of physical affection and warmth between mother and child during

[8] Relevant to this is a study of gender differences in responsivity to touch in humans in response to the stress of hospitalization (Whitcher & Fisher, 1979). Results revealed that, under stress, touch produced more favorable affective, behavioral, and physiological (especially cardiovascular) effects in females than was true for males, and touch was actually experienced as aversive by males.

stressful circumstances have been tied to normal HPA activation profiles in response to stress in offspring (e.g., Flinn & England, 1997; Chorpita & Barlow, 1998; Hertsgaard, Gunnar, Erickson, & Nachmias, 1995). In humans (as well as in non-human primates), these processes appear to be mediated by mother-infant attachment, with securely-attached offspring less likely to show elevated cortisol in response to challenging circumstances (e.g., Gunnar, Brodersen, Krueger, & Rigatuso, 1996; Gunnar, Brodersen, Nachmias, Buss, & Rigatuso, 1996; Nachmias, Gunnar, Mangelsdorf, Parritz, & Buss, 1996).

Nurturing behavior under stressful conditions may not only quiet and soothe offspring, but also have discernible effects on health-related outcomes, directly affecting the likelihood that offspring will survive and mature properly.[9] For example, in humans, inadequate physical maternal care has been tied to growth retardation, social withdrawal, and poor interpersonal relatedness, among other complications (e.g., Harlow, 1986; Shaffer & Campbell, 1994). Premature human infants given a pacifier or massage grow better, become calmer, and become more tolerant to pain (Bernbaum, Pereira, Watkins, & Peckham, 1983; Field & Goldson, 1984; Scafidi, Field, & Schanberg, 1993; Uvnas-Moberg, Marchini, & Winberg, 1993). In experimental investigations with humans, touch and massage have been found to increase immune function, decrease pain, reduce subjective reports of stress, and maintain normal growth in infants (Field, 1995, 1996; Ironson et al., 1996; Scafidi & Field, 1996).[10]

If mothers, in particular, exhibit nurturing behavior under conditions of stress, it should also be possible to see behavioral evidence for this prediction in parenting behaviors. Such evidence is provided by Repetti's (Repetti, 1989, 1997) studies of the effects of stressful workdays on parenting behavior. Repetti interviewed both fathers and mothers about their workdays and their behaviors at home on those days, and also interviewed children regarding their experiences with their parents on those days. She found that fathers who had experienced an interpersonally conflictual day at work were more likely to be interpersonally conflictual in the home in the evenings. Fathers who had had highly stressful workdays, but not involving interpersonal conflict, were more likely to withdraw from their families (Repetti, 1989). A very different pattern was found for mothers. Specifically, women were more nurturant and caring toward their children on their stressful work days. In particular, on days when women reported that their stress level at work had been the highest, their children reported that their mothers had shown them more love and nurturance (Repetti, 1997). A second study replicated these differences in mothers' and fathers' responses to offspring under stress (Repetti, 2000).[11]

The underpinnings of the tending response appear to be oxytocin-based initially, at least in rodent and animal species, and possibly also in human females[12]; prolactin, endogenous opioids, and social learning may be more important for sustaining the tending response, once the behavior pattern has developed (Panksepp, 1998). The extent to which the tending response is hormonally regulated over the long term is unclear, however. Rat studies show that tending responses under stress (e.g., pup retrieval) lose their complete dependence upon hormonal regulation relatively quickly, and are thought to be socially maintained instead, in response to distress vocalizations (DeVries & Villalba, 1999). Tending responses in human females also appear to depend, in part, on characteristics of human infant cries, and such qualities as pitch and tone convey often quite subtle information to mothers about the urgency and nature of the infant's need (Bates, Freeland, & Lounsbury, 1979; Crowe & Zeskind, 1992; Zeskind, 1980, 1987; Zeskind & Collins, 1987; Zeskind, Sale, Maio, Huntington, & Weiseman, 1985). The human female not only brings the possibility of social evocation by offspring to stress situations, but a large neocortex as well, and so tending behavior in human females may be oxytocin-based, socially mediated, mediated by higher-order brain functions, or some combination of these three processes.

In summary, whereas male responses to stress may be tied to sympathetic arousal and to a fight-or-flight pattern that is at least, in part, organized and activated via androgens, female stress responses do not show these androgen links and instead, may be tied, at least in part, to the release of oxytocin and its biobehavioral links to caregiving behavior. Oxytocin is believed not only to underlie attachment processes between mothers and offspring, but it may also be implicated in other close social bonds. We extend this analysis in the next section by arguing that female responses to stress are also characterized by affiliation with social groups because group living provides special benefits for females.

Befriending Among Females

Group living is generally regarded as an evolutionary adaptation among many species that benefits both males and females (Caporeal, 1997). Groups provide more eyes for the detection of predators, and most predators are reluctant to attack potential prey if they believe there are others who might come to that prey's rescue (Rubenstein, 1978; Janson, 1992). Moreover, groups can create confusion in a predator. If a predator charges a large group, the group may disband in many directions, which may confuse the predator long enough to reduce the likelihood that any one member of the group can be taken down. Group life, then, is fundamental to primate existence, making it an important evolutionary strategy by which primates have survived (Caporeal, 1997; Dunbar, 1996). As we have noted, female stress responses have likely evolved in ways that not only protect the female herself, but also protect her offspring. As such, group life is likely

[9] Bowlby's (1988) theory of attachment maintains that the formation of an attachment bond between infant and mother (or a suitable substitute) is essential for adequate socialization. For example, human play behavior and exploration in early ages is heavily dependent upon physical proximity to a caregiver with whom that infant has formed a strong bond (see Hazan & Shaver, 1994).

[10] It should be noted that touch (Panksepp et al., 1999) and smell (Kendrick, Levy, & Keverne, 1992) have been implicated in animal studies of maternal-infant attachment, and these same behaviors may be implicated in human mother-infant attachment processes to some degree as well (e.g., Fleming, Steiner, & Corter, 1997).

[11] There appears to be an upper limit on this phenomenon, inasmuch as chronically stressed or distressed mothers are somewhat more likely to show withdrawal behavior on especially stressed days, rather than increases in affection (Repetti & Wood, 1997).

[12] Oxytocin may have important effects on social learning and social memory (de Wied, 1997; Popik, Vetulani, & Van Ree, 1992). For example, low doses of oxytocin strengthen social memories and, as such, oxytocin may play a role in learning and memory for social bonds, infant caregiving, and friendships.

to have been an especially important adaptation for females and offspring, because of the limitations of fight-or-flight as a female response to stress. Like human males, human females required successful defense against external predators, such as tigers, leopards, hyenas, packs of hunting dogs, and other primates. In addition, human females have much to fear from human males, in the form of rape, assault, homicide, and abuse of offspring.[13] The pairing of human females with human males may be, in part, an evolutionary adaptation that protects females and offspring against random assault by males. However, under some conditions, human females also have reason to fear their own male partners. In North America, estimates of the percentage of women who have been assaulted by their partners range from 20% to 50% (Bray, 1994; Goodman, Koss, Fitzgerald, Russo, & Keita, 1993; Koss, Goodman, Browne, Fitzgerald, Keita, & Russo, 1994; Malamuth, 1998; Straus & Gelles, 1986), and statistical analyses of assault and homicide data reveal that human females are most likely to be assaulted or killed by their own partners (see Daly & Wilson, 1988; Daly, Wilson, & Weghorst, 1982). There is no reason to believe that this is a particularly modern phenomenon. Thus, evolved mechanisms of female survival likely protected against a broad array of threats, including those from males of her own species.

If the above reasoning is true, one would predict a strong tendency among females to "affiliate" under conditions of stress. There is animal data consistent with this analysis. Crowding has been found to stress male rodents, but to calm female rodents, as assessed by corticosteroid levels (specifically, spatial crowding is problematic for males, whereas number of other animals present is positively related to calming in females) (Brown, 1995; Brown & Grunberg, 1995). McClintock (1998) has reported that female rats housed together in five-female groupings live 40% longer than females housed in isolation.[14] Research on prairie voles, a preferred species for studying behavioral concomitants of oxytocin, has found that, under conditions of stress, female prairie voles show selective preference for their same-sex cage companions (DeVries & Carter, unpublished data, cited in Carter, 1998).

Human Evidence for Affiliation Under Stress

Research on human males and females shows that, under conditions of stress, the desire to affiliate with others is substantially more marked among females than among males. In fact, it is one of the most robust gender differences in adult human behavior, other than those directly tied to pregnancy and lactation, and it is the primary gender difference in adult human behavioral responses to stress (Belle, 1987; Luckow, Reifman, & McIntosh, 1998). In their analysis of gender differences in coping, Luckow et al. (1998) found that the largest difference arose on "seeking and using social support," and the combined significance of their effect was significant beyond the $p < .0000001$ level. Of the 26 studies that tested for gender differences, one study showed no differences and 25 favored women; there were no reversals (Luckow et al., 1998). Indeed, so reliable is this effect that, following the early studies on affiliation in response to stress by Schachter (1959), most subsequent research on affiliation under stress used only female participants.[15]

Nonetheless, some research has compared males' and females' responses to stress. Bull et al., (1972) found that exposure to noise stress led to decreased liking among male participants, but greater liking by females toward familiar others. Bell and Barnard (1977) found that males prefer less social interaction in response to heat or noise stress, whereas females preferred closer interpersonal distance. Affiliation under stress, however, is not random (Bull et al., 1972; Kenrick & Johnson, 1979; Schachter, 1959). Women's affiliative tendencies under stress are heavily to affiliate with other women (Schachter, 1959). When given a choice to affiliate with an unfamiliar male versus alone prior to a stressful experience, women choose to wait alone (Lewis & Linder, 1999). In summary, then, women are more likely than men to choose to affiliate in response to a laboratory challenge, but affiliation appears to be selectively with similar others, especially other women.

Across the entire life cycle, females are more likely to mobilize social support, especially from other females, in times of stress. They seek it out more, they receive more support, and they are more satisfied with the support they receive. Adolescent girls report more informal sources of support than do boys, and they are more likely to turn to their same-sex peers for support than are boys (e.g., Copeland & Hess, 1995; see Belle, 1987, for a review). College student females report more available helpers and report receiving more support than do males (e.g., Ptacek, Smith, & Zanas, 1992; see Belle, 1987, for a review). Adult women maintain more same-sex close relationships than do men, they mobilize more social support in times of stress than do men, they rely less heavily than do men on their spouses for social support, they turn to female friends more often, they report more benefits from contact with their female friends and relatives (although they are also more vulnerable to network events as a cause of psychological distress), and they provide more frequent and more effective social support to others than do men (Belle, 1987; McDonald & Korabik, 1991; Ogus, Greenglass, & Burke, 1990). Although females give help to both males and females in their support networks, they are more likely to seek help and social support from other female relatives and female friends than from males (Belle, 1987; Wethington, McLeod, & Kessler, 1987).[16]

Women are also more engaged in their social networks than are men. They are significantly better at reporting most types of social network events than men, such as major illnesses of children, and they are more likely to report being involved if there is a crisis event in the network (Wethington et al., 1987). In an extensive study of social networks, Veroff, Kulka, and Douvan (1981) reported that women were 30% more likely than men to have

[13] Although abuse of children does not differ significantly by gender of perpetrator (U.S. Department of Health & Human Services, 1999), correcting for time spent with children yields considerably higher rates for men than women. Stepfather status is a particularly potent predictor of abuse (Rosenthal, 1988; Daly and Wilson, 1996).

[14] No males were included in this particular study.

[15] The late Stanley Schachter maintained, in several contexts, that he had not found affiliative behavior in men under stress and, consequently, conducted his subsequent studies on affiliation using females only.

[16] It should be noted that, although men are less likely to seek and give social support than women, they are often recipients of social support, and such support, especially from a female partner, close relative, or close female friend, appears to be successful in reducing physiological arousal in response to stress (e.g., Kirschbaum, Klauer, Filipp, & Hellhammer, 1995). Similar findings emerge in the primate literature. Sapolsky reports that males who are the recipients of grooming efforts by females have better physiological functioning (Sapolsky, 1994).

provided some type of support in response to network stressors, including economic and work-related difficulties, interpersonal problems, death, and negative health events. So consistent and strong are these findings that theorists have argued for basic gender differences in orientation toward others, with women maintaining a collectivist orientation (Markus & Kitayama, 1991) or connectedness (Clancy & Dollinger, 1993; Niedenthal & Beike, 1997; Kashima, Yamaguchi, Choi, Gelfand, & Yuki, 1995) and males, a more individualistic orientation (Cross & Madson, 1997). These findings appear to have some cross-cultural generalizability: In their study of six cultures, Whiting and Whiting (1975) found that women and girls seek more help from others and give more help to others than men do, and Edwards (1993) found similar sex differences across 12 cultures.

In stressful circumstances where resources are scarce, female networks for child care and exchange of resources often emerge and become very well developed. Large kin networks among disadvantaged African-Americans, as well as the fictive kin networks that often evolve when real kin are not available are well-documented (Stack, 1975). Newman (1999) described the all-female economic networks that impoverished Dominican women develop, so as to protect themselves and their children when male breadwinners are unemployed or leave the family. Studies of Black families, White working class families, White ethnic families, and low-income families of all races reveal the importance of the instrumental assistance and emotional support shared among female kin, friends, and neighbors, especially around the tasks of child-rearing (Belle, 1987).[17]

The preceding analysis is not intended to suggest that males are not benefitted by social group living or that they do not form social groups in response to external threats or stress. But anthropological accounts, as well as survey literature, suggest that the functions of the groups that men and women form and/or turn to under stress are somewhat different. In a broad array of cultures, men have been observed to form groups for purposes of defense, aggression, and war (Tiger, 1970). They tend toward larger social groups than is true of women (Baumeister & Sommer, 1997), and these groups are often organized around well-defined purposes or tasks. Although men orient toward and invest in a large number of social relationships, many of these emphasize hierarchies of status and power, rather than intimate bonding (Baumeister & Sommer, 1997; Spain, 1992). Female groupings tend to be smaller, often consisting of dyads or a few women, and although some such groups are focused around tasks (such as food preparation, sewing, or collective child care), these groups often have the establishment and maintenance of socioemotional bonds at their core, a characteristic less true of male groupings (Cross & Madson, 1997). Women in women's social groups show more affiliative behaviors, including smiling, disclosure, attention to others, and ingratiation (Baumeister & Sommer, 1997; Pearson, 1981), and they interact at closer interaction distances than do men's groups (Patterson & Schaeffer, 1977).

A Neuroendocrine Perspective on Affiliation Under Stress

Studies of affiliative behaviors in animal studies suggest a mechanism whereby enhanced social activity of females may occur under conditions of stress. In particular, they suggest that oxytocin reduces stress and enhances affiliation. For example, social contact is enhanced, and aggression diminished, following central oxytocin treatment in estrogen-treated female prairie voles (Witt et al., 1990), and the exogenous administration of oxytocin in rats causes an increase in social contact and in grooming (Argiolas & Gessa, 1991; Carter, DeVries, & Getz, 1995; Witt, Winslow, & Insel, 1992). With reference to humans, Carter (1998) suggests that oxytocin may be at the core of many forms of social attachment, including not only mother-infant attachments, but also adult pair bonds and friendships (Drago et al., 1986; Farbach et al., 1985; Pankesepp, 1998). Keverne et al. (1999) suggested that female-to-female bonding may have piggybacked onto maternal/infant bonding attachment processes. Consistent with Keverne et al.'s (1999) hypothesis, research has reported that animals prefer to spend time with animals in whose presence they have experienced high brain oxytocin and endogenous opioid activities in the past (Panksepp, 1998), suggesting that friendships may be mediated by the same neurochemical systems that mediate maternal urges. As is true of the maternal-infant caregiving system, contact with a friend or a supportive other person during stressful events downregulates sympathetic and neuroendocrine responses to stress and facilitates recovery from the physiological effects of acute stress (Christenfeld, Gerin, Lindon, Sanders, Mathur, Deich, & Pickering, 1997; Fontana, Diegnan, Villeneuve, & Lepore, 1999; Gerin, Milner, Chawla, et al., 1995; Gerin, Piper, Levy, & Pickering, 1992; Glynn, Christenfeld, & Gerin, 1999; Kamark, Manuck, & Jennings, 1990; Kirschbaum, Klauer, Filipp, & Hellhammer,1995; Kors, Linden & Gerin, 1997; Lepore, Allen, & Evans, 1993; Roy, Steptoe, & Kirschbaum, 1998; Sheffield, & Carroll, 1994; Thorsteinsson, James, & Gregg, 1998). Both men and women experience these stress regulatory benefits of social support, but women disproportionately seek such contact, and the stress-reducing benefits are more consistent when the support provider is female rather than male (e.g. Gerin et al, 1995).

The enhanced desire for social contact that females demonstrate

[17] Studies of human female networks suggest that matrilinear and matrilocal societies are typically characterized by peaceful interfemale relations (Glazer, 1992). When generations of related women and girls live together all their lives and participate in cooperative work groups, interfemale aggression is reported to be low (Benedict, 1934; Glazer, 1992; Murphy & Murphy, 1974). Reliably, however, when women join patriarchal extended families, interfemale aggression is considerably higher, especially between in-laws. These findings are true both for human social groupings and for primate social groupings (Glazer, 1992; Keverne et al., 1999).

An intriguing study of hunting among women of the Agta Negrito of Luzon (the Philippines) underscores the functions of networks of female kin. Women's hunting has largely been regarded as biologically impractical, because hunting is assumed to be incompatible with the obligations of maternal care of offspring (Dahlberg, 1981; Hiatt, 1970; Lee, 1979). Specifically, hunting forays are thought to impair women's abilities to nurse, care for, and carry children, and female odor itself may constitute a handicap to effective hunting. However, studies of cultures where the females do hunt suggest exceptions that prove the rule. Agta women participate actively in hunting precisely because others are available to provide child care responsibilities (Goodman, Griffin, Estioko-Griffin, & Grove, 1985). When women were observed to hunt, they either brought nursing children with them, or gave the child to their mothers or oldest female siblings for care. Whereas men typically hunted alone, women almost always hunted with dogs and/or in groups, often with other females, especially sisters. Thus, proximity to hunting grounds, use of dogs, hunting in groups, and cooperation in child care appear to be the key factors that make it possible for Agta female hunters to be successful.

under conditions of stress, relative to males, may also be modulated by endogenous opioid mechanisms. Endogenous opioid peptides are released during stress, and are believed to influence social interaction (Benton, 1988; Jalowiec, Calcagnetti, & Fanselow, 1989). Animal studies suggest that higher levels of endogenous opioids are associated with higher levels of social interaction and maternal behavior. For example, Martel et al. (1993) found that administration of naloxone (an opioid antagonist) in female rhesus monkeys reduced both maternal behavior as well as social grooming of other females. Further support for this hypothesis and for its possible differential relevance for females is provided by an experimental investigation of the effects of opioids on affiliative behavior in humans. Jamner, Alberts, Leigh, and Klein (1998) found that administration of naltrexone (a long-acting opioid antagonist) increased the amount of time women spent alone, reduced the amount of time that they spent with friends, and reduced the pleasantness of women's social interactions, as compared with men; in addition, women given naltrexone initiated fewer social interactions than when they received a placebo. Thus, endogenous opioids appear to play a role in regulating social interactions, especially for women. Endogenous opioids also moderate the release of other peptides in the limbic system (e.g., oxytocin, vasopressin), as well as other "stress-related" neurohormones, such as norepinephrine (Keverne et al., 1999), and cortisol (Klein et al., 1998), which may contribute to the sex differences observed in social behavior under conditions of stress.

Advantages of Affiliation Under Stress

What are the advantages of social affiliation under stress, and why do females to do it more? Why does female affiliation under stress appear to be at least somewhat selectively with other females? We reasoned that examining evidence from humans' closest relatives, namely Old World non-human primates, may provide some insights into the patterns and functions of female affiliative responses to stress.[18]

Female-female networks of associations are common in non-human primate societies. Among many Old World primates, female coalitions and networks are formed early and are in place when they are needed (Dunbar, 1996; Wallen & Tannenbaum, 1997). For example, in Gelada baboons, a mother and her two daughters, or a sister, mother, and daughter may form an alliance to provide support against threat. These long-term commitments are solidified through grooming behavior, which may take up as much as 10% to 20% of an animal's time (Dunbar, 1996). Intrasexual aggression within these matrilineal groupings is reported to be low among females (although high among males), while the reverse is true of affiliative behavior, with females exhibiting more affiliative behaviors than males. These findings appear to be similar across several species of monkeys and other primates (Burbank, 1987; Glazer, 1992; Keverne et al., 1999). Although these bonds and their functions appear to be stronger when kin relationships are involved (Silk, 2000), unrelated females in several primate species form similar bonds. Wallen and Tannenbaum (1997) found that rhesus monkeys establish social bonds with female peers, which provide security and promote the maintenance of a matrilineal social system. Squirrel monkeys typically associate with females of roughly the same age and spend considerable time in close association (Baldwin, 1985; Mason & Epple, 1969). In captive situations, female squirrel monkeys show signs of distress in response to being separated from their cage mates. In an experimental investigation, when female squirrel monkeys were introduced to a novel environment, they showed more distress when alone than when they experienced the new environment in the company of their same-sex cage mates (Hennessy, Mendoza, & Kaplan, 1982); these adverse reactions were stronger for lactating mothers with infants than for non-lactating females (Jordan, Hennessy, Gonzalez, & Levine, 1985).

The so-called "harem" structure that characterizes the breeding patterns of many primates also suggests what some of the protective functions of female groups may be (Wrangham, 1980). The harem structure typically consists of a dominant male and several females and their offspring. Primatologists have tended to emphasize the benefits that the harem structure has for males, enabling them to have all their eggs in one basket, so to speak, and have somewhat overlooked the functions that the harem may afford to females and offspring. Evidence suggests, however, that the female harem may provide protection for females. With reference to the Gelada baboons, Dunbar (1996) notes that daughters mature into a harem grouping of females to join their mothers, older sisters, aunts, and female cousins in a "coalition of great intensity and loyalty…these alliances are formed at birth, the product of being born to a particular mother" (p. 20). Mother-daughter, sister-sister, and female friend grooming are all widely documented and are described by Dunbar as "the cement that holds alliances together," (p. 20). Although males rarely groom each other, adult females will often groom their close female relations and friends in this fashion. Grooming does not occur at random, but rather, takes place within the context of clearly defined social relationships, most of which involve matrilinear relatives or special friends (see also De Waal, 1996; Wrangham, 1980).

Grooming can be an indication of status as well as a form of hygiene and an expression of friendship. The frequency with which a female is groomed by others predicts how likely it is that those others will come to her aid if she is attacked by members of another harem, the male in her own harem, or an outside predator (Dunbar, 1996; Wrangham, 1980). In his studies of rhesus monkeys, Saroj Datta (cited in Dunbar, 1996, p. 25) noted that whether a particular female is attacked may depend on such factors as whether that female's mother or other females with whom that female has formed alliances are nearby. The probability of attack is reduced if the targeted female is of high status or if her mother is of high status, because there is greater potential to enlist the support of other females to drive off a potential attacker. Grooming behavior appears to be enhanced by oxytocin and may be moderated by endogenous opioid mechanisms. For example, among monkeys, naxolone has been found to reduce mothers' grooming behavior toward their infants and toward other group members (Martel et al., 1993).

These female groups may also provide protection for females from their own males. On the one hand, the harem itself may be protected by a dominant male who attempts to keep the females in

[18] Old World primates include bonobos, gorillas, orangutans, and chimpanzees (which are believed to be the closest relations of humans), as well as certain monkeys, including baboons and macaques. New World monkeys are the capuchins, muiriquis, and squirrel monkeys.

line, in particular, preventing them from breeding with other males. On the other hand, if he is overly aggressive or threatening to a particular female, the chances that her female relatives will come to her aid and threaten the male as a group is very high. Dunbar (1996) describes an example of this protection:

> The harem male's attempts to ride herd on his females when they stray too far from him often backfire. The luckless victim's grooming partners invariably come to her aid. Standing shoulder-to-shoulder, they outface the male with outraged threats and furious barks of their own. The male will usually back off, and walk huffily away, endeavoring to maintain an air of ruffled dignity. However, occasionally, the male will persist, feeling, perhaps, unusually sensitive about his honor and security. This only leads to more of the group's females racing in to support their embattled sisters. The male invariably ends up being chased 'round the mountainside by his irate females in an impressive display of sisterly solidarity (pp. 20-21).[19]

Similar accounts are found in De Waal (1996).

Female bonded groups also appear to be important for the control of resources related to food (Silk, 2000; Wrangham, 1980). Wrangham (1980) suggested that female bonded groups may have evolved, in part, because of the competition that exists for high-quality food patches under conditions of limited feeding sites. Cooperative relationships among females may provide for the sharing of information about food sites and also help supplant others from preferred food patches (Silk, 2000; Wrangham, 1980). Matrilocal primate groupings also provide opportunities for the exchange of caretaking responsibilities under some circumstances (Wrangham, 1980), and examples of one female taking care of the offspring of another female appear commonly throughout the primate literature (e.g., De Waal, 1996).

Studies of primates suggest that these groups of females and their offspring may also be a critical mechanism by which juvenile females gain experience in the tending of infants, enabling them to observe the behaviors of other mothers. For example, studies with rhesus macaque monkeys have reported that females who have not yet given birth frequently help care for younger siblings (Keverne et al., 1999). Research that has deprived monkeys of maternal or social contact during the first eight months of life reveals significant adverse effects on subsequent maternal care, including infanticide and abuse; social contact and opportunities to provide maternal care subsequently improves maternal care, but that care does not approach that of feral mothers (e.g., Ruppenthal, Harlow, Eisele, Harlow, & Suomi, 1974). When mothers and infants are given opportunities to form bonds with each other, abandonment of infants is rarely observed (Keverne et al., 1999; Mendoza & Mason, 1999), but in captive-reared animals and other circumstances when mother-infant bonds have not formed, mothering behavior can be inadequate. This maternal behavior is believed to be mediated, in part, by endogenous opioid mechanisms. Related findings appear in studies of human affiliative behavior (Jamner et al., 1998).

Although oxytocin and endogenous opioid mechanisms may be important in affiliative and maternal behavior in primates and humans, the important role of higher brain functioning must also be noted. As Keverne et al. (1999) point out, the development of a large neocortex in primates has allowed affiliative behavior and maternal caregiving to take place without the hormonal regulation prompted by pregnancy and parturition that elicits similar behaviors in rats. Freeing behavior from exclusive neuroendocrine control enables females to engage in affiliation and infant caregiving through learning by modeling other females. These points suggest an important socialization role for these all-female social groupings. Indeed, Keverne et al. (1999) argue that, through such learning, females provide social stability and group cohesion, with their affiliative processes helping to maintain the continuity of the group over successive generations.

Two caveats regarding the research on female networks in primate groups are warranted. First, there are over 130 different primate species, and there is substantial variability in the specifics of female networks. For example, female associations are based on kin in some primate social groupings, but on non-kin dominance hierarchies in others. In most primate species, networks of females are responsible for rearing offspring, but in titi monkeys, fathers are responsible for the rearing of offspring, and titi females actually show aversion to being left alone with their offspring (Mendoza & Mason, 1999). While it would be unwise to draw direct links from primate behavior to humans, it would be foolish to claim that there is nothing to be learned from primate behavior, merely because there is variability among primate species. Thus, although these primate examples should be interpreted with caution, they provide illustrations of the befriending patterns common to many primates, including human females.

Second, the preceding analysis runs the risk of romanticizing the networks that females create. It must be noted that these networks are by no means stress-free, particularly non-kin female networks (e.g., Silk, 2000). Studies of primates reveal how more dominant females in the hierarchy may harass less dominant females, a behavior that can have many adverse effects, including the suppression of fertility (Abbott, Saltzman, Schultz-Darken, & Smith, 1999; Shively, Laber-Laird, & Anton, 1997). A more extreme response has been reported by Fossey (1983) in gorillas and by Goodall (1986) in chimpanzees; in both species, dominant females, together with their oldest female offspring, were found, on occasion, to cannibalize the young of less dominant females. In humans, interpersonal strain, conflict, and the potential for misunderstanding and mistreatment are common in social groups, and all-female groups are no exception. The networks that women help create and may become enmeshed in are themselves sources of stress, and women report that interpersonal stressors are the most common and stressful types of stressors they experience (Davis, Matthews, & Twamley, 1999). Nonetheless, on the whole, these female networks may confer more benefits than harm.

Conclusions, Implications, and Limitations

We have proposed a theory of female responses to stress characterized by a pattern termed "tend and befriend." Specifically, we proposed that women's responses to stress are characterized by patterns that involve caring for offspring under stressful circumstances, joining social groups to reduce vulnerability, and contributing to the development of social groupings, especially those involving female networks, for the exchange of resources and responsibilities. We have maintained

[19] We are not suggesting that the female kin network evolved primarily or even significantly to protect females against their own partners. It is, however, likely that females have evolved mechanisms that protect them and their offspring against jealous and suspicious partners, and female kin networks may be one basis for so doing.

that aspects of these responses, both maternal and affiliative, may have built on the biobehavioral attachment/caregiving system that depends, in part, on oxytocin, estrogen, and endogenous opioid mechanisms, among other neuroendocrine underpinnings. We suggest that these patterns may have evolved according to principles of natural selection and by virtue of differential parental investment. We propose this theory as a biobehavioral alternative to the flight-or flight response (Cannon, 1932), which has dominated stress research of the last five decades and has been disproportionately based on studies of males.

To evaluate our theory, we examined several empirical literatures that provide convergent support. A neuroendocrine literature on stress hormones and their relation to behavior derived largely from studies with male rats and, to a lesser extent, on non-human primates, suggests that the fight-or flight response may be heavily tied to androgenic prenatal or post-natal organization of an aggressive response to threat that is activated, in part, by testosterone. A substantial neuroendocrine literature from animal studies with females suggests, in contrast, that sympathetic and HPA responses may be downregulated by oxytocin under stressful circumstances, and that oxytocin, coupled with endogenous opioid mechanisms and other sex-linked hormones, may foster maternal and affiliative behavior in response to stress. The neuroendocrine model links to a literature on humans suggesting that oxytocin and endogenous opioid mechanisms may have similar maternal and affiliative concomitants. Finally, literatures on both human and non-human primates point to differential maternal and affiliative activities among females, compared with males, and provides evidence of a substantial female preference to affiliate under stress. The tend-and befriend pattern may be maintained not only by sex-linked neuroendocrine responses to stress but by social and cultural roles as well.

Theoretical and Empirical Limitations

There are limitations in our analysis. We have combined observations from stress literatures on rats, primates, and humans in a manner that requires considerable leaps, both empirically and inferentially. As noted, the reason for this unusual mode of argumentation is because the neuroendocrine mechanisms are addressed heavily by one literature (rodent), and the behavioral responses to stress by two others (primate, human). It is impossible to build a coherent and informed biobehavioral model that covers what is known about female stress responses without drawing on these diverse and largely unintegrated sources of evidence. This need does not diminish the risks that such an analytic strategy entails, however.

Some of the points in the preceding argument remain conjectural. In particular, we have suggested that oxytocin and endogenous opioids may play important roles in female responses to stress, and it remains to be seen if these are as significant players as we have suggested. It should be noted that the present argument does not posit that oxytocin and endogenous opioids are either necessary or sufficient bases for the behavioral responses identified: We have argued that the "tending" response is consistent with maternal investment in offspring, and maternal behavior under stressful conditions is socially responsive to distress vocalizations by offspring and is likely to be mediated by cortical processes as well. The "befriending" pattern is one of the most robust sex differences reported in the literature on adult human behavior under stress (e.g., Belle, 1987; Luckow et al., 1998), and it, too, may depend heavily on social and cortical processes. At present, the potential roles of oxytocin and endogenous opioids in mediating these patterns are sufficient to be considered credible hypotheses, but they are not definitively established.

Our analysis has included little consideration of the nature of the stressor in moderating stress responses. Neuroendocrine responses under stress are not uniform, but depend upon the stress stimulus involved and other environmental conditions such as predictability and chronicity of a stresssor (e.g., Glass & Singer, 1972; Sapolsky, 1992a; Staub, Tursky, & Schwartz, 1971). Under certain stressful circumstances, we might find the tend-and-befriend pattern to be quite descriptive of female responses to stress and, in other cases, not descriptive (Jezova et al., 1996). In addition, because different stressors elicit different patterns of stress hormones, oxytocin may be involved in some kinds of stressful events, but not others (cf. Sapolsky, 1992b; Kalin, Gibbs, Barksdale, Shelton, & Carnes, 1985).

Another limitation is that, at present, the model largely ignores the very reason why stress responses in females have been so understudied: cyclical variation. If the hypothesized neuroendocrine underpinnings of female stress responses are correct, then we might expect to see cyclical variation in these responses, as well as a degree of dependence upon critical reproductive-related events in a woman's life, including onset of puberty, pregnancy, lactation, and menopause. For example, if estrogen is involved in the modulation of oxytocin-related affiliative or maternal responses, the so-called tending/befriending pattern may be stronger during the late luteal phase of cycle, as opposed to the follicular phase, and diminished in post-menopausal women. Consistent with these suggestions, in rhesus monkeys, females are most social around the time of ovulation or when they are treated with estrogen (Wallen & Tannenbaum, 1997), and oxytocin, in interaction with estrogen, has been suggested as the mechanism by which this sociability occurs (Carter, 1998). At present, however, more evidence is needed to assess the validity of these hypotheses.

Social and Political Implications

The issue arises as to whether sex differences in human behavior might not be better understood as differences in social roles, rather than as evolved biobehavioral responses (Eagley and Wood, 1999). For example, given substantial human behavioral flexibility, one can question whether maternal investment in offspring continues to be higher than that of fathers.[20] In response, we note that current differences between men and women in parental investment do not matter so much as differential parental

investment during the period of time that stress responses evolved. An evolutionary biobehavioral argument does not constrain current human behavior, but neither is it necessarily

[20] Survey data (Staines & Pleck, 1980; Burden & Googins, 1987; Ferber, O'Farrell, & Allen, 1991), interview data (Hochschild, 1989), and analyses of time use diaries (Robinson & Godbey, 1997) indicate that women continue to bear the major responsibility for childcare, whether or not they work for pay. These estimates suggest that mother's childcare exceed father's childcare by a factor of approximately three to one, on average.

challenged by current human behavioral flexibility. We also note that, although human social roles vary substantially across cultures and may, in some cases, prescribe behavioral patterns for women similar to the tend-and-befriend pattern, social roles alone are unlikely to account for it. A social role position does not address the cross-species similarities we have identified, nor can it account for the underlying biological evidence for our position. Nonetheless, it will be important for future research to detail the parts of our biobehavioral model that are sensitive to environmental input.

An analysis that posits biological bases for gender differences in behavior raises important political concerns as well. Many women feel, with some justification, that such models can be used to justify patterns of discrimination and social oppression. To head off any such effort, we emphatically point out that our analysis makes no prescriptive assumptions about the social roles that women occupy. Our analysis should not be construed to imply that women should be mothers, will be good mothers, or will be better parents than men by virtue of these mechanisms. Similarly, this analysis should not be construed as evidence that women are naturally more social than men or that they should shoulder disproportionate responsibility for the ties and activities that create and maintain the social fabric.

Other political concerns, however, may be based on false assumptions about what biological underpinnings signify. Biological analyses of human behavior are sometimes misconstrued by social scientists as implying inflexibility or inevitability in human behavior or as reductionist efforts that posit behavioral uniformity. These perceptions constitute unwarranted concerns about biological bases of behavior. Biology is not so much destiny as it is a central tendency, but a central tendency that influences and interacts with social, cultural, cognitive, and emotional factors that results in substantial behavioral flexibility (Crawford & Anderson, 1989; Tooby & Cosmides, 1992). The last few decades of biological research have shown that, just as biology affects behavior, so behavior affects biology, in ways ranging from genetic expression to acute responses to stressful circumstances. Rather than viewing social roles and biology as alternative accounts of human behavior, a more productive theoretical and empirical strategy will be to recognize how biology and social roles are inextricably interwoven to account for the remarkable flexibility of human behavior.

Implications For Future Research

The present analysis suggests several areas of research for future investigation. We have presented a relatively primitive neuroendocrine model, ascribing a heavy role to oxytocin, endogenous opioid mechanisms, and estrogen. However, other neurohormones such as serotonin (e.g., Bagdy & Arato, 1998; Insel & Winslow, 1998; Knutson et al., 1998), prolactin (Insel, 1997; Panksepp, 1999), vasopressin (Panksepp et al., 1999), dopamine (Berridge & Robinson, 1998; Kreek & Koob, 1998), and norepinephrine (Kraemer, 1992; Panksepp et al., 1999) may also be implicated in these pathways as well, in ways not yet fully identified. Examination of the patterning of these neuroendocrine responses in subsequent studies of both lower animals and humans may help to clarify the neuroendocrine model further. Additional behavioral sequelae of these patterns merit investigation, such as suppression of sexual behavior in females under stress; the role of stress responses in moderating gender differences in negative affect, especially high levels of depression and anxiety in females (Craske & Glover, in press; Frasch, Zetzsche, Steiger, & Jirikowski 1995; Levine, Lyons, & Schatzberg, 1999); and the neuroendocrine and behavioral underpinnings of eating behavior, social withdrawal, and substance abuse under conditions of stress.

The range of female responses to stress, as outlined in this paper, go beyond the acute fight-or-flight response that has been argued to be the foundation of stress responses. Our analysis suggests, instead, that aspects of a coordinated stress response are structurally in place, which are then activated under conditions of stress. This is not a particularly novel observation, inasmuch as group living is precisely such a structural adaptation. The interplay of such structural adaptations with acute stress conditions suggests how primate and human stress responses may have assumed increasingly complex forms as non-human primates and humans encountered an ever more diverse array of stressors. Indeed, it suggests a layering and patterning of means for responding to stress that may provide a quite flexible set of reactions to a broad array of situations and, as such, may be suited to managing chronic stress, as well as acutely stressful conditions.

In this context, there may be value in thinking about the fight-or-flight response as only part of a range of equally flexible male responses. Fight-or-flight may have garnered disproportionate attention in the scientific literature, because of the potent behavioral responses it produces, such as aggression, and from the risks it may create for men's health, such as the early development of cardiovascular disease (CVD). Other male responses to stress may be meritorious of investigation. For example, some aspects of the tend-and-befriend model may characterize male responses to stress under some conditions as well. A more complete model would also consider a broader range of male behavioral responses to stress, such as affiliative behavior, protective behavior, and social withdrawal; a broader array of stress-related disorders, including substance abuse, accident rates, and homicide/suicide; and a broader range of neuroendocrine responses, such as the roles of serotonin, oxytocin, vasopressin, and endogenous opioid mechanisms in mediating or moderating male responses to stress. For example, some intriguing effects of vasopressin in male prairie voles include guarding of territory, self defense, and guarding of females in response to stress, and studies of the effects of oxytocin in male rodents reveal effects on pair-bonding and affiliation (see Carter, 1998, for a review). In short, much remains to be discovered about men's responses to stress as well.

Although our analysis has focused on human stress responses, the present analysis may apply to some other mammalian species as well. Under what circumstances should we see tending and befriending responses to stress in females? Evidence of female "tending" under conditions of stress may be especially pronounced under conditions where there are long gestational periods of offspring, when females spend a high proportion of their life in activities related to pregnancy, nursing, and the rearing of offspring, and in any species in which offspring remain biologically immature for a long period of time. The "befriending" response may be especially prevalent under conditions of resource scarcity; in any species where females are smaller and less powerful than males; when males are unavailable and/or there is a high differential mortality between the sexes; when there is a high rate of rape or attack of females; and when males commonly

abandon their partners or where monogamous associations are otherwise unlikely or unstable.

The present analysis is suggestive of health implications for females. If a downregulated stress response in females produces relaxation and affiliation, this may help to explain the seven-and-a-half nonspecific years that women live longer than men. That is, a stress response moderated by a counter-regulatory system such as the tend-and-befriend pattern proposed here may reduce women's vulnerability to a broad array of stress-related disorders, including episodes of violence, such as homicide and suicide; dependence upon stress-reducing substances, such as alcohol or drugs; stress-related accidents and injuries; and patterns of cardiovascular reactivity that represent risk factors for CVD.

The analysis also suggests important implications for social support processes. It is now well-established that both animals and humans show health benefits from social contact (e.g., House, Umberson, & Landis, 1988). Positive physical contact in the form of touching, hugging, cuddling, and the like is known to release oxytocin which, in turn, has anti-stress properties. The present analysis suggests some mechanisms whereby social support may provide health protection, in particular, by engaging a counterveiling anabolic response to stress characterized by decreased sympathoadrenal activity, decreased hypothalamic-pituitary-adrenocortical responses (HPA), and increased parasympathetic activity and accompanying relaxation. As such, oxytocin may confer health benefits (cf. Ryff & Singer, 1998).

Finally, the present analysis underscores the importance of studying both sexes in investigations of stress and stress responses. We have contended that the disproportionate representation of males in studies of stress has obscured significant influences on and patterns of responses to stress in females. Similarly, virtually all of the studies on affiliation under stress have been conducted on women; the absence of male data makes interpretation of these patterns difficult. Strenuous arguments against the inclusion of single-sex samples for understanding the pathology and treatment of health and mental health disorders (with the exception of sex-linked disorders) have prompted major changes in requirements for clinical trials and treatment evaluation. The threat that single-sex investigations pose to basic research endeavors is no less significant, both because the knowledge that is gained is skewed in favor of one sex's life experiences, and because basic knowledge often becomes the basis for subsequent clinical intervention.

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Received July 30, 1998
Revision received January 26, 2000
Accepted February 29, 2000