LUST, ATTRACTION, AND ATTACHMENT IN MAMMALIAN REPRODUCTION

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This paper proposes that mammals exhibit three primary emotion categories for mating and reproduction: (1) the sex drive, or lust, characterized by the craving for sexual gratification; (2) attraction, characterized by increased energy and focused attention on one or more potential mates, accompanied in humans by feelings of exhilaration, "intrusive thinking" about a mate, and the craving for emotional union with this mate or potential mate; and (3) attachment, characterized by the maintenance of close social contact in mammals, accompanied in humans by feelings of calm, comfort, and emotional union with a mate. Each emotion category is associated with a discrete constellation of neural correlates, and each evolved to direct a specific aspect of reproduction. The sex drive is associated primarily with the estrogens and androgens; it evolved to motivate individuals to seek sexual union. The attraction system is associated primarily with the catecholamines; it evolved to facilitate mate choice, enabling individuals to focus their mating effort on preferred partners. The attachment system is associated primarily with the peptides, vasopressin, and oxytocin; it evolved to motivate individuals to engage in positive social behaviors and assume species-specific parental duties.

During the evolution of the genus *Homo,* these emotion systems became increasingly independent of one another, a phenomenon that contributes to human mating flexibility and the wide range of contemporary human mating and reproductive strategies.

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William James implied that emotions are discrete phenomena—that each is associated with a unique pattern of peripheral physiological events. Schachter and Singer (1962) replaced this model with their two-factor emotion theory, the concept that different emotions are the result of the same basic undifferentiated arousal plus specific cognitions. William James's model for the unique psychophysiology of specific emotions has recently come back into favor, however. As psychologist Richard Davidson reports, "The notion that different emotional states are associated with unique patterns of central nervous system activity must, in a trivial sense, be true if we subscribe to the belief that no mental modification occurs without a corresponding change in brain activity. . . . The challenge for us is to specify what the natural categories [of emotion] are" (1994:240).

In 1872, Darwin discussed several natural categories of emotion in *The Expression of the Emotions in Man and Animals.* Since then many scientists, including Watson (1930), Izard (1977), Plutchik (1980), Panksepp (1986), MacLean (1990), and Ekman (1992), have defined specific categories of emotions (see Ekman and Davidson 1994; Lazarus 1991). This paper reassembles current data with the purpose of defining the primary categories of emotion associated specifically with mammalian reproduction.[1] It places particular emphasis on attraction, the least well-known of these emotion systems.

In this paper, it is hypothesized that mammals have evolved three primary, discrete, interrelated emotion systems for mating and reproduction; each is associated with a specific constellation of neural correlates, and each evolved to direct a specific aspect of mammalian reproduction. The sex drive (the libido, or lust) is characterized by the craving for sexual gratification; it is associated primarily with the estrogens and androgens; and it evolved primarily to motivate individuals to seek sexual union with *any* conspecific. The attraction system is characterized by increased energy and focused attention in mammals, as well as by exhilaration, "intrusive thinking," and the craving for emotional union in humans. Attraction is associated primarily with the catecholamines; and it evolved to *facilitate* mate choice, enabling individuals to focus their mating effort on *preferred* conspecifics. The attachment system is characterized by territory defense and/or nest building, mutual feeding, grooming, maintenance of close proximity, separation anxiety, shared parental chores, and other affiliative behaviors in mammals, and with feelings of calm, security, social comfort, and emotional union in humans. Attachment is associated primarily with the neuropeptides vasopressin and oxytocin; this emotion system evolved to enable individuals to engage in positive social behaviors and / or sustain affiliative connections long enough to complete species-specific parental duties.

As reproductive strategies vary according to the degree of mating effort and parental investment required of each species and each individual (Lancaster and Kaplan 1994; Trivers 1972), the distribution of brain sites for hormone and neurotransmitter receptors associated with each of these emotion categories, as well as the duration, intensity, and types of activities at these neural sites, are expected to vary from one species to the next.

Evidence of this variation is discernible among different species of voles; for example, in monogamous prairie voles (*Microtus ochrogaster*) the distribution of limbic system receptor sites for oxytocin, one of the peptides associated with attachment, varies from that of montane voles (*Microtus montanus*), an asocial relative (Insel et al. 1993). Moreover, data on binding activities at oxytocin receptor terminals in limbic brain areas of the monogamous prairie vole versus similar data on the asocial montane vole suggest that it is not variations in gene structure but a phylogenetic shift in regulatory sequences that directs varied mammalian parenting strategies. "In other words, the evolution of monogamy might result from relatively minor changes in promoter sequences, directing the expression of the same receptor protein [oxytocin] to very different neural circuits" (Leckman et al. n.d.:26). Further investigation should establish many species-specific variations in the expression and neurophysiology of the sex drive, attraction, and attachment.

The neural mechanisms governing these emotion systems also can be expected to vary between individuals *within* a species. Individual variations in the sex drive are commonly reported among humans and among individuals of other primate species. Tennov (1979) reports individual variations in the frequency and duration of human attraction. Behavioral variations in the expression of attachment are documented among monogamous prairie voles. After initial copulation, almost 90% of males remain with a mate to rear offspring as a team; however, the remaining 10.9% abandon the reproductive unit (Carter et al. 1995; Insel and Carter 1995). Cross-cultural and within-culture divorce rates illustrate individual variations in human attachment behaviors as well (Fisher 1989, 1992, 1994, 1995). Although cultural and ecological forces clearly contribute to these individual human variations in the sex drive, attraction, and attachment, these individual variations most likely have neural correlates.

The neural mechanisms mediating the sex drive, attraction, and attachment also can be expected to vary across the life course. Data on voles confirm it. Insel reports that at parturition, when the female montane vole first affiliates with her infants, "the expression of OT (oxytocin) receptors changes in the direction of the pattern observed in the highly parental prairie vole" (Insel 1992:4). The neural mechanisms associated with these emotion systems for mating can be expected to vary according to sex/gender and in response to environmental opportunities and exigencies as well; however, discussion of these variations is beyond the scope of this paper.

Extensive data indicate that the hormonal and neurotransmitter systems underlying these three emotion categories interact with one another and with other bodily systems. Recent data on male prairie voles, for example, indicate that testosterone, which promotes mounting and intromission, can facilitate the production of vasopressin and thus, indirectly, the regulation of male parental care (De Vries 1990; De Vries, Wang et al. 1994; Wang et al. 1994). Several studies report that oxytocin administered centrally to virgin female rats induces maternal behaviors within minutes (Fahrbach et al. 1984a, 1984b, 1985; Pedersen and Prange 1979; Pedersen et al. 1982; Wamboldt and Insel 1987), but the response is dependent on priming with gonadal steroids (Leckman and Mayes, in press). For more examples, oxytocin affects dopaminergic activity (Sarnyai and Kovacs 1994), and serotonin can alter the synthesis, release, or function of several neuropeptides (Fuller 1996).

A host of data also indicate that these three emotion systems not only inhibit and/or enhance one another, they can inhibit or enhance conjoining systems and independent neurohormonal systems (Crawley and McLean 1996; Herbert 1996; Nyborg 1994; Sitsen 1988; see Ziegler and Lake 1984). These interactions are expected. As psychologist Jaak Panksepp writes, "one of the persistent problems is that there is considerable overlap in the autonomic and endocrine outputs of the various basic emotional systems, *which is to be expected.* The main function of the autonomic and endocrine changes is to bring various bodily reactions in line with behavioral/psychological demands of each emotional system" (Panksepp 1994:258, emphasis added).

Nevertheless, under some circumstances these three emotion systems can act independently. Male gibbons *(Hylobates lar)* have been documented to express attachment toward a mate by dueting, grooming, and displaying coordinated territorial defense within the same time frame that they express attraction toward a female in a neighboring territory (Palombit 1994). The independence of these emotion systems, however, is most clear in humans. Men and women can express attachment for a spouse or long-term mate, attraction toward a different conspecific, and the sex drive in response to visual, verbal, or mental stimuli that are *unrelated* to either the spouse or the individual to whom they are romantically attracted. Further examination of data on specific species is necessary to illustrate how each emotion system is differentially expressed and how it interacts with the others and with other bodily systems.

Psychologists distinguish between the sex drive, attraction (standardly termed "passionate love" or "obsessive love"), and attachment (standardly termed "companionate love"; see Hatfield and Rapson 1996; Hatfield and Sprecher 1986; Hatfield 1988; Shaver et al. 1988). But they have not discussed the neural correlates of these emotion systems, the specific role of attraction in mammalian reproduction, the evolution of these emotion systems in *Homo sapiens*, or the impact of these three *distinct* emotion systems on contemporary human patterns of mating and reproduction. So the present paper defines and distinguishes these three emotion systems for mating, reports on data suggesting the primary hormones and / or neurotransmitters associated with each emotion system, proposes that the attraction system evolved to facilitate mate choice in mammals, and concludes that during the course of hominid evolution these three emotion systems became increasingly independent from one another, a neurophysiological artifact that contributes to current patterns of human mating flexibility and the wide range of contemporary human reproductive strategies.

LUST

The sex drive, otherwise known as lust, the libido, or the urge for sexual consummation, is a multidimensional phenomenon; many parts of mammalian anatomy and physiology are involved. Myriad ecological stimuli including seasonal light, temperature, and olfactory cues influence this emotion system as well. In primates, learning also plays an important role in triggering the sex drive. The present paper does not review the ecological or social cues that influence the sex drive; instead it examines the primary neural correlates associated with this emotion category in order to establish the sex drive as an emotion system distinct from that of attraction or attachment.

For several decades, the sex drive has been regarded as a distinct emotion system associated with specific hormones and primary neural structures (Beach 1948, 1976; see Komisaruk et al. 1986). This neural circuitry varies between species, but it is known to be innate, and common aspects of this neural circuitry are known to be present in all mammals. The sex drive is regulated, in large part, by the preoptic area of the anterior hypothalamus, which is one source of gonadotropin-releasing hormone (GnRH), also known as luteinizing hormone–releasing hormone. GnRH traverses a portal vascular system to the anterior pituitary to stimulate production of follicle-stimulating hormone (FSH) and luteinizing hormone (LH). FSH and LH stimulate the gonads to produce the sex steroids, including testosterone, and testosterone can be metabolized to dihydrotestosterone, estradiol, and other estrogens. Other areas of the brain are associated with the sex drive in specific mammalian species, but these regions and the sex steroids are associated with sexual arousal in all mammals (see Komisaruk et al. 1986).

When testosterone is administered to castrated male rats, mice, or pigs, their sex drive returns (see Beach 1948; 1976; Nyborg 1994). In humans, androgens are associated with increased libido in both sexes (Sherwin 1994). Women with higher levels of circulating testosterone have more sexual thoughts, greater desire for sex, and higher mean levels of sexual activity (Morris et al. 1987; Persky et al. 1978). Older men and women who receive injections of testosterone report that sexual thoughts and sexual motivation increase (Sherwin and Gelfand 1987; Sherwin et al. 1985). The androgens have long been associated with the male sex drive (Beach 1948). Now there is also "compelling evidence that libido, or sexual motivation, in women is dependent on androgens" (Sherwin 1994:428).

Estrogen also plays a role in the sex drive. Rising levels of estradiol (primarily) triggers estrus and sexual behavior in female mammals; rhesus monkeys are an example (Wallen and Tannenbaum 1997). The link between increasing levels of estradiol and increasing sexual motivation and behavior is significantly reduced in humans; nevertheless, some women report that they have more sexual desire just before they ovulate, when ovarian estrogen levels peak (Judd and Yen 1973). Small amounts of adrenal androgens convert to estrogen in aging men, contributing to their sex drive too. In fact, injections of testosterone and other androgens may initiate sexual behavior in castrated female mammals and injections of estrogens may trigger sexual behavior in castrated male mammals.

The testosterone/estrogen relationship and its function in relation to other bodily systems is a complex phenomenon (see Nyborg 1994). Nevertheless, the brain circuitry for the sex drive is clearly independent of the neural correlates for attachment in mammals; all mammals engage in sexual activity, yet individuals in only 3% of mammalian species form a long-term attachment to a mating partner (Kleiman 1977). The relationship between the sex drive and attraction is more problematic. Mammals regularly express the drive for sexual consummation, yet most prefer some partners over others—an indication that the sex drive and attraction are somewhat distinct phenomena. Evidence that these three emotion systems are distinct is clearest in *Homo sapiens*. Humans can feel and express sexual desire toward individuals for whom they feel no romantic attraction, as well as for conspecifics to whom they are not emotionally attached.

The sex drive and attraction are regularly lumped together in ethological discussions of mammalian mating behavior, a custom that stems from the work of Frank Beach. Beach (1976) defined three distinct stages of sexual behavior in female mammals: attractivity, proceptivity, and receptivity. *Attractivity* refers to masculine appetitive (approach) reactions to females as attractive sexual stimuli, expressed most frequently when a female is secreting maximum levels of estrogens. *Proceptivity* refers to feminine appetitive sexual reactions toward males, also associated with maximum levels of estrogen (although Beach also implicates the androgens in the sex drive of both male and female mammals). *Receptivity* refers to consummatory acts of mating in both sexes.

Beach does not distinguish between the neural correlates associated with the sex drive and those associated with attraction. He does acknowledge attraction in mammalian species, referring to it as "favoritism," "selective proceptivity," "individual preference," "distinct preferences for some partners and strong aversion to others," and "sexual choice" (Beach 1976:124). He notes that "the occurrence or nonoccurrence of copulation depends as much upon individual affinities and aversions as upon the presence or absence of sex hormones in the female" (Beach 1976:130; see Phoenix 1973). He states that "proceptive and receptive behavior may depend upon *different* anatomical and neurochemical systems in the brain" (Beach 1976:131; emphasis added). And he reports data that confirm this distinction between the sex drive and attraction: "The mating behavior of female rats treated with monoamine receptor blocking agents indicates that 'lordotic behavior and soliciting behavior may be mediated by anatomically and possibly neurochemically separate systems' " (Beach 1976:131; see Ward et al. 1975). But Beach (1976) concludes that mammalian attractivity and receptivity are controlled primarily by estrogen, whereas proceptive behavior may be stimulated when androgens are added.

Beach's conclusion that the androgens and estrogens both play a primary role in the sex drive has been supported. But there is no evidence that the androgens (or estrogens) play a primary role in attraction—the emotion system that enables individuals to focus their mating effort on specific *preferred* sex partners. When menopausal women are injected with androgens, for example, their sex drive is enhanced, but there is no evidence that injections of androgens evoke feelings of romantic attraction or attachment to specific individuals. When rats, monkeys, and other mammals are injected with estrogens and/or androgens, they exhibit increased appetitive sexual behaviors but they do not display increased favoritism, increased partner preference, or increased focused attention on preferred conspecifics.

Beach's (1976) model of attractivity, proceptivity, and receptivity is useful for distinguishing between stages of the sex drive. But this model does not adequately distinguish a second emotion system for mating that may operate *in tandem* with the sex drive in most mammalian species, attraction.

ATTRACTION

The close physiological and behavioral association between the sex drive and attraction in mammals may account for the scarcity of investigation into the brain correlates of attraction. Nevertheless, naturalists and scientists have acknowledged attraction as a discrete emotion system for over a century. When Darwin (1859, 1871) proposed the concept of sexual selection to explain patterns of sexual dimorphism in secondary sexual characteristics and mating behaviors in birds and mammals, he proposed two selective agents: competition between individuals of one sex and *preference* for certain traits exhibited by the opposite sex. Central to Darwin's model was "female choice," also known as mate choice or mate preference. Since then, many articles have discussed aspects of mate preference (attraction) in birds and mammals (see Andersson 1994; Campbell 1972).

Implicit in Darwin's model of sexual selection and subsequent discussions of mate choice is the understanding that some type of emotion system is activated when individual mammals focus their energy and mating effort on preferred mating partners. So it is proposed in this paper that mate preference has two fundamental aspects: First, factors that *trigger* mate preference, such as symmetry, the display of resources, the display of fertility, and/or other biological and behavioral factors that stimulate *to whom* one becomes attracted; second, the emotion system that *facilitates* this mate preference, including increased energy and intent focus on this conspecific. In humans, for example, timing, state of health, access to resources, childhood experiences, and myriad other cultural and biological forces play crucial roles in triggering to whom one becomes attracted. But as this choice emerges, *a specific emotion system is activated,* enabling the individual to focus his/her mating effort on this preferred individual.

Since myriad species-specific anatomical, chemical, and behavioral phenomena have evolved in mammalian species expressly to stimulate attraction from conspecifics, it is parsimonious to suggest that these sexually selected stimuli activate a specific emotion system in *all* mammals. So it is hypothesized that attraction constitutes a discrete emotion system; that this emotion system is associated with a specific constellation of neural correlates; that the neural circuitry for attraction is interrelated with the neural circuitry for the sex drive (and most likely with the attachment system); and that the mammalian attraction system evolved to enable individuals to focus their mating effort on preferred conspecifics, generally those displaying genetically superior traits. This excitatory emotion system is hereby labeled *attraction;* in humans, intense attraction is hereby labeled infatuation, romantic love, "being in love," passionate love, and / or obsessive love.

Descriptions of mammalian mating interactions characteristically include reports of increased energy and focused attention directed toward preferred conspecifics. Yet the behavioral components of the attraction system in nonhuman mammals are undefined, and cross-species comparative descriptions of the attraction system have not been compiled. In rats and other mammals, however it is likely that attraction-associated behaviors are short-lived, whereas in humans these behaviors are longer-term and intensely expressed (Fisher 1992; Jankowiak and Fisher 1992). So the attraction system is best examined in humans.

Intense attraction, commonly known as romantic love, is recorded in all human cultures for which data are available. Jankowiak and Fischer (1992) surveyed 166 contemporary societies and found evidence of romantic love in 147 of them; they note that the 19 negative cases are due to ethnographic oversight. Historical and literary sources indicate that attraction was also evident in ancient Sumeria and Egypt, classical Greece and Rome, and in the preindustrial civilizations of India, China, Japan, Europe, Africa, and the Americas (Alarcon 1992; Bullfinch 1993; Cole 1963; Fowler 1994; Hamill 1996; Hurford 1995; Melville 1990; Moore and Beier 1984; Wolkstein 1991). So Jankowiak and Fischer (1992:154) conclude that attraction constitutes a "human universal" or "near universal."

Some psychologists see the development of human passionate love as rooted in childhood experiences. They focus their investigations on the effects of mother-infant bonding in order to explain variations in the form, duration, and / or frequency of adult passionate relationships (see Hatfield and Rapson 1996; Shaver et al. 1988; Sternberg and Barnes 1988). These data on the development of passionate love from childhood experiences are not the focus of this paper: The present paper does not discuss *the context* in which romantic attraction develops across the human life course, *when* it develops, *toward whom* it is directed, *why* it is directed toward specific individuals rather than others, *how often* one experiences attraction, or *how long* an individual maintains attraction for a partner or a spouse. Instead, the present paper is a preliminary investigation of the specific constellation of neural correlates associated with this primary emotion category.

First it is necessary to discuss the psychophysiological properties of human attraction, since this suite of traits gives some indication of the neural substrate involved in this emotion system. Several psychologists have investigated the properties of attraction. Using a series of questionnaires and in-depth interviews of approximately 2,000 individuals, Tennov (1979, personal communication 1997) isolated a suite of psychological traits associated with "being in love," a state she calls *limerence.* Hatfield and Sprecher (1986) have also isolated a suite of traits commonly associated with attraction, a state they call "passionate love." Reviewing these data, as well as the past 25 years of psychological literature on attraction, Harris (1995) compiled a list of characteristics associated with romantic attraction that has been frequently cited and is well supported.

In a current synthesis of these data, the author and colleagues (Fisher et al. n.d.a) have compiled a more extensive list of psychophysical properties associated with attraction:

1. the loved person takes on "**special meaning.**" As one of Tennov's informants phrased it, "My whole world had been transformed. It had a new center, and that center was Marilyn" (Tennov 1979:18). This phenomenon is coupled with the **inability to feel romantic passion for more than one person** at a time;
2. **intrusive thinking** about the loved person;
3. crystallization, or the **tendency to focus** on the loved person's positive qualities and overlook or falsely appraise his/her negative traits;
4. **labile psychophysiological responses** to the loved person, including exhilaration, euphoria, buoyance, spiritual feelings, feelings of fusion with the loved person, increased energy, sleeplessness, loss of appetite, shyness, awkwardness, trembling, pallor, flushing, stammering, aching of the "heart," inappropriate laughing, gazing, prolonged eye contact, butterflies in the stomach, sweaty palms, weak knees, dilated pupils, dizziness, a pounding heart, accelerated breathing, uncertainty, anxiety, panic, and/or fear in the presence of the loved person;
5. a longing for **emotional reciprocity** coupled with the desire to achieve **emotional union** with the loved person;
6. **emotional dependency** on the relationship with the loved person, including feelings of hope, apprehension, possessiveness, preoccupation with the beloved, hypersensitivity to cues given by the beloved, inability to concentrate on matters unrelated to the beloved, jealousy, emotional vulnerability, fear of rejection by the beloved, fantasies about the loved person, separation anxiety, and swings in mood associated with the fluctuating state of the relationship, as well as feelings of despair, lack of optimism, listless-

ness, brooding, and loss of hope during a temporary setback in the relationship or after rejection by the loved person;
7. a powerful sense of **empathy** toward the loved person, including a feeling of **responsibility** for the beloved and a willingness to **sacrifice** for the loved person;
8. a **reordering of daily priorities** to be available to the loved person coupled with the **impulse to make a certain impression** on the loved person, including changing one's clothing, mannerisms, habits, or values;
9. an intensification of passionate feelings caused by **adversity** in the relationship;
10. a **sexual desire** for the target of infatuation coupled with the desire for **sexual exclusivity;**
11. the **precedence of the craving for emotional union** over the desire for sexual union with the beloved;
12. the feeling that one's romantic passion is **involuntary and uncontrollable.**

Some of these psychophysiological properties of attraction suggest specific neural correlates. Psychiatrist Michael Liebowitz (1983) has proposed that the exhilaration of romantic attraction is associated with heightened levels of one or more of the monoamine neurotransmitters, dopamine, norepinephrine, and serotonin, and/or phenylethylamine (PEA) in mesolimbic "reward centers" of the brain. Other properties of attraction listed above, including heightened energy, "intrusive" thinking, and focused attention, also suggest that the monoamine neurotransmitters are involved. To test Liebowitz's hypothesis that one or more of these monoamine neurotransmitters play a primary role in human romantic attraction, the rest of this section examines current data on the monoamines.

Dopamine (DA) is a catecholamine. Increased concentrations of dopamine in the brain are associated with euphoria (Wise 1988), loss of appetite (Colle and Wise 1988), hyperactivity (Post et al. 1988), increased mental activity, a delay of the onset of fatigue, and decreased need for sleep (Kruk and Pycock 1991). Hence dopamine is a likely agent for the exhilaration, heightened energy, sleeplessness, and reduced appetite associated with passionate attraction in humans. In rats, blocking the activity of dopamine diminishes proceptive behaviors, such as hopping and darting reactions (Herbert 1996). Data on some drugs of abuse also support the hypothesis that dopamine is a primary agent of attraction: Cocaine and amphetamines increase concentrations of dopamine in the brain (Wise 1989, 1996) and produce the exhilaration, excessive energy, sleeplessness, and loss of appetite that are characteristic of individuals who report being passionately in love.

Increased concentrations of dopamine in the brain have also been associated with heightened attention, motivation, and goal-directed behaviors in humans and other mammals (Kiyatkin 1995; Salamone 1996; Scatton et al. 1988), suggesting that the focus, motivation, and goal-directed behaviors characteristic of infatuated humans and other mammals are due to heightened concentrations of central dopamine. Dopamine neurons innervating the prefrontal cortex are stimulated during exposure to a novel environment (Tassin et al. 1980); this may occur when an individual is exposed to the novelty of a new partner. In addition, increased concentrations of central dopamine have been associated with "a hyperreactive, fearlike state" (Lee et al. 1988:324) and with anxiety and panic (Post et al. 1988); both are properties of intense romantic attraction.

Norepinephrine (NE) is a catecholamine chemically derived from dopamine. The effects of norepinephrine (and dopamine) are varied, depending on the receptors that they trigger. Nevertheless, increasing levels of central norepinephrine are generally associated with exhilaration, excessive energy, sleeplessness, loss of appetite, and other excitatory responses commonly associated with attraction. Amphetamine and related drugs of abuse increase concentrations of norepinephrine (Seiden et al. 1988), and amphetamines are regularly associated with euphoria, increased energy, loss of appetite, and wakefulness—all properties of romantic attraction. Norepinephrine has been associated with imprinting in an avian species (Davies et al. 1985), and the focused attention characteristic of romantic attraction could be considered a form of imprinting on the beloved. Norepinephrine is also associated with increased memory for new stimuli (Griffin and Taylor 1995), a trait that could be associated with the phenomenon of "crystallization," the increased recall of moments spent with the beloved that infatuated informants report (Tennov 1979).

After administering monoamine oxidase inhibitors to "lovesick" patients, Liebowitz (1983) concluded that the exhilaration of attraction is, at least in part, associated with phenylethylamine. Phenylethylamine (PEA) is chemically and pharmacologically related to the catecholamines (Sabelli and Javaid 1995). Sabelli and Javaid (1995:6) report that PEA may be a neuromodulator at aminergic synapses that modulates both NE and DA synapses; they conclude that PEA works in concert with these catecholamines to elevate mood. Hence it is likely that PEA plays a secondary role in the emotion system referred to here as attraction.

Observational data on nonhuman mammals include many incidences in which individuals display increased energy, focused attention, and goal-directed behavior while courting. And several studies conclude that the catecholamines play a crucial role in the preparatory phase of sexual behavior, specifically motivation and sexual arousal (Melis and Argiolas 1995). For example, when female prairie voles are exposed to a drop of male urine on the upper lip, norepinephrine is released in specific areas of the brain olfactory bulb, stimulating the release of estrogen and concomitant proceptive behavior (Dluzen et al. 1981). In most mammalian species, attraction may occur as a spontaneous, brief, catecholaminergically induced, excitatory reaction to a conspecific that initiates sexual physiology and behavior.

Serotonin (5-HT) is an indoleamine derived from tryptophan that has at least fifteen receptor subtypes, some of which may be associated with appetitive reproductive behaviors. In general, however, high levels of central serotonin have been associated with the consummatory and satiating aspects of sexual behavior and a loss of sexual interest; no specific appetitive sexual behaviors have been linked with high concentrations of central serotonin (Herbert 1996; Robbins and Everitt 1996). The data relating serotonin specifically to attraction in humans are conflicting. Increased concentrations of central serotonin can suppress appetite (Cooper 1996) and produce sensations of well-being, properties associated with infatuation. But increased concentrations of central serotonin generally accelerate and prolong sleep and reduce anxiety and fearfulness (Hardman et al. 1996; Stein and Stanley 1994); these are not properties of infatuation.

Low levels of serotonin may be associated with attraction, however. Insomnia, a common property of passionate attraction, is associated with low concentrations of central serotonin (Hardman et al. 1996). In addition, serotonin-reuptake inhibitors, which increase serotonin at the synapse, are currently the agents of choice in treating most forms of obsessive-compulsive disorder (Flament et al. 1985; Hollander et al. 1988; Thoren et al. 1980), suggesting that low levels of central serotonin may contribute to obsessive "intrusive thinking," a primary element of passionate love.

Dosage effects of the above-mentioned monoamines, interactions between these monoamines, and interactions between these monoamines and other central and peripheral emotion systems make analysis of this emotion system, attraction, highly complex. Yet the similarities between the psychophysiological properties of romantic attraction (listed above) and the psychophysiological properties of these monoamines suggest that dopamine, norepinephrine, and serotonin may play central roles in this emotion category (Table 1).

Liebowitz (1983) proposed that the brain architecture associated with romantic attraction involves mesolimbic "pleasure centers." The brain's "pleasure centers" were first described in the 1950s (Olds 1956; Olds and Milner 1954; see Wise 1996). But recent advances in the neurophysiology of addiction, as well as other studies, have refined our understanding of

Table 1. The Three Proposed Emotion Categories for Mammalian Mating and Reproduction and Their Associated Hormones and Neurotransmitters in the Brain (Listed are molecules that have an action in the brain and that play a major, but not exclusive, role in lust, attraction, or attachment. Evidence for the role of these molecules in the different emotions comes from rodent and human data.)

Lust (Sex Drive)	*Attraction (Obsession/Attention)*	*Attachment (Comfort, Parenting)*
Androgens	Catecholamines:	Oxytocin
Estrogens	Dopamine	Vasopressin
	Norepinephrine	
	Phenylethylamine (PEA)†	
	Serotonin	

†PEA is associated with catecholaminergic cells and sympthomimetic functional effects. It may be a modulator of aminergic synapses and not a classic neurotransmitter.

some of the primary areas of the brain's "reward circuitry," and the mesocorticolimbic dopamine system is strongly implicated (Wise 1996).

Wise (1989, 1996) proposes that a central component of the brain's reward circuitry is increased concentrations of dopamine at dopamine receptors localized to specific subpopulations of neurons in the nucleus accumbens and prefrontal cortex. Discussing the neurobiology of motivation and reinforcement, Robbins and Everitt (1996:229) concur, implicating the mesolimbic dopamine system that projects from the ventral tegmental area to the ventral striatum, including the nucleus accumbens (Figure 1). Several neuroscientists report that related structures are most likely also involved, including the basolateral amygdala, the hippocampal formation, and the prefrontal cortex (Gallagher and Chiba 1996; Robbins and Everitt 1996). The amygdala is a phylogenetically old brain structure that is centrally involved in the function of the autonomic nervous system (Kilts et al. 1988). So specific areas within the amygdaloid complex associated with dopamine (Kilts et al. 1988) and the control of arousal (Gallagher and Chiba 1996) most likely play central roles in the peripheral excitatory responses associated with attraction.[2]

The specific neural circuitry of the brain's system for motivation, reinforcement, pleasure, and/or reward is complex (see Kalivas and Nemeroff 1988). Other brain areas associated with catecholaminergic activity could be involved (Figure 1), and neurotransmitters other than dopamine are currently being investigated (Robbins and Everitt 1996). Nevertheless, this mesocorticolimbic reward system in the brain is associated with heightened energy, motivational processes, and goal-directed behavior in a range of mammalian appetitive categories of emotion, including the search for *preferred* foods and *preferred* drugs (Kiyatkin 1995; Robbins and

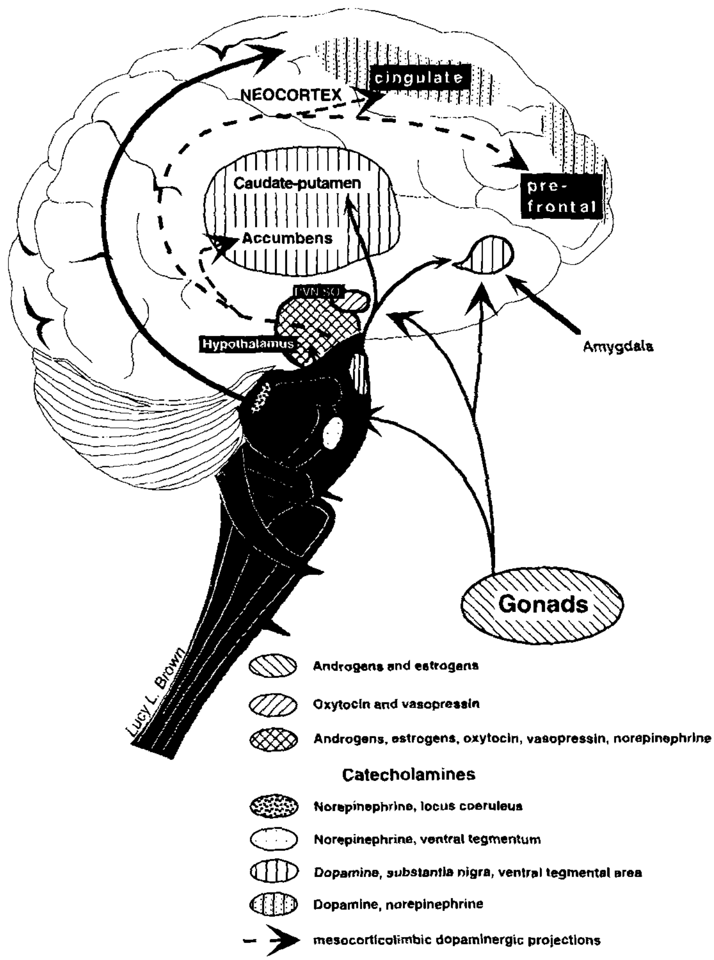

Figure 1. Brain areas and primary hormones and neurotransmitters associated with lust, attraction, and attachment. The simplified human brain drawing shows the principal sources and targets of the hormones and neurotransmitters implicated in the emotions of lust (androgens and estrogens), attraction (catecholamines), and attachment (oxytocin and vasopressin). Sources of the hormones for lust are the gonads; sources of the hormones for attachment are the PVN/SON of the hypothalamus. Sources of the catecholamines are cell groups in lower hindbrain areas including the locus coeruleus, ventral tegmental area, and substantia nigra. Targets of the hormones tend to be in lower brain areas whereas major targets of the catecholamines are in the forebrain. The mesocorticolimbic dopaminergic projections are known for their role in euphoria and positive reinforcement and may play a primary role in the emotions associated with attraction in humans. PVN/SON refers to the paraventricular and supraoptic nuclei of the hypothalamus.

Everitt 1996). So it is parsimonious to suggest that this neural system is part of the constellation of neural correlates associated with some of the properties of attraction, including exhilaration; increased energy; autonomic reactions such as loss of appetite, sleeplessness, and a pounding heart; motivation; goal-oriented behaviors; and focused attention on a *preferred* mate.

Attraction may be associated with a range of other neural regions as well. As Davidson (1994:241) writes, "emotion-specific patterning at the discrete emotion level may be found in those brain circuits that are not exclusively devoted to emotional processing, but also are involved in higher-order cognitive processes." Since cultural rules and childhood experiences contribute a great deal to human mating behavior, it is logical to suggest that a range of higher-order cognitive processes and corresponding cortical structures also are involved in human attraction.

Hatfield and Walster (1978) distinguish between reciprocated love, associated with fulfillment and ecstasy, and unrequited love, associated with emptiness, anxiety, and despair. Their data, along with the many descriptions of romantic love in other psychological literature and descriptions of attraction in thousands of myths, legends, stories, novels, poems, and works of nonfiction cross-culturally, suggest that passionate romantic attraction takes a variety of graded forms, from elation to despair, from calm to anxiety. So it is expected that the constellation of neural correlates associated with these *gradations* of attraction will vary accordingly. For example, most likely the relationship among the catecholamines and serotonin varies in specific ways as a romantic relationship becomes more or less reciprocated. Analysis of infatuated subjects, using in-depth questionnaires in conjunction with functional magnetic resonance imaging of the subjects' brains, may establish more definitively some of the fundamental anatomical and neurochemical components of mammalian attraction (Fisher et al. n.d.a, n.d.b).

Data already exist, however, to suggest that attraction is a discrete emotion category distinct from the sex drive: 61% of Tennov's female informants and 35% of male informants agreed with the statement, "I have been in love without feeling any need for sex"; 95% of Tennov's female informants and 91% of her male subjects rejected the statement, "The best thing about love is sex" (Tennov 1979:74). These informants distinguished between the sex drive and feelings of romantic attraction. Moreover, humans can feel the urge for sexual consummation with a partner without feeling romantic attraction toward this partner. The distinction between attraction and lust is also observable in other mammals. Mammals regularly express the drive for sexual consummation, yet most prefer some partners and reject others.

So it is parsimonious to conclude that the constellation of neural correlates associated with attraction are distinct from those associated with the sex drive; that these emotion systems operate along conjoining and/or closely linked neural circuits; and that each of these emotion categories evolved to direct a distinct aspect of mammalian reproduction: Lust evolved to motivate individuals to seek sexual gratification with *any* conspecific, and attraction evolved to enable individuals to focus their mating effort on *preferred* mating partners.

In humans, attraction is mediated by a host of cultural stimuli. *When* an individual falls in love, *where* they fall in love, *with whom* they fall in love, *how* they court, even *whether* they choose to act on their bodily sensations of attraction can be expected to be influenced by childhood experiences, by myriad other cultural forces, and by individual volition. But the actual *feeling* an individual experiences *as* he/she becomes attracted to a preferred conspecific is a product of the evolution of the mammalian brain designed to enable individuals to choose genetically superior mating partners.

ATTACHMENT

Many scientists have discussed mother-infant bonding and its role in aspects of adult attachment (Ainsworth 1969, 1989; Ainsworth et al. 1978; Shaver and Hazan 1993; Shaver et al. 1988). But these investigations concentrate on *types* of psychological attachment and the *development* of psychological attachment through the life course; instead, the present paper defines this emotion system, specifies some of the neural mechanisms associated with all forms of attachment behavior, and cites data to establish that this emotion system, attachment, is distinct from that of the sex drive and attraction.

Neuroscientists currently distinguish appetitive and consummatory behaviors as distinct behavioral and physiological phenomena; they regard the neural substrates of these categories of emotion as distinct (see Robbins and Everitt 1996); and they regard attachment as an emotion associated with consummatory behavior (see Pedersen et al. 1992). Psychologists have recognized attachment as a specific emotion system since John Bowlby began to investigate and record attachment behaviors in humans and other mammalian species in the 1950s (see Bowlby 1969, 1973, 1980). Bowlby (1969:179) regarded attachment behavior "as a class of social behaviour of an importance equivalent to that of mating behaviour . . . *that had a biological function specific to itself*" (emphasis added). He described attachment behavior as "what occurs when certain behavioural systems are activated" (Bowlby 1969:179).

Attachment behaviors in social mammals include recognizing conspecifics to whom one is attached, preferring the company of these conspecifics, maintaining proximity (often close body contact), exhibiting species-specific patterns of touch, displaying separation anxiety when apart, and attempting to restore close contact after separation (Bowlby 1969; Mendoza and Mason 1997). Attachment behaviors also include monogamous male-female affiliative gestures and monogamous parental behaviors, such as territory defense, nest building, mutual feeding, grooming, and shared parental chores (see Carter et al., eds. 1997; Pedersen et al. 1992). In humans, the above-mentioned behavior patterns associated with attachment are accompanied by reported feelings of closeness, security, peace, social comfort, mild euphoria, and reduced anxiety when in contact with a partner, and separation anxiety when apart for a length of time (Liebowitz 1983). Psychologists describe human attachment as "the affection we feel for those with whom our lives are deeply entwined" (Hatfield 1988:205).

Several neuropeptides have been implicated in male-female bonding, group bonding, and mother-infant bonding in mammals (see Carter et al. 1997; Insel 1992; Pedersen et al. 1992). But recent data indicate that oxytocin and vasopressin released in the central nervous system are the primary hormones that produce monogamous male-female attachment and monogamous parenting behaviors in mammals (Carter 1992; Carter et al. 1995; Insel et al. 1993; see Pedersen et al. 1992; Winslow et al. 1993). Vasopressin is produced primarily in the supraoptic (SON) and paraventricular (PVN) nuclei of the hypothalamus. Oxytocin, which varies from vasopressin by two amino acids, is also produced primarily in the supraoptic and paraventricular nuclei of the hypothalamus (Carter 1992).

Carter and colleagues report that among monogamous prairie voles, "no evidence currently exists that gonadal hormones play a role in the partner preference component of pair bonding" (Carter et al. 1997:263); instead oxytocin and vasopressin play a predominant role in maintaining these sustained monogamous attachments (see Carter et al. 1997). And although the neural correlates of attachment are associated with those for the sex drive (Insel 1992), several neuroscientists view the constellation of neural correlates associated with attachment as a specific emotion category (Carter 1992; Carter et al. 1995; Insel et al. 1993; see Pedersen et al. 1992; Winslow et al. 1993).

Observational data on humans support the hypothesis that the neural correlates of attachment are distinct from those of the sex drive and those of attraction. Arranged marriages, for example, are common cross-culturally (Frayser 1985), as are long-term marriages (Fisher 1989, 1992, 1994, 1995). Spouses in arranged marriages and long-term marriages regularly maintain attachment to one another, express feelings of attachment for one another, and display mutual parental duties *without* displaying or reporting feelings of attraction or sexual desire for one another.

HUMAN MATING FLEXIBILITY

A primary characteristic of human reproductive strategies is monogamous marriage. Monogamous marriage is the predominant mating tactic in all contemporary societies (Fisher 1989, 1992; Lancaster and Kaplan 1994; Murdock 1949; van den Berghe 1979). All cultures have procedures for initiating and sustaining monogamous marriage, traditions for overcoming the trauma of separation anxiety at the termination of monogamous marriage, and means for negotiating monogamous remarriage. Sexual jealousy is also universal to human cultures; humans, as a rule, do not share long-term partners to whom they are attached unless the environmental and cultural perquisites considerably outweigh the deficits. Because monogamous attachment is not characteristic of the African apes, it is parsimonious to suggest that the specific constellation of neural correlates associated with sustained monogamous attachment evolved at some point in hominid evolution.[3]

But *sustained* monogamous attachment is not an exclusive hominid reproductive strategy; secondary opportunistic reproductive strategies are also prevalent in humans. Opportunistic *serial* monogamy is universal to human societies (Fisher 1992). Opportunistic polygyny occurs in 83% of human cultures (van den Berghe 1979).[4] Opportunistic polyandry occurs in .5% of cultures (van den Berghe 1979). Opportunistic extra-pair attachments occur in all cultures for which data are available (Fisher 1992), and humans exhibit other secondary forms of attachment in association with a range of environmental variables (Lancaster and Kaplan 1994). Mating flexibility is a hallmark of *Homo sapiens*.

These data suggest that during the course of hominid evolution the constellations of neural correlates associated with lust, attraction, and attachment became increasingly independent of one another, enabling hominids to exercise mating flexibility and engage (sometimes simultaneously) in a range of primary and secondary opportunistic reproductive strategies.

CONCLUSION

Many scientists have presented lists of primary categories of emotion in mammals. Panksepp and colleagues (1997:80) note that for several of these emotions "existing neurobiological data are affirming that distinct brain circuits exist." The present paper attempts to isolate the primary categories of emotion associated with mammalian reproduction; to present these emotion systems as a useful model for categorizing aspects of mating behavior in mammals; to propose the evolutionary relationship between attraction, mate choice, and sexually selected, species-specific traits; and to offer a hypothesis for the flexibility and range of contemporary patterns of mating and reproduction in *Homo sapiens.*

It is proposed that mammals exhibit three interrelated, bidirectional, yet, in some species, distinct emotion systems for mating that evolved to regulate three primary aspects of mammalian reproduction: the sex drive, associated primarily with the androgens and estrogens, motivates individuals to seek sexual gratification with *any* conspecific; the attraction system, associated primarily with the catecholamines, motivates individuals to focus their mating effort on *preferred* conspecifics; and the attachment system, associated primarily with oxytocin and vasopressin, motivates individuals to assume species-specific parental duties.

The precise composition, duration of activation, and activities of the neural mechanisms associated with each of these three emotion systems can be expected to vary according to the primary reproductive strategy of each species. These emotion systems can also be expected to vary within species from one individual to the next, across the life course, according to gender, and in response to specific environmental opportunities and exigencies. These emotion systems can also be expected to be closely interrelated and to work in concert with one another and with other bodily systems.

Nevertheless, the constellations of neural correlates associated with the sex drive, attraction, and attachment are also proposed to be distinct from one another in some mammals, including humans. Men and women can express attachment for a long-term mate, attraction to a different conspecific, and the sex drive in response to stimuli unrelated to either of these individuals. The independence of these emotion systems in humans evolved to take advantage of rare mating opportunities and to pursue a mixture of short-term and long-term reproductive strategies simultaneously or in succession. Hence the independence of these emotion systems enabled mating flexibility in hominid populations of the past and contributes to contemporary patterns of human serial monogamy, extra-pair copulations, and other variations in the wide range of human mating and reproductive behaviors.

At least 25% of homicides in the United States involve spouses, sexual partners, or sexual rivals (Daly and Wilson 1988). Any given year, approximately 1.8 million wives in the United States are beaten by their husbands (Strauss 1978); male jealousy is the most common cause of wife battering cross-culturally (see Smuts 1992; Daly and Wilson 1988). Fifty-six percent of American college women in one study reported being harassed by a rejected lover (Jason et al. 1984). An untold number of husbands receive physical abuse from wives as well, and many other crimes of passion, as well as incidences of stalking and cases of clinical depression and suicide, are commonly associated with romantic attraction cross-culturally (Hatfield and Rapson 1996; Tennov 1979). So the model presented here for identifying attraction as a specific emotion system, independent from the sex drive and from attachment, may be useful to understanding some patterns of human criminal, social, and reproductive behavior.

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NOTES

1. Discussion of avian mating systems is beyond the scope of this paper, but it is likely that avian species exhibit related anatomical and neurohormonal emotion systems for mating.
2. Because depletion of dopamine in the brain's reward circuitry has been proposed as a consequence of drug withdrawal (Wise 1996), a similar drop in dopamine levels in the central reward system may account for the feelings of depression, loss of energy, and lack of motivation associated with rejection by a conspecific to whom one is attracted.
3. It is hypothesized that selection for the neurohormonal circuitry associated with hominid serial monogamy occurred at the basal radiation of the hominid clade when the vicissitudes of the woodland/grassland environment required

pairing in conjunction with rearing young through infancy (Fisher 1989, 1992, 1994, 1995).

4. In two-thirds of polygynous societies, less than 20% of men take two or more wives simultaneously; in one-third of polygynous societies, around 20% or more men engage in polygyny at some point during their lives (Lancaster and Kaplan 1994).

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