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SERIAL MONOGAMY AND CLANDESTINE ADULTERY:

Evolution and consequences of the dual human reproductive strategy

Considerable data suggest that *Homo sapiens* has evolved a dual reproductive strategy: life long and/or serial monogamy in conjunction with clandestine adultery (Fisher 1992). This paper explores the underlying biochemical and genetic mechanisms likely to contribute to this flexible, yet specific human reproductive system and explores some of the implications of this dual human reproductive strategy for contemporary partnerships.

Neurobiology of human attachment

Pair-bonding is a hallmark of humanity. Data from the Demographic Yearbooks of the United Nations on 97 societies canvassed in the 1980s indicate that approximately 93.1% of women and 91.8% of men in that decade married by age forty-nine (Fisher 1989; Fisher, 1992). Worldwide marriage rates have declined somewhat since then; but today 85% to 90% of men and women in the United States are projected to marry (Cherlin 2009). Cross-culturally, most individuals wed one person at a time: monogamy. Polygyny is permitted in 84% of human societies; but in the vast majority of these cultures, only 5% to 10% of men actually have several wives simultaneously (Frayser, 1985; van den Berghe, 1979). Because polygyny in humans is regularly associated with rank and wealth, monogamy may have been even more prevalent in prehorticultural, unstratified societies (Daly and Wilson 1983). Human monogamy is not, however, always life long. Nearly half of all marriages in the US end in divorce. By age 35, 10% of American women have had three or more husbands

(Cherlin 2009). Data collected from the Demographic Yearbooks of the United Nations on 58 societies from 1947 to 1989, as well as a host of ethnographic studies, indicate that divorce and remarriage are also common cross-culturally (Fisher 1992; Fisher 1989).

Several data suggest that this human disposition for pair-bonding has a biological basis. The contemporary psychological investigation of human attachment began with Bowlby (Bowlby 1969; 1973) and Ainsworth (Ainsworth et al 1978) who proposed that, to promote the survival of the young, primates have evolved an innate attachment system designed to motivate infants to seek comfort and safety from their primary caregiver, generally mother. Since then extensive psychological research has been done on the behaviors and feelings associated with this attachment system in adults (Fraley and Shaver 2000); and researchers have proposed that this biologically-based attachment system remains active throughout the life course, serving as a foundation for attachment between pair-bonded spouses for the purpose of raising offspring (Hazan and Diamond 2000; Hazan and Shaver 1987). Hatfield refers to the human feelings associated with these attachment behaviors as companionate love, which she defines as "a feeling of happy togetherness with someone whose life has become deeply entwined with yours." (Hatfield et al. 1988:191).

The human penchant to form pair-bonds is rare among mammals; only 3% form pair-bonds to rear their young. But pair-bonding is common in avian species; some 90% of more than 8,000 avian species practice pair-bonding to rear their young. Moreover in all avian and mammalian species where monogamy is the primary reproductive strategy, it is associated with a particular suite of behaviors, including mutual territory defense and/or nest building, mutual feeding and grooming, maintenance of close proximity, affiliative behaviors and shared parental chores. The ethological literature commonly regards this constellation of pair-bonding behaviors as a behavioral syndrome that evolved primarily to motivate mating partners to sustain an affiliative connection long enough to complete species-specific parental duties.

The most informative biological research on pair-bonding in mammals has been collected on prairie voles (*Microtus ochrogaster*). These individuals mate soon after puberty and maintain a monogamous relationship throughout their life course, raising a series of litters as a team; and some of the neural underpinnings of their pair-bonding behaviors have been established. When prairie voles engage in sex, copulation triggers the activity of oxytocin (OT) in the nucleus accumbens among females and arginine vasopressin (AV) in the ventral pallidum among males, which then facilitates dopamine release in these reward regions and motivates females and males to prefer a particular mating partner, initiate pair-bonding and express attachment behaviors (Lim, Murphy & Young 2004; Carter, 1992; Lim and Young, 2004).

These data are corroborated in other species. Promiscuous white-footed mice and promiscuous rhesus monkeys do not form pair-bonds or express attachment behaviors for a specific mate, and the males of these species do not express the same distribution of V1a receptors in the ventral pallidum (Bester-Meredith et al., 1999; Wang et al., 1997; Young, 1999; Young et al., 1997). Moreover, when scientists (Pitkow et al 2001; Lim and Young 2004) transgenically inserted the genetic variant in the vasopressin system associated with pair-bonding in male prairie voles into the ventral pallidum of male meadow voles, an asocial promiscuous species, vasopressin receptors were up-regulated; these males also began to fixate on a particular female and mate exclusively with her, even when other females were available (Lim et al., 2004). When this gene was inserted into non-monogamous male mice, these creatures also began to exhibit attachment behaviors (Young et al., 1999).

A number of groups have reported that the basic human motivations and emotions arise from distinct systems of neural activity and that these brain systems derive from mammalian precursors

(Davidson 1994; Panksepp 1998). So it is parsimonious to suggest that the underlying physiology associated with human monogamy is similar to that of other mammalian pair-bonding species. Moreover, activity in the ventral pallidum has been linked with longer-term pair-bonding in humans (Aron et al., 2005; Acevedo et al., 2008; Acevedo et al., in press; Fisher et al 2010). And although the AVPR1A gene among *Homo sapiens* is not homologous to the one found in prairie voles, humans do have similar alleles in this genetic region (Walum et al 2008), suggesting that a related biological system plays a role in human monogamy.

INFIDELITY

Monogamy is only part of the human reproductive strategy. Infidelity is also widespread (Buunk & Dijkstra, 2006; Fisher, 1992). The National Opinion Research Center in Chicago reports that some 25% of American men and 15% of American women philander at some point during marriage (Laumann et al 1994). Other studies of American married couples indicate that 20%-40% of heterosexual married men and 20%-25% of heterosexual married women have an extramarital affair during their lifetime (e.g., Greeley, 1994; Laumann et al., 1994; Tafoya & Spitzberg, 2007); still other researchers indicate that some 30% to 50% of American married men and women are adulterous (Gangestad and Thornhill 1997). When polled, approximately 2%-4% of American men and women had had extramarital sex in the past year (Forste & Tanfer, 1996).

The Oxford English Dictionary defines adultery as sexual intercourse by a married person with someone other than one's spouse. But current researchers have broadened this definition to include sexual infidelity (sexual exchange with no romantic involvement), romantic infidelity (romantic exchanges with no sexual involvement) and sexual and romantic involvement (Glass & Wright, 1992). When considering these varieties of adultery, statistics vary. In a meta-analysis of 12 studies of infidelity among American married couples, Thompson (1983) reported that 31% of men and 16% of women had had a sexual affair that entailed no emotional involvement; 13% of men and 21% of women had been romantically but not sexually involved with someone other than their spouse; and 20% of men and women had engaged in an affair that included both a sexual and emotional connection.

Currently 70% of American dating couples report an incidence of infidelity in their partnership (Allen & Baucom, 2006). Furthermore, in a recent survey of single American men and women, 60% of men and 53% of women admitted to "mate poaching," trying to woo an individual away from a committed relationship to another to begin a relationship with them instead (Schmitt & Buss, 2001). Mate poaching is also common in 53 other cultures (Schmitt et al, 2004).

Infidelity was also widespread in former decades. Reports in the 1920s indicated that 28% of American men and 24% of women were adulterous at some point after wedding (Lawrence, 1989). In the late 1940s and early 1950s, approximately 33% of men and 26% of women in an American sample were adulterous (Kinsey et al., 1948; Kinsey et al., 1953); in the 1970s, some 41% of men and 25% of women reported infidelity (Hunt, 1974); and data collected in the 1980s indicated that 72% of men and 54% of women were unfaithful at some point during their marriage. Infidelity was also common among the classical Greeks and Romans, among the pre-industrial Europeans, among the historical Japanese, Chinese and Hindus and among the traditional Inuit of the arctic, Kuikuru of the jungles of Brazil, Kofyar of Nigeria, Turu of Tanzania and many other tribal societies (Fisher, 1992). Extra-pair copulations also occur frequently in every other society for which data are available (Frayser 1985). Human testes size suggests that adultery by both sexes was also common in hominid prehistory (Short, 1977; Moller 1988)

Extra-pair copulations (EPCs) are prevalent in over 100 species of monogamous birds and several mammalian species examined (Mock & Fujioka 1990; Westneat, Sherman, & Morton, 1990;

Wittenberger & Tilson, 1980). Only 10% of some 180 species of monogamous songbirds are sexually faithful to their mating partners; the rest engage in EPCs. Among swift foxes (*Vulpes velox*) over 59% of a female's offspring were not genetically related to the male with whom she was pair-bonded (Kitchen et al 2006). Extra-pair copulations are also common among gibbons (*Hylobates lar*) (Reichard 1995).

In fact, infidelity is so widespread and persistent in monogamous avian and mammalian species, including humans, that scientists now refer to monogamous species as practicing "social monogamy," in which partners display the array of social and reproductive behaviors associated with monogamy while not necessarily displaying sexual fidelity as well.

Myriad psychological, sociological and economic variables play a role in the frequency and expression of infidelity (Tsapelas, Fisher and Aron, 2010). But recent genetic studies suggest that biology plays a role. Walum et al (2008) investigated 552 couples biologically, psychologically and socially. All were either married or co-habiting for at least five years. Men carrying the 334 allele in a specific region of the vasopressin system scored significantly lower on a questionnaire, the Partner Bonding Scale, indicating less feelings of attachment to their spouses. Moreover, their scores were dose dependent: those carrying two of these alleles showed the lowest scores for feeling of attachment, followed by those carrying only one allele, followed by those carrying no copies of this allele. Men carrying the 334 allele also experienced more marital crises (including threat of divorce) during the past year. These results were also dose-dependent; men with two copies of the allele were approximately twice as likely to have had a marital crisis as those who had inherited either one copy or no copies. Men with one or two copies were also significantly more likely to be involved in a partnership without being married. Last, the spouses of men with one or two copies of this allele in the vasopressin system scored significantly lower on questionnaires measuring marital satisfaction.

This study did not measure infidelity directly; instead it measured several factors likely to contribute to infidelity. Nevertheless, among prairie voles, polymorphisms in a similar gene in the vasopressin system contribute to the *variability* in the strength of the monogamous pair-bond (Hammock & Young 2002), including the degree to which individuals express sexual fidelity (Ophir, Wolff, & Phelps, 2008). Moreover, in a more direct recent study of infidelity in a sample of 181 young adult humans, Garcia and colleagues (Garcia et al 2010) found a direct link between specific alleles in the dopamine system (DRD47R+) and a greater frequency of uncommitted sexual intercourse (one night stands) and a higher frequency of sexual infidelity.

Another biological system may contribute to infidelity. In the now classic “sweaty t-shirt” experiment, women sniffed the t-shirts of several anonymous men and selected the t-shirts of those they felt were the sexiest. They selected the shirts of men with different genes (from themselves) in a specific part of the immune system, the major histocompatibility complex (MHC) (Wedekind et al., 1995). In a subsequent investigation, women married to men with similar genes in this part of the immune system were also more adulterous; and the more of these genes a woman shared with her spouse the more extra-dyadic partners she engaged sexually (Garver-Apgar et al., 2006).

Brain architecture may also contribute to infidelity, due to the connections between three distinct yet interrelated brain systems that evolved for mating, reproduction and parenting: the sex drive; romantic attraction; and attachment (Fisher 1998). In mammals, the sex drive is associated primarily with the estrogens and androgens; however in humans only the androgens, particularly testosterone, are central to sexual desire in both men and women (Sherwin 1994; Van Goozen et al 1997). Studies (fMRI) indicate that specific networks of brain activation are associated with the sex drive, among the regions involved is the hypothalamus (Arnow et al., 2002; Karama et al 2002) and amygdala (Karama et al 2002). Romantic attraction (also known as romantic love, obsessive love, passionate love or being in love) is primarily associated with elevated dopamine activity in reward pathways of the brain (Fisher et al 2005; Aron et al 2005; Bartels and Zeki 2000; Bartels and Zeki 2004; Acevedo et al 2008; Acevedo et al., in press; Fisher et al 2010). As discussed above, attachment in humans and other mammals is associated primarily with oxytocin and vasopressin activity in the nucleus accumbens and ventral pallidum respectively (Lim, Murphy & Young 2004; Lim and Young 2004; Acevedo et al., in press; Fisher et al 2010).

These three basic interrelated but distinct neural systems interact with one another and many other brain systems in myriad flexible, combinatorial patterns to provide the range of cognitions, emotions, motivations and behaviors necessary to orchestrate our complex human reproductive strategy (Fisher et al 2002). Nevertheless, these three brain systems are not always directly connected, making is possible for one to express deep feelings of attachment for one individual, *while* one feels intense romantic attraction toward another, *while* one feels the sex drive for more extra-dyadic partners (Fisher, 2004). The relative biological independence of these three neural systems for mating and reproduction enable *Homo sapiens* to engage opportunistically in social monogamy and clandestine adultery simultaneously (Fisher 2004).

EVOLUTION OF MONOGAMY

Monogamy could have evolved at any point in hominid evolution. However two lines of possible evidence suggest that the neural circuitry for human pair-bonding evolved with the basal radiation of the hominid stock (Fisher 1992), most likely in tandem with the hominid adaptation to the woodland/savannah eco-niche some time prior to 4 million years BP. *Ardipithecus ramidus*, currently dated at 4.4 my BP, displays traits associated with reduced sexual dimorphism; so Lovejoy (2009) suggests that human monogamy had evolved by this time. Anthropologists have also re-measured *Australopithicus afarensis* fossils for skeletal size; and they report that by 3.5 million years BP hominids exhibited roughly the same degree of sexual dimorphism in several traits as the sexes exhibit today, thus they have proposed that these hominids were "principally monogamous" (Reno et al 2003:1073).

The emergence of facultative bipedalism may have been a primary contributing factor to the evolution of the neural circuitry for hominid monogamy (Fisher 1992). While foraging and scavenging in the woodland/savannah eco-niche, bipedal Ardipithecine females were most likely obliged to carry infants in their arms instead of on their backs, as quadrupedal female apes do, thus needing the protection and provisioning of a mate while they transported nursing young. Meanwhile, Ardipithecine males may have had considerable difficulty protecting and providing for a harem of females in this open woodland/savannah eco-niche. But a male could defend and provision a single female with her infant as they walked near one another, within the vicinity of the larger community.

So the exigencies of facultative bipedalism in conjunction with hominid expansion into the woodland/savannah eco-niche may have pushed Ardipithecines over the "monogamy threshold," selecting for the brain chemistry and brain architecture for pair-bonding and associated attachment behaviors (Fisher 1992; 2004).

EVOLUTION OF *SERIAL* MONOGAMY

Contemporary cross-cultural patterns of divorce suggest that *serial* social monogamy may have also evolved as part of the suite of traits associated with hominid adaptation to the expanding woodland/savannah eco-niche prior to 4 my BP. Data on 58 human societies taken from the Demographic Yearbooks of the United Nations between 1947 and 1989 indicate three worldwide divorce patterns. Divorce occurs most frequently among couples with one dependent child; among couples at the height of their reproductive and parenting years (ages 25-29); and among couples married a modal duration of four years (Fisher 1989; Fisher 1992). Because four years is the common duration of birth spacing in hunting/gathering societies, and because many monogamous avian and mammalian species form pair-bonds that last only long enough to rear the young through infancy, this human cross-cultural modal divorce peak may represent the remains of an ancestral hominid reproductive strategy to remain pair-bonded at least long enough to raise a single child through infancy, about four years (Fisher 1992).

Children in hunting/gathering societies characteristically join a multi-age playgroup soon after being weaned, becoming the responsibility of older siblings and other relatives in the band. So in the EEA, the ecological pressure on couples to remain pair-bonded *after* offspring weaning would have been substantially reduced, unless the couple conceived another child. Moreover, ancestral hominids that practiced serial social monogamy in association with offspring weaning would have created disproportionately more genetic variety in their lineages, an adaptive phenomenon (Fisher 1992).

EVOLUTION OF CLANDESTINE ADULTERY

Infidelity often involves considerable time and metabolic energy. It also involves risk; adultery can lead to diseases, unwanted pregnancy, and many adverse social consequences, including losing one's home, spouse, children, job, community and/or health. Yet, despite near universal disapproval of infidelity, this worldwide phenomenon occurs with regularity. Most curious, regardless of the many correlations between relationship dissatisfaction and adultery (see Tsapelas, Fisher and Aron 2010), Glass and Wright (1985) report that among Americans who engage in infidelity, 56% of men and 34% of women rate their marriage as "happy" or "very happy." Because philandering is prevalent worldwide; because it is associated with a wide range of psychological and sociological factors; because it is correlated with several biological underpinnings discussed above; because promiscuity is the primary reproductive strategy among our closest primate relatives, bonobos and common chimps; and because infidelity occurs even in "happy" and "very happy" marriages today; it is likely that infidelity is a core aspect of our primary human reproductive strategy, and that it evolved in tandem with hominid serial social monogamy for adaptive purposes.

Many scientists have offered hypotheses regarding the selective value of infidelity (see Buss 1994). Among these, it has been proposed that in the ancestral woodland/savannah eco-niche, philandering males and females would have disproportionately reproduced, as well as reaped the reproductive benefits of genetically more varied offspring (Fisher 1992). Unfaithful females may have also garnered economic resources from extra-dyadic liaisons, as well as parenting support if their primary partner died or deserted them (Fisher 1992). Hence clandestine infidelity (in conjunction with serial and/or life long social monogamy) may have had reproductive payoffs for both males and females throughout the EEA, selecting for the biological underpinnings of infidelity in both sexes today.

Along with the evolution of serial/lifelong social monogamy and clandestine adultery, several other neural systems may have evolved. Three are considered next: the brain system associated with feelings of intense romantic attraction to a *specific* individual; four proposed temperament dimensions that may have begun to play a guiding role in mate choice; and the brain networks associated with rejection in love. All of these neural systems most likely served other purposes among our hominoid forebears prior to the hominid radiation into the woodland/savannah eco-niche. Nevertheless, these neural systems may have taken on new functions with the evolution of the hominid dual reproductive strategy.

EVOLUTION OF ROMANTIC ATTRACTION

Human romantic love (also known as passionate love, obsessive love, and “being in love”) is a cross-cultural phenomenon (Jankowiak and Fischer 1992). In a survey of 166 societies, Jankowiak and Fischer (1992) found evidence of romantic love in 147 of them. No negative evidence was found;

in the 19 remaining cultures, anthropologists had failed to ask the appropriate questions, cases of ethnographic oversight. Jankowiak and Fischer concluded that romantic love constitutes a "human universal… or near universal"(Jankowiak and Fischer 1992).

Romantic attraction is associated with a specific suite of psychological, behavioral and physiological traits (Fisher 1998; Gonzaga et al. 2001; Hatfield et al. 1988; Hatfield and Sprecher 1986; Harris 1995; Tennov 1979). Romantic love generally begins as an individual starts to regard another individual as special, unique. The lover focuses his/her attention on the beloved, aggrandizing the beloved's worthy traits and overlooking or minimizing their flaws. The lover expresses increased energy, ecstasy when the love affair is going well, and mood swings into despair during times of adversity. Adversity and social barriers tend to heighten romantic passion, "frustration attraction"(Fisher 2004). The lover often suffers "separation anxiety" when apart from the beloved, and a host of sympathetic nervous system reactions when with the beloved, including sweating, stammering, butterflies in the stomach and/or a pounding heart. Lovers are emotionally dependent; they change their priorities and daily habits to remain in contact with and/or to impress the beloved. Smitten humans also exhibit increased empathy for the beloved; many are willingness to sacrifice, even die for this "special" other. The lover also expresses sexual desire for the beloved, as well as intense sexual possessiveness, "mate guarding." Yet the lover's craving for emotional union with the beloved tends to supersede his/her craving for sexual union with him or her. Most characteristic, the lover thinks obsessively about the beloved, "intrusive thinking." Romantic attraction is also involuntary and difficult to control.

Several neuroimaging studies of romantic love indicate the physiological underpinnings of this near-universal human experience (Fisher et al 2003; Aron et al 2005; Bartels and Zeki 2000; Bartels and Zeki 2004; Ortigue et al 2007; Acevedo et al 2008; Fisher et al 2010). Human romantic love is predominantly associated with increased activity in several regions of the reward system, mediated most likely by increased dopamine release (Fisher et al 2005; Aron et al, 2005; Acevedo et al., in press; Fisher et al 2010). But activity in the ventral tegmental area (VTA), a central region of the brain's reward system associated with pleasure, general arousal, focused attention and motivation to pursue and acquire rewards (Schultz 2000; Delgado et al 2000; Elliot et al 2003) is central to the experience.

Considerable data suggest that the human brain system for romantic attraction arose from mammalian antecedents. Like humans, all birds and mammals exhibit mate preferences; they focus their courtship energy on favored conspecifics (Fisher 2004). This phenomenon is so common that the ethological literature regularly uses several terms to describe it, including "female choice," "mate preference," "individual preference," "favoritism," "sexual choice" "female choice," "selective proceptivity" (Andersson 1994) and "courtship attraction" (Fisher 2004). Furthermore, most of the basic traits associated with human romantic love are also characteristic of mammalian courtship attraction, including increased energy, focused attention, obsessive following, affiliative gestures, possessive mate guarding, goal-oriented behaviors and motivation to win a preferred mating partner (Fisher et al 2002; Fisher 2004).

The biological underpinnings of human romantic attraction and mammalian courtship attraction are also similar. When a female laboratory–maintained prairie vole (*Microtus ochrogaster*) is mated with a male, she forms a distinct preference for him associated with a 50% increase of dopamine in the nucleus accumbens (Gingrich et al 2000), a central region of the reward system. When a dopamine antagonist is injected into the nucleus accumbens, the female no longer prefers this partner; and when a female is injected with a dopamine agonist, she begins to prefer the conspecific who is present at the time of the infusion, even if she has not mated with this male (Gingrich et al., 2000; Wang et al., 1999). An increase in central dopamine is also associated with courtship attraction in female sheep (Fabre-Nys et al 1998). In male rats, too, increased striatal dopamine release has been shown in response to the presence of a receptive female rat (Montague et al. 2004; Robinson et al. 2002). In most species courtship attraction is brief, however, lasting only minutes, hours, days or weeks; while in humans, intense, early-stage romantic love can last 12 to 18 months (Marazziti et al. 1999) or much longer (Acevedo et al., in press).

Because human romantic attraction shares many behavioral and biological characteristics with mammalian courtship attraction, it is likely that human romantic love is a developed form of this mammalian courtship biobehavioral mechanism (Fisher 1998; Fisher 2004). The hominid variation of this neural system may have began to develop prior to 4 my PB, as facultative bipedality became necessary for the carrying of tools, weapons, food and infants in the woodland/savannah eco-niche, selecting for individuals who formed monogamous partnerships to rear their young through infancy. The sex drive served to motivate individuals to seek copulation with a range of partners; romantic attraction evolved to motivate individuals to focus their mating energy on a single partner; and the neural system for attachment evolved to motivate Ardipithecine individuals to sustain this partnership at least through the infancy of a single offspring (Fisher 1998; Fisher 2004).

EVOLUTION OF MATE CHOICE

The evolution of romantic love, serial social monogamy and clandestine adultery may have also stimulated new patterns of mate choice. Mate selection is governed by myriad cultural and biological factors. Men and women tend to be more attracted to individuals who have similar attitudes and values (Shaikh and Suresh 1994; Krueger and Caspi 1993); those from a similar socio-economic and ethnic background (Buston and Emlen 2003; Byrne, Clore and Smeaton 1986; Cappella and Palmer 1990; Rushton 1989; Laumann et al 1994; Pines 1999); those with a similar level of education and intelligence (Buston and Emlen 2003; Byrne, Clore and Smeaton 1986; Cappella and Palmer 1990; Laumann et al 1994; Pines 1999); and those who share their religious and political views and social goals (Laumann et al 1994; Pines 1999). Men and women also gravitate to individuals with a similar degree of financial stability, sense of humor and social and communication skills (Buston and Emlen 2003; Byrne, Clore and Smeaton 1986; Cappella and Palmer 1990; Galton 1884; Laumann et al 1994; Pines 1999). Freud (1905) (and many others) have proposed that one's parents play a primary role in one's romantic choices; and Harris (1999) proposes that individuals choose a partner who reflects the values, interests, ideals and goals of the friends they knew during their formative years. Timing also plays a role (Hatfield 1988), as does proximity (Pines 1999). And the MHC component of the immune system may play a role in mate choice (Wedekind et al 1995).

But temperament may play a role as well (Fisher 2009). Personality is composed of two basic types of traits: traits that an individual acquires, dimensions of character; and traits with biological underpinnings, dimensions of temperament (Cloninger 1994). Many traits of temperament are heritable, relatively stable across the life course and linked to specific gene pathways and/or hormone or neurotransmitter systems. Moreover, although many neural systems orchestrate human survival and reproduction, only four brain systems are regularly associated with human cognition, feelings, motivations and behaviors: the dopamine, serotonin, testosterone and estrogen/oxytocin systems (Fisher 2009; Fisher et al 2010a; 2010b; 2010c).

A literature review indicates that each of these four neural systems is associated with a distinct *constellation* of related biobehavioral traits (temperament dimensions or behavior syndromes). Variations in the dopamine system (DA) have been linked with exploratory behavior, thrill, experience and adventure seeking, boredom susceptibility, and disinhibition (Zuckerman, 2005; Cloninger et al., 1991; 1994); mania and hypersocial behavior (Depue & Collins, 1999); enthusiasm (Goreman &

Wesman, 1974; Zuckerman, 1994); lack of introspection (Cloninger et al., 1991; Ebstein et al., 1996; Gerbing, Ahadi & Patton, 1987); energy, motivation and achievement striving (e.g., Depue & Collins, 1999; Wacker et al., 2006); exploration (Espejo, 1997); abstract intellectual exploration (DeYoung et al., 2002); cognitive flexibility (Ashby et al., 1999); plasticity (DeYoung et al., 2005); curiosity (e.g., Olson, Camp & Fuller, 1984); and idea generation and verbal and non-linguistic creativity (Flaherty, 2005).

The suite of biologically based traits associated with the serotonin system (5-HT) include sociability (Golimbet et al., 2004), lower levels of anxiety, higher scores on a scale of hypomania and extroversion, and lower scores on a scale of “No Close Friends” (Golimbet et al 2004), as well as with positive mood (Flory et al., 2004; Opbroek et al., 2002), religiosity (Borg et al, 2003), conformity (DeYoung et al.,2002), orderliness (DeYoung & Gray, 2005), conscientiousness (Manuck et al., 1998), concrete thinking (Zuckerman 1994), self-control (Manuck et al., 2000), sustained attention (Zuckerman 1994), low novelty seeking (Serretti et al., 2006) and figural and numeric creativity (Reuter et al., 2006)

The biobehavioral traits currently linked with prenatal testosterone (T) expression are heightened attention to detail, intensified focus, and restricted interests (e.g., Baron-Cohen et al., 2005; Knickmeyer et al., 2005). Testosterone activity is also associated with emotional containment (Dabbs & Dabbs, 1997), emotional flooding, particularly rage (Manning, 2002), social dominance and aggressiveness (e.g., Dabbs, 1990; Knickmeyer et al., 2005; Mazur et al., 1997), less social sensitivity (Baron-Cohen et al., 2005) and heightened spatial and mathematical acuity (See Nyborg 1994).

The constellation of biobehavioral traits associated with the estrogen (E) and related oxytocin (OT) systems include verbal fluency and other language skills (Baron-Cohen et al., 2005; Knickmeyer et al., 2005; Manning, 2002), empathy, nurturing, the drive to make social attachments, and other prosocial skills (Baron-Cohen, 2002; Kendrick, 2000, Pedersen et al., 1992; Taylor et al., 2000), contextual thinking (Baron-Cohen et al., 2005; Dabbs & Dabbs, 2000; Fisher, 1999), imagination (Fisher, 2009), and mental flexibility (Skuse et al., 1997).

To study the possible role of these four broad temperament dimensions in human mate choice, first a questionnaire was designed to measure the traits constellations associated with each of these brain systems. This measure consisted of 56 questions: 14 questions to measure an individual's expression of each scale (i.e. the dopamine, serotonin, testosterone and estrogen/oxytocin scales). Data were collected and the questions modified on these four scales regularly between 2006-2007, using an Internet dating site, Chemistry.com, a division of Match.com, until reliability was obtained in a United States sample of 39,913 anonymous men and women. Participants completed demographic information, the questionnaire, and 12 validity questions with the goal of finding a romantic partner. Respondents ranged in age from 18 to 88 years (*M* = 37.0; SD= 12.6); 56.4% were female (*N* = 22,521); 89.6% (*N* = 35,759) were seeking an opposite-sex partner. All individuals expressed all four temperament dimensions; yet individuals varied in the degree to which they expressed each.

The final measure was named the Fisher, Rich, Island Neurochemical Questionnaire (FRI-NQ) (Fisher et al 2010a; 2010b; 2010c). The Cronbach's alpha internal consistency coefficient in the final US sample of 39,913 was .79 for the proposed dopamine scale; .79 for the proposed serotonin scale; .80 for the proposed testosterone scale; and .78 for the proposed estrogen/oxytocin scale. The FRI-NQ measure was then placed on an international dating site (Match.com) in 39 other countries and data to measure reliability were collected on 15,000 individuals in five of these translations: German, French, Spanish, English (Australian sample), and Swedish. The alpha coefficients reflected acceptable levels (ranging from .71 to .82) across the four scales in these five other countries.

After this questionnaire had achieved adequate reliability and had correlated positively with 12 validity measures (Fisher 2009; Fisher et al 2010; Fisher et al 2010a; Fisher et al 2010b; Fisher et al 2010c; Fisher et al in preparation), it was employed to investigate the initial attraction phase of mate choice. A random sample of anonymous participants from the online dating website Chemistry.com® was examined. The sample consisted of 28,128 heterosexual adults (17,776 men; 10,352 women) who had just had an initial meeting with a potential partner and who had given a positive or blank rating of their partner after returning from this first date.

Men and women who predominantly expressed the constellation of biobehavioral traits associated with the proposed dopamine scale were significantly more likely to choose to meet individuals who predominantly expressed this same temperament dimension. Those who predominantly expressed the constellation of traits associated with the proposed serotonin scale were also significantly more likely to select to meet individuals biochemically similar to themselves. But individuals who predominantly expressed traits associated with the proposed testosterone scale were significantly more likely to choose to meet their opposite, those who predominantly expressed traits associated with the proposed estrogen/oxytocin dimension, and vice versa (Fisher 2009; Fisher et al 2010c)

It has been hypothesized that variations in human personality stem from their reproductive advantages in the shifting ecological and social environment of prehistory (Buss 1991; MacDonald 1995). Although these four temperament dimensions may have evolved among mammals long before the hominid radiation into the woodland/savannah eco-niche, their roles in human mate choice may have emerged by positive selection as our hominid forebears became obliged to form longer-term attachments prior to 4 my BP (Fisher 2009). Unions between individuals predominantly expressing testosterone and those predominantly expressing estrogen and oxytocin may have increased their fecundity by pooling suites of complementary temperament traits; while mates who were both expressive of the proposed serotonin system may have capitalized on some very effective parenting traits, including loyalty, calm and caution; while mates who were both expressive of the proposed dopamine system (and equally novelty-seeking, curious and creative) may have engaged in more extra-pair copulations and serial partnerships, thereby producing disproportionate genetic variety in their lineages.

So it is proposed that the human predisposition to seek partners with specific biochemical profiles evolved in conjunction with the evolution of monogamy to facilitate more effective mate choices in the expanding woodland/savannah environment of southern and eastern Africa prior to 4 my PB (Fisher 2009).

EVOLUTION OF ROMANTIC REJECTION

The evolution of serial/long-term social monogamy coupled with clandestine adultery most likely elevated the trauma of rejection in love. To study the neural systems associated with romantic rejection, ten female and five male college-age heterosexuals were studied, using functional Magnetic Resonance Imaging (fMRI); all had recently been rejected by their partners but reported that they were still intensely in love (Fisher et al 2010). The average length of time since the initial rejection and the participants' enrollment in the study was 63 days. All scored high on the Passionate Love Scale (Hatfield and Sprecher 1986), a self-report questionnaire that measures the intensity of romantic feelings. All participants said that they spent more than 85% of their waking hours thinking of the person who rejected them and yearned for their abandoning partner to return to the relationship.

Brain activations coupled with romantic rejection included activity in the ventral tegmental area (VTA) associated with feelings of intense romantic love, the nucleus accumbens and orbitofrontal/prefrontal cortex associated with craving and addiction, the insular cortex and the anterior cingulated associated with physical pain and the distress associated with physical pain, and the ventral pallidum associated with feelings of attachment (Fisher et al 2010). Thus, rejected individuals are experiencing extreme feelings of romantic passion, intense craving, and severe physical and mental distress.

Rejected individuals also often experience "abandonment rage"(Meloy 2001). The primary rage system is closely connected to centers in the prefrontal cortex that anticipate rewards (Panksepp 1998); and animal studies indicate that these reward networks and rage circuits are intertwined (Panksepp 1998), producing a response to unfulfilled expectations known as "frustration-aggression." Abandonment rage stresses the heart, raises blood pressure and suppresses the immune system (Dozier 2002). Romantic rejection can also stimulate feelings of resignation, despair, lethargy, despondency and depression (Najib et al 2004; Panksepp 1998); some broken-hearted lovers die from heart attacks or strokes caused by their depression (Rosenthal 2000).

Few men or women cross-culturally avoid the suffering of rejection at some point over the life course. In one American college community, 93% of both sexes queried reported that they had been spurned by someone they passionately loved; 95% reported they had rejected someone who was deeply in love with them (Baumeister et al 1993). Moreover, rejected individuals most likely suffer for evolutionary reasons. They have wasted precious courtship time and metabolic energy; and their social alliances and reproductive future have been jeopardized. So rejected individuals are most likely fighting a strong survival system that evolved to provide them with the energy and motivation to renew or sustain a foundering partnership crucial to reproduction in the EEA (Fisher 2004).

CONCLUSION

Critics of evolutionary psychology fail to find the profound value of this budding discipline. For example, people have long regarded romantic love as part of the supernatural, or as an invention of the Troubadours in 12th century France, or as the result of childhood training and cultural experiences.

On the contrary, romantic love engages primary regions of the brain's primitive "reward system" associated with focus, energy, craving and intense motivation to win and/or sustain a partnership; it most likely emerged from mammalian antecedents during hominid evolution to enable our forebears to focus their mating energy on a single mate and initiate a pair-bond essential to their reproductive and genetic survival. If the medical and legal communities were to understanding that romantic love is an evolved drive (Fisher 2004) that can lead to severe social and personal consequences, they might develop new procedures for dealing with the negative aspects of this powerful neural mechanism.

Indeed, it would be appropriate to treat romantic rejection as a biologically-based addictive state. Because romantic love is associated with focused attention, euphoria, craving, obsession, compulsion, distortion of reality, personality changes, emotional and physical dependence, inappropriate and dangerous behaviors, tolerance, withdrawal symptoms, relapse, and loss of self-control, several psychologists have regarded romantic love as an addiction (Peele 1975; Carnes 1983; Halpern 1982; Tennov 1979; Hunter et al 1981; Mellody et al 1992; Griffin-Shelley 1991; Schaef 1989). Data from neural imaging confirm this; romantic rejection activates three basic brain regions associated with craving and addiction (Fisher et al 2010).

Researchers and therapists might also design their therapies differently if they were to acknowledge the varying ways that the sexes process rejection (Baumeister et al 1993; Buss 1994; Hatfield and Rapson 1996). Men are two to three times more likely to commit suicide after being rejected (Hatfield and Rapson 1996); and men are more likely to stalk a rejecting partner, as well as batter or kill her (Meloy et al 2001).   Rejected women report more severe feelings of depression (Mearns 1991) and more chronic strain and rumination after being rejected (Nolen-Hoeksema et al 1999). Women are also more likely to talk about their trauma, sometimes inadvertently re-traumatizing themselves (Hatfield and Rapson 1996). Equally important to know is that feelings of romantic love after rejection recede with time. Neural imaging (fMRI) indicates that the greater the number of days since rejection, the less activity there is in the brain region associated with attachment, the right ventral putamen/pallidum (Fisher et al 2010). Also, areas associated with reappraising difficult emotional situations and assessing one's gains and losses are activated after rejection, suggesting that rejected individuals are trying to understand and learn from their difficult situation.

Knowledge of evolutionary psychology could also help professionals (and many others) understand the underlying (evolutionary) predispositions that lead to unstable partnerships. The brain mechanisms associated with serial monogamy and clandestine adultery surely contribute to many contemporary cross-cultural patterns of philandering and divorce, as well as the high cross-cultural incidence of sexual jealousy, partner stalking, spousal abuse, love homicide, love suicide and clinical depression (Meloy and Fisher 2005).

Last, I feel it is essential that the medical and legal communities begin to embrace the possible consequences of contemporary antidepressant usage (Fisher and Thomson 2007). Over 100 million prescriptions for antidepressants are written annually in the United States; most are for SSRIs, Selective Serotonin Reuptake Inhibitors that elevate serotonin at the synapse. It is well known that these drugs cause sexual dysfunction in as many as 73% of patients. But these drugs may also adversely affect the neural system for romantic love, blunting this powerful brain mechanism for mate choice (Fisher 1999; Fisher and Thomson 2007) . These drugs may also jeopardize several other specific neural systems that evolved to enable people to assess potential mates, prefer and choose specific partners, feel extended romantic passion, and and/or sustain feelings of attachment during a long-term relationship (Fisher 1999; Fisher and Thomson 2007). The number of neural mechanisms associated with mate selection, romantic love and long-term partnership stability are unknown, and many operate outside of conscious awareness. If professionals prescribing these medications for *long* *term use* were aware of their potential effects on conscious and unconscious neural systems associated human reproduction, they might consider informing patients of their potential side effects, as well as undertake far more expansive studies of these drugs, particularly their effects on the neural systems for romantic love and attachment (Fisher and Thomson 2007).

Anthropologists, psychologists, sociologists, economists, primatologists, zoologists, and many other scholars have painstakingly accumulated a wealth of data on aspects of human behavior and its counterparts in many other species, using the perspective of evolutionary psychology. These data can add valuable understanding into many issues affecting human marital and sexual relationships.

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