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Source: *Philosophical Transactions: Biological Sciences*, Dec. 29, 2006, Vol. 361, No. 1476, The Neurobiology of Social Recognition, Attraction and Bonding (Dec. 29, 2006), pp. 2173-2186

Published by: Royal Society

Stable URL: https://www.jstor.org/stable/20209808

PHILOSOPHICAL
TRANSACTIONS
OF
THE ROYAL
SOCIETY B

Phil. Trans. R. Soc. B (2006) **361**, 2173–2186
doi:10.1098/rstb.2006.1938

Romantic love: a mammalian brain system for mate choice

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Mammals and birds regularly express mate preferences and make mate choices. Data on mate choice among mammals suggest that this behavioural 'attraction system' is associated with dopaminergic reward pathways in the brain. It has been proposed that intense romantic love, a human cross-cultural universal, is a developed form of this attraction system. To begin to determine the neural mechanisms associated with romantic attraction in humans, we used functional magnetic resonance imaging (fMRI) to study 17 people who were intensely 'in love'. Activation specific to the beloved occurred in the brainstem right ventral tegmental area and right postero-dorsal body of the caudate nucleus. These and other results suggest that dopaminergic reward and motivation pathways contribute to aspects of romantic love. We also used fMRI to study 15 men and women who had just been rejected in love. Preliminary analysis showed activity specific to the beloved in related regions of the reward system associated with monetary gambling for uncertain large gains and losses, and in regions of the lateral orbitofrontal cortex associated with theory of mind, obsessive/compulsive behaviours and controlling anger. These data contribute to our view that romantic love is one of the three primary brain systems that evolved in avian and mammalian species to direct reproduction. The sex drive evolved to motivate individuals to seek a range of mating partners; attraction evolved to motivate individuals to prefer and pursue specific partners; and attachment evolved to motivate individuals to remain together long enough to complete species-specific parenting duties. These three behavioural repertoires appear to be based on brain systems that are largely distinct yet interrelated, and they interact in specific ways to orchestrate reproduction, using both hormones and monoamines. Romantic attraction in humans and its antecedent in other mammalian species play a primary role: this neural mechanism motivates individuals to focus their courtship energy on specific others, thereby conserving valuable time and metabolic energy, and facilitating mate choice.

Keywords: mate choice; romantic love; dopamine; oxytocin; vasopressin; evolution

1. ROMANTIC LOVE: A MAMMALIAN BRAIN SYSTEM FOR MATE CHOICE

Individuals of many species exhibit mate preferences and focus their courtship energy on these favoured conspecifics. The phenomenon of 'courtship attraction' is so common in nature that the ethological literature regularly uses several terms to describe it, including 'female choice', 'mate preference', 'individual preference', 'favouritism', 'sexual choice' and 'selective proceptivity' (Andersson 1994). Charles Darwin regarded this phenomenon, what has become known as 'mate choice', as a central aspect of intersexual selection, the type of sexual selection by which individuals of one sex evolve traits that *attract* members of the opposite sex (Darwin 1871/n.d).

Mammalian and avian species (as well as other species) have evolved many physical and behavioural characteristics by means of mate choice. The peacock's tail feathers are the standard example. But investigations have focused on the traits that 'display producers' have evolved to attract mates. The corresponding neural mechanism by which 'display choosers' become attracted to these traits and focus their mating energy on particular preferred individuals, thereby making a mate choice, has not been defined. Therefore, it has been proposed (Miller 2000; Fisher *et al.* 2002*a*,*b*) that two aspects of intersexual selection evolved in tandem: (i) traits that evolved in the 'display producer' to attract mates, and (ii) corresponding neural mechanisms in the 'display chooser', the viewer of the display, that evolved to enable him/her to discriminate between various displays, become attracted to some and pursue these specific preferred individuals.

Several brain systems most probably operate in tandem to orchestrate mate choice, including the neural systems for sensory perception, memory, and cognitive and emotional responses. But the specific brain mechanism discussed in this review is the neural mechanism that *motivates* the display chooser to *pursue* a *preferred* mating partner, the courtship attraction

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One contribution of 14 to a Theme Issue 'The neurobiology of social recognition, attraction and bonding'.

system. Courtship attraction is characterized in mammals by increased energy, focused attention, obsessive following, affiliative gestures, possessive mate guarding and motivation to win a preferred mating partner (Fisher 2004).

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). Thus, it is parsimonious to suggest that a mammalian brain mechanism for courtship attraction is also active in *Homo sapiens*. Moreover, because human romantic love (also known as passionate love, obsessive love and 'being in love') is a universal human phenomenon (Jankowiak & Fischer 1992), because romantic love's central characteristic is mate *preference* and because 'being in love' exhibits many of the other traits associated with mammalian courtship attraction, it has been hypothesized that human romantic love is a developed form of this mammalian neural mechanism for mate choice (Fisher 1998). In most species, courtship attraction is brief, lasting only for minutes, hours, days or weeks; in humans, intense early stage romantic love can last 12–18 months (Marazziti *et al.* 1999) or more.

This review discusses the present evidence for this brain system in mammals and humans, focusing on recent neuroimaging studies of romantic love in humans (Bartels & Zeki 2000, 2004; Aron *et al.* 2005; Fisher *et al.* 2005*a*,*b*). It examines how this brain system varies from the sex drive and how it changes across time (Aron *et al.* 2005). It also discusses preliminary data on neural mechanisms associated with romantic rejection (Fisher *et al.* 2005*a*,*b*). Finally, it proposes that this brain system is one of the three primary mating drives which interact in many ways and which have evolved in mammalian and avian species to direct various aspects of reproduction. (i) The sex drive evolved to motivate individuals to seek copulation with a *range* of partners, (ii) courtship attraction/romantic love evolved to enable 'display choosers' to focus their mating energy on *specific* mates, thereby conserving courtship time and metabolic energy, and (iii) partner attachment evolved to motivate mating individuals to remain together long enough to perform species-specific parental duties (Fisher 1998).

2. MAMMALIAN COURTSHIP ATTRACTION

'It was evidently a case of love at first sight, for she swam about the new-comer caressingly...with overtures of affection' (Darwin 1871/n.d.). Darwin was describing a female Mallard duck. Blackbirds, thrush, black grouse, pheasants, these and many other birds, were reported as 'fell in love with one another' (Darwin 1871/n.d.).

A myriad of other descriptions of courtship attraction have been reported by ethologists (Andersson 1994). Gladikas (1995) reports of a free-ranging orangutan living in the Tanjung Putting Reserve, Borneo, 'The object of TP's adoration was Priscilla ... I thought that TP would have chosen a more comely female. But ... TP was smitten with her ... He couldn't take his eyes off her. He didn't even bother to eat, so enthralled was he by her balding charms'. Housing conditions are likely to alter the display of mate preferences among laboratory animals when not presented with a choice, but free-ranging individuals regularly exhibit sexual favouritism.

Yet despite hundreds of ethological descriptions of courtship attraction in a wide array of mammalian and avian species, ethologists have traditionally lumped this motivation/emotion system together with the sex drive. However, there are exceptions. Beach (1976) made a distinction between the sex drive and the courtship attraction, writing that the occurrence of copulation depended as much on individual affinities and aversions as upon the presence or absence of sex hormones and that proceptive and receptive behaviour in the female may depend upon different anatomical and neurochemical systems in the brain. Hutchison & Hutchison (1983) proposed that courtship entailed a sequence of choices, each requiring different mechanisms, and they questioned whether the sex hormones had any specific role in the establishment and expression of mating preferences. Pfaff (2002) distinguishes between the hormone-dependent facilitation of sexual arousal and the expression of approach and other courtship behaviours, regarding these as distinct aspects of mating behaviour and physiology. Kendrick & Dixson (1986) have shown that anteromedial hypothalamic lesions block proceptivity but not receptivity in the female common marmoset. Finally, Goodall (1986) reported that males of many primate species 'show clear-cut preferences for particular females, which may be independent of cycle stage'.

Various neurochemical mechanisms have also been associated with courtship attraction. Darwin hypothesized that female mate preferences arose from their innate sense of beauty. But he (understandably) offered no hypothesis regarding which specific neural mechanisms might be involved (Darwin 1871/n.d.). Miller (2000) noted that several faculties must have evolved to discern and respond to the courtship traits of display producers, referring to this constellation of neural mechanisms as 'mental machinery' and 'sexual choice equipment'. Miller (2000) also distinguished between 'cold choosers', such as insects that become attracted to ornamental displays without any sensation of pleasure, and 'hot choosers', animals whose choice of mates is directed by subjective feelings of pleasure; and he proposed that the endorphins may be involved in the mate choices of hot choosers. Beach (1976) suggested that the monoamines were involved in mate preference, saying, 'The mating behaviour of female rats treated with monoamine receptor blocking agents indicates that lordotic behaviour and soliciting behaviour may be mediated by anatomically and possibly neurochemically distinct systems'.

Present research supports Beach's hypothesis. 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 in dopamine in the nucleus accumbens (Gingrich *et al.* 2000). When a dopamine antagonist is injected into the accumbens, the female no longer prefers this partner and when a female is injected with a dopamine agonist, she begins to prefer the conspecific that is present at the time of infusion, even if she has not mated with this male (Wang *et al.* 1999; Gingrich *et al.* 2000). An increase in central dopamine is also associated with courtship attraction in female sheep (Fabre-Nys 1997, 1998). In male rats, too, increased striatal dopamine release has been shown in response to the presence of a receptive female rat (Robinson *et al.* 2002; Montague *et al.* 2004).

Recent data on several peptides also suggest that central dopamine plays a role in regulating mate preference. Kendrick & Dixson (1985) showed that in marmosets, luteinizing hormone-releasing hormone specifically facilitated female proceptive behaviours, and oxytocin and vasopressin have been shown to facilitate social recognition in mammalian species. All of these peptides facilitate monoamine release (Kendrick 2000). Therefore, it has been suggested that mate preference may be influenced as these peptides rewire brain circuits so that sensory and other stimuli from specific individuals have more potent effects on monoamine release, particularly release of dopamine in brain reward centres (Lim *et al.* 2004).

The extensive ethological literature on sexually dimorphic traits that evolved to attract mates, in conjunction with the above physiological data on mate preference in several species, suggests that intersexual selection involves interactions between the display traits of display producers and a brain system for mate preference in display choosers, courtship attraction. Moreover, the data suggest that the brain system for courtship attraction is distinct from, yet operates in tandem with, the sex drive to orchestrate proceptivity in birds and mammals. Finally, the dopaminergic reward pathways may be involved.

3. HUMAN ROMANTIC LOVE

It was appropriate to investigate this brain system in *Homo sapiens* for several reasons. Foremost, intense romantic love is a cross-cultural universal. In a survey of 166 societies, Jankowiak & Fischer (1992) found evidence of romantic love in 147 of them. No negative data were found; in the 19 remaining cultures, anthropologists had failed to ask the appropriate questions; all were cases of ethnographic oversight. Jankowiak & Fischer (1992) concluded that romantic love constitutes a 'human universal … or near universal'. Moreover, romantic love is associated with a specific set of physiological, psychological and behavioural traits (Tennov 1979; Hatfield & Sprecher 1986; Shaver *et al.* 1987; Hatfield *et al.* 1988; Harris & Christenfeld 1996; Fisher 1998; Gonzaga *et al.* 2001); and most of these traits are also characteristic of mammalian courtship attraction, including increased energy, focused attention, obsessive following, affiliative gestures, possessive mate guarding, goal-oriented behaviours and motivation to win a preferred mating partner (Fisher *et al.* 2002*a*,*b*; Fisher 2004).

Romantic love begins as an individual starts to regard another individual as special and unique. The lover then focuses his/her attention on the beloved, aggrandizing the beloved's worthy traits and overlooking or minimizing his/her 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 barriers heighten romantic passion, what has been referred to as 'frustration attraction' (Fisher 2004). The lover suffers 'separation anxiety' when apart from the beloved and a host of sympathetic nervous system reactions when with the beloved, including sweating and a pounding heart. Lovers are emotionally dependent; they change their priorities and daily habits to remain in contact with and/or impress the beloved. Smitten humans also exhibit empathy for the beloved; many are willing to sacrifice, even die for this 'special' other. The lover expresses sexual desire for the beloved, as well as intense sexual possessiveness, mate guarding. Yet the lover's craving for emotional union supersedes his/her craving for sexual union with the beloved. Most characteristic, the lover thinks obsessively about the beloved, 'intrusive thinking'. Rejected lovers first experience a phase of protest, during which they try to win back the beloved and often feel abandonment rage; then they move into the second stage of rejection, associated with resignation and despair. Romantic love is also involuntary, difficult to control and generally impermanent.

Since romantic love shares many characteristics with mammalian courtship attraction, it has been hypothesized that this human preference system would also be associated with the monoamines, specifically elevated activity of central dopamine and/or central norepinephrine (Liebowitz 1983; Fisher 1998).

4. ROMANTIC LOVE: FUNCTIONAL MAGNETIC RESONANCE IMAGING RESEARCH

To investigate the constellation of neural correlates associated with romantic love, Fisher, Aron, Brown and colleagues recruited 10 women and 7 men who were intensely in love. The age range was 18–26 years ($M=20.6$; median $=21$); the reported duration of 'being in love' was 1–17 months ($M=7.4$; median $=7$). Each participant was orally interviewed in a semi-structured format to establish the duration, intensity and range of his/her feelings of romantic love. Each also completed the Passionate Love Scale (PLS), a 9-point Likert scale self-report questionnaire which measures traits commonly associated with romantic love (Hatfield & Sprecher 1986; Cronbach's alpha for questionnaire reliability in this study $=0.81$; Cronbach 1951).

A preliminary investigation had identified a photograph of the beloved as an effective stimulus for eliciting feelings of intense romantic love (Mashek *et al.* 2000). Thus, the protocol employed photographs and consisted of four tasks presented in an alternating block design: for 30 s, each participant viewed a photo of his/her beloved (positive stimulus); for the following 40 s, each performed a countback distraction task; for the following 30 s, each viewed a photograph of an emotionally neutral acquaintance (neutral stimulus); and for the following 20 s, each performed a similar countback task. The countback task involved viewing a large number, such as 8421, and mentally counting backwards (beginning with this number) in increments of seven. We included the countback task to decrease the carry-over effect after the participant viewed the positive stimulus because it is difficult to quell intense feelings of romantic love. This four-part sequence (or a counterbalanced version beginning with the neutral stimulus) was repeated six times; the total stimulus protocol was 720 s (12 min). Pre-scanning instructions were to think about a non-sexual euphoric experience with the beloved; post-scanning interviews established that the participants had engaged in romantic thinking and feeling.

Group activation specific to the beloved occurred in several regions, including the right ventral tegmental area (VTA) localized in the region of A10 dopamine cells (Aron *et al.* 2005). The VTA is a central region of the brain's reward system (Wise 1996; Schultz 2000; Martin-Soelch *et al.* 2001), associated with pleasure, general arousal, focused attention and motivation to pursue and acquire rewards (Schultz 2000; Delgado *et al.* 2000; Elliot *et al.* 2003).

The VTA sends projections to several brain regions (Gerfen *et al.* 1987; Oades & Halliday 1987; Williams & Goldman-Rakic 1998), including the caudate nucleus where we also found group activations, specifically in the right medial and postero-dorsal body (Aron *et al.* 2005). The caudate plays a role in reward detection and expectation, the representation of goals and the integration of sensory inputs to prepare for action (e.g. Schultz 2000; Martin-Soelch *et al.* 2001; Lauwereyns *et al.* 2002; O'Doherty *et al.* 2002). Zald *et al.* (2004) found that predictable monetary reward presentation caused dopamine release in the medial caudate body where we found activation.

Using functional magnetic resonance imaging (fMRI), Bartels & Zeki (2000) also investigated brain activity in 17 men and women who reported being 'truly, deeply and madly in love'. Eleven were women; all looked at a photograph of his/her beloved, as well as photographs of three friends of similar age, sex and length of friendship. But the participants in that study had been in love substantially longer than those in our study (28.8 months versus 7.4 months $t[32]=4.28$, $p<0.001$). They were also less intensely in love. This was established because both study groups were (serendipitously) administered the same questionnaire on romantic love, the PLS (respective scores were 7.55 versus 8.54, $t[31]=3.91$, $p<0.001$). In spite of these differences in protocol, Bartels & Zeki (2000, 2004) found activity in regions of the ventral tegmental area and caudate nucleus, as we did.

These data are consistent with the above animal literature, suggesting that mesolimbic dopamine pathways in the reward system of the brain play a role in the pleasurable feelings, focused attention, motivation and goal-oriented behaviours associated with romantic love. However, activation of subcortical dopaminergic pathways of the VTA and caudate nucleus may comprise only the 'general arousal' component (Pfaff 1999) of this brain system for mate preference and mate pursuit (Fisher 2004).

Other neurotransmitters are likely to be involved, including glutamate in the mesocortical system, owing to their role in the release of dopamine in the VTA (Legault & Wise 1999) and/or their fast signals in the prefrontal cortex regarding reward (Lavin *et al.* 2005). Central norepinephrine may also be associated with courtship attraction (Fisher 1998). This was hypothesized because increased activity of norepinephrine generally produces alertness, energy, sleeplessness and loss of appetite (Coull 1998; Robbins *et al.* 1998), increased attention (Posner & Peterson 1990) and increased memory for new stimuli (Griffin & Taylor 1995), some of the primary characteristics of human romantic love (Tennov 1979; Hatfield & Sprecher 1986; Fisher 2004). As norepinephrine is also associated with peripheral sympathetic nervous system responses, including increased heart rate, sweating and trembling, central norepinephrine may contribute to these aspects of romantic love/courtship attraction as well (Fisher 1998).

The above data suggest that mammalian courtship attraction and human romantic love are associated with dopaminergic reward pathways in the brain. These data also support the hypothesis that romantic love is distinct from the sex drive (Aron & Aron 1991; Fisher 1998).

5. THE SEX DRIVE

The sex drive is characterized by the urge for sexual gratification. It is associated with the androgens and oestrogens in non-primate mammalian species and primarily with the androgens in many primates, especially humans (Edwards & Booth 1994; Sherwin 1994; Van Goozen *et al.* 1997). Humans with higher circulating levels of testosterone tend to engage in more sexual activity (Edwards & Booth 1994; Sherwin 1994). Women tend to feel more sexual desire during and around ovulation, when testosterone activity increases (Van Goozen *et al.* 1997). Both sexes have fewer sexual fantasies, masturbate less regularly and engage in less intercourse as levels of the androgens decline with age (Edwards & Booth 1994).

The balance between the androgens, oestrogens and other bodily systems, as well as childhood and adult experiences and a host of other biological and environmental factors play a role in when, where and how often individuals express the sex drive (Nyborg 1994). Nevertheless, the androgens are central to the sex drive and these gonadal and adrenal hormones have not been associated with human romantic love. Moreover, when humans self-administer androgens to boost sex drive, they do not report that they fall in love. These two neural systems do not always act in tandem in *Homo sapiens*.

Several fMRI studies support the hypothesis that the sex drive is associated with specific networks of brain activation and that these networks are largely distinct from those associated with human romantic love/mammalian courtship attraction. Arnow *et al.* (2002) reports that when young male heterosexual subjects look at erotic video material while wearing a custom-built pneumatic pressure cuff around the penis, their sexual arousal is associated with strong activations in the right subinsular region, including the claustrum, left caudate and putamen, right middle occipital/middle temporal gyri, bilateral cingulate gyrus, right sensorimotor and pre-motor regions, and right hypothalamus.

Using fMRI, Beauregard *et al.* (2001) measured brain activation in men as they viewed erotic film excerpts. Activations occurred in limbic and paralimbic structures, including the right amygdala, right anterior temporal pole and hypothalamus. Using fMRI, Karama *et al.* (2002) also recorded brain activity while men and women viewed erotic film excerpts. Activity increased in the anterior cingulate, medial prefrontal cortex, orbitofrontal cortex, insula and occipitotemporal cortices, as well as in the amygdala and ventral striatum. Men showed activation in the thalamus and significantly greater activation than women in the hypothalamus, specifically in a sexually dimorphic area associated with sexual arousal and behaviour. Animal studies also indicate that several brain structures are associated with the sex drive and sexual expression, including the medial amygdala, medial preoptic area, paraventricular nucleus and periaqueductal gray (PAG; Heaton 2000), as well as the septum and the ventromedial hypothalamus (Dixson 1998).

Although the neural regions associated with the sex drive overlap those associated with courtship attraction, these two neural systems show many differences, suggesting that the primary brain system for the sex drive is distinct from the brain system associated with human romantic love (Aron & Aron 1991; Fisher 1998). Anecdotal behavioural data in humans support this hypothesis. (i) The sex drive is focused on a specific goal, sexual union with another, and romantic love is focused on a different goal, emotional union with another. (ii) The sex drive is often expressed towards a *range* of individuals and romantic love is focused on one particular individual. (iii) The sex drive is often temporarily quelled when satisfied and romantic love does not decrease with coitus and often persists unabated for months, even years. (iv) Most liberated adults have engaged in coitus with individuals for whom they felt no romantic love and many have also been 'in love' with someone with whom they have had no physical contact.

Several lines of investigation indicate that the sex drive and the courtship attraction/romantic love are distinct neural systems, designed to orchestrate different aspects of the reproductive process. The sex drive enables individuals to initiate courtship and mating with a range of partners; courtship attraction/ romantic love motivates them to focus their mating energy on specific individuals, thereby conserving time and metabolic energy.

Nevertheless, the brain systems for the sex drive and the courtship attraction regularly interact to coordinate mammalian mate choice.

6. THE SEX DRIVE AND MATE PREFERENCE: INTERACTIONS

The biological relationships between the sex drive and the courtship attraction are most likely dose dependent and variable, depending on which brain regions are involved and many other biological and environmental factors. However, data suggest that these brain systems have a positive correlation.

Animal studies indicate that elevated activity of dopaminergic pathways can stimulate a cascade of reactions, including the release of testosterone and oestrogen (Wenkstern *et al.* 1993; Kawashima &Takagi 1994; Ferrari & Giuliana 1995; Hull *et al.* 1995, 1997, 2002; Szezypka *et al.* 1998; Wersinger & Rissman 2000). Likewise, increasing levels of testosterone and oestrogen promote dopamine release (Hull *et al.* 1999; Auger *et al.* 2001; Becker *et al.* 2001; Appararundaram *et al.* 2002; Creutz & Kritzer 2002; Pfaff 2005). When a male rat is placed in an adjacent cage, where he can see or smell an oestrous female, activity of central dopamine increases and contributes to sexual arousal and pursuit of the female (West *et al.* 1992; Wenkstern *et al.* 1993; Hull *et al.* 1995, 1997, 2002). When the barrier is removed and the male is allowed to copulate, activity of dopamine continues to rise in the medial preoptic area (Hull *et al.* 1995). When dopamine is injected into specific brain regions of the male rat, the infusion stimulates copulatory behaviour (Ferrari & Giuliana 1995). Blocking the activities of central dopamine in rats diminishes several proceptive sexual behaviours, including hopping and darting (Herbert 1996). Finally, electrochemical studies in male rats show increased dopamine release in the dorsal and the ventral striatum in response to the presence of a receptive female rat (Robinson *et al.* 2002; Montague *et al.* 2004). Pfaff (2005) reports that in male rats, dopamine increases male sexual behaviour in at least three ways: it increases sexual arousal and courtship behaviour; it potentiates the motor acts of mounting; and it facilitates genital responses to stimulation.

This positive relationship between elevated activity of central dopamine, elevated sex steroids and elevated sexual arousal and sexual performance (Herbert 1996; Fiorino *et al.* 1997; Liu *et al.* 1998; Pfaff 2005) also occurs in humans (Walker *et al.* 1993; Clayton *et al.* 2000; Heaton 2000). When individuals exhibiting hypoactive sexual desire disorder are treated with dopamine-enhancing medications, libido improves (Segraves *et al.* 2001). When patients suffering from depression take drugs that elevate central dopamine activity, their sex drive often improves (Walker *et al.* 1993; Ascher *et al.* 1995; Coleman *et al.* 1999). In fact, since elevated activity of central serotonin is inhibitory to the sex drive (Rosen *et al.* 1999; Montejo *et al.* 2001), some patients taking serotonin-enhancing antidepressants supplement this therapy with medications that elevate the activity of dopamine (and norepinephrine) solely to maintain or elevate sexual appetite and arousal (Walker *et al.* 1993; Ascher *et al.* 1995; Coleman *et al.* 1999; Rosen *et al.* 1999).

Animal studies indicate that norepinephrine is also positively linked with sexual motivation and sexual arousal (Van Bockstaele *et al.* 1989; Clayton *et al.* 2002; Fraley 2002; Pfaff 2005). When a female prairie vole is exposed to a drop of male urine on the upper lip, norepinephrine in the olfactory bulb contributes to the release of oestrogen and concomitant proceptive behaviour (Dluzen *et al.* 1981). The reverse also occurs; oestradiol and progesterone contribute to the release of norepinephrine in the hypothalamus to produce lordosis in rats (Etgen *et al.* 1999). Moreover, when ovariectomized, sexually receptive female rats receive injections of oestrogen and are then permitted to mate, copulation produces the release of norepinephrine in the lateral ventromedial hypothalamus (Etgen & Morales 2002). Drug users attest to this positive chemical relationship between norepinephrine and the sex drive. In the right oral dose, amphetamines (norepinephrine and dopamine agonists) enhance sexual desire (Buffum *et al.* 1988).

The complex interaction between these catecholamines and gonadal hormones suggests why the sex drive and the courtship attraction have traditionally been lumped into a single behavioural category, proceptivity. Instead, these distinct neural systems appear to work in tandem to enable display choosers to explore an array of mating partners, focus their courtship attention on preferred individuals and then sustain attraction and sexual arousal long enough to complete species-specific mating behaviours.

7. PARTNER ATTACHMENT

The full array of brain systems associated with courtship, mating and parenting and the interactions between these brain systems need further investigation (Fisher & Thomson in press). Nevertheless, the available literature suggests that at least three distinct, yet interrelated neural systems play a role in reproduction: the sex drive, courtship attraction and partner attachment. Each of these motivation/emotion systems is associated with a different behavioural repertoire, each is associated with a different and dynamic constellation of neural correlates and each evolved to direct a different aspect of reproduction (Fisher 1998). The relationship between courtship attraction/romantic love and the sex drive has been discussed above, and partner attachment is considered next.

Partner attachment, or pairbonding, in birds and mammals is characterized by mutual territory defence and/or nest building, mutual feeding and grooming, maintenance of close proximity, separation anxiety, shared parental chores and affiliative behaviours. The ethological literature commonly infers that this constellation of attachment behaviours associated with pairbonding evolved primarily to motivate mating partners to sustain an affiliative connection long enough to complete species-specific parental duties. This parental attachment system has been associated with the activity of the neuropeptides, oxytocin (OT) in the nucleus accumbens and arginine vasopressin (AVP) in the ventral pallidum (Carter 1992; Winslow *et al.* 1993; Wang *et al.* 1994; Carter *et al.* 1997; Young *et al.* 1998; Lim & Young 2004; Lim *et al.* 2004), although the brain's opioid system (Moles *et al.* 2004) and other neural systems are involved as well (Kendrick 2000).

Bowlby (1969, 1973) and Ainsworth *et al.* (1978) proposed that, to promote 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 their mother. More recently, researchers have emphasized that this attachment system remains active throughout their life and serves as a foundation for attachment between spouses as they raise children (Hazan & Shaver 1987; Hazan & Diamond 2000). Data from the Demographic Yearbooks of the United Nations on 97 societies suggest the prevalence of this attachment system in humans. Approximately 93.1% of women and 91.8% of men marry by age 49 (Fisher 1992). Pairbonding and attachment behaviours are central aspects of the multi-part human reproductive strategy (Fisher 1992).

Hatfield (1988) refers to feelings of attachment as companionate love, which she defines as 'a feeling of happy togetherness with someone whose life has become deeply entwined with yours'. Extensive research has been done on this attachment system in adults (Fraley & Shaver 2000), but this literature does not regularly distinguish between feelings of attachment and feelings of romantic love (Aron *et al.* 2006). However, cross-cultural and historical data indicate that people in other societies and centuries do distinguish between feelings of romantic love and attachment.

Nisa, a !Kung Bushman woman of the Kalahari Desert, Botswana, reported, 'When two people are first together, their hearts are on fire and their passion is very great. After a while, the fire cools and that's how it stays. They continue to love each other, but it's in a different way—warm and dependable' (Shostak 1981). The Taita of Kenya say that love comes in two forms, an irresistible longing, a 'kind of sickness', and a deep enduring affection for another (Bell 1995). In Korea, 'sarang' is a word close to the western concept of romantic love, while 'chong' is more like feelings of long-term attachment; Abigail Adams, wife of America's second president, distinguished these feelings when writing to John Adams in 1793, 'Years subdue the ardor of passion, but in lieu thereof friendship and affection deep-rooted subsists, which defies the ravages of time' (McCullough 2001).

Current brain imaging investigations in humans and animal studies indicate some of the neural correlates of this attachment mechanism. These data also suggest that the neural correlates for attachment are distinct from those for early-stage intense romantic love in humans and courtship attraction in other mammalian species, yet these two brain systems interact.

8. NEUROIMAGING AND ANIMAL STUDIES OF ATTACHMENT

As discussed earlier, using fMRI, Bartels & Zeki (2000) studied 17 men and women who were in love. However, their subjects were in love for an average of 28.8 months, a considerably longer period of time compared with our participants who were in love for an average of 7.4 months (Aron *et al.* 2005); their subjects were less passionately in love (Aron *et al.* 2005). Their participants also exhibited activity in several brain regions where our subjects showed none, including the anterior cingulate cortex and mid-insular cortex.

These varying results stimulated us to examine the subset of our subjects in longer relationships, specifically those who were in love between 8 and 17 months. In our subset of individuals in longer relationships, several regions showed activations, including the right anterior and posterior cingulate cortex, and right mid-insular cortex (Aron *et al.* 2005).

Thus, we confirmed Bartels & Zeki's (2000) findings that the anterior cingulate and insular cortex are involved in longer term love relationships.

More relevant to this discussion, we also found activation in the ventral putamen/pallidum (Aron *et al.* 2005). Activity in this region, associated with a specific distribution pattern of vasopressin (V1a) receptors, has been linked with pairbonding and attachment behaviours in monogamous prairie voles (Lim & Young 2004; Lim *et al.* 2004), monogamous California mice and monogamous marmosets, whereas promiscuous white-footed mice and promiscuous rhesus monkeys do not express pairbonding/attachment behaviours or this distribution of V1a receptors in the ventral pallidum (Wang *et al.* 1997; Young *et al.* 1997; Bester-Meredith *et al.* 1999; Young 1999). Hence, activity in the ventral pallidum is greater in longer term human relationships than in shorter ones and activity in the ventral pallidum, specifically associated with vasopressin, is evident in other pairbonding/attaching mammals.

But vasopressin activity in the ventral pallidum also affects partner preference, a central characteristic of mammalian courtship attraction and human romantic love. Lim & Young (2004) report that arginine vasopressin antagonists infused into the ventral pallidum prevented partner preference formation among male prairie voles. Yet they also report that V1aR activation in this region is necessary for pairbond formation (Lim & Young 2004).

Activity of central oxytocin in the nucleus accumbens also contributes to both pairbonding and partner preference (Lim *et al.* 2004). Williams *et al.* (1994) report that when oxytocin was administered intracerebroventricularly, ovariectomized female prairie voles preferred the partner who was present at the time of infusion; and Lim, Murphy and Young report that when an oxytocin receptor (OTR) antagonist is infused directly into the nucleus accumbens of a female prairie vole, this antagonist blocks partner preference formation (Young *et al.* 2001; Lim *et al.* 2004). Yet they also conclude that among monogamous prairie voles, OTRs and vasopressin V1a receptors (V1aR) in the ventral forebrain play critical roles in the formation of pairbonds.

Research on the genetic basis of pairbonding also lumps partner preference and attachment behaviours. Pitkow *et al* (2001) reported that structural differences in the V1 receptor gene of socially monogamous male voles (as opposed to asocial promiscuous voles) increased levels of the expression of this receptor in the ventral pallidum; moreover, these males also exhibited heightened levels of social affiliation. They formed a preference for a specific female and began to cohabit with her, even though they had not mated with this female. Lim, Young and colleagues report that when they transfected this genetic variant (the monogamous version) into the pallidum of meadow voles, an asocial promiscuous species, vasopressin receptors were upregulated; each male also began to fixate on a *particular* female and mate exclusively with her, even though other females were available (Lim *et al.* 2004).

The activities of central oxytocin and vasopressin have been associated with both partner preference and attachment behaviours, while dopaminergic pathways have been associated more specifically with partner preference. So Lim *et al.* (2004) integrate these data, proposing that when monogamous prairie voles and other pairbonding creatures engage in sex, copulation triggers the activity of vasopressin in the ventral pallidum and oxytocin in the nucleus accumbens and facilitates dopamine release in these reward regions, which motivates males and females to prefer a current mating partner and initiates attachment/pairbonding behaviours. Moreover, males of promiscuous species (who lack one link in this chain for encoding the V1a receptor for vasopressin in the ventral pallidum) most probably feel attraction, but do not associate this pleasurable feeling with their specific mating partner so they do not initiate a longer term attachment. In species that do not form these bonds, this relationship with dopamine reward centres is much weaker (Kendrick 2000).

Like the brain systems for the sex drive and the courtship attraction, the neural mechanism for attachment is complex, flexible, varies in its threshold and intensity and is most likely integrated with many other brain systems (Kendrick 2000), probably including the opioids (Moles *et al.* 2004). Nevertheless, the above data suggest that the neural systems for courtship attraction and partner attachment work in tandem in a pairbonding species, motivating individuals to prefer a specific mating partner and also motivating them to form an attachment to this mate. These data also suggest that courtship attraction and partner attachment can operate independently in non-monogamous species, enabling individuals to prefer specific mating partners yet avoid long-term attachments.

Data on the neural correlates of maternal love support the proposition that feelings of attachment and feelings of romantic love are distinct yet interrelated neural systems. Bartels & Zeki (2004) used fMRI to measure brain activity in mothers while each looked at a photo of her own infant, an infant with whom she was acquainted, an adult best friend and an adult acquaintance. They then compared these data on the neural mechanisms associated with maternal attachment with their data on the neural correlates of (later stage) romantic love (Bartels & Zeki 2000). Maternal love activated several specific brain regions that differed from those associated with romantic love, including the lateral orbitofrontal cortex and the PAG. Maternal love also activated some brain regions that were the same as those activated by romantic love, including regions of the medial insula, anterior cingulate gyrus and caudate nucleus. Finally, activity associated with maternal love and romantic love overlapped in brain areas rich in oxytocin and vasopressin receptors, including the substantia nigra (Bartels & Zeki 2004).

The neural flexibility of these brain systems for reproduction and their interactions with one another and other brain systems are complex (Kendrick 2000). For example, central dopamine (and norepinephrine) can stimulate the release of oxytocin and vasopressin in neurohypophyseal tissues (Kendrick *et al.* 1992; Ginsberg *et al.* 1994; Galfi *et al.* 2001); but increasing activity of central dopamine can also inhibit release of central oxytocin (Seybold *et al.* 1978; Vizi & Volbekas 1980). Increasing activity of central oxytocin can stimulate release of norepinephrine and dopamine (Kendrick 2000) or interfere with dopamine and norepinephrine pathways (Schwarzberg *et al.* 1981; Kovacs & Telegdy 1983; Kovacs *et al.* 1990; Van de Kar *et al.* 1998). Finally, a small microsatellite repeat sequence in the gene coding for V1aR controls its density of expression in the ventral pallidum and this gene region is subject to a number of polymorphisms that contribute to variability in the strength of monogamous bonding in male prairie voles (Hammock & Young 2005). The *Homo sapiens* version of this gene has similar polymorphisms, which might contribute to individual differences in human monogamous pairbonding as well.

The above data suggest that the mammalian attachment system is distinct from, yet interacts with, the neural mechanisms for courtship attraction and the sex drive. This flexible, combinatorial system would provide individuals of myriad species with the range of motivations, emotions and behaviours necessary to pursue their species-specific reproductive strategy.

These data on attachment and romantic love also lend perspective to another aspect of reproduction, rejection in love.

9. REJECTION IN LOVE

Romantic love is expressed in many graded forms, but it has two extremes: love that is returned and love that is rejected. To understand the range of neural mechanisms associated with mate choice, Fisher, Aron, Brown and colleagues used fMRI to study 10 women and 5 men who were still very much in love but had recently been rejected by their romantic partner (Fisher *et al.* 2005*a*,*b*). We used the same protocol as with our happily in-love subjects (Aron *et al.* 2005). Rejected participants alternately viewed a photograph of their abandoning beloved (positive stimulus) and a photograph of a familiar, emotionally neutral individual (neutral stimulus), interspersed with a distraction–attention task.

Preliminary analysis of the positive–neutral contrast showed significant group effects in the right nucleus accumbens/ventral putamen/pallidum, lateral orbitofrontal cortex and anterior insular/operculum cortex (Fisher *et al.* 2005*a*,*b*). We then compared these data on rejected lovers with the results from our study of 17 happily in-love individuals (Aron *et al.* 2005). Rejected lovers expressed significantly greater activity in the ventral striatum/putamen/pallidum than did those who were happily in love (figure 1).

Other studies have shown that the nucleus accumbens/ventral pallidum/putamen region where we found activity becomes more active as an individual chooses a high-risk investment associated with big gains or big losses, making it an uncertain gain (Kuhnen & Knutson 2005), or anticipates a money reward (Zald *et al.* 2004); data from rat studies are consistent with the idea that the nucleus accumbens core is important for choices for uncertain rewards and delayed reinforcement (e.g. Cardinal & Howes 2005); activity in the nucleus accumbens has also been associated with pairbond formation and maintenance in prairie voles (Lim *et al.* 2004). The region of the anterior insula/operculum cortex where we found activity has been associated with skin and muscle pain and with anxiety (Schreckenberger *et al.* 2005). The region of the lateral orbitofrontal cortex where we found activity has been associated with theory of mind (Vollm *et al.* 2006), evaluating punishers (Kringelbach & Rolls 2004), implementing appropriate adjustments in behaviour (Ridderinkhof *et al.* 2004), obsessive/compulsive behaviours (Evans *et al.* 2004) and with controlling anger in recently abstinent cocaine-dependent individuals (Goldstein *et al.* 2005).

Figure 1. Three axial sections through the human brain at 2 mm intervals show a consistent activation difference between a group happily in love and a group in love but recently rejected (yellow colour, $p < 0.01$). Those who were recently rejected show greater activation in the right ventral putamen–pallidum and accumbens core (side definition is radiological convention) than those who were happily in love. These regions have been associated with reward, especially uncertain large gains and losses in gambling, and uncertain reinforcement in rats. (Figure data from Aron *et al.* 2005 and a preliminary report, Fisher *et al.* 2005*a*,*b*).

These results suggest that brain systems associated with reward and motivation remain active in recently romantically rejected men and women, but differ in their precise location. These preliminary results also suggest that neural regions associated with risk-taking for big gains or losses, physical pain, obsessive/compulsive behaviours, ruminating on the intentions and actions of the rejecter, evaluating options, and emotion regulation increase in their activity when someone is rejected by a beloved.

Our study is the second investigation of romantic rejection. Najib *et al.* (2004) studied nine women who were ‘actively grieving’ over a recent romantic break-up. Our preliminary comparisons uncovered no commonalities; in fact, in several regions where we found activations, they found deactivations. Since our subjects regularly reported anger and hope for reconciliation, while subjects in the Najib *et al.* (2004) study more regularly reported acceptance, we suspect that our subjects were in the initial stage of romantic rejection, the protest phase, while their participants were largely in the subsequent resignation/despair phase.

The combined aforementioned data may contribute understanding to the high cross-cultural rates of stalking, homicide, suicide and clinical depression associated with rejection in love (Meloy & Fisher 2005).

10. THE DRIVE TO LOVE

The psychological literature distinguishes between emotions (affective states of feeling) and motivations (brain systems oriented around the planning and pursuit of a specific want or need). Aron has proposed that romantic love is not primarily an emotion, but a motivation system designed to enable suitors to build and maintain an intimate relationship with a preferred mating partner (Aron & Aron 1991; Aron *et al.* 1995).

The fMRI and animal experiments we have reviewed above support Aron's hypothesis. The VTA is directly associated with motivation- and goal-oriented behaviours, as is the caudate nucleus. Moreover, the caudate nucleus has widespread afferents from all of the cortex except primary visual areas (Kemp & Powell 1970; Selemon & Goldman-Rakic 1985; Saint-Cyr *et al.* 1990; Eblen & Graybiel 1995; Flaherty & Graybiel 1995) and is organized to integrate diverse sensory, motor and limbic functions (Brown 1992; Parthasarathy *et al.* 1992; Eblen & Graybiel 1995; Parent & Hazrati 1995; Parent *et al.* 1995; Brown *et al.* 1998; Haber 2003). Thus, regions of the caudate nucleus could effectively integrate the behavioural and biological actions associated with a complex state, such as romantic love.

In fact, these findings suggest that romantic love is a primary motivation system, a fundamental human mating drive (Fisher 2004). Pfaff (1999) defines a drive as a neural state that energizes and directs behaviour to acquire a particular biological need to survive or reproduce and he reports that all drives are associated with the activity of dopaminergic pathways and a few other specific neural systems (as well as other neural systems specific to each individual drive state). Romantic love has many characteristics in common with drives (Fisher 2004). (i) Like drives, romantic love is tenacious and emotions ebb and flow, (ii) romantic love is focused on a specific reward and emotions are associated with a range of phenomena instead, (iii) romantic love is not associated with a distinct facial expression and the primary emotions are all associated with specific facial expressions, (iv) romantic love is difficult to control and all of the basic drives are difficult to control, and (v) human romantic love and mammalian courtship attraction are associated with dopamine-rich neural regions and all the basic drives are also associated with dopaminergic pathways. Drives lie along a continuum. Thirst is almost impossible to control, while the sex drive can be redirected, even quelled. Romantic love is evidently stronger than the sex drive because when one's sexual overtures are rejected, people do not kill themselves or someone else. Instead, abandoned lovers sometimes stalk, commit suicide or homicide or fall into a clinical depression.

More investigations need to be made to understand the flexibility, variability and durability of this neural mechanism for mate choice, romantic love. Data could be collected on how the neural mechanisms for romantic love vary in conjunction with specific traumatic childhood experiences; how specific personality profiles affect the biological expression of romantic love; how specific diseases, such as schizophrenia and Parkinson's disease, and addictions, such as cocaine, amphetamine and alcohol addiction, facilitate or inhibit the biological expression of romantic love; how the constellation of neural correlates associated with romantic love varies during the course of a long-term relationship; how the biology of romantic love varies according to sexual orientation; and how this brain system varies in cultures with different marital patterns and in different mammalian species with diverse reproductive strategies. More research into the brain mechanisms associated with romantic love may also help to explain some of the basic principles of brain lateralization and lend further understanding of the reward system and its interactions with cognitive and emotional processes that together produce complex behaviours.

It might also be valuable to investigate gender differences in the constellation of neural correlates associated with early stage (and later stage) romantic love. In a preliminary study of gender differences, we did a between-subject analysis of our 10 women and 7 men who were happily in love. Although men and women were similar in many ways, we did find gender differences. Men tended to show more activity than women in a region of the right posterior dorsal insula that has been correlated with penile turgidity (Arnow *et al.* 2002) and male viewing of beautiful faces (Aharon *et al.* 2001). Men also showed more activity in regions associated with the integration of visual stimuli (Narumoto *et al.* 2001). Women tended to show more activity than men in regions associated with attention, memory and emotion (Gray *et al.* 2002; Maddock *et al.* 2003; Velanova *et al.* 2003).

Extensive cross-cultural data indicate that courting men respond more strongly than women to visual signals of youth and beauty (Buss *et al.* 1990); hence, we speculate that the above male activation pattern evolved, in part, to enable ancestral men to respond to the visual signals of women who could bear them viable young (Fisher 2004). Cross-cultural data indicate that women are more attracted than men to potential mates who offer status and resources (Buss *et al.* 1990). To calculate the reproductive value of a man, a woman must remember the promises and provisioning record of her potential partner. Thus, we speculate that the above female activation pattern evolved, in part, to enable ancestral women to remember male behaviour patterns and thus make adaptive long-term mate choices (Fisher 2004). But more research is necessary to confirm this hypothesis, to establish the cultural variables that contribute to gender differences and to find more gender differences in the brain associated with romantic love.

We expect that human romantic love will be found to engage a wide range of varying, overlapping and dynamic brain systems, as would be appropriate of a multi-faceted phenomenon that has significant social, reproductive and genetic consequences. Nevertheless, the primary neural correlates associated with intense, early-stage romantic love are likely to remain similar across individuals and cultures, even among species, because this neural mechanism evolved to direct a crucial aspect of mammalian reproduction, mate choice.

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