Neuroendocrinology Letters Special Issue, Suppl.4, Vol.23, December 2002
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REVIEW ARTICLE

The Neural Mechanisms of Mate Choice: A Hypothesis

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Submitted: *September 9, 2002*
Accepted: *September 15, 2002*

Key words: **mate choice; attraction; proceptivity; dopamine; fMRI scanning; brain circuits**

Neuroendocrinology Letters 2002; ***23*** *(Suppl.4):92–97 pii: NEL231002R09 Copyright © Neuroendocrinology Letters* ***www.nel.edu***

Abstract Scientists have described many physical and behavioral traits in avian and mammalian species that evolved to attract mates. But the brain mechanisms by which conspecifics become attracted to these traits is unknown. This paper maintains that two aspects of mate choice evolved in tandem: 1) traits that evolved in the "display producer" to attract mates and, 2) corresponding neural mechanisms in the "display chooser" that enable them to become attracted to these display traits. Then it discusses our (in-progress) fMRI brain scanning project on human romantic attraction, what we believe is a developed form of "courtship attraction" common to avian and mammalian species as well as the primary neural mechanism underlying avian and mammalian mate choice. The paper hypothesizes that courtship attraction is associated with elevated levels of central dopamine and norepinephrine and decreased levels of central serotonin in reward pathways of the brain. It also proposes that courtship attraction is part of a triune brain system for mating, reproduction and parenting. 1) The sex drive evolved to motivate birds and mammals to court any conspecifics. 2) The attraction system evolved to enable individuals to discriminate among potential mating partners and focus courtship activities on particular individuals, thereby conserving mating time and energy. 3) The neural circuitry for attachment evolved to enable individuals to complete species-specific parental duties.

Introduction

Charles Darwin distinguished between two types of sexual selection, intrasexual selection, by which members of one sex evolve traits that enable them to compete directly with one another to win mating opportunities; and intersexual selection, by which individuals of one sex evolve traits that are preferred by members of the opposite sex [1]. The second of these two processes for mating success has become known as "mate choice." This paper maintains that two aspects of mate choice evolved in

tandem: 1) traits that evolved in the "display producer" to attract mates and, 2) corresponding neural mechanisms in the "display chooser," the viewer of the display, that enable the viewer to become attracted to these display traits.

It is well established that many creatures have mate preferences and make mate choices. In fact, the phenomenon of mate choice is so common in nature that the ethological literature regularly uses several terms to describe it, including "mate choice," "female choice", "mate preference", "individual preference", "favoritism", "sexual choice" and "selective proceptivity." And in past decades scientists have described many physical and behavioral traits that evolved in birds and mammals by means of mate choice [2, 3]. The peacock's elaborate tail feathers are the standard example. But no one had defined the corresponding neural mechanisms in the display chooser, the brain mechanisms by which the chooser internally processes these display traits, comes to prefer certain traits, rejects other traits, and focusses mating energy on particular conspecifics, thereby making a mate choice. So this paper attempts to define the primary neural mechanisms that facilitate mate preference, the mechanisms by which the chooser prefers and pursues certain conspecifics. We call this neural mechanism "courtship attraction."

We hypothesize that courtship attraction is associated with a specific and distinct constellation of neural correlates, an "attraction system;" that this attraction system operates in tandem with other neural systems, including the sex drive and circuits for sensory perception, discrimination and memory; that courtship attraction is expressed at different times and to different degrees in different species according to each species' specific reproductive strategy; and that this neural attraction circuit evolved to enable display choosers to perform three essential tasks of courtship: 1) discriminate among courtship displays; 2) prefer those displays that advertise superior genes, better resources and/or more parental investment; and 3) motivate the display chooser to focus courtship attention on and pursue particular mating partners, thereby conserving courtship time and energy.

It is hypothesized that in most mammalian and avian species this excitatory state of courtship attraction is brief; attraction lasts only minutes, hours, days or weeks. In humans, the neural mechanisms associated with courtship attraction are more developed, forming the physiological basis of what is commonly known as passionate love, obsessive love, "being in love", and/or romantic love.

Overview Of The Field

Psychologists regularly distinguish between the affective state of romantic attraction (passionate love, obsessive love, or "being in love") and the sex drive [4, 5, 6, 7, 8]. But this motivation-emotion system, courtship attraction, is not clearly described in the ethological literature. Instead, ethologists generally lump attraction with the sex drive and call this behavioral/physiological state "proceptivity." There are exceptions. In 1976 Frank Beach made a distinction between the sex drive and attraction, writing: "The occurrence or non-occurrence of copulation depends as much on individual affinities and aversions as upon the presence or absence of sex hormones in the female…proceptive and receptive behavior may depend upon different anatomical and neurochemical systems in the brain."[9]. More recently Donald Pfaff and colleagues have distinguished between the hormone-dependent elevation of courtship arousal and the expression of approach and other courtship behaviors, regarding these as distinct aspects of mating behavior and physiology [10].

A few scientists have also considered the anatomical and/or neurochemical mechanisms that produce and direct courtship attraction. Darwin proposed that female mate preferences arose from their innate sense of beauty. But he (understandably) offered no suggestion as to how this feminine attraction to beauty operates in the brain. He wrote, "It is, however, difficult to obtain direct evidence of their capacity to appreciate beauty" [11].

Hutchison and Hutchison propose that courtship could entail "a sequence of choices each requiring different mechanisms" and they speculate on some of the underlying neural mechanisms associated with mate preference [12]. They question whether the sex hormones are involved, saying, "Hormones are well known to be closely related to sexual behaviour. But whether sex hormones have any specific role in the establishment and expression of mating preferences… does not appear to be known" [13]. Yet they conclude that testosterone and some of the androgenic metabolites could be involved in some aspects of avian mate choice.

Geoffrey Miller has hypothesized that the endorphins are involved in mate choice. He notes that "display-judgers" must have evolved several faculties to discern and respond to the displays of "display-producers," including aspects of sensory perception, cognition, memory, judgement and feelings of pleasure. He calls this constellation of neural mechanisms in both sexes "mental machinery" and "sexual choice equipment" [14]. Miller then distinguishes 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 writes, "The hot chooser has a big pleasure-meter in its brain – it may be something like the level of endorphins floating around its nervous system" [15]. Miller maintains that both sexes inherit and pass to their offspring the genes that underlie this mental machinery for mate preference [16].

Frank Beach also recognized that proceptive behavior was a composite of more than one neurochemical system and suggested that the sex hormones may have operated in tandem with the monoamines. As he reported, "The mating behavior of female rats treated with monoamine receptor blocking agents indicates that 'lordotic behavior and soliciting behavior may be mediated by anatomically and possibly neurochemically

separate systems" [17, 18]. Subsequently it has been established that some of the monoamines, specifically dopamine and norepinephrine, play significant roles in regulating aspects of proceptivity [19, 20, 21, 22, 23, 24, 25, 26].

We hypothesize that some of the monoamines, specifically elevated levels of central dopamine and norepinephrine and decreased levels of central serotonin, are the primary neural mechanisms associated with mate choice [27]. We arrived at this hypothesis after launching a three-part investigation of courtship attraction in humans. We chose to study attraction in humans because this motivation-emotion system is universal to human societies, extensively described in the psychological literature, and more easily tabulated and quantified than is courtship attraction in other species. The rest of this paper reports on this in-progress investigation of human courtship attraction, what we regard as the primary neural mechanism underlying mate choice.

Phase I: The Hypothesis

In their survey of 166 societies, Jankowiak and Fischer found evidence of romantic attraction in 89% of these cultures. People sang love songs, composed love poems, practiced love magic, described myths and legends about love, and/or committed suicide or homicide due to unrequited love. The authors found no negative evidence; in the balance of these societies the lack of evidence was attributed to ethnographic oversight. So Jankowiak and Fischer conclude that romantic attraction is a universal affective state [28].

In phase I of the investigation of this neural circuit, the currently available American psychological literature was canvassed and a list of psychophysiological properties regularly associated with this excitatory state was compiled [29, 30, 31, 32]. These primary psychophysiological characteristics of romantic attraction were then compared with the behavioral effects of central dopamine, norepinephrine and serotonin [33]. Several correlations (listed below) suggest that elevated levels of central dopamine and norepinephrine and decreased levels of serotonin are involved in human courtship attraction.

1) Romantic attraction is associated with focussed attention on a specific, preferred other. Elevated concentrations of central dopamine and norepinephrine are associated with heightened and focussed attention [34, 35, 36]. These parallels suggest that elevated levels of central dopamine and norepinephrine contribute to the lover's focussed attention on the beloved.
2) The lover tends to regard the beloved as novel and unique. Elevated concentrations of central dopamine are associated with exposure to novelty [37].
3) The lover tends to remember tiny details of the beloved and their times spent together. Elevated levels of central norepinephrine are associated with increased memory for new stimuli [38].
4) The lover becomes highly motivated to seek affiliation with the beloved and exhibits diverse goal-oriented behaviors designed to achieve affiliative contact. Elevated levels of central dopamine are associated with motivation and goal-directed behaviors [39, 40, 41].
5) Characteristic of the lover is emotional dependence on the relationship with the beloved and longing, even craving, for emotional union with the beloved. Emotional dependency and craving are aspects of addiction associated with dopamine and norepinephrine pathways in the brain [42, 43, 44].
6) When people are "in love," they characteristically express heightened energy, sleeplessness and often loss of appetite, as well as labile emotional states, predominated by euphoria. Elevated levels of dopamine and norepinephrine are associated with hyperactivity [45], sleeplessness [46], loss of appetite [47] and feelings of euphoria [48, 49].
7) Adversity intensifies feelings of attraction. Known as the "Romeo and Juliet Effect," this phenomenon is most likely also associated with elevated levels of dopamine. When a reward is delayed, dopamine-producing cells in the Ventral Tegmental Area of the midbrain increase their activity [50]. (This neural mechanism probably evolved, in part, to drive birds and mammals to work even harder in times of adversity to acquire genetically desirable partners.)
8) The most prominent aspect of romantic attraction is obsessive thinking about the beloved. Obsessive thinking is commonly associated with low levels of central serotonin [51, 52, 53].

Focussed attention, motivation, goal-oriented behaviors, heightened energy, sleeplessness, loss of appetite, feelings of euphoria, obsessive thinking about the beloved, and heightened attraction during adversity in the relationship are all aspects of romantic attraction and all of these traits are associated with elevated levels of central dopamine and norepinephrine and/or decreased levels of central serotonin. These correlated data led to the hypothesis that romantic attraction to a preferred conspecific is associated with elevated levels of central dopamine and norepinephrine and decreased levels of central serotonin in corresponding brain regions. Passionate attraction takes a variety of graded forms, however, ranging from romantic love that is returned to unrequited love. So it is expected that these gradations of attraction are associated with different combinations of central dopamine, norepinephrine and serotonin, as well as with the activities of many other neural systems.

Phase II: Protocol Design

In phase II of this project the authors devised an experiment to establish which of several stimuli would produce feelings of romantic attraction. Eleven female and three male volunteers who reported that they had "just fallen madly in love" were first orally interviewed; data were also collected regarding their romantic rela-

tionship via a series of questionnaires. Then these subjects used a computer-based response device to indicate the intensity of their current feelings of romantic love while being exposed to a series of stimuli, including a visual image of the beloved, a smell, a song, a love note, a memory of the beloved and an anticipated event with the beloved. Their responses were recorded and compared to their responses while reacting to a neutral stimulus in each of the above categories; and a statistical analysis was made. It was established that feelings of romantic attraction are stimulated most effectively by photographs of the beloved, "thinking back" to specific relationship events, and songs relevant to the relationship [54].

These data formed the basis of the protocol for the functional Magnetic Resonance Imaging (fMRI) investigation, Phase III of this project.

Phase III: fMRI Investigation

In Phase III of this project, volunteers between the ages of 18 and 28 who reported that they had "just fallen madly in love" were interviewed to establish the extent of their romantic passion and their appropriateness for fMRI brain scanning. Subjects were then educated regarding the fMRI procedure and the protocol of the experiment and administered several questionnaires; then the brain scanning session was scheduled and completed. Among the tasks that each subject was required to do during the brain scanning process was to look at a photograph of the beloved and a photograph of a familiar individual for whom the subject felt no strong positive or negative feelings. During this twelve minute experiment, 3,200 brain images were collected for each subject.

This fMRI study is currently in progress. It is predicted that some of the brain regions associated with the feeling of intense romantic attraction will be those with high concentrations of receptor sites for dopamine, norepinephrine and serotonin, such as the caudate and the putamen and other regions associated with the "reward system" in the brain [55, 56, 57].

Discussion

Bartels and Zeki completed a similar fMRI experiment using 17 men and women who reported being "truly, deeply and madly in love" [58]. These scientists found a specific constellation of brain activity associated with romantic attraction and concluded that "a unique network of areas is responsible for evoking this affective state" [59]. In their study, bilateral activation occurred in the medial insula, the anterior cingulate cortex, the posterior hippocampus, the head of the caudate nucleus and the putamen. Deactivations occurred in the right prefrontal, parietal and middle temporal cortices, the medial prefrontal cortex, the posterior cingulate gyrus and the posterior amygdaloid region.

The caudate nucleus is associated with motivation and goal-oriented behaviors and 80% of receptor sites for central dopamine reside here. These data suggest that our hypothesis is at least partially correct: courtship attraction is primarily a motivation system that arises, in part, from the basal ganglia and is associated with dopamine pathways in the reward system of the brain.

Data from animal studies also support our hypothesis that elevated levels of central dopamine play a primary role in courtship attraction in mammalian species. In rats, blocking the activities of dopamine diminishes proceptive behaviors, including hopping and darting [60]. When a female lab–raised prairie vole is mated with a male, she forms a distinct preference for this partner. This preference is associated with a 50% increase of dopamine in the nucleus accumbens [61]. When a dopamine antagonist is injected directly into the nucleus accumbens, females no longer prefer this partner. And when a female is injected with a dopamine agonist, she begins to prefer a conspecific who is present at the time of infusion, even if the female has not mated with this male [62].

Data on animals also suggest that norepinephrine is involved in the courtship attraction response. When a female prairie vole is exposed to a drop of male urine on the upper lip, norepinephrine is released in parts of the olfactory bulb; this contributes to the release of estrogen and concomitant proceptive behavior [63]. Ovarian hormones, estradiol and progesterone, act to determine the release of norepinephrine in the hypothalamus to produce lordosis behavior in rats, a primary aspect of courtship behavior in this species [64]. And when ovariectomized, sexually receptive female rats receive injections of estrogen and are then permitted to mate, mating produces release of norepinephrine in the lateral ventromedial hypothalamus [65].

Conclusion

Fisher (1998) has hypothesized that avian and mammalian species have evolved three distinct brain systems for courtship, mating, reproduction and parenting [66].

1) The sex drive is characterized by a craving for sexual gratification.
2) Attraction (favoritism, sexual preference, or mate choice) is characterized by focussed attention on a preferred partner, heightened energy, motivation and goal-oriented courtship behaviors.
3) Attachment is characterized by the maintenance of proximity to a mating partner, affiliative gestures and expressions of calm when in social contact with this mating partner, separation anxiety when apart, and parental behaviors such as territory defense, nest building, mutual feeding, grooming and other parental chores [67, 68, 69, 70].

Each of these motivation-emotion systems, lust, attraction and attachment, is associated with a different constellation of brain circuits, different behavior patterns and different affective states. Each varies according to the reproductive strategy of each species. And each motivation-emotion system evolved to play a distinct

role in reproduction [71]. The sex drive evolved principally to motivate individuals to seek sexual union with *any* appropriate member of the species. Attraction evolved to motivate individuals to select among potential mating partners, prefer particular conspecifics, and focus their courtship attention on this/these individuals, thereby making a mate choice. And the neural circuitry for adult male/female attachment evolved primarily to motivate individuals to sustain these affiliative connections long enough to complete species-specific parental duties [72].

This paper focusses on the neural circuitry of the attraction system. It hypothesizes that mate choice in mammalian and avian species is associated with two phenomena that evolved in tandem: 1) traits of the "display producer" and, 2) a corresponding neural mechanism that enables the "display chooser" to prefer certain display traits, an "attraction system." Primary to this neural courtship attraction system in avian and mammalian species is elevated levels of central dopamine and norepinephrine and decreased levels of central serotonin in corresponding brain regions.

Among the brain regions likely to be involved in the neural circuitry of attraction and mate choice are: 1) The caudate nucleus and other regions of the basal ganglia associated with focussed attention, motivation, goal-oriented behavior, craving and addiction. 2) The anterior cingulate cortex and other regions of the Limbic System associated with emotion, feeling and affect. 3) The insular cortex, which processes emotions and bodily states. 4) Structures in the prefrontal cortex associated with reward assessment, planning and monitoring (most likely regions of the dorsolateral prefrontal cortex) and cortical structures associated with emotion processing (most likely regions in the ventromedial prefrontal cortex).

Some of the neural circuits associated with the sex drive have been identified [73, 74, 75]. It is hypothesized that the neural system for courtship attraction is distinct from but closely linked to some of these primary circuits associated with the sex drive and that these two neural systems, attraction and the sex drive, operate in tandem in most avian and mammalian species. This courtship attraction circuit must also operate in tandem with neural systems associated with the discrimination of colors, sizes, shapes, vocal tones, odors, postures, gestures and other brain systems associated with sensory perception, memory, reward assessment, planning and motor activities.

Last, it is hypothesized that this attraction circuit varies in duration and intensity according to each species' reproductive strategy. Yet this neural motivation-emotion system plays a similar role in reproduction across species: It enables both males and females to distinguish among potential mating partners, prefer particular conspecifics, and focus their courtship attention on the pursuit of these favored individuals, thereby conserving mating time and energy by making a mate choice. In humans this motivation-emotion system has evolved into a brain network that has come to be called romantic love.

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