12

The Varieties of Love and Lust

Neural Control of Sexuality

"What kind of love . . . is it that sanctifies marriage?" he asked hesitatingly. . . .

"True love. . . . When such love exists between a man and a woman, then marriage is possible," she said.

"Yes, but how is one to understand what is meant by 'true love'?" said the gentleman with the glittering eyes timidly and with an awkward smile.

"Everybody knows what love is," replied the lady, evidently wishing to break off her conversation with him.

"But I don't," said the man. "You must define what you understand. . . ."

"Why? It's very simple," she said, but stopped to consider. "Love? Love is an exclusive preference for one above everybody else," said the lady.

"Preference for how long? A month, two days, or half an hour?" said the gray-haired man and began to laugh.

Leo Tolstoy, *The Kreutzer Sonata* (1889)

CENTRAL THEME

Male and female sexuality are subservient to distinct brain controls, although they also share many influences. The primordial plan for both female and male fetuses, in mammals but not in birds, is initially feminine. Some have called this the "default" plan, since masculinization results from the organizational effects of fetal testosterone, which, in humans, occur during the second trimester of pregnancy. Others would call it the "without fault" plan, since the female brain coordinates the use of both cerebral hemispheres more effectively than does the male brain. Contrary to some creation myths, in mammals maleness arises from femaleness, rather than the other way around. If all biochemical events go according to the masculinization plan during this phase of gender specialization, the initially feminine brain is masculinized in utero by the timed secretion of testosterone and its conversion to the active organizational hormone, estrogen. The developing female brain is protected by prophylactic molecules, such as alpha-fetoprotein, which neutralize the effects of maternal estrogens that would otherwise tend to masculinize the brain. To be masculinized means that certain areas of the brain, especially specific nuclear groups in the anterior hypothalamus, grow larger in males than in females, while other areas remain smaller, such as the corpus callosum, which connects the two cerebral hemispheres. These brain organizational effects of early hormone secretions go a long way toward explaining some homosexual tendencies, for the hormones that ultimately trigger the organization of the male brain (testosterone aromatized to estrogen) are distinct from those that trigger the organization of the male body (testosterone converted to dihydrotestosterone, or DHT, by 5α-reductase). Due to this branching of control factors for brain and body organization, it is quite possible for a male-type body to contain a female-type brain, and for a female-type body to contain a male-type brain. It has been repeatedly shown in animal models that maternal stress can hinder the normal process of brain masculinization by desynchronizing the underlying physiological processes: If neonatal testosterone is secreted too early, before receptors are available to receive the message, normal masculinization does not occur. Maternal stress also impairs aromatase activity, which retards conversion of testosterone to estrogen. These different gender potentials in the brain, laid down during fetal development, are activated by the maturation of gonadal steroid synthesis during puberty. It is also known that male and female sexual urges emerge from different neural systems. Perhaps this is clearest in songbirds, where male courting-song systems in the brain grow and

shrink in phase with the breeding season. However, mammals also exhibit major brain functional differences between the sexes. For instance, preoptic area damage has more deleterious effects on male sexual behavior than on female behavior, while ventromedial hypothalamic damage has the opposite effect, compromising female urges more than those of males. These brain areas are organized differently in males and females. To have a male or female brain means many things, but among the best-established effects are the higher prevalence of arginine-vasopressin (AVP) circuits in males and more extensive oxytocin circuits in females. Several other neuropeptides control sexuality differentially between the sexes. The existence of such systems in the brain will eventually help explain many of the behavioral and emotional differences in male and female sociosexual tendencies. We are now on the verge of understanding the powerful feelings that control sexuality, but a great deal of affective neuroscience remains to be done before precise knowledge replaces credible hypotheses.

On the Nature of Sociosexual Feelings

Warm and friendly companionship is essential for mental health in humans, and probably most other mammals. Justifiably, some call the most fulfilling long-term relationships love, but sex is also essential to most vertebrate species.[1] Some humans are prone to call even the transient passions of sexual lust by the name of love. It is wonderful when the forms of "love" go together, but in humans all too often they do not, and in animals the concept of love is deemed to be highly suspect by the scientific community. Many confusions and disagreements have arisen from the failure to distinguish the two major forms of love. As Tina Turner sings: "What's love got to do with it?" And as that creative explorer of the human soul, Leo Tolstoy, expounded in *The Kreutzer Sonata*, a great deal of social chaos can emerge when we confuse the two. Members of our species regularly demonstrate that sex and social warmth or nurturance need not go together, and in primitive areas of the brain that elaborate such feelings, confusion also prevails. Sexuality and nurturance are to some extent independently and to some extent interdependently controlled. The Janus-faced nature of human passions and human warmth can only be understood by unveiling the underlying networks of the brain.

Clearly, humans can experience many social feelings. Some of them arise from our erotic nature, and some from the gentler feelings of friendly acceptance, nurturance, and social bonding. Filial love—the love between parent and child—seems outwardly quite distinct from sexual desire, but as Freud suspected, they may share important features. As we will see, findings from modern psychobiology can now be used to bolster this view; key molecules such as oxytocin are involved in both, albeit by actions on different parts of the brain. Although our cultural evolution has sought to bind our desire for sex and our need for social bonding together in an inextricable whole called the institution of marriage, there is no guarantee in the recesses of the brain that such cultural unions will succeed. And so, Tolstoy, through his protagonist in *The Kreutzer Sonata*, cries out in despair: "'Yes, I know,' the gray haired man shouted. . . . 'You are talking about what is supposed to be, but I am speaking of what is. Every man experiences what you call love for every pretty woman'" (p. 120). He proceeds to assert that many people marry only for the opportunity to copulate "and the result is either deception or coercion. . . . And . . . when the husband and wife have undertaken the external duty of living together all their lives, and begin to hate each other after a month, and wish to part but still continue to live together, it leads to that terrible hell" (p. 171) of mutually inflicted psychic pain and alienation.

Indeed, it seems likely that human bonding is not totally monogamous by nature, but our neurobiology is compatible with long-term serial and parallel relationships. The views fashioned by our cultural heritage may choose to disagree. In any event, evolutionary psychologists have now clearly demonstrated that men and women are typically looking for different attributes when they seek mates: Many surveys of human mate preferences indicate that females are seeking companions who are powerful and willing to invest resources in their behalf, whereas males are swayed more by youth and beauty, namely, external indicators of reproductive fitness.[2]

Sexual Feelings

Many psychobiological processes exist in the human brain to facilitate successful social and sexual connections. The tyranny of lust can lead one to feelings of moral degradation and physical dissipation, while acceptance of the power of lust can lead to incomparable ecstasies of psychophysical delight. Full acceptance of one's passionate nature, as elaborated in Tantric Buddhist philosophies, has even been touted as a path to enlightenment. In any event, it is an inescapable fact of life that evolution has built uncompromising feelings of sexual desire into the brain, as well as the potential for social devotion and deception, which can serve to maximize reproductive success. (This, of course, is an excessively casual way to express the matter, since evolution has no ends; it merely reels out endless patterns of reproductive possibilities—some successful, others not—depending on local social and environmental conditions.)

We experience the various feelings we call sexual love and lust because our biological nature has made us social creatures. Brain evolution has not given us, or any other animal, the innate cognitive appreciation that our sense of physical beauty and the pleasures of copulation are designed to service reproductive ends. That is something the human species had to learn

through insight, and it is still a difficult lesson for many to accept. Cognitive insights commonly govern sexual behavior less than do the insistent feelings of lust, which diminish only with age, stress, and illness.

Although we cannot definitively explain how erotic feelings are created in the brain, during the past few decades, neuroscience has given us the essential pieces of the puzzle. Although we have yet to see PET or MRI images of sexual arousal or orgasm, the first evidence concerning the neural sources of human sexual feelings were provided by Robert Heath almost 30 years ago. He found that during sexual arousal humans exhibit massive changes in brain electrical activity, including spiking in the septal area. When he placed acetylcholine (ACh) into that brain area in one schizophrenic woman, she described feelings of imminent orgasm. Such feelings have also been evoked there by electrical stimulation of the brain (ESB).[3]

Paul MacLean mapped out the monkey brain for sites from which genital arousal (erections) could be evoked by localized ESB. He discovered a broad swath of tissue, in higher limbic areas, where sexual responses could be elicited.[4] They included, prominently, areas such as the septal area, bed nucleus of the stria terminalis, and preoptic areas, all of which converge through the anterior hypothalamus into the medial forebrain bundle of the lateral hypothalamus. These brain regions will figure heavily in our discussion of the neural substrates of sexual behavior in this chapter and of maternal behavior in the next. However, before I proceed to detail the mass of neurobehavioral evidence that is now available, let us briefly consider the broader social contexts in which sexuality must develop.

The Sociobiology of Sexual Attachments

The tortured protagonist of *The Kreutzer Sonata* contrasted the stark reality of male sexual urges with the softer fabric of feminine social expectations. Which view is correct—the image of the male who desires nothing but sex or the image of the female who seeks devotion? Obviously, both, but the desires of men and women are not as distinct as Tolstoy portrayed them. Women need sex as much as males need devotion, and it is hard to find devotion in marriage without sex. Only when one's sexual appetite is slaked with lots of reproductive activity, or perhaps when one has become wizened with age, is loving companionship enough. Thus, younger people need more sexual passion in their lives, while older ones tend to be more satisfied with friendly companionship. But everyone is capable of experiencing both commitment and deceit in the quest for reproductive success. Marriage, of course, is a human invention to assure that the former will generally outweigh the latter. Other species have gone to great lengths to minimize male philandering (Figure 12.1).

For marital relationships to last, the frailness of human commitments typically needs to be solidified by cultural mandates. Still, at present, some estimate that one marriage in every two ends in divorce. Why does this happen? Perhaps because nurturance, sexual motivation, and the quest for power are partially independent but also intertwined in the brain in ways that we do not yet fully comprehend. Evolution progresses via the continual magnification and reinforcement of strategies promoting reproductive fitness. In certain species and under certain circumstances, it may be a wise evolutionary strategy to reproduce and leave someone else to care for the offspring. Males make a smaller biological investment, not only because of their ability to produce exorbitant quantities of sperm but also because they do not get pregnant, and so are more likely to depart without establishing long-term commitments than are females, who carry and gestate the fetus. Hit-and-run tactics become counterproductive, however, when a single individual is bound to have great difficulty rearing offspring successfully to reproductive age. Thus, the amount of male investment varies enormously in mammalian and avian species. Some species make no lasting bonds, while others remain paired for life.[5]

Reproductive strategies have left indelible marks on the behavior of each creature. In certain fish, the male is more devoted to the offspring than the females; in many birds, males share responsibilities equally with females, while in most mammals the responsibilities are left more to the mother.[6] Some species are exceptional, such as humans, where the father has become an increasingly active participant in many cultures. There are even a few mammals, such as the titi monkeys of South America, where fathers naturally take greater care of the young than mothers, perhaps as a strategy to allow the mother adequate time to seek nourishment. Indeed, recent cultural thought in the West has sought to coax men increasingly toward an avian or titi monkey psychology, even though there is no assurance that the neural underpinnings of male nature are in total agreement with such a plan. Many human males remain satisfied with less commitment than society desires,[7] while others exhibit sustained devotion.

Since there is such marked variability in reproductive strategies among mammals, we should be cautious in generalizing from one species to another. Also, in some species there are great interindividual differences. There is, in fact, no single anthropoid plan that can be discerned among our brethren great apes: Whereas gibbons appear to mate for life with a single partner, gorillas prefer a harem-type family structure, orangutans tend to be social isolates, with the sexes coming together mostly for copulatory purposes, while chimpanzees are quite social and promiscuous, sharing partners rather indiscriminately. Thus, even our closest evolutionary cousins provide no clear insight about our intrinsic sexual nature.[8] Humans, with help from their rich imaginations, can partake of all these viewpoints.

Since human females exhibit "concealed estrus," with no seductive display of skin or smell to advertise ovulation, most assume that our sexuality has become strongly dissociated from immediate reproductive concerns. Human sexuality is probably as closely aligned with social bonding as it is with propagation. Thus, my discussion of "lower" species can only offer clarity in thinking about certain underlying issues. The biological constraints that all mammals share contain no prescription for what human sexual behavior should be. As always, in the subcortical reaches of the brain, the evidence can only tell us what *is*; it does not inform us about what *should* or *could* be, especially when it comes to creatures as complex as humans.

Although we cannot fathom the thoughts of other species, evolutionary psychologists have recently advised us that humans may have various intrinsic cognitive tendencies that guide our thinking about sexuality. Probably the most obvious fact is that the human male brain has many "simpleminded" feature detectors for various aspects of the female body, which easily generate sexual arousal. Female eroticism is not so visually captivated, but male bodies obviously also convey many sexual and other social messages. For instance, it has recently been argued that male-pattern baldness helps signal that one is relatively mild-mannered and not very threatening, while a large bush, especially on the face, tends to convey the opposite message.[9]

Sociobiologists have also suggested that the human brain is cognitively prepared to deliberate upon a large variety of reproductive issues—ranging from sexual competition to consummation, from parental care to social alliances that maximize inclusive fitness. Although it is unlikely that other mammals have similar thoughts, they appear to be spontaneously prepared to cope emotionally with very similar concerns. The tendency to help kin is widespread in nature.

It is now widely believed that reproductive urges have ruled the evolution of many subtle brain and bodily mechanisms. Indeed, the whole discipline of *sociobiology* is premised on the analysis of psychological, behavioral, and genetic complexities that have emerged in evolutionary history in the service of reproductive fitness.[10] Although sexual feelings cannot be observed directly, it is an inescapable fact that they exist, probably in all mammals, and they can be as intense as other bodily needs such as thirst and hunger. Indeed, sexuality lies at the very fulcrum of our attempts to distinguish processes that psychologists have traditionally called motivations, in which a bodily need is subserved by a behavior, from those called emotions, for which no bodily need is evident. Obviously, sex is not essential for the bodily survival of any individual member of a species, "merely" for the survival of the species itself. In other words, it is not just a peripheral bodily need but a brain need that has profound consequences for each species. Thus it is not surprising that it is a bodily and psychological function that is highly politicized in both animal and human societies.

We now know with considerable assurance that sexual feelings emerge from primitive hormonally regulated mechanisms of the emotional-limbic brain that we share to a substantial extent with other mammals. It was a remarkable feat of nature to weave powerful sexual feelings and desires in the fabric of the brain, without also revealing the reproductive purposes of those feelings to the eager participants. Unfortunately, routine sex education for young humans rarely attempts to clarify the types of neural fabric from which lust and erotic desires arise. Partly this is surely because most people are really not very interested in such neural details. Here, however, I will focus forthrightly on the brain substrates of those lusty passions that we have inherited from ancestral species. The little that we humans have learned about such matters—about the many erotic brain molecules and brain areas that fuel our sexual desires and behaviors—has emerged only during the past few decades. However, most of the peripheral hormonal mechanisms have been known for a much longer time.

The fact that gonadal hormones govern sexual behaviors has long been recognized and was experimentally characterized in the middle of the last century, starting with A. A. Berthold's studies of castrated roosters in 1849.[11] Berthold demonstrated that adult sexual characteristics did not emerge in roosters whose gonads had been removed, but that the roosters' full spectrum of male vigor was restored by reimplantation of the testes. During the early part of this century, the active factor controlling both the physical and the psychological expressions of male sexuality was demonstrated to be testosterone. However, almost a century passed before the role of specific brain systems in elaborating sexuality began to be recognized. Now we know there is really no other way to understand the basic nature of sexual lust and passion than through the intricacies of psychoneuroendocrinology and brain research. I will dwell no further on the peripheral genital and hormonal machinery, for that is well covered in many texts.[12] Instead, I will focus on the more recently discovered neuroanatomical, neurochemical, and neurobehavioral issues that are now ready to be linked to psychology.

Unfortunately, brain scientists are prone to restrict their discussions to sexual behavior and tend to ignore sexual feelings, for such neurodynamics cannot be directly observed. Thus, it will require some imagination and theoretical courage to discern the vague outlines of the primitive brain mechanisms that create the sociosexual feelings that are our foremost concern here. However, we can only scientifically probe such emotions in the context of objective behavioral and brain data. As previously argued, in affective neuroscience, these levels of analysis—the behavioral, psychological, and neurological—must always go together.

Varieties of Sexual Behaviors

It is wondrous to behold the varieties of courting and other sexual strategies that have evolved in the service of reproductive fitness.[13] For instance, the sexual skills and proclivities of various species of fish suggest that we should accept behavioral variety as the norm rather than the exception. For the deep-sea angler fish, the very limited male role is to bite into the body of the female, becoming a permanent sperm-donating "slave" that dangles from her more massive body, their reproductive functions under her hormonal command (Figure 12.1). On the other hand, sea bass have developed a strategy of "egg trading" in which pairs of animals reciprocally take male and female roles during successive reproductive episodes, so as to minimize the potential influence of male philandering (i.e., to minimize hit-and-run tactics in males that would provide no follow-up investment in rearing the young). Then there are hermaphrodites, such as killifish, which under adverse environmental circumstances indulge in self-fertilization. Such "peculiarities" are not restricted to lower animals.

Certain mammals also exhibit memorable sociosexual tendencies. For instance, as mentioned in Chapter 10, female hyenas have an enlarged clitoris (or pseudopenis) that, by any measure, is as impressive as the male organ and is quite capable of erectile activity. This appendage is used primarily for purposes of sociosexual communication, especially dominance displays. Baby hyenas are also delivered, perhaps quite painfully, via the narrow uterine canal that exits through this enlarged clitoral organ. The unusual reproductive apparatus of female hyenas highlights a key aspect of their social reality—the exceedingly powerful role of females in hyena societies. Females are consistently dominant over the males. How evolution promoted social power and dominion in female hyenas remains unclear, but it was probably achieved, at least in part, by hormonally induced masculinization of certain brain processes and body parts. In many mammals, the vigor of male sexuality and male assertiveness (i.e., social dominance) tend to go together, and we are finally beginning to understand the underlying neural conjunctions. The fact that male sexuality and aggression interact to a substantial extent in subcortical areas of the brain is now a certainty (see Chapter 10). The meaning of this interaction for human sexuality remains regrettably pregnant with ambiguities.

Most of our understanding concerning the brain substrates of sexuality has come from the analysis of how hormones modify brain activities in animals. There has been some puritanical resistance to accepting the implications of this work for the human condition, perhaps representing a culturally ingrained societal stance of separating the present cultural condition of humans from our animal past. The failure to recognize the common mammalian underpinnings of sexuality is also due in part to the dazzling diversity of sexual strategies in nature, as well as the obvious fact that many human strategies are cognitively mediated, yielding complex ideas and voluntary selection of gender stances that most smaller brains simply cannot assume. Accordingly, it is too widely believed that the underlying brain details may vary so markedly among species that useful translations are impossible. However, as more and more neurobiological evidence accumulates, such beliefs are becoming less and less tenable. It is unfortunate that in this important area of human experience, so many psychologists and other social scientists attempt to construct wishful belief systems that do not reflect physical realities.[14]

Still, surface variety is remarkable across species. For instance, the neural timing of sexual receptivity is dramatically different between animals that remain receptive throughout the year and seasonal breeders

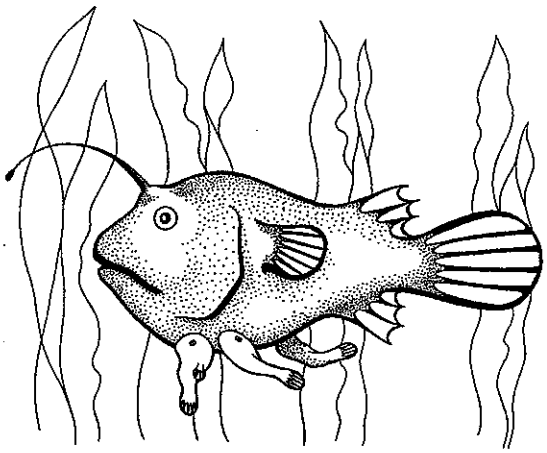

Figure 12.1. Drawing of a female deep-sea angler fish, with three males permanently attached to her body as ventral appendages. Through her hormones, she controls the testicular secretions of the fully "captivated" males. (Adapted from Crews, 1987; see n. 26.)

whose gonads grow and regress in early spring and autumn as the availability of daylight increases or decreases. Seasonal reproducers typically go to great lengths to advertise their receptive status, unlike humans and other species, including laboratory rats, that remain sexually active throughout the year. Despite such variety, we can be confident that many general principles of sexuality have been conserved in all mammalian species; here I will focus on those issues that seem most likely to apply to the human condition. This is not to say that humans cannot choose to override these mechanisms with their free will. They certainly can, especially if they are either skilled at deception or exceptionally saintly. Fortunately, other animals, which cannot lie and have no apparent urge to exercise willpower, speak their minds quite transparently through their behaviors.

To approximate the biological nature of things, the first tenet we need to accept is that male and female sexualities are as differently organized in male and female brains as they are in bodies. Although learning mechanisms are of obvious importance in generating the details of gender identity, the different sexes value substantially different things because of the distinct types of brain mechanisms and psychobiological values with which they are endowed. As already mentioned, human males are enticed by youthful beauty, while females are enticed by resource commitment. We also see this in other primate societies. Male chimpanzees usually fight over meat and sexual issues and also during social reunions, while females exhibit aggression largely in the context of seeking protection, competing for plant foods, and protection of the young.[15]

To some extent, especially in humans, the different gender expectations are culturally biased, but there are many psychobiological differences that are not simply a matter of choice or learning. For instance, males are more aggressive and power-oriented, while females are more nurturant and socially motivated. Indeed, recent brain metabolic evidence in humans indicates that temporal lobe areas (where aggression circuitry is concentrated) are more active in males, while cingulate areas (where nurturance and other social emotional circuitries are concentrated) are more active in females.[16] Such natural gender differences (at least at a population level) should no longer be a matter of debate, for the empirical facts seem overwhelming. However, we should doubt claims made for facts that have been poorly collected. For instance, in our estimation, rough-and-tumble play tendencies are quite comparable among males and females, at least in laboratory rats (see Chapter 15). Data on humans and other primates are not sufficiently well collected that we can exclude the effects of social learning on the gender differences that have been reported. In any event, we should come to terms with the fact that there are intrinsic neurochemical and psychobehavioral mechanisms in our brains that help create certain sex differences. Indeed, without the biological underpinnings, there would be no human sexuality or nurturance. It is truly remarkable how far back these differential controls go in brain evolution.

Evolutionary Sources of Mammalian Sexuality

If one places a small, naturally occurring, nine–amino acid peptide called *vasotocin* into the brains of male frogs and lizards, they begin to exhibit courting sounds and sexual behaviors. Given the opportunity, males treated with vasotocin mount and clasp females and copulate. In other words, a simple brain chemical system can trigger complex and coordinated sequences of sexual behavior.[17] It is not clear exactly what triggers the release of this transmitter in the reptilian brain under natural conditions, but it is clear that testosterone promotes vasotocin synthesis, and a host of social stimuli probably arouse the system into action. In fish the evolutionarily related hormone is *mesotocin*.

In mammals, two evolutionary offspring of these reptilian and piscine hormones (Figure 12.2), vasopressin and oxytocin, assume key roles in controlling certain aspects of sexual behaviors. Each differs from vasotocin by only one amino acid. Oxytocin has more effect on female sexual and social behavior, while vasopressin (which differs from oxytocin by only two amino acids) retains the ability to govern male sexuality.[18]

Intellectually, it is quite satisfying to discover that these descendants of more ancient molecules still control social and sexual behaviors in mammals. Vasopressin, which is more abundant in the male brain, is especially important in the mediation of many aspects of male sexual persistence (including courtship, territorial marking, and intermale aggression). Oxytocin, which is more abundant in female brains, helps mediate female social and sexual responsivity (especially the tendency of female rodents when mounted to exhibit lordosis postures, a characteristic, arch-backed, female receptivity reflex).[19] It is even more remarkable that after the birth of the young, these same synaptic modulators encourage parents, especially the mothers but at times also the fathers, to take care of their offspring (see Chapter 13).

To the best of our present knowledge, the segregation of male and female sex-related chemistries in the mammalian brain is incomplete. Vasopressin systems may help energize some of the more aggressive aspects of maternal behavior (i.e., protecting the young from harm); conversely, oxytocin systems may sustain some of the gentler aspects of male behavior (e.g., the tendency of fathers to be nonaggressive and supportive toward their offspring).[20] It cannot be emphasized too much that brain oxytocin is not completely reserved for female functions. It also has some role in governing male sexuality, just as vasopressin may have some role in females (i.e., reducing sexual readiness and increasing maternal aggressiveness).

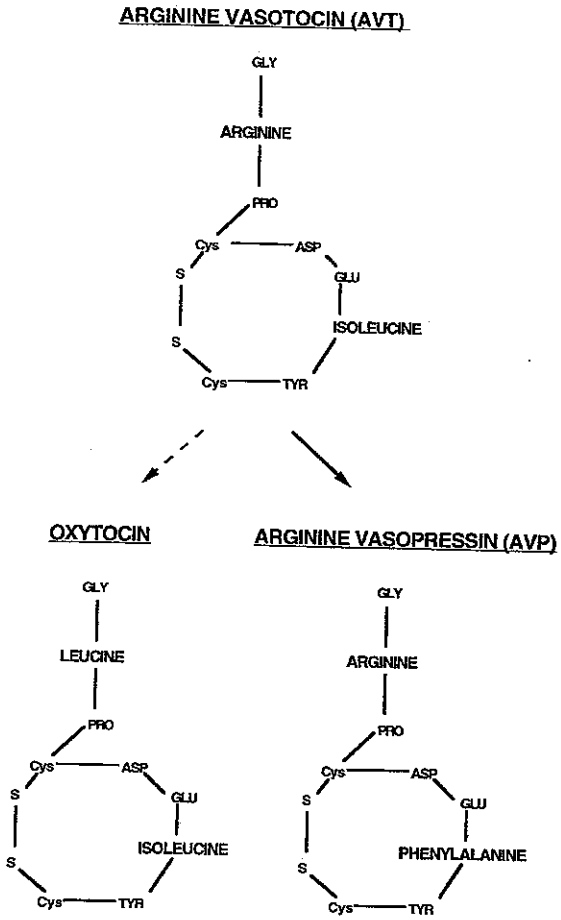

Figure 12.2. Summary of the structures of mammalian arginine-vasopressin (AVP) and oxytocin (OXY) as compared with the structure of the ancestral avian posterior pituitary neuropeptide arginine vasotocin (AVT). Each of the mammalian peptides differs from AVT by a single amino acid.

In males, oxytocin placed directly into many brain areas promotes sexual arousal (i.e., induces erections), ejaculation, and orgasm.[21] It is somewhat perplexing that the hippocampus would be a highly sensitive brain tissue to generate such effects, since it has generally been thought to function mainly in the conversion of short-term memories to long-term ones. This, of course, leads to the possibility that oxytocin produces erections there by activating sexual memories. In any event, brain oxytocin also appears to help mediate the behavioral inhibition, or "refractory period," that follows orgasm in males. Perhaps this peptide helps mediate postorgasmic feelings such as the "afterglow" that commonly follows copulation, at least in humans.[22]

It may seem paradoxical that the same brain chemical can mediate both sexual arousal and sexual satiety, but such subtleties no longer surprise neuroscientists. Reversals in behavioral effects are common in neuropeptide research and may correspond to the dynamics of the evoked psychological processes.[23] Just as a little alcohol can facilitate sociability, higher levels are bound to impair. As discussed more extensively in the following, similar effects can be obtained with endogenous opioids, where low doses of morphine can promote sexuality, while high doses impair it. Such effects may be mediated by slightly different circuits, receptor systems, or other yet unfathomed emotional dynamics of these systems in action as a function of how much of a given neuromodulator has been released over time.

There are many other situations in which social neuropeptides have one effect at low doses and a diametrically opposite effect at higher doses. One relevant example, which will be discussed more fully later, is the ability of low doses of oxytocin to solidify social memories, while high doses impair such memories.[24] Thus, at modest levels, brain oxytocin activity appears to help cement social bonds that may be the foundations for future reciprocities and "friendships," while excessive activity may lead to social aloofness.[25] One thing modern neuroscience has revealed is that the brain is full of apparent puzzles and paradoxes, and that logic is not as good a guide to knowledge in the natural sciences as careful observation!

Let us now consider how the basic impulses for male and female sexuality are organized in the mammalian brain. To understand sexuality, it is essential to recognize important differences in male and female brain organization, some of which occur during fetal development and some of which become apparent only when those differential plans are activated by the increasing hormonal tides of puberty. I will shift readily between animal data and human implications, since the evidence suggests that at the basic subcortical levels the neuronal machinery is remarkably similar.[26]

Genetic Sex and Fetal Sexual Differentiation

The ever-increasing appreciation of the differences between the *organizational* and *activational* components of sexuality has deepened our understanding of what it means to be male or female. A photographic analogy helps us envision these distinct processes. The hormonal patterns that are set in place during the organizational phase of fetal development help "expose" the imprint of maleness or femaleness on maturing brain circuits, as well as on bodily appearance. The hormones secreted at the onset of puberty eventually "develop" the exposed "negative," thereby activating the latent male or female sexual proclivities that have remained comparatively dormant within brain circuits since infancy. If brain and body organization do not match up, the individual will have to discover, through painful

experience, which gender was predominantly imprinted within his or her brain, and to what extent. This can be a stressful and lonely psychological journey.[27]

Animal research has indicated that the male and female poles of brain sexuality reflect extremes of a gradient that allows for many intermediary types. Although male and female sexuality are distinct to a substantial extent, each sex does in fact possess circuits for both forms of behavior, but typically to different degrees. The fact that male and female brains have distinct but related psychosocial proclivities allows sexual urges to become quite complicated in the real world. The possible permutations allow for cross-sexual variants that society is still trying to reconcile with long-standing cultural expectations, which are sometimes based on ignorance and intolerance. This issue was poignantly highlighted when President Clinton attempted to open the doors of the military to homosexuals at the start of his presidency in 1993, but the forces of ignorance and discrimination prevailed.

Brain scientists have suspected for many decades that there are intrinsic brain organizational patterns that promote certain forms of homosexuality.[28] The remarkable confirmatory story that has now been worked out in animal models is only slowly percolating into our general cultural imagination. To highlight this story for my students, I typically ask them a seemingly inane question: "How many genders or sexes are there?" At first they look puzzled, but courageous students are willing to provide the reasonable and expected answer: "two." I tell them how curious it is that our modern society still holds on to such prescientific views, for "four or more" is certainly a more accurate answer. Indeed, this is the belief some Native American tribes held as the correct description of their social world. They believed that in addition to the prevailing variants of *man within man* and *woman within woman,* nature sometimes created a *man's mind within the body of a woman* and a *woman's mind within the body of a man.* The essential accuracy of this view has now been affirmed by years of scientific research on the development and expression of sex circuits inside the rodent brain. Indeed, one could argue that there can be an "infinite number" of permutations along the biochemically determined gradients of brain and body masculinization and feminization. However, for our purposes "four" is certainly a more accurate answer than "two" as an estimate of the major types of gender (brain/mind) and sex (body) identities that actually exist in the world. Although the details have been worked out in lower animals, existing evidence suggests that similar principles also operate in humans.

In simplest terms, the brain *organizational* story goes like this. One is typically born either genetically female (with the XX pattern of sex chromosomes) or genetically male (with the XY pattern). What the Y chromosome provides for the male is testis determining factor (TDF), which ultimately induces the male gonadal system to manufacture testosterone.[29] The XX pattern allows things to progress in the ongoing feminine manner, unless some external source of testosterone (or, more accurately, one of its metabolites) intervenes. The actual manner in which male brain and body development proceeds is determined by the timing and intensity of the resulting hormonal organizational signals, namely, testosterone and two closely related metabolic products, estrogen and dihydrotestosterone (DHT). These last two steroid hormones normally control the final trajectory of brain and body development, respectively, while the XY baby is still in the womb—still hidden from the cultural influences of its future social world (Figure 12.3).

These hormones can similarly affect female development if they happen to be present in sufficiently high levels during pregnancy. Howevér, the XX sex chromosome pattern informs the female body to manufacture proteins such as the steroid-binding factor *alpha-fetoprotein,* which can thwart the cross-gender organizational influences of sex steroids during early development.[30] This protects the female fetus from being masculinized by the generally high levels of maternal estrogens. If there is not enough of this fail-safe factor, or if the maternal levels of estrogens are so high that they saturate the available alpha-fetoprotein, the female will proceed toward a male pattern of development—sometimes in both body and mind, sometimes in one but not the other, depending on the hormonal details that have transpired.

The four major types of organizational permutations can yield the obvious forms of cross-sexual gender identities: the presence of malelike brains in female bodies and of female brains in malelike bodies. The fact that individuals who look like men on the outside can come to feel like women on the inside, and individuals who look like women on the outside can come to feel like men on the inside, arises from a simple biological fact. The signals that trigger babies' brains and bodies to take the various possible gender and sex paths are separate (Figure 12.3). Initially, all fetuses are femalelike, and masculinity emerges from distinct prenatal signals that tell the brain and body to be masculinized. After the TDF gene has induced the male fetus to manufacture testosterone, several critical events must take place before the male brain and body phenotypes can be fully expressed (Figure 12.3). First, testosterone needs to be converted in two distinct one-step reactions to estrogen and DHT. The final organizational signal that tells the brain to masculinize is estrogen, and the signal that tells the body to develop along male-typical lines is DHT. Of course, these sexual potentials, laid down in the brain and body during gestation and infancy, do not become fully manifested until puberty.

With our current understanding of this organizational phase of psychosexual development, it is no longer a surprise that estrogen, a steroid hormone that is associated with female sexuality in the popular imagi-

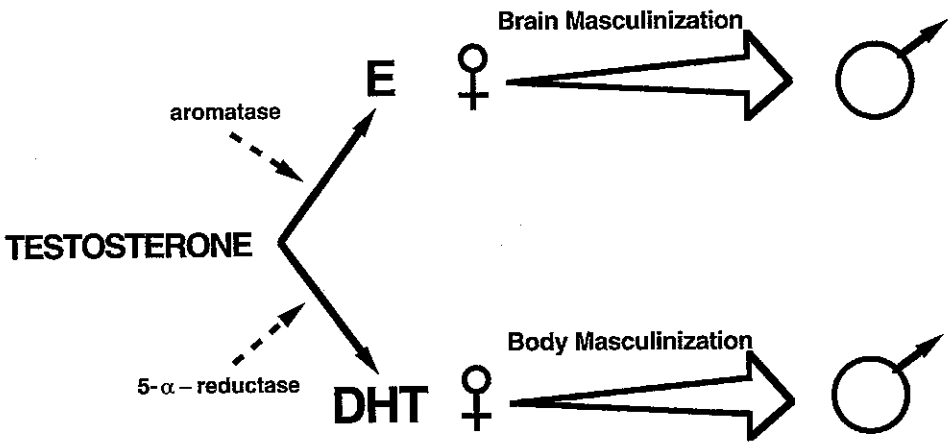

Figure 12.3. Both the brain and body of mammals are initially organized according to a female characteristic plan. Maleness emerges from two distinct influences of testosterone on body tissues—masculinization of the brain being mediated by estrogen (E) and of the body by dihydrotestosterone (DHT). Different tissues can convert testosterone to different products because of the enzymes they contain. DHT is manufactured in cells containing 5-α-reductase, and E is manufactured in those that contain aromatase.

nation, helps organize the intrinsic brain aspects of male gender identity in many species. To understand this, we need to consider the metabolism of testosterone (Figure 12.3). After testosterone has been synthesized from cholesterol, via many steps that include the intermediates progesterone and dihydroepiandrosterone, it can be biochemically modified in two distinct ways. Along one metabolic path, it can be converted into DHT with the assistance of the enzyme *5-α-reductase*. Along the other path, it can be converted into estrogen by the enzyme *aromatase*. These products of testosterone metabolism are critical ingredients that dictate whether a genetic male will continue along the male path in terms of body and brain development, both before and after puberty.[31] Various forms of homosexuality and bisexuality are promoted if "errors" occur in the various control points of these biochemical processes—if the developing male brain is not bathed in testosterone at the sensitive time or if it is missing the enzyme aromatase that converts testosterone to estrogen.

If the female brain is exposed to too much estrogen during the sensitive periods of development (the precise time varies from species to species), it will assume malelike characteristics while leaving the body feminine.[32] Females such as these will preferentially exhibit male-typical behaviors at maturity, but only if their brains are exposed to the activational effects of testosterone at that time. Indeed, in humans, tomboyishness in females has been promoted by maternal injections of diethylstilbestrol (DES), an estrogenic hormone that was given to pregnant mothers during the second trimester to prevent miscarriages in the 1940s and 1950s.[33]

Conversely, in the absence of fetal estrogen but with sufficient DHT, a male body can emerge with female-type circuits hidden within the brain. A naturally occurring instance of this type of organizational development has been found in a small group of individuals in the Dominican Republic. These boys, called *guevedoces,* which literally means "penis at 12," are genetically deficient in 5-α-reductase.[34] They have a female appearance at birth, with some enlargement of the clitoris and no apparent testicles (which are present but remain undescended within the body). However, their fetal gonads do apparently secrete testosterone at the usual time, and since they have normal aromatase activity, it is converted to estrogen but not DHT. Accordingly, their brains, but not their bodies, are fully organized along male lines. When such boys enter puberty and begin to secrete testosterone, they develop male-typical bodies—with an increase of body hair, deepening of the voice, enlargement of the penis, and, finally, the descent of the testes. Male-typical sexual urges also begin to emerge. Thus, the boys' pubescent erotic desires come to be directed toward females, even though they were reared as girls throughout childhood! This probably indicates that the male brain is instinctively prepared to respond to certain features of human femaleness, including facial and bodily characteristics, voice intonations, as well as ways of being.

There are yet other fascinating variants of psychosexual expression in humans that are probably biologically based but less well understood. For instance, some males have an extra female chromosome (i.e., XXY) and exhibit *Klinefelter's syndrome*, which is characterized by exceptionally small gonads. Such children are

often temperamentally passive, socially dependent, and mentally slow. On the other hand, boys with an extra male chromosome (i.e., XYY) have been claimed to be more hostile and aggressive than normal males, even though these findings are debatable. In addition, many drugs can modify the normal progression of the underlying psychosexual organizational processes, which should caution women against taking any drugs or being exposed to environmental toxins during pregnancy.[35]

These fascinating details of early development inform us of a profound fact of nature: Although male and female are the most typical biologically ordained poles of sexual identity, a vast number of gradations can be produced by normally occurring variations in the underlying hormonal control mechanisms that guide gender differentiation. Because of this, the biological forms of homosexuality do not represent psychological perversity resulting from aberrant psychosocial experiences but simply represent natural variants that can occur in the course of development. Of course, this does not exclude the possibility that humans sometimes voluntarily select gender roles in accord with their whimsical or neurotic cognitive desires. It is possible for someone to be halfway on the biological gradient of masculinity-femininity, and we might expect such individuals to be highly bisexual, with a maximal choice as to which direction they wish to orient their erotic tendencies. Since the real causes are typically hidden in the brain, it will be difficult to distinguish who is who, and it should not matter. Obviously, one's erotic choices should remain an individual matter, as long as no coercion or child abuse is involved.[36]

In sum, the major role of sex chromosomes is to dictate which enzymes and hormones will be manufactured by the developing reproductive apparatus. The XY chromosome pattern tells the male's body to manufacture testosterone at critical periods of development, setting in motion a cascade of changes in the protoypical female-type brain. This type of brain masculinization can also occur in females, which can promote cross-sexual behavioral and erotic tendencies in adulthood. The traditional XX pattern of femaleness will emerge, even in genetic males, if such early hormone secretions do not occur. Thus, the brain substrates for sexuality that are organized by these early hormonal experiences help determine what type of gender identities, erotic desires, and sex behaviors individuals will exhibit at puberty, when the elevations in hypothalamic gonadotrophic hormones and gonadal sex steroids begin to "activate" sexual tendencies (Figure 12.4).

Although the exact details of the hormonal cascades controlling these early organizational events vary somewhat among species, they are sufficiently similar in rats and humans that work on the former has elucidated the patterns that were subsequently found in the latter. But there presumably are differences in the magnitude of the cross-gender effects that can be achieved in different species. For instance, existing evidence suggests that rats exhibit larger brain changes during fetal masculinization than do humans, which would be in line with the larger average differences in body size between males and females. Usually the average gender difference in body size is considered an index of the extremity of sex roles in a species. Thus, it is to be expected that "tournament species" such as elks and walruses, in which intermale competition and the seeking of dominion over females are extreme, will exhibit the largest dimorphism between the sexes. In comparison with such creatures, the relative biologically based gender differences are modest in humans. On the other hand, in such species as the spotted hyena, we would predict that the tables would be turned, but sufficient brain data have not yet been collected.

What Is Organized in the Male Brain by Fetal Testosterone?

Much confusion in earlier discussions of hormones and sexuality arose from the failure to draw a clear distinction between the ways hormones *organize* male and female brains during fetal development and how they later *activate* the physiological and neuropsychological changes that accompany puberty. Because of the bifurcation of hormonal control of body and brain development (Figure 12.3), we now understand why intrinsic gender identity and body morphology do not always match up. To summarize, both humans and rats can have female-type brains in male-type bodies (if DHT was present in sufficient quantities but estrogen was not) or male-type brains in female-type bodies (where estrogen was present but DHT was not).

Although such biological facts are unlikely to explain all homosexual tendencies, they probably account for many cases, especially those including explicit internal desires for transsexual transformations, which in our modern society can prompt individuals to have sex-change operations. Recent evidence indicates that transsexuals have demonstrable differences in the bed nucleus of the stria terminalis, one of many brain areas that control sexual motivation. Thus, many males who have sought to be surgically converted to females do have more female types of brain organization.[37] Understandably, most people would desire that their internally experienced sexuality and gender identity should match their external appearance. There are bound to be many variants in the organization of the underlying circuits, but at present we have woefully little detailed information on such matters.

Although socialization certainly influences the sexual roles individuals choose, it now appears less crucial than has been widely believed in the arena of basic sexual feelings. For instance, the Dominican XY males who lacked 5-α-reductase did not experience extreme difficulty in reorienting their lives as males following puberty, even though they had been reared as girls. In

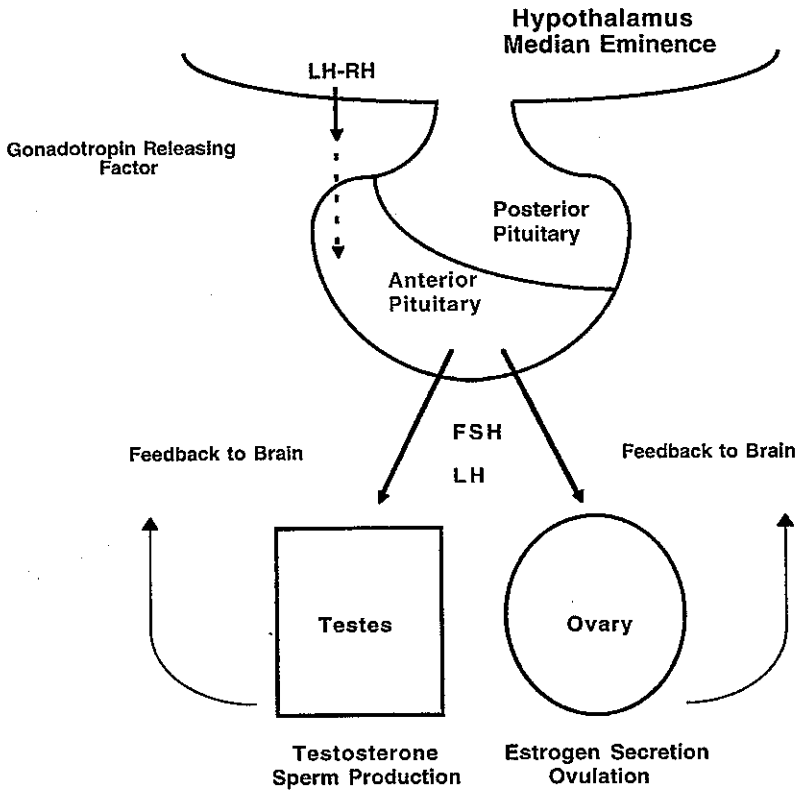

Figure 12.4. Overview of the hypothalamic and anterior pituitary control of sex steroid secretion. Hypothalamic gonadotrophin-releasing hormone, also known as LH-RH (leutenizing hormone-releasing hormone), activates the release of leutenizing hormone and follicle-stimulating hormone, which promote estrogen secretion from the ovary and testosterone production in the testes.

contrast, boys who have lost their genitalia early in life and have been reared as girls throughout their childhood have been found to experience considerable emotional distress and confusion at puberty when they are expected to behave like women. This is probably because they have the imprint of maleness stamped firmly in their brains.

What does it mean precisely when we assert that a brain has been masculinized? Although all the details have not been resolved, male and female brains differ in many important respects. For instance, females generally exhibit greater hemispheric coordination, since their right and left lobes are integrated more extensively via the larger fiber connections of the corpus callosum. This may have important implications for higher brain functions, such as the tendency of females to use both hemispheres in speech while males tend to use only the left side of their brains.[38] Accordingly, females often recover speech more readily after left hemisphere strokes than do men. Unfortunately, because of the lack of appropriate animal models, this is not well understood at the neuronal level. The most widely studied sex-related brain differences are found in subcortical areas. Remarkably clear neuroanatomical and neurochemical distinctions are found in neural systems that contain high levels of sex-steroid receptors, which are known to exist in all of the distinct varieties that one might expect—including different ones for testosterone, DHT, estrogen, and progesterone.

The largest subcortical differences have been found in the anatomy and chemistry of the medial *preoptic area* (POA), where males in practically all species studied have significantly larger neuronal densities than females.[39] In rats, the most highly masculinized zone is called the sexually dimorphic nuclei of the preoptic area (SDN-POA). In females, many neurons in this part of the brain die during fetal development for lack of testosterone, or more precisely its product estrogen, which is a powerful growth factor for these neurons. In humans the homologous brain areas are called the interstitial nuclei of anterior hypothalamus (INAH). Several studies have now documented that sex differences in

specific INAH nuclei of human brains closely resemble those found in rats, albeit the sexual dimorphic growth of these areas is not as great.[40] This probably helps explain why behavioral sex differences are not as great in humans as in some other species, in which these hypertrophied hypothalamic circuits do participate in the elaboration of male-typical sex behaviors. Even though a great deal is known about such matters in rats, there is, at present, little direct evidence in humans. Hence, generalizations are hazardous, but they may help guide our thinking.

Brain Control of Male Sexual Behavior

Following puberty, these organizational effects in the POA influence male sexual tendencies in all mammals that have been carefully studied. If the POA area is damaged, male sexual behavior is severely impaired (Figure 12.5).[41] In certain creatures, such as rats, lots of early play experience can partially overcome such deficits.[42] In others, such as cats, play does not promote restoration of sexual functions.[43] Overall, the influences of this area on sexuality presently appear to be more evident in the behavioral than the psychological realms, as highlighted by studies that have contrasted POA lesion–induced changes in sexual behavior and sexual motivation.

In sexually experienced rats, this area is more important for the generation of sexual *behavior* than sociosexual *motivation*. Following lesions of the POA, male rats that have had abundant sexual experience still seek access to receptive females, even though they do not attempt to copulate with them.[44] In other words, their social memories, situated perhaps in the cingulate cortex, amygdala, and nearby areas of the temporal lobes, are still capable of motivating social approach, although sexual engagement is no longer initiated. Perhaps this is because they can no longer experience sexual pleasure. Neurophysiological studies in primates indicate strong neural arousal in the POA not only when animals are copulating but also when males are approaching the subject of their desire.[45] Comparable effects are not seen when they approach other objects of desire, such as a bunch of bananas!

The SDN-POA of male rats contains abundant testosterone receptors, which activate male sexual tendencies at maturity.[46] In some species the less abundant DHT receptors also contribute to arousal. Castrated male rats that have lost their sexual ardor can be reinvigorated simply by placing testosterone directly into the POA. Indeed, male rats that are not very active sexually (so-called duds) have fewer testosterone receptors in this part of the brain than sexually vigorous animals (the so-called studs).[47] Estrogen, although it helped organize this tissue in male-typical ways during infancy, has no apparent role to play in activating adult male sexuality.

Major sex differences in brain anatomies and neurochemistries have also been found in various other brain areas such as the amygdala, especially in medial areas, where high concentrations of sex steroid receptors are found (areas that also play an important role in elaborating rage and intermale aggression). Neurons in the anterior areas of the medial amygdala of male rats respond equally to copulatory experiences as well as aggressive ones, while some of the cells in more posterior areas appear to respond selectively to the ejaculatory, and hence perhaps their orgasmic, experiences.[48] Androgen as well as estrogen receptors are concentrated in many of the same brain areas, including the POA,

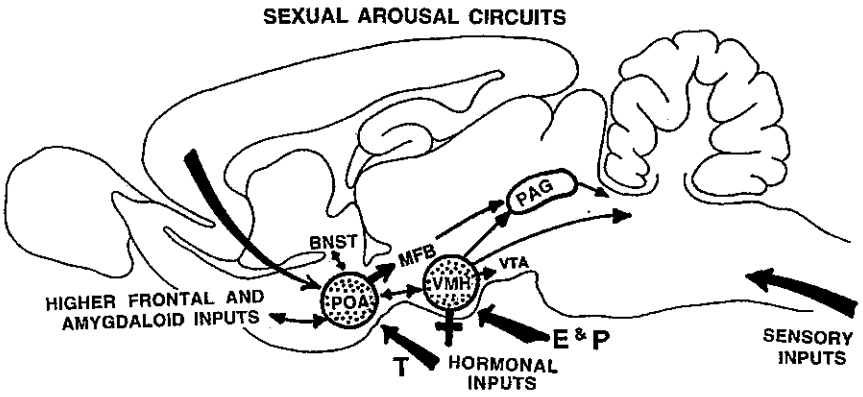

Figure 12.5. Lateral view of the rat brain summarizing two major areas that provide differential control over male and female sexual behaviors. Males contain a larger POA, and this area is essential for male sexual competence. The VMH is clearly more influential in female sexual responsivity. These systems operate, in part, by sensitizing various sensory input channels that promote copulatory reflexes. The extent to which these circuits control the affective components of sexual behavior remains uncertain.

the ventromedial hypothalamus, the periaqueductal gray, and down to the lower reaches of the spinal cord, where both male and femal sexual reflexes are controlled.[49] There are fine anatomical and neurochemical differences between males and females in all these areas, with the most striking one in the lower spinal cord being the *nucleus of the bulbocavernosus*, which is distinctly larger in males than in females. As already indicated, there are also some differences in the cortex, as well as in the commissures that connect the two hemispheres, which no doubt contribute to distinct cognitive styles in men and women.

Many brain areas exhibit neurochemical differences, but we are just beginning to fathom which of them control the various aspects of sexual behavior, sexual desire, sexual pleasure, and the many other sex differences documented in the behavioral tendencies of animals and humans—especially in urges such as aggressiveness, exploration, fear, and nurturance.[50] It is also reasonable to assume that comparable brain differences in humans control the strength of psychological and behavioral strategies that human males and females employ in seeking reproductive success, but there is precious little objective evidence to bolster such beliefs. Indeed, it is hard to imagine how documentation could be obtained, not only because of the pervasive methodological difficulties (e.g., it is impossible to control for differential learning factors in humans) but also because of the pervasive influence of issues of political correctness in this arena of knowledge.

In our society, many find it difficult to accept any intrinsic differences among the sexes. It also seems that others would be delighted to embellish any intrinsic differences with "naturalistic phallacies" that attempt to transform factual "is" statements into ethical "should" statements, thereby promoting various reactionary gender-biased political agendas. Abundant neuroscience data now suggest how brain and neurobiological differences between the sexes can promote or hinder certain psychological and behavioral tendencies—from aggression to nurturance. These are bound to have consequences for the emergence of long-term changes that we might seek in the sociopolitical arena of human affairs. How we will deal with these emerging facts, and incorporate them into our worldviews gracefully, remains a major challenge to our culture. Obviously, our search for equity must increasingly empower pro-social human qualities that ennoble us as caring creatures (see Chapter 13 and "Afterthought," Chapter 16).

Stress-Induced Suppression of Brain Masculinization

Although nature is strongly disposed toward creating relatively clear-cut male brains within male bodies and female brains within female bodies, we have now seen that it can easily produce other permutations. These may have adaptive consequences under certain circumstances. For instance, they can lead to different courting strategies that might actually increase reproductive fitness: Less strongly masculinized males might succeed with females by exhibiting behaviors that some would find more attractive than the tendency toward male brutishness that is so evident in many tournament species. Alternatively, the presence of such individuals in the social group may provide psychological dispositions that increase the reproductive advantage of their relatives (e.g., increased helping behaviors in male homosexuals). One additional idea is that under certain conditions, such as periods of high social and environmental stress, increased levels of homosexuality may be adaptive by limiting reproduction that could prove wasteful.[51] In any event, it is now well established that mother rats who have been heavily stressed during pregnancy tend to have a high incidence of homosexual male offspring. Maternal stress sets in motion internal neurochemical changes that tend to leave the brains of male offspring in their primordial femalelike condition.

When a pregnant rat is exposed to any of a variety of stressors during the last trimester (third week) of the three-week gestation period, many of the male offspring exhibit gender ambiguity when they reach puberty. Commonly, the experimental stress imposed on such mothers has consisted of prolonged immobilization, with continuous exposure to bright light, which rats dislike and which also generates thermoregulatory discomfort. However, many other stressors, such as foot shock or overcrowding, have also been used with comparable results. In a normal litter from unstressed mothers, approximately 80% of the males become "studs" at puberty, while the rest remain asexual "duds," which exhibit little male- or female-typical sexual behavior. Among the male pups of stressed mothers, however, only about 20% become "studs," while about 60% either are bisexual (exhibiting male behavior with a highly receptive female, and female behavior in response to a "stud" male) or else exhibit exclusively female sex behaviors (i.e., they exhibit lordosis, the characteristic female-specific receptivity pattern, when mounted by a sexually aroused male). The remaining 20% are asexual, as in unstressed litters. From the perspective that homosexuality may promote nurturance, it is noteworthy that the homosexual and bisexual males from stressed mothers are also more likely to exhibit maternal behaviors than their normal counterparts.[52]

These ratios can be altered substantially by the pups' social rearing conditions: The male offspring of stressed mothers exhibit more "normal" sexual behavior if they are housed continuously during adulthood with sexually experienced females. Although the expression of homosexual tendencies varies as a function of environmental conditions, the dramatic increase in the potential for this kind of gender ambiguity is now known to arise from the fact that maternal stress causes physio-

logical changes that work against the normal masculinization of the male brain.

The fetal spurt of testosterone that normally masculinizes male rats occurs several days prior to birth (around 19 days of fetal age).[53] Under conditions of maternal stress, the critical cascade of events is disrupted so that the peak of testosterone secretion occurs several days earlier than it should, when brain tissues are not yet ready to receive the organizing message. It is as if the organizational camera shutter had been clicked without the lens cap being removed: Although enough testosterone is secreted, it simply comes too early, and the neural image of maleness is not adequately imprinted upon the brain. In addition, maternal stress impairs enzymes that help synthesize testosterone in the gonads. Delta^5-3ß-hydroxysteroid dehydrogenase is inhibited, especially around days 18 and 19 of gestation, when the enzyme is normally available in highest levels. Likewise, brain aromatase, which allows testosterone to be converted to estrogen, is inhibited at the same time. These factors combine in such a manner that the brains of the affected males remain more femalelike. For instance, the SDN-POA becomes feminized because of the normal female-typical progression of cell loss in that area, since the effect of estrogen in promoting nerve growth is absent.[54]

Recent work has clarified whether it is the psychological consequences of maternal stress that cause demasculinization or whether stress-related physiological changes suffice: The effect seems to be a direct result of the mother's bodily stress response. Of the several prominent stress hormones, excess opioid (perhaps ß-endorphin) secretion appears to mediate the demasculinizing effect of stress. Pituitary ß-endorphin release is partly a counterregulatory hormonal mechanism that helps prevent other excessive stress responses, such as those arising from adrenocorticotrophic hormone (ACTH) secretion. The possible role of an opioid component in stress-induced neurodevelopmental changes has been evaluated simply by blocking opioid receptors during maternal stress with long-acting drugs such as naltrexone; the result was a complete restoration of masculinization. Stress-induced abnormalities in various biochemical parameters, such as reduced aromatase production, were also rectified.[55]

Since opiate receptor blockade can mildly increase the psychological perception of stress in humans, these results suggest that the opioid component of the stress response, as opposed to any psychological response to the stressor, is the critical element in the cascade of events that lead to the failure in fetal masculinization. This line of research also suggests that external administration of opioids to pregnant mothers may demasculinize males, and there is some evidence for this in animals.[56] One must wonder whether similar changes would occur in the male offspring of women addicted to opiates during pregnancy. At present we do not know, but the prediction is clear: Boys born to mothers using opiates during the second trimester would be expected to have a higher incidence of homosexuality than the offspring of nonaddicted women.

Does maternal stress also affect the development of the female offspring? The answer was thought to be no, but some behavioral differences in females have now been detected. The most noteworthy, in the present context, is that female offspring of stressed mothers exhibit weaker maternal tendencies than those from nonstressed mothers—just the converse of the pattern seen in males, who tend to become more nurturant.[57] Such changes in nurturance have been evaluated using a "sensitization" or "concaveation" procedure, whereby virgin animals (either male or female) are given free access to rat pups. Across several days of exposure, these initially nonmaternal animals begin to exhibit such behaviors as retrieving pups and huddling over them (see also Chapter 13). The females from stressed mothers take longer to exhibit this type of sensitization, while the males begin to exhibit nurturant behaviors more rapidly than controls.[58]

Another urgent question is whether human babies exhibit similar brain changes when their mothers are confronted by stress. Although several positive findings are available, they are generally deemed controversial. For instance, it has been documented that one highly stressful historical period, namely, the years of declining fortunes for Germany during World War II, led to a higher incidence of homosexual individuals, as measured by their sexual preferences in later years. In other words, boys born during the peak years of wartime stress were reported to have a higher incidence of homosexuality than those born during the years of peace before and after the war.[59] Also, there has been some work relating the levels of perceived stress during the various trimesters of pregnancy to homosexuality in male offspring. Elevated stress during the second trimester has been reported by some investigators to be related to a higher incidence of homosexuality in the offspring.[60]

Of course, scientific caution is always advised in trying to extrapolate from animal data to the human condition. As one scientist who has done much of this work points out, "The optimistic conclusion . . . that this (i.e., stress) syndrome provides a direct explanation of homosexuality in human males should be greeted with some caution."[61] At the same time, however, to insist that such findings have no implications for human issues is to sustain an excessively cautious stance about the underlying dynamics of the human body and brain.

In sum, even though environmental effects clearly modify one's self-perceptions, the sources of gender identity, as genetic sex itself, are heavily rooted in biology. Although it would be foolish to conclude that sexual preferences are completely controlled by nature, we can no longer discount innate biological influences. The reason such factors were not considered more fully

during earlier eras of cross-sex research was because the efforts of most investigators were focused on the role of hormone patterns that occur during the activational phase of sexuality at the onset of puberty rather than those that guide the organizational phases of fetal development.[62] Obviously, those early hormone secretions are still difficult to study in humans, so we must be satisfied with the snippets of indirect evidence that may be gleaned from clinical evidence.

Female and Male Sexual Behaviors: The Activational Phase

The imprint that is made on male and female fetal brains by early hormonal tides is finally developed at puberty (Figure 12.4). The passionate potentials of the nervous system are brought to life by renewed tides of hormone secretion. When animals copulate, neurons in widespread areas of the brain "light up," as seen through Fos immunocytochemistry. The areas are widespread in medial subcortical zones, but especially in areas that have high concentrations of hormone receptors.[63] These brain areas manufacture transmitters, partly under the control of sex hormones, that are especially important for normal sexuality. Obviously, a multiplicity of controls—emotional, cognitive, behavioral, and physiological—must be synchronized for competent sexual behavior in both males and females. Thus, scientific progress in this area will arise from our ability to follow and quantify these various components objectively, rooting out pervasive methodological problems, not to mention cultural biases. This makes the relevant human research remarkably difficult.

The most evident features of sexuality are behavioral, and excellent techniques exist to study the appetitive (proceptive) and consummatory (receptive) aspects of sexual behavior in lower animals. Accordingly, my focus here will be largely on the behavior of laboratory rats. However, we must remember that even in the brain research laboratory, much more work has been devoted to the consummatory (i.e., copulatory) components than to the proceptive, courting, or appetitive components of sexual behavior. Even more regrettably, more empirical work has been done on male than female sexual proclivities, and hence our factual coverage will remain a bit lopsided. This sex bias in the questions being asked has gradually been changing as increasing numbers of female investigators have entered this field of inquiry.

In general, experienced male rats housed alone in their cages are always ready for a little sex. Females, on the other hand, are not. Female rats typically have four-day sexual (estrus) cycles, and only for several hours on the day of estrus are they willing to participate in copulation. Nature has assured, for most species, that sexual arousal in females is tightly coordinated with peak fertility.

A few species, including humans, exhibit no such correspondence, and human females can remain receptive throughout the monthly cycle. In other words, human females exhibit a "concealed ovulation" with no clear "estrus cycle," which makes sexual behavior around the peak of the monthly cycle a less probable event than it is in most other species. This means that sexual urges and the likelihood of fertilization have been dissociated to a substantial extent in our species, which may help promote male investment and pair-bonding with individual women. In other words, a human male cannot identify which female is ovulating by any external sign. Hence, for reproductive success, he needs to be more attentive to one female's needs for longer periods of time than is characteristic of most mammals.[64]

If a human female is willing to offer sufficient sexual gratification to one male, the probability that he will squander or invest his resources elsewhere is reduced. This would obviously set female sexuality in humans apart from that found in most other species. However, this could have been effected by fairly modest shifts in the motivational substrates, such as a shift toward a male pattern of testosterone-mediated eroticism, while sustaining the other subcortical principles of female sexuality summarized earlier. We also must remember that the neural programs for sexuality are much more "open" to higher mental influence in humans than in other species. This is especially important when we come to the stereotyped sexual behavior exhibited by males of most species.

In rats and most other mammals, the general male strategy (facilitated by testosterone) is to exhibit fairly persistent searching for numerous sexual interactions (the word *cruising* has been used for this behavior pattern), followed by the emission of vigorous overtures (*courting* patterns, with characteristic 50 KHz vocalizations), which, if the female does not object, culminate in stereotyped consummatory (or *copulatory*) behavior.[65] During this final phase, the male mounts the female from the rear, palpating her flanks with his forepaws to arouse an arched-back, rump-raised receptive posture called *lordosis*. Whereupon, the male rat exhibits sets of rapid thrusting movements called *intromissions*, which, if well guided, lead to entry of the penis into the vagina. After a series of intromissions, the male ejaculates, which is accompanied by a "deep thrust," and then he pushes off, often falling over in the process. He then attends to personal matters, with intense grooming of his genital area, with a shift to 22 KHz defeat-type (or "I'm not in the mood") vocalizations. Presumably, all this is accompanied by various emotional shifts, but we can only infer such states from external signs such as changes in vocal patterns and specific affective measures, such as place-preference tests.

The sexually aroused female rat also has a variety of active behaviors to attract males. These "flirtatious" appetitive or *proceptive* behaviors appear designed to capture the attention of a male and entice him to pur-

suit. The most evident behaviors in the rat are repeatedly running toward and away from the male, or past him in a hopping, darting fashion with the head wiggling and many 50 KHz vocalizations.[66] Many of these behaviors also characterize play solicitation behaviors, which precede rough-and-tumble juvenile wrestling (see Chapter 15). If the male is aroused to pursue and mount the female, she makes entry easy for him: As he palpates her flanks, she assumes the lordosis posture—which, to amplify on the previous description, consists of a momentary rigid immobility, with a helpful arching of the back in such a way that the rump is elevated and the tail is flexed laterally to permit intromission and ejaculation by the male.

One common measure of female sexual receptivity is the *lordosis quotient*, which is the ratio of the number of mounts required to evoke the lordosis reflex. A great deal is known about how the rodent brain elaborates this reflex, but there is an unfortunate paucity of information about brain mechanisms that mediate the active appetitive components of female sexual behavior. Because the female shows no behavioral component similar to ejaculation (whether they experience anything like orgasm is unknown), it is more difficult to speculate about the nature of sexual experiences in female rats than in males. In short, the nature of sexual reward in the female remains less well understood than similar processes in males.

Physiological Substrates of Sexual Activation in Females

In most species (perhaps even humans), the hormonal changes that periodically prepare an egg for fertilization (i.e., gradually increasing estrogen followed by a rapid rise of progesterone) also prepare the female brain for heightened sexual receptivity. This consists of several discrete neuropsychological changes, including (1) a decrease in aggressiveness toward sexually aroused males, (2) an active tendency to solicit male attention, and (3) a sensitization of the female copulatory reflex of lordosis.[67] In many species, ovulation is accompanied by evident external signs of sexual readiness, such as a swelling and reddening of the anogenital region or the production of attractive odors. In the laboratory, one can use an experienced male rat as a detective to identify females that are in heat: He will spend a great deal more effort investigating the anogenital region of receptive females than nonreceptive ones, and, if permitted, copulation will follow rapidly.[68]

It is clear that the female lordosis reflex involves a spinal mechanism that is presensitized by higher brain mechanisms to respond to hormone patterns that help constitute sexual receptivity. This is because the latency of the lordosis reflex from the moment of flank stimulation is shorter than the conduction speed necessary for spinal neurons to send information up to the brain and back to the spinal cord.[69] Thus, female physical receptivity is imposed by readiness potentials emerging from higher brain areas. Critical circuits that sensitize the lordotic spinal reflex via tonic descending influences arise from the central gray of the midbrain and the ventromedial hypothalamus (VMH)—brain areas that, as we have seen, figure heavily in energy-balance regulation, as well as the elaboration of many other emotions (suggesting a way in which sexual readiness might be influenced by other emotional and motivational processes). It appears likely that females' diminished food intake and heightened sexual receptivity during estrus may reflect the common effect of hormonally induced sensitivity changes in these parts of the brain.[70] It may also be worth noting that starved animals are much less likely to mate than are well-fed ones, and the linkage between energy balance and mating readiness may be neurally negotiated directly within the VMH. Obviously, it is unwise to seek reproduction when energy resources are low, and nature has assured that this is unlikely to happen.

As already indicated, the hormonal patterns that induce receptivity in females are high circulating levels of estrogen followed by a rapid rise in progesterone (which typically occurs when the egg arrives in the fallopian tubes). Sexual receptivity can be reliably evoked in rats if one simulates this hormonal pattern by the appropriate regimen of injections.[71] In contrast, human females are more willing than most other mammals to indulge in sex independently of their hormonal status, but it is also clear that better studies concerning the sexual-emotional motivation of women need to be done before we exclude the importance of hormonal fluctuations. At best, human females exhibit only a modest trend for increased receptivity during ovulation.[72] Indeed, as we will see, the hormonal control of female sexuality in humans may be considerably different than in other species. Also, at present there are not enough studies analyzing feelings of eroticism in humans as a function of the menstrual cycle to draw any definitive conclusions concerning the role of ovarian hormones in modulating psychological responses related to sexuality.

Neurochemical Activation of Adult Sexuality: Male and Female Erotic Hormones in Action

Although we are beginning to understand what it means for the brain to be masculinized or feminized, what types of dynamic neurochemical changes actually mediate male and female sexual desires at maturity? Since this story is complex, and still in the preliminary phases of development, I will restrict my discussion to several key examples from brain chemistries that have been considered on previous pages. These same chemistries will also be important in subsequent chapters on the other social emotions.

As noted in Chapter 11, the male brain has more AVP, especially in neurons situated in several parts of the brain, including the amygdala, septal area, and anterior hypothalamus. The levels of AVP in some of these circuits increase as juveniles go through puberty and sexual urges begin to emerge.[73] These chemical systems help invigorate persistent male-characteristic behaviors, both aggressive and sexual. Indeed, when extra AVP is placed into the POA of male rodents, they obsessively patrol and mark their territory, and become substantially more combative. These are the same behaviors that are elevated by the onset of puberty and testosterone. They are also diminished after castration. Indeed, as mentioned earlier, when this part of the brain is damaged, male sexuality rapidly diminishes, while female sexuality remains largely unaffected.[74] In males who have been made sexually sluggish through castration, sexual eagerness can be restored by placing testosterone directly into this brain area.[75] This may occur in part because testosterone stimulates the manufacture of AVP in sex-control circuits through a direct effect on the genetic machinery that codes for the expression of AVP. The proximity of sexual and aggression control circuits in the male brain should also lead us to pause and wonder about possible functional relationships.

In a certain sense, this is the male dilemma: The hormonal stimuli that promote sexuality also increase certain types of aggressiveness.[76] If male animals are castrated, both their sexual ardor and their pugnacity diminish gradually, as do levels of AVP in approximately half the neural systems of the brain. Although sexuality can continue without brain AVP, it is sluggish, lacking the high level of persistence characteristic of sexually aroused males. While castration leads to a gradual decrease of sexuality in normal males, it leads to a rapid cessation of sexuality in genetically impaired animals that have little vasopressin in their brains to begin with (e.g., rats of the Brattleboro strain).[77]

During sexual activity, AVP is released from the pituitary into the circulation during the anticipatory phase of male sexual arousal that precedes ejaculation (Figure 12.6), and AVP appears to be more important in male than in female sexual craving. Indeed, when AVP is artificially increased in the female brain, sexual receptivity plummets.[78] Perhaps the presence of this male sex factor impairs female sexuality by making the females more aggressive (see Chapter 10). Indeed, soon after giving birth, brain AVP is elevated in females, and perhaps this neurochemical change helps pave the way for maternal aggression.[79] Of course, AVP has other functions in the brain, including overall arousal, attention, and perhaps some forms of memory, especially social memories. It should come as no surprise that quite a few circuits in the female brain contain this peptide. Thus, when investigators deem AVP to be predominantly a male sexual factor, it must be kept in mind that they are speaking only in relative terms.

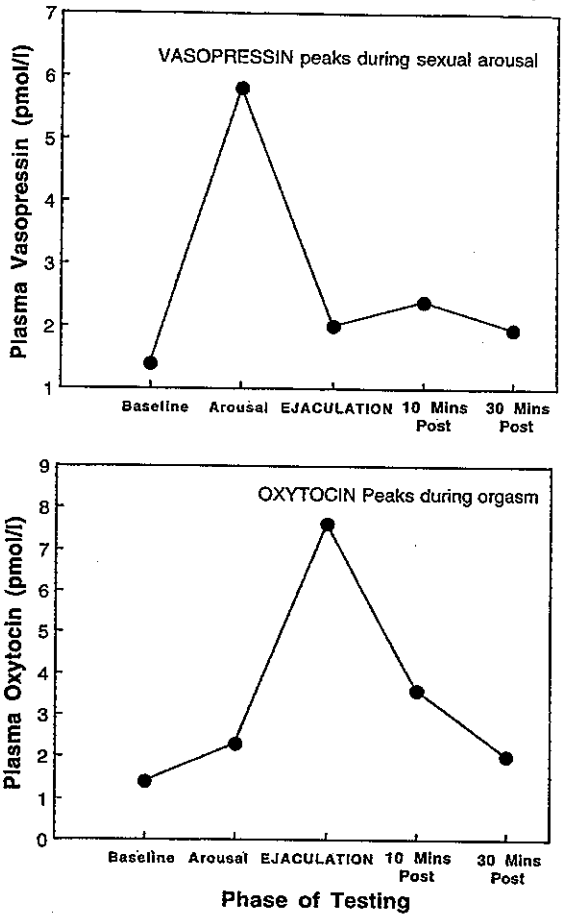

Figure 12.6. Effects of sexual arousal, ejaculation, and postejaculatory interval on average plasma oxytocin (OXY) and arginine-vasopressin (AVP) levels in human males. (Adapted from Murphy et al., 1987; see n. 87.)

By contrast, the female brain contains more oxytocin neurons than the male brain, and the genetic manufacture of oxytocin is under the control of the ovarian hormone estrogen.[80] The role of this neuropeptide in sexuality is not as lopsided as that of vasopressin in the male brain. Administration of oxytocin directly into the brain can increase both male and female sexuality, but seemingly in different ways. In males, oxytocin promotes erectile capacity, and it is released into the circulation in large amounts at orgasm (Figure 12.6). Unfortunately, no comparable data appear to be available for females. In any event, at present, brain oxytocin release is a key candidate for being a promoter of orgasmic pleasure and hence one of the mediators of behavioral inhibition commonly seen in males following copulation.[81]

There is a certain beauty in the fact that oxytocin, a predominantly female neuromodulator, is an especially important player in the terminal orgasmic components of male sexual behavior. In that role it may allow the

sexes to better understand each other. Indeed, we shall see that sexual activity can invigorate this chemical system in the male brain, thereby helping to promote nurturant behaviors (see Chapter 13). While oxytocin does modulate the orgasmic phase of male sexual activity, in females it appears to be important for both the courting and copulatory phases. In less clinical terms, it activates female flirtatiousness as well as sexual ardor. These urges are probably promoted by specific changes in specific parts of the brain.[82]

As already mentioned, a major area of the brain where sensitization of female sexual eagerness transpires is the ventromedial nucleus of the hypothalamus (see Figure 12.5). It has long been known that this area is uniquely important for normal female receptivity. Damage can seriously impair female sexual responsivity while having little effect on male sexuality. We now understand how this happens. The sex hormones that prepare the body for fertilization also dramatically change neurochemical sensitivities in this part of the brain. Indeed, hormonally induced receptivity (i.e., estrogen injections for several days, followed by progesterone a few hours before behavioral testing) leads to clear-cut anatomical and neurochemical changes in the medial hypothalamus.[83] A major neurochemical principle mediating this change is oxytocin. Hormone priming (just like normal estrus) leads to a proliferation of oxytocin receptors in the medial hypothalamus, as well as an expansion of the dendritic fields, which physically expand, reaching out toward the incoming oxytocinergic nerve terminals arising from more rostral neurons. This completes a circuit that sensitizes the lordosis reflex of the spinal cord (and presumably prepares the female psychologically to interact seductively with males). It is to be expected that the opening and closing of this gate will have substantial effects on the affective erotic feelings of a female.

Female receptivity can be markedly increased by administering oxytocin into various brain areas that normally contain oxytocin circuits, but only if the females have been adequately primed with estrogen. Conversely, sexual receptivity is compromised by administration of oxytocin antagonists into these brain areas.[84] Following brain oxytocin receptor blockade, females exhibit no sexual receptivity and actively reject the eager advances of males. Indeed, they squeal and complain if a male attempts to mount them, and they may even attack.[85] Of course, the befuddled males remain in hot pursuit, for their olfactory senses convince them that the female must be in a receptive state. Male sexual behavior is also strongly diminished with oxytocin antagonists,[86] again indicating that males and females do share some factors in the control of their sexual urges. We should note that, unlike the case of visual titillation in human males (which presumably reflects well-processed visual input into amygdalar tissue in the medial temporal lobes), in rats the smell of a female is more essential than physical appearance in the control of sexual urges.

At present, we know very little directly about the role of these chemical systems in the control of human sexuality (because of the difficulty of obtaining such evidence), but, as already noted, some interesting parallels have been obtained from an analysis of plasma peptides in males. AVP is elevated during the arousal phase of masturbation but declines rapidly at orgasm. Oxytocin, on the other hand, remains low during the preliminaries of sexual arousal but is released vigorously during orgasm and remains high for some time thereafter (Figure 12.6).[87] These changes probably correspond to erotic mood changes that are transpiring within the brain—with AVP promoting sexual eagerness and oxytocin promoting sexual pleasure.

Primitive areas of all mammalian brains contain affective systems designed to assure that males and females seek each other's sexual companionship. As we will see in the next chapter, these same chemistries have been utilized to construct circuits through which parents are eventually coaxed to take care of their offspring. These same chemical systems also appear to establish attachment bonds between mother and child, and they may also cement love, friendships, and social preferences among adults (see Chapters 13 and 14). However, there is a darker side to this story.

Sexual arousal may set the stage for sexual jealousies. For instance, one especially intriguing finding is that a male's "jealous" attachment to a female may be dependent on the fact that AVP was active in his brain during sexual activity. At least in prairie voles, the only species studied so far, sexual activity can increase the likelihood that a male will attack potential interlopers. Males that are allowed to copulate will become aggressive toward other males that enter their territory. However, if an AVP antagonist is placed into the brain just prior to the sexual activity, these field mice do not develop such a jealous attitude. On the other hand, if one simply puts AVP into the brain of a male in the presence of a female, with no sexual activity allowed, the males still begin to treat other males in threatening ways.[88] If one is willing to generalize from these behavioral results to human feelings, one might hypothesize that tendencies for sexual jealousy are promoted in the male brain by the release of AVP during sexual activity. Of course, animal behaviorists are unlikely to use such subjective terms as *jealousy* in the interpretation of their work, for such subtle emotional issues can only be evaluated through human research. However, the likelihood that such work will ever be done in humans seems remote, but if an orally effective AVP antagonist is discovered, we might anticipate that it will take the edge off sexual jealousy in men.

The Neurochemistry of Sexual Pleasure

A key emotional question related to sexuality is: What does it mean, in neurochemical and neurophysiologi-

cal terms, to have experienced sexual pleasure? This is a difficult question to answer on the basis of available evidence, and to a substantial extent we must rely upon mere speculation. Indeed, sexual pleasures should probably be subcategorized into neurologically distinct pre- and postorgasmic phases. At present, we have no absolute assurance that other animals even experience orgasm. It might be easier to argue that males do, since they exhibit the explicit response of ejaculation, which in humans is highly related to the emotional experience of orgasm, but the issue is much harder to judge for females. There is no outward sign as clear as ejaculation in females. Indeed, it could be argued that there is no clear adaptive value for female orgasm in creatures that are as hormone-bound in their sexual appetites as are the females of most other mammalian species. Only when there emerged a major social payoff for extended sexuality (as is the case in humans) was there significant evolutionary pressure for the emergence of reasonably stable pattern of female orgasms. As will be discussed more extensively in a subsequent section, perhaps orgasms evolved as an internal signal that one had found "Mr. Right." Even though females of other species may not experience orgasm, this is not to say that they do not enjoy sex. Obviously, positive erotic feelings in both sexes are likely to be critical in sustaining sexual activities.

Although brain oxytocin and vasopressin circuits are excellent candidates for organizing both the behaviors and the emotional feelings associated with sexuality, they are only two especially prominent candidates in a growing list of chemistries that elaborate libido. For instance, one neuromodulator we have yet to mention is luteinizing hormone releasing hormone (LH-RH), which controls secretion of gonadotrophins from the pituitary (see Figure 12.4) and is represented by extensive systems within the brain that generally parallel the oxytocin neural system. Administration of LH-RH into the brain can selectively increase female sexual receptivity in rats, and it has been of some clinical interest to determine whether this agent can increase libido in humans.[89] Some success in treatment of sexual disorders has been achieved by administration of this agent peripherally in both females and males (with more positive effects observed in females), but no one has yet injected it directly into the human brain to ascertain if subjective effects are produced.

At present, one of the few ways we can determine which chemistries participate in sexual reward is through the conduct of place-preference studies in animals. One approach that has been taken is to evaluate preferences for those locations where animals have had the opportunity to copulate. (In such studies, animals were allowed to have sex in one of two environments, and male animals chose to spend more time in the environment in which they have had sex.)[90] Since both dopamine and opioids have been implicated in the mediation of brain reward, investigators have determined whether the sex-induced place preference could be modified by either dopamine- or opiate-blocking agents. Such experiments have clearly indicated that opiate blockade is more effective than dopamine blockade in attenuating sexual reward in males. Indeed, this effect has been obtained by the restricted blockade of opiate receptors within the preoptic area, where the sexually dimorphic nucleus is situated.[91]

In this context, it is also noteworthy that opiate addicts who "mainline" strong drugs such as heroin report feeling an orgasmic rush, with a warm erotic feeling centered in the abdomen, when the drug hits their system. Thus, it seems that both sexual pleasure and taste pleasure (see Chapter 9) are mediated by similar chemistries, but perhaps in different brain areas. But surely other chemistries are also involved. For instance, as mentioned at the outset of this chapter, administration of ACh into the septal area has induced orgasmic feelings in humans. However, since ACh is important in so many brain functions, it will not be of much use in the treatment of sexual or erotic disorders. Also, as previously indicated, the probability that oxytocin secretion contributes to orgasmic feelings is high, but it may well be that the larger part of the orgasm-correlated secretion (e.g., Figure 12.6) is due to concurrent opioid release within the brain.

What is needed now are more animal studies that concurrently evaluate the role of several neuropeptide systems, such as vasopressin, oxytocin, and LH-RH, in this type of reward. All such studies need to control for social-reward effects that are independent of sexual reward. In addition, we desperately need more studies along these lines that focus on the female side of the sexual interaction. Until such work is more vigorously pursued, the subjective erotic effects of sex behavior–mediating systems of the brain will remain veiled in mystery.

Some Evolutionary Issues concerning Orgasmic Responses in Humans

Presumably, reproductive issues have helped guide the evolution of various sexual interactions, as well as sexual pleasure mechanisms in each species. For instance, why is it that human females are capable of multiple orgasms, while human males need periods of repose (i.e., postejaculatory pauses) before they can resume sexual activity? We do not know, but perhaps it is because the male body must have time to restore sperm resources before it makes biological sense to continue sexual activity, while females have no such constraint. Why is it that males can generally achieve orgasm more rapidly and reliably than females? We do not know, but perhaps it is because essential reproductive reflexes (i.e., ejaculation) are more tightly linked to orgasmic experiences in males than in females. Reproduction would not be possible without male ejacu-

lation, and it is easy to understand why the approach of orgasm in males would further invigorate sexual activity. Egg fertilization, on the other hand, apparently can proceed effectively without female orgasm, although it remains possible that such responses promote sperm extraction and propulsion up the uterine canal and even into the fallopian tubes.

Since the human female's orgasm appears to be largely independent of simple reproductive issues, it may be related to more complex social ones such as bonding. From this vantage, it might be understandable why females would be capable of multiple but less predictable orgasms (at least during interpersonal sex) than males. Orgasm may provide a novel emotional route for identifying and reinforcing certain male qualities. Mechanistically, the female orgasm may simply arise from the brain mechanisms that evolved to mediate male orgasm; alternatively, it may be an evolutionarily emerging state, perhaps as an exaptation derived from aspects of male orgasmic mechanisms. Obviously, it is attractive to believe that male and female orgasms are fundamentally similar in terms of brain neurophysiology (just as the penis and clitoris develop from the same primordial tissue), but such a commonality remains to be demonstrated.

One important line of evidence that supports the idea that male and female eroticism have converged in humans is the finding that sexual desire in females is more dependent on adrenal testosterone than in other mammals,[92] whose receptivity relies more critically on ovarian estrogen and progesterone. If, in fact, female orgasm is a process that is presently emerging in an evolutionary sense, one provocative idea is that it may help females identify males who have the right characteristics for social bonding and hence are likely to support the woman's future needs. However, the bottom line is that, at present, we simply do not know.

It still remains possible that male and female sexual reward differ in some fundamental ways in the brain, and a large number of neurochemistries, from galanin to cholecystokinin in the preoptic area, may eventually shed light on this important facet of human life. However, without a good animal model of female sexual gratification, it will be most difficult to evaluate such issues. Also, since the hormonal control of sexual urges is so different in human females than in other animals, it may be impossible to devise a simple laboratory model for such processes.

Learning within the Sexual Systems of the Brain: The Case of Birdsong

As has been observed with all of the other basic emotional systems, sexual circuits of the brain can promote learned behaviors. Indeed, for a long time it was commonly assumed that gender identity was learned, but we now recognize that to be, at best, only half true. Although human choice cannot be denied, the greatest part of sexuality is guided, as in other animals, by the types of neural systems nature has provided within male and female brains. Of course, how each organism uses sexuality in the world is subject to a great deal of learning, especially with respect to courting rituals and specific sexual preferences. Such issues are most provocatively highlighted by recent discoveries about how song is elaborated in the avian brain (also see Appendix B).

It is typically the case that males sing, both to attract females and to ward off competing males that would enter their living space. Song usually occurs at the time of year, namely, springtime, when birds' gonads are rapidly growing to their maximal size, following the shrinkage that occurred during the previous fall and winter. It has been a remarkable observation that along with the changing size of the gonads, the circuits of the brain that mediate singing also sprout forth and recede with the seasons.[93] Unlike brain tissues in mammals, avian brains sustain the ability to manufacture new neurons even in adulthood. During springtime, males are endowed with increasing amounts of neural tissue especially in the areas of the brain that generate singing. These events are mediated by fluctuating testosterone levels. When testosterone falls, the areas of the male brain that mediate singing regress and remain, in relative terms, as small as their gonads.

A series of higher brain structures in birds have now been found to be under the neurotrophic control of testosterone, and it has been demonstrated that these structures acquire much of their eventual behavioral competence as a result of early learning.[94] Although there is considerable variability from one species of bird to the next, the most common theme is that birdsong is not completely formed within the genetically connected components of their song circuits; rather, in most species, there is only a rudimentary form of the species-characteristic "score" embedded within the genetically dictated connections of those circuits. To become complete, circuit functions need to be optimized through learning, and the birds need to be able to hear their own fledgling attempts at song production. Without early exposure to their own song, the males of most passerine species (i.e., songbirds) will exhibit only a few fragments of their ancestral tunes.[95] In the absence of any better role model, some species are able to approximate the songs of other species heard during their youth, but most will fully perfect only the song of their own species. And this perfection requires experience. The refinement process occurs in those specific areas of the brain where neural circuits can be invigorated by increasing tides of testosterone.

In the sexual arena, as elsewhere, it is clear that nature and nurture go hand in hand, with experience bringing the organic potentials of genetically ingrained systems to their full potential. Human courtship and sexual styles are obviously learned. The passions that accompany them are not. It seems likely that biological factors are as influential in the hidden desires of the human heart as they are in the birdsong of springtime.

AFTERTHOUGHT: More On the Nature of Sexual Pleasure

So, let us ask once more: To what extent do the animal studies summarized here have implications for the human condition? While the higher levels of cortical influence in the human brain provide overriding principles of cultural control, the power of subcortical emotional circuits may be decisive in the sexual quality of individual lives—the ability to sustain receptivity and potency and to have experiences of intimacy and pleasure. Neuroscience will eventually provide new forms of assistance to such aspirations of the human heart, and future remedies will be much more effective than the aphrodisiacs of the past.

Already there have been anectodal reports that intranasal oxytocin is able to facilitate sexual performance in humans.[96] As mentioned earlier, this peptide is quite effective in increasing both male and female sexual activity in rodents. Could this type of knowledge be used routinely to promote sexual functioning in humans? We can be sure that many pharmaceutical firms are presently searching for new aphrodisiacs based on a solid knowledge of the mammalian brain as opposed to wild hunches from folklore and the approximations of ancient traditions. Powdered rhinoceros horn may continue to be sold in some part of the world as long as there is a market for superstitions and the body parts of endangered animals, but such practices are based more on faith and the power of placebo effects than on solid knowledge. As we saw in Chapter 8, the mammalian brain is designed to construct belief systems, and once they are solidified, they are as hard to move as mountains.

One molecule with scientifically established aphrodisiac qualities is yohimbine,[97] which blocks brain norepinephrine receptors of the alpha-1_A variety. In addition, the MAO-B inhibitor l-deprenyl has been found to sustain sexual vigor and longevity in aging male rats.[98] Although more needs to be learned about these fascinating systems before useful connections to psychiatric issues can be formulated, it does seem that basic sexual urges are controlled by similar neurochemistries in both rats and humans. But this is not to say that the road from biology to behavior is a one-way street. There is also feedback from behaviors to biological processes. As with most complex brain systems, there are complex two-way interactions between the brain and the environment in which it operates. Several fascinating phenomena have been discovered when people have monitored changes in the sex hormones as a function of various social challenges.

Animals have been found to exhibit remarkably consistent hormonal fluctuations as a function of their social successes, and similar changes are also evident in humans. As mentioned in Chapter 10, the winners of social encounters typically exhibit elevations in circulating testosterone, while losers exhibit declines.[99] It is reasonable to expect that such changes would promote neurochemical activities that facilitate male libido (and thereby increase their reproductive success), even though such effects remain to be documented.

Conversely, it is also interesting in this context to consider how environmental psychosocial variables might modify the physiological substrates of sexual and reproductive tendencies in females. Many fascinating observations have been made: (1) Young females, including humans, typically become sexually mature more rapidly when strange males enter their environments. (2) Social stimulation can modify levels of bodily enzymes controlling the manufacture and processing of sex steroids. (3) Groups of female primates, as well as wolves and other species, exert physiological influences over each other to control which animals will reproduce in the group (perhaps via olfactory cues). (4) Finally, we are beginning to find that the olfactory senses of human beings may also be acutely sensitized to certain smells that can synchronize sexual cycles and hence may coordinate sociosexual activities.[100]

Humans are generally less dependent on olfactory cues for sexual arousal than are most other mammals, but recent work indicates that human sexuality is still linked to certain bodily odors.[101] Visionary entrepreneurs in the perfume industry are paying close attention to these findings, hoping to profit through the manufacture and distribution of smells that can amplify moods that control our behaviors at the affective fringes of our consciousness. The emerging knowledge concerning the existence of a vomeronasal organ and an accessory olfactory system in humans will undoubtedly figure heavily in the success of such efforts.[102]

Suggested Readings

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