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Sexual Motivation: A Comparative Approach in Vertebrate Species

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Abstract
Purpose of the Review We review three different components of sexual motivation: appetitive behaviors, sexual incentive motivation, and paced mating in rats, mice and voles. These components occur in semi-natural or natural conditions. We also described behaviors in other species that are indicative of sexual motivation.
Recent Findings Sexual motivation is the mechanism responsible for activating, directing, and causing persistence of behaviors directed towards a sexual incentive. Appropriate sexual motivation is crucial for the survival of any species that reproduces sexually, but not for the survival of any individual. We describe the possible role of the social decision-making network in sexual motivation whereby dopamine is involved in wanting sex, opioids are involved in liking sex, and oxytocin is involved in pair bond formation. Brain areas and neuromodulators in the social decision-making network are common across vertebrate lineage.
Summary Understanding the variables involved in sexual motivation in different species can lead to a framework of basic mechanisms of sexual motivation, and such a framework could help us understand human sexual motivation.

Keywords Appetitive behaviors · Sexual incentive motivation · Paced mating · Reward · Dopamine · Opioids · Social decision-making network

Defining Sexual Motivation

Sexual motivation in humans involves awareness, goals, and intentions [1], as well as the representation of sexual incentives (fantasies) and social learning [2]. A definition of sexual motivation that can apply to humans and animals considers sexual motivation as the mechanism activating, directing, and causing persistence of behaviors directed towards a sexual incentive [3, 4]. The stimuli that produce an approach behavior usually have rewarding properties and are called incentives [5••]. In humans, we can ask if an incentive is rewarding and we can obtain a detailed description of the physiological changes induced by the incentive, which are associated with reward. In the case of the animals, we infer the rewarding value of an incentive from the approach behavior displayed by the subject. For example, there is evidence indicating that a female rat is an unconditioned sexual incentive for a male, and the intensity of approach behavior is not increased by sexual experience [6]. This finding suggests that under adequate conditions, a receptive female will induce approach behavior by a male increasing the probability for a sexual encounter.

Although sexual motivation is considered a primary need, such as feeding, there are considerations that make sex different from other motivated behaviors. For example, in rodents, motivation to eat increases as the time without access to food increases, and the reward by feeding is correlated with this time period. In contrast, there is no evidence that the time between episodes of sexual activity is positively correlated with the motivation to mate or the sexual reward experienced [2]. Additionally, sexual activity might be totally absent in the lifespan of individuals with no relevant consequences for their survival, as is the case of non-copulating males described in several species, such as rats, mouse, rams, guinea pigs, hamsters, and gerbil [7]. These non-copulating males do not have hormonal, physiological, or behavioral alterations; they only lack motivation to mate [8–10]. It is not clear if there are non-

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copulating females. In one study, several intact females were injected with estradiol to evaluate sexual behavior in paced mating tests (see below). Depending on the time spent with a male, three different subpopulations of females were identified: "approachers," "normal" females, and "avoiders." The group of females identified as avoiders spent less time with a male and displayed fewer proceptive behaviors than the other groups. They also received fewer mounts, intromissions, and ejaculations than the normal control group, but they still displayed sexual behavior [11]. These females resemble the sexually sluggish male rats, but not the non-copulating males.

We recently reviewed the different methods used to evaluate sexual motivation in rodents [12], and there are other reviews that have addressed this topic [13–15]. In the present review, we employ a comparative approach to describe how sexual motivation is inferred in rodents and in some non-mammalian species. A general description of the neural mechanisms involved in the regulation of sexual motivation is also presented.

Evaluating Sexual Motivation in Rodents: Appetitive Behaviors, Sexual Incentive Motivation, and Paced Mating

There are different methods to measure sexual motivation. How an animal approaches a sexual incentive varies depending on the conditions and options available [4]. Early studies focused on measuring motivation with instrumental and conditioning strategies, and they have been extensively described elsewhere [13, 14]. The use of learning paradigms or other methods that are not in the natural setting of the animals, such as crossing an electrified grid to gain access to a sexual incentive for example, can add valuable insight to the study of sexual motivation, but these paradigms also represent confounding variables in the interpretation of the results. Therefore, in the present review, we focus on behaviors that occur in natural and semi-natural conditions that reflect naturally occurring behavior. We will focus on appetitive behaviors, sexual incentive motivation (SIM), and paced mating (PM), which are observed in rats, mice, and voles.

Appetitive Behaviors

Appetitive behaviors are considered as "sexual readiness" signals that attract potential sexual partners and serve to start and maintain mating. In sexually receptive female rats, appetitive or proceptive behaviors consist of a series of stereotyped motor patterns displayed to attract the attention of a male, including ear wiggling, hoping, and darting [16]. There is evidence for and against considering proceptivity as an indication of sexual motivation depending on the experimental conditions. For example, in traditional mating tests with one male and one female, behavioral studies have shown that a higher rate of proceptive behaviors is observed at the start of mating, markedly just before receiving the first intromission from the male. Proceptivity declines, but is not inhibited, as sexual stimulation continues [17–19]. If a new male is introduced, an increase in proceptive behaviors by the female is observed, evidence of the Coolidge effect in females [4, 17]. These fluctuations in the rate of proceptive behaviors once mating is initiated could indicate a change in sexual motivation as a result of the sexual stimulation received. On the other hand, studies in semi-natural conditions where several females and male rats are housed simultaneously in a large arena have shown that the transition from non-sexual receptivity to sexual receptivity in females is immediate [20•]. Proceptive behaviors appear abruptly, remain unchanged during mating and disappear in the same way as they appeared. Under this condition, both sexes are equally involved in initiating and maintaining mating, and the female is fully receptive and displays proceptive behaviors from the beginning to the end of the behavioral estrus [20•]. These observations in semi-natural conditions contrast with those in laboratory settings where one male and one female mate. For example, ovariectomized females primed with estradiol benzoate and progesterone were tested every 3 h for 12 h. The lordosis response decreased over time, and the decline in receptivity was faster in paced than in non-paced mating (non-PM) conditions [21]. The effects of repeated testing in seminatural conditions need to be evaluated because it has been shown that sexual experience alters the display of paced mating behavior [22•]. Together, these observations suggest that sexual motivation inferred from proceptive behaviors depends on the testing conditions and sexual experience.

Classical studies in males used the latency for the first mount and intromission as an index of sexual motivation. This notion was supported by conditions that induce sexual satiety, where males stop mounting females due to the reduction of sexual motivation caused by mating itself [23]. However, there is extensive evidence indicating that latencies do not reflect the intensity of sexual motivation. For example, several pharmacological treatments can reduce the latencies to initiate mating by other factors not associated with changes in sexual motivation including an increase in general activity, increase in the sensitivity of the male abdominal skin that could facilitate mounts or intromissions [4]. There are also compounds like dexmedetomidine (a noradrenergic $\alpha 2$ receptor agonist) which facilitate ejaculation latency without affecting indices of sexual motivation [24]. These results indicate that latencies are not a good measure of sexual motivation, and as we discuss below, there are other methods that directly measure sexual motivation.

In socially monogamous prairie voles, sexual motivation is expressed differently compared to other rodents, such as rats and mice. Female prairie voles do not display sexual receptivity at the time of puberty (i.e., first estrous cycle); instead,

sexual receptivity is first induced by the presence of an unfamiliar male. Estrous behavior is not induced by pheromones of familiar males, such as their fathers or brothers [25, 26]. Investigation of the anogenital area of an unfamiliar male and direct nasal contact with his pheromones for 24 to 48 h induces a surge in estrogens that leads to sexual receptivity and copulatory behavior inducing ovulation [27]. In this species, mating for 6 h or cohabitation without sexual interaction for 24 h, with an unfamiliar, unrelated vole from the opposite sex induces pair bonding. Pair bonding is characterized by a clear preference for the mating partner, selective aggression towards other males or females, and biparental care of the offspring.

Currently, appetitive behaviors such as pursuit and approach to the female or the male by conspecific of the opposite sex are considered more reliable measures of sexual motivation than those involving some type of learning or instrumental conditioning [6], even in the absence of any physical contact between the subjects and the stimulus animals. In fact, approach and appetitive behaviors allow a more direct measurement of sexual motivation, using paradigms where animals are not able to physically interact, such as the SIM test [6].

Sexual Incentive Motivation (SIM)

According to the incentive salience model, sexual motivation can be triggered by sexual stimuli or cues that the individual perceives as rewarding [4]. Once an animal is in contact with the sexual stimulus, the neural representation of the incentive activates approach behavior. With subsequent encounters, rewarding experiences make the incentive more attractive, wanted, and pursued [28–30]. This process is influenced by a complex relationship between the animal's internal state (i.e., hormone levels, age) and the characteristics of the incentive [1, 4, 31••].

Based on this model, the SIM test evaluates the time spent by subjects in the vicinity of two simultaneously presented incentives with different characteristics such as a sex (male vs female) or hormonal condition (gonadally intact vs gonadectomized). In this way, the experimental subject moves throughout the arena spending more time near the stimulus animal that he or she finds more attractive. The subjects can smell, see, and hear the stimulus animals, but there is no physical contact because the incentives are confined in cages located in opposite sides of the arena, separated by a wire mesh [19]. Rats with optimal gonadal hormones levels spend more time in the vicinity of a sexual over a social incentive. In addition, subjects (male or female) that have recently mated spent less time near a sexual incentive indicative of reduced sexual motivation [19]. In contrast to the partner preference test where subjects interact physically and mate [32], the SIM test has the advantage of evaluating the intensity of approach behaviors towards a sexual incentive without the confounding variables associated with the execution of sexual behavior.

Recently, using the SIM test, it was demonstrated that ultrasonic vocalizations (USV) do not have incentive value for rats [33•, 34]. This is consistent with the observation that devocalized animals mate normally, suggesting that vocal cues are not crucial for sexual motivation [35]. A detailed study evaluating the role of different sensory modalities to determine the stimuli required to induce approach behavior showed that a single sensory modality, olfaction, vision, or audition is not sufficient to induce approach behavior for a sexually receptive female rat. However, the combination of two sensory modalities, among which olfaction is crucial, is necessary to induce approach behavior by a male rat for a sexual incentive over a social incentive, suggesting that cooperative functioning of two sensory modalities is necessary to induce approach behavior for a potential mate [36]. Sexual incentive motivation has also been studied in mice. Ovariectomized female mice were tested with a gonadectomized male mouse (i.e., social incentive) and a gonadally intact male (i.e., sexual incentive). Females in this hormonal condition prefer equally the social and sexual incentives [37]. Hormonal replacement with estradiol and progesterone increases sexual incentive motivation but not social motivation [37]. Contrary to the description in rats where USV are not sufficient to induce approach behavior, in male mice, the emission of USV attracts females [38, 39]. Male mice emit longer and simpler calls and sequences when they sing to females, but they emit complex calls when they are exposed to female urine. Female mice show a clear preference for complex songs or vocalizations. Chabout and collaborators propose that complex songs can be used to lure females and the simpler sequences are used for direct courtship attracting females to come closer, facilitating sexual interaction [40].

The evaluation of SIM is a better method to directly evaluate sexual motivation than those involving some type of learning or than those in which the execution of the behavior is present, like in the partner preference test in which physical interaction is allowed. When SIM is evaluated, no variables such as learning or mating interfere with the interpretation of the intensity of approach behaviors towards a sexual incentive, that is sexual motivation. The same can be measured in partner preference tests in which no physical interaction is possible.

Paced Mating (PM)

Classic studies evaluating sexual interactions in the wild [41] or in large mating spaces resembling semi-natural conditions [42] have shown that mating in rats is promiscuous and occurs in groups, where both males and females mate and control the rate of sexual stimulation. During group mating, several males are present and estrus is synchronized in females living

together [43]. Males and females mate with several partners repeatedly changing partners in the middle of copulation [44]. In females, an ejaculation is not necessarily preceded by several intromissions because she can start mating with a male that had already been mating with other females. The male could be in the middle or at the end of a copulatory series; therefore, he could display few intromissions with any given female before ejaculation. As such, a female can receive mounts, intromissions, and ejaculations from the same or from different males. In rats, males can mount and intromit with the same female until ejaculation or they can mount and intromit with different females, which is usually the case, until ejaculation [44–46]. Therefore, in group mating, although both sexes can have a different temporal pattern of copulation, males and females both control (i.e., pace) the rate of the sexual interaction by having multiple mates available at any given moment.

In laboratory conditions, different methods are used to evaluate PM. For example, bilevel chamber studies in rats allow the female to move from one level of the cage to the other with the male following closely behind [47]. The method to evaluate PM that is most extensively used and where physiological advantages have been described in detail is the one developed by Mary Erskine [48]. In this method, the mating cage is divided by a partition with a hole in the middle that allows the female, but not the male, to go from one compartment to the other. The male cannot follow the female because of its larger size. Cages with four holes and where the male is trained not to cross to the other compartment are also used to evaluate PM behavior [49, 50]. The physiological and behavioral advantages of PM over non-PM have been extensively described [51–53]. Briefly, when females pace the sexual interaction, they required fewer intromissions to get pregnant or pseudo-pregnant and they secrete higher levels of prolactin than when they cannot control the rate of the sexual interaction [51]. The interval between intromissions is longer when females pace the sexual interaction, and the latency to return to the male side is longer after an ejaculation than after an intromission. In addition, the return latency after an intromission is longer than after a mount. These observations indicate that females that pace the sexual interaction can differentiate the intensity of the stimulation they receive [51].

When the subjects mate without the barrier, the male paces the rate of the sexual stimulation. Using this paradigm, we have shown that only when subjects (males or females) pace the sexual interaction, a positive affective, reward state is induced, as evaluated by the conditioned place preference (CPP) paradigm [54]. The positive affective or reward state in animals is inferred from the approach behavior by the subject to an incentive. In the case of CPP, the subjects change their original preference for a compartment after conditioning with a putative rewarding event, in this case sexual behavior. We assume that the association of the physiological state induced by the rewarding stimulus (i.e., mating) induces an approach behavior that reflects a CPP [52]. The reward state induced by PM is mediated by opioids, reviewed in [5••]. The systemic administration of the opioid antagonist naloxone in male [55] and female [56] rats blocks the reward state induced by mating. Moreover, infusion of naloxone into the medial preoptic area (MPOA) in males [57] and into the MPOA, the ventromedial hypothalamus (VMH), or the amygdala (AMG) in females [58] blocks the reward state induced by mating, suggesting that these brain regions are part of a neural system involved in sexual reward.

In rodents, the appropriate selection of a mating partner and the display of sexual behavior depend on the integrity of the olfactory system and its connections with other brain regions. The formation of new neurons in the adult brain, a process known as neurogenesis, is produced in the dentate gyrus of the hippocampus and the subventricular zone (SVZ)-rostral migratory stream (RMS)-olfactory bulbs (OB) system of mammals. The cells born in the SVZ migrate for 2 weeks through the RMS until they reach and integrate in functional circuits of the OB (reviewed in [59, 60]). In a series of studies, we have tested if sexually relevant odors and mating induce changes in these neurogenic regions. We have shown that sexual behavior in rats induces multiple effects on proliferation and neurogenesis along the SVZ-RMS-OB system, a detailed description can be found elsewhere [61••]. When males or females pace the sexual interaction, a higher number of cells and/or neurons are observed in the RMS and different layers of the main and accessory olfactory bulbs. The cells and/or neurons are labeled the first time the subjects mate and are observed 15 or 45 days later after they migrate and incorporate into functional pre-existing circuits in the OB [61••], a brain region crucial for the expression of sexual behavior. Interestingly, the neurogenesis induced by sexual behavior is blocked by the administration of naloxone [62]. Together, these results indicate that pacing sexual interactions induces long-lasting plastic changes, specifically neurogenesis in the OB. The release of opioids during sexual behavior could contribute not only to the reward state induced by mating, but opioids might participate in the long-lasting plastic changes during neurogenesis in the SVZ-RMS-OB system. Additional studies need to determine the role of the new cells/neurons induced by mating; a possible role could be enhancing motivational processes to assure that the behavior will be repeated in the future enhancing the probability of the survival of the species. Furthermore, we need to determine the type of these new cells/neurons induced by mating.

The effects of pacing the sexual interaction in female mice have been evaluated in laboratory conditions. Contrary to what is observed in rats, where females are smaller than males, male and female mice are about the same size and therefore a barrier with holes will not allow the female to pace the sexual

interaction because the male could follow her. Therefore, for mice, the mating cage is equally divided by a small barrier and the male is tethered to one side of the cage by a collar around his neck allowing free movement only in one side of the cage. The female is free to move between both compartments by jumping or climbing over the barrier escaping and avoiding the male [63]. A limitation of this test is that the male is constrained, and this can affect the display of normal sexual behavior. Using this procedure, it has been demonstrated that female mice take longer to return to the male after an ejaculation, in comparison with the return latency after a mount or an intromission, observations which are consistent with what is observed in rats. However, the return latency after an intromission and a mount does not differ. Females in the non-PM condition receive more mounts than females in the PM condition [63].

In socially monogamous prairie voles, we demonstrated that mating, in an acrylic cage without a divider for 6 h or mating until one ejaculation, induces a reward state, as evaluated by CPP, in males but not in females. This reward state is mediated by opioids, facilitating pair bonding formation [64]. Thus, in male voles, sexual stimulation to one ejaculation or 6 h of mating contributes to the formation of long-lasting bonding. In this condition, where the male paces the sexual interaction, females do not develop a reward state, but they do pair bond. When PM conditions and non-PM conditions are compared in female voles, no significant differences are observed in latency to start mating, in the duration of mating, the number of mating bouts, percentage of pairs that mated, or litter size [65••]. Additional studies are needed to determine if PM behavior is rewarding or a less stressful experience for female voles. It also needs to be evaluated if a longer cohabitation time induces a reward state in female voles.

Measuring Sexual Motivation in Other Non-mammalian Species

In other species, different behaviors associated with reproduction can be used to infer sexual motivation. Most of these observations have been done in natural or semi-natural conditions, and their interpretation as sexually motivated behaviors is unclear. The examples describe below illustrate the variety of behaviors that favor reproduction using different strategies. For example, in female mosquito fish (*G. holbrooki*), preference for a male mosquito fish changes with sexual experience and depends on the social context. Sexually experienced females prefer males that exhibit moderate sexual activity and avoid highly sexually active males when only one female is present with a male. However, if several females mate with males that display moderate or high sexual activity, females show a clear preference for the highly sexually active males [66]. Frequent and intense mating can lead to genital trauma, decreases foraging efficiency, and increases predator risk [66].

In some fish (*Poecilia reticulata* and *mexicana*) and sand gobies, females prefer to mate with dominant high-quality males that display bright colors and are larger. However, this preference changes in the presence of predators when smaller and paler males are preferred [67, 68].

Sexual motivation also depends on the reproductive state of the animals. During the reproductive season (late May–Jun), male midshipman fish build and defend a nest; they also call or hum to attract the females. Only gravid females (i.e., females ripe with eggs) are strongly attracted to the hum (phonotaxis) [69]. This auditory cue allows them to localize the male and deposit their eggs in the male's nest. Once the females release all their eggs, they leave the nest and only the male takes care of the offspring [70].

In the female quail, proceptivity and sexual motivation can be evaluated by hopping and darting, approaches, and pecking (i.e., gentle pecks at male flanks). These behaviors initiate or increases male sexual activity. Sexually receptive females spend more time close to a sexually active male and prefer him over another female; this component of sexual motivation is estrogen dependent [71].

From the above described experiments, it is clear that sexual preference in fish is influenced by different factors including sexual experience, sexual activity display by the males, social hierarchy, and the presence of predators. In birds, sexual motivation can be evaluated by hopping, darting (as in rats), by pecking, and as it will be described in the following section by singing, which induces CPP.

Neural Regulation of Sexual Motivation

The social decision-making network is a large system that integrates important processes for an individual's adaptation and survival within the environment [72]. In this system, two important brain circuits convey, with homology in different vertebrate lineages, and integrate external and internal stimuli: the social behavior network (SBN), important in the regulation of sexual behavior; and the mesolimbic reward system, important for reward, including reward associated with sexual incentives. The SBN includes brain areas such as the MPOA, the AMG, the anterior hypothalamus, and the VMH; the mesolimbic reward system includes the ventral tegmental area (VTA) and nucleus accumbens (NAcc) among other brain regions [72, 73]. These two circuits contribute to various aspects of sexual motivation.

Depending on the information and nature of the stimuli received, an individual can display a specific motor response through NAcc projections to the basal ganglia, which are involved in voluntary musculoskeletal control [1, 74]. In the presence of a potential sexual partner, an individual's internal state will activate visceral and motor responses to approach the sexual incentive. If mating occurs, sexual reward will

induce associative learning which in turn facilitates the repetition of the behavior in the future [5••].

During this process, at least three main neuromodulators act in different brain areas localized in the social decision-making network: dopamine (DA) in "wanting" that induces approach behavior or motivation [28, 29], opioids in reward [5••], and oxytocin in sexual motivation and pair-bonding; the latter important in monogamous species such as prairie voles.

Studies that evaluate appetitive behaviors have found that the MPOA is a key brain area regulating sexual motivation [75]. For example, non-copulating male rats, which do not present any hormonal or physiological alterations but only a lack of motivation to mate, have a lower aromatase expression in the MPOA [76] compared to copulating males. Moreover, testosterone or estradiol implants into the MPOA induce sexual activity in these non-copulating animals [77]. Classic studies in females have shown that lesions of the MPOA increased lordosis response, but when given the chance to pace the sexual interaction, females avoid the male and do not mate indicative of reduced sexual motivation to mate after the lesion [50, 78]. The NAcc is also important for sexual motivation: DA is released in anticipation and prediction of reward [28, 29]. For example, classic studies using in vivo micro-dialysis in male [79, 80] and female rats [81] showed that there is DA release in the NAcc with the presentation of a sexual partner behind a wire mesh. In males, DA release is higher when mating starts and decays gradually [79, 80], whereas in females, extracellular DA increases just before intromissions, but only during PM conditions [82]. More recent studies have shown that sexually experienced male rats have higher extracellular DA levels in the NAcc after they are exposed to odors from sexually receptive females, in comparison to sexually naïve males [83]. However, both groups also showed a DA release when exposed to male odors, indicating that DA participates in other contexts, such as expectation of social behavior [84]. Other experiments using mutant male mice with low expression of the DA transporter, resulting in higher DA levels in the synaptic space, show an increased expectation or wanting for a sweet reward [85]. Moreover, different events enhance DA release in the NAcc, among them eating and drinking, as well as other motivated contexts, even aversively motivated contexts, such as during tail pinch, restraint stress, foot-shock, social defeat, and aggressive encounters (see [86] for a review). Together, these results indicate that DA is involved in the wanting response for different motivated behaviors.

In female rodents, mating is largely dependent on gonadal hormones [87]. During behavioral estrus, when females are sexually receptive, females show higher extracellular striatal DA levels, than during non-receptive days [88]. The sequential estradiol and progesterone administration modifies D1/D2 receptors ratio and receptor binding, in relevant brain areas such as the MPOA. This functional change induced by hormones in specific brain regions such as the MPOA may contribute to the modulation of sexual motivation. Neurons of the MPOA discharge when females display proceptive behaviors but are inactive when females receive intromissions [89].

As described above, mating induces a reward state that is mediated by opioids in both male and female rats [5••]. Opioids also modulate the long-lasting plastic changes that induce the formation of new cells and neurons in the ventricular zone, rostral migratory stream olfactory bulb system [61••]. The opioid system also participates in other motivational processes. For example, in male rats, the administration of the μ-opioid receptors agonist, DAMGO (D-Ala [2], *N*-MePhe [4], Gly-ol-enkephalin) into the central nucleus of the amygdala enhances the incentive value of food and an antagonist reduces it [90, 91]. When DAMGO is administered in the dorsolateral striatum, the incentive value of cues related to food reward are increased in subsequent presentations [92•]. Taken together, these results suggest that opioids are released during naturally occurring behaviors, inducing a reward state thus increasing the probability that the behavior will be repeated.

There is also evidence in birds demonstrating the important role of DA, opioids, and the MPOA in sexual motivation. In some birds, songs induce sexual motivation. At the onset of the spring breeding season, female starlings (*Sturnus vulgaris*) search for nest sites and are attracted to a male courtship song [93, 94]. Courtship songs are rewarding to females because they can associate a reward state with a chamber in which they heard a male courtship song. Thus, courtship can induce a positive affective reward state [95]. Interestingly, some female starlings do not explore or defend nest locations and these females are not attracted to male courtship songs [95, 96]. Infusion of the opioid receptor antagonist naloxone into the MPOA (analogous to the MPOA in rodents) of male starlings increases courtship singing in low-singing birds suggesting that high density of mu receptors in the MPOA actively suppresses singing in these males. However, the same treatment in high singing birds decreases song production. The authors suggest that these effects are due to the inverted U-shaped relation between opioids and behavior, whereby opioid-dependent behaviors are observed at high rates when opioids are released at intermediate levels. If high or low levels of opioids are released, opioid-dependent behaviors are produced at low rates [97••]. In female starlings, opioid labeling with met-enkephalin-positive cells in the VMN (analogous to the VMN in rodents) correlated positively with the reward state, as evaluated by CPP, induced by hearing male courtship songs [95]. In females, the administration of a non-selective dopamine reuptake inhibitor (GBR-12909) increases the time females responds to a non-biologically relevant cue such as the song of a different strain male (Purple Martin song) [96]. In Japanese quail, the activation of

dopamine (DA) D1 and D2 receptors in the MPOA facilitates rhythmic cloacal sphincter movements. These movement increases when the male has visual contact with a female. Extracellular DA in the MPOA is released in male quail anticipating contact with a female [98, 99]. In addition, consummatory sexual behaviors, such as neck-grab, mount attempt, mount and cloacal contact movements, are facilitated by activation of the D1 and D2 receptors [98]. From the above described data in rodents and birds, it could be argued that DA participates in the consummatory aspects of mating, whereas opioids are involved in the reward state associated with mating in birds. A similar hypothesis has been presented for rats [5••], which is also consistent with the wanting and liking hypothesis presented before by Berridge and Robinson [100].

The role of oxytocin in sexual motivation in rats has also been studied. The systemic administration of an oxytocin receptor antagonists in males reduced the amount of time spent with a receptive female [101]. Another study evaluated the role of oxytocin and vasopressin in mate guarding behavior in which female rats that mated for the first time display guarding behavior for a male when another competitor female is present. Female rats displaying mate guarding behavior had more double label cells for Fos and oxytocin in the supraoptic and paraventricular nuclei. Moreover, administration of oxytocin or vasopressin increased mate guarding behavior. The authors suggest that the first sexually rewarding experience in females induces changes to bonding networks in the brain, when paired with the same male [102].

In voles, mating induces the release of oxytocin and DA, allowing the female to associate the cues of the partner with mating, producing pair bonding. In this species, pair bonding depends on the activation of brain structures such as the bed nucleus of the stria terminalis, the MPOA, the NAcc, the AMG, and the VTA [103, 104•].

Figure 1 illustrates the brain areas involved in different aspects of sexual motivation and the role of DA, opioids, and oxytocin. The mesolimbic reward system could be activated by a sexual incentive that, after DA release, will induce approach behavior. If the approach behavior eventually leads to mating, the release of opioids in brain regions of the SBN would induce a reward state. The connections between both components of the system (i.e., the SBN and the mesolimbic reward network) will associate the cues of the incentive with the reward state, increasing the probability of repeating the behavior in the future. When the subject encounters the same incentive again, or another one with similar characteristics, DA may activate a wanting response (approach behavior to an incentive; motivation) through the mesolimbic reward system in anticipation of opioid release and the "liking" response (reward state). In the case on monogamous species, like the prairie vole, the release of DA and opioids induces the release of oxytocin facilitating pair bonding.

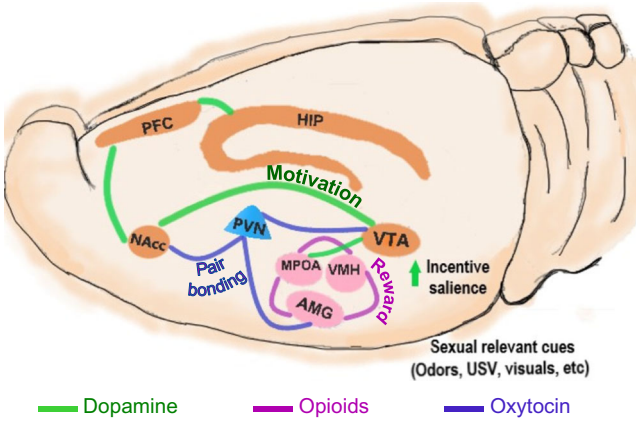

Fig. 1 A representative model of the neurobiology of sexual motivation, sexual reward, and pair bonding processes. Brain areas that are part of the mesolimbic reward system (MRS, in orange) and areas from the social behavior network (SBN, in pink) converge in the social decision network, important for an individual to recognize and respond to potential sexual partners and in subsequent encounters. This network regulates motivation to mate, mainly through dopamine actions on the MRS. Once mating occurs, a sexual reward state is induced by opioid release in structures of the SBN (AMG, VMH, and MPOA). For monogamous species, pair bonding is facilitated by mating and oxytocin release from the PVN and the activation of brain areas including the NAcc, the AMG, and the HVM. PFC prefrontal cortex, HIP hippocampus, NAcc nucleus accumbens, PVN paraventricular nucleus of hypothalamus, MPOA medial preoptic area, VMH ventromedial hypothalamus, AMG amygdala

Conclusions

Different models are used to understand sexual motivation, defined as the mechanisms that direct behavior towards a sexual incentive. Many models use learning tasks or methods such as crossing electrified grids that are not in the natural setting of the animals, adding confounding variables to the interpretation of the results [12]. The possibility of studying behaviors or components of sexual motivation that occur in semi-natural or natural conditions such as appetitive behaviors, sexual incentive motivation, and PM can give us more direct information of the mechanisms controlling sexual motivation.

Evidence from different lines of evidence demonstrates that the release of DA in the social decision network induces an approach behavior and the release of opioids induces a reward state, increasing the probability of repeating the behavior in the future with the same or a similar incentive whereby DA activates the wanting response and opioids the liking response [100].

Evidently, the factors influencing human sexual motivation are more complex than those involved in animals. In humans, there are numerous sociocultural factors and beliefs that profoundly modulate different motivations to engage in sex [2, 105]. Humans have the capacity to have high levels of sexual motivation, even in the absence of a sexual partner, from thoughts, fantasies, and mental representations of what is

sexually attractive with large variations between people and cultures [2]. Despite these differences, there are many analogies between sexual behavior in humans and animals that have been described and discussed in detail before [14, 105]. The possibility to understand the mechanism involved in sexual motivation in different species can lead to a framework of basic mechanisms to further understand human sexuality.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflicts of interest.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

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