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Sexual behavior in ewes and other domestic ruminants

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Abstract

Similarities as well as differences across species in the control of sexual behavior are helping to fully understand the subtle relations between physiology and eco-ethological constraints and how the brain integrates such information. We will illustrate this with sexual behavior in domestic ruminants and especially ewes. Females of these species like humans, but unlike rodents, have a long luteal phase. A prolonged exposure to progesterone (Pg) before the preovulatory estradiol rise is necessary for estrous behavior to be displayed. Estradiol action and receptor localization is very similar to that observed in other species. But not too surprisingly, the role of Pg is rather different with a priming effect not observed in rodents. However, as in rodents, Pg also has an inhibitory effect, is necessary for the display of proceptivity and is responsible for the timing of the different periovulatory events.

These steroids act on the central nervous system in similar areas across mammalian species to regulate estrous behavior. Steroid fluctuations during the estrous cycle cause changes in catecholaminergic activity in the hypothalamus. Interestingly, these neurotransmitters seem to have very similar effects in ewes and rats as illustrated by the norepinephrine rise after male–female interactions observed in both species. Similar comparisons can be made regarding the action of some neuropeptides, including oxytocin and GnRH, and more integrative processes like sexual differentiation and modulation of reproduction by social interactions. Data on sheep, goats and cows will be compared with those of rodents.
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In all mammals, reproduction depends on internal fertilization of a female gamete by a male one. To achieve this, a male and female of adequate reproductive status have to come into close contact. This is only possible through a coordinated control of the pairing which will bring the male and female together at a time when the production of mature gametes has occurred. It is not surprising therefore, in evolutionary terms, that the mechanisms underlying the control of these events are very similar across species. Yet along with these similarities, important variations among species occur. Understanding the similarities and differences among species and why they exist will increase our knowledge of the basic principles governing the control of sexual behavior. The aim of this paper is to review the data on the neuroendocrine control of sexual behavior in ewes and to compare them with data in related species such as goats or cows as well as rodents.

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Description of sexual behavior

Behaviors leading to internal fertilization are obviously very different across species. They vary according to the anatomy of the sexual partners and to the physical and social environment in which this behavior takes place. Generally, related species looking very much alike and sharing the same eco-ethological conditions present very similar types of behaviors.

Social context

In domesticated ungulates as well as in laboratory rats, reproduction is regulated by human intervention. However, in most species it only occurs in a specific social context. In wild or feral types of the domesticated ruminant species, males and females live most of the year in segregated unisex troupes (Alexander et al., 1980). Male and female groups come together during the breeding season. They then form a multimale–multifemale group in which reproduction is of the promiscuous

type. Estrous females may mate with several males during one estrous period and males may mate with several females on the same day. This type of reproduction is also seen in laboratory rats when observed in a semi-natural environment approaching that of the field (McClintock and Anisko, 1982). Changes in partners in Norway rats, can even occur within one copulatory sequence.

Reproduction, however, does not occur at random. In feral sheep and goats (Mc Taggart, 1971; Grubb and Jewell, 1973), mountain sheep or goats (Geist, 1965, 1968), and American bison (Lott, 1981), males engage in numerous fights at the onset of the breeding season and form a hierarchy. Most estrous females mate with the dominant male, generally the oldest and the strongest. Subordinate males, however, are rarely totally excluded from reproduction. A similar observation has been made in domestic sheep when a clear social order is evident among males, which is not obligatory. If the dominant male is infertile this can lead to a significant decrease in the proportion of pregnant females in the flock (72% versus 91%; Fowler and Jenkins, 1976). Some competition can also be observed among females. In a mixed sex group of ungulates, estrous females often gather about the dominant male and form a sort of harem competing with other females for male attention. However the competition between females of these species rarely results in the exclusion of subordinate females from reproduction.

Behavioral patterns

In domestic ruminants and in most mammals, as Beach (1976) proposed, it is helpful to distinguish 3 components in female sexual behavior: attractivity, proceptivity and receptivity. Attractivity refers to the female's value as a sexual stimulus whereas proceptivity consists of appetitive activities shown by females. Attractivity depends on stimuli passively emitted by females as well as on female behavior. To differentiate attractivity from proceptivity we will consider in attractivity only the non-behavioral stimuli.

In feral or mountain sheep and goats, males leave their group to look for females when the breeding season is approaching (Grubb and Jewell, 1973; McDougall, 1975; Dunbar et al., 1990). What is responsible for this attraction is not clear but it is probably not an estrous-specific attractiveness. Mating only occurs several weeks after males have joined the female group (Grubb and Jewell, 1973) which suggests that when males moved, the females were still not cycling. In fact, it is likely that, as in domestic sheep and goats (Martin et al., 2004), reindeer (Shipka et al., 2002), or muskox (Rowell et al., 2003) the sudden exposure of an anoestrous female to males is responsible for the onset of seasonal cyclicity, a phenomenon called the male effect. Preference for specific females has been shown in cattle and sheep (Hayman, 1964; Lees and Weatherhead, 1970; Rouger, 1974). Tilbrook and Lindsay (1987) found that one of the reasons for this preference in sheep is that females differ in their attractiveness, an attribute which is relatively stable from one cycle to the next and independent from the dose of estradiol used to induce estrus. Olfaction is certainly important as sexually experienced rams and bulls are able to discriminate between the smell of an estrous female and a non-estrous one just as rats do (Carr et al., 1966; Stern, 1970) and anosmia impairs ram partner seeking activity (Fletcher and Lindsay, 1968). The shape of the female and the context of the interaction also matters (Rouger, 1974; Tilbrook and Lindsay, 1987). In any case, the most important cue for attracting males is the females' proceptive behavior.

An increase in motor activity is observed in most female ruminants as well as in rodents when estrus starts. At that time, cows, goats and ewes tend to leave the main flock and look around for males. This increase in walking activity in cows is even seen within a unisex group and is used in some dairy farms to detect estrus (Senger, 1994). The ram seeking activity of ewes is frequent: 75% of estrous ewes display it and older females display it more than nulliparous ones. Ewes employ sight and not smell to seek out and locate rams (Fletcher and Lindsay, 1968) and estrous ewes in a two choice test will choose to approach a male or a life sized picture of its face whereas anestrous females prefer the female (Kendrick et al., 1995).

In addition to this searching behavior, females can display specific behavioral patterns which will increase the males' interest as with hopping and darting in rats. Cows and goats, when in estrus are agitated, vocalizing and gathering with other estrous or proestrous females into a "sexually active group"(Blockey, 1978). Within this group, females display male-type courtship behavior and reciprocal mounting. This behavior attracts males and stimulates sexual activity in bulls and male goats (Blockey, 1978; Geary and Reeves, 1992; Shearer and Katz, 2006). Ewes on the contrary, are rather undemonstrative in their display of estrus. Apart from their seeking activity, they only express a few motor patterns such as a movement of the head toward the male, and tail fanning, but the main display that they show is just to stand still near the male (Banks, 1964). In sheep as in rats, the expression of this proceptive behavior is of major importance when males are not highly motivated or when many females are in estrus at the same time (Lindsay and Fletcher, 1972; Madlafousek et al., 1976). This can explain the reduced fertility of young ewes when in a large group with older females (Edey et al., 1978; Dyrmundsson, 1981).

For internal fertilization to occur in mammals, the two partners need to be in close contact and in a proper orientation and this is only possible if the female remains still. The receptive behavior of the ewe, the female goat or the cow in estrus only consists of an "active immobilization" during which the female will resist if you try to push her (Alexander et al., 1980). There is no pattern such as the lordosis of rodents, just a slight arching of the back during immobilization. In ewes as in does, immobilization is a sign both of proceptivity and receptivity. In the ram, the male goat and the bull, ejaculation generally occurs after the first intromission and only lasts a few seconds (Alexander et al., 1980). There is no need for a series of intromission although the reproductive success of the ewe is enhanced if mating occurs more than once (Synnott et al., 1981). So the amount of vaginal stimulation is very limited in these species, contrary to what occurs in rodents. In ruminants, as in rodents, it seems that the duration of the estrous period is reduced by abundant behavioral interactions with the male (Erskine, 1985; Fletcher and Lindsay, 1971; Romano and Fernandez Abella, 1997).

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