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Sociosexual stimuli and gonadotropin-releasing hormone/luteinizing hormone secretion in sheep and goats

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Abstract

Sociosexual stimuli have a profound effect on the physiology of all species. Sheep and goats provide an ideal model to study the impact of sociosexual stimuli on the hypothalamic-pituitary-gonadal axis because we can use the robust changes in the pulsatile secretion of luteinizing hormone as a bioassay of gonadotropin-releasing hormone secretion. We can also correlate these changes with neural activity using the immediate early gene *c-fos* and in real time using changes in electrical activity in the mediobasal hypothalamus of female goats. In this review, we will update our current understanding of the proven and potential mechanisms and mode of action of the male effect in sheep and goats and then briefly compare our understanding of sociosexual stimuli in ungulate species with the "traditional" definition of a pheromone.

Keywords: Pheromones; Olfactory; Reproduction; Kisspeptin; GnRH; LH

1. Introduction

All mammals, particularly those that live in large groups, are immersed in a rich and complex social environment that is full of the sights, sounds, and smells of their neighbors, mates, and offspring [1]. These sensory inputs, the sociosexual signals, can profoundly alter many physiological and behavioral processes, including reproduction [2,3]. For example, in both female and male ungulates, exposure to a prospective mate induces an almost immediate increase in gonadotropin-releasing hormone (GnRH)/luteinizing hormone (LH) secretion, phenomena termed the "male effect" and "female effect," respectively (Fig. 1). Olfactory signals, often called "pheromones," are among the most potent of the sociosexual stimuli and can stimulate GnRH/LH secretion and induce ovulation in females, even in the absence of additional sociosexual stimuli [4–6]. Changes in GnRH secretion into the hypophyseal circulation have not been measured directly in female sheep or goats exposed to males. However, the well-established relationship between GnRH and LH secretion [7] makes the measurement of LH secretion in the peripheral circulation a reliable bioassay of GnRH secretion. Nonolfactory stimuli also help to achieve the optimum neuroendocrine and ovulatory response of females to males [8–10], but recent work has shown that these stimuli play a relatively minor role and are unable to substitute for the full complement of sociosexual stimuli in sheep or goats [10–12]. The field of pheromone research has evolved dramatically since the initial concept of pheromones was proposed by Karlson and

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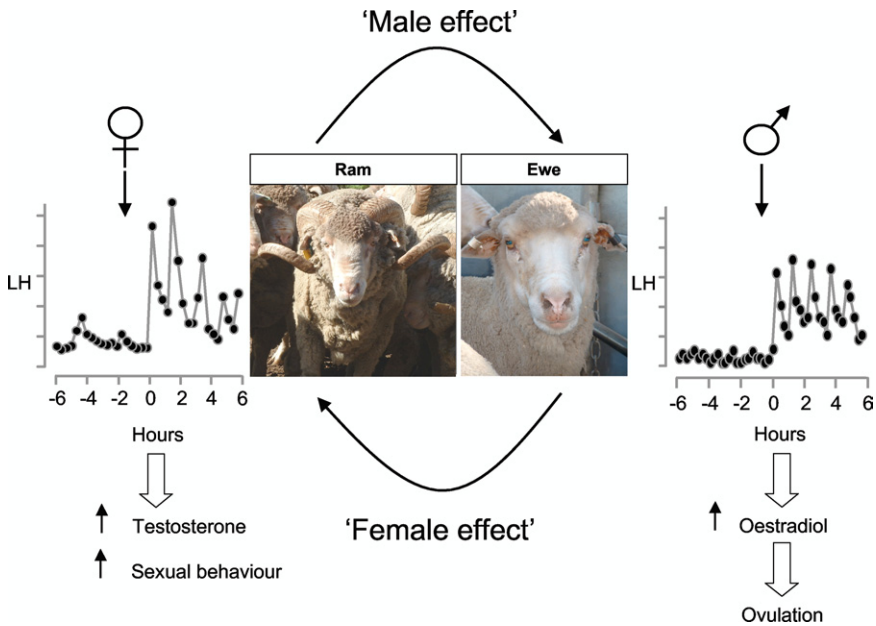

Fig. 1. Schematic representation of the impact of sociosexual stimuli from a prospective mate on the reproductive physiology of female sheep (the "male effect") and male sheep (the "female effect").

Lüscher [13], with the emergence of pheromone feedback loops between GnRH neurons and regions of the brain responsible for olfactory processing [14], increasing evidence of convergence between the main and accessory olfactory systems [15], and the proposed distinction between pheromones and olfactory signatures [16]. Even in the early 1980s, there was sufficient evidence for Martin et al [2] to question whether the male pheromone in sheep and goats "fits" the traditional definition of a pheromone. In this review, we will update our current understanding of the mechanism and mode of action of the male effect in sheep and goats and then briefly expand on the discussion outlined by Delgadillo et al [17] on how the male pheromone in ungulate species compares with the "traditional" definition of a pheromone.

2. Mechanism

It is logistically difficult to study the mechanism through which sociosexual stimuli impact GnRH secretion because of the sheer complexity of the phenomenon. For example, the time course of the neuroendocrine response of females to males stems from an initial "acute" response (0 to 6 h after initial exposure to males; Fig. 1) to the changes in LH and estradiol secretion that precede the preovulatory surge of LH and ovulation [2]. The nature of sociosexual stimuli is wide ranging and female responsiveness is markedly affected by the method of exposure (ie artificial simulation with visual images compared with exposure of anosmic females to males) [9,11] and is not necessarily driven by the odors that we, as humans, associate with males [18]. It can also be difficult to differentiate between stimulation associated with social stimuli (ie identification of familiar or novel conspecifics or offspring) [review; 19] and sexual stimuli (ie male pheromone). This complexity is perhaps the reason why few studies have attempted to conclusively identify the mechanism driving the impact of sociosexual stimuli on GnRH secretion. Histologic assessment of neural activation is a particularly useful technique to study the impact of sociosexual stimuli on GnRH secretion because the neural response to an internal or external stimulus can be quantified using the immediate early gene *c-Fos*. The Fos protein is only present in the nucleus of recently activated cells for up to 2 h after the initial stimulation, so we can use immunohistochemistry or in situ hybridization to map the time course of neural activation relative to a given stimulus [20–22]. In this section, we will summarize our current understanding of the proven and potential mechanisms involved in mediating the effects of sociosexual stimuli from males on the reproductive axis of sexually experienced female sheep and goats (Fig. 2).