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Sexually active bucks are a critical social cue that activates the gonadotrope axis and early puberty onset in does

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ABSTRACT

In rodents, early exposure to adult male is well known to induce an early puberty in females (Vandenbergh effect). This phenomenon has been less studied in other mammals. In goats, despite our extensive knowledge about the “male-effect” phenomenon in adults (i.e. ovulation induced by the introduction of the male during the anestrous), there are few data on the consequences of an early exposure of females to males. Here, we evaluated the puberty onset of young alpine goats when raised since weaning with intact bucks (INT), with castrated bucks (CAS) or isolated from bucks (ISOL). The INT group had the first ovulation 1.5 month before the two other groups. Despite the earlier puberty the INT group of females had normal and regular ovarian cycles. Morphological study of the genital tract showed that at 6 months, uterus of INT goats was 40% heavier than CAS and ISOL goats. Moreover, INT females had a myometrium significantly thicker and INT was the only group having *corpora lutea*.

In our study, INT females were pubescent in the month following the entry of bucks into the breeding season, suggesting that only sexually active bucks provide the signal responsible for puberty acceleration. By removing direct contact with the bucks, we showed that somatosensory interactions were dispensable for an early puberty induction.

Finally, no difference in the GnRH network (fiber density and number of synaptic appositions) can be detected between pubescent and non-pubescent females, suggesting that the male stimulations triggering puberty onset act probably on upstream neuronal networks, potentially on kisspeptin neurons.

1. Introduction

Puberty is a complex process that requires morphological, physiological and behavioral modifications that render individuals able to reproduce (Ebling, 2005). During puberty, the hypothalamic-pituitary-gonadal (HPG) axis, which remained quiescent since childhood, is reactivated leading to the secretion of gonadotropin-releasing hormone (GnRH). GnRH stimulates the secretion of gonadotropin, leading to the onset of the cyclical ovarian activity in females (Grumbach, 2002).

Many factors, including genetic, metabolic and environmental influences, can affect the age at puberty (Bronson and Rissman, 1986; Dýrmundsson, 1981). Among environmental factors, interactions with conspecifics of the opposite-sex can dramatically modulate the dynamics of the onset of puberty. Indeed in rodents, pre-pubertal exposure to an intact male or to its odor induces an acceleration of puberty onset in females; this phenomenon is known as the “Vandenbergh effect” (Vandenbergh, 1976, 1969, 1967). By contrast, exposure to a castrated male has no impact on the age at puberty, suggesting that stimulating signals from the male are androgen-dependent (Jouhanneau et al., 2014; Vandenbergh, 1969).

In rodents, the most common non-invasive measure used to determine the age at puberty is the timing of vaginal opening (Rodriguez et al., 1997). However, this measure is not the best predictor of the attainment of puberty because the first ovulation is not well correlated with vaginal opening (Safranski et al., 1993). In larger mammals, such as sheep or goats, the age at puberty can be established more precisely by monitoring blood progesterone levels to assess ovulation. Moreover, in these species serial blood sampling over a long period could be performed without affecting the animal's physiology, allowing close monitoring of LH pulses, the frequency of which increases during the

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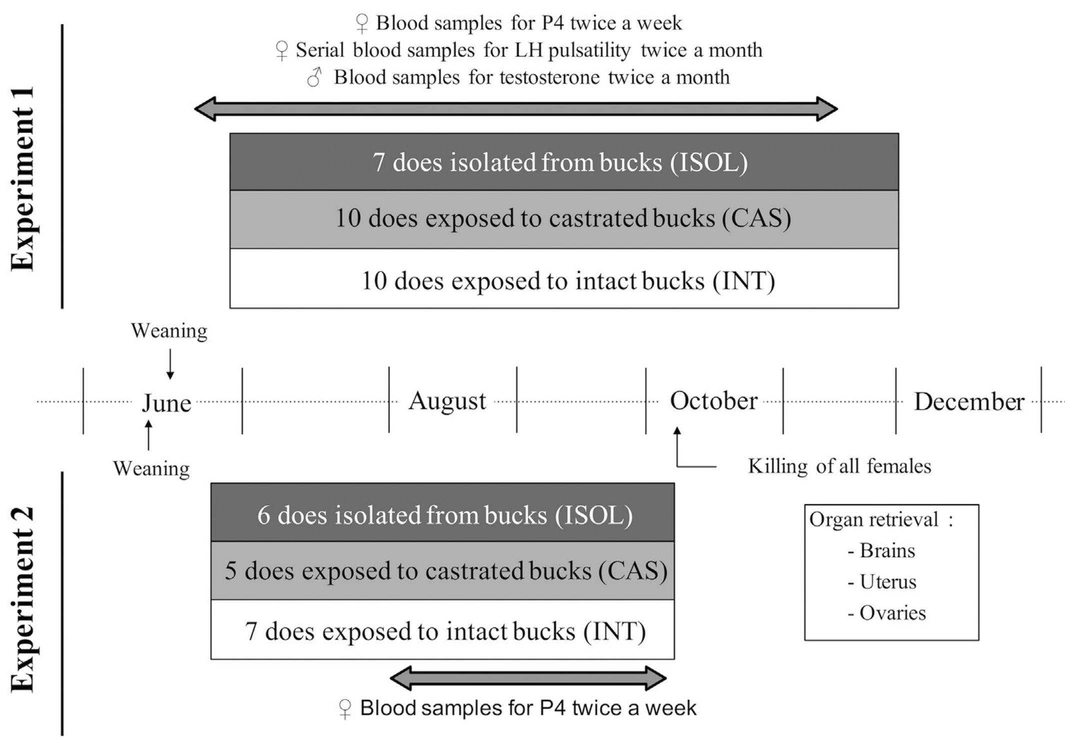

Fig. 1. Diagram of the experimental design. Females were weaned at 2.5 months and then divided in 3 groups, one isolated from bucks (ISOL), one exposed to castrated bucks (CAS) and one exposed to intact bucks (INT). In CAS and INT groups, stimulation was continuous behind a fence and three times a week we allowed direct contact for 1 h by introducing a buck into females' pen. Behavior of males and females was observed during this hour. For experiment 2, females were euthanized early October to collect brain, uterus and ovaries.

pubertal transition (Huffman et al., 1987; Watanabe and Terasawa, 1989). Despite the technical advantages of working with large animals, almost all studies investigating the pubertal induction due to male exposure have been carried out in rodents. Hence in rodents, it is well known that intact males provide chemosignals in their urine that induce a precocious vaginal opening and an increase of uterus weight in young females (Jouhanneau et al., 2014; Lombardi et al., 1976; Vandenbergh, 1969, 1967). Information regarding these phenomena and underlying mechanisms are lacking in non-rodent species. Some studies in sheep (Abecia et al., 2016; Dýrmundsson and Lees, 1972; Oldham and Gray, 1984; Williams, 1981) and pigs (Brooks and Cole, 1970; Pearce and Paterson, 1992) have suggested the possibility of accelerating puberty through male exposure. However, these demonstrations were quite incomplete, as none of them evaluated the impact of the presence of the male on the gonadotropic axis, including the dynamics of gonadotropin secretions, on the genital tract maturation, or on neuroendocrine regulation.

Goats are a good model to study the physiological consequences of early exposure to males on females sexual maturation. We have shown that the reproductive axis of mature female goats is highly sensitive to socio-sexual signals provided by bucks. For example, the introduction of a male induces ovulation and estrous behavior in anestrous does (Chasles et al., 2016; Chemineau, 1987; Shelton, 1960). This effect is known as the "male-effect" and studies investigating factors influencing its efficiency demonstrated that the level of sexual activity of the buck is the most important. Indeed, an inactive buck fails to trigger female reproductive activity, whereas the presence of a sexually active buck induces ovulation within 4 days in > 80% of females (Flores et al., 2000; Martinez-Alfaro et al., 2014; Ramírez et al., 2016). In addition, it has been demonstrated that exposure to the fleeces of sexually active bucks induces an increase of LH pulse frequency and ovulation in anestrous goats (Claus et al., 1990). Nevertheless, exposure to a sexually active buck that provides the buck odor but that has been sedated to prevent the expression of sexual behaviors fails to induce ovulation in anestrous females (Martinez-Alfaro et al., 2014; Vielma et al., 2009). Therefore, the nature of the signal provided by the buck that regulates does reproductive activity remain unclear.

One study reported possible impacts of buck exposure on the sexual maturation of young goats (Amoah and Bryant, 1984). Unfortunately, females from the control group (isolated females) were exposed to males before they reached spontaneous puberty, so no comparison of the age at puberty was possible. Moreover, females were considered pubescent when they accepted to be mounted by a buck, but this criterion is misleading because in young goats ovulations are often not associated with estrous behavior (Zarazaga et al., 2009). Hence, our goal was to study the physiological consequences of an early exposure to bucks in pre-pubertal does at different levels of the gonadotropic axis including occurrence of the first ovulation, genital tract maturation, induction of LH pulses and modifications of the GnRH neuronal network. In this experiment, we also investigated the nature of the signal provided by the buck that reactivates the gonadotropic axis by modifying the modalities of interactions between males and females.

2. Materials and methods

2.1. Animals

Experiments were carried out from March 2015 to December 2017 in Nouzilly, France (latitude 47° 32N and longitude 0° 46E) on alpine goats (*Capra hircus*). A total of 70 animals were used, 58 pre-pubertal females and 12 adult males sexually experienced. Animals were fed daily with barley straw, lucerne hay and commercial concentrate, with free access to water and mineral blocks. Throughout all experiments females were weighed monthly to detect a possible metabolic effect and to ensure that mean body weight remain similar in all groups, indeed in small ruminants we know that the body condition can impact on breeding performance (Cave et al., 2011; Rivas-Muñoz et al., 2010). No weight difference was observed between groups at any time point in the