



Major role of suckling stimulation for inhibition of estrous behaviors in lactating rabbits: Acute and chronic effects

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ABSTRACT

Lactation in rabbits induces anestrus: sexual receptivity and scent-marking (chinning) are reduced despite the brevity of suckling (one daily nursing bout, lasting around 3 min). The mechanisms underlying this effect are unknown but, as chinning, lordosis, and ambulation in an open field are immediately inhibited by the peripheral stimulation received during mating we hypothesized that, across lactation, suckling stimulation would provoke a similar effect. To test this possibility we provided litters of 1, 3, 5, or 10 pups across lactation days 1–15 and quantified chinning and ambulation frequencies, the lordosis quotient, and milk output. Baseline chinning frequency, determined before the daily nursing bout, was low across lactation days 1–15 in does nursing 3, 5 or 10 pups but it increased steadily across days 1–10 in rabbits suckling one pup. Yet, a single young was sufficient to abolish chinning for about 1 h, after which this behavior rose again. Suckling litters of all sizes reduced (but did not abolish) ambulation frequency, both chronically (baseline levels declined across days 1–5) and acutely. Sexual receptivity was significantly reduced on lactation day 15 only in does that had nursed 10 pups. Large litter size promoted a larger milk output and a normal duration of nursing episodes. Results support a major role of suckling stimulation for the suppression of estrous behaviors and ambulation through as yet unidentified mechanisms.

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Introduction

In most studied mammals lactation induces anestrus, a condition during which sexual receptivity is minimal and ovulation does not occur. This effect has been studied mainly in rats, cows, sheep, and swine (for review see: [Mc Neilly, 2006](#)). These mammals nurse their progeny several times a day and the duration and frequency of suckling bouts vary according to the stage of lactation (for reviews see: [González-Mariscal and Poindron, 2002](#); [Numan et al., 2006](#)). Rabbits, by contrast, nurse their young only once a day for around 3 min throughout the 30 days of lactation ([Drewett et al., 1982](#); [González-Mariscal et al., 1994](#); [González-Mariscal, 2007](#); [Zarrow et al., 1965](#)). Despite its brevity, the single daily nursing bout is sufficient to induce anestrus, as evidenced by the inhibition of sexual receptivity (the lordosis reflex; [Beyer and Rivaud, 1969](#)) and chinning, a scent-marking behavior characteristic of estrous does ([González-Mariscal et al., 1990](#)). It consists of the rubbing of the female's chin onto solid objects in the environment to deposit secretions produced by the submandibular glands and thus advertise to males her willingness to mate ([Melo and González-Mariscal, 2010](#)). The single daily nursing bout is also necessary to maintain lactational anestrus in rabbits: suppressing

a single nursing bout in early lactation leads to the restoration of estrus 24 h later. If does are then mated ([Bonanno et al., 1999](#)) or artificially inseminated ([Alvariño et al., 1998](#); [Castellini et al., 1998](#); [Theau-Clément and Mercier, 1999](#)) reflex ovulation occurs and a new pregnancy is initiated concurrently with lactation. This pattern is in marked contrast with that observed in most studied mammals in which the latency for estrus resumption following weaning takes several days, varies greatly across species, and is related with the number of suckled young ([Lindblom et al., 1985](#); [Schirar et al., 1990](#); [Van der Schoot et al., 1978](#); [Wettemann et al., 1978](#)). Moreover, in such mammals the occurrence of ovulation is independent of mating (spontaneous ovulators; for review see: [Freeman, 2006](#)) and, in some cases (e.g., ungulates), it is also modulated by the duration of photoperiod (for reviews see: [Goodman and Inskip, 2006](#); [Malpoux, 2006](#)).

From the above it is clear that rabbits present a unique model for exploring how a small amount of suckling stimulation received once a day is sufficient to induce anestrus and necessary to maintain this state. Little is known, however, about the ways by which chinning and sexual receptivity are suppressed across lactation ([Beyer and Rivaud, 1969](#); [González-Mariscal et al., 1990](#)). We do know that both behaviors are stimulated by estradiol because they are abolished by ovariectomy and reinstated by the injection of estradiol ([Hudson et al., 1990](#)). Progesterone (P) inhibits lordosis and scent-marking because: a) its administration to estradiol-primed ovariectomized (ovx) rabbits inhibits chinning and sexual receptivity ([Hudson et](#)

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al., 1990), effects counteracted by injecting the antiprogesterin RU486 (Hoffman and González-Mariscal, 2006); b) during pregnancy – when P concentrations are high (González-Mariscal et al., 1994) – both behaviors are markedly reduced (Beyer and Rivaud, 1969; González-Mariscal et al., 1990; Soares and Diamond, 1982); c) injecting human chorionic gonadotrophin (a procedure that provokes ovulation and leads to P secretion from the corpus luteum despite the absence of mating) inhibits chinning and sexual receptivity (Hoffman et al., 2010). Yet, P concentrations are negligible in lactating rabbits (González-Mariscal et al., 1994) because, unlike rats (Van der Schoot et al., 1978), the amount of prolactin released at each nursing bout (Fuchs et al., 1984) is apparently insufficient to maintain the corpus luteum. Consequently, other (non-steroidal) pathways must operate to inhibit the expression of estrous behaviors during lactation in rabbits. Indeed, a P-independent mechanism, triggered by mating, inhibits chinning, lordosis, and ambulation in an open field *immediately* post-copula (González-Mariscal et al., 1997). These effects do not involve the action of P or its receptor because: a) P secretion begins several hours after mating (Ramírez and Beyer, 1988); b) the previous injection of the antiprogesterin RU486 does not prevent the *immediate* mating-induced inhibition of the above behaviors in intact does (Hoffman and González-Mariscal, 2007); c) this behavioral inhibition is observed even in ovx estradiol-primed rabbits (Hoffman and González-Mariscal, 2007). These results show that, in estrous rabbits, chinning and lordosis can be *acutely* inhibited by a specific form of peripheral stimulation (vaginocervical), thus opening the possibility that in lactating does suckling stimulation may provoke a similar effect. To explore this issue in the present work we investigated the immediate and long-term consequences of suckling on the expression of lordosis and the frequency of chinning and ambulation in lactating does. To further establish whether, as in rats (Lindblom et al., 1985; Södersten et al., 1983), a relationship exists between the size of the suckling litter and the magnitude of estrous behavior inhibition we provided a different number of pups to specific groups of nursing does, ranging from 10 young (which is the usual litter size in New Zealand rabbits; Castellini et al., 2003; Lebas, 1987) to a single one.

Materials and methods

Animals and housing conditions

New Zealand white rabbits (3.5–4.5 kg body weight) bred in our colony were used. They were kept in wire mesh maternal cages (90 cm long × 60 cm wide × 40 cm high) inside the rabbit colony under controlled light (14 h light:10 h darkness; lights off at 2100 h) and natural temperature (13–25 °C) conditions. Water and Purina rabbit pellets were provided *ad libitum*. Throughout this work animal care complied with the Law for the Protection of Animals (Mexico). Females were mated with sexually active bucks of the same strain inside a round (1 m in diameter) wire mesh arena. On pregnancy day 21 a wooden nest box (50 cm long × 30 cm wide × 32 cm high) with a rectangular (20 cm × 22 cm) opening on one side was introduced into the female's cage to allow the construction of the maternal nest, as previously described (Chirino et al., 2007).

Behavioral measurements

Starting on pregnancy day 30 females were spot-checked across the day to determine the approximate time of delivery. Mothers were left undisturbed for the following 5–8 h after which the pups were removed from the nest box and counted. Litter size was then adjusted for four independent groups of females, as follows: 1 pup (n=9), 3 pups (n=9), 5 pups (n=9), or 10 pups (n=8). They were kept away from their mothers inside a box containing paper shavings, under a mild heat source. Across the next 15 days, at 10:00 h, the pups were weighed, introduced into the nest box, and

the mother was allowed to enter it for nursing. The following parameters were quantified daily: a) the mother's time inside the nest box, i.e., the time elapsed between the mother's entrance into the nest box and her voluntary exit from it (as seen in Results this time was usually around 3 min and only in the one-pup condition did it approach 30 min), b) the pups' milk intake (determined by comparing their body weight before and after nursing), and c) the impact of nursing on chinning and ambulation. To quantify these two behaviors females were introduced into a square wire-mesh arena (1 m × 1 m) placed inside the rabbit colony. A grid was painted on the floor of this arena and three piles of bricks were put inside it. The number of lines crossed and the number of chin-marks made onto any of the bricks were recorded simultaneously for 10 min. The chinning/ambulation tests were performed at the following times: before nursing (around 1000 h; "baseline"), immediately afterwards (time "zero"), 1, 5, and 10 h after nursing. Does were returned to their home cages between behavioral measurements. On lactation day 15, to determine sexual receptivity, females were allowed to nurse and were then mated as described above. Their sexual receptivity was determined by counting the number of times they showed lordosis in response to three mounts made by the male. As mating inhibits chinning (González-Mariscal et al., 1997) this behavior was not scored on lactation day 15 following copulation.

Statistical analysis

A Kruskal–Wallis ANOVA was used to compare differences *among* the responses (chinning, ambulation, milk output) of the four experimental groups across time. When pertinent ($p < 0.05$) this was followed by Mann–Whitney's U test to compare the frequencies of chinning and ambulation and the amount of milk output between two groups at specific time points. Friedman's ANOVA was used to compare the responses, across time, of animals *within* a given experimental group. When pertinent ($p < 0.05$) this was followed by a Wilcoxon test to compare, within a group, the values of chinning and ambulation between two specific time points. As the lordosis quotient was quantified only once it was simply compared between two experimental groups with a Mann–Whitney U-test. A chi-square test was used to compare, between two groups, the proportions of females that showed lordosis, were inseminated and became pregnant (Siegel and Castellan, 1988).

Results

Effects of litter size on chinning and ambulation

Fig. 1 shows the baseline (i.e., pre-suckling) values of chinning frequency observed on selected days of lactation (1, 5, 10, and 14).

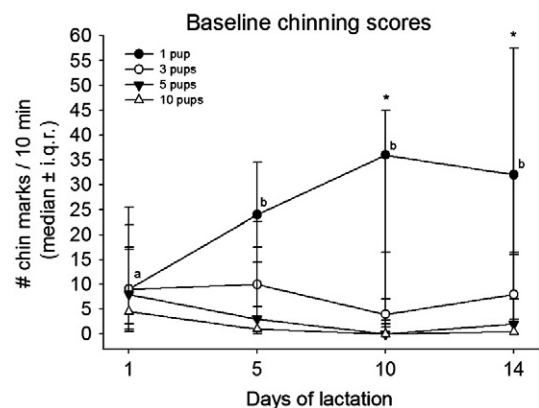


Fig. 1. Effect of nursing litters of different sizes on the frequency of chinning displayed before the suckling episode of the corresponding day. * $p < 0.01$, 1 pup vs 5 and 10 pups. Data points *within* a group not sharing the same letter differ from each other at $p < 0.05$.

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