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Endocrine regulation of postpartum ovarian activity in cattle : a review ⁽¹⁾

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Summary. The problem of postpartum anoestrus is a real one because it results in prolongation of the time between calvings. The interval between the calving and resumption of cyclic ovarian activity depends on several factors, *i.e.*, amount of feeding before and after parturition, level of milk yield, age of the animal, calving difficulty, presence of a bull in the herd, season and its photoperiodism and particularly the suckling or lactating status of the cow. The anoestrus period is longer in suckled cows (30 to 110 days) than in milked cattle (20 to 70 days).

The physiology of the hypothalamic-pituitary-ovarian axis is still far from clear. Nevertheless, some events are very well demonstrated. The pulsatile release of LH and GnRH and the pituitary sensitivity to GnRH increase gradually after calving. They are inhibited by suckling, which acts more on LH and GnRH release than on their synthesis. Suckling or the presence of a calf can exercise its action via oestrogens. Suckling inhibits oestrogen synthesis by follicular cells and diminishes their feed-back positive effect on the hypothalamic-pituitary axis. The suckling effect depends on oestrogen concentrations and on time after calving. The progressive LH release induces the synthesis of progesterone. After calving, the first luteal phase is shorter and the progesterone plasma concentrations are lower than what is observed during a normal cycle. Amongst some hypotheses proposed, premature luteolysis induced by uterine prostaglandins offers a new and very interesting field of research related to the utero-ovarian relationship after calving. The effects of FSH, prolactin and glucocorticoids hormones are much less understood.

1. Clinical aspects of postpartum anoestrus.

Clinically, the postpartum period is characterized by a period of behavioural anoestrus, the duration of which differs in different breeds.

If the detection of oestrus is optimal, anoestrus lasts for 20 to 70 days in dairy cows (Graves *et al.*, 1968 ; Callahan *et al.*, 1971 ; Schams *et al.*, 1978 ; Pirchner *et al.*, 1983 ; Richardson *et al.*, 1983 ; Etherington *et al.*, 1984). This period is highly variable in suckled cows and lasts from 30 to 110 days (Wiltbank and Cook 1958 ; Oxenreider 1968 ; Graves *et al.*, 1968 ; Casida *et al.*, 1968 ;

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Short *et al.*, 1972 ; Nancarrow *et al.*, 1977 ; Holness *et al.*, 1978 ; Wettemann *et al.*, 1978 ; Short *et al.*, 1979 ; Dunn and Kaltenbach, 1980 ; Kesler *et al.*, 1980 ; Randel, 1981 ; Montgomery, 1982 ; Peters and Riley, 1982 . Jainudeen *et al.*, 1982/1983 ; Bastidas *et al.*, 1984 ; King and Mc Leod, 1983/1984 ; Hansen and Hauser, 1984 ; Montgomery *et al.*, 1985).

Assay of progesterone in plasma or milk has shown that 88 % of animals of dairy breeds have an luteal activity present by 35 days after calving (Ball and Lamming, 1983) and 95 % within 50 days (Bulman and Lamming, 1978). According to different authors, the first rise of progesterone appears between 16 and 69 days after calving in dairy cows (Webb *et al.*, 1977, 1980 ; Pirchner *et al.*, 1983) and between 56 and 96 days in suckled cows (Fonseca *et al.*, 1980 ; Peters and Riley 1982 ; Jainudeen *et al.*, 1982/1983 ; Montgomery *et al.*, 1985).

It is possible to detect ovarian follicles by rectal palpation in both milked and suckled cow from the second week after calving (Saiduddin *et al.*, 1968 ; Callahan *et al.*, 1971 ; Kesler *et al.*, 1979 ; Webb *et al.*, 1980 ; Kesler *et al.*, 1980 ; Stevenson *et al.*, 1983). The size of the follicles increases during the subsequent weeks. But in the suckled cow, there is generally an absence of follicular development until the final stage, namely ovulation.

2. Factors affecting postpartum anoestrus.

In our European agricultural areas, an average 12-month calving interval is generally considered as the ultimate goal of economic efficiency in cattle reproduction. In both suckled and milked cows, postpartum anoestrus is a paramount obstacle affecting this goal.

The length of the anoestrus period is variable and depends on several factors.

Most authors admit that before or after calving, extended periods of over- or underfeeding of cows (10 to 20 % of the required needs) can affect ovarian function and consequently the duration of postpartum anoestrus (Wiltbank *et al.*, 1962, 1964 ; Dunn *et al.*, 1969 ; Lammond, 1970 ; Corah *et al.*, 1975 ; Whitman *et al.*, 1975 ; Duffour, 1975 ; Holness *et al.*, 1978 ; Carstairs *et al.*, 1980 ; Dunn and Kaltenbach, 1980 ; Gauthier and Thimonnier, 1982 ; Peters and Riley, 1982 ; King and Mc Leod, 1983/1984 ; Rutter and Randel, 1984). Some authors have found that overfeeding improves ovarian (Wiltbank *et al.*, 1962, 1964 ; Hansen *et al.*, 1982) or pituitary (Beal *et al.*, 1978 ; Jordan and Swanson, 1979 ; Lishman *et al.*, 1979 ; Moss *et al.*, 1982) function. Others have found no relation between feeding and the ovarian (Lishman *et al.*, 1979 ; Carstairs *et al.*, 1980) or pituitary (Hill *et al.*, 1970 ; Dunn *et al.*, 1974 ; Spitzer *et al.*, 1978 ; Haresign, 1981 ; Rutter and Randel, 1984) activity.

Little is known about the mechanism under which diet exerts its effect. It is conceivable that feeding influences the ovarian response to gonadotropins (Gombe and Hansel, 1973). There was a positive correlation between the degree of fatness of an animal and the plasma concentration of 17 β -oestradiol, 7 weeks after calving (Lishman *et al.*, 1979).

Feeding affects the release of luteinizing hormone (LH) and subsequent luteal function (Dunn *et al.*, 1974 ; Spitzer *et al.*, 1975 ; Apgar *et al.*, 1975 ; Beal *et al.*,

1978). It has been observed that the release of LH induced by gonadotropin releasing hormone (GnRH) injection was greater in underfed heifers (Beal *et al.*, 1978 ; Gauthier and Mauleon, 1983), underfed ewes (Haresign, 1981) and underfed rats (Campbell *et al.*, 1977) than in normally fed controls. Other reports have failed to record any difference (Cummins *et al.*, 1975 ; Beal *et al.*, 1978) or have noted a lower release of LH (Lishman *et al.*, 1979 ; Jordan and Swanson, 1979 ; Echterkamp *et al.*, 1982).

In the same way, underfed animals after calving have lower plasma (Terqui *et al.*, 1982 ; Echterkamp *et al.*, 1982 ; Gauthier *et al.*, 1983) or pituitary LH concentrations (Beal *et al.*, 1978). On the contrary, overfeeding does not induce variations in LH plasma concentrations or in pituitary response to GnRH (Rutter and Randel, 1984).

These contradictory results may be due to differences between studies in the nature of feed treatments, *i.e.*, the quantitative or qualitative aspects of the ration given to or absorbed by the animal. In general, the amount of food actually absorbed by the animal in connection with the state of its own reserves has not been considered. Now it appears that animals which remain in good condition after calving have, irrespective of the rations received, higher LH plasma concentrations and a greater pituitary response to GnRH and consequently a shorter calving — first oestrus interval (Gauthier *et al.*, 1983 ; Rutter and Randel, 1984).

Some workers have reported a positive relationship between milk yield and time to first oestrus or ovulation (Marion and Gier, 1968). The duration of anoestrus also depends on the age of the animal. Heifers have a longer calving-first oestrus interval than pluriparous cows (Germ Plasm Evaluation Program, 1975, King and Mc Leod, 1983/1984 ; Tervit *et al.*, 1977). It also depends on calving difficulty. Dystocia and retained placenta, both of which extend the duration of uterine involution, reduce the rate of pregnancies 100 days after calving (Laster *et al.*, 1973) and result in a longer acyclic period after calving (Erb *et al.*, 1958). The presence of a bull in a herd reduces the time before resumption of cyclic activity (male effect) (Zalesky *et al.*, 1984).

Season or photoperiod (Tucker, 1982) also changes the duration of anoestrus after calving (Thibault *et al.*, 1966 ; Montgomery *et al.*, 1980). The longer the duration of illumination at the time of calving, the shorter the duration of anoestrus (Bulman and Lamming, 1978 ; Peters and Riley, 1982 ; Hansen and Hauser, 1983). Animals calving between May and November have a calving-first ovulation interval significantly shorter than those calving between December and April (Lamming *et al.*, 1981 ; Peters and Riley, 1982 ; King and Mc Leod, 1983/1984). This effect is even more important in primiparous than in pluriparous animals. It is also increased by an inadequate diet (Hansen and Hauser, 1983 ; Montgomery *et al.*, 1985). How this effect works is still rather vague. Higher plasma LH (Mc Natty *et al.*, 1984) and prolactin concentrations (Munro *et al.*, 1980 ; Mc Natty *et al.*, 1984) in summer than in winter could be the explanation, though it is not corroborated by some authors (Hansen and Hauser, 1984). Moreover feeding factors can also have a direct or indirect effect upon the process.

The suckling or lactating status of the animals must be considered as the determining factor. It is unanimously admitted that suckling induces a lengthening of the calving-first oestrus interval (Clapp, 1937 ; Graves *et al.*, 1968 ; Morrow *et al.*, 1969 ; Short *et al.*, 1972 ; Randel and Walker, 1976 ; Edgerton, 1980). This interval is shortened by early weaning (Smith and Vincent, 1972 ; Laster *et al.*, 1973 ; Bellows *et al.*, 1974 ; Carter *et al.*, 1980) or by a temporary suspension (48 to 72 hr) of suckling (Smith *et al.*, 1979 ; Dunn *et al.*, 1985).

This influence depends on the intensity of the mammary stimulation. According to some authors (Wettemann *et al.*, 1978) but not to others (Peters and Riley, 1982), a cow suckling two calves will have a longer anoestrus (96 days vs 67 days) than a cow suckling only one calf. It also depends on the duration and the frequency of this stimulation (Kaiser, 1975). As a matter of fact, the duration of anoestrus is longer when access to the mammary glands is *ad libitum* than if it is restricted to one or a few daily periods (Carruthers and Hafs, 1980 ; Montgomery, 1982 ; Randel and Walker, 1976).

3. Hormonal mechanisms of postpartum anoestrus.

Several steroid or peptide hormones are directly or indirectly involved in the physiology of the hypophysis and the hypothalamus, the main centers regulating reproduction.

3.1. *Luteinizing hormone (LH).*

Pregnancy has an inhibitory effect on the sensitivity of the pituitary to hypothalamic GnRH (Schallenberger *et al.*, 1978).

The sensitivity of the hypophysis to GnRH and LH plasma concentrations gradually increases after calving. The same holds true for GnRH pulsatile release which increases from 0-0,25 pulse an hour to 0,25-1,25 pulse an hour (Echterkamp and Hansel, 1973 ; Kesler *et al.*, 1977 ; Webb *et al.*, 1980 ; Carruthers *et al.*, 1980 ; Peters *et al.*, 1981 ; Gauthier *et al.*, 1982 ; Humphrey *et al.*, 1983). These changes are principally emphasized during the days preceding the first increase in progesterone and the first ovulation in dry as well as in lactating or suckling animals. In addition, LH concentrations in suckled cows are lower than those in milked or non suckled postpartum cows (Short *et al.*, 1972 ; Humphrey *et al.*, 1976 ; Webb *et al.*, 1977 ; Kesler *et al.*, 1977 ; Schallenberger *et al.*, 1978 ; Fernandes *et al.*, 1978 ; Stevenson et Britt, 1979 ; Carruthers and Hafs, 1980 ; Carruthers *et al.*, 1980 ; Rawlings *et al.*, 1980 ; Webb *et al.*, 1980 ; Foster *et al.*, 1980 ; Peters *et al.*, 1981 ; Ramirez-Godinez *et al.*, 1982 ; Azzazi *et al.*, 1983).

The time of appearance of this pulsatile release and of pituitary sensitivity varies according to breed. In dairy cows, the pulsatile release of LH and the sensitivity of the pituitary to hypothalamic GnRH appears 10 days after calving and is greater between 12 and 15 days after calving (Echterkamp and Hansel, 1973 ; Kesler *et al.*, 1977, 1979 ; Peters *et al.*, 1981). On the other hand, in suckled cows, suckling induces a difference in the time of appearance and

intensity of this response, extending up to 20-30 days after calving (Radford *et al.*, 1978 ; Carruthers *et al.*, 1980 ; Irvin *et al.*, 1981 ; Peters *et al.*, 1981).

But neither the mechanism by which suckling interferes with the hypothalamic-hypophyseal axis, nor the nature of specific stimuli required to produce this effect are well-defined. Recent work has suggested that mechanical manipulation of teats does not in itself constitute an exteroceptive stimulus capable of altering LH release patterns in the cow (Williams *et al.*, 1984). It is possible that other factors such as physical presence of a calf or social interaction are necessary in order for teat stimulation to be effective.

Suckling may have an effect at three levels.

It reduces the frequency (Carruthers and Hafs, 1980 ; Walters *et al.*, 1982a ; Edwards, 1985) and amplitude of LH release (Radford *et al.*, 1978 ; Carruthers and Hafs, 1980 ; Troxel *et al.*, 1980 ; Webb *et al.*, 1980 ; Peters *et al.*, 1981), pituitary sensitivity to GnRH (Carruthers *et al.*, 1978 ; Smith *et al.*, 1981) and pulsatile release of GnRH by the hypothalamus (Carruthers *et al.*, 1980 ; Walters *et al.*, 1982c ; Schallenberger and Peterson, 1982).

The inhibitory effect of suckling on resumption of cyclic activity after calving acts more on the LH and GnRH release and action mechanism than on their synthesis. Many demonstrations support this proposition.

Pituitary concentrations of LH (Saiduddin *et al.*, 1968 ; Graves *et al.*, 1968) and hypothalamic concentrations of GnRH (Carruthers *et al.*, 1978) are similar in both milked and suckled cows. Suckling is capable of inhibiting the positive effect of endogenous or exogenous oestradiol on the release of pituitary LH (Nancarrow *et al.*, 1977 ; Short *et al.*, 1979 ; Stevenson *et al.*, 1983).

Temporary weaning (48 hr) induces an increase of the plasma LH concentrations (Smith *et al.*, 1977 ; Walters *et al.*, 1982b) which decrease to pre-calf removal concentrations within 4 hrs of calf return (Walters *et al.*, 1982d). It also induces an increase of the follicular concentrations of LH receptors (Walters *et al.*, 1982a). Calf removal stimulates an increase in LH concentration by increasing LH pulse frequency but the induced activity appears to be in relation to LH plasma concentrations and pulse frequency before calf removal (Edwards, 1985).

Suckling not only delays but also reduces the amount of LH released in response to GnRH injection. Temporary removal enhances over time the amount of LH release induced by GnRH injection (Dunn *et al.*, 1985).

The number of animals, whether being milked or suckled, which respond positively to injection of GnRH or oestradiol increases during the postpartum period. On the other hand, suckled cows are less likely to respond by LH release after injection of oestradiol or GnRH than milked cows during the first 15 days after calving. This difference diminishes during subsequent weeks (Schams *et al.*, 1973 ; Britt *et al.*, 1974 ; Kesler *et al.*, 1977 ; Webb *et al.*, 1977 ; Schallenberger *et al.*, 1978 ; Carruthers *et al.*, 1980 ; Smith *et al.*, 1981 ; Walters *et al.*, 1982c).

At last, as well as a diminution in the interval between injection of oestradiol or GnRH and the LH peak, there is also an increase in the amplitude of this peak during the first 4 weeks after calving (Stevenson *et al.*, 1983 ; Azzazi *et al.*, 1983). The magnitude of the GnRH-induced release of LH was directly proportionnal to

follicular diameter (Smith *et al.*, 1983 ; Lishman *et al.*, 1979) and oestrogen concentrations in postpartum cattle (Fernandes *et al.*, 1978).

3.2. Follicle stimulating hormone (FSH).

Concentrations of FSH vary in an unpredictable manner (Schams *et al.*, 1978 ; Manns *et al.*, 1983) but tend to increase during the first few days after calving (Webb *et al.*, 1980 ; Peters *et al.*, 1981).

Suckling does not affect FSH plasma concentrations (Carruthers *et al.*, 1980 ; Convey *et al.*, 1983) or the number of ovarian receptors to FSH (Walters *et al.*, 1982a). It seems that during the early days of the postpartum period, the role of this hormone is of a facilitating or permissive nature (Webb *et al.*, 1980 ; Walters *et al.*, 1982c ; Peters and Lamming, 1984) because it induces the formation of LH receptors on granulosa cells under influence of oestrogen (Richards *et al.*, 1976).

3.3. Oestrogens.

Concentrations of oestrogens (17 β -oestradiol and oestrone) in blood plasma progressively increase toward the end of pregnancy and are at their highest 24-48 hours before calving (Smith *et al.*, 1973 ; Arije *et al.*, 1974 ; Stellflug *et al.*, 1978). Peripheral levels of oestradiol-17 β fall after calving and then fluctuate considerably before first ovulation (Pope, 1982).

Oestrogens such as 17 β -oestradiol and to a lesser extent oestrone (Azzazi and Garverick, 1984) are involved in the effects of suckling on the hypothalamo-hypophyseal axis. In the hypothalamus, suckling increases the threshold of sensitivity to the negative retro-action of oestradiol on the tonic center (Acosta *et al.*, 1983). Suckling inhibits oestrogen synthesis by the follicular cells (Bellin *et al.*, 1984) for a few days but not for three weeks after calving (Walters *et al.*, 1982a). This fact is important because in rats it was demonstrated (Richards *et al.*, 1976) that follicular sensitivity to gonadotropins depends partly on their oestrogen and androgen concentrations.

In the pituitary, suckling diminishes the LH response to exogenous oestradiol (Short *et al.*, 1979). Oestrogens have a positive effect on the amplitude of the LH peak and on LH release induced by injection of GnRH. These effects may occur by an increase in the rate or amplitude of GnRH secretion or an increase in pituitary sensitivity to GnRH stimulation (Zolman *et al.*, 1974 ; Yen *et al.*, 1974 ; Kesler *et al.*, 1977 ; Beck *et al.*, 1978 ; Hsueh *et al.*, 1979 ; Zaied *et al.*, 1980 ; Kesner *et al.*, 1981 ; Azzazi *et al.*, 1983 ; Peters, 1984).

This effect depends on the dose of oestrogens. High doses (10 mg) of oestradiol benzoate inhibit the pituitary response to GnRH (Barraclough, 1973 ; Manns and Richardson, 1976) and low doses increase this response (Hobson and Hansel, 1972). It also depends on the right time of injection in relation to calving (Stevenson *et al.*, 1983) and on the period of injection. In ovariectomised ewes treated (for a period equivalent to that of gestation) with a daily dose of oestradiol equivalent to that which occurs during gestation, there is a progressive reduction in the amount of LH released following GnRH injection and also a fall in pituitary LH, both these parameters being directly correlated. Simultaneously there was an

increase in the number of GnRH receptors in the pituitary (Crowder *et al.*, 1982). After calving, injection of oestrogens for 7 days with a dose sufficient to produce plasma concentrations similar to those present before calving, at first increased and then diminished the amount of LH released after GnRH injection, a positive effect which also occurred after the injections had ceased. The decrease of the amount of LH released may have resulted from a negative effect of oestrogens on LH synthesis. The second increase could have been due to progressive development of GnRH receptors (Azzazi *et al.*, 1983). Perhaps oestrogens stimulate the synthesis of LH but inhibit its release (Tang, 1977).

3.4. Progesterone.

Concentrations of progesterone in the plasma of cows are high throughout gestation. They diminish slowly during the final 3-4 weeks and rapidly 2-3 days before calving (Short, 1958 ; Randel and Erb, 1971 ; Smith *et al.*, 1973).

Milked or suckled cows, 50 to 80 % of the time, have a first luteal phase which is shorter and progesterone plasma concentrations which are lower than observed during a normal cycle (Donaldson *et al.*, 1970 ; Edgerton and Hafs, 1973 ; Humphrey *et al.*, 1976 ; Schams *et al.*, 1978 ; Stevenson and Britt, 1979 ; Kesler *et al.*, 1980 ; Webb *et al.*, 1980 ; Odde *et al.*, 1980 ; Lavoie *et al.*, 1981 ; Peters and Riley, 1982 ; Troxel *et al.*, 1983 ; Pirschner *et al.*, 1983 ; Manns *et al.*, 1983). That hormonal abnormality can result in embryonic mortality (Ramirez-Godinez *et al.*, 1982b ; Troxel *et al.*, 1983).

More precise studies of hormones have shown that two types of luteal activity occur after calving (Troxel *et al.*, 1983). The first is a luteal phase lasting 6-12 days and referred to as the short luteal phase (or SLP), while the second is a luteal phase of normal duration, lasting more than 14 days, but accompanied by progesterone concentrations lower than normal (inadequate luteal phase or ILP). The reason for this is not fully understood. Such a dual possibility has also been observed after GnRH injection (Webb *et al.*, 1977 ; Lishman *et al.*, 1979 ; Kesler *et al.*, 1980 ; Fonseca *et al.*, 1980 ; Sheffel *et al.*, 1980 ; Troxel *et al.*, 1983) or after early weaning (Odde *et al.*, 1980) or limited suckling with (Dunn *et al.*, 1985) or without (Flood *et al.*, 1979) GnRH injection.

Many hypotheses have been put forward to explain this.

Morphological and endocrine studies (Manns *et al.*, 1983) indicate that these first short-lived corpora lutea are not destroyed by the usual luteolytic process, but by a loss of ability to synthesize progesterone.

The lower FSH plasma concentration before oestrus preceding a short cycle may imply a possible influence of this hormone on the lifespan of the corpus luteum (Ramirez-Godinez *et al.*, 1982a).

Progesterone might be formed by a follicle which has failed to ovulate (Tribble *et al.*, 1973 ; Corah *et al.*, 1974 ; Webb *et al.*, 1980). The absence of differences in LH plasma concentrations observed before or after an oestrus associated with a short cycle does not lead one to a conclusion of an insufficient LH synthesis (Ramirez-Godinez *et al.*, 1982a).

The reduced lifespan might be related to GnRH-induced LH surge having a short duration (Troxel *et al.*, 1980). However the luteal receptors for LH or the

number of granulosa cells (Channing *et al.*, 1981) may not be sufficient to give an optimum response to this luteotropic stimulus (Schams *et al.*, 1979). As a matter of fact, while the corpus luteum from cows with regular cycles gives a positive response *in vitro* to LH addition in culture medium, this response cannot be observed with a corpus luteum whose formation has been induced by injection of GnRH. This difference may be because the luteal tissues are unable to recognize LH (Kesler *et al.*, 1981). Histological studies have indicated that the response of postpartum corpora lutea to LH *in vitro* is similar in all the first three cycles, but that is related to the integrity of luteal tissue at the time of removal (Duby *et al.*, 1985).

These last two observations support the concept of a premature luteolysis.

The presence of a luteolytic agent such as prostaglandin F₂ α (PGF₂ α) synthesized after calving by the caruncular uterine tissues (Guilbaut *et al.*, 1981, 1984b) may be responsible for this premature luteolysis and short luteal phase (Troxel and Kesler, 1984b). In fact, concentrations of one of the metabolites of PGF₂ α , 13, 14 dihydro-15-ceto-PGF (PGFM), increase during and after calving. They reach peak values on days 2 or 3 postpartum and return progressively to a basal concentration by 2 or 3 weeks after calving both in milked (Edqvist *et al.*, 1978 ; Thatcher *et al.*, 1980 ; Lindell *et al.*, 1982 ; Kaker *et al.*, 1984 ; Madej *et al.*, 1984 ; Guilbaut *et al.*, 1984a) and suckled (Troxel *et al.*, 1984) cows. Its concentration decreases after the increase of progesterone in the blood (Lewis *et al.*, 1984). It is generally agreed that PGF₂ α is not luteolytic during the first 4 or 5 days of the cycle. Nevertheless, its repeated injection during this period reduces progesterone concentration during the rest of cycle (Beal *et al.*, 1980).

Oxytocin injected (Troxel *et al.*, 1984) or released in response to milking or suckling or the presence of uterine infection (Roberts *et al.*, 1975 ; Lindell *et al.*, 1982 ; Watson, 1984) may be responsible for an increased concentration of PGFM and consequently earlier luteolysis and earlier resumption of a normal luteal phase (Madej *et al.*, 1984). It has also been shown that intrauterine infusion of indomethacin, an inhibitor of prostaglandins synthesis, not only diminishes basal or induced concentrations of oxytocin and of the PGF metabolite (Troxel *et al.*, 1984) but also prolongs the life of corpora lutea induced by GnRH (Troxel and Kesler, 1984a).

These various observations have led research workers to study the physiological significance of abnormal luteal phases and with experiments to determine the effects of treatments with progestagens or progesterone before an injection of GnRH. Injection of progesterone (25 or 100 mg) 12 days after calving and 48 hrs before GnRH injection (Williams *et al.*, 1982) or implantation of norgestomet for 8 days, starting 17 days after calving, followed by an injection of 250 mcg GnRH 24 hrs after removal of the implant (Troxel and Kesler, 1984c) have beneficial effects on the amount of progesterone secreted by the corpora lutea thus induced (Ramirez-Godinez *et al.*, 1981 ; Sheffel *et al.*, 1982 ; Pratt *et al.*, 1982). Such pretreatment is without effect if applied 40 days after calving (Troxel *et al.*, 1980).

The mechanism of this effect is still unknown.

A direct effect on the ovary cannot be ruled out, although experiments on

rats have failed to confirm the role of progesterone in follicular development (Saiduddin and Zassenhaus, 1978).

A local utero-ovarian mechanism has also been proposed. In the first days after calving, the ovary bearing the gestation corpus luteum produces smaller follicles than the contralateral ovary (Lewis *et al.*, 1984). The oestrogen concentration of these follicles is also smaller (Bellin *et al.*, 1984). This has also been observed during the oestrus cycle (Matton *et al.*, 1981 ; Brantmeier *et al.*, 1984). Thirty days after calving, a corpus luteum or a follicle is less often palpated on the ipsilateral ovary than on the contralateral ovary (Lewis *et al.*, 1984), which confirms earlier reports about the location of the first ovulation (Marion and Gier, 1968). It is possible that through the prostaglandins it synthesizes, the involuting pregnant horn influences the ipsilateral ovary more than the contralateral ovary (Guilbaut *et al.*, 1983). It has been suggested that progesterone could influence the concentrations of luteolytic and luteotropic factors (Pratt *et al.*, 1982). It has been shown that progesterone pretreatment induces low and constant concentrations of PGFM, though not to a significant degree (Troxel and Kesler, 1984c).

An effect of progesterone on the hypothalamo-hypophyseal axis cannot be ruled out. It is well known that during the oestral cycle progesterone decreases the pulsatile secretion of LH (Ireland and Roche, 1982), because it has a negative feedback effect on its synthesis in the pituitary (Echterkamp and Hansel, 1973 ; Convey *et al.*, 1977). This effect acts on higher nervous centers since progesterone modifies neither the LH content nor the number of GnRH receptors in the pituitary (Moss *et al.*, 1981). This sensitivity of the pituitary to negative feedback exercised by progesterone increases during the postpartum period (Peters *et al.*, 1983). During the postpartum period, the amplitude and the duration of the LH peak induced by GnRH injection is higher in animals pretreated with progesterone (Troxel *et al.*, 1980 ; Troxel and Kesler, 1984c). Such an effect has not been confirmed by others (Williams *et al.*, 1982 ; Azzazi *et al.*, 1983). This observation should be taken in the context of the higher frequency of ovulation which occurs after progesterone treatment (Troxel and Kesler, 1984c). However, this did not occur after norgestomet treatment 40 days after calving (Troxel *et al.*, 1980).

The opposing effects of progesterone on LH release are not necessarily contradictory. They may depend on the timing of the experiment in the period after calving. Thus the effect may be inhibitory during the first 3 weeks (Williams *et al.*, 1982 ; Azzazi *et al.*, 1983) and stimulatory later (Troxel *et al.*, 1980 ; Troxel and Kesler, 1984c). The further away from calving it is given, the more likely it is for progesterone to have a favourable effect on LH release and the amount of progesterone synthesized by the resulting corpus luteum (Peters *et al.*, 1983). This inhibitory effect is brought about by a decrease in the amount of GnRH released, by a decrease of the self-regulating (or self-priming) effect of GnRH (Kesner *et al.*, 1982 ; Padmanabhan, 1982) or by oestradiol acting on the pituitary receptors of GnRH (Azzazi *et al.*, 1983).

3.5. Prolactin.

During lactation, prolactin is released in response to a mammary stimulation (Tucker, 1971). In rats (Amenomori *et al.*, 1970) and in women (Rolland *et al.*,

1975), the high blood prolactin concentrations are closely correlated with the gonadotropin synthesis inhibition. On the other hand, the high induced blood prolactin concentrations in rats (Fraser *et al.*, 1982) or gestation or lactation (Reeves *et al.*, 1982) is accompanied by a reduction of the number of pituitary GnRH receptors.

In the bovine, the anti-gonadotropic effect of prolactin cannot be accepted.

The prolactin plasma concentrations are the same in milked or suckled cows (Goodman *et al.*, 1979 ; Smith *et al.*, 1981), and in dairy cattle they are associated with increased milk yields (Akers *et al.*, 1980). Prolactin release is not systematically connected with suckling (Gimenez *et al.*, 1980 ; Convey *et al.*, 1983). Moreover, anoestrus length was observed by some (Chang *et al.*, 1981) but not others (Webb *et al.*, 1980) to be closely correlated with plasma prolactin concentrations. Finally, the injection of prolactin (Forrest *et al.*, 1980) or of bromocriptin (Williams and Ray, 1980), an inhibitor of prolactin release, influences neither the variations of LH or FSH concentrations nor the resumption of cyclic activity after calving delay at least in bovines. However, we cannot rule out an ovarian local effect of this hormone on the synthesis of progesterone (Mc Natty *et al.*, 1976, 1977) and on follicular development (Tsai-Morris *et al.*, 1983). The prolactin follicular concentration and the number of LH receptors are in fact significantly higher in weaned cows than in suckled cows (Walters *et al.*, 1982a).

3.6. Other hormonal factors.

Experiments carried out with ovariectomized animals confirm that the ovary and its steroidal or peptide factors (Channing, 1978 ; Fraser, 1982 ; Sharpe, 1982) cannot play a determining part in the LH release mechanism after calving.

The presence of higher concentrations of glucocorticoids in the blood of suckled than non suckled cows before (Wagner and Oxenreider, 1972 ; Schallenberger *et al.*, 1982) or after (Dunlap *et al.*, 1981 ; Ellicott *et al.*, 1981) a weaning period indicated that might play a role in LH release, the more so as they are likely to inhibit LH secretion in bovines (Wagner and Li, 1982). Recent work (Convey *et al.*, 1983) has failed to confirm glucocorticoid release during suckling in non ovariectomized animals and again set the problem of the exact part played by those steroids in postpartum anoestrus in cows.

Conclusions.

Clinical and physiological studies lead to the conclusion that suckling has a major inhibitory effect on the resumption of regular sexual activity following parturition in the bovine species. Most specialists in bovine reproduction have tried to demonstrate and understand hormonal manifestations of the hypothalamo-hypophyso-ovarian axis during the postpartum weeks. They have stated the action mechanism of enhancing and determining factors and shown the importance of a pulsatile discharge of LH under GnRH control. So new approaches emerge. An increasing influence on follicular growth is attributed to the involuting uterus. Moreover, the isolation and purification of ovarian cybernins will allow a better understanding of the determinism of anoestrus. It would

also be interesting to elucidate more precisely the effect of stresses such as parturition and suckling on neuromediators and endorphins at the level of the central nervous system level. Epidemiological research in bovine reproduction is now expanding. Because of its application in animal husbandry, it must define more accurately the respective roles of the different factors involved in anoestrus and clarify the economic implications of the therapeutic means already proposed to improve the fertility and fecundity of cattle.

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Résumé. *Régulation endocrinienne de l'ovaire au cours du postpartum dans l'espèce bovine.*

Dans l'espèce bovine, l'intervalle entre vêlages dépend notamment de la durée de l'anoestrus du postpartum. Plusieurs facteurs sont susceptibles d'influencer la physiologie de l'ovaire après la parturition : l'alimentation avant et après le vêlage, le niveau de production laitière, l'âge de l'animal, la nature du vêlage, la présence d'un taureau dans le troupeau, la saison et son photopériodisme mais surtout le caractère lactant ou allaitant de la vache. L'anoestrus est plus long chez la vache allaitante (30 à 110 jours) que chez la vache traite (20 à 70 jours).

Bien qu'encore incomplètes, les connaissances relatives à la physiologie de l'axe hypothalamo-hypophyso-ovarien au cours du postpartum ne cessent de progresser. Plusieurs faits apparaissent maintenant bien établis. La libération pulsatile de la LH et du GnRH ainsi que la sensibilité hypophysaire à la GnRH augmentent progressivement après le vêlage. Elles sont inhibées par l'allaitement qui agit plus sur la libération que sur la synthèse de la LH et du GnRH. La diminution de la synthèse d'œstrogènes par les follicules et la réduction de leur rétro-action positive sur l'axe hypothalamo-hypophysaire constituent la manifestation physiologique de cet effet inhibiteur. Après la parturition, la première phase lutéale est de plus courte durée et la synthèse de progestérone inférieure à celle observée au cours d'un cycle normal. Il est possible qu'une lutéolyse prématurément induite par les prostaglandines d'origine utérine soit à l'origine de cette particularité. Les effets de la FSH, de la prolactine et des corticoides, apparaissent nettement moins bien définis. De nouvelles voies d'approche se font jour. Nous citerons celles qui ont pour but de préciser le rôle de l'utérus en involution sur la croissance folliculaire ainsi que celles relatives aux cybernines ovariennes. L'étude du mécanisme d'action des facteurs de stress pourrait aussi revêtir des implications pratiques. Enfin, les recherches épidémiologiques en reproduction bovine permettront de cerner davantage l'effet respectif des différents facteurs impliqués dans l'anoestrus.

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