Changes in Peripheral Levels of Immunoreactive Inhibin and Gonadotropins in Cattle Induced to Superovulate by Porcine Follicle-Stimulating Hormone

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Summary. Concentrations of inhibin in peripheral blood were determined in cattle treated with porcine follicle-stimulating hormone (FSH). Changes in plasma concentrations of FSH, luteinizing hormone (LH), estradiol and progesterone were also examined. These results were compared with hormonal profiles in the intact estrous cycle prior to FSH treatment of the same cows. Plasma levels of estradiol before ovulation and of progesterone after ovulation during the period of treatment with porcine FSH were much higher than those in the intact cycle. Concentrations of plasma inhibin rose promptly after injections of porcine FSH and maintained high levels for a longer period than estradiol after the LH surge. Changes in plasma concentrations of inhibin were not correlated to those of progesterone in superovulating cattle. In the superovulating animals, peaks of the preovulatory FSH surge were suppressed to 70.4% of the intact cycle, though LH peaks were not significantly suppressed. These results indicate that high levels of inhibin after treatment with porcine FSH may be involved in a partial suppression of the preovulatory surge of FSH in superovulating cattle. These findings also suggest that unovulated follicles maintain the ability to secrete inhibin and that the corpus luteum in superovulating cattle is not the active source of inhibin secretion.

KEY WORDS: PERIPHERAL INHIBIN, ESTRADIOL, GONADOTROPINS, SUPEROVULATING CATTLE.

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Ovarian inhibin is one of the important factors which regulate FSH secretion in female animals and suppressed FSH biosynthesis in gonadotrophs (de Jong, 1988).

In cattle, inhibin is thought to be involved in the divergencies between FSH and LH secretion in the estrous cycle. For example, FSH concentrations during the follicular phase did not change whereas LH levels increased 2 or 3 fold (Ireland and Roche, 1982; Padmanabahn *et al*, 1984). Further, a small elevation of FSH was observed after the preovulatory gonadotropin surges though concentrations of LH decreased to low levels (Dobson, 1978; Walters and Schallenger, 1984; Quirk and Fortune, 1986). Inhibin is probably involved in regulation of folliculogenesis by means of the negative feedback effects on FSH secretion, as suggested by Quirk and Fortune (1986).

There were several reports dealing with hormonal profiles in superovulating cattle (Saumande, 1980;

Saumande and Lopetz-Sebastian, 1982; Jensen *et al*, 1982; Lauria *et al*, 1982; Donaldson, 1985), though patterns of FSH and, in particular, inhibin were not examined.

In this study, we have investigated changes in peripheral levels of inhibin in cattle induced to superovulate by treatment with porcine FSH. Effects of elevation of inhibin levels on preovulatory FSH and LH secretion were also examined in relation to hormonal profiles during the intact estrous cycle.

Materials and Methods

Reagents

Porcine FSH preparation (pFSH; Denka Seiyaku, Co., Kawasaki, Japan) and prostaglandin F_{2α} (PG; Daiichi Seiyaku Co., Tokyo, Japan) were used to induce superovulation. The weight of 40 Armour Units (A. U.) of porcine FSH preparation was 31.8 mg.

Treatments and blood sampling

Four Japanese brown cattle, clinically normal with regular estrous cycles were used. Animals were given s.c. twice daily injections of pFSH (10:00 and 16:00) for 4 successive days starting 10 days after estrus (6 and 5 A.U. on the first day, 5 and 4 A.U. on the second day, 4 and 3 A.U. on the third day and 3 and 2 A.U. on the fourth day). Fifteen mg PG was administered i.m. two times at 48 and 56 hr after the first pFSH injection. Estrous behavior (standing estrus) was checked every 4 hr. Blood samples were obtained via venipuncture every day from one day before the beginning to the end of pFSH treatment. When animals came into estrus, blood sample were taken every 2 hr for 16 hr and afterwards, every 4 hr until 72 hr after the beginning of estrus. Daily blood sampling was further continued by 7 days after estrus. Patterns of hormonal changes after pFSH treatment were compared with those in the intact estrous cycles of the same animals just before pFSH treatment. Blood samples were collected every 24 hr from 5 or 6 days before anticipated estrus. When estrous behavior was noted, blood samples were obtained from each cow with the same frequency as mentioned previously in pFSH treated animals.

Determination of ovarian responses

Number of ovulations was determined by counting corpora lutea through rectal palpation performed 7 days after estrus.

Hormone assays

Concentrations of LH in plasma were measured by radioimmunoassay (Echternkamp *et al.*, 1976) using anti-ovine LH serum (DJB-3-1211), USDA-bLH-I1 for radioiodination and USDA-bLH-B-5 as a standard. The sensitivity of the assay, based on a 95% confidence limit of the mean for 6 replicate tests for the zero standard, was 0.006 ng/tube. The intra- and inter- assay coefficients of variation were 6.6% and 11.7% respectively.

Concentrations of FSH in plasma were measured by radioimmunoassay (Bolt and Rollins, 1983) using anti-bovine FSH β -subunit antiserum (USDA-5-0012), purified bovine FSH (USDA-FSH-BP3) for radioiodination and USDA-FSH-B1 as a reference standard. The sensitivity of FSH assay was 0.48 ng/tube. The intra- and inter- assay coefficients of variation were 5.9% and 4.9% respectively. Cross reaction between pFSH and antiserum against β -subunit of bovine FSH was 6.3%, and antiserum against ovine LH was 0.6%, respectively, at 50% of the binding in each assay.

Concentrations of estradiol and progesterone were

determined as described previously (Taya *et al.*, 1985) using antisera to estradiol-17 β (GDN 244; Korenman *et al.*, 1974) and progesterone (Gunma OGP-1; Takahashi *et al.*, 1985). In the assay of estradiol, samples were defatted twice with the solution of mixture of 2 ml n-hexan and 0.5 ml 50% methanol (v/v). The sensitivity of the assay were 0.63 pg/tube for estradiol and 1.25 pg/tube for progesterone. The intra- and inter- assay coefficients of variation were 6.0% and 12.4% for estradiol and 6.1% and 18.5% for progesterone, respectively.

Concentrations of inhibin in peripheral plasma were measured by a homologous double-antibody radioimmunoassay as described previously (Hamada *et al.*, 1989) using antisera to bovine 32 kDa inhibin (TNDH-1). Pooled bFF was used as a reference standard and values estimated by the present radioimmunoassay were expressed as nl bFF/ml. One nl of this reference standard corresponds to 5.17 pg of purified 32 kDa bovine inhibin. The intra- and inter-assay coefficients of variation were 8.3 and 17.4%, respectively.

Statistics

The time of the preovulatory LH peak of each estrous cycle was designated as 0 hr on Day 0 and hormonal profiles in the intact estrus cycle and those after the treatment with pFSH were compared. Plasma concentrations of LH, FSH, inhibin, estradiol and progesterone were subjected to a split plot in time design with repeated measurements (Gill and Hafs, 1971). Comparisons between hormonal concentrations of the intact cycle and those of the corresponding time after pFSH treatment were made using paired t-test. A value of $p < 0.05$ was considered to be significant.

Results

Ovarian responses

The number of ovulations (corpora lutea) determined by rectal palpation after pFSH treatment were 3 in cows Nos. 1 and 4, and 5 in cow No. 3 and 10 in cow No. 2.

Changes in concentrations of plasma FSH and LH (Fig. 1, A and B)

In the intact cycle, basal levels of plasma FSH ranged from 10 to 20 ng/ml. Concentrations of FSH were significantly higher during the period of treatment with pFSH than those in the intact cycle from 12 to 72 hr before the LH peak. The basal concentrations of plasma LH were under 1.5 ng/ml both in the intact cycle and after pFSH treatment.

Fig. 1. Changes in plasma concentrations of LH (A) and FSH (B) relative to the preovulatory LH peak (0 hr) in cattle after the administration of porcine FSH preparation (pFSH; a total doses of 32 A.U.) and prostaglandin $F_{2\alpha}$ (PG; a total doses of 30 mg) (●) or during the intact estrous cycle (○). Results are expressed as mean $\pm$ S.E.M. for four animals. Arrows indicate injections of pFSH and PG. * $p < 0.05$ compared with the value for the respective control (paired t-test).

The mean value of preovulatory FSH peaks was 84.9 ± 13.0 ng/ml in the intact estrous cycle, whereas it was suppressed to 59.8 ± 6.7 ng/ml after the treatment with pFSH, being 70.3% of intact one ($p < 0.05$). On the other hand, the preovulatory LH peaks were not significantly suppressed.

Changes in concentrations of plasma inhibin (Fig. 2, A)

Plasma concentrations of inhibin in the intact estrous cycles were 43.1 nI/ml 5 days before estrus (Day 0) and increased to 76.5 nI/ml on estrus.

Plasma concentrations of inhibin significantly increased 48 hr after the first pFSH injection (48 hr before the LH peak) when compared to the levels before the first pFSH injection (96 hr before the LH peak) and reached the maximum concentration of 947.5 nI/ml on estrus (Day 0). During the period of pFSH treatment, plasma concentrations of inhibin were higher than those in the control cycle from -48 to 48 hr of the LH peak.

Changes in concentrations of plasma estradiol (Fig. 2, B)

Plasma concentrations of estradiol in the intact estrous cycle increased gradually during the follicular phase and reached peak values of 10 pg/ml on estrus, and then decreased less than 5 pg/ml 8 hr after the LH

Fig. 2. Changes in plasma concentrations of inhibin (A), estradiol (B) and progesterone (C) relative to the preovulatory LH peak (0 hr) in cattle after the administration of porcine FSH preparation (pFSH; a total doses of 32 A.U.) and prostaglandin $F_{2\alpha}$ (PG; a total doses of 30 mg) (●) or during the intact estrous cycle (○). Results are expressed as mean $\pm$ S.E.M. for four animals. Arrows indicate injections of pFSH and PG. * $p < 0.05$ compared with the value for the respective control (paired t-test).

peak. Concentrations of estradiol further declined thereafter (under 2 pg/ml).

Concentrations of estradiol significantly increased 72 hr after the first pFSH injection (24 hr before the LH peak) compared to pre-injection levels (96 hr before the LH peak) and reached the maximum level of 88.8 pg/ml. During the period of treatment with pFSH, plasma concentrations of estradiol significantly higher than those in the intact estrous cycle from -24 to 32 hr of the LH peak.

Changes in concentrations of plasma progesterone (Fig. 2, C)

Plasma concentrations of progesterone in the intact estrous cycle decline from 6.2 to less than 1 ng/ml 48 hr before the LH peak and remained under 0.3 ng/ml until 64 hr after the LH peak. Thereafter, concentrations of progesterone increased and reached levels of 3.3 ng/ml 7 days after estrus.

In animals treated with pFSH, injections of PG induced luteolysis as seen by a fall in progesterone.

Concentrations of progesterone after injections of PG were higher during the period of pFSH treatment than those in the intact estrous cycle from -24 to 16 hr of the LH peak. Progesterone levels increased to high levels of 25 ng/ml 7 days after estrus, significantly higher than intact levels.

Discussion

The present results indicate that peripheral immunoreactive inhibin increased progressively in cattle treated with pFSH for induction of superovulation in agreement with the previous reports in cows (Hasegawa *et al.*, 1987) and ewes after the infusion of FSH (McNeille *et al.*, 1989).

Present results also indicate that plasma inhibin maintained high levels for a longer period than estradiol after the LH surge. The source of inhibin during these period is not clear. Large number of unovulated antral follicles of various sizes were detected after ovulation in FSH primed cows (Pierson and Ginther, 1984; Yadav *et al.*, 1986). Inhibin- α and - β A mRNAs were detected in bovine antral follicles (Rodgers *et al.*, 1989) and granulosa cells from small or atretic follicles produced detectable amounts of inhibin (Henderson *et al.*, 1984). On the other hand, after ovariectomy, half life of serum inhibin for the initial rapid decrease, represented most of the overall decay process, was determined to be 15 min in the female rats (Robertson *et al.*, 1988). Therefore, it was suggested that unovulated follicles secreted inhibin and might be involved in the maintenance of elevated inhibin levels after the LH surge.

Any parallel changes between concentrations of plasma inhibin and progesterone were not observed in pFSH treated cows. These results were consistent with the previous study in which α - and β A-inhibin mRNAs were not detectable in fully developed bovine corpora lutea (Rodgers *et al.*, 1989). Bovine corpus luteum did not produced detectable amounts of inhibin bioactivity (Henderson *et al.*, 1981, 1983).

The present results clearly demonstrated that peaks of the preovulatory surge of FSH but not of LH were significantly suppressed in superovulating cattle, consistent with our preliminary examination (Kaneko *et al.*, 1989). Tsukamoto *et al.* (1986) demonstrated that a marked increase in inhibin secretion completely blocked the periovulatory FSH surge, and further, Sasamoto *et al.* (1987) have demonstrated a quantitative relationship between inhibin secretion and suppression of the preovulatory FSH surge in superovulating rats. Tsonis *et al.* (1988) suggested that the supra physiologic-

al levels of inhibin suppressed the occurrence of the FSH surge in ewes infused with ovine FSH. Therefore, a marked increase in inhibin secretion during the periovulatory period seemed to be responsible for the partial suppression of the FSH surge in the present experiments. Changes in endogenous FSH and LH during pFSH injections (from -72 to -12 hr from the LH peak) could not be determined due to the cross reaction between pFSH and antisera against bovine FSH- β subunit and ovine LH.

Previous reports indicated that a large amount of inhibin partially suppressed the LH surge in the intact (Rush *et al.*, 1981) or in superovulating rats (Tsukamoto *et al.*, 1986; Sasamoto *et al.*, 1987) and superovulating ewes (Tsonis *et al.*, 1987). Moreover, bovine or porcine follicular fluid and 32 kDa porcine inhibin suppressed LH secretion stimulated by luteinizing hormone releasing hormone (LH-RH) in rat pituitary cell culture (de Jong *et al.*, 1979; Fukuda *et al.*, 1987). In the present study, however, a consistent and significant decrease in the preovulatory LH peak was not observed in superovulating cattle. The reasons why neither the partial suppression of the LH surge nor completely inhibition of the FSH surge occurred in superovulating cattle is not clear. Species differences may exist in the potency of inhibin effects on gonadotropin secretion.

It seems unlikely that high levels of estradiol before gonadotropin surges were responsible for the suppression of the FSH surge. Estradiol induced an FSH surge in ovariectomized cattle (Kesner and Convey, 1982; Kesner *et al.*, 1982) probably by increasing pituitary sensitivity to LH-RH due to an increase in the receptors for LH-RH in pituitary cells (Schoenemann *et al.*, 1985; Clarke *et al.*, 1988) and LH-RH pulse frequencies (Clarke and Cummins, 1985). In addition, progesterone also did not seem to contribute to the suppression of the preovulatory FSH surge, since progesterone levels after luteolysis induced by PG were under 1 ng/ml

In summary, the present results indicate (1) that a marked increase in inhibin secretion partially suppressed the preovulatory surge of FSH, (2) that plasma inhibin rose earlier and high levels of plasma inhibin were maintained for a longer period than estradiol, and (3) that the corpus luteum may have no ability to secrete detectable amounts of inhibin, in cattle induced to superovulate with pFSH.

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FSH製剤投与による過排卵誘起牛における末梢血中インヒビンおよび性腺刺激ホルモンの変化

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豚由来の FSH 製剤を投与したウシの末梢血中のインヒビン, FSH, LH, エストラジオールおよびプロジェステロン濃度を測定した。結果は, 同一牛の無処置の発情周期中におけるホルモン濃度の変化と比較した。FSH 投与群では, 排卵前のエストラジオールおよび排卵後のプロジェステロンの血漿中濃度は無処置時に比べて著しく高値であった。血漿中インヒビン濃度は FSH 製剤投与後, 急激に上昇し, LH サージ後もエストラジオールより長時間高値を維持した。血漿中インヒビンと

プロジェステロン濃度は, 過排卵誘起牛では関連した変化を示さなかった。過排卵誘起群では排卵前の FSH サージのピーク値が無処置群の70.4%に抑制されたが, LH サージは抑制されなかった。これらの結果より, FSH 製剤投与後の高濃度のインヒビンが排卵前の FSH サージを抑制するものと推察された。また, これらの知見から, 残存卵胞がインヒビン分泌活性を保持していること, 並びに黄体は過排卵誘起牛ではインヒビンの主要な分泌源ではないことが示唆された。