Primary modulation by oestradiol of the production of an oviduct-specific glycoprotein by the epithelial cells in the oviduct of newborn golden hamsters

H. Abe, T. Satoh and H. Hoshi

Research Institute for the Functional Peptides, Shimojo, Yamagata 990, Japan

The effects of steroid hormones (oestradiol and progesterone) on the appearance of a golden hamster oviduct-specific glycoprotein (GHOGP) in the epithelium of the oviduct of the newborn golden hamster were investigated by immunoblotting and immunohistochemical staining with a GHOGP-specific monoclonal antibody. Newborn golden hamsters (1.5 days old) were injected daily with oestradiol (1 µg) or progesterone (10 µg). An oviductal extract of oestradiol-treated golden hamsters for 4 days apparently immunoreacted with the monoclonal antibody on a broad band with a molecular mass of more than 200 kDa by immunoblotting under reducing conditions. This broad band was consistent with the migration of GHOGP in an extract of adult oviducts. Consecutive daily injections of oestradiol induced the appearance of GHOGP in undifferentiated epithelial cells of the oviduct of neonates. In oviducts of oestradiol-injected animals, GHOGP was first detected in the Golgi region and then increased in amount to fill the supranuclear cytoplasm of the epithelial cells. The inductive effect of oestradiol was dose-dependent. In contrast, consecutive daily injections of progesterone had no effect on the appearance of GHOGP in the oviductal epithelium. The effects of oestradiol and progesterone in organ culture of oviducts were examined *in vitro*, by culturing oviductal organs from 1.5-day-old newborn golden hamsters in chemically defined medium supplemented with oestradiol or progesterone for 2 days and then subjected to immunohistochemical staining. The immunoreaction was detected only in the epithelial cells of oestradiol-treated oviducts at concentrations of $> 0.01 \text{ ng ml}^{-1}$, but not in the cells of untreated and progesterone-treated oviducts. These results indicate that the production of GHOGP in the epithelial cells of the oviduct of newborn golden hamsters is induced by oestradiol both *in vivo* and *in vitro*. It is suggested that oestradiol may be involved in the synthesis of GHOGP in the oviduct during postnatal development of golden hamsters.

Introduction

The mammalian oviduct is a tubular conduit that is the site of extremely important processes, including the final maturation of male gametes, fertilization, and the early development of embryos. The nonciliated secretory cells of the mammalian oviduct produce and secrete oviduct-specific glycoproteins (OGPs) that may regulate or be involved in various reproductive events (Hunter, 1994; Malette *et al.*, 1995a). Some of the OGP associated with the ovulated eggs or developing embryos have been identified and characterized in several species, such as mice (Kapur and Johnson, 1985), golden hamsters (Leveille *et al.*, 1987), pigs (Bui *et al.*, 1993), goats (Abe *et al.*, 1995a), cows (Boice *et al.*, 1992) and monkeys (Boice *et al.*, 1990a). Several OGPs become associated with the surface of spermatozoa (Sutton *et al.*, 1984; McNutt *et al.*, 1992; Abe *et al.*, 1995b) and may, thereby, affect fertilization and other

functions of spermatozoa (King *et al.*, 1994; Boatman and Magnoni, 1995; Abe *et al.*, 1995b; Satoh *et al.*, 1995).

In previous studies, it was demonstrated that an oviductal glycoprotein (GHOGP) from the golden hamster is associated with the zona pellucida of ovulated eggs of golden hamsters (Oikawa *et al.*, 1988; Abe *et al.*, 1992). Monoclonal antibodies (mAbs) specific for this GHOGP were used to clarify the ultrastructural localization of GHOGP in the oviductal epithelium, and ultrastructural evidence was obtained for an association between GHOGP and the zona pellucida or perivitelline matrix of the golden hamster egg (Abe and Oikawa, 1990a, 1991). In sexually mature golden hamsters, GHOGP is secreted primarily by ampullary and isthmic secretory cells and then accumulated in the ovarian bursal sac. These observations suggest regional differences in the production of GHOGP by epithelial cells (Abe and Oikawa, 1991). However, the critical functions of the GHOGP remain to be determined.

A recent study showed that consecutive injections of oestradiol induced the cytodifferentiation of the secretory cells

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in the oviduct of newborn golden hamsters, whereas injections of progesterone significantly enhanced the rate of appearance of ciliated cells but not of secretory cells (Abe and Oikawa, 1993). These findings suggest that the cytodifferentiation of epithelial cells in the oviduct of newborn golden hamsters is regulated by steroid hormones. During postnatal development, GHOGP appears in the epithelium of the oviduct between 9 and 10 days after birth (Abe and Oikawa, 1990b). This study also suggested a relationship between the morphological differentiation of secretory cells and the appearance of the GHOGP in the secretory cells of the oviduct of newborn golden hamsters. In prepubertal female golden hamsters, a significant increase in FSH occurred in serum between 7 and 12 days after birth (Vomachka and Greenwald, 1979) and the binding of this gonadotrophin was first detected in the granulosa cells of small preantral follicles at 10 days after birth (Shaha and Greenwald, 1983). These studies suggest that the production of steroid hormones by the ovary occurs approximately at 10 days after birth, and provide the basis for the hypothesis that the biosynthesis of GHOGP is initiated by ovarian steroid hormones in the oviductal epithelium of golden hamsters during postnatal development.

Study of the influence of hormones on the initiation of GHOGP biosynthesis in the oviduct of the newborn golden hamster is important for clarifying the physiological function of this glycoprotein and the functional maturation of the oviduct. The present study was designed to investigate the hormonal control of GHOGP production in the epithelial cells of the oviduct in newborn golden hamsters. An immunohistochemical examination was undertaken to determine the effects of oestradiol and progesterone on the appearance of GHOGP in the oviducts of hormone-injected newborn golden hamsters and in the oviducts of neonates cultured in chemically defined medium *in vitro*.

Materials and Methods

Animals and hormone treatments

Golden hamsters (*Mesocricetus auratus*) were supplied with water and a commercial diet *ad libitum*. They were maintained at $23 \pm 2^\circ\text{C}$ and a relative humidity of 50–60%, with a controlled light cycle of 12 h of fluorescent light per day.

Oestradiol (Sigma Chemicals, St Louis, MO) and progesterone (Nakarai Chemicals, Kyoto) were dissolved in sesame oil and stored at -20°C . The 1.5-day-old female golden hamsters were injected daily with oestradiol or progesterone at 12:00 h each day. The injection volume was 0.01 ml per hamster for each hormone; i.p. injections were administered from the dorsal side. Control hamsters were injected with sesame oil alone in the same manner. Animals were killed by cervical dislocation 24 h after the last injection and their oviducts were excised.

Monoclonal antibody

In all immunolabelling experiments, culture supernatants that contained mAb C11E8, raised against materials obtained from the golden hamster oviduct (Abe *et al.*, 1992), were used for the detection of GHOGP. The characterization of mAb C11E8 was

described by Abe *et al.* (1992). In western blotting analysis, mAb C11E8 bound specifically to a broad band that corresponded to macromolecules of > 200 kDa in oviductal extracts of the golden hamster that had been subjected to SDS-PAGE under reducing conditions. During indirect enzyme immunostaining, mAb C11B8 reacted with epithelial cells of the oviduct and, to a lesser extent, with some other tissues of the golden hamster. mAb C11E8 reacted selectively with the zona pellucida of oviductal eggs of golden hamsters but not with that of ovarian eggs.

Electrophoresis and immunoblotting

The biochemical characteristics of antigens that crossreacted with the mAb C11E8 were determined by immunoblotting. Tissues were homogenized on ice with a glass homogenizer in PBS (pH 7.4) that contained 1 mmol phenylmethylsulfonyl fluoride l^{-1} (PMSF; Sigma). The suspensions were centrifuged at $20\,000\text{ g}$ for 20 min. Aliquots of the resulting supernatants, containing 5–10 μg protein, were separated by SDS-PAGE (Laemmli, 1970) on gradient gels (3–15% polyacrylamide) and were transferred to nitrocellulose membranes. The membranes (blots) were washed in PBS and incubated in 3% (w/v) BSA in PBS at 37°C for 1 h or at 4°C overnight. The blots were then incubated with the culture supernatant that contained the mAb (concentration of IgG, $60\text{ }\mu\text{g ml}^{-1}$) as the primary antibody for 1–2 h at room temperature and washed in PBS. After the washing step, the second antibody, horseradish peroxidase (HRP)-conjugated antibodies raised in rabbit against mouse immunoglobulin (DAKOPATTS, Glostrup), diluted 1:500 in PBS, was allowed to react with the blots for 1 h at room temperature. After washing in PBS, the blots were incubated with the colour-development solution, Tris-HCl buffer (pH 7.2) that contained 0.5% (w/v) diaminobenzidine (DAB) and 0.025% H_2O_2 . The blots were then washed in water and air-dried.

Immunohistochemical staining

Oviducts were fixed in 10% formalin in distilled water. The specimens were embedded in paraffin wax and cut at $5\text{ }\mu\text{m}$ thickness. Immunohistochemical staining was performed by the methods described by Abe and Oikawa (1990b, 1991). Deparaffinized and rehydrated sections were treated with 1% H_2O_2 in methanol for 10 min at room temperature to eliminate the endogenous peroxidase activity. After they had been washed in distilled water and PBS, the sections were treated with 3% BSA in PBS for 30 min at 37°C to reduce the extent of nonspecific binding of the primary antibody. The sections were then incubated with mAb C11E8 as the primary antibody for 1–2 h at room temperature. After they had been washed in PBS (three times, 5 min each), the sections were incubated with HRP-conjugated antibodies raised in rabbit against mouse immunoglobulin, which had been diluted 1:50 in PBS, as the second antibody. The sections were then washed with PBS and incubated with the DAB containing colour-development solution for 10 min at room temperature. The colour reaction was stopped by washing the sections with PBS. After the development of colour, the sections were washed thoroughly in water,

Fig. 1. Immunoblots of golden hamster oviductal extracts after fractionation by SDS-PAGE under reducing conditions and immunostaining with mAb C11E8. Lane A: extract from an adult oviduct. Lanes B–D: extracts from oviducts after four consecutive daily treatments with oestradiol (lane B), progesterone (lane C), or vehicle (lane D).

Fig. 2. The percentages of oviduct-specific glycoprotein-producing oviducts (GP-PO) in golden hamsters subjected to consecutive daily treatments with 1 µg oestradiol (●), 10 µg progesterone (■), or vehicle (○). The numbers in parentheses represent the numbers of oviducts examined.

counterstained with 1% (w/v) methyl green and mounted in Canada balsam for examination under a light microscope (BH2; Olympus Optical Co., Ltd, Tokyo).

Controls for immunolabelling

In control experiments, sections or blots were incubated with the supernatant from a culture of the myeloma cells that

Fig. 3. The percentage of oviduct-specific glycoprotein-producing oviducts (GP-PO) in golden hamsters after two consecutive daily treatments with oestradiol at various doses. The numbers in parentheses represent the numbers of oviducts examined.

had been used for the preparation of the hybridomas or with a mAb directed against a surface antigen of sea urchin spermatozoa (an IgG that had been prepared in our laboratory by the same method as that used to prepare mAb C11E8) instead of the supernatant that contained mAb C11E8.

Organ culture of oviducts

Oviducts were excised from 1.5-day-old female golden hamsters under sterile conditions. The oviducts were dissected from the uterus and ovary, and they were trimmed to remove the fat and connective tissue under a stereoscopic microscope. The tissues were rinsed twice with Ca²⁺- and Mg²⁺-free PBS and transverse segments of the oviducts, of approximately 2 mm length, were cut from the ampullary to the isthmic region. The segments of oviducts were distributed in the wells of a 24-well microplate (Nunc, Roskilde) and were cultured in TCM-199 (Nissui Pharmaceutical Co., Tokyo) at 37°C in a humidified atmosphere of 95% air: 5% CO₂ for 2 days. The oviducts were incubated in TCM-199 plus oestradiol, progesterone, or a solvent control (0.1% ethanol). After the incubation, the oviducts were fixed in 10% formalin in distilled water, embedded in paraffin wax, and cut at 5 µm thickness. The sections were subjected to immunohistochemical staining as described above.

Results

Proteins with a broad range of molecular masses above 200 kDa in the oviductal extract obtained from golden

Fig. 4. Immunostaining with mAb C11E8 of sections of oviducts from golden hamsters that had been subjected to consecutive daily treatments with 1 μ g oestradiol (a, b), 10 μ g progesterone (c), or vehicle (d). (a) Immunoreactive materials (arrows) appeared in the oviductal epithelium (E) after 1 day of treatment with oestradiol. (b) Hypertrophy of the epithelial cells was observed and large amounts of immunoreactive material filled the supranuclear cytoplasm (double arrows) in the oviduct after 4 days of treatment with oestradiol. Immunostaining with mAb C11E8 was negative in the oviductal epithelium after 4 days of treatment with progesterone (c) or with vehicle (d). Lu, lumen; S, stroma. Scale bars represent 50 μ m.

hamsters after 4 days of consecutive daily treatments with 1 μ g oestradiol were stained by mAb C11E8 (Fig. 1, lane 2). This band showed the same pattern of migration as crossreactive materials in an extract of adult oviducts (Fig. 1, lane 1). No reactivity with mAb C11E8 was observed with oviductal extract from golden hamsters after 4 days of consecutive injections of 10 μ g of progesterone (Fig. 1, lane 3) or in an extract from control animals (Fig. 1, lane 4).

A large number of oviducts of different golden hamsters were fixed after consecutive daily treatments with oestradiol (1 μ g), progesterone (10 μ g), or vehicle (control). They were immunostained with mAb C11E8 and examined for the presence of immunoreactive GHOGP from the ampulla to the isthmus under a light microscope. If even a faint reaction was found in the epithelium of a given oviduct, it was judged to be a glycoprotein-producing oviduct (GP-PO). The percentages of

Table 1. Effects of oestradiol and progesterone on the production of oviduct-specific glycoprotein in the oviducts of newborn golden hamsters cultured in chemically defined medium *in vitro*

Hormone	Concentration (ng ml ⁻¹)	Number of GP-PO/ number of oviducts examined (%)
Control	—	0/12 (0)
Oestradiol	1 × 10 ⁻⁴	0/9 (0)
	0.01	15/16 (94.0)
	1	9/10 (90.0)
	100	9/11 (81.8)
Progesterone	100	0/10 (0)
	1 × 10 ⁻⁴	0/9 (0)

GP-PO, glycoprotein-producing oviduct, in which immunostaining with mAb C11E8 was recognized.

oviducts that were judged to be GP-PO at various times after the start of hormone treatments are shown (Fig. 2). On day 1 of treatment with oestradiol, most oviducts (94%) were judged to be GP-PO. After two consecutive daily treatments with oestradiol, GHOGP was detected in the epithelium of all oviducts examined. In contrast, materials reacting with mAb C11E8 were never detected in the epithelium of oviducts from animals subjected to four consecutive daily treatments with progesterone or from control animals.

The golden hamsters were injected with oestradiol at various doses (0.1 ng, 10 ng, and 1 µg) after two consecutive daily treatments and the percentages of GP-PO were determined by immunohistochemical staining (Fig. 3). Treatment with oestradiol increased the percentage of GP-PO in a dose-dependent manner.

The presence of materials that reacted with mAb C11E8 in the oviductal epithelium at various times after the start of consecutive daily treatments with oestradiol (1 µg) or progesterone (10 µg) are shown (Fig. 4). After two consecutive daily treatments with oestradiol, the immunohistochemical reaction was observed in the oviductal epithelium, in particular, in the apical region and the Golgi area of the epithelial cells (Fig. 4a). After four consecutive daily treatments with oestradiol, most of the epithelial cells became hypertrophied and their supranuclear cytoplasm was abundant with mAb C11E8-reactive materials (Fig. 4b). In contrast, the oviducts from progesterone-treated or control animals did not react with mAb C11E8 and the hypertrophy of epithelial cells was not observed (Fig. 4c, d).

Oviducts from 1.5-day-old hamsters were cultured in chemically defined medium supplemented with oestradiol or progesterone at various concentrations for 2 days and the oviducts were subjected to immunohistochemical staining to examine the effect of oestradiol and progesterone on the appearance of GHOGP in the oviduct *in vitro*. The numbers and percentages of oviducts that reacted with mAb C11E8 are shown (Table 1). A large number of GP-PO were observed in many segments of oviducts *in vitro* in the presence of oestradiol. No reaction was detected in segments of oviducts in the presence of progesterone or in control medium.

Fig. 5. Immunostaining with mAb C11E8 of sections of oviducts from 1.5-day-old golden hamsters after culture in medium containing 100 ng oestradiol ml⁻¹ (a) or 100 ng progesterone ml⁻¹ (b), or in control medium (c) for 2 days. (a) Immunoreactive material (arrows) was visible in the supranuclear cytoplasm of epithelial cells (E) of oviducts that had been cultured in oestradiol-containing medium. No immunohistochemical staining was observed in oviducts that had been cultured in medium that contained progesterone (b) or in control medium (c). S, stroma. Scale bar represents 50 µm.

The presence of materials that reacted with mAb C11E8 in the epithelium of oviducts when they were cultured in oestradiol (100 ng ml⁻¹) or progesterone (100 ng ml⁻¹) for 2 days are shown (Fig. 5). The reactive materials were detected in the apical region and supranuclear cytoplasm of epithelial cells, as they were in the oviducts of oestradiol-injected neonatal hamsters *in vivo* (Fig. 5a). The oviducts cultured in the presence of progesterone or in the control medium indicated no crossreactivity with mAb C11E8 (Fig. 5b, c).

No specific reaction was observed in any sections or on any blots with the mAb directed against a surface antigen of sea urchin spermatozoa or with the supernatant from myeloma cell cultures (data not shown).

Discussion

Mammalian oviducts synthesize and secrete specific glycoproteins. The rates of biosynthesis of these OGP's fluctuate during the oestrous cycle and seem likely to be regulated by steroid hormones in many mammalian species, including pigs (Buhi *et al.*, 1992), sheep (Murray, 1992, 1993), cows (Boice *et al.*, 1990b; Abe *et al.*, 1993; Sendai *et al.*, 1994), primates (Fazleabas and Verhage, 1986; Verhage *et al.*, 1989) and humans (Verhage *et al.*, 1988). In most species, the rate of OGP synthesis is oestradiol-dependent. However, the previous results were obtained from studies with mature animals, and limited information is available about any possible correlation between oestradiol and the onset of the biosynthesis of GHOGP during ontogeny. The results of the present study revealed that exogenous oestradiol induces the appearance of GHOGP in epithelial cells of the oviduct of newborn golden hamsters. In addition, a recent indirect immunofluorescence study demonstrated that the production of a GHOGP, oviductin, which is similar to the glycoprotein investigated in the present study, was induced in oestradiol-treated prepubertal animals (Malette *et al.*, 1995b). These findings strongly suggest that oestradiol is of primary importance for the production of GHOGPs by secretory cells of the oviduct during postnatal development in golden hamsters, although it remains to be determined whether the initiation of GHOGP production, which normally occurs in oviducts of newborn golden hamsters *in vivo*, is induced in an oestrogen-dependent manner.

A previous study demonstrated that the marked morphological differentiation of oviductal epithelial cells and of secretory cells, in particular, occurred approximately 10 days after birth (Abe and Oikawa, 1989). Subsequently, it was shown that GHOGP can be detected in the Golgi apparatus and secretory granules of these developing secretory cells at the same time, suggesting a coincidence between the morphological differentiation of secretory cells and the initiation of the biosynthesis of GHOGP in the golden hamster oviduct during postnatal development (Abe and Oikawa, 1990b). Exogenous oestradiol induces the morphological differentiation of secretory cells in the oviducts of newborn golden hamsters (Abe and Oikawa, 1993). Oestradiol also induces various ultrastructural changes, such as the development of Golgi apparatus and rough endoplasmic reticulum and the appearance of secretory granules, indicative of the differentiation to secretory cells, in undifferentiated epithelial cells. The present study demonstrates that injection of oestradiol induces the appearance of GHOGP in the Golgi area of undifferentiated epithelial cells in oviducts of neonatal golden hamsters. The results strongly suggest that there is a correlation between the beginning of cytodifferentiation and the onset of production of GHOGP in the oviductal secretory cells of newborn golden hamsters.

In organ culture, oestradiol also induced the appearance of GHOGP in the epithelial cells of oviducts cultured in the chemically defined medium, as occurred *in vivo* in oviducts of

oestradiol-injected golden hamsters. Thus, it appears that oestradiol acts directly on the oviduct, although it is unclear whether the epithelial (secretory) cells of the oviduct are the direct target of oestradiol. It is well known that the actions of steroid hormones are mediated by their intracellular receptors. However, previous studies have suggested that intercellular mediators must also be involved in the actions of steroid hormones in the reproductive organs (Cunha *et al.*, 1985; Brenner *et al.*, 1990). In particular, it has been suggested that some hormonal effects of sex steroids on the epithelium are mediated indirectly, through the stroma, in the oviduct of the rhesus monkey (Brenner *et al.*, 1990). The inducible mechanisms of oestradiol on the biosynthesis of GHOGP in the secretory cells of the golden hamster oviduct require further analysis, such as an investigation of putative receptors for oestradiol in the oviductal epithelium.

The biological functions of OGP's have been studied in many species (King *et al.*, 1994; Abe *et al.*, 1995b; Gandolfi, 1995; O'Day-Bowman *et al.*, 1996; Hill *et al.*, 1997; Schmidt *et al.*, 1997; Vansteenbrugge *et al.*, 1997). It has been suggested that a GHOGP (oviductin) may influence the penetration of spermatozoa (Boatman and Magnoni, 1995) or the interaction between spermatozoa and the zona pellucida (Kimura *et al.*, 1994) during fertilization *in vitro*. However, the critical biological functions of GHOGPs *in vivo* remain unclear. The production of GHOGP in the oviduct of sexually mature animals has not yet been shown to be oestrogen-dependent, and strong immunohistochemical staining by mAb C11E8 has been observed in the epithelium of the oviduct of adult golden hamsters throughout the oestrous cycle (H. Abe and H. Hoshi, unpublished). Ovarian steroid hormones control the functional state of the epithelium of the mammalian oviduct, for example the secretory activity (Brenner and Maslar, 1988). If the exact functional role of GHOGP in reproductive events are to be determined, the influences of various hormones on the biosynthesis of GHOGP in the epithelial cells of the oviduct need to be investigated in detail.

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