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Influence of photoperiod on the ultrastructure of the hypophysial pars tuberalis of the Djungarian hamster, *Phodopus sungorus*

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Summary. Conspicuous cytological differences are found between specific secretory cells of the hypophysial pars tuberalis of Djungarian hamsters exposed to long and short photoperiods. The cells differ with respect to the shapes of perikarya and nuclei and show diverse amounts of secretory granules, lysosome-like bodies and glycogen.

Key words: Photoperiods – Pituitary gland, pars tuberalis – Ultrastructure – *Phodopus sungorus*

In the hypophysial pars tuberalis at least two types of cells are discernible as shown in several mammalian species and in the chicken and newt (Dellmann et al. 1974). A comparison with cell types of the pars distalis is difficult since ultrastructural features differ in both areas, and also because immunocytochemical examinations of the pars tuberalis have led to controversial findings and indicate species differences (Gross 1983, Girod 1983). However, the presence of LH- and FSH-containing cells seems to be established, at least in the rat (Baker and Yu 1975, Gross 1978) and rhesus monkey (Antunes et al. 1979). The number of these gonadotropic cells is small and increases gradually from rostral to caudal regions. In addition, recent results have also ascertained the presence of TSH-producing cells in the pars tuberalis of rat (Gross 1983) and man (Baker 1977, Osamura and Watanabe 1978), and thereby suggest a specific endocrine activity.

Dellmann et al. (1974) mentioned regressive changes in secretory cells of the pars tuberalis during hibernation in the garden doormouse, and thus, for the first time, drew attention to possible ultrastructural alterations dependent upon the annual cycle. Under natural illumination, Djungarian hamsters show distinct annual changes in body weight and pelage color as well as in structure and function of the reproductive organs (Hoffmann 1979). Under experimental conditions, these changes are induced by alteration in the duration of the daily photoperiod. Short photoperiods induce regression of gonads and accessory glands, decrease in body weight and molting into winter pelage; long photoperiods have the opposite effects (Hoffmann 1981a, b). Changes in plasma and pituitary levels of gonadotropins and of prolactin induced by photoperiods have also been reported in this species (Simpson et al. 1982; Yellon and Goldman 1984). Results of several experiments suggest that the photoperiodic effects are mediated by melatonin secreted from the pineal organ (Hoffmann 1981a, b; Carter and Goldman 1983a, b). The hypothalamus, in connection with the pituitary, seems to act as the main effector organ for melatonin. As a first step in an analysis of hypothalamic pituitary complex we have examined the ultrastructural aspects of the hypophysial pars tuberalis in Djungarian hamsters maintained under long and short photoperiods.

Materials and methods

Adult (6–7 months old) male Djungarian hamsters were used. Half of them had been maintained under long photoperiods (LD 16:8) from birth and, accordingly, were in physiological summer condition. Testicular weight was high ($M \pm SE$: 831 ± 25 mg; $N=6$) as was body weight (44.6 ± 0.7 g); all animals were in summer pelage. The other half had also been raised under long photoperiods, but was maintained under short photoperiods (LD 8:16) for the last 12 weeks. Accordingly, these animals were in physiological winter condition. Testes had regressed (74 ± 8 mg; $N=6$), body weight had decreased (32.8 ± 1.3 g), and the animals had started to change into winter coat.

After this pre-treatment all animals were sacrificed under Nembutal (Na pentobarbital) anaesthesia (dosage: 400 mg/kg body weight i.p.) by intracardial perfusion with the following solutions: 1. Rheomacrodex 10% containing liquemin; 2.2% glutaraldehyde and 2.5% paraformaldehyde in 0.1 m phosphate buffer (pH 7.35). Two hours after perfusion brains were dissected out; tissue blocks containing medial hypothalamus with hypophysis were postfixed in 1% OsO_4, dehydrated in alcohol, and embedded in Epon or Durcupan. Alternating semithin and ultrathin frontal sections were cut from the rostral border of the median eminence with pars tuberalis up to formation of the infundibular stem. Semithin sections were stained with toluidine blue and pyronin G (Ito and Winchester 1963). Ultrathin sections were contrasted with uranyl acetate and lead citrate (Reynolds 1963). From each animal about 10 semithin and 10 ultrathin sections were examined by light and electron

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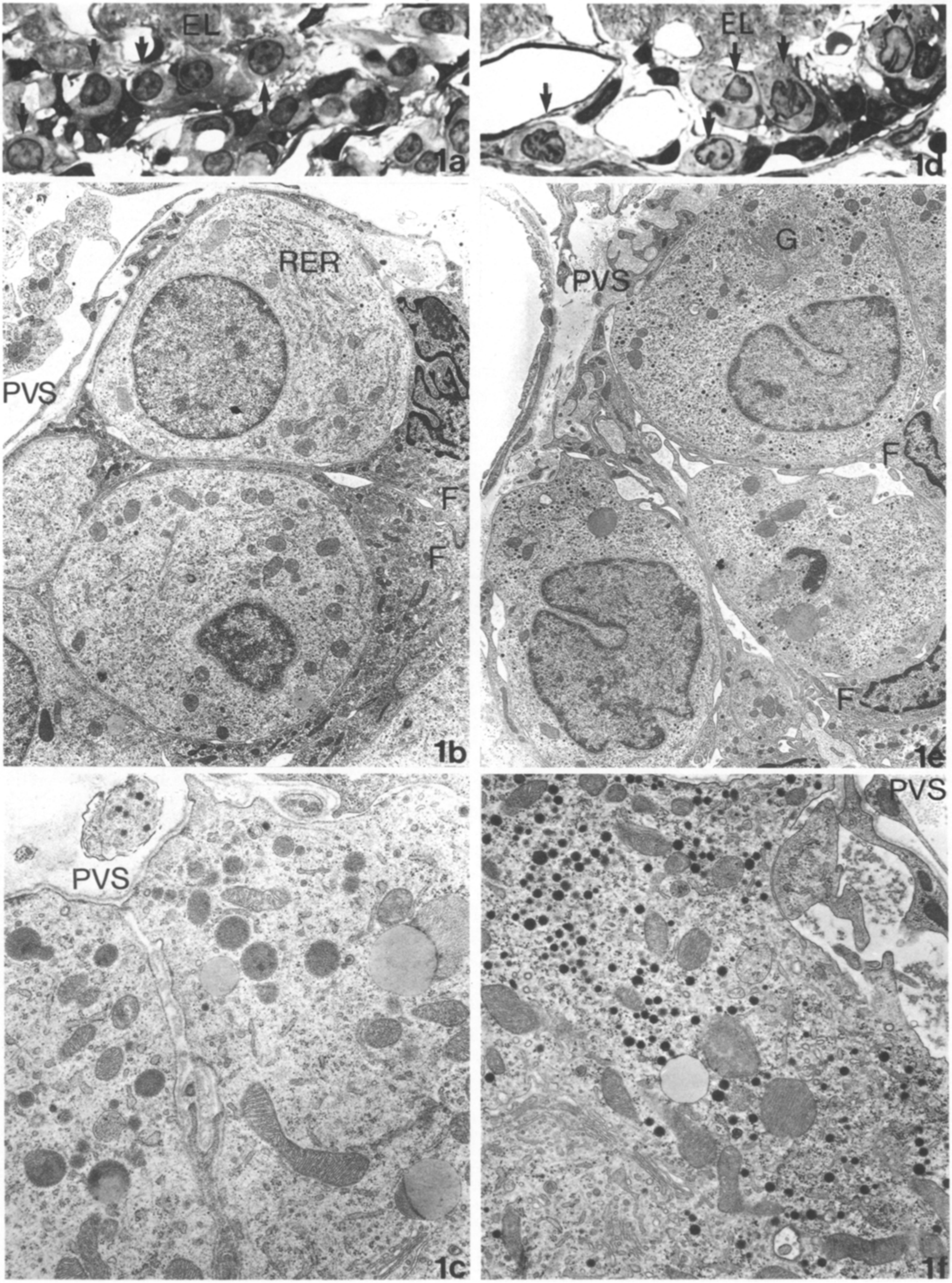
Dedicated to Professor H. Rollhäuser, Münster, on the occasion of his 65th birthday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microscopy. Corresponding areas of the pars tuberalis were compared.

Results and discussion

General morphological characteristics of the pars tuberalis

As in other mammals (Dellmann et al. 1974) two types of cells are discernible in the cell cords of the pars tuberalis surrounding the median eminence in Djungarian hamsters:

1. Specific secretory cells with clear signs of an endocrine activity including the presence of secretory granules aggregated in regions of the cytoplasm displaying contact with the perivascular space of portal vessels (Fig. 1b, e).

2. Follicular cells with an undifferentiated appearance devoid of any secretory granules. These cells are small, elongated and arranged in concentric groups surrounding cavities of varying extension. These cavities frequently are filled with an amorphous dense material. Follicular cells (Fig. 1b, e) also give rise to long, small processes lining the inner and outer surface of the pars tuberalis and surrounding specific secretory cells with exception of their vascular poles which contain secretory products.

Pars tuberalis. Hamsters raised under long photoperiods (Fig. 1a–c)

The majority of specific secretory cells shows round to oval, light nuclei with smooth contours. Perikarya often have rounded or oval contours (Fig. 1a, b). Lysosome-like bodies and lipid inclusions are frequently observed, whereas only few secretory granules with a diameter of 90–130 nm are found. All these inclusions are primarily located in peripheral parts of the cytoplasm facing the vascular space (Fig. 1c). A well-developed rough endoplasmic reticulum, many mitochondria and Golgi complexes are also characteristic of these cells.

Pars tuberalis. Hamsters maintained under short photoperiods (Fig. 1d–f)

In contrast to animals held under long photoperiods, specific secretory cells of animals exposed to short photoperiods exhibit irregularly formed nuclei with deep invaginations of the nuclear membrane (Fig. 1d, e). Outlines of the perikarya are often irregular, angular and show processes directed to the vascular space. An additional conspicuous difference is the high number of secretory granules measuring 100–180 nm in diameter found in the periphery of the cells (Fig. 1e, f). The presence of lysosome-like bodies is reduced. No apparent morphological differences are found concerning Golgi zones or lipid inclusions, whereas the amount of rough endoplasmic reticulum is markedly reduced. High amounts of glycogen are observed in many cells.

Conspicuous alterations of the follicular cells were not found.

The differences described in the cytological features of specific secretory cells in animals exposed to long and short photoperiods are found over the whole extent of the pars tuberalis from the rostral beginning up to the formation of the infundibular stem. They indicate markedly different functional stages of the pars tuberalis in summer and in winter. Short photoperiods induced alterations that speak in favor of a change in secretory activity. The storage of high amounts of granules suggests a "reserve stage" (Girod 1984) of these endocrine cells. There are no signs of increased lysosomal activity ("crinophagy") indicative of a suppression of excretion (Girod 1984). The decrease of the amount of rough endoplasmic reticulum as compared with the secretory cells from animals under long photoperiods suggests a reduction of protein synthesis.

Short photoperiods, in the golden hamster, regularly result in a depression of LH and FSH in plasma as well as in the pars distalis of the pituitary (Berndtson and Desjardins 1974, Reiter and Johnson 1974). Moreover, studies in the Djungarian hamster show an increase in plasma and pituitary levels of LH and FSH in young animals after transfer to long photoperiods (Simpson et al. 1982; Yellon and Goldman 1984).

Ultrastructural alterations in the pars tuberalis caused by different physiological conditions have only been mentioned by Dellmann et al. (1974) for the garden doormouse. These authors found a reduction of secretory granules in hibernating animals as well as a decrease of the amount of rough endoplasmatic reticulum and an aggregation of increasing amounts of glycogen granules.

From immunocytochemical investigations it is known that, after castration and especially following hypophysectomy, LH- and FSH-producing cells of the pars tuberalis become hypertrophic and hyperplastic (Gross and Page 1979; Gross 1983). Gross (1983) reported that, in the rat, the activity of TSH-producing cells decreased after hypophysectomy. These cells seem to predominate among the secretory cells of the pars tuberalis in this species. Photoperiod also influences the pituitary-thyroid axis as was reported for the golden hamster; a suppression by short photoperiods was found (Vriend 1983).

In general, our results support the assumption that the pars tuberalis has a specific function differing from that of the pars distalis. A better interpretation will be possible

Fig. 1a–c. Characteristic aspects of pars tuberalis of hamsters maintained under long photoperiods. **a** Two types of cells are discernible: secretory cells with oval nuclei (↑) and follicular cells with dark, elongated nuclei. External layer of the median eminence (*EL*). Semithin section. ×825. **b** Secretory cells with typical smooth outlines of perikarya and nuclei, a well-developed rough endoplasmic reticulum (*RER*) and few secretory granules. Lamellar processes of follicular cells (*F*) surround secretory cells. Perivascular space (*PVS*). ×7360. **c** Portions of secretory cells facing perivascular space (*PVS*) containing many lysosome-like bodies and lipid droplets but few secretory granules. ×16000. **d–f.** Characteristic aspects of pars tuberalis of hamsters raised under short photoperiods. **d** Nuclei of secretory cells (↑) are irregularly formed and show deep invaginations. Follicular cells without altered shape. External layer of the median eminence (*EL*). Semithin section. ×825. **e** Cytoplasm of secretory cells is filled with numerous secretory granules. Note the nuclear invaginations. Golgi apparatus (*G*). Follicular cells (*F*). Perivascular space (*PVS*). ×7360. **f** Vascular process of a secretory cell filled with secretory granules, mitochondria and glycogen. Perivascular space (*PVS*). ×16000 after further morphometric and immunocytochemical investigations including the pars distalis.

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