Transformed centrioles in adult and aged cat pinealocytes

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Abstract

The ultrastructural modifications of the centrioles in adult and aged cat pinealocytes are described. In the 7-month-old cat, pinealocytes show centrioles of normal structure. From the first year onwards, the centriole undergoes transformation including elongation and wall disruption. In old cats, most if not all of the centrioles are transformed. Centriolar transformation affects the pinealocytes exclusively, and may possibly be considered as an ultrastructural marker of this cell type.

Introduction

The centrioles of pinealocytes in different species of rodents have a peculiar configuration. Wolfe (1965) first described 'microtubular sheaves' in the centrosomal region of adult rat pinealocytes, and considered them as centriolar derivatives. Centriolar transformation into microtubular sheaves is produced during differentiation of rat pinealocytes (Lin, 1970; Calvo and Boya, 1983). Transformed centrioles, *i.e.* those elongated with a ruptured wall, have been described not only in rats but also in the adult guinea pig (Lin, 1972), and the adult golden hamster (Bucana *et al.*, 1974; Lin *et al.*, 1987).

In the course of studies on the ultrastructure of the pineal gland of adult and aged cats, we detected transformed centrioles in the pinealocytes, a finding not previously described in this species. In the present work, the characteristics of the centriolar transformation in cat pinealocytes are discussed.

Materials and methods

Ten healthy cats of both sexes were used and kept under natural lighting conditions (approximately 40° N latitude). Two cats (female and male) were sacrificed at each of 7 months, 1, 2, 4, and 12 years of age. The animals were anaesthetized with sodium penthobarbital and killed at 1100 h during July, August and September. The pineal gland was carefully removed and fixed by immersion in cold 3% glutaraldehyde in 0.1 M phosphate buffer. The tissue blocks were rinsed in 0.1 M phosphate buffer, postfixed in 1% osmium tetroxide in the same buffer and embedded in Vestopal W. Ultrathin sections were stained with uranyl acetate and lead citrate and examined in a Philips EM201.

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Results

In all phases studied, transformed centrioles in the cat pinealocytes were evident. They appeared more frequently with age. Pineal astrocytes never showed centriolar transformation in any of the phases investigated.

At the 7th postnatal month, pinealocytes showed isolated centrioles or more frequently diplosomes of normal structure, as previously described (Wartenberg, 1968). They occurred in the cell body, associated with the Golgi apparatus, generally close to the nucleus. Occasionally, the centrioles were located superficially, in relation to a short cilium in the pinealocytes. Modified centrioles were very seldom detected at this age.

From the first year of age onwards, the frequency of transformed centrioles in pinealocytes increased. Initially, diplosomes were observed with one of the centrioles showing a normal structure while the other was under transformation (Figure 1). The centriolar transformation was nearly complete in the oldest cats examined (Figures 2 to 7), in which it was very difficult to find either structurally normal centrioles or cilia.

The transformation of the centrioles in cat pinealocytes consisted of two modifications: centriolar elongation and disruption of the wall. In longitudinal sections, the transformed centrioles appeared as tubular structures >2.0—2.5 μm in length, showing frequent wall discontinuities (Figure 2). The outer surface of the centriolar wall showed a striped border (Figure 5), as described in rodents by Lin (1972). The rupture and dissociation of the centriolar wall determined open profiles in transverse and oblique sections (Figures 3, 4 and 5). Occasionally nine microtubular triplets were identified in these open profiles (Figure 6). Two or three separate structures containing triplets of microtubules (Figure 3) were frequently discovered. Densely packed microfibrils associated with the transformed centrioles were also found (Figure 3), together with some unusual configurations (Figure 7).

Opposite

Figure 1 One-year-old male. Diplosomes near the Golgi complex. One of the centrioles looks normal while the other is fragmented (arrows). x12,000.

Figure 2 Two-year-old male. Diplosome showing an elongation in one of the centrioles. x14,400.

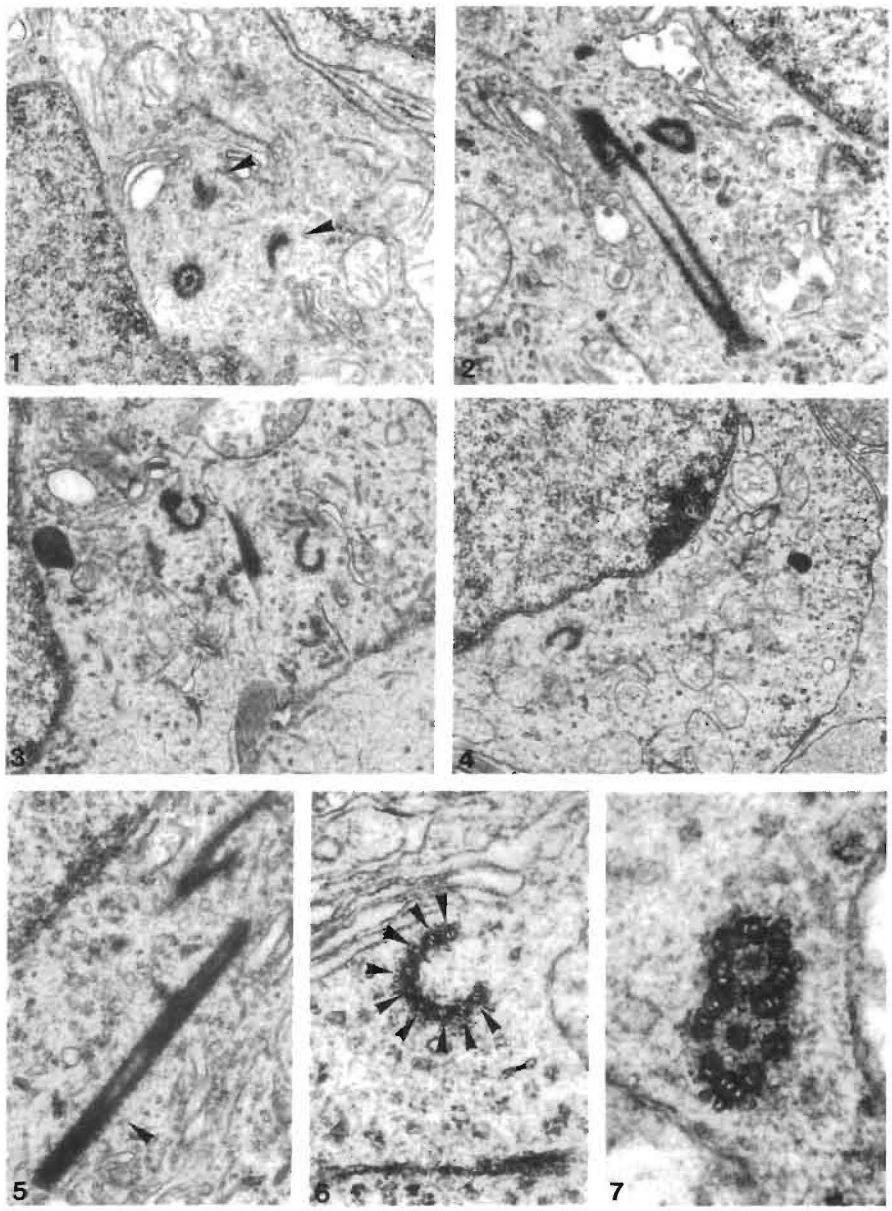
Figure 3 Four-year-old female. Two centrioles with ruptured walls, and between them a dense material resembling a tangentially sectioned centriole. x14,000.

Figure 4 Twelve-year-old female. Nuclear centrioles juxtaposed and showing ruptured walls. x12,800.

Figure 5 Four-year-old male. Elongated centrioles with striped borders (arrow). x20,000.

Figure 6 Twelve-year-old female. Ruptured centriole wall. Arrows indicate the position of the nine microtubular triplets. x28,800.

Figure 7 Twelve-year-old male. Two merged centriole-like structures whose walls are formed by microtubular triplets. x45,600.



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Discussion

The presence of transformed centrioles in the pinealocytes of adult and aged cat pinealocytes has been demonstrated. Such modifications have not been described by previous workers (Duncan and Micheletti, 1966; Wartenberg, 1968). Centriolar ultrastructural modifications appear to be exclusive to pinealocytes. Adjacent pineal astrocytes show normal centrioles even in the oldest cats studied. In rodents, modified centrioles were also exclusive to the pinealocytes (Wolfe, 1965; Lin, 1970, 1972; Calvo and Boya, 1984; Bucana *et al.*, 1974; Lin *et al.*, 1987).

This work is the first description of centriolar transformation in the pinealocytes of a non-rodent mammal, although it may occur in mammals other than rodents and cats. Ultrastructural studies on the pineal gland of species other than rodents are few (for review see Vollrath, 1981; Karasek, 1983). Moreover, such studies were always performed on young or adult animals, and no evidence of transformed centrioles in the pineal gland of adult dogs was found by Calvo *et al.* (1988). Centriolar transformation in cat pinealocytes was seen mainly in the oldest animals.

Centriolar transformation in cat pinealocytes includes elongation and rupture of the centriolar wall, similar to previous descriptions for rodents (Wolfe, 1965; Lin, 1970, 1972; Calvo and Boya, 1983; Bucana *et al.*, 1974; Lin *et al.*, 1987). In cats, most centrioles showed a simple opening, with little tendency to fragmentation in multiple bundles or 'microtubular sheaves', as has been described for rodents (Wolfe, 1965; Lin, 1970, 1972; Calvo and Boya, 1984; Bucana *et al.*, 1974; Lin *et al.*, 1987).

The mechanism of centriolar transformation is unknown. Alteration of the proteins linking the microtubular triplets may lead to a complete separation of all the triplets rather than a mere wall rupture at a single point. On the other hand, the rupture of the wall of the centriole is associated with elongation. Perhaps the growth of the centriole beyond its normal size may elicit some kind of mechanical stress resulting in wall rupture.

The significance of centriolar transformation in the pinealocytes is unknown. In those species showing centriolar transformation (rat, guinea-pig, hamster, cat), cilia are rare or absent in pinealocytes (for review see Vollrath, 1981). Phylogenetically, mammalian pinealocytes were derived from sensorial photoreceptor cells present in non-mammalian vertebrates linked to the sensorial cell line defined by Collin (1971). The presence of centrioles and cilia with a 9 + 0 pattern in different mammalian species (Pevet and Saboureau, 1973; Pevet, 1974; Pevet and Collin, 1976; Pevet *et al.*, 1976; Pevet and Racey, 1981), reinforces this analogy, provided that the 9 + 0 cilium is considered as a rudimentary outer segment.

In those species where centriolar transformation is present, cilia disappear, and no rudimentary outer segments are formed (Pevet and Collin, 1976). Alternatively, Vollrath (1981) suggested that centriolar transformation in

pinealocytes could be an aborted production of outer segments or cilia. However, centriolar transformation is confined to postnatal life, mainly in adult and old animals. Normal centrioles and cilia have been found in several species before centriolar transformation (rat: Lin 1970; Calvo and Boya, 1983; Zimmerman and Tso, 1975; cat: present study). Therefore, cilia apparently disappear after centriolar transformation.

Karasek (1983) indicated that centriole-derived microtubular sheaves may play a central role in the development of synaptic bars. However, these structures appear in adult animals only in a limited number of species, while synaptic bars occur in many species throughout postnatal life. Transformed centrioles might prove to be ultrastructural markers for pinealocytes in at least some species.

References

BUCANA C. D., Nadakavukaren M. J. and Frehn J. L. 1974. Novel features of hamster pinealocyte ultrastructure. *Tissue Cell* **6** 85–94.

CALVO J. and Boya J. 1983. Postnatal development of cell types in the rat pineal gland. *J. Anat.* **137** 185–95.

CALVO J. and Boya J. 1984. Ultrastructure of the pineal gland in the adult rat. *J. Anat.* **138** 405–9.

CALVO J., Boya J. and Garcia-Mauriño E. 1988. Ultrastructure of the pineal gland in the adult dog. *J. Pineal Res.* **5** 479–87.

COLLIN J. P. 1971. Differentiation and regression of the cells of the sensory line in the epiphysis cerebri. *In* The Pineal Gland. CIBA Foundation Symposium. pp 79–125. Edited by G. E. W. Wolstenholme and J. Knight. Churchill Livingstone, Edinburgh.

DUNCAN D. and Micheletti G. 1966. Notes on the fine structure of the pineal organ of cats. *Tex. Rep. Biol. Med.* **24** 576–87.

KARASEK M. 1983. Ultrastructure of the mammalian pineal gland: its comparative and functional aspects. *In* Pineal Research Reviews. Vol 1, pp 1–48. Edited by R. J. Reiter. Alan R. Liss, Inc. New York.

LIN H. S. 1970. The fine structure and transformation of centrioles in the rat pinealocyte. *Cytobios* **2** 129–51.

LIN H. S. 1972. Transformation of centrioles in pinealocytes of adult guinea pigs. *J. Neurocytol.* **1** 61–8.

LIN H. S., Chen W. P. and Tsai A. I. 1987. A centrosomal inclusion (striped nebulous body) in pinealocytes of the golden hamster. *Cell Tissue Res.* **248** 257–65.

PEVET P. 1974. The pineal gland of the mole (*Talpa europaea* L.). I. The fine structure of the pinealocytes. *Cell Tissue Res.* **153** 277–92.

PEVET P. and Collin J. P. 1976. Les pinéalocytes de mammifère: diversité, homologies, origine. Etude chez la Taupe adulte (*Talpa europaea* L.). *J. Ultrastruct. Res.* **57** 22–31.

PEVET P. and Saboureau M. 1973. L'épiphyse du Hérisson (*Erinaceus europaeus* L.) mâle. I. Les pinéalocytes et leur variations considérées au cours du cycle sexuel. *Z. Zellforsch.* **143** 267–385.

PEVET P. and Racey P. A. 1981. The pineal gland of nocturnal mammals. II. The ultrastructure of the pineal gland in the Pipistrelle bat (*Pipistrellus pipistrellus* L.): presence of two populations of pinealocytes. *Cell Tissue Res.* **216** 253–71.

PEVET P., Ariëns Kappers J. and Nevo E. 1976. The pineal gland of the Mole-rat (*Spalax ehrenbergi* Nehring). I. The fine structure of pinealocytes. *Cell Tissue Res.* **174** 1–24.

VOLLRATH L. 1981. *The pineal organ.* Handbuch der mikroskopischen Anatomie des Menschen. VI/7. Springer-Verlag, Berlin.

WARTENBERG H. 1968. The mammalian pineal organ: electron microscopic studies on the fine structure of pinealocytes, glial cells and on the perivascular compartment. *Z. Zellforsch.* **86** 74–97.

WOLFE D. E. 1965. The epiphyseal cell: an electron-microscopic study of its intercellular relationship and intracellular morphology in the pineal body of the albino rat. *Progr. Brain Res.* **10** 332–86.

ZIMMERMAN B. L. and Tso M. O. M. 1975. Morphologic evidence of photoreceptor differentiation of pinealocytes in the neonatal rat. *J. cell Biol.* **66** 60–75.

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