

Transdifferentiation of Mucus Cells into Ciliated Cells in the Quail Oviducte (Coturnix Coturnix Japonica) II- Estroprogestative Treatment, Follow-up of Progestogenic Treatment

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Abstract

Transdifferentiation is the process by which a cell that is not stem cell is differentiated into another cellular type without a dedifferentiation step. Transdifferentiation of secretory cells into ciliated cells was studied in ovariectomized quail oviduct after stimulation with Estroprogestatif and progesterone treatments. Cytological technique was applied. Semi thin sections realized in the blocks were observed and photographed by the Ultraphot II ZEISS. Estroprogestatif treatment (estradiol benzoate: 20ug +progesterone: 1mg/day) during six days induces differentiation of almost all epithelial cells into secretory cells. When this treatment is followed by progesterone alone during six days, about 50% of secretory cells transdifferentiation into ciliated cells. Following these treatments, neither DNA replication nor mitosis seems necessary for transdifferentiation of secretory cells into ciliated cells in quail oviduct.

Keywords: Transdifferentiation, Secretory Cells, Ciliated Cells, Quail Oviduct, Steroid Hormones.

Introduction

In all organisms, the different tissues are put in place during embryonic development, during which the cells differentiate. Certain cells, like nerve cells, will acquire their terminal differentiation. They will involute and die, but cannot divide or change orientation. However, many other cells retain embryonic characters. These are stem cells, which actively divide over the life of the individual. Their terminal differentiation allows the formation of a number of cell types, which ensure the replacement of differentiated cells which are involved. Once differentiated, these cells having reached their terminal differentiation can no longer evolve. This type of involution or cell death process is apoptosis or programmed cell death beneficial to the tissue or organism.

We accept in advanced multicellular organisms, notably in Vertebrates, a stability of differentiation. A differentiated cell, having therefore acquired a specificity to perform a given function, cannot acquire new specificities for another function.

There are, however, some exceptions to this general principle in which already specialized cells can replace other cell types. This process corresponds to cell conversion [1, 2]. This cell conversion, described as transdifferentiation, is observed in Pisces, Amphibians, Bird embryos or human fetuses [1, 3, 4]. During a

transdifferentiation, the differentiated stem cell leaves its path of differentiation to give another cell [2]. Besides the tissues elicited, this cellular transdifferentiation would exist in the oviduct of birds [5, 6]. The objective of this study is to highlight it.

In the oviduct of birds, during natural development, the epithelial cells differentiate under the action of steroid hormones [7-13]. In the quail magnum at the end of development corresponding to the laying female, the epithelial cells bordering the light differentiate into mucus cells and ciliated cells. In the laying animal the epithelium does not include undifferentiated stem cells [14, 15].

In sections of quail magnum laying eggs, dead ciliated cells flake in the lumen of the oviduct, unlike mucus cells [15]. However, on all the sections of magnum of quail in oviposition examined, the proportion of these two cell types remains constant (50% of each type). At the same time, mucus cells with ciliogenesis have sometimes been observed in the oviduct of quail laying eggs [15].

The transformation of mucus cells into ciliated cells, however very rare, seems evident in the oviduct of quail laying eggs. This process could help maintain the balance between the two cell types [15]. So at the level of the quail magnum in laying takes place a cellular transdifferentiation [7, 16].

Since transdifferentiation rarely occurs in the magnum of the quail laying eggs, it has been caused by hormonal treatments in

ovariectomized quails. Varying doses of hormones have been tested by who concluded that estrogen-progestogen therapy (estradiol benzoate 20 µg / d, progesterone 1 mg / d) for six days allowed the differentiation of all epithelial cells into secretory cells [17]. Certain cells secreting this epithelium can transform into ciliated cells following a six-day progestin treatment. Thanks to the present work it has been possible to study the hormonal control of this transdifferentiation.

Materials and Methods

Animal Material

The present works were carried out from 1981 to 1983 at the experimental Cytology center of Ivry sur Seine (France). The quails used (*Coturnix coturnix japonica*) came from the Dombes farm (France). They were raised in battery in a room maintained at 21 ° C, with 11 hours of light per day. They were fed ad libitum, consisting of granules (UAA 115, UAA Villemoisson, and France) and water. Under these conditions, the abomasum which arrives at the laboratory at the age of two weeks develop normally and become adults after six weeks. These animals weigh, on average, 100 g at 3 weeks, and 200 g at 7 weeks.

Methods

Natural Development

The natural development considered as a succinctly presented “control study” was carried out according to the weight of the magnum and not the age of the animal.

Hormonal Treatment

The magnum, or albumin genic segment of the oviduct, is a model for studying the action of steroid hormones at the cellular and molecular level. The study of development induced by hormone treatments was carried out on three-week-old ovariectomized quails in which the endogenous natural sources of sex steroids were eliminated.

One week after the ovariectomy, the quail received a daily intramuscular injection of estradiol benzoate (20 µg) and progesterone (1 mg) dissolved in 0.1 ml of olive oil for 6 days. The treatment is continued for 1 to 6 days by injections of progesterone alone, at a rate of 1 mg / day dissolved in 0.1 ml of olive oil. All quails were sacrificed 24 hours after the end of treatment. The medium magnams are removed, fixed by immersion in 3% glutaraldehyde in 0.05M phosphate buffer (Sorensen), at pH 7.4.

Cytological Technique

After one hour of fixation in 3% glutaraldehyde, within the framework of natural development and following hormonal treatments, all the samples are rinsed in phosphate buffer, postfixed for 1 hour in 1% osmium tetroxide in Veronal buffer, gradually dehydrated in increasing ethanol baths (70 °, 95 ° and 100 °) after rinsing in Veronal buffer. The samples were included in the araldite.

For light microscopy, semi-thin sections, made in blocks using a Porter Blum MT2 ultra microtome, are mounted on glass slides and stained with the Azure / methylene blue mixture, according to [18]. These sections were examined and photographed with the Ultraphot II Zeiss.

Fine sections made in these same blocks using a Reichert ultra-microtome, placed on grids, are contrasted by alcoholic uranyl acetate and by lead citrate prepared according to [19, 20]. These

sections were then observed and photographed using a Philips EM 300 transmission electron microscope.

Results

Morphology and Internal Anatomy of the Laying Quail

Adult female quail have conventional plumage characteristics (Figure 1). The reproductive system of female quail is asymmetrical and odd. The right portion consists of an atrophied ovary and oviduct. The left portion is differentiated to give a functional device consisting of a left ovary and oviduct. This asymmetry is very visible from the establishment of the reproductive organs. It is very marked in quail laying eggs (Figure 2A & 2B). During the maturity of the quail, the establishment and differentiation of the reproductive system takes place gradually. It begins between the third and fourth week in immature individuals. The two organs, namely the ovary and the oviduct, increase in size and volume.

The oviduct, at the immature stage, is a threadlike tube whose size and diameter increases during differentiation. White in immature stage, it becomes pale pink and vascularized in the laying female (Figures 2A & 2B). In addition, during the differentiation, a regionalization of the organ appears which is subdivided into five segments: the infundibulum, the magnum, the isthmus, the uterus, the vagina and the cloaca. It is the magnums collected at the different stages of their evolution which were the subject of the microscopic study.

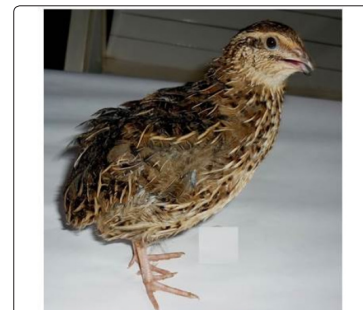


Figure 1 : Morphologie d'une caille femelle âgée de 7 semaines

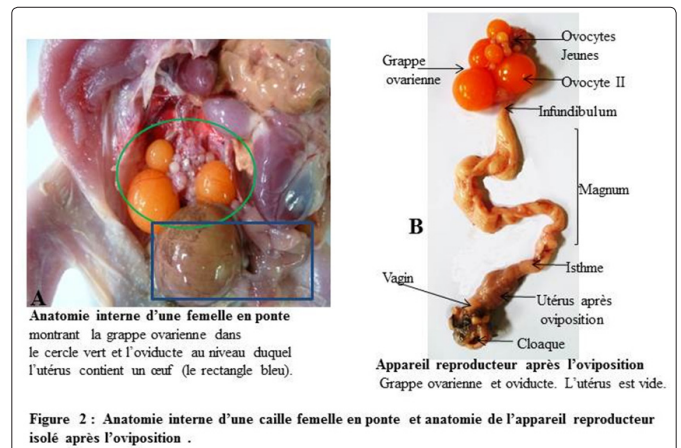


Figure 2 : Anatomie interne d'une caille femelle en ponte et anatomie de l'appareil reproducteur isolé après l'oviposition .

Brief Summary of the Natural Development of the Quail Magnum:

Structure and ultrastructure of the magnum

The chronological study was carried out according to the weight of the magnum.

The magnum of an immature quail weighs 20-30mg. Its wall is characterized, at the histological level, by the presence of small villi of approximately 300 µm in height (Figure. 3A). These villi consist

of a palisade epithelium formed of simple undifferentiated cells. This epithelium surmounts a compact stroma comprising fibroblasts and collagen fibers surrounding blood capillaries. This whole unit rests on a muscularis (Figure 3A). During development, cell proliferation occurs in the epithelium. It is characterized by cell divisions in the epithelium (Figure 3B) and in the stroma (Figure 3C) which leads to an increase in the height and width of the villi.

At the ultrastructural level, the pubertal quail magnum epithelium is a simple epithelium, made up of cells 5 to 6 μm high (Figure 3D). These cells contain few cytoplasmic organelles. A distinction is made in the nuclei of epithelial cells and of the stroma, the mass of condensed chromatin associated with nucleoli. This epithelium covers a dense stroma consisting of fibroblasts and bundles of collagen fibers (Figure 3D).

During development, the weight of the magnum evolves until it reaches 1g. The height of the villi goes from 300 μm to around 900 μm (Figure 4A). During this process the epithelial cells become invaginated and form tubular glands (Figure 4A & 4B). The other

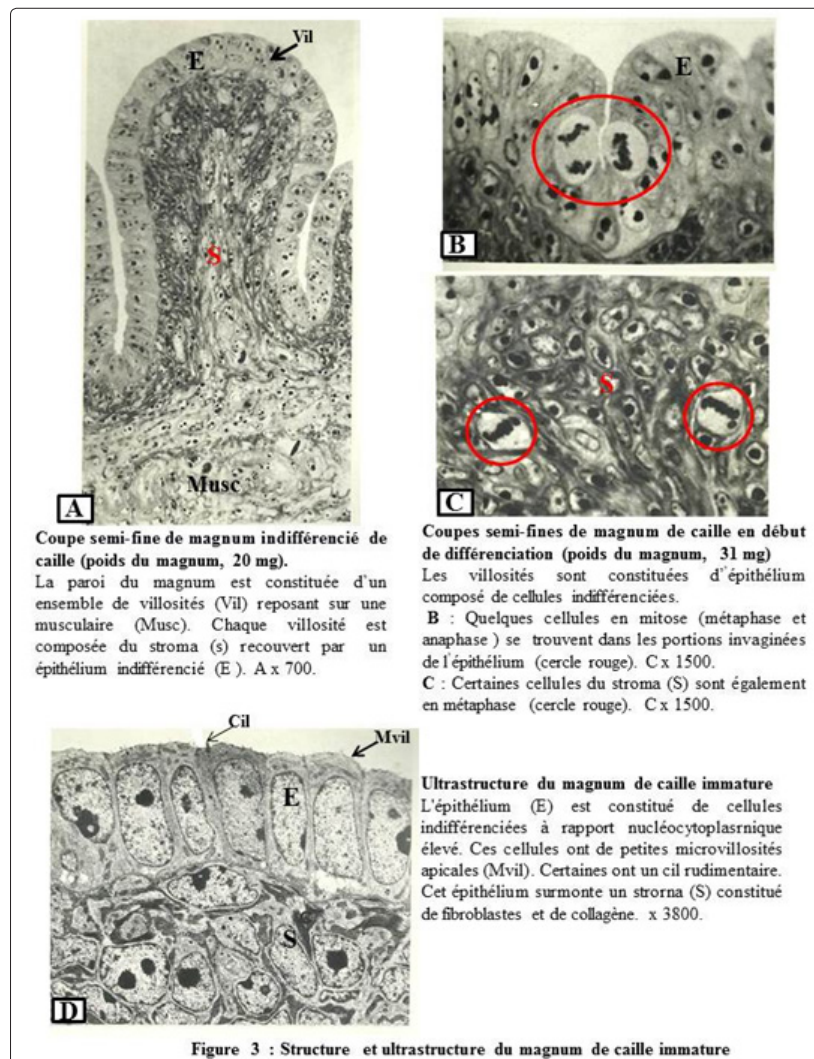
cells of the luminal epithelium differentiate into ciliated cells (Figure 4A & 4B). Goblet cells with a basal nucleus, containing a few grains of mucus, also differentiate in the epithelium before the end of the proliferative phase (Figure 4B).

Differentiation of Ciliated Cells

At the ultrastructural level, the cells at the end of ciliogenesis or the ciliated cells are high cells of 20 to 30 μm (Figure 4C). Their apical surface is terminated by numerous eyelashes of approximately 5 μm long alternating with microvilli of 2 μm (Figure 4C). Their hyaloplasm is very clear, compared to that of mucus cells. Their nucleus, ovoid or lobed, occupies a median or apical position.

Differentiation of Mucus Cells

Ripe mucus cells are like ciliated cells, 20 to 30 μm high (Figure 4D). In principle, the nucleus of these cells is rejected. They contain little hyaloplasm and few cytoplasmic organelles. Almost the entire cytoplasm of these cells is occupied by grains of mucus, except in the zone of the spindle (Figure 4D).



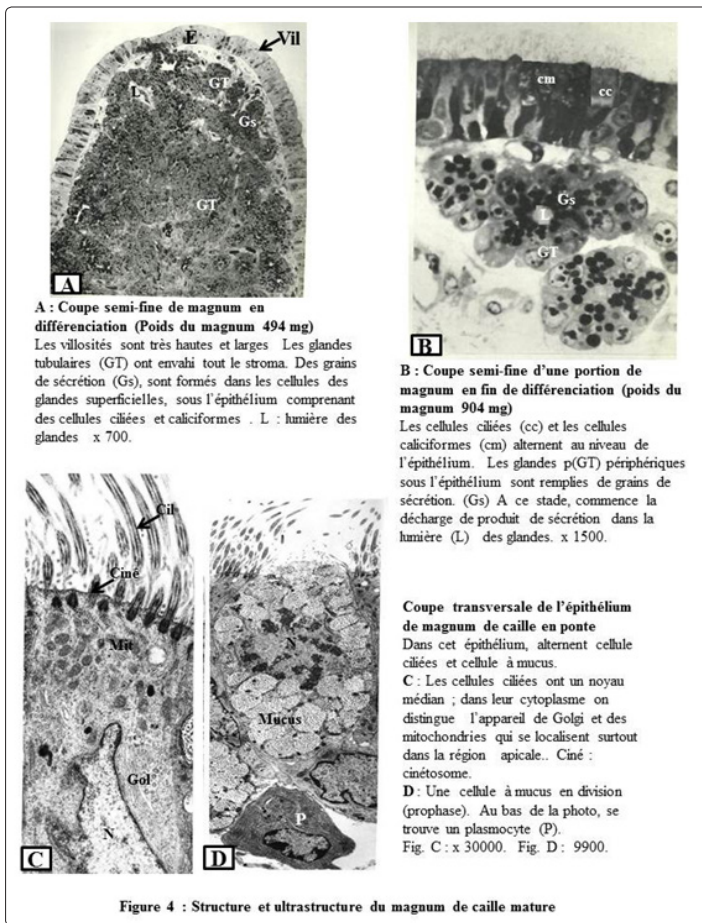


Figure 4 : Structure et ultrastructure du magnum de caille mature

Magnums of immature quail (three weeks old), before or just after ovariectomy have the same characteristics (Figure 3A & 3D). These are small villi of about 300 μm made up of an epithelium formed from simple undifferentiated cells 5 μm high. It overcomes a compact stroma comprising fibroblasts and collagen fibers. This whole unit rests on a muscularis (Figure 3A & 3D).

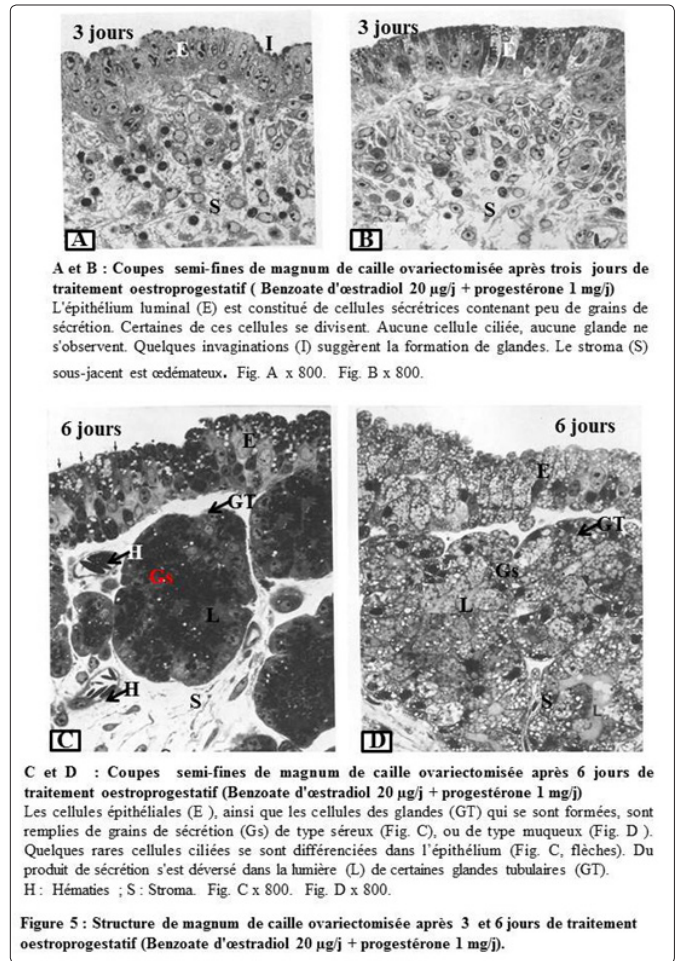
Effects of Hormone Treatments

This part concerns the incidence of hormonal treatments on the evolution of the ovariectomized quail magnum (Figure 3A & 3D). The study is limited to the epithelium because transdifferentiation concerns the ciliated cells and the mucus cells which constitute this epithelium. 3-3-1 Three days of estrogen-progestogen treatment; estradiol benzoate 20 μg / d, progesterone 1mg / d.

Following this treatment, the epithelial cells are actively divided (Figure 5A & 5B). The epithelium is made up of 5 μm high secretory cells (Figure 5A & 5B). The few grains of secretion observed are grouped in the apical region of the cells. In this epithelium, which rests on an edematous stroma, no ciliated cell is observed, no gland has formed, but certain epithelial cells begin to invade in the stroma (Figure 5A) for subsequent formation of the glands tubular.

Six Days of Estrogen-Progestogen Treatment; Estradiol Benzoate 20 μg / d, progesterone 1mg / d.

In semi-thin sections, cell divisions continue at the level of the epithelium. The epithelial cells have become very tall. They are approximately 34 μm high (Figure 5C and 5D). They are filled with grains of secretion of the serous type (Figure 5C) or of the mucous type (Figure 5D). Only 0.4 to 0.3% of the epithelial cells are ciliated (Figure 5C). Many glands have formed (Figure 5C & 5D) by pushing back the cells of the stroma.



At the ultrastructural level, the six-day estrogen-progestogen treatment made it possible to differentiate almost all the epithelial cells of the quail magnum into secretory cells (Figure 6A). These cells have small apical microvilli, and are filled with secretory grains of various aspects. Some rare cells containing secretory grains are ciliated or in ciliogenesis (Figure 6B & 6C). In their cytoplasm, we distinguish mitochondria and the Golgi apparatus typical of ciliated cells. The majority of epithelial cells are however secretory cells similar to those of (Figure 6A).

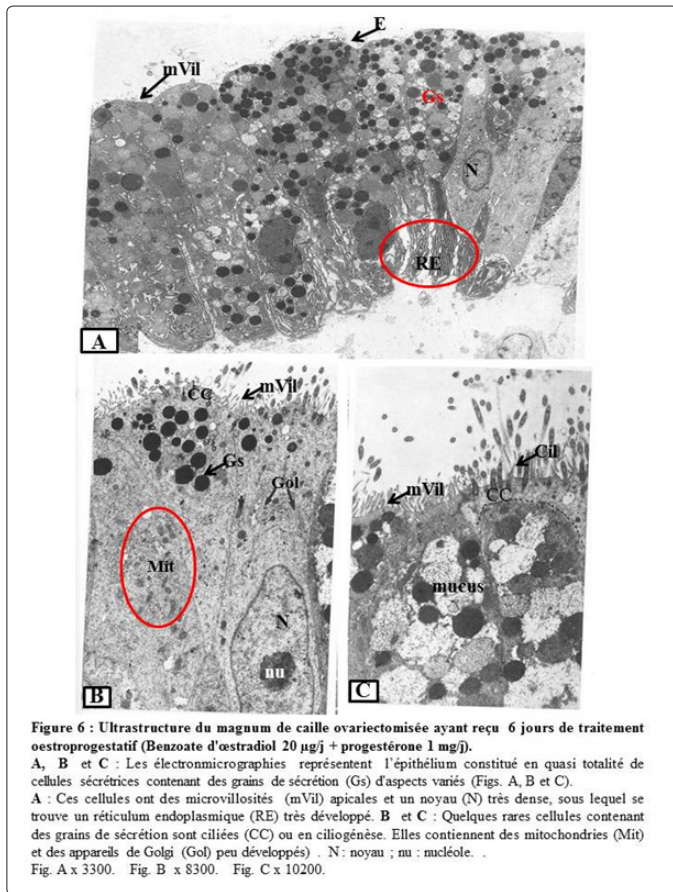
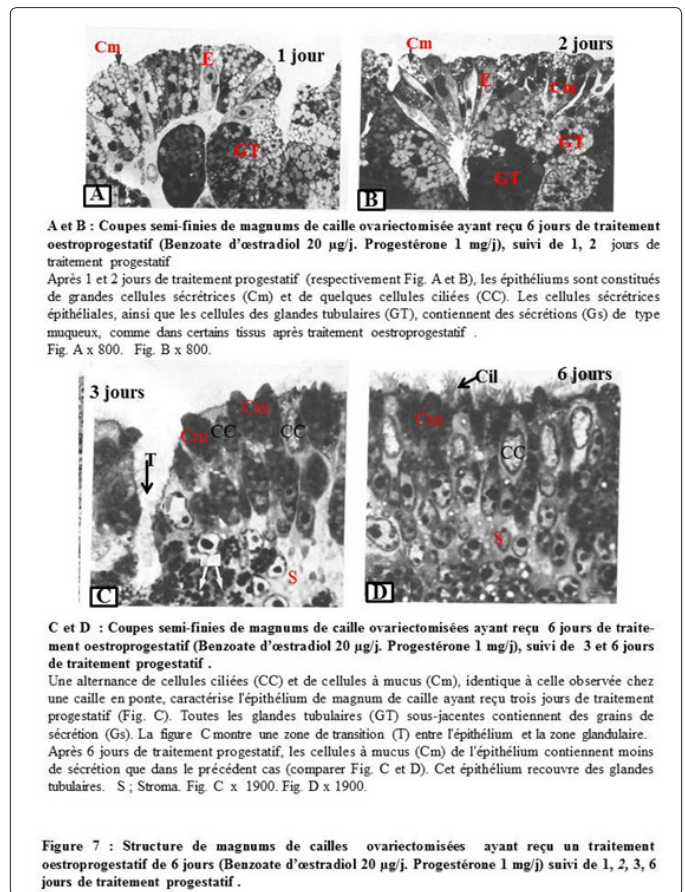


Figure 6 : Ultrastructure du magnum de caille ovariectomisée ayant reçu 6 jours de traitement oestrogen-progestatif (Benzoate d'œstradiol 20 µg/j + progestérone 1 mg/j).
 A, B et C : Les électromicrographies représentent l'épithélium constitué en quasi totalité de cellules sécrétrices contenant des grains de sécrétion (Gs) d'aspects variés (Figs. A, B et C).
 A : Ces cellules ont des microvillosités (mVil) apicales et un noyau (N) très dense, sous lequel se trouve un réticulum endoplasmique (RE) très développé. B et C : Quelques rares cellules contenant des grains de sécrétion sont ciliées (CC) ou en ciliogénèse. Elles contiennent des mitochondries (Mit) et des appareils de Golgi (Gol) peu développés. N : noyau ; m : nucléole.
 Fig. A x 3300. Fig. B x 8300. Fig. C x 10200.



A et B : Coupes semi-finies de magnums de caille ovariectomisée ayant reçu 6 jours de traitement oestrogen-progestatif (Benzoate d'œstradiol 20 µg/j. Progestérone 1 mg/j), suivi de 1, 2 jours de traitement progestatif.
 Après 1 et 2 jours de traitement progestatif (respectivement Fig. A et B), les épithéliums sont constitués de grandes cellules sécrétrices (Cm) et de quelques cellules ciliées (CC). Les cellules sécrétrices épithéliales, ainsi que les cellules des glandes tubulaires (GT), contiennent des sécrétions (Gs) de type muqueux, comme dans certains tissus après traitement oestrogen-progestatif.
 Fig. A x 800. Fig. B x 800.
C et D : Coupes semi-finies de magnums de cailles ovariectomisées ayant reçu 6 jours de traitement oestrogen-progestatif (Benzoate d'œstradiol 20 µg/j. Progestérone 1 mg/j), suivi de 3 et 6 jours de traitement progestatif.
 Une alternance de cellules ciliées (CC) et de cellules à mucus (Cm), identique à celle observée chez une caille en ponte, caractérise l'épithélium de magnum de caille ayant reçu trois jours de traitement progestatif (Fig. C). Toutes les glandes tubulaires (GT) sous-jacentes contiennent des grains de sécrétion (Gs). La figure C montre une zone de transition (T) entre l'épithélium et la zone glandulaire. Après 6 jours de traitement progestatif, les cellules à mucus (Cm) de l'épithélium contiennent moins de sécrétion que dans le précédent cas (comparer Fig. C et D). Cet épithélium recouvre des glandes tubulaires. S ; Stroma. Fig. C x 1900. Fig. D x 1900.
Figure 7 : Structure de magnums de cailles ovariectomisées ayant reçu un traitement oestrogen-progestatif de 6 jours (Benzoate d'œstradiol 20 µg/j. Progestérone 1 mg/j) suivi de 1, 2, 3, 6 jours de traitement progestatif.

Six days of combined hormonal treatment followed by a six-day single progesterone injection.

This treatment allows the maintenance of the secretory activity of the tissue (Figures 7A, 7B, 7C & 7D). During the first two days of progestational treatment, the epithelium is mainly composed of secreting cells presenting varied aspect of mucus (Figure 7A & 7B). After three days of progesterone injection, the epithelium similar to that of a quail egg (Figure 7C). It consists of ciliated cells alternating with mucus cells, but here there is an apical outgrowth of goblet cells (Figure 7C).

After six days of progestogen treatment, the mucus cells have less grain than after three days of the same treatment but the structure of the epithelium is identical (Figures 7A, 7B, 7C & 7D). The alternation of ciliated cells and mucus cells persists. Only half of the cells in the epithelium underwent transdifferentiation. Transdifferentiated cells do not appear to contain grains of secretion. In addition, no dividing cell was observed (Figures 7C & 7D).

Evolution of transdifferentiation and mitosis

In the case of prolonged estrogen-progestogen treatment with progesterone injections, approximately 50% of the epithelial cells are ciliated or in ciliogenesis from the 3rd day, and this percentage does not change after six days of progesterone injections.

As for cell divisions, progesterone alone does not trigger divisions. The formation of 50% of ciliated cells in the epithelium, during these treatments, irrevocably demonstrates that secretory cells can transdifferentiate into ciliated cells without dividing beforehand.

Discussion

Birds have an odd reproductive system. The highly developed left ovary and left oviduct constitute the female reproductive system [21-25]. The left oviduct which occupies a large part of the abdominal cavity in the laying animal is in the form of a tube extending from the ovarian cluster to the cloaca. The anatomical and functional differences allow it to be divided into five parts succeeding each other from the anterior end to the cloaca: 1 infundibulum, magnum, isthmus, uterus, and vagina. The magnum, or albuminogenic segment making "the white of the egg" is the fragment concerned in the present works [21-26].

The present studies were carried out in quail, unlike most of the work concerning the action of hormones on the oviduct of birds, which are carried out in hens. Quail has the advantage of being able to be ovariectomized without the rudimentary right gonad becoming a testicle, as in the hen. We can therefore work on quail from which the endogenous natural sources of sex steroids have been eliminated.

The immature female quail magnum has an undifferentiated structure described by [5, 27, 28].

In the present work and also described by in adult females especially laying females, at level of the epithelium occurs ciliogenesis which results in the formation of ciliated cells [5, 6, 15, 16]. Goblet cells containing grains of mucus, differentiate from other epithelial cells. These cells can still divide.

In the quail oviduct, mucus cells divide as mentioned [10]. In addition, they are capable of transdifferentiating into ciliated cells [15, 16, 17]. In contrast, ciliated cells in mitosis, unlike mucus cells have never been observed. In addition, ciliogenesis in quail oviduct according to and in bronchial epithelium according to, is a process of terminal differentiation of epithelial cells [15, 30].

These data suggest that the ciliated cells are at the end of a chain of differentiation, and that this differentiation is irreversible. These ciliated cells in the quail oviduct die from apoptosis and flaking. But in the Birds' oviduct, the hair cells are constantly renewed.

According to the literature, there is no epithelium made up entirely of ciliated cells. All have, as in the oviduct, either secretory cells, either secretory cells or undifferentiated cells, such as the trachea, Discoglossus seminal vesicle, uterine endometrium or the bronchial epithelium [31-35].

In these latter cases, undifferentiated cells, basal or parabasal cells ensure the renewal of ciliated cells or other flaking cells. This is the case of the bronchial epithelium [30].

The quail oviduct has no undifferentiated stem cells, nor basal or parabasal cells capable of renewing squamous ciliated cells.

In the absence of undifferentiated cells, as in the quail oviduct, little work has been done on the renewal of flaky ciliated cells.

In the quail oviduct, the ciliogenesis mixed mucus cells have been identified and described [15]. The rarity of this transdifferentiation on sections of oviduct of quail in laying does not allow to properly identify the phenomenon and study it. On the other hand, this transdifferentiation can be induced on a large scale by hormonal treatments [16]. In his work mentioned that transdifferentiation corresponds to the change of destiny of a differentiated cell and that the best known examples are induced experimentally [36]. To support this idea, mentioned that this process of transdifferentiation is a rare phenomenon, but most of the cases of transdifferentiation described in mammals are performed artificially [37].

It is therefore an experimental study that was adopted to demonstrate transdifferentiation in the quail magnum. Varying doses of hormones have been tested by who concluded that estrogen-progesterone therapy (estradiol benzoate 20 µg / d, progesterone 1 mg / d) for six days allowed the differentiation of all epithelial cells into secretory cells. Stopping the injection induced ciliogenesis, in the presence or absence of progesterone [16].

It is an estroprogestative treatment (estradiol benzoate 20µg/ d, progesterone 1mg / d) and progesterone which allowed the study of transdifferentiation at the level of the quail oviduct. This

transdifferentiation shows the plasticity of the epithelial cells of the quail oviduct. Since all undifferentiated epithelial cells can differentiate into secretory cells. The undifferentiated epithelial cells are therefore not predetermined, since they can differentiate all into secretory cells or by giving a mucociliary epithelium according to hormonal treatment. In the opinion of, transdifferentiation is just the direct reprogramming from one differentiated state to another without going through a stem cell stage [38]. This transformation is possible thanks to the plasticity of the cells concerned. This plasticity must exist between the mucus cells and the ciliated cells in the quail oviduct. On the contrary, consider ciliated cells and mucus cells to be two perfectly distinct cell types [29, 32, 39].

The observation of mixed cells (mucus cells in ciliogenesis), after estroprogestative stimulation, also shows that the epithelial cells are not predetermined [10]. At the doses used, estrogen-progesterone treatment almost completely inhibits ciliogenesis. The inhibition of ciliogenesis is lifted in the present case by the injection of progesterone alone. We can therefore deduce that in the case of transdifferentiation there is the lifting of blockage of ciliogenesis and not its stimulation.

Obtaining 50% of ciliated cells supposes that there is a topographic regulation preventing a secretory cell surrounded by two ciliated cells from differentiating into a ciliated cell. This regulation is not known.

The decrease in secretory activities after six days of treatment with progesterone alone, a secretory stimulating substance, is probably due to the decrease in the number of progesterone receptors, the synthesis of which is controlled by estrogens [40].

During transdifferentiation, differentiated cells dedifferentiate by losing a large part of their original characteristics, and undergo at least one division before giving a new cell type [41]. His argument echoes that of that, after the loss of specificity, the cells become accessible to a new genetic program [42]. However, for this new program to be expressed, a new cell cycle must be established [1, 3, 43].

In the quail magnum, dedifferentiation of mucus cells is not required for them to transdifferentiate into ciliated cells. These cells do not completely lose their secretory grains before transdifferentiating. The idea is supported by the work of [4]. According to the latter, significant dedifferentiation and reshaping of the cells do not seem essential during the regeneration of the lens. This hypothesis is similar to that of which somatic transference cells pass directly from one differentiated state to another without going through a stem cell stage [2].

Depending on the physiological state of the tissue, secretory cells transdifferentiate into ciliated cells after desquamation of a ciliated cell. These secretory cells may or may not divide before transforming. This transdifferentiation would allow fine regulation of the regular topographic alternation between the ciliated cells and the mucus cells at the level of the quail magnum. The mucus cell can be considered as the adult stem cell at the level of the quail magnum [6].

The present experimental study shows, however, that for the change of cell phenotype in the quail magnum DNA replication and mitosis

are not necessary contrary to what is generally accepted [6, 44].

Conclusion

The transdifferentiation phenomenon is a mode of organ regeneration in vertebrates [1, 44]. It is often preceded by the loss of specificity of the cells concerned, by DNA synthesis, and cell proliferation.

The quail oviduct made it possible to study the transdifferentiation of secretory cells into ciliated cells. In this material, this transdifferentiation is caused by an estroprogestative treatment followed by progesterone injection. Transdifferentiation is a mode of cell renewal in the quail oviduct, which does not have undifferentiated stem cells. The mucus cells, although differentiated, therefore appear as adult stem cells in this material [6]. However, in the case of the magnum, a reservation is expressed regarding the generalization of the different stages of transdifferentiation, as they have been described so far [44]. In quail, the mucus cells do not necessarily divide before transdifferentiating. They do not reject all their secretions, and therefore do not lose their specificity before transdifferentiating into ciliated cells.

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