

BEHAVIOUR OF THE ALCALINE PHOSPHATASE IN THE »WOLFFIAN LENS-REGENERATION«

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In the last two decades the eye, and especially the crystalline lens, has become the favourite object of regenerative researches. As it is known, if the lens of some inferior animals is removed, it regenerates out of the dorsal margin on the iris, because in these animals (urodela, anura) not only the embryonic calyx, but the differentiated eye as well possesses the faculty of forming the lens. *Wolff* (1895) was the first to give an exact morphological analysis of the process. Nevertheless the character of the factors inducing and maintaining the process of regeneration remained unexplained up to now in spite of the fact that the problem occupied the interest of a great many workers for several decades. They thought to have found the cause of the phenomenon in some external and internal factors, until *Speeman* and, later *Wachs* and his school formed a hypothesis according to which it is the retina which is responsible for the regeneration of the lens (induction of the lens). These experiments being of operative and exclusively morphological character were unable to clear up the biochemical processes going on in the retina and connected with the regeneration of the lens. So they did not produce any direct proof concerning the role of the retina in the process. Since it is known that some fermentative processes show an increased activity in the regenerative phenomena, the supposition seemed justified to us that we shall succeed in registering some changes in the enzymic processes also during the lens regeneration, and further that we shall be able to draw conclusions on the activity of the retina in the course of the regeneration of the lens.

On the basis of these suppositions we examined the behaviour of the phosphatase histochemically and chemically in connection with the regeneration of the lens of tritons. We chose the examination of the alkaline phosphatase for the reason because we possess already numerous literary data concerning the action of it in other regenerative processes, in developing organs and (in general) in normal tissues, — based on cytochemical and microchemical examinations.

Material. Methods

We experimented upon 110 *Triton cristatus* gathered without selection. The removal of the lens of their right eyes was executed in ether narcosis. The left eye preserved intact has served as the control of the right eye. After the operation, till their sacrifice, the animals were regularly fed. For the histochemical examinations we sacrificed the animals by decapitation in groups of 8 to 12, on the 3rd, 5th, 8th, 10th, 12th, 14th, 18th, 22nd days following the operation. The fixation was carried out in 80 per cent alcohol kept for 8 hours in the ice-box. After the fixation we removed the skull-bones through operation instead of decalcination. We chose this technique because a further considerable loss of enzymes would have been inevitable during the decalcination. Further, we treated our materials according to the method elaborated by *Gomori* (1939, 1941) and by *Takamatsu* (1939) for the histochemical determination of the phosphatase. The *pH* of our incubating solution was 9.5. For incubation time we fixed, on the basis of previous investigations, 18 hours. As a result of the reaction a black precipitate (CoS), highly apt to microscopical analyses appears on the places corresponding to the phosphatase. This proceeding alone was not sufficient, because there is hardly any difference in the colour of the precipitate and the black pigment which is present in a great quantities on the place of the reaction, especially in the iris and this makes evaluation difficult. Therefore we changed the method of *Gomori—Takamatsu* as follows: we transformed the calciumphosphate — arisen in consequence of the enzyme-activity and precipitated in the tissues — into lead phosphate, and later by the help of potassium bichromate into lead chromate; so we succeeded in localizing the enzyme as a yellow, insoluble, readily identifiable precipitate.

The microchemical analyses were executed on the 3rd, 8th, 10th, 12th, 14th, 18th, resp. 22nd days of development. As material of our investigations we used partly the normal and the »experimental« eye of the same triton, partly the eyes of non-treated animals. We obtained these materials by removing the bulbs of the animals narcotized in ether and by cleaning them carefully from all connective tissue. There too, we made comparisons, between the normal and operated eyes of the same animals on the one hand, and between the normal eyes of non-operated animals on the other hand. After the removal we weighed the bulbs, and adding a drop of chloroform, we triturated each of them separately in a small tube, taking care especially of the retina. Then we pipetted 1,5 ml. 0,2 M. concentrated glycerophosphate Na solution adjusted to *pH* 9,5 in both tubes, and we stirred it until the suspension became homogenous; then we incubated it for 18 hours at 37° C. For each examination we took off from the above-mentioned suspension 0,5 ml. and after removal of the proteins we determined its inorganic phosphate contents by means of the *Martland—Robison* colorimetric micro-method (1923).

Experiments

To estimate properly the results of our experiments it seems necessary to go over the process of a normal lens-regeneration (*Sato*, cit. *Mangold*, p. 316). The successive process of a lens-regeneration in the circumstances in which we made our experiments is as follows: After the removal of the lens the edge of the iris swells and grows rich in pigment (1st—5th day). After this the depigmentation of the iris takes place and a gap appears between its two layers (5th—10th day). Then the edge of the iris begins to proliferate and to form a hollow epithelial vesicle (10th—15th day), in which fibres appear (17th and 18th day) Finally the new, regenerating lens detaches from the dorsal edge of the iris (18th—21st day). The new lens is quite normal in its structure and differentiation, but it is smaller than the original lens and reaches normal size only later. Nevertheless this regenerating process is greatly subject to individual variations; therefore we found it proper to evaluate the changes of the phosphatase occurring in the operated eye during the regeneration on the basis of comparisons with the normal eye of the same animal. The above-mentioned terms of the successive sacrifices were chosen with regard to the same points of view.

Histochemical investigations

We examined first the phosphatase content of the eyes of the control animals (Fig. 1). We found it equal in both eyes of the same animal without any difference in quantity or localization. We obtained a general, slightly positive mainly nuclear reaction. It may be observed that the reaction is stronger in the external and internal granular layers and in the ganglion cells of the retina than in the other layers, where it is scarcely visible. In the epithelium



Fig. 1.

Left eye of a non-operated *Triton taeniatus*. Phosphatase reaction. A diffuse, moderated nuclear reaction is to be seen. *General remark.* Signs occurring in most of the figures: *B* = left (control) eye; *J* = right (experimental) eye; *r* = retina; *i* = iris; *ch* = choroid; *c* = cornea *L* = lens of the eye; *l* = lens vesicle.

of the lens, in the cornea and in the peribulbar tissue, we may notice a kind of nuclear reaction like the one observed in the retina. As for the iris, only the cells of the frontal and dorsal epithelial layer show a moderate nuclear reaction. The choroid, the sclera may be practically considered as free from enzyme. It may be observed that the retinal reaction is not stronger than the nuclear reaction of the environment: only a greater density of cells makes it more striking. We may remark that the analysis of the iris and chorioid was made with the above-described lead-chromate modification.

On the 3rd and 5th days following the operation microscopical examination showed a general increase of the reaction in the regenerating cornea. A pronounced reaction was observed in the fornices. The retinal reaction did not

change significantly (Fig. 2). In several cases a scarcely perceptible increase of activity could be observed on the experimental and the control retina visible rather beside the iris.

8 days after the removal one may observe that, in comparison with the earlier phases, only the experimental eye showed a changed reaction (Fig. 3), though a slight rise of activity might be found in the control eye too. In this phase the retina of the experimental eye gives already a stronger reaction than that of the control eye. The strengthening of the reaction is parti-

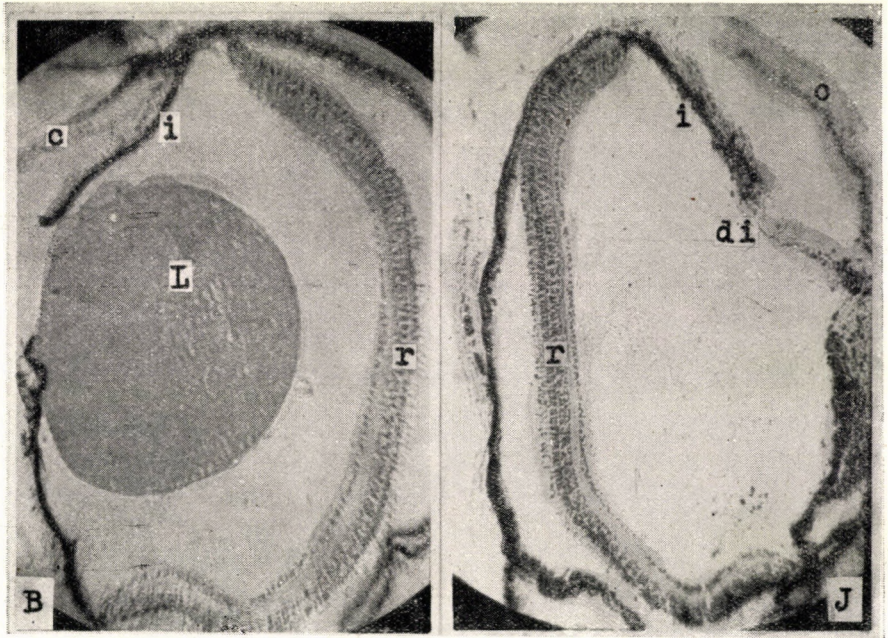


Fig. 2.

Five days after removal of the lens (Sato's 1st phase). Both eyes of *Triton taeniatus*. Phosphatase reaction. There is no important difference between the activity of the two retinæ. Note, in the experimental eye (J) the swollen margin of the dorsal iris (di) and the hypertrophic cornea (c).

cularly visible in the external granular layer, whilst towards the inside it keeps diminishing. One may observe that the increase of the reaction begins in both eyes beside the iris. But the proliferation of cells occurring on the dorsal edge of the iris does not show any increase of activity.

On the 10th day of regeneration the already mentioned positivity appears in the retina of the normal eye beside the iris and there mainly in the external granular layer (Fig. 4). In contrast to this the reaction in the retina of the operated eye proves to be diffuse and more intense (Fig. 4, 5), though a careful observation may show that it is, even in this case, darker on the peripheral

parts. Higher magnifying clearly indicates that the intensity of reaction shows a gradually diminishing tendency from the external cellular layer of the retina towards the internal parts (Fig. 5). The reaction observed in the outer and especially in the inner epithelial layer of the dorsal iris is of the same intensity as in the retina. The newly formed lens vesicle shows, on the contrary, only a mild reaction.

The reaction of the retina increases considerably on the 12th and 14th day which is especially well visible in the 14 days old animals (Fig. 6). The

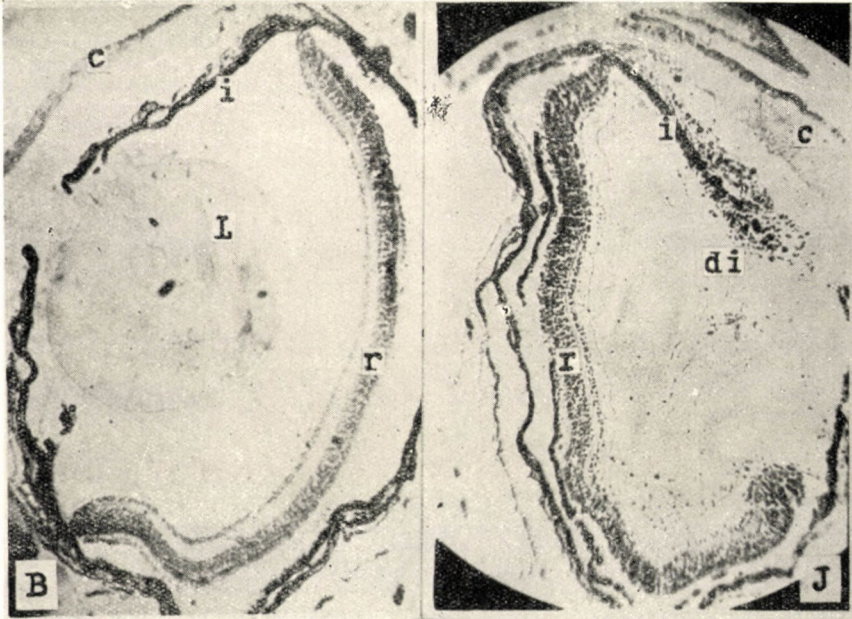


Fig. 3.

Eight days after operation (Sato's 3rd phase). Both eyes of *Triton taeniatus*. Phosphatase reaction. Enzymic activity is slightly greater in the retina (*r*) of the experimental eye (*J*) than in the control eye (*B*). The cellular swelling on the dorsal margin of the iris (*di*) is deficient in enzymes. In the retina of the control eye a slight marginal reaction is to be observed.

massive reaction in the retina of the experimental eye is much stronger than the reaction in the control retina, though we may find here also as in the preceding cases — some enzyme activity on the edges. The regenerating cornea, the conjunctiva (mainly in the fornix) is very active; while on the contrary the regenerating lens, in which the first signs of the formation of lenticular fibres appear, presents a very faint reaction.

In the 18 days old animals we may observe a considerable decrease of the retinal reaction of the experimental eye, and now, excepting some parts, where a slight difference is still visible no difference may be found any more between

the two, the experimental and the control retinae (Fig. 7). Nevertheless the regenerating cornea gives in many cases an important degree of reaction. In this phase of regeneration newly formed concentric fibres fill up the cavity of the lens vesicle.

22 days after the removal of the lens the regenerating lens shows a differentiation similar to that of the original lens, only it is smaller (Fig. 8). In no

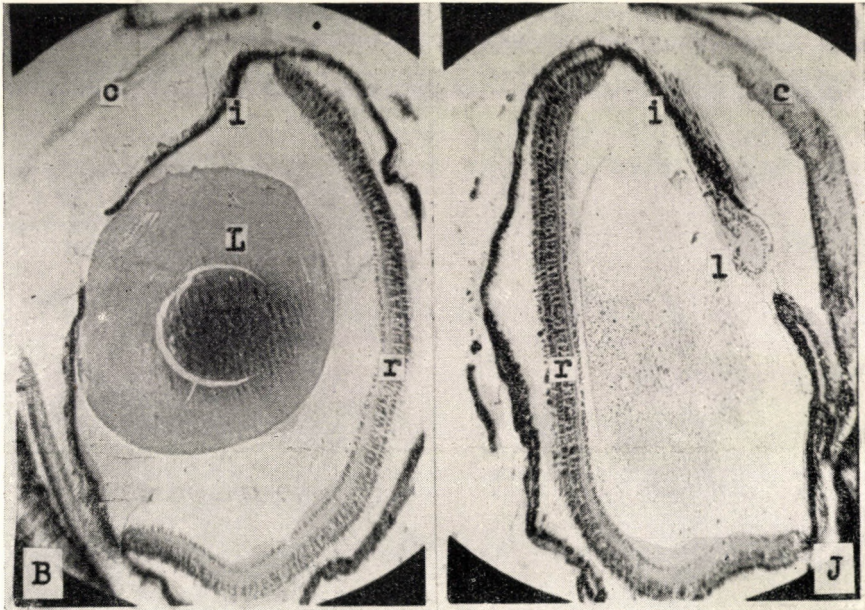


Fig. 4.

Ten days after removal (Sato's 4th phase). Both eyes of *Triton taeniatus*. Phosphatase reaction. Note, in the retina (*r*) of the experimental eye (*J*) the diffuse uniform reaction, — more intense than the retinal reaction of the control eye (*B*). The lens vesicle (*l*) visible on the dorsal margin of the iris contains scarcely any enzymes. In the lens (*L*) of the control eye and on the marginal parts of its retina enzymic activity is to be remarked.

instance of this phase could we observe any difference between the activity of the two retinae. The picture resembles the reaction found in the eyes of non-operated animals (Fig. 1).

Chemical investigations

On Table I. we summarized the results of the microchemical investigations carried out with the above-mentioned methods and phases of development. By activity we mean the quantity of free phosphate of 5 experimental, resp. control eyes (bulbus) split off in 18 hours by 1 mg. (wet weight) under the above-mentioned circumstances (at the temperature of 37° C., at 9,5 pH in

0,2 M Na-glycerophosphate). The comparison of these values of the experimental and the control eyes supplied us the percent-specification of the increase of the activity in the operated eye as it is visible on Fig. 9. The increase of the enzymic activity starts after the 8th day, attains its culmination on the 14th day, when the enzyme activity of the operated eyes shows an 83 per cent increase compared with the control eyes. In the following phases the enzymic activity of the experimental eye approaches rapidly the normal value.

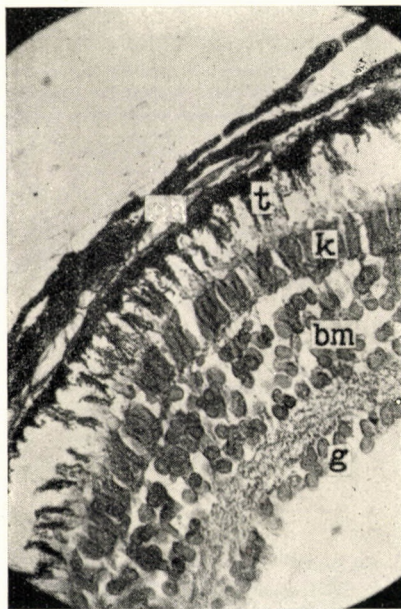


Fig. 5.

Ten days after operation. Detail of retina of the experimental eye (*J*). Phosphatase reaction. Note, the decrease of intensity of the reaction from the outer cellular layer (*k*) towards the layer of the ganglion cells (*g*). *t* = tapetum, *bm* = inner nuclear layer.

Table I.

Days after the operation	3 rd	8 th	10 th	12 th	14 th	18 th	22 nd
Activity of operated eye in mg	0,0266	0,0275	0,0286	0,0280	0,0396	0,0281	0,0214
Activity of normal eye in mg	0,0227	0,0204	0,0208	0,0171	0,0218	0,0207	0,0191
Increase of activity in %, in favour of the operated eye	17,5	34,5	37,5	64	83	36	10

Activity = free phosphate split by 1 mg wet weight of 5—5 eyes (bulbs) at 37° C and pH 9,5 in 0,2 M Na-glycerophosphate in 18 hours (mg).

Discussion

Speeman's opinion, that the lens-formation induced by the retina (*Törö* 1932), was built out by *Wachs* and his school into the theory of a secretory equilibrium between the lens and the retina. According to them there exists a secretory equilibrium — probably a chemical one — between the retina and the lens, because the secretion of the lens neutralizes the secretion of the retina, which induces the regeneration of the lens after its removal. The following

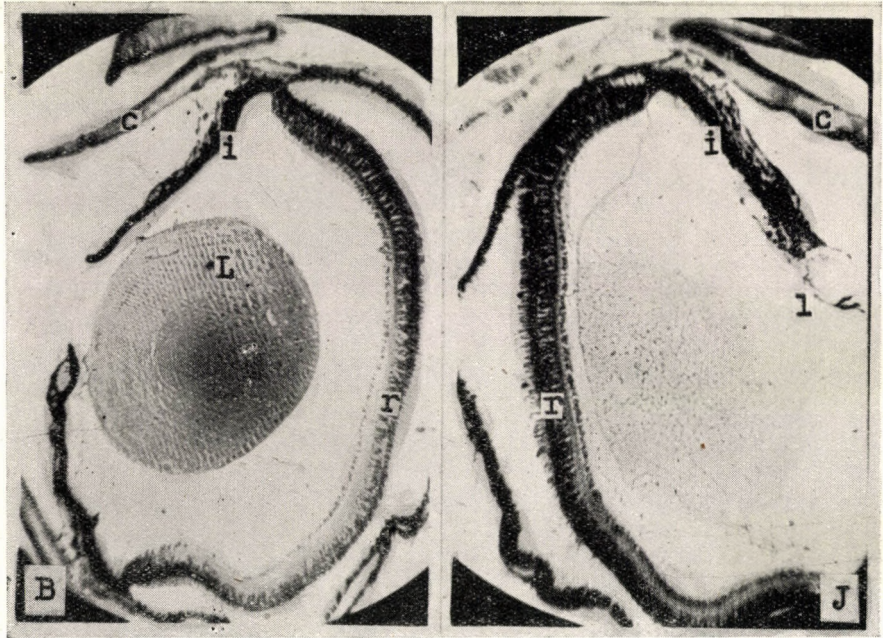


Fig. 6.

Fourteen days after removal (*Sato's* 6th phase). Both eyes of *Triton taeniatus*. Phosphatase reaction. In the retina (*r*) of the experimental eye (*J*) very intensive enzymic activity is to be seen. The regenerating lens (*l*) dyes pale. Note characteristic marginal reaction in the retina of the control eye (*B*). The lens (*L*) too contains phosphatase.

experiments may argue in favour of the inhibiting influence of the lens :

1. A part of the dorsal edge of the iris implanted into the dorsal chamber of an eye still possessing a lens did not form a lens, but after the removal of the original lens, it did in 7 cases out of 8 (*Wachs, Sato* cit. by *Mangold*, p. 327).
2. If a larger lens was replaced by a smaller one, then on condition of a good adjustment regeneration was checked in most cases (*Wachs*, cit. by *Mangold*, p. 327).
3. But if the lens of a Triton, imbedded in paraffine, was implanted into the place of the removed lens of another Triton (*Kesselyák*, 1935), a lens or a lens vesicle regenerated. The influence of the retina on the inducing and

maintenance of regeneration is proved by the following facts: 4. Dorsal iris transplanted into the labyrinth of another animal (embryo) without retina does not regenerate lens (5 cases), but with retina it does (2, resp. 6 cases of 9) (*Wachs*, 1914, cit. by *Mangold*, p. 327). 5. If the whole retina is removed together with the lens, the retina regenerates first, and then the lens. (*Wachs*, 1920 cit. by *Mangold*, p. 327.)

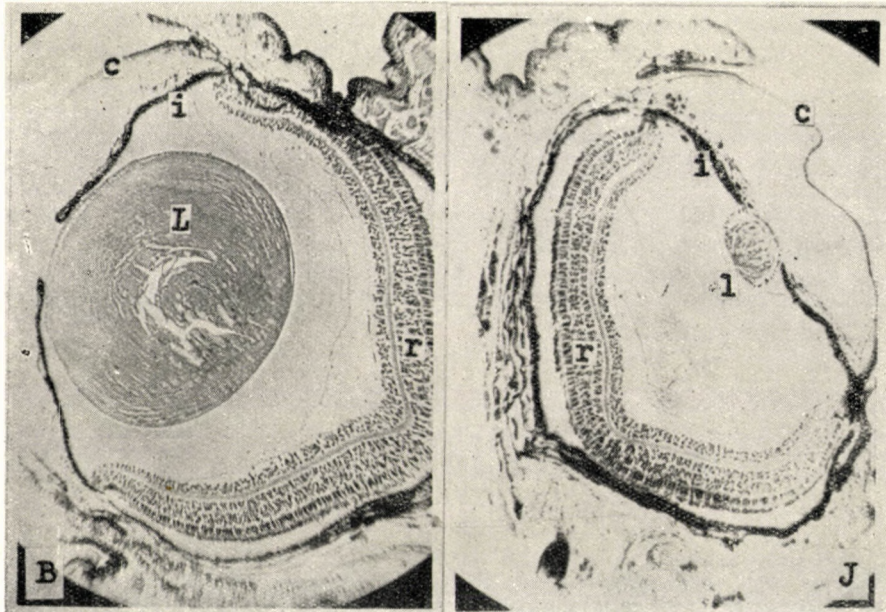


Fig. 7.

Eighteen days after operation (*Sato's* 10th phase). Both eyes of *Triton taeniatus*. Phosphatase reaction. The difference between the activity of the retina (*r*) of the experimental eye (*J*) and of the control eye (*B*) is scarcely perceivable. The regenerated lens (*l*) is already segmented from the dorsal margin of the iris.

Naturally many objections could have been and also were raised against these experiments. Partly because of the small number of the animals used for the experiments, partly because of the occasional circumstance that some cells of hurt retina may also transform into lens-like structures, into the so-called lentoids (*Törő*, 1932; *Reyer*, 1948). This concerns especially the experiment No. 4., which shows only two absolutely positive cases, the four other cases are probably lentoids. In spite of the objections, the above described experiments prove the importance of the retina in the induction of the lens-regeneration, they could, however, not demonstrate a direct evidence of the determining role of the retina in the regeneration.

The results derived from our experiments form the first phase of a series of experiments which will try to analyze the lens regeneration from the biochemical, resp. histochemical point of view.

Our observations concerning the normal eye correspond to some literary data: *Santoni* (1938) himself has found the phosphatase-content of the lens very small; and according to *De Concilis* (1934), there is some alkaline phosphatase in the retina too. *Verkstern* (1946 cit. by *Baur*, p. 572) affirms that the presence of adenosintri-phosphatase in the retina shows a similar picture. Up to now no difference has been found between the adaptation of the retina to light or to darkness (cit. by *Baur*). *Lindeman* (1949) has found

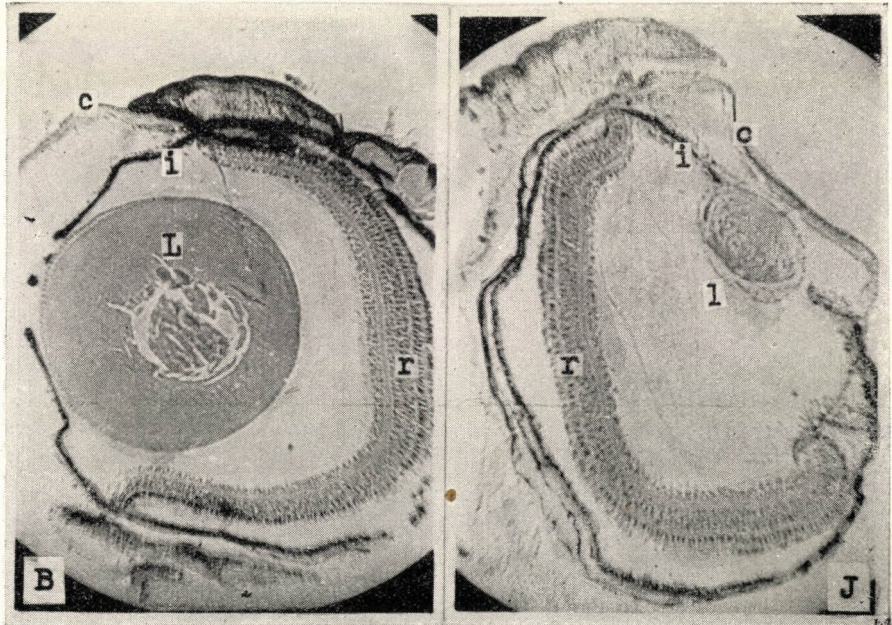


Fig. 8.

Twentytwo days after removal (*Satos's* 13th phase). Both eyes of *Triton taeniatus*. Phosphatase reaction. No difference between the enzymic activity of the retina (r) of both eyes. Note the segmented new lens (l).

an important increas of phosphatase activity during the differentiation of the retina of the chicken embryo. *Sülmann* (1947, cit. by *Baur*, p. 572) has found also alcali-mono- and diesterase in the cells of the cornea.

According to our researches there is (in comparison with the normal eye) a considerable increase of enzyme activity in the retina of the experimental eye. It is manifest that this phenomenon is connected with the regenerating lens, as far as in certain morphologically demonstrated forms of development we may find a determined increase of the retina activity. If we observe, in the course of the regenerating process, the increase of activity in the retina of the experimental eye, we may find that it is confined to the period (from about the 8th day till the 18th) in which the lens is developing from the dorsal margin

of the iris. But even within this period activity increased during the appearance and formation of the fibres of the lens (Fig. 4 and 6). At the same time the regenerating lens contains scarcely any enzymes.

These examinations show that certain processes take place in the retina during their egeneration of lens and in these processes the enzyme phosphatase plays an important role.

The phosphatases cooperate considerably in the metabolism of some organs or cells, and take part in their specific functions too. Thus they occur also in the illuminated retina (Reis, 1940), but their quantity seems to be independent of the light stimulus. Their role seems to be proved in the metabolism of nuclein acids, nucleotids and, in general, in that of nucleoproteins

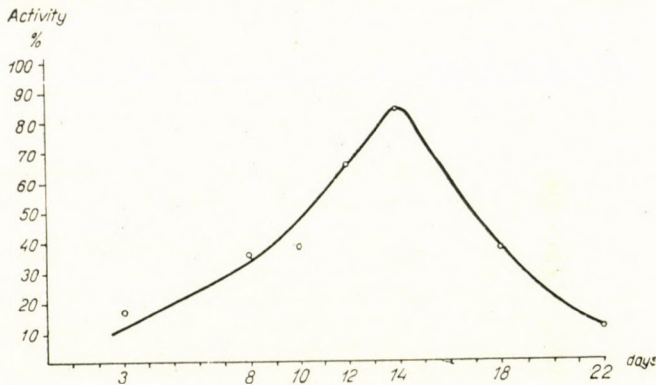


Fig. 9.

Increase of the phosphatase activity of the experimental eyes in percentage during the lens regeneration.

(Sulkin, 1948). Certain experimental data show the close connection of the phosphatase with the (collagenous) fibrogenetic processes too (Danielli, 1943, Bourne, 1943, Lorch, 1947) etc.

Taking into consideration, moreover, the circumstance that the increase of activity is intensified at the time of the formation of the lens and especially of the lenticular fibres, we may suppose that during regeneration such processes are going on in the retina which have an important role in or are perhaps responsible for the formation of the albumines of the lens.

Our experiments show further that the phosphatase-activity of the retina begins to change substantially only after the 5th day (Fig. 3, 4 and 6) though the introductory symptoms of regeneration — a strong depigmentation of the iris and formation of the gap — appear already before that time.

These data show that at the beginning of the regeneration the activity of the retina is not increased yet as much as could be expected on the basis of the increase of enzyme-activity observed in the later phases of regeneration.

So we may suppose that the role of the retina is smaller at the beginning of the regeneration than at the time of the formation of the lens. Perhaps the local destructive processes following the operation (*Reinke*, cit. by *Mangold*, p. 326), resp. the specific changes of metabolism connected with them, may induce the regeneration. This opinion is supported by the conclusion of *Striganova* (1950), concerning the regeneration of axolotl limbs.

The hypothesis arising from the numerous analyses which prove the undoubtedly important role of the retina in the induction of the lens-regeneration (*Wolff*, *Speeman*, *Wachs*, *Mangold*, *Törö* etc.) seems to be more probable. On the basis of these we may say that the retina is responsible for the induction of the regeneration; but the processes taking place this time in the retina could not be demonstrated by means of phosphatase analyses — probably because in these processes it is not the phosphatase that plays the essential role.

Consequently, it seems that the changes occurring in the retina at the time of the formation of the lens differ in character from the changes responsible for the induction of the regeneration.

Comparing the enzyme content of the retina in the normal eye of the operated animals with that of the lens, there seems to be a certain connection between the phosphatase content of the retina and the lens. This opinion is supported by our finding according to which in the later phases of regeneration, especially on the 10th, 12th, 14th days, when even the retina of the normal eye shows some increase of activity, this activity goes parallel with the proportional increase of activity in the lens.

The changes of the enzyme contents of the control eyes prove that in the course of the regeneration of the organ (during the different phases of growth and differentiation) (Fig. 3, 4, 6) the process going on in the retina of the regenerating eye does not remain a local phenomenon, but influences the other eye and, probably, the whole organism. There are two possibilities for the extension of this process. One of them is that the retina of the regenerating eye produces a substance that would stimulate specifically the other eye through the blood stream. The other supposition is that the stimulation would excite, through the nervus opticus, the respective part of the central nervous system and this stimulation would effect the reaction on the other side. Taking into consideration the works of *Speranski* and his school, we suppose the latter to be more probable. This observation is proved by the fact, — borne out by many literary data, — that the central nervous system of the triton is able to register, receive and transmit certain stimulations (connected with regeneration). *Polshaev* (1950) demonstrated in frogs the effect of the central nervous system and of the hypophysis on the regeneration of the limb. We may remark that these problems of the lens-regeneration of the triton are not yet cleared up and we plan to undertake further investigations in this field.

Our chemical results correspond, on the whole, with our histochemical ones, confirming them, except the beginning and the end of the regeneration (Fig. 9) when the chemical analyses show a certain increase of the enzyme activity of the experimental eye, a phenomenon which cannot be confirmed histochemically. This may be explained by the fact that we used up the whole bulb for our chemical estimations, and so the phosphatase-content of the cornea and conjunctiva and of the other tissues may have produced the difference which we disregarded and ignored in our histochemical investigations where we compared only the retinal reaction.

Summary

1. The authors examined histochemically and chemically the behaviour of the alkaline phosphatase in the regeneration of the lens of tritons.

2. Both histochemically and chemically, the increase of the enzymic activity could be observed in the retina on the 8th—16th days following the removal of the lens. This may be connected with some phenomena of the lens-formation giving us the convincing certitude, that during the lens-regeneration processes of decisive importance are going on in the retina.

3. On the first 5 days no increase could be observed in the retina of the experimental eye. It is likely that in connection with the induction of regeneration processes, of such character are taking place in the retina in which alkaline phosphatase has no essential role.

4. During regeneration we observed some variations of the enzyme contents of the control eyes too.

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ПОВЕДЕНИЕ ЩЕЛОЧНОЙ ФОСФАТАЗЫ ВО ВРЕМЯ РЕГЕНЕРАЦИИ ХРУСТАЛИКА ПО ВОЛЬФУ

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Резюме :

1. Мы исследовали гистохимически и химически поведение щелочной фосфатазы в процессе регенерации хрусталика тритонов.

2. Через 8—16 дней после удаления хрусталика мы наблюдали с гистохимической а также с химической точки зрения повышенную активность энзима в сетчатке глаза. По нашему мнению, это явление стоит в связи с процессом регенерации хрусталика а является прямым доказательством того, что в сетчатке глаза во время регенерации хрусталика происходят очень важные процессы.

3. Во время первых 5 суток регенерации мы не установили повышенной активности энзима в сетчатке подопытного глаза. Мы считаем вероятным, что в этот период происходят начальные процессы регенерации, в которых щелочная фосфатаза не играет существенной роли.

4. В течение регенерации мы наблюдали некоторые изменение содержания энзима и в контрольных глазах.