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STUDIES ON THE LIGHT- AND DARK-ADAPTATION OF THE COLOUR OF THE CRAYFISH, *ASTACUS LEPTODACTYLUS* ESCHSCHOLZ (DECAPODA) CONTROLLED BY THE SECRETORY ACTIVITY OF THE CENTRAL NERVOUS SYSTEM. II. HISTOMORPHOLOGICAL PICTURE OF THE NEUROENDOCRINE SYSTEM RELATED TO THE CHANGES IN ILLUMINATION

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Many questions are unanswered yet in connexion with the neuroendocrine system regulating light- and dark-adaptation. The purpose of our investigations was to clarify the mechanism of colour changes in two related crayfish species (*Astacus leptodactylus* and *Astacus astacus*) showing, however, different types of light and dark-adaptation owing to the difference of the biotopes they live in.

As a continuation of physiological experiments published in a previous paper, this paper contains some data from our histological investigations.

Material and Methods

Adult specimens of *Astacus leptodactylus* collected from Lake Balaton were used in our experiments. They were stored in running Balaton water at a temperature of 10 to 15° C.

In some experimental groups, after 24 hours permanent exposure to illumination or darkness, the eyestalks were ligated (KONOK 1961). The animals in this state were put, each in the other basin, kept there for another 24 hours and then prepared histologically. Two other groups of crayfish with their eyestalks ligated were kept in unchanged light conditions for six days and then prepared.

In other groups of animals submitted to total eyestalk extirpation (KONOK 1961) were kept in identical conditions and treated in the same way. The same applies to the control group.

In another series of experiments one group of animals was kept permanently exposed to light for 6 days (1,000 lux). On the 7th day specimens were prepared as control and the other animals were transferred into completely darkened basins. Every 2nd hour the brains and the eyestalks were fixed during 10 hours.

Another group was kept in complete darkness for 6 days, then after taking control specimens they were transferred into permanently illuminated basins. The material was then processed as in the previous group.

The state of the chromatophores of the carapace and the position of their pigments were investigated in each animal.

The material (brains and eyestalks) was fixed with BOUIN's fluid* then having embedded them in celloidin-paraffin they were serially dissected into

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4 to 6 μ sections. The sections were stained with aldehyde-fuchsin according to GOMORI's (1950) method modified by HALMI (1952). The total number of animals used in the various experiments was about fifty.

Results

The investigations of the changes in the histological picture of the neuroendocrine centres (supraesophageal ganglion and eyestalk) due to light- and dark-adaptation have led — in the succession of the findings — to the following results:

1. In permanent illumination (after 144 hours) the chromatophores of the animals showed normal adaptation. The red pigments were found dispersed, the white and blue ones, concentrated in the chromatophores of the carapace.

The examination of the eyestalks revealed that the rhabdoms in the ommatidia had assumed a violet colour and a bubbled structure without any transverse stratification. Most of the proximal retinal pigment had withdrawn above the basilar membrane stained dark violet, and had surrounded the rhabdoms. Immediately below the basilar membrane, in the subretinal blood vessels, hyaline and granular cells could be observed in large numbers, the latter ones containing a varying quantity of granules stained violet. Less granular cells were found in the eyestalk, chiefly basally in the intersegmental plicae, in the subepithelial lacunes and also in the medulla externa and the medulla terminalis.

The terminations of the sinus gland axon fibres were found to have been stained violet and looked homogenous.

Both A-type and B-type secretory cells (KONOK 1960) could be observed in the eyestalk in various positions not only on the medulla terminalis (medulla terminalis X-organ) but also on the surface of the medulla externa and medulla interna laterally or rather stuck between the individual medullae in various positions. Even within larger, possibly mixed groups, certain minor groups of secretory cells could be found separated from each other *(Fig. 1.)*.

The plasm of the giant cells A in general got stained intensively violet; it is of a spumous structure and fine-granuled. They are in an active phase, some with vacuoles. The picture of the B-type secretory cells varies according to their place. In general they are all active but in some only a hull of secretory products can be observed around the nucleus. Others are full of granules. In others again the plasm contains large violet-stained granules.

Many granular cells can be found in the brain and also peripherally, within the neurilemma. Hyaline cells can also be observed in large number.

The A-type giant secretory cells in the brain are generally stained a light colour, have a finely granulated plasm of spumous structure and are partly vacuolized. Most of the B-type cells are in an inactive phase, their plasm is empty, and traces of activity can only be detected in some small groups.

In animals kept in light for 6 days and then in darkness for 2 hours some 80 to 90 per cent of the pigments of the red chromatophores are still in a state of diffusion, the white pigments are completely contracted whereas some 60 to 70 per cent of the blue pigments are diffused.

The rhabdoms stained red and showing transverse stratification are still covered with the proximal retinal pigment which however, has markedly withdrawn below the basilar membrane. A large number of granular cells filled with violet granules can be observed in the subretinal blood vessels *(Fig. 2.)*. There is a similarly large number of granular cells in the blood vessels of the medulla externa *(Fig. 3.)*.

The terminations of axon fibres in the gland assume a marked violet colour and contain purple droplets.

The A-type secretory cells of the eyestalk are active. Giant cells with pink-, red- and violet-stained plasm can be observed mainly laterally. The B-type cells on the medulla externa between the terinations of axon fibres in the sinus gland are filled with secretory product *(Fig. 4)*, and so are those on the medulla interna. In-between, but chiefly at the basal end of the medulla terminalis markedly vacuolized empty B-type cells can be found.

A large number of granular cells can be observed in the brain, in its periphery and around it *(Fig. 5—6)*. Usually the A-type giant cells are in an active phase, some stained light-red, with spumous granulated plasm, others filled with secretory material, others again, with large vacuoles. In some of the B-type cells stained secretion can only be observed around the nuclei. They are, however, full with fine granules and they are partly vacuolized.

In animals kept for four hours in darkness the distribution of chromatophores shows complete adaptation, *i. e.* the red and the white pigments are contracted and the blue ones diffused.

The rhabdoms in the ommatidia show no transverse stratification. The proximal retinal pigment has withdrawn partly above the rhabdoms, partly below the basilar membrane. There is an unusually small number of granular cells in the subretinal vessels, whereas the number of the hyaline cells is relatively high.

The sinus gland is dark-violet, with purple-coloured droplets in some of the axon fibre terminations.

The A-typ cells, chiefly those situated distally, are filled with secretory product. The B-type cells also display strong activity and are filled with secretory material. In some of them vacuoles can be observed chiefly laterally and proximally.

In the brain and around it there are very few granular cells, Most of the A-type cells are filled and vacuoles can be seen only here and there. The B-type cells are similarly filled.

In the 6-, 8-, 10-hour specimens of the series the chromophores, as in the 4-hour specimens, show the dark-adaptation, and the histological picture is also the same. This makes it unnecessary to give detailed data.

2. In the series of inverse experiments, however, we could observe the following:

In the chromatophores of animals kept for 6 days in darkness the pigment diffusion showed the normal adaptation: the red and the white pigments were contracted the blue ones, diffused.

The proximal retinal pigment has withdrawn almost entirely below the basilar membrane. Many granular cells filled with violet granules can be observed in the subretinal blood vessels.

The sinus gland is filled with secretory products and stained dark-violet.

The A-type cells of the eyestalk are pale, some have slightly red, spumous plasm, with few granules and are vacuolized. The B-type cells are partly vacuolized, partly filled with secretory materials.

The plasm of the A-type cells of the brain is granulated, with vacuoles. The B-type cells contain many vacuoles and are generally empty.

The chromatophorous pigments of the carapace of animals exposed to 2 hours light are in a transitional state. Some 60 to 70 per cent of the red pigments but only some 20 to 30 per cent of the white ones are already diffused, while of the blue ones some 80 to 90 per cent are still diffused.

The proximal retinal pigment is about half-way up toward the top of the basilar membrane. A large number of filled granular cells can be observed in the subretinal vessels.

The sinus gland is full and is stained dark-violet.

The A-type cells of the eyestalk are very different. Some are empty, others have granules only around the nuclei. Most of them, however are filled with secretory product. The A-type cells, more pronouncedly than the B-type ones, can be seen to form isolated small groups within the larger groups and these minor groups are in different secretory phases *(Fig. 1.)*. Those on the medulla externa are active, are well stained, but some cells of the medulla terminalis are empty and not stained. Here again the cells of other groups are filled and only slightly vacuolized.

There are many granular cells in the brain and around it *(Figs 5—6)*. The A-type cells are generally characterized by strong activity, are filled with secretory product and slightly vacuolized peripherally. The majority of the B-type cells can also be found in an active phase and only some of them (in isolated groups) are empty.

The chromatophores of animals prepared after four hours exposition to light show almost complete adaptation: the white pigments are diffused, the blue ones contracted while of the red ones only some 80 per cent are in a state of diffusion.

In the eyestalk the proximal retinal pigment can still be found beneath the basilar membrane. In the subretinal blood vessels the blood cells are chiefly hyaline cells and only very few are granular cells.

The terminations of the axon fibres in the sinus gland are stained pale-violet with few red patches in them.

The A-type giant cells are active, filled, some being vacuolized.The B-type cells are active likewise: some groups of them are filled and partly vacuolized, some (fewer) are empty.

In the brain and around it there are only few blood cells containing granules. The A-type cells are markedly stained, whereas the B-type cells contain less granules and many vacuoles.

The 6-, 8- and 10-hour specimens of the series have yielded similar results which will not be treated in detail. The sixth group of the series, *i. e.* the animals exposed to light for 10 hours, must, however, be dealt with. Unlike as in group 3, here the red pigments were found entirely diffused and the white ones (some 40 per cent) started to contract (Konok 1961). The proximal retinal pigment had almost entirely withdrawn above the basilar membrane and the evacuated fibres were stained bluish-violet. Besides, the number of granular cells was small.

Again unlike the other groups of the series, the sinus gland was light-violet with bright-red spots in places.

3. In the experiments with ligated and extirpated eyestalks the controls show the above-mentioned histological picture of light- and dark-adaptation.

In the group with ligated eyestalks, symptoms of degeneration could be observed distally from the ligatures in the eyestalk after 6 days. The rhabdoms show a spiral structure, are narrow and elongated, while in the group illuminated they are crumbled. The nuclei of both A- and B-type cells are generally shrunk and the cell-membranes are not visible.

In the groups kept in darkness very few granular cells can be seen, the hyaline cells prevail. Here the A-type cells still show signs of secretion and are normally vacuolized, yet their nuclei are also substantially smaller than those of the normal cells.

In all animals either kept in darkness or exposed to light, the granular cells (filled with violet granules) accumulate before the ligature. Especially in the group kept in darkness they can be discerned in large number in and around the brain, too.

The sinus glands are very pale in both groups and the individual axon terminations of unusually small size (in the group kept in darkness this is even more pronounced) are few and rather dispersed, chiefly on the surface of the medulla externa.

In both groups the A- and B-type cells of the brain are equally pale and contain large vacuoles. In the group illuminated before the ligature the nerve fibres on the brain side are stained more and more markedly violet.

4. After the extirpation of the eyestalks the chromatophores in both groups show the normal light-adaptation. In the group kept in darkness an extremely high number of granular cells and a smaller number of hyaline cells can be observed around and in the brain The A-type cells of the brain are active, large, with many vacuoles. The B-type cells are less active, are pale, with many vacuoles.

There is a very large amount of granular cells in the group was illuminated too. The A-type cells are pale, filled with granules and partly vacuolized. The majority of the B-type cells are markedly vacuolized, and few cells contain secretory product.

Discussion

There is a most conspicuous connexion between the number and saturation of the granular cells, the single phases of light-adaptation (pigment distribution in the chromatophores) and the changing morphologic picture of the sinus gland *(Fig. 7.)*. There is a good agreement between pigment migration, resp. the appearance of the hormones responsible for it in the hemolymph and on the other hand the change in the proportion of the hyaline cells and granular cells in the blood stream.

References to the connexion between hyaline cells and granular cells have been made long (Cuénot 1895). Our experiments seem to support the view (Maynard 1960) that the granular cells represent in fact the functional phase of the hyaline cells. *i. e.* that they are actually hyaline cells playing a part in the transportation of certain substances in the blood fluid. In our case it seems obvious that the hyaline cells play a significant direct or indirect part — as can be assumed in the case of insects (WIGGLESWORTH 1956) — in the transportation of the hormones in the hemolymph. This statement seems to be supported by the connexion that exists between the physiological state of the sinus gland and the number of the granular cells or rather their saturation, between the adaptation of different directions and their phases. Further corroboration can be found in the connexions discovered by other authors

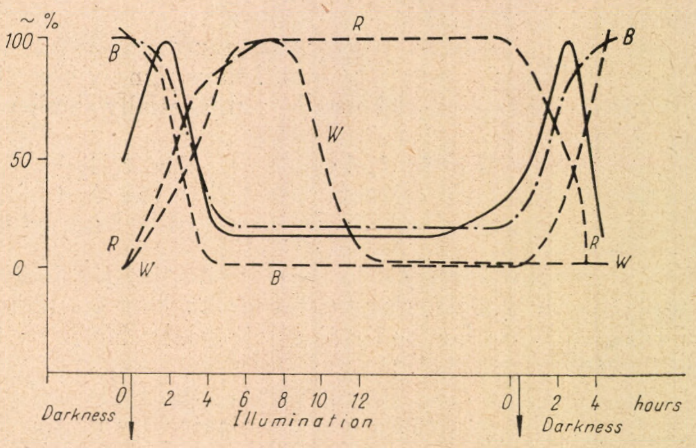

Fig. 7. Connexions between the number of granular cells (—), the hormone content of the sinus gland (— · —), the expansion of the red (R), white (W) and blue (B) chromatophores (- - -), in percentage of the maximum values

7. ábra. Összefüggések a granulocyták száma (—), a sinus gland hormontartalma (— · —), továbbá a piros- (R), fehér- (W) és kék (B) kromatofórok (- - -) expandáltsága között, a maximális értékek %-ában

between the changes in the number of granular cells and the physiological processes, known to be controlled by hormones, of the moulting and sexual cycles (AUSTREY 1952).

The stream of granular cells can be followed throughout the circulation system, including the capillaries of the brain and of the medullae of the eyestalk. As can be seen from the sections, they accumulate in large numbers in the segmental plicae, at the basal part of the eyestalks and on the surface of the brain: chiefly outside, but also inside the neurilemma. They can be seen whithin groups of secretory cells *(Fig. 8.)*, usually in larger numbers along the nerves issuing from the brain below the neurilemma, caught in the net of connective tissue *(Fig. 9.)*.

The circulation of the granular cells in the subretinal blood vessels running immediately below the basilar membrane — when related to what we know about the hormonal control of the retinal pigment system (FINGERMAN, LOWE and SUNDARARAJ 1959, FINGERMAN and MOBBERLY 1960) — again seems to stress the important part the granular cells playing in the transportation of hormones.

The experiments with ligated eyestalks raise another problem in connexion with the granular cells. The point is that by ligating the eyestalks the blood circulation was stopped in them. Before the ligature granular cells could be observed to accumulate in large number. Considering the results of our experiments in which after ligating the eyestalks the animals were interchanged in the basins (*i. e.* the animals kept in darkness were exposed to light and vice versa), and a normal colour-adaptation could be observed (KONOK 1961), the conclusion obviously suggests itself that the release of the hormones into the blood stream takes place not exclusively — in the given case only — through the sinus gland.

By ligating the eyestalks the immediate nervous connexion between the eye and the brain is not ceased, only the circulation is stopped. Nevertheless even in this state the colour-adaptation was normal in spite of the fact that the hormone-supplying function of the sinus gland was suspended — in a well controllable manner. This fact seems to show that under the effect of an adequate impulse the hormone was presumably released immediately from the brain (since this organ displayed a chromatophototropic activity to a similar extent to that of the eyestalk). Obviously it is highly probable that this function exists also in normal conditions. This is indicated also by the peripheral accumulation of the granular cells. This assumption is supported by the results of investigations undertaken by other authors as well (WEYGOLDT 1961).

The comparative study of the secretory cells of the eyestalks and of the brain has not proved particularly helpful for the localization of the hormones. A great obstacle in the way of correct estimation is the fact that the secretory activity is, in all probability, a continuous one, increasing or decreasing according to the requirements. At any rate it must be emphasized that neither the A-type cells nor the B-type ones, and these even less so, can be considered indentical in physiological sense. Although they cannot be discerned morphologically with sufficient certainty, the arrangement, e. g. of B-type cells, belonging to the same morphological type, in separated minor groups within the larger one, and the often differing secretory phases of these minor groups make it probable that the hormones produced in these cells may be different. This highly probable and justified assumption seems to be corroborated among other things, by the identity of the extent of dispersion of the granules within a small secretory group and, at the same time, by its dissimilarity from the adjacent but well delimited group of cells (otherwise of identical type). The fact that in two cell groups of identical morphological character the plasma was stained at the same time in an identical manner both in the brain and, e. g. on the medulla terminalis but they were stained in a way different from the other similar cells, seems to justify the above assumption and to indicate that identical hormones may be produced both in the eyestalk and in some cell groups of the brain.

Although necessitating further investigation, some phenomena observed, such as for instance the formation, like the terminations of axon fibres arranged in one layer on the chiasma externa (below the lamina ganglionaris), whose morphological picture is identical with that of the sinus gland in every phase *(Fig. 10.)*, must not be left unmentioned. Another noteworthy feature is an axon tissue between the above-mentioned formation and the lamina ganglionaris, always stained a more or less intensive violet and arranged perpendicularly to the axis of the eyestalk. In addition to this it is interesting to note that when the proximal retinal pigment has withdrawn above the basilar membrane, the fibres arising from the retinal cells also assume a violet colouration.

The well discernible movement of the proximal retinal pigments, characteristic of the individual phases of adaptation, also supports the fact that light-adaptation takes place less quickly than dark-adaptation. In this connexion, now in the case of the *Astacus leptodactylus*, the unanswered question of the mechanism of light-adaptation arises. No factor or factors either expanding red and white pigments or contracting blue ones have so far been extracted, nor has their existence been directly proved. We have, however, obtained reliable data indirectly from our own experiments (KONOK 1961) and from the experiment of others (FINGERMAN and MOBBERLY 1960, FINGERMAN and MOBBERLY 1960) to support their existence. Hence, we have evolved the following hypothesis concerning the mechanism of light-adaptation in the *Astacus*.

The slow diffusion of the red and the white pigments and the contraction of the blue ones could be observed after the extirpation of the eyestalks (KALMUS 1938, KONOK 1961). These and other physiological observations (KONOK 1961) suggest that in the hemolymph there exists a hormone level of adequate concentration and of antagonistic effect (responsible for light-adaptation) which — in the absence of counter-action — always causes the red and the white pigments to diffuse and the blue ones to contract. As to the source of these hormones we still have to do without satisfactory data.

What has been said about the function of the granular cells seems to contradict our assumption concerning light-adaptation. This contradiction, however, is not exclusive any longer and further experiments will surely enable us to reveal the mechanism of light-adaptation.

Conclusions

The histological assessment of various experiments on the light-adaptation of the *Astacus leptodactylus* on the basis of brain and eyestalk sections has led to the following conclusions:

1. The number of the granular cells in the blood and their saturation with granules varies in the hemolymph according to the phases of adaptation.
2. The granular cells should in fact be regarded as hyaline cells which, among other things, play an active part in the transportation of the chrom-activating hormones in the hemolymph.
3. The circulation of granular cells below the basilar membrane, in the subretinal blood vessels is conspicous. Hence it seems probable that they have something to do with the hormonal regulation of the motion of the retinal pigments.
4. Granular cells and hyaline cells accumulate in the basal part of the eyestalks, immediately below the epithelium, and also on the periphery of the brain, outside and also below the neurilemma.
5. The stream of granular cells in the brain and in the capillaries of the individual medullae of the eyestalks, as well as within the individual groups of secretory cells between the cells can clearly be observed.
6. The changes in the histomorphological picture of the sinus gland closely follow the course of the release of hormones corresponding to dark-adaptation.

7. In the A- and B-type cells of the brain and the eysetalk the chromatophorotropic factors of a dark-adapting character and capable of being isolated, could not be localized. The secretion of certain hormones presumably goes on incessantly, the rate of secretion may, however, accelerate or decelerate according to the prevailing conditions.

8. The secretory cells of the eyestalk are not condensed on the medulla terminalis but, both groups of A- and B-type cells can be observed on the medulla interna as well as is on the medulla externa, in a lateral or intermedullar position, what is more, even between the sinus gland axon fibre terminations.

9. Also within the morphologically uniform major groups of secretory cells clearly isolated minor cell groups can be seen near each other. These groups are in a synchronous functional phase. It may be presumed that even in the morphologically identical B-type cells various hormones may be produced.

10. The results of the experiments with ligated eyestalks indicate that hormones are released into the hemolymph directly from the brain, too.

11. On the chiasma externa a formation situated in one layer below the lamina ganglionaris and reminiscent of the terminations of axon fibres can be observed. It shows an activity similar to, and synchronous with, that of the sinus gland.

12. The fibres running from the retinal cells to the lamina ganglionaris assume a violet colour after the withdrawal of the proximal retinal pigment above the basilar membrane. The axon tissue arranged perpendicularly to the axis of the eyestalk below the lamina ganglionaris stains in a similar way.

13. The movement of the proximal retinal pigments of the ocelli and the pigment migration in the chromatophores indicate that light-adaptation is a slower process than dark-adaptation.

14. The hypothesis that light-adaptation (unlike the mechanism of dark-adaptation) is due to the constant hormonal concentration, at a given level, of the hemolymph, seems to be supported in different respects. The hormonal concentration becomes active when the secretion by factors inducing dark-adaptation of an antagonistic character is suspended.

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VIZSGÁLATOK A KECSKERÁKON, *ASTACUS LEPTODACTYLUS* ESCHSCHOLZ (DECAPODA), A KÖZPONTI IDEGRENDSZER SZEKRÉCIÓS TEVÉKENYSÉGE ÁLTAL SZABÁLYOZOTT FÉNY- ÉS SÖTÉTSÉG-ADAPTÁCIÓVAL KAPCSOLATBAN. II. A NEUROENDOKRIN RENDSZER HISZTOMORFOLÓGIAI KÉPE, ÖSSZEFÜGGÉSBEN A VÁLTOZÓ MEGVILÁGÍTÁSSAL

KONOK ISTVÁN

Összefoglalás

Az *Astacus leptodactylus*on végzett különböző fényadaptációs kísérletek hisztológiai értékelésénél, agyból és szemnyelekből készült preparátumok alapján a szerző ta következő megállapításokat tette:

A vérben levő granulociták az adaptáció egyes fázisaival összefüggésben, változó számban és granulumokkal különböző mértékben telten figyelhetők meg a hemoimfában.

A granulociták tulajdonképpen hyalocitáknak tekintendők, melyek az egyes neuroendokrin forrásokból származó — többek között — kromatoforotrop hormonok hemolimfában való transzportjában is szerepet játszanak.

Feltűnő a granulociták áramlása közvetlenül a bazális membrán alatt, a szubretinális véredényekben. Ennek kapcsán szerepük a proximális retina pigmentek mozgásának hormonális szabályozásában is valószínűnek látszik.

Granulo- és hyalociták felhalmozódása figyelhető meg a szemnyelek bazális részén, az epithelium alatt közvetlenül, továbbá az agy perifériáján, főleg a neurilemmán kívül, de az alatt is.

Jól megfigyelhető a granulociták áramlása az agyban és a szemnyelek egyes medulláiban húzódó csatornácskákban, valamint az egyes szekréciós sejtcsoportokon belül, a sejtek között is.

A szinusz-mirigy hisztomorfológiai képének változása jól követi a sötétséghez való adaptációnak megfelelő hormonelválasztás menetét.

A szemnyél és az agy A- és B-típusú sejtjeiben az izolálható, „dark-adapting" jellegű kromatoforotrop faktorok lokalizálása nem volt lehetséges. Az egyes hormonok szekréciója feltehetőleg állandóan folyik, s ennek üteme valószínűleg szükség szerint gyorsulhat, vagy lassúbbodhat.

A szemnyél szekréciós sejtjei nem tömörülnek a medulla terminálison, hanem mind az A-, mind a B-típusú sejtek csoportja megfigyelhető a medulla internán és externán egyaránt, laterális vagy intermedulláris elhelyezkedésben, sőt a szinuszmirigy axon terminálisai között is.

A szekréciós sejtek egyes nagyobb, morfológiailag egységes csoportján belül is jól izolált kisebb sejtcsoportok foglalnak helyet egymás mellett. Ezek a csoportok szinkron működési fázisban vannak. Feltehető, hogy az egyébként morfológiailag azonos B-típusú sejtekben is különböző hormonok termelődnek.

Szemnyél-lekötéses vizsgálatok eredményei arra utalnak, hogy hormonelválasztás a hemolimfába közvetlenül az agyból is végbemegy.

A chiasma externán, a lamina ganglionáris alatt egy rétegben elhelyezkedő, axon terminálisokra emlékeztető képlet figyelhető meg, mely a szinusz-mirigyhez hasonló és azzal szinkron aktivitást mutat.

A retinális sejtekből a lamina ganglionárisig húzódó rostok, a proximális retina pigment bazális membrán fölé húzódása után lilára festődnek. Hasonlóképpen festődik a lamina ganglionáris alatt a szemnyél tengelyére merőleges irányba rendeződött axon szövedék is.

Az ocellusok proximális retina pigmentjeinek mozgása, s a kromatofórokban való pigmentvándorlás is azt mutatja, hogy a „light"-adaptáció kialakulása hosszabb ideig tart, mint az ellentétes folyamat.

Több vonatkozásban alátámasztottnak látszik az a feltevés, hogy a fény-adaptációt (ellentétben a sötétséghez való adaptáció mechanizmusával) a hemolimfának egy bizonyos szintű állandó hormonkoncentrációja idézi elő, mely akkor jut érvényre, amikor az antagonista jellegű „dark"-adaptációt indukáló faktorok elválasztása szünetel.

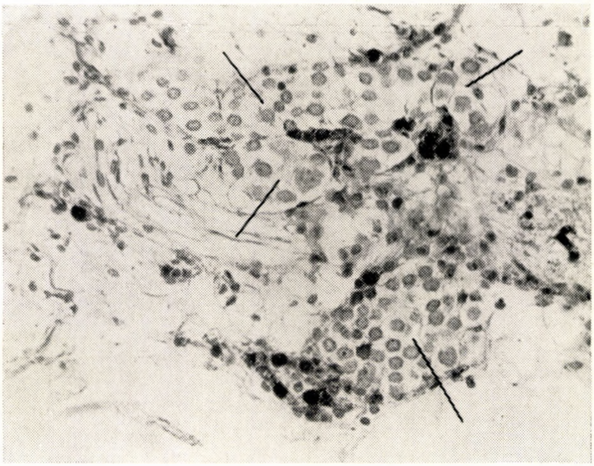

Fig. 1. Group of B-type cells isolated within a major group of secretory cells on the medulla terminalis (eyestalk of *Astacus)*

1. ábra. Nagyobb szekréciós sejtcsoporton (medulla terminalis X-szerv) belül izolált B-típusú sejtek csoportja *(Astacus* szemnyél)

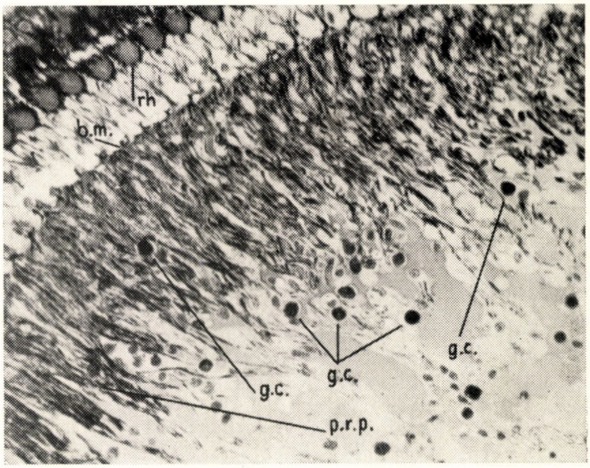

Fig. 2. Granular cells in the subretinal blood vessels (eyestalk of *Astacus).* b. m. = basilar membrane; g. c. = granular cells; p. r. p. = proximal retinal pigment; rh. = rhabdoms

2. ábra. Granulocyták a subretinalis véredényekben *(Astacus* szemnyél). b. m. = basalis membran, g. c. = granulocyták, p. r. p. = proximal retinal pigment, rh = rhabdomok

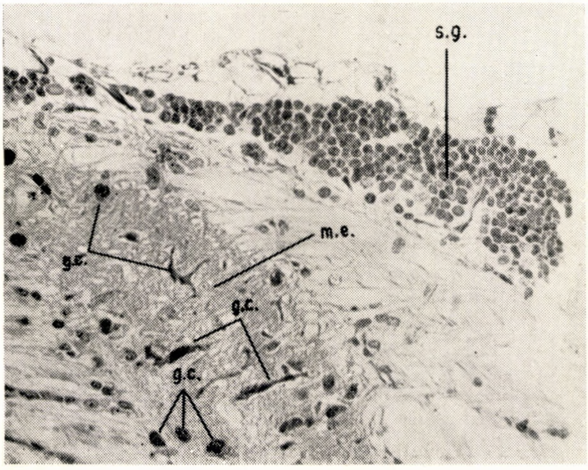

Fig. 3. Granular cells is the medulla externa (eyestalk of *Astacus).* g. c. = granular cells; m. e. = medulla externa; s. g. = sinus gland

3. ábra. Granulocyták a medulla externaban *(Astacus* szemnyél). g. c. = granulocyták, m. e. = medulla externa, s. g. = sinus gland

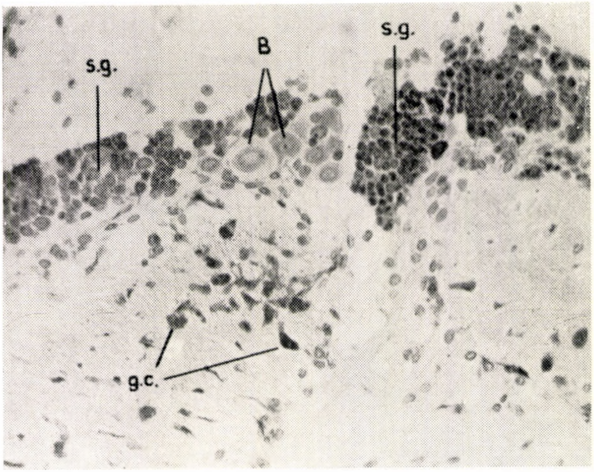

Fig. 4. B-type secretory cells between the terminations of axon fibres of the sinus gland (eyestalk of *Astacus*). B = B-type cells; g. c. = granular cells; s. g. = sinus gland

4. ábra. B-típusú szekréciós sejtek a sinus gland axon terminalisai között (*Astacus* szemnyél). B = B-típusú sejtek, g. c. = granulocyták, s. g. = sinus gland

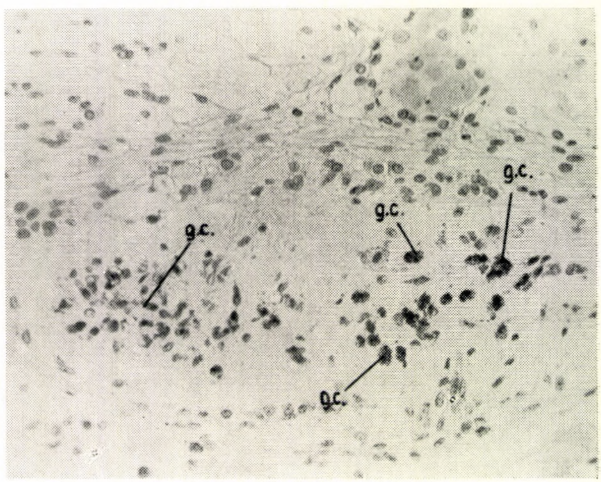

Fig. 5. Granular cells in the mass of the brain (*Astacus*). g. c. = granular cells

5. ábra. Granulocyták az agy tömegében (*Astacus*). g. c. = granulocyták

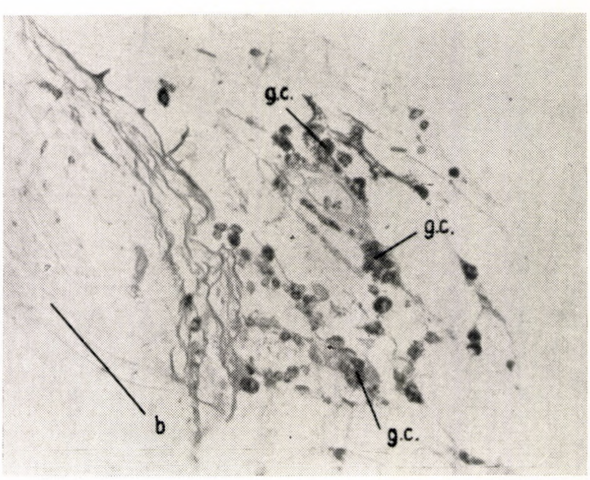

Fig. 6. Granular cells on the periphery of the brain (*Astacus*). b = brain; g. c. = granular cells

6. ábra. Granulocyták az agy periferiáján (*Astacus*). b = brain, g. c. = granulocyták

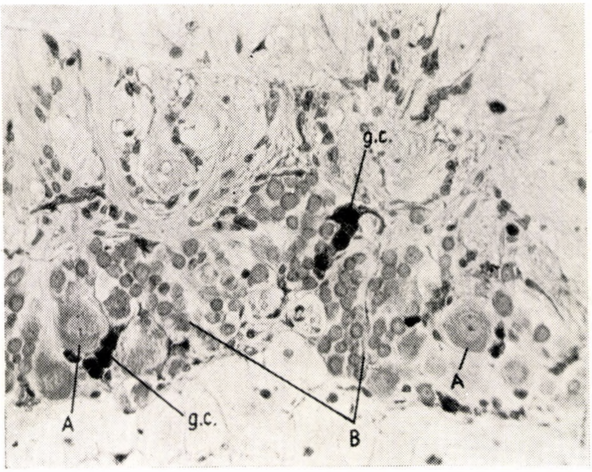

Fig. 8. Granular cells between the secretory cells (brain o-*Astacus)*. A = A-type cellsf B = B-type cells; g. c. = gra; nular cells

8. ábra. Granulocyták a szekréciós sejtek között *(Astacus* agy). A = A-típusú sejtek, B = B-típusú sejtek, g. c. = granulocyták

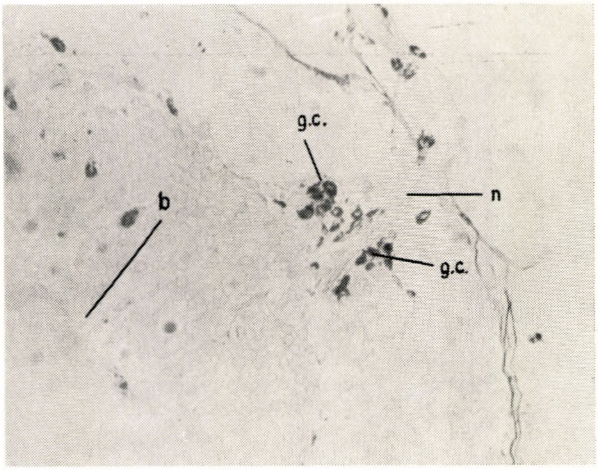

Fig. 9. Granular cells around an issuing nerve (brain of *Astacus)*. b = brain; g. c. = granular cells; n = nerve

9. ábra. Granulocyták kilépő ideg körül *(Astacus* agy). b = brain, g. c. = granulocyták, n = ideg

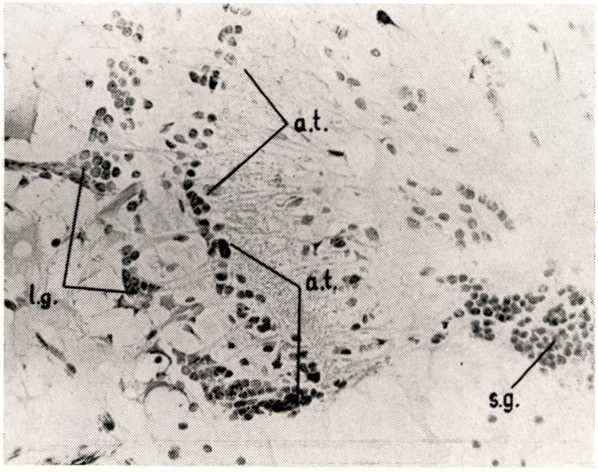

Fig. 10. See legend in the text. a. t. = terminations of axon fibres; l. g. = lamina ganglionaris; s. g. = sinus gland

10. ábra. Magyarázat a szövegben a. t. = axon terminalisok, l. g. = lamina ganglionaris, s. g. = sinus gland