

REGULATION OF THE BRANCHIAL CILIARY ACTIVITY

IN THE MUSSEL

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LAGEN

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by

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I. Introduction

The question whether the ciliary mechanism, which in lamellibranchs ensure the water and food supply, can be regulated at will by the animals themselves has long been a subject for research and debate. The phenomenon that, even in gills or fragments of gills, removed from the animals, the cilia can remain active for hours and even days on end, in a form and co-ordination of movement which to all appearances looks quite normal, has often convinced scientists that the ciliary activity is an autonomous movement, quite outside the animal's control.

There is no doubt indeed that those co-ordinated ciliary movements are autonomous to a high degree. BABAK (1913) supposed that the branchial nerve might control the activity, though - as we judge his paper - he hardly had a reason. NELSON (1951; 1960), however, was possibly the first to record that the animal can influence its ciliary activity to a certain extent, as he found that the pauses, which normally occur in the beat of the lateral cilia, could not be observed in filaments which were cut apart from the branchial nerve. He therefore concluded that they must be caused by inhibitory impulses, originating in that nerve. He worked with the oyster *Crassostrea*, an eulamellibranch for which it had already been discovered (ELSEY, 1935) that ramifications of the nervus branchialis reach as far as the gill filaments. At that time nerve ramifications could not be traced quite as far in filibranchs (GRAY, 1922; LUCAS, 1931b). For want of anatomical evidence the very plausible notion that in animals such as *Modiolus* (LUCAS, 1932a) and *Mytilus* (FIELD, 1922; LUCAS, 1932a) the observed periodical pauses in the beat of the lateral cilia -

quite similar to those described by NELSON for oysters - were of neural origin, was rejected as often as it recurred.

It was not before 1965 when AIELLO & GUIDERI succeeded in observing ramifications of the branchial nerve in the gill filaments of *Mytilus*, running at the basis of the lateral cells. In addition nerve branches were observed under the frontal and post-lateral cells in the same species by PAPARO (1972), after similar structures at corresponding locations had been found by SATIR & GIULIOLA (1970) in the fresh water mussel *Elliptio*.

Thus the morphological base was laid for the explanation of results which in the meantime had been obtained by AIELLO (1957; 1960) with *Mytilus*. In those experiments he demonstrated in a way much resembling NELSON's technique that the branchial nerve influences the activity of the gill's cilia. Contrary to NELSON, however, he concluded to an excitatory action. This conclusion was supported when AIELLO & GUIDERI (1964) found that a repetitive electric stimulation of the branchial nerve soon results in an increase of the beat frequency of the lateral cilia in *Mytilus*. Their results were confirmed by TAKAHASHI & MURAKAMI (1968) who found, moreover, that one single impulse to the nerve induces an abrupt short pause in the movement of the lateral cilia. These observations reconcile the conclusions of NELSON and of AIELLO, the first concluding that inhibitory impulses originate in the branchial nerve and the latter that its action is excitatory.

In the years after the first indications had been found (AIELLO 1957; 1960) that serotonin (5-hydroxytryptamine) was an important excitatory mediator, great progress has been made in unraveling the physiological processes which accompany the neurally controlled ciliary activity in a number of lamelli-

branch species (AIELLO, 1970; PAPARO & FINCH, 1972; AIELLO & PAPARO, 1974). From this work, summarized by JØRGENSEN (1975), we may conclude that the regulation mechanism of the mussel gill is now for the greater part revealed. However, because the studies were done on heavily mutilated animals, the remark made more than a decade ago by AIELLO & GUIDERI (1965) is still valid: this knowledge does not help in understanding the way in which the intact animal makes use of it. Though our research of the feeding mechanism of the mussel was only connected indirectly with problems of cilia regulation, it did contain some observations which may be of interest in this respect and partly fill in the upmentioned gap. Moreover, the ciliary movement in fragments of gills - which of course can only concern the autonomous ciliary movement - can be compared with the movement in intact animals, thus informing us about a possible interference by the animals in the autonomy of the ciliary movement. After a very brief earlier report (DRAL, 1970) a more detailed account is presented here.

During our study the frontal and marginal gill cilia were greatly neglected; our interest was primarily directed to the lateral and latero-frontal cilia. The latter cilia and their movements have been elaborately described in an earlier paper (DRAL, 1967). A detailed description of the movements of the lateral cilia in undamaged mussels seems not to exist as yet. For this reason some relevant details will receive more attention in the present paper.

Acknowledgement. I am indebted to Dr. J. Verwey for stimulating interest during the observations and for his helpful criticism in the preparation of the manuscript.

II. Methods

The observations were carried out on very young mussels, their shells being still sufficiently transparent to observe the internal functions in the undamaged animal. The animals were kept in a perspex cuvette, through which a constant current of sea water was kept up. A more detailed description is given by DRAL (1967).

In various experiments, besides the young mussels, some gill fragments cut out of adult mussels were put into the cuvette and fixed by some glass threads. The fragments were taken from the ventral side of a gill lamella, including the food groove, so that during the treatment the mutual connections between the filaments were better maintained. The dorsal boundary of the cut ran through the middle of the lamella so that the cut did not contain any part of the branchial nerve which runs through the axis of the gill.

In such fragments the cilia may keep on moving for a long time, but usually the lateral cilia lose their activity after a few hours. To reduce the risk that for this reason a series of experiments would have to be broken off its duration had to be kept as short as possible, with the drawback that changes in temperature and salinity had to be effected at a very fast rate.

The beat frequencies of the lateral and in a few instances also of the latero-frontal cilia were measured by synchronization with stroboscopical illumination. In intact animals as well as in isolated gill fragments the beat frequency of the cilia varies not only in the course of time, but also at various locations in the same object. In order to avoid effects of the latter phenomenon, the measurements of any series were carried out at the same spot of the object.

In observations with a changing watertemperature two thermometers were fixed in the water current, one where it entered and one where it left the cuvette. The mean between the two readings was taken to represent the temperature in the cuvette. The various chlorinities in a series of experiments were obtained by mixing a quantity of sea water with the necessary amounts of either distilled water or of a sea water concentrate (Flüssiges Meersalz "Dangasal", Ulrich Sabarth KG, Hage, Germany). The chloride content of the mixtures was determined by titration.

III. Observations

1. Pauses

In young mussels, as observed in our studies, periodic stops of the lateral ciliary activity were an ever existing phenomenon. In Fig. 1 their occurrence in an otherwise fairly constant activity is shown. This represents an "average case". The pauses may occur more or less often and may last for a shorter or a longer time. They may involve all the filaments together, or only a small number, or a single filament, or even only part of one row of lateral cilia. As a rule they tend to occur more beats per sec.

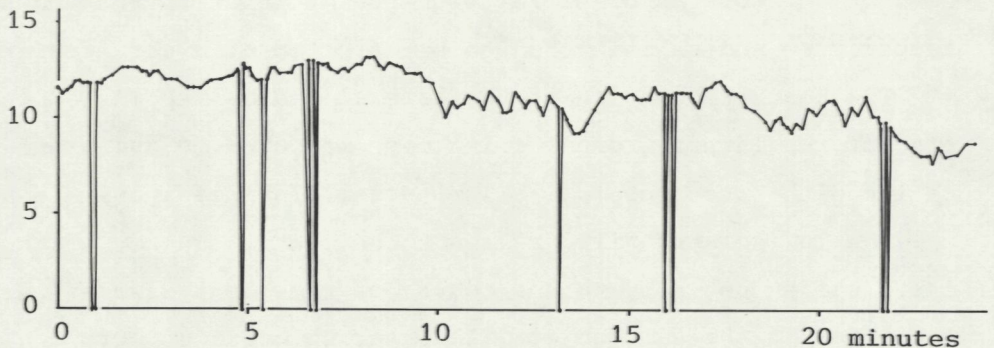


Fig. 1. Beat frequency of the lateral cilia of a young mussel, measured at short intervals.

often if suspended particles are present in the current.

We have observed that pauses of a similar kind may be evoked as a reaction to external incidents. When the experimental set-up is tapped lightly, or the illumination suddenly turned down, the beat of the lateral cilia is stopped immediately for a short and sometimes a long time. After such a pause has been evoked in the same way for a few times in succession the animal ceases to react for a certain time. At normal temperatures the pauses follow the stimulus so promptly that it is difficult to imagine any other cause than a nervous inhibition. Besides, however, many pauses occur in seemingly constant conditions, without any apparent external cause.

From an earlier description (DRAL, 1967) it follows that the remarks made in the previous paragraph with respect to the lateral cilia, also hold for the latero-frontal ciliary activity. It should be repeated here that pauses need not occur simultaneously in both epithelia, nor are necessarily of equal duration.

Contrary to NELSON's (1951; 1960) findings with *Crassostrea* but in accordance with LUCAS' (1931 a) findings with some other species we have also observed these pauses in fragments cut out of *Mytilus* gills, in which certainly no connection remained with the nervus branchialis. This holds for the lateral cilia. In this respect nothing can be said about the latero-frontal cilia, because in gill fragments these cilia rarely show movements of any regularity (DRAL, 1967), so eventual pauses can not be discerned.

2. The beat frequency of the lateral cilia

To compare the beat frequencies measured in a constant environment in the lateral cilia of an undamaged young mussel

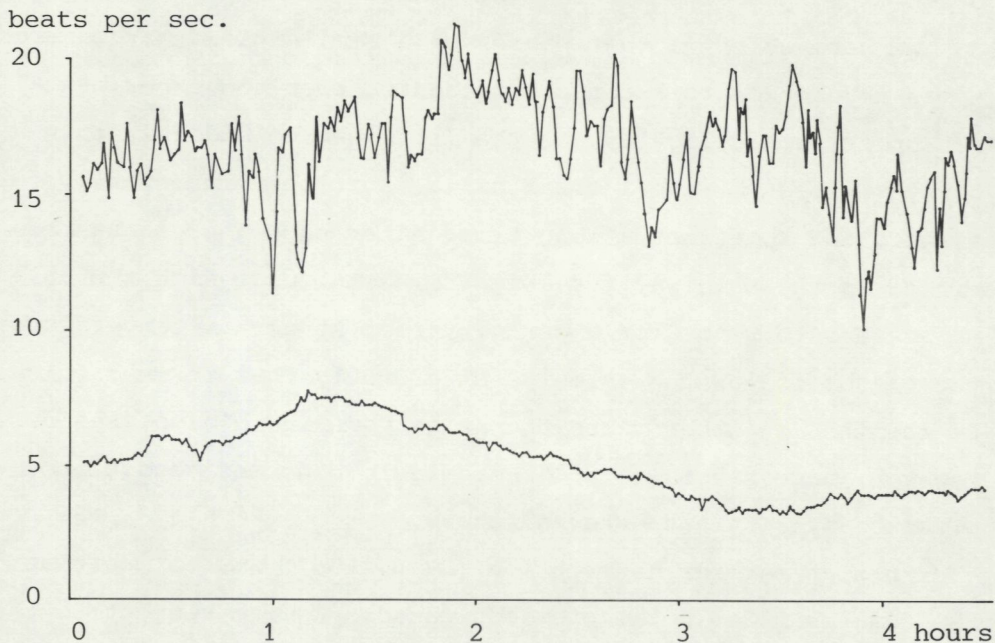


Fig. 2. Beat frequency of the lateral cilia of an undamaged young mussel and of a gill fragment in a constant environment.

with those in a gill cut we turn to Fig. 2. It must be emphasized that in this and all following figures the above mentioned short pauses are left out. Attention is also drawn to the difference in scale with the previous figure.

It is clear that in the gill fragment variations in beat frequencies are smaller and more gradual than in the undamaged mussel. The argument might be advanced that this is due to the differences in ciliary behaviour in an adult and a young mussel respectively. In fact, in another context such a difference has been stressed by MACGINITIE & MACGINITIE (1968, appendix 98), though without any argumentation. As has been demonstrated previously (DRAL, 1967) there is no support for the assumption of a difference in behaviour, rather the contrary seems true: the young and the adult animal act alike. We conclude that Fig. 2

illustrates the steering of the animal of the autonomous ciliary activity.

3. The influence of temperature

a. The lateral cilia

Fig. 3 represents the results of a series of experiments in which three young mussels, kept in flowing sea water of a constant chlorinity of 16.5 ‰, were exposed to a temperature which for over twelve hours decreased by about one centigrade per hour. Each point in this diagram shows the average of a number of measurements during 5 - 10 minutes, so that the mean activity of the lateral cilia is reflected, while the rapid and often considerable variations in beat frequency are for the greater part eliminated.

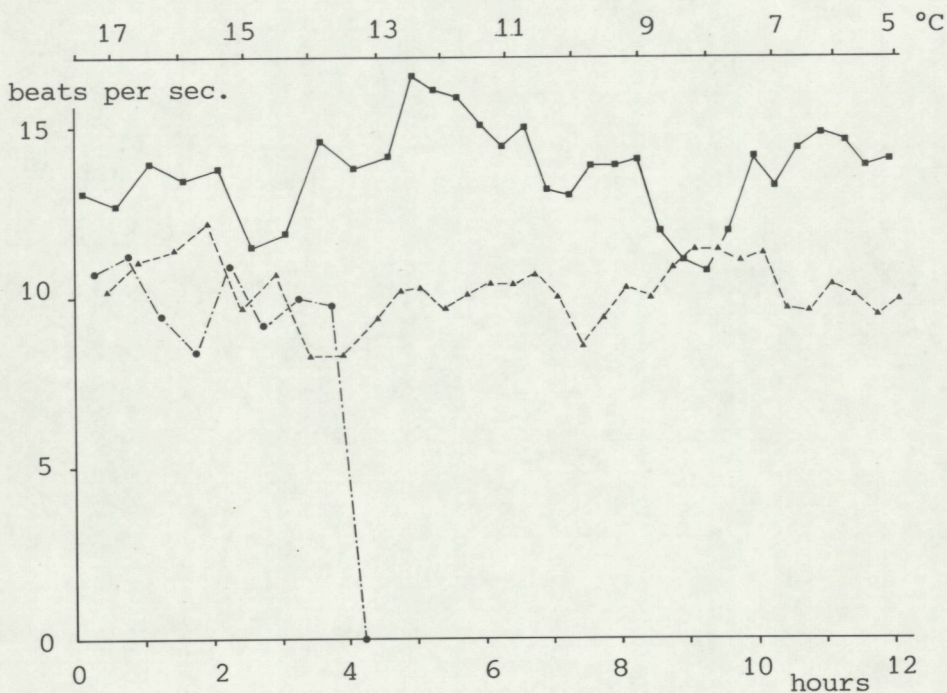


Fig. 3. Beat frequency of the lateral cilia of three young mussels at falling temperature.

One of the animals stopped altogether after four hours of observation, the two other animals did not show any influence of temperature. In fact, the curves might just as well represent the results of experiments at a constant temperature.

The results of other experiments carried out in about the same way as the previous one, different however in rate and/or direction of the change of temperature, are summarized in Fig. 4. Again, with one exception (the curve indicated by an arrow), there is no evidence that the temperature had any influence on the lateral ciliary beat frequency.

In a third series of experiments young mussels were used

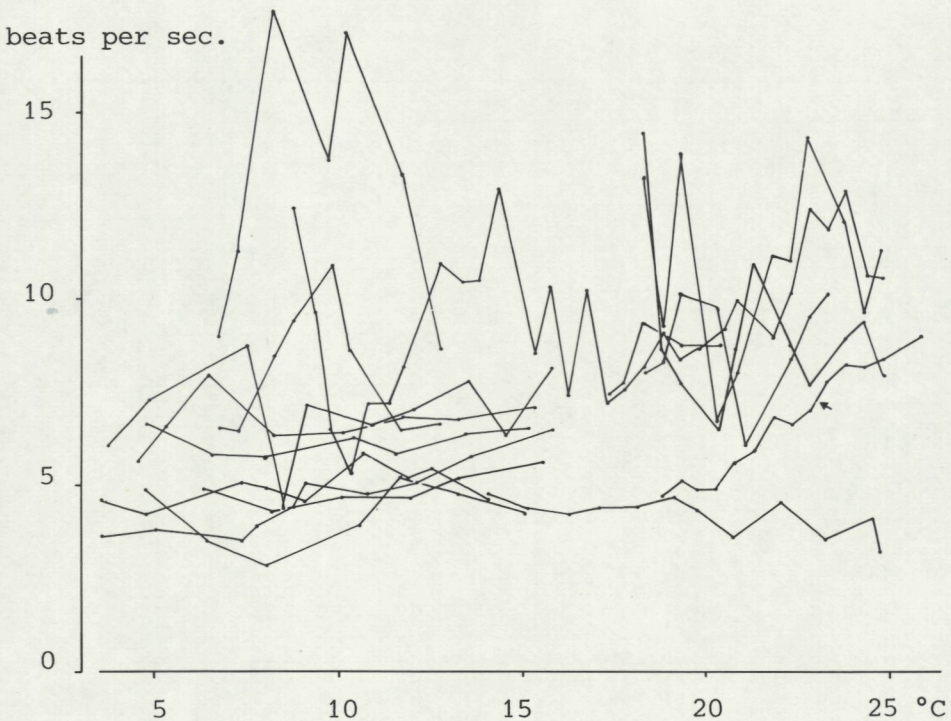


Fig. 4. Beat frequency of the lateral cilia of young mussels at varying temperatures.

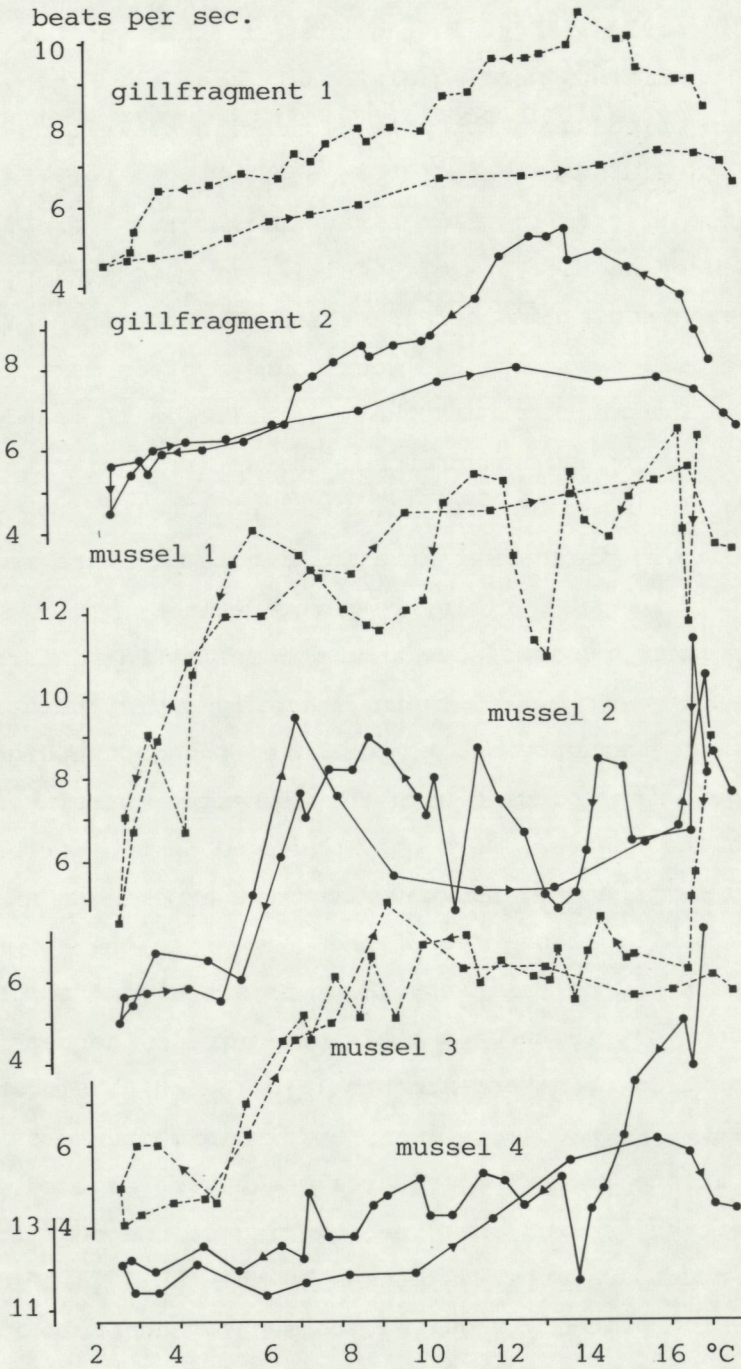


Fig. 5. Beat frequency of the lateral cilia of gill fragments and of young mussels at falling and rising temperature respectively.

simultaneously with gill fragments. In this way the environmental conditions were equal for all objects. Fig. 5 represents a series of measurements with decreasing as well as rising temperature. The changes in temperature were very fast: it fell from 17° to 2.5° C at a rate of about 1° per 15 minutes, followed by an increase of about 1° per 5 to 6 minutes. This must have been a considerable stress for the animals.

Two gill fragments and four young mussels were used. For the gill fragments a reasonable correlation is found between beat frequency and temperature, though (not quite in accordance with the findings of AIELLO, 1955 and 1960; GRAY, 1928 and LUCAS, 1932b) the values at a falling temperature were not equal to those at a rising temperature.

The young mussels show a more complicated picture. At temperatures above 7° C there is hardly any correlation between beat frequency and temperature, though the highest observed frequencies coincide with the highest temperatures. Those high values however, were only observed in the series with falling temperature, shortly after the experiment started. They are due to the adaptation of the animals to the experimental conditions and no value should be attached to them. Below 7 or 8° C, however, in three out of four animals the beat frequency decreased. In other experiments (Fig. 3 and 4), in which the temperature changed much less rapidly, a decrease of beat frequency at the lower temperatures was never recorded. It must therefore be assumed that the lowering of the beat frequency at lower temperatures was caused by the rapid fall in temperature, which probably required too much of the animal's adaptability.

The curve indicated by an arrow in Fig. 4 was obtained from

a mussel which had passed the night before the experiment in sea water of 28° C. The fact that in this case a temperature influence was found indicates that the animal's condition had suffered from the preceding high temperature. This effect might well be comparable with that observed in Fig. 5 at the lower temperatures, so that the conclusion, that the beat frequency in intact animals is not influenced by temperature, remains valid.

Overlooking the experiments described above we may conclude that under natural conditions changes of temperature within relatively wide limits do not affect the beat frequency of the lateral cilia of *Mytilus*.

b. The latero-frontal cilia

The relation between temperature and beat frequency of the latero-frontal cilia was studied by an experiment in which the temperature of the sea water was lowered from 20 to 9° C in the course of $4\frac{1}{2}$ hours, during which time the beat frequencies of the lateral and latero-frontal cilia was measured alternately. The average values for periods of 10 minutes (each value from about 4 measurements) are plotted in Fig. 6.

As we saw before, the lateral cilia show great variations in activity. It has been remarked earlier (DRAL, 1967) that the latero-frontal ciliary beat tends to follow these variations, though with a much smaller amplitude. Such a tendency can also be noticed in the details of the variations shown in Fig. 6. Apart from this, however, and in contrast with the lateral cilia, the beat frequency of the latero-frontal cilia shows a positive correlation with the temperature. We never saw a similar change in beat frequency of the latero-frontal cilia during many observations on animals in unchanging external conditions.

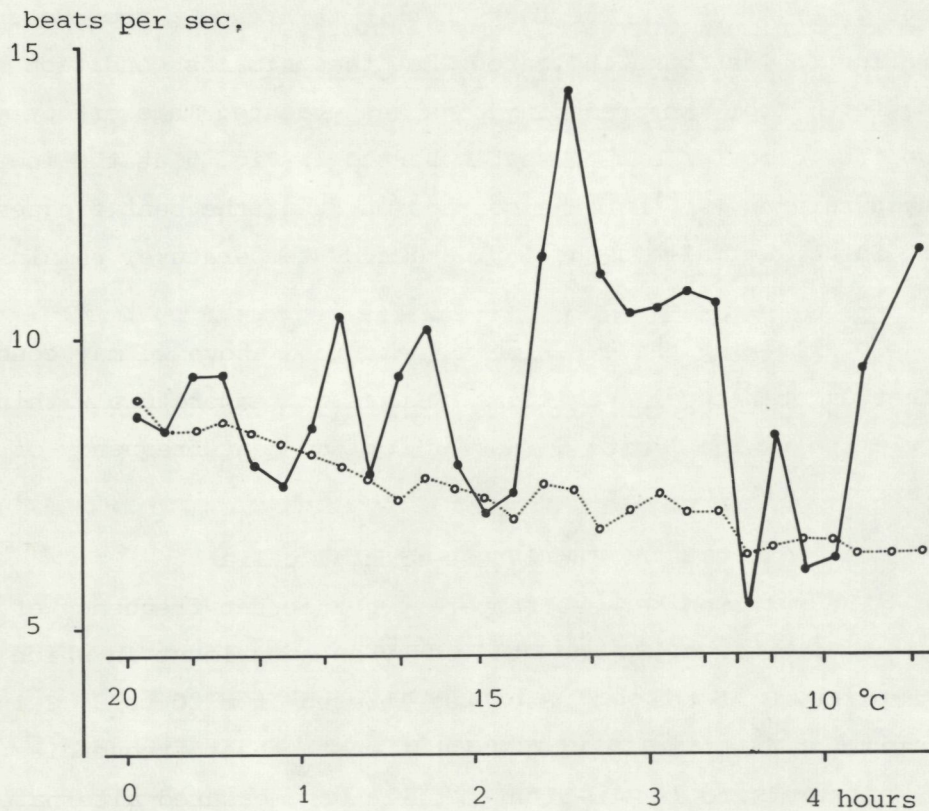


Fig. 6. Beat frequencies of the lateral (solid dots) and latero-frontal (open dots) cilia of a young mussel at falling temperature.

4. The influence of chlorinity

a. The lateral cilia

In the experiments of which the results are summarized in Fig. 7 the chlorinity of the sea water was lowered by steps of about 1.5 ‰ Cl' from 17.46 to 8.88 ‰ and then back to the original concentration in the same way, all this within eight

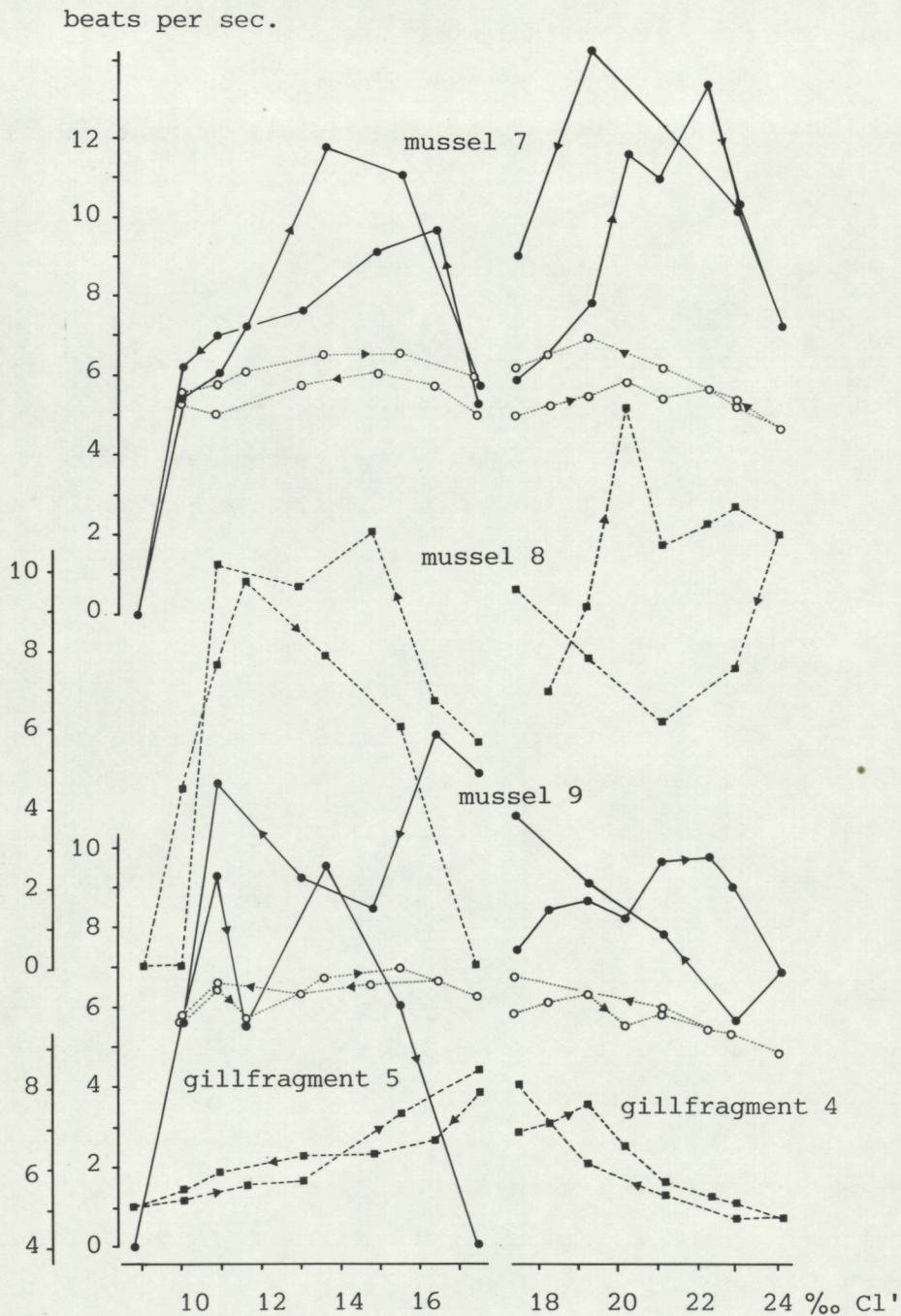


Fig. 7. Beat frequencies of the lateral cilia of a gill fragment and of the lateral (solid dots) and latero-frontal (open dots) cilia of some young mussels at varying chlorinities.

hours. On the next day the animals were subjected to an increase of the chlorinity by the same steps, up to 24.09 ‰ Cl', followed by a decrease to the original concentration in a period of nine hours in all. On the second day of the experiment the gill cut was replaced by a fresh one. On both days the temperature varied between 16.8 and 17.8° C.

Apparently (Fig. 7) there exists a fairly regular and reversible correlation between chlorinity and activity of the lateral cilia in isolated gill fragments. The intact animals reacted very differently. Apart from the complete stand-still at 8.88 ‰ Cl', where they all had closed their shells, the animals showed a similarity in the relatively low activities in the unmodified sea water (17.46 ‰). We have no explanation for the latter fact. Except for these points, however, the mussels' reactions varied much individually.

A few more experiments were carried out in which the chlorinity was changed either stepwise or gradually. With intact animals a correlation between chlorinity and lateral ciliary beat frequency was never found and we must conclude that such a correlation does not exist.

b. The latero-frontal cilia

Measurements of the beat frequency of the latero-frontal cilia in varying chlorinities are given in Fig. 7 for two intact mussels. Again we may expect that these curves follow on a smaller scale the main course of those for the lateral cilia in the same animal. This is indeed the case. In our opinion, however, there are some slight indications - especially in the range of 18 to 24 ‰ Cl' - that these variations are superimposed on a trend, correlative with chlorinity. By lack of more reliable observations no conclusion can be drawn.

IV. Discussion

That the co-ordinated movements of the cilia of a mussel's gill must be ascribed to some property of the ciliary epithelium may be concluded from the fact that such movements can persist in one single cell, isolated from the tissue. (a.o. GRAY, 1922). By their (autonomous) movement the lateral gill cilia give rise to a current of food- and oxygen-bearing sea water through the mantle cavity and it seems natural that the animal might use its neural mechanism to regulate this ciliary activity and therewith the supply of food and oxygen.

It appears from the experiments with changing temperature and chlorinity that the animals try to compensate the influence of those changes in environment by regulation. Under natural circumstances they will certainly succeed. Thus the pumping performance will be maintained at a satisfactory level. The significance of such a function seems evident.

The mediating structures - ramifications of the branchial nerve - have been found at the basis of the lateral cells. Similar structures were found at the basis of the frontal cells. The frontal ciliary activity was not included in the present study. That it is under at least inhibitory nervous control may be concluded from observations by GALTSOFF (1957) in *Crassostrea* (similar observations also hold for the cilia in the terminal food grooves). In view of the different functions - water propulsion in lateral and food transport in frontal cilia - one might expect their regulation to be mutually independent. Indeed some occasional observations (GRAY, 1926; AIELLO, 1960) point at such an independence; on the other hand there are indications for a common regulation of both epithelia (AIELLO & GUIDERI, 1965). That this is of some interest in connection

with the latero-frontal cilia is explained as follows.

On anatomical grounds one must assume that the cells, bearing the latero-frontal cilia, are not contacted by nerves. So nervous regulation should not be expected. Parallel variations in beat frequency of the lateral and latero-frontal cilia - the latter with a smaller amplitude - are almost everytime observed. As has been explained before (DRAL, 1967), these slight variations in the beat frequency of the latero-frontal cilia are of neglectable importance to their food filtering function. We are led to suppose, therefore, that the variations in the latero-frontal ciliary beat are not more than a secondary effect of the regulation of the lateral cilia. Basically, the activity of the latero-frontal cilia would be an autonomous movement, independent from that of the lateral cilia and, unlike the latter, not regulated to counter-balance the direct influence of external factors like temperature and chlorinity. Indeed, the evidence reported in this paper - however few it may be - seems to support this idea. Also in agreement are the facts that prolonged periods of activity or inactivity as well as short pauses occur in complete mutual independence in lateral and latero-frontal cilia. SEGERDAHL (1922), GRAY (1928) and AIELLO (1960) also mention differences in reaction or behaviour of the ciliary groups in question.

Still we observe parallel variations in beat frequency.

The reasoning that a change of frequency of beat of the lateral cilia will change the velocity of the water current and therefore the external resistance to the latero-frontal cilia, might suggest that the parallism of the variations has mechanical reasons. Such an effect has indeed been described (DRAL, 1967) but, as it appeared to be very slight, it is highly improbable that it is responsible for the phenomenon under dis-

cussion. Alternatively one should consider a direct influence by the regulating mechanism. According to PAPARO (1972) nerve fibers are found under only one of a series of ciliated lateral cells; neighbouring cells must be excited by passive spread of current from directly stimulated ones. Presumably the same course of events takes place in the frontal epithelium. If the current should diffuse beyond the borders of the "own" epithelium, it eventually might reach the latero-frontal cells. In virtue of its proximity the frontal epithelium, to which the latero-frontal cells are directly bordering, would be the first possible source, while the lateral epithelium, from which the latero-frontal cells are separated by unciliated cells, is only a second candidate. However, parallel variations in beat frequency have been observed for the latter two types of cilia. Would that mean that frontal and lateral cilia are subject to a common regulation? It certainly is worth while to eliminate the above speculations and find answers to the questions.

For forty years (or maybe more) nervous control of the ciliary activity in the mussel's gill has been denied, based on lack of anatomical support. One may wonder now how sure we can be about the absence of nervous (or any other) regulation in the latero-frontal cilia. As far as we know (DRAL, 1967) the latero-frontal cilia are the most sensitive ones to external disturbances and the only ones which are able a. to shorten the trajectory of beat (without alteration of the frequency); b. to perform two types of beat: the "regular" and the "angular" one and c. to be sticky or not. The fact that these unique capacities are brought into practice whenever that seems useful, makes us nearly expect that some regulating mechanism will be found one of these days.

Returning to known facts, a few remarks should still be

made.

AIELLO & GUIDERI (1965) affected the beat frequency of the lateral cilia of small groups of filaments by fitting an electrode to various points on the visceral ganglion, from which the branchial nerve originates. The ability of the regulatory mechanism to select groups of filaments can be observed in function when much suspended matter is present (DRAL, 1968). In these circumstances the activity of the lateral cilia on a varying number of caudally situated filaments can be greatly diminished and finally stopped, while the activity of these cilia on filaments of more anterior positions remains practically unaffected. We hope to enter this matter more elaborately in a separate paper and confine ourselves at this place to the remark that by this mechanism the handling of large amounts of suspended material is greatly facilitated. In connection with the upmentioned observations by AIELLO & GUIDERI it should be added that in transparent young mussels occasionally a similar inactivity of some anterior filaments can be seen; even a small group of inactive filaments between active ones has rarely been observed.

Finally we want to return for a moment to the short pauses in the ciliary activity. The pauses induced by external disturbances are certainly of nervous origin and it seems obvious to conclude that this function is performed by innervation through the *nervus branchialis*, as described by TAKAHASHI & MURAKAMI (1968). It seems possible that a rather long pause may also be induced by this nerve. When the animal is about to shut the shell we notice that all cilia stop abruptly, while the demibranchs are retracted into the mantle cavity. Only when the adductor muscle relaxes the cilia resume their movements.

In isolated gill fragments, where short pauses also occur, we may rule out any function of the nervous system. Moreover, that such pauses can occur in only a part of a row of lateral cilia (LUCAS, 1932a; DRAL, 1967; MURAKAMI, 1968) seems to indicate that they may be part of the autonomous movement mechanism of the ciliary epithelium. In that case we shall have to discriminate between two principally differing kinds of pauses, voluntary and involuntary, which, however, do not differ in any way in their outward manifestation.

V. Summary

In mussels the movement of the cilia on the gill are basically autonomous and influenced by environmental factors. The branchial nerve has an inhibitory as well as a stimulating effect on the activity of the lateral cilia. The reactions of these cilia to changing temperature and chlorinity in isolated gill fragments and in undamaged young mussels were compared. It is concluded that the activity of the lateral cilia is regulated in such a way that the direct influence of the studied environmental factors is compensated.

Probably the latero-frontal cilia are not under such a nervous control.

The functionality of the regulation of the various ciliary tracts in the mussel gill is discussed.

VI. References

- AIELLO, E.L., 1955. Coordinated ciliary movement on the gill of the ribbed mussel, *Modiolus demissus plicatula*.-Biol. Bull. mar. biol. Lab., Woods Hole 109: 344.
- , 1957. The influence of the branchial nerve and of 5-hydroxytryptamine on the ciliary activity of *Mytilus* gill.-Biol. Bull. mar. biol. Lab., Woods Hole 113: 325.
- , 1960. Factors affecting ciliary activity on the gill of the mussel *Mytilus edulis*.-Physiol. Zool. 33: 120-135.
- , 1970. Nervous and chemical stimulation of gill cilia in bivalve molluscs.-Physiol. Zool. 43: 60-70.
- AIELLO, E.L. & G. GUIDERI, 1964. Nervous control of ciliary activity.-Science, N.Y. 146: 1692-1693.
- , 1965. Distribution and function of the branchial nerve in the mussel.-Biol. Bull. mar. biol. Lab., Woods Hole 129: 431-438.
- AIELLO, E.L. & A. PAPARO, 1974. A role for acetylcholine in the regulation of ciliary activity.-Comp. Gen. Pharmac. 5: 285-297.
- BABAK, E., 1913. Zur Regulation des Atemstromes bei den Lamellibranchiaten. Zugleich ein Beitrag zur Physiologie der Flimmerbewegung.-Z. allg. Physiol. 15: 184-188.
- DRAL, A.D.G., 1967. The movements of the latero-frontal cilia and the mechanism of particle retention in the mussel (*Mytilus edulis* L.).-Neth. J. Sea Res. 3: 391-422.
- , 1968. On the feeding of mussels (*Mytilus edulis* L.) in concentrated food suspensions.-Neth. J. Zool. 18: 440-441.
- , 1970. Regulation of ciliary movement in *Mytilus*.-Neth. J. Zool. 20: 405.
- ELSEY, C.R., 1935. On the structure and function of the mantle and gill of *Ostrea gigas* (Thunberg) and *Ostrea lurida* (Carpenter).-Trans. R. Soc. Canada 5: 131-158.
- FIELD, I.A., 1922. Biology and economic value of the sea mussel *Mytilus edulis*.-Bull. U.S. Bur. Fish. 38: 127-259.
- GALTSOFF, P.S., 1957. Observations on muscle attachments, ciliary motion, and the pallial organ of Oysters.-Proc. Nat. Shellfish Ass. 48: 154-161.

- GRAY, J., 1922. The mechanism of ciliary movement.—Proc. R. Soc. (Biol.) 93: 104-121.
- , 1926. The mechanism of ciliary movement. V. The effect of ions on the duration of beat.—Proc. R. Soc. (Biol.) 99: 398-404.
- , 1928. Ciliary movement. Cambridge Univ. Press: 1-152.
- JØRGENSEN, C.B., 1975. On gill function in the mussel *Mytilus edulis* L.—*Ophelia* 13: 187-232.
- LUCAS, A.M., 1931a. An investigation of the nervous system as a possible factor in the regulation of ciliary activity of the lamellibranch gill.—*J. Morph. Physiol.* 51: 147-193.
- , 1931b. The distribution of the branchial nerve in *Mytilus edulis* and its relation to the problem of nervous control of ciliary activity.—*J. Morph. Physiol.* 51: 195-203.
- , 1932a. Co-ordination of ciliary movement. I. Methods of study and the relation of ciliary co-ordination to ciliary inhibition.—*J. Morph. Physiol.* 53: 243-263.
- , 1932b. Co-ordination of ciliary movement. II. The effect of temperature upon the ciliary wave length.—*J. Morph. Physiol.* 53: 265-276.
- MACGINITIE, G.E. & N. MacGINITIE, 1968. Natural history of marine animals, 2nd ed. McGraw-Hill, New York, London, Sydney: 1-523.
- MURAKAMI, A., 1968. Response of cilia to electrical stimulation of *Mytilus* gill.—*J. Fac. Sc. Tokyo (Sect. IV)* 11: 373-384.
- NELSON, T.C., 1951. Nervous control of lateral cilia in the gill of young spat of the oyster *Ostrea virginica*.—*Anat. Rec.* 111: 576.
- , 1960. The feeding mechanism of the oyster. II. On the gills and palps of *Ostrea edulis*, *Crassostrea virginica* and *C. angulata*.—*J. Morph. Physiol.* 107: 163-203.
- PAPARO, A., 1972. Innervation of the lateral cilia in the mussel, *Mytilus edulis* L.—*Biol. Bull. mar. biol. Lab., Woods Hole* 143: 592-604.
- PAPARO, A. & C.A. FINCH, 1972. Catecholamine localization, content, and metabolism in the gill of two lamellibranch molluscs.—*Comp. gen. Pharmac.* 3: 303-309.

- SATIR, P. & N.B. GIULULA, 1970. The cell junction in a lamellibranch gill ciliated epithelium. Localization of pyroantimonate precipitate.- J. Cell. Biol. 47: 468-487.
- SEGERDAHL, E., 1922. Investigations on the effect of a direct electric current on the ciliary motion of the *Anodonta* gill.-Skand. Arch. Phys. 42: 62-76.
- TAKAHASHI, K. & A. MURAKAMI, 1968. Nervous inhibition of ciliary motion in the gill of the mussel, *Mytilus edulis*.-J. Fac. Sc. Tokyo (Sect. IV) 11: 359-372.