J. Fac. Fish. Anim. Husb.
Hiroshima Univ. (1968), 7: 193~207

Studies on the Optomotor Reaction of Fishes

I. Examination of the Conditions Necessary to Induce the Reaction of the Japanese Killifish, *Oryzias latipes* TEMMINCK et SCHLEGEL.

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(Figs. 1-7; Plate 1)

The optomotor reaction on fishes has been applied in many previous studies of their visual sense[1)~4)], their orientating behavior in stream[5),6)] or their swimming speed[5),7)], because this reaction was considered as a so-called unconditioned response which organisms show immediately when placed in a moving scene. However, the systematic study does not seem to have been conducted yet about the conditions which affect this occurrence: namely the physiological conditions, such as the degree of maturation, the nutrition of fishes, etc. or the ecological conditions, such as biotic and abiotic.

The purpose of the present research is to analyse the nature of the optomotor reaction of fishes, from various points of view, and to find out the availability of it for practical purposes, for instance, means of controling the behavior of fish in pisciculture ponds or of gathering fish on fishing grounds.

This paper reports some results obtained through experiments concerned with the possibility of occurrence of the optomotor reaction under various rearing conditions. As a model, the Japanese killifish was used, for reasons of its schooling nature and also its small size that it was easier to handle.

The authors wish to express their hearty thanks to Dr. Tamotsu TAMURA, Professor of Nagoya University, Dr. Takashi HIBIYA, Professor of Tokyo University, and Dr. Isao HANYU, Associate Professor of Tokyo University, for their scientific advice and criticism to these experiments.

This study was partly supported by a grant from the Japanese Ministry of Education.

MATERIALS AND METHODS

The fish used were obtained locally in October of 1967. They had been held in outdoor tanks for about one month until the experiments were to start. These tanks had been constantly supplied with water of about 17°C. In order to keep them in

Contribution No. 2 from the Kumano Freshwater Biological Station, Hiroshima University.

healthy condition, the fish were fed with plentiful amount of pelet once every evening. Six individuals which were swimming around lively, were picked out and put into an opaque plastic tank in the laboratory. This tank radially partitioned by net into six parts was filled with circulating water of a constant temperature (19 ± 1°C.) and each fish was kept in these six different partitions in order to avoid possible confusion. The individual discrimination made it possible to follow up the occurrence of the reaction of each fish historically.

The apparatus used is shown schematically in Fig. 1. This is a device with slight modification from that used by CRONLY-DILLON and MUNTZ (1965)[3]. The whole set of this apparatus was placed in a dark room.

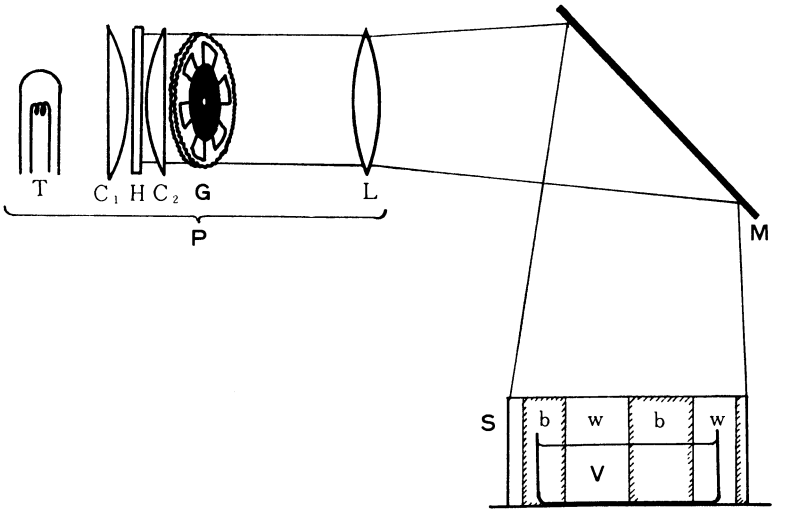

Fig. 1. Schematic diagram of apparatus

P; projector T; 750 W projection lamp
C_1, C_2; condenser lenses
H; heat filter
L; projection lens (130 mm F 2.8)
G; gear with 6 radiating holes and a black plastic plate
M; mirror
V; glass vessel
S; cylindrical screen w; light stripes
b; dark stripes

During the experiment the fishes were placed in a cylindrical glass vessel (**V**), 30 cm in diameter and 15 cm deep, whole bottom of which was lined with a black rubber sheet. This vessel was filled with water up to 10 cm. The temperature of water inside the vessel was kept at 19 ± 1°C. during experiments.

The gear (**G**) with radiating holes from its centre was inserted between a condenser lens (C_2) and a projection lens (L) of the projector (**P**). By using a mirror (**M**) as shown in Fig. 1, the gear could be projected upon the inner surface of the cylindrical screen (**S**) to cast an alternating pattern of light and dark stripes having the

same widths. Since the cylindrical screen was about 40 cm in diameter, a space of 4 to 6 cm width could be left between the outer periphery of the vessel and the inner surface of the screen. A black circular plastic plate was fixed to the centre part of the gear to cast shade of itself upon the whole bottom inside of the cylindrical screen. In this way, it can be said that the fish in the vessel can react only to the stripes projected on the screen. The gear was combined with a motor through some other gears. The angular velocity of its rotation was controled easily from 10 to 72°/sec. by using the transformer attached to the motor. In these experiments, five kinds of gears having 4, 6, 8, 12 and 16 radiating holes were prepared, because it was stated by OKA (1935)[8] that the response of organisms upon moving stripes could be affected by the width of stripes and their moving speed. However, only the gear having 6 holes was used for these experiments, since the preliminary tests did not show any difference of the reaction of the fish, caused by the different width of stripes, and also because the six stripes were found to be more convinient for observation than others.

The light source used was provided by a 750 W projection lamp (T); the light intensity measured around the glass vessel with a selenium barrier-cell photometer was 2800 to 3000 lux at the parts of light stripes.

The fish was singly placed in the glass vessel and left for more than 5 minutes to settle down before observations began. During this time interval, the motor has been driven on already in order to make the pattern of stripes go around clockwise on the screen with a constant speed during the experiment, but the projection lamp yet remained switched off. As soon as the projection lamp was turned on, observation could begin. During the period of one experiment, 5 minutes long, the following data were collected every 15 seconds: number of sets consisting of a light and a dark stripe (n_1) which were outrun by the fish, and number of sets (n_2) which outran the fish. In such a way, we got a series of 20 sets of those numbers for each one experiment. At the beginning and the end of each experiment, we measured with a stop watch the angular velocity of rotation of the gear, from which the number of sets of stripes (k) passing through at the definite point on the screen for each 15 seconds was calculated in combination with the number of radiating holes of the gear. Based upon those records for each 15 seconds, the ratio, $100\ (k+n_1-n_2)/k$, was calculated in per cent. In this paper the authors call them "the optomotor reaction rate" or shortly "the reaction rate", because they should be considered to reflect the relative movement of fish following the running stripes on the screen; namely, the rate of 100 % means that the fish followed the same set of stripe during the period of 15 seconds, while the value of 0 % occurs when the fish stayed at the same point in the glass vessel. Of course, there were some fish which swimmed against the direction of the movement of stripes. In this case, the reaction rate comes within a range of negative values.

For the purpose of clearing the relationship between the occurrence of the optomotor reaction and the adaptation of fish eyes to light intensity, retinomotor reaction in fish eyes was examined through histological treatment. The fish held in a complete darkness for about 24 hours were put into the glass vessel of the work-

ing apparatus. Out of them, six pairs of fish were successively taken at the time of 1, 2, 3, 4, 5, and 10 minutes after being put in the apparatus, and their heads were cut off at the position just behind the posterior margine of eye orbit to be put into BOUIN's solution. After the fixation of 48 hours, the excised eyes of them were washed, dehydrated, cleared and embeded in paraffin, in the ordiary manner. Sections were cut at 9 μ, subsequent to staining with MEYER's haematoxyline and eosin. In the same way the preparations of the dark- or light-adapted eyes were provided from the fish held in a complete darkness or those exposed to continuous illumination at 2000 lux for more than 24 hours, respectively. Measurements were made with an ocular micrometer on the following items for the sections of retinas in the region of fundus, according to TAMURA (1957)[9]; namely, the thickness of retina (from the base of pigmental layer to the external limiting membrane), the position of ellipsoids of cones (from the base of pigmental layer to their centres) and the position of tips of pigment (from the base of pigmental layer to its protuberence).

RESULTS

Preliminary observations were carried out in the above-mentioned apparatus for the purpose of examining the validity of our interpretation on the optomotor reaction rates which was described in the previous section. The fish used in these observations were different individuals from the six fishes for the main experiments. While the fish were left to settle down for more than 5 minutes in the glass vessel which was illuminated at the intensity of about 1000 lux just above the water surface by a flood lamp from the ceiling of dark room, they sometimes remained quietly and sometimes swam about slowly. But when the moving stripes were projected upon the screen soon after the flood lamp has been switched off, the fish began to swim about more actively.

The results of some preliminary observations revealed the followings; when the fish was observed to follow the moving stripes clearly, the values of n_1 and n_2 both appeared very small and their difference too was always standing near to zero. In this case the optomotor reaction rate could be obtained as about 100 %. For instance, in the most occasional case of these experiments in using the six-holed gear rotating at angular velocity of 36°/sec or 10 sec/revolution ($k=9$; 6 sets of stripe multiplied by 15 seconds of period of observation divided by angular velocity of 10 sec/rev.), n_1 and n_2 were measured by 4 to 5. On the other hand when the fish showed only a slight reaction n_2 surpassed n_1 in keeping their difference at the values near to k. In such cases, especially n_2 stood at considerable high level. Namely, under the same experimental condition as above-mentioned ($k=9$), n_2 were measured by 20 to 25, while n_1 stood 10 to 16. Here the reaction rates ranged from +33 % to −11 %. Very rarely n_2 surpassed n_1 by much more than k, from which the reaction rate could be calculated as smaller values than −50 %.

These results should be considered as proof to verify our interpretation that the optomotor reaction rate coincides with the facts. Moreover, the result indicates

that there is no need to count both n_1 and n_2 but that it is enough to count just only their difference during each observation of 15 seconds. The optomotor reaction rates above +50 % can be regarded as the criteria showing the occurrence of positive reaction, while those below −50 % signify the occurrence of negative reaction in fact. However, in reality, the latter circumstances were observed very rarely, at least in the case of the Japanese killifish used in these experiments.

By using the above-mentioned criteria, the authors have analysed the obtained data.

Effect of Training

Since the preliminary observations revealed that unexperienced wild fish could not react positively to the movement of stripes, the effect of training upon the occurrence of the optomotor reaction was examined for six fishes individually identified respectively. The results obtained for one fish is shown, for example, in Fig. 2.

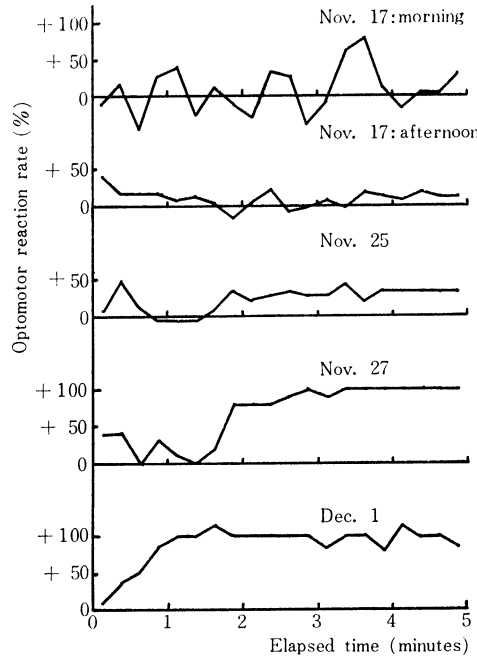

Fig. 2. Development of optomotor reaction in a fish during its experience.

This individual was introduced into the apparatus for the first time on November 17. At the time of first three trials which were performed on 17 and 25 of November, it did not show any optomotor reaction at all during the whole periods of experiments, as shown in the upper part of Fig. 2. At the fourth trial performed on 27 of the same month, the fish responded clearly and positively to the moving stripes, although the reaction began 2 minutes after the experiment was started. At

the fifth trial, the optomotor reaction was induced clearly and positively even within the first 1 minute of experiment and it was maintained until the end of experiment. (see the lowest part of Fig. 2) Thereafter the fish showed consistently the same pattern of behavior such as mentioned above, as far as it would be held under such appropriate conditions as will be discussed elsewhere in this paper. This is the reason why the results obtained after the sixth trial have been omitted from Fig. 2. Data obtained for the other five individuals also indicated an identical tendency, although some of them showed an individual variation in the number of trials necessary for fish to be trained unto showing clear reactions from the first 1 minute of the experiment. However, even well trained, no fish could start a clear positive reaction within the first 30 seconds of the experiment.

In conclusion it can be said that exclusively the fish trained with three to five trials, say enough trained, should be used for further examination of the conditions necessary to induce the optomotor reaction, and that the well-trained fish show typical tendency to be characterized by the chronological series of optomotor reaction rates where their values are increasing unto 100%, in 30 to 60 seconds after the experiment began, and such a high value is kept steadily thereafter.

Effect of Rearing Conditions

Also some rearing conditions were observed preliminarily to affect the possibility for the optomotor reaction to occur, especially the conditions concerning some properties of the container in which fish was held before experiment.

Three well-trained fishes were used for these experiments. Two of them were kept, before being put into the apparatus, for about 24 hours in glass beakers of 300 ml, filled with water up to 10 cm. Another one was kept in a white plastic (opaque) beaker of 300 ml, in the same manner as the two others. These three fishes were treated in such a way as the others held in the six-partitioned tank, in excepting that they were kept in small beakers with stagnant water as mentioned above.

The results obtained are shown in Fig. 3.

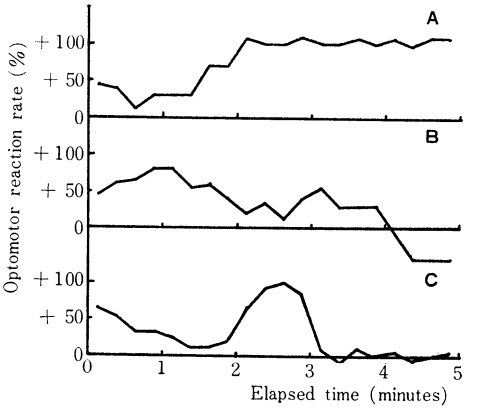

Fig. 3. Optomotor reaction shown by fish reared in small opaque container (A) or in small glass container (B, C).

As shown in Fig. 3, B and C, the optomotor reaction rates for two fishes held in the glass beakers were usually at lower level, sometimes showing values higher than 50 %, and fluctuated more irregularly over the whole period of experiments than those for one fish held in a white plastic beaker, as shown in Fig. 3, A. Although the reaction rates obtained for fish held in the plastic beaker were maintained at about 100 % level in the latter half period of the experiment, the beginning time of clear optomotor reaction was slightly more delayed than that of the typical reaction shown by fish held in a ordinary way.

Irregularity of the occurrence of the optomotor reaction shown by fish held in the glass beaker may be due to the transparency of its wall, while the delaying of reactions seemed to be due to the fact that the fish was held in a smaller container with stagnant water.

Reaction of Fish shown the Stripes in Advance

For these experiments, one trained fish was used. It was kept for more than 5 minutes beforehand in the glass vessel of the apparatus where the stripes had been made on the screen already, although they stayed at rest. Measurements of the optomotor reaction were started when the stripes had been driven on. The process of the occurrence of the optomotor reaction shown by such treated fish was traced and compared with that of the same fish treated in the ordinary way beforehand.

Results are shown in Fig. 4.

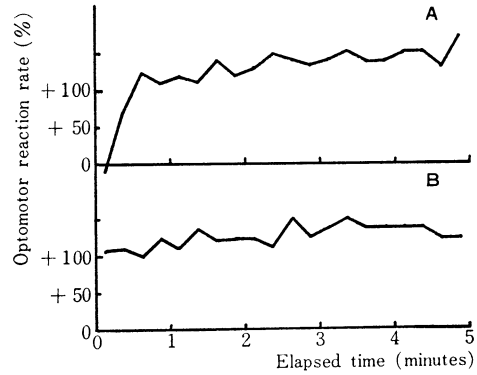

Fig. 4. Optomotor reaction shown by a fish when it was not shown (A) or when it was shown (B) stripes prior to experiments.

While the reaction rates for the ordinarily treated fish have been increasing during the first 30 seconds and reached the 100 % level about 45 seconds after the experiment began, the fish shown the stripes reacted clearly and positively to their movement even at the beginning time of the experiment already; this can be proved clearly by the comparison of both curves in Fig. 4.

These experiments may suggest that the pre-perception of the presence of the pattern of stripes make fish ready to react to its movement. Yet more experiments

are needed to verify such a tendency, for reasons of the delicacy with which this kind of effect is at work.

Effect of Dark Adaptation of Eyes

This subject seemed to us one of the most interesting problems on the optomotor reaction of fish, since it is considered to be concerning the relationship between reaction and visual sense in fish. Therefore the study was carried out in more details; namely in parallel with the examination of the difference betwee the optomotor reactions shown by the same fish when they were held in darkness or under illumination, the light adaptation of fish retina was examined histologically.

In the observations of optomotor reaction, two trained fishes were used. At the first time, one of them was held in a completely dark room for more than 24 hours before being put into the apparatus, and the other was held in a tank illuminated continuously at 2000 lux for more than 24 hours before the experiment. The former was tested after being kept for 5 minutes in the dark apparatus without the light of flood lamp from the ceiling, while the latter was tested in the ordinary way, i.e. after being kept in the apparatus illuminated by the flood lamp from the ceiling. The second time, the treatment prior to experiments was made in a reverse way.

The results are shown in Fig. 5.

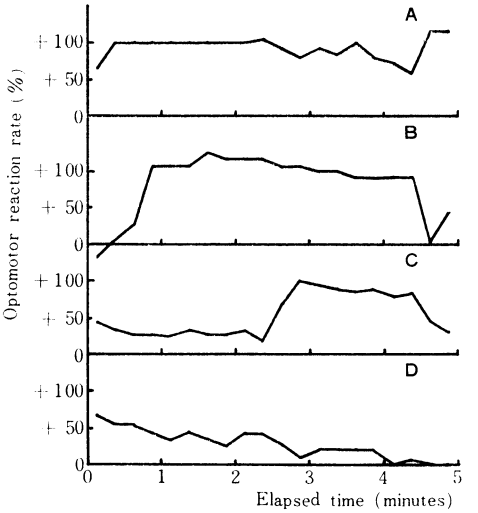

Fig. 5. Optomotor reaction of fish reared for 24 hours in light (A, B) or in darkness (C, D). One fish was used for experiments A and C, while another one for experiments B and D.

A clear positive reaction can be seen for the fish held under illumination already within first 30 seconds of experiment (in Fig. 5, A); this is rather uncommon when the pattern of stripes is not shown to fish prior to experiment. The

other fish showed the same typical pattern of behavior such as the above-mentioned ones for fish treated in a ordinary way (in Fig. 5, B). However, held in darkness for 24 hours, the clear positive reaction may occur at 3 minutes after the experiment began, or may not be observed at all at least during the period of experiment (see C and D in Fig. 5), although in the latter case fish was observed to react clearly and positively to the movement of stripes soon after the end of the experiment and continued to react at least for one minute, but those details of the reaction have not been measured regrettably. That is, keeping fish in darkness for a long time would be responsible for the delaying of the beginning time of the clear positive optomotor reaction by 2 to $4\frac{1}{2}$ minutes in comparison with the time shown by ordinarily treated fish.

For examination of retina in reference to the light conditions, a total of 16 fishes were taken. They had been paired into 8 sets and each set was treated in different ways. The microscopic photographs of the sections of retinas prepared by the previously described histological treatment (see p. 196) are shown in Plate. Plate is including only five photographs showing sections of retinas from five differently treated fishes: from a fish kept in darkness for 24 hours, from a fish kept under continuous illumination at ca. 2000 lux for 24 hours and from three fishes kept in the working apparatus for 3, 5 and 10 minutes, respectively, after being held in darkness for 24 hours. As shown in Photograph A of Plate, keeping fish in darkness for 24 hours can make its retina completely dark-adapted; namely, the tips of the protuberences of pigment and the ellipsoids of cones can be located near the base of the pigmental layer. In contrast to such circumstances, these clearly noticeable elements of retina can be found near the outer limiting membrane for fish which had been exposed to continuous illumination for 24 hours, as shown in Photograph B. Some intermediate circumstances between the two extremes can be seen in Photographs C, D and E showing the sections of retinas of fish which were held in working apparatus for a various duration after being once adapted to darkness. For the purpose of quantitative indication of spatial and temporal movement of cones or tips of pigment, some measurements were made with ocular micrometer by the previously described method (see p. 196). 25 measurements were made for each retina on the previously described items. The positions of cones or tips of pigment in retina were indicated, according to TAMURA (1957)[9], as the relative position to the thickness of retina in per cent. The frequency distributions of these relative positions of cones and of tips of pigment for each fish individually treated are shown separately in Fig. 6 and 7, respectively.

Tips of protuberneces of pigment can be found most occasionally at 45 % of thickness of retina from the base of pigmental layer, in dark-adapted eyes, while they can be located at 85 % in the light-adapted eyes, as shown in Fig. 7. A full span of their movement can be calculated as about 40 % of thickness of retina. On the other hand ellipsoids of cones can be found to move in the restricted range of only 20 to 30 % of thickness of retina, since their relative positions were measured most frequently by 65 % of thickness of retina from the base of pigmental layer for the dark-adapted eyes and by 85 to 95 % for the light-adapted eyes, as shown

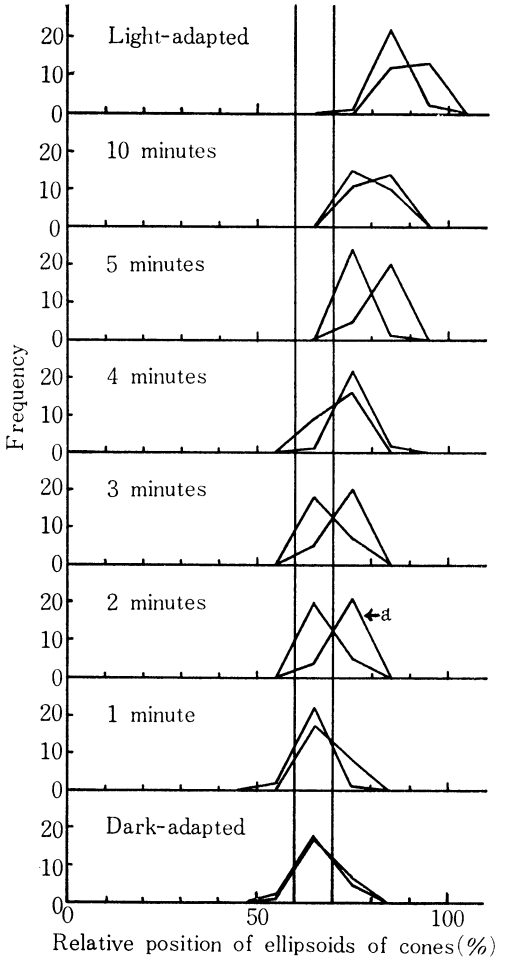

Fig. 6. Chronological change in frequency distribution of relative position of cones measured from base of pigmental layer in fish retinas adapting to light condition.

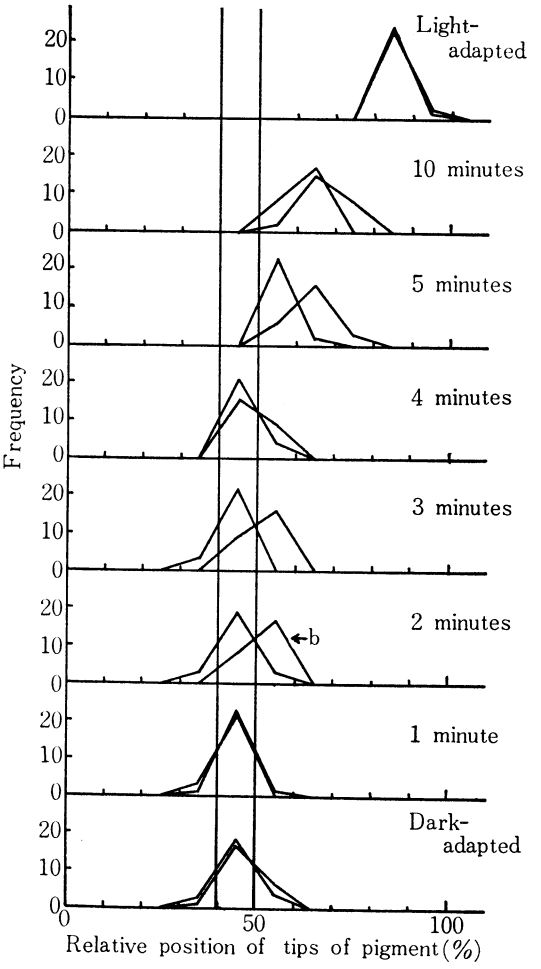

Fig. 7. Chronological change in frequency distribution of relative position of tips of pigment measured from base of pigmental layer in fish retinas adapting to light condition.

in Fig. 6. Here some difference in spatial pattern of movement would be noticed between both elements of retina. However, by just inspecting the chronological change of the frequency distribution of both elements, it can be seen that there is a common temporal pattern of movements for both elements in retina which can be supposed to be on the way of light adaptation; namely, in some retina (a in Fig. 6 and b in Fig. 7), both elements began their forward movement even within 2 minutes after being replaced into the working apparatus from dark condition but the distinct movement can be seen after 5 minutes. (see the frequency distributions of positions of cones, in Fig. 6, and tips of pigment, in Fig. 7, for the retinas of fish held for 5 minutes in the working apparatus) Even if exposed to the light condition for 10 minutes, the retina of fish is far from completely light-adapted at least com-

pared to the retinas of completely light-adapted fish. The beginning time of the retinomotor reaction can be estimated to range from 2 to 5 minutes after the fish has been placed into the working apparatus and the time is in good coincidance with the time when the clear positive optomotor reaction begins in the dark-adapted fish.

DISCUSSION AND CONCLUSION

It has been verified by CLAUSEN (1931)[10] that stream dwelling fishes can respond to a moving background better than lake dwelling ones. The Japanese killifish used in the present experiments is one of the most common fresh water fishes, dwelling in ponds or small streams. It is well known that fish of this species orientate head upstream in groups, when they are found in small streams, except for the cold season when they become very inactive and demersal. And so they can be regarded to belong to "stream dwellers" rather than to "lake dwellers", in the words of CLAUSEN and can be expected to show the positive optomotor reaction. In fact, this expectation is supported by the fact obtained here, that they can nearly all the time follow clearly the moving pattern of stripes as far as they have been trained enough and the appropriate conditions are kept.

However, the present authors have some doubt as to whether the response of fish to moving background is an unconditioned reflex, as stated by PAVLOV (1966)[6], or not, for the results obtained here induce us to think that training is one of the indispensable conditions to make fish react to the moving scene surrounding them, at least as far as this fish species is concerned. MIYAUCHI (1953)[11] and HARDEN JONES (1963)[12] have suggested the same possibility by relating the nature of the response to moving background for the Japanese killifish and the herring, respectively, although they did not verify the opinion.

Perception of the pattern of stripes by fish immediately prior to the experiment has the before-mentioned effect, which could probably be regarded as the phenomenon called a "set" in the psychological term. The irregular occurrence of the optomotor reaction shown by the fish previously held in a container with transparent walls seems to suggest that such a container has a kind of psychological effect to the fish, but further discussion must be reserved until more will be known about this aspect.

The delayed responses were observed when fish was kept either in small containers or in darkness before making the experiment. Although the same phenomenon of delaying the reaction appears commonly, in each case different mechanisms could be supposed to have been at work. Namely, when fish is kept in darkness, the state of adaptation of its eye might be the most important factor for the reaction delay, while delay of response shown by fish held in smaller containers might be due to some other physiological factors whose nature yet remains unknown to us.

The present experiments confirm the fact that the dark-adapted fish can not

show clear optomotor reaction until the retinomotor reaction starts in the eye itself. This conclusion is in accord with the facts observed by many previous authors. BRETT and ALI (1958)[13] and ALI and HOAR (1959)[14] found that the down stream migration of pink salmon was initiated when their retinas were only partially adapted to decreasing illumination and from these findings they also stated that the nocturnal movement of the salmon to migrate down stream might be caused by reduction of their visual contact with surrounding environments. ALI (1959)[15] showed the fact that dark-adapted salmon schooled by using visual sense even when retinas of their eyes were not yet maximum state of light adaptation. In her paper dealing with examinations of retinomotor reaction of marine fishes attracted by artificial light, GIRSA (1967)[16] stated that young mullet entering into the light zone, had retinas with cones on the way to light adaptation, the pigment however still remaining near the base of the pigmental layer.

After consideration of all the above-mentioned data, we must conclude that only fish well trained and put in favorable conditions physiologically and psychologically all the time can be taken up for studies of optomotor reaction; if these conditions are not kept, reproducible results can not be expected.

SUMMARY

Some experiments of the optomotor reaction using the Japanese killifish, *Oryzias latipes* TEMMINCK et SCHLEGEL, were carried out in the apparatus slightly modified from the one used by CRONLY-DILLON and MUNTZ (1965) consisting in rotating pattern of alternating light and dark stripes around the glass vessel in which fish are held. The results obtained can be summarized as follows.

1. Wild fish do not show any clear positive optomotor reaction until they are well trained by 3 to 5 trial experiments. It takes 30 to 60 seconds even for well-trained fish to come to the state of following completely the moving pattern of stripes.

2. Fish show irregular optomotor reaction when they are reared in a small glass container, even if they have been duly trained. Besides, when reared in a small opaque container, they begin to react several minutes later than they do when normally reared.

3. Fish that have been shown the pattern of stripes prior to the experiment begin to react to the moving pattern of stripes earlier than those which have not been shown.

4. The starting time of the optomotor reaction in fish kept in darkness (dark-adapted) is delayed correlatively to the time at which the process of light adaptation begins in retinas of fish held in the working apparatus.

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要　　約

1. ガラス円形水槽の周囲に明暗の縞模様が廻転するように考案されたCRONLY-DILLON and MUNTZの装置を改良した実験装置を用い，メダカの運動視反応の発現と飼育条件の関係を調べて，次の様な結果を得た．

2. 野生のメダカは少くとも3～5回訓練して，始めて明瞭な運動視反応を確実に現わすようになる．しかし廻転する縞模様に完全に追随する迄には30～60秒を要する．

3. 充分に訓練したメダカでも，これをガラス容器内で飼育して置くと，その運動視反応は極めて不規則となり，又狭い容器内に飼育した場合には，運動視反応は遅れて現われる．

4. 更に，実験装置内で予め縞模様を見せて置くと，メダカは縞の運動開始と殆んど同時にそれを追い始める．

5. 暗い中で飼育し暗順応状態になっているメダカは，実験開始後数分経ってから運動視反応を呈するが，この反応の発現の遅れは，実験装置内に入れられた暗順応状態のメダカの網膜において，錐体楕円部及び色素層とが明順応状態への網膜運動を開始するのに要する時間と一致する．

EXPLANATION OF PLATE

Microscopic photographs of sections cut at 9 μ of retinas of the Japanese killifish, *Oryzias latipes* TEMMINCK et SCHLEGEL, each of which was treated differently as follows;

Photo. A : kept in darkness for 24 hours to be regarded as dark-adapted,

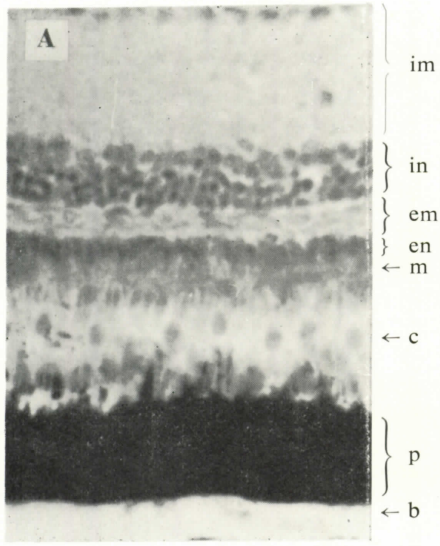
Photo. B : kept under continuous illumnation at ca. 2000 lux for 24 hours to be regarded as light-adapted,

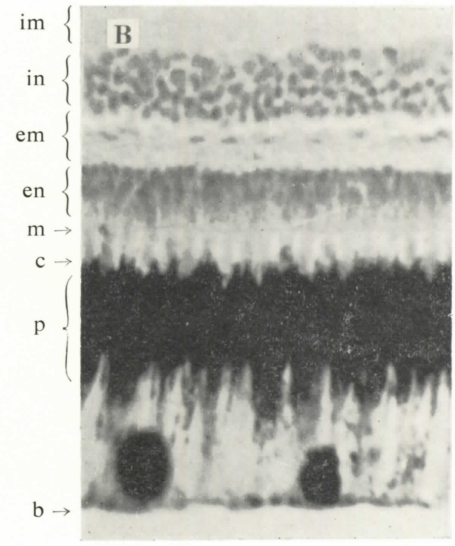
Photo. C : kept in working apparatus for 3 minutes after dark-adapted,

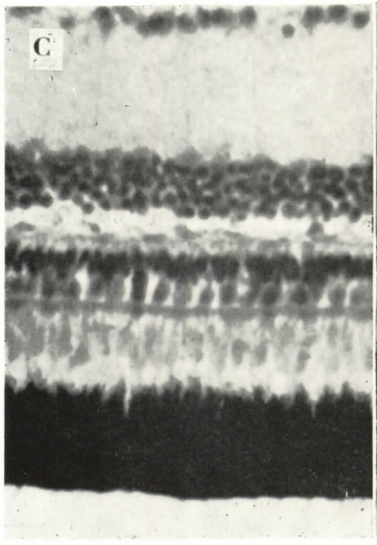
Photo. D: kept in working apparatus for 5 minutes after dark-adapted,

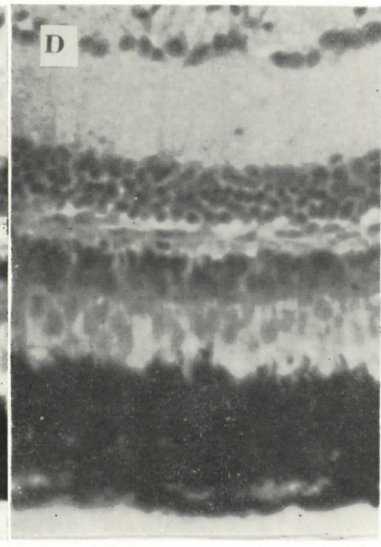
Photo. E : kept in working apparatus for 10 minutes after dark-adapted.

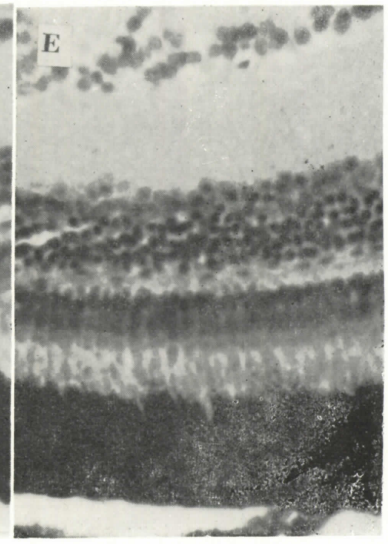
b; base of pigmental layer, p; pigment, c; ellipsoid of cone, m; external limiting membrane, en; external nuclear layer, em; external molecular layer, in; internal nuclear layer, im; internal molecular layer.


A
im
in
em
en
m
c
p
b


B
im
in
em
en
m
c
p
b


C


D


E