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The Optokinetic Response of the Rainbow Trout *Salmo gairdnerii*

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The optokinetic response (OKR) of rainbow trout was investigated using rotating vertical black and white stripes. The rainbow trout showed two kinds of OKR patterns, Sliding-OKR (S-OKR) and Circular-OKR (C-OKR). S-OKR means the response as the fish follows the rotating stripes like a hand of a clock, while C-OKR is the response as the fish follows the stripes along the inner wall of an experimental trough. The S-OKR appeared mainly when the stimulus velocity (the rotating velocity of the stripes) was low (20 deg/s), while the C-OKR was dominant when the stimulus velocity was high (more than 60 deg/sec). With the stimulus velocity within an appropriate range, the fish followed the stimulus as fast as the stimulus itself.

The maximum followable velocity (V_{max}) depended upon the stripe width and the illumination intensity, while the minimum followable velocity (V_{min}) was not affected by these factors. An abnormal OKR (very rapid response to only one stimulus direction) was produced by unilateral eye-enucleation. The unilateral tectal-ablation had the same effect on the OKR as the contralateral eye-enucleation. These results suggest that visual input from both eyes is necessary for normal OKR and that most of these inputs project to the contralateral optic tectum.

In a variety of animals, moving patterns elicit a stereotyped optokinetic response (OKR), which includes eye or head nystagmus^{1,2,4-7,10,14,17,24} or following behavior.^{9,13,16,18-23} The OKR is a basic visual response and can be a useful model for the analysis of many kinds of visually-related behavior. In teleosts, for example, the OKR is used to examine the ontogeny of visual acuity.¹³ It is also used with regard to the rheotactic response,⁹ schooling behavior^{19,20} or feeding behavior²³. For the further analysis of these studies, the basic quantitative data of the OKR are required.

In order to elucidate the neural substratum of the OKR, the OKR in monocular vision has been investigated in many species of vertebrates. Among them, frogs,^{1,14} their tadpoles,^{16,21} turtles,¹⁰ guinea pigs,¹⁰ and rabbits⁴ display a clear, unidirectional OKR, reacting to only one stimulus direction. We found that rainbow trout, with monocular vision, also showed a clear unidirectional response.

This paper attempts (1) to describe quantitatively the OKR in rainbow trout and (2) to examine the effects of monocular deprivation on the elicitation of the OKR.

Materials and Methods

Thirty-eight rainbow trout parrs between 11

and 13 months old (body length: 10.4-12.0 cm) were used. Fig. 1 shows the experimental apparatus, consisting of a trough, a rotatable drum and a video tape recorder. The trough (glass beaker; 15 cm in diameter and 18 cm in height), in which the fish were individually placed, was

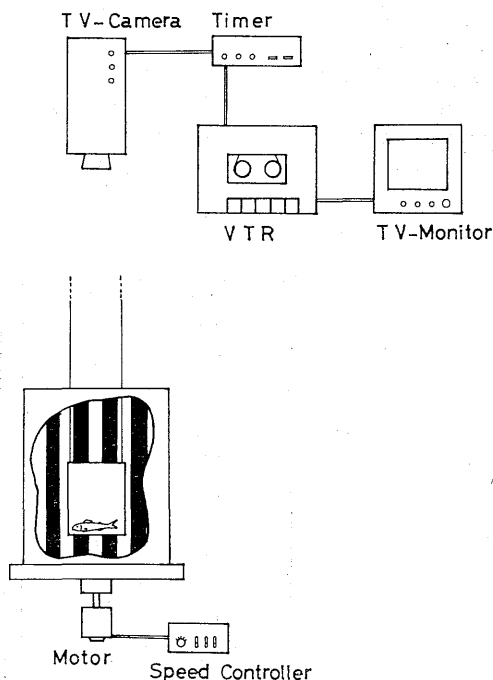


Fig. 1. Experimental apparatus (See the text.).

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hung inside the rotatable drum (42 cm in diameter and 40 cm in height). The drum was lined with vertical black and white stripes of equal widths. As a visual stimulus, the drum was then rotated clockwise or counterclockwise. The rotating speed of the drum (stimulus velocity) ranged from 5 to 560 deg/s. As a rule, the stripe width was 10 mm, which provided a visual angle of 4 degrees if the fish saw it from the periphery of the trough. A gray-colored panel was used as the control stimulus. The illumination intensity was 100 lx at the bottom of the trough. The water temperature was kept at 8.0–9.5°C. After 3 min of adaptation, the stimulus was given alternately in each direction. The inter-stimulus interval was 1 min. The behavior of the fish was recorded on the video tape recorder through a camera right above the experimental apparatus and was analyzed by means of images played back on the screen of a monitor television.

The effects of eye-enucleation and tectal-ablation on the OKR were examined. The fish were anesthetized by 0.03% tricaine methane sulfonate (MS-222) and placed in a holder. The gills were perfused alternately with water and MS-222 during the operation. The unilateral eye was removed with ophthalmological scissors. The whole optic tectum of the unilateral side was ablated with scalpels and forceps. The sham operation for eye-enucleation was just anesthetization, holding, and gill perfusion, while that for tectal ablation was the exposure of the brain surface. Observation was made about 24 h after the operation.

The statistics were based on the Student's *t*-test.

Results

Basic Patterns of the OKR

When the stimulus was given, that is, when the black and white stripes were rotated, the fish bent its tail in the direction opposite to the stimulus.

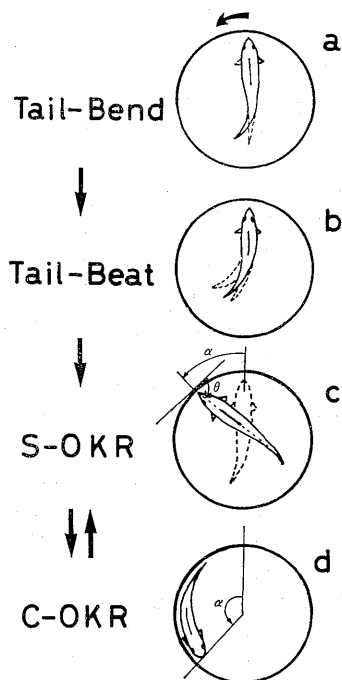


Fig. 2. Basic patterns of the OKR.

Arrow in a: Stimulus direction
 in c, d: Turning angle of the fish
 in c: Angle between the body axis of the fish
 and the tangent line to the wall of the trough

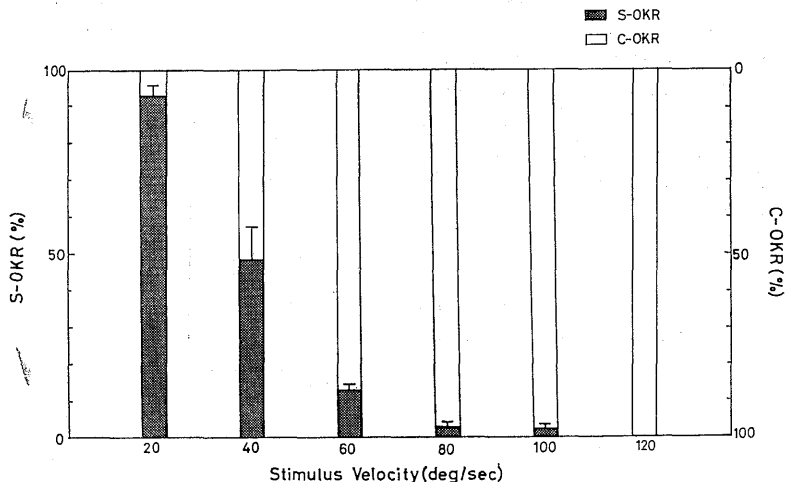


Fig. 3. Relationship between the stimulus velocity and the duration of the S-OKR (or C-OKR).

Duration of the S-OKR (or C-OKR) per 30 seconds was measured 5 times in each stimulus direction in 5 fish. Bars indicate standard error of the mean.

We called this response the Tail-Bend Response (Fig. 2-a). The fish then began to swing the bended tail bilaterally. We called this response the Tail-Beat Response (Fig. 2-b). A few seconds after the onset of the stimulus, the fish began to follow the stripes in the rotating direction. There were two kinds of following responses to the stimulus: (1) when the stimulus velocity was low, the fish, keeping its body axis perpendicular to the wall of the trough, pivoted to the stimulus direction like a hand of a clock (Fig. 2-c), and (2) when the stimulus velocity became faster, the fish followed the stripes along the inner wall of the trough (Fig. 2-d). In this paper, the former response is called the Sliding OKR (S-OKR), while the latter is called the Circular-OKR (C-OKR), according to the nomenclature of SOKABE and SANO^{2,1)} regarding the OKR of *Xenopus* tadpoles. When the fish kept the angle between its body axis and the tangent line to the wall of the trough (θ in Fig. 2-c) more than 70 degrees for more than 1.0 s, we defined this response as the S-OKR, while the others were identified as the C-OKR.

The relationship between the stimulus velocity and the duration of S-OKR (or C-OKR) was examined. As is shown in Fig. 3, the S-OKR mainly appeared at a stimulus of a low velocity (20 deg/s), and its incidence decreased as the stimulus velocity increased. At the velocity of 120 deg/s, only the C-OKR appeared. At intermediate stimulus velocities (40 or 60 deg/s),

the two kinds of OKR appeared alternately.

The relationship between the stimulus velocity and the turning angle of the fish (α in Fig. 2-c, d) is shown in Fig. 4. At a stimulus velocity as low as 20 deg/s, the fish followed the stripes slower than the stimulus velocity (closed circles). As has already been shown, the S-OKR was dominant at this stimulus velocity. At a stimulus velocity of 100 deg/s, the fish followed the stripes by the C-OKR at a nearly constant velocity, as fast as the stimulus velocity (closed triangles). At a higher stimulus velocity such as 200 deg/s, however, the fish seldom showed the following response (open triangles). When the gray panel was rotated, no response was elicited at any velocity.

In order to obtain the maximum and minimum limits of the followable velocity of the fish (V_{max} and V_{min}), gains (swimming velocity of the fish/stimulus velocity) were calculated at several stimulus velocities (Fig. 5). Here, the swimming velocity of the fish was estimated from the time needed for the fish to take 5 turns in the trough, as it followed the stimulus. At stimulus velocities between 40 and 160 deg/s, the fish followed the stimulus with a gain of nearly 1.0; that is, the swimming velocity of the fish was the same as the stimulus velocity. When the stimulus velocity was slower than 30 deg/s or faster than 180 deg/s, though, the gain became less than 1.0, which means that the swimming velocity of the fish became slower than the stimulus velocity. We

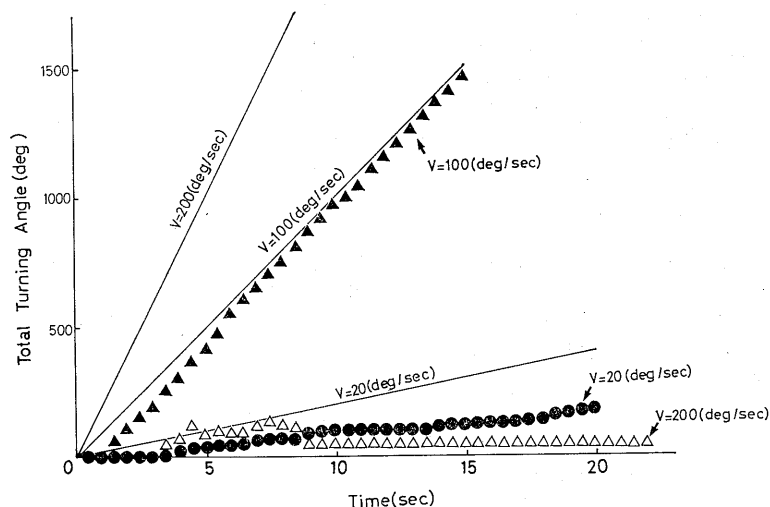


Fig. 4. Relationship between the stimulus velocity and the turning angle of the fish.

The stimulus velocities used were 20 deg/s (closed circles), 100 deg/s (closed triangles), and 200 deg/s (open triangles). The three lines in the figure indicate the rotating angles of the drum. Data were taken from the same individual.

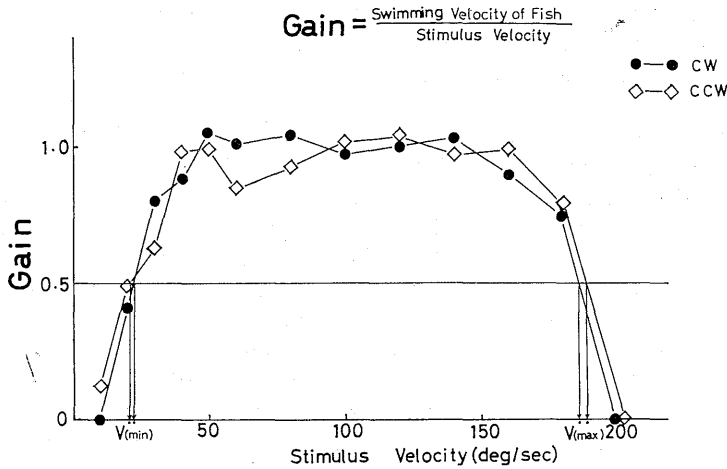


Fig. 5. Relationship between the stimulus velocity and the gain (swimming velocity of the fish/stimulus velocity).

At each stimulus velocity, measurements were taken of the same individual, once in the clockwise direction (closed circles), and once in the counterclockwise one (open squares).

V_{max} : Maximum limit of the followable velocity of the fish

V_{min} : Minimum limit of the followable velocity of the fish

defined the V_{max} and V_{min} as follows:

$$V_{max} = v_1 + 20(g_1 - 0.5)/(g_1 - g_2)$$

where g_1 is the gain when the stimulus velocity is v_1 deg/s and g_2 is the gain when the stimulus velocity is $(v_1 + 20)$ deg/s. Here, the value of g_1 must be larger than 0.5, and that of g_2 , smaller than 0.5.

$$V_{min} = v_1 - 10(g_1 - 0.5)/(g_1 - g_2)$$

where g_1 is the gain when the stimulus velocity is v_1 deg/s and g_2 is the gain when the stimulus velocity is $(v_1 - 10)$ deg/s. The value of g_1 must be larger than 0.5, and that of g_2 , smaller than 0.5. The V_{max} and V_{min} under both clockwise and counterclockwise stimuli are shown on the abscissa in Fig. 5.

Relationship between the Stripe Width and the V_{max} and V_{min}

The V_{max} and V_{min} were measured at stripe widths (width of each black or white vertical line) of 3, 10, 20, and 40 mm. These stripe widths gave the visual angles of 1.2, 4, 8, and 16 degrees respectively when the fish saw them from the periphery of the trough. As is shown in Fig. 6, the V_{max} increased with the stripe width. However, its rate of increase (slope of the curve) decreased as the stripe width increased. In contrast, the V_{min} stayed constant at each stripe width.

Relationship between the Illumination Intensity and the V_{max} and V_{min}

The V_{max} and V_{min} were measured at illumination intensities ranging from 10 to 500 lx. Fig. 7 shows the results. At the low illuminations from

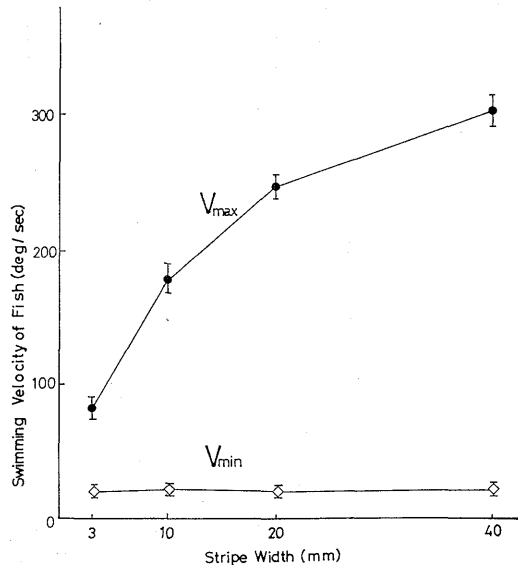


Fig. 6. Relationship between the stripe width and the V_{max} and V_{min} .

At each stripe width, the V_{max} (closed circles) and V_{min} (open squares) to both stimulus directions were measured 4 times for each fish ($n=6$). Bars indicate standard error of the mean.

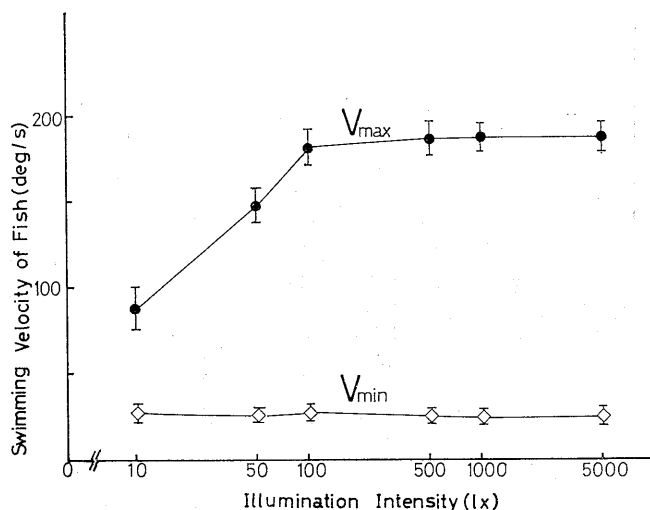


Fig. 7. Relationship between the illumination intensity and the V_{max} and V_{min} .

At each illumination intensity, the V_{max} (closed circles) and V_{min} (open squares) to both stimulus directions were measured 4 times for each fish ($n=6$). Bars indicate standard error of the mean.

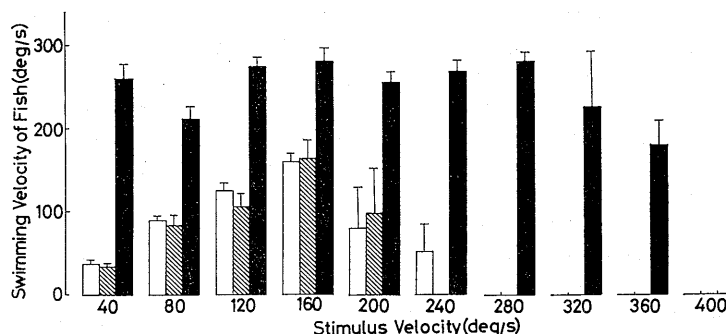


Fig. 8. Effects of eye-enucleation on swimming velocity of the fish.

Open columns: Swimming velocity of intact fish ($n=5$)

Hatched columns: Swimming velocity of sham-control fish ($n=4$)

Shaded columns: Swimming velocity of operated fish (mean of 2 fish with right-eye and 2 fish with left-eye enucleation)

The response to the clockwise (counterclockwise) direction was examined in the right (left)-eye-enucleated fish. In each fish, measurements were taken 4 times in each stimulus direction. Bars indicate standard error of the mean.

10 to 100 lx, the V_{max} increased with the illuminations and reached a plateau at 100 lx. On the contrary, the V_{min} was kept constant, regardless of the illuminations.

Effects of Eye-enucleation

After the eye-enucleation, the response to the stimulus in a temporo-nasal direction was exaggerated: that is, when the right eye was enucleated, the fish responded mainly to the clockwise stimulus. Similarly, when the left eye was enucleated, the response to the counterclockwise

stimulus became dominant. Therefore, the temporo-nasal direction was used as the stimulus. In the operated fish, the S-OKR decreased remarkably even at the low stimulus velocity and was replaced by the C-OKR. Fig. 8 shows the relationship between the stimulus velocity and the swimming velocity of the fish. At stimulus velocities ranging from 40 to 320 deg/s, the operated fish swam in the trough faster than the stimulus velocity. The swimming velocities in the operated fish at each stimulus velocity were always faster than those in the intact ($p < 0.005$)

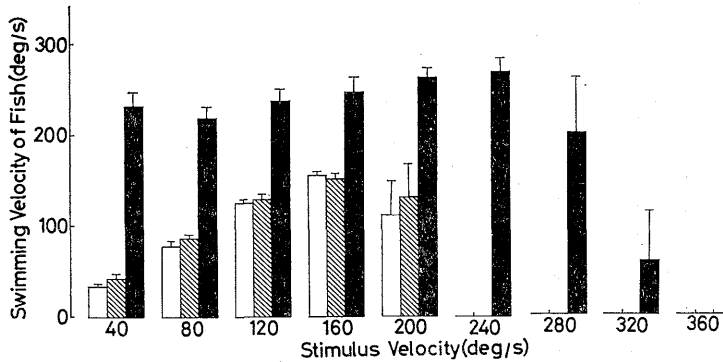


Fig. 9. Effects of tectal ablation on the swimming velocity of the fish.

Open columns: Swimming velocity of intact fish ($n=5$)

Hatched columns: Swimming velocity of sham control fish ($n=4$)

Shaded columns: Swimming velocity of operated fish (mean of 2 fish with right-tectum and 2 fish with left-tectum ablation)

The response to the counterclockwise (clockwise) direction was examined in the right (left) tectum ablated fish. In each fish, measurements were taken 4 times in each stimulus direction. Bars indicate standard error of the mean.

and sham-control fish ($p < 0.005$). The V_{max} values of these fish (352.0 ± 31.7 deg/s) were also significantly larger than those of the intact (209.6 ± 31.0 deg/s; $p < 0.005$) and sham-control fish (196.5 ± 21.3 deg/s; $p < 0.005$).

Effects of Tectal-ablation

Tectal-ablation produced nearly the same results as eye-enucleation except for the stimulus direction to which the fish responded. When the right optic tectum was ablated, the fish responded mainly to the counterclockwise stimulus, while when the left optic tectum was ablated, they responded to the clockwise one. In these operated fish, the C-OKR was dominant even at a low stimulus velocity. At stimulus velocities ranging from 40 to 240 deg/s, the swimming velocities of these fish were higher than those of the intact ($p < 0.005$) and sham-control fish ($p < 0.005$) and also higher than the stimulus velocity (Fig. 9). The V_{max} values of these fish (297.7 ± 25.6 deg/s) were also significantly larger than those of the intact (202.0 ± 17.1 deg/s; $p < 0.005$) and sham-control fish (211.5 ± 19.3 deg/s; $p < 0.005$).

Discussion

Rainbow trout showed two kinds of OKR patterns: (1) S-OKR, pivoting in the trough like a hand of a clock and (2) C-OKR, turning along the inner wall of the trough.

At a low stimulus velocity, the fish mainly

displayed the S-OKR (20 deg/s in Fig. 3). However, the fish followed the stimulus slower than the stimulus velocity (Fig. 4, closed circles and Fig. 5). This suggests, by means of the S-OKR, that the fish are unable to follow the stripes with the same stimulus velocity, even when it is slow.

The V_{max} depends on two factors: (1) the visual acuity of fish to discriminate the change in black and white patterns, and (2) their ability to swim following the moving stripes. Therefore, it can be said that at a small stripe width (e.g., 3 mm in Fig. 6), the V_{max} mainly reflects the visual acuity of fish, while at a large stripe width (e.g., 40 mm in Fig. 6), their swimming ability has large effect on the V_{max} .

HARDEN JONES reported that whiting, whiting-pout, cod, and smelt could follow the moving stripes at a velocity of 1–2 x body length/s, while herring could follow the stripes as fast as 3–4 x body length/s⁹. Although our results cannot directly be compared with his because of the differences of the experimental conditions, the rainbow trout used in the present study could follow the moving stripes as fast as 3–4 x body length/s, which indicates that the rainbow trout could swim as fast as herring.

Under a low illumination intensity (less than 100 lx), the V_{max} was affected by the illumination intensity (Fig. 7). For this reason, an illumination of more than 100 lx is desired to study the visually-related behavior in this fish.

On the other hand, the V_{min} was independent

of the illumination intensity as well as of the stripe width. This value stays at 3–4 cm/s. In stickleback and whiting-pout⁹⁾, the minimum stimulus required to elicit the OKR (nearly corresponding to V_{min} in the present experiment) is 0.03 cm/s, which is smaller than the value in rainbow trout. According to HARDEN JONES,¹⁰⁾ this value is related to the rheotactic response in fish.

The rainbow trout, with monocular vision, showed a clear unidirectional response: it responded to the stimulus of one direction (from temporal to nasal) with very rapid swimming for more than 95% of the observation time, but mostly did not respond to another stimulus direction. The effects of unilateral tectal-ablation on the OKR were nearly the same as those of contralateral eye enucleation. Although the unidirectional response in monocular vision has been reported in goldfish,²²⁾ it is not so clear as in rainbow trout: the right-eye-enucleated goldfish followed the clockwise rotating stimulus for about 83% of the observation time, but it also followed the counterclockwise rotation for more than 60% of the observation time. These results suggest that, in rainbow trout, the interaction of the visual inputs from both eyes is more important for the normal OKR than in goldfish and that most of these inputs project to the contralateral optic tectum.

There are two explanations of the unidirectional response in fish. One is based on rheotaxis:¹⁶⁾ as the fish spends all its life swimming toward the water current, movements of objects from the nasal to the temporal direction are usual, and therefore uninformative, whereas movements in the opposite direction are rare and informative, which thus attract the attention of fish. The other comes from physiological results: directional selective neurons have been found in the optic tectum of perch,⁸⁾ goldfish,¹¹⁾ and Japanese dace.¹²⁾ Most such neurons have a preference for stimuli in the temporo-nasal direction rather than those in the reverse direction. As was discussed by EASTER,²⁾ the directional selectivity of the tectal neurons might interpret the unidirectional response in monocular vision.

The unidirectional response in monocular vision has been reported in frogs,^{1,14)} their tadpoles,^{16,21)} turtles,¹⁰⁾ guinea pigs,¹⁰⁾ and rabbits,⁴⁾ while in pigeons^{6,7)} and chickens⁵⁾ with monocular vision the OKR to one stimulus direction did not completely disappear, but became weaker than that to the other stimulus direction. In cats²⁴⁾

and primates,¹⁷⁾ the OKR is symmetrical for both directions. FUKUDA hypothesized that the OKR asymmetry was due to the total decussation of the optic nerve.⁵⁾ This assumption does not hold true with fish, however, since ipsilateral retinal projections have been reported in various kinds of fish.³⁾ According to BONAVENTURE *et al.*¹⁾ the characteristics of the OKR are related to the position of the eyes (degree of the binocular visual field). Animals with eyes in the lateral position (small binocular visual field) show an asymmetrical OKR, while animals with eyes in the frontal position (large binocular visual field) show a symmetrical OKR. This hypothesis works very well in fish which have a small binocular visual field (about 30 degrees).

Although the role of the accessory optic system in the optokinetic nystagmus has been reported in pigeons⁷⁾ and frogs,¹⁴⁾ it remains to be established in fish.

The biological significance of the OKR has been discussed by many investigators. It has been said that the optokinetic eye movement is related to the feeding behavior of several kinds of teleosts,¹³⁾ although in *Leteolabrax* moving objects with a constant velocity are not attractive as food.²³⁾ In carangid fishes,¹⁹⁾ the similarity between the OKR and certain features of schooling behavior has been suggested, although the OKR is elicitable even from fish prior to the stages of school formation and from nonschooling species.²⁰⁾ Further investigation is thus required to explain the full biological significance of the OKR.

Acknowledgements

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