Orientation of fish to gravity

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ABSTRACT

The equilibrium position about the transverse axis was studied in three species of Characinoidei, following the original work of von Holst.

The equilibrium position was measured in intact fish and in fish with one utricular statolith removed, under conditions in which the weight was increased from 1.0 to 2.2 g through centrifuging. Some specimens were fixed and cleared so that the position of the utricular statoliths relative to the long axis could be photographed.

The experiments show: (1) The equilibrium function is a feedback process of peripheral and central factors, with the sensory receptor built into the system as the external control element. (2) Removal of one utricular statolith results in a marked weakening of the peripheral equilibrium component, but is not equal to an exact halving as should be expected from the results of other workers. This suggests that one of the other statoliths may be acting in maintaining the equilibrium position around the transverse axis. (3) The direct measurement of the morphological angle of the utricular statoliths imbedded in the body of the fish was compared with the calculated value obtained by centrifuging the whole animal.

A. Positional reactions

When we turn a living fish around its longitudinal or transverse axis thereby forcing it to assume an abnormal angle, we observe changes of position of the eyes and compensating movements of the fins, producing a torsional moment adequate to bring the animal back into its normal position (Figs. 1a and 1b). The receptors for controlling such postural responses are the utricular statoliths in the labyrinth (Fig. 2). The location of these receptors has been demonstrated in many experiments in which the various parts of the statolith system have been eliminated one by one (see Lowenstein 1957).

The statolith of the utriculus is a flat stone of high specific gravity. It lies on the hairs of a sensory epithelium which is covered with an elastic gelatinous material. For a long time it was not known just how the statolith of the utriculus functioned in enabling the animal to maintain its vertical position. It was thought that it either stimulated the epithelium by exerting pressure on it, or that the statolith might stimulate the sensory epithelium by a force parallel to its surface (shearing force) when the body was turned. Working with free swimming fish, von Holst (1950) succeeded in demonstrating what the effective stimulus was. In his studies he used fish in which the statolith of the utriculus lies in a horizontal plane when the fish is in its normal upright position. He had earlier discovered that some species of bony fish also use their eyes for orientation in space (v. Holst 1935). When illuminated from one side, they swim with a longitudinal tilt toward the light (Fig. 1c) without showing the torsional moments described. If the statoliths of both utriculi are removed and the fish are subjected to diffuse light from all sides, or in the absence of light, such fish are completely lacking in orientation, turning around aimlessly in all directions. If, however, they are illuminated from one side, they will swim with their backs directed exactly towards the light. In horizontal light beams, for example, their dorsoventral axis will be horizontal, i.e., the fish is on its side. If an intact fish is illuminated laterally, its dorsoventral axis will be oblique, the angle assumed being the resultant between the torsional moment produced through the
Figure 1. Equilibrium reactions of a fish tilted around its longitudinal axis to the left side. a. Side view. b. Front view. The arrows show the direction of operation of the fins. c. In horizontal light beams (L), the reactions seen in a and b disappear. The assumed tilt toward the light is the equilibrium position. $\alpha =$ angle between dorsoventral axis and vertical; $\beta =$ angle between dorsoventral axis and direction of light; $\gamma =$ angle between direction of light and vertical (after von Holst 1950).

Figure 2. Drawing of fish labyrinth: St-statoliths, Cu-cupulae of the semicircular canals. The statolith lying horizontal on its epithelium is the utricular statolith (Ut) (after von Holst 1950).

Figure 3. Sketch to illustrate the behavior of the fish with $g$ doubled when the light intensity and the angle of light entry into the eye is kept constant. The measured angle of inclination is so changed that the shearing force (s) acting perpendicular to the sensory hairs remains constant. The pressure component (d) may increase considerably. $1g$ is the normal gravitational field (after von Holst 1950).

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Positional adjustments. It also seems clear that in the absence of one of these sources of sensory input, the behavior of the fish is controlled by the other.

**B. The adequate stimulus of the utricular statoliths**

From the introductory observation (Figs. 1a and 1b) on a fish which is not in equilibrium we might expect that, if illuminated from one side, it would show less tilting response when the “weight” of its statoliths was increased. This means that the angle between its dorsoventral axis and the vertical decreases. It is possible to increase the weight acting upon the fish at any quantitative rate by the addition of a centrifugal force. In such an experiment the fish swims within an experimental tank, against a stream of water, so that it remains in one spot. The tank is mounted on an arm of a centrifuge so that it can rotate freely when the centrifuge is operated. The fish assumes a position such that its longitudinal axis is in a plane vertical to the resultant of the force of gravity and the statoliths and the tendency to turn its back to the light. Thus it seems clear, in the described reaction, that the eyes, responding to the direction of illumination, and the utricular statoliths are the only sense organs involved in providing information to the central nervous system for bringing about...
centrifugal force, while the dorsoventral axis of the fish is parallel to the resultant. This resultant force will be measured in g units, 1 g being equal to the normal gravitational field. Laterally to the fish a luminous sidewall is mounted, so that the dorsoventral axis of the fish deviates at a certain angle from the direction of g.

The experimental fish chosen were angel fish (Pterophyllum eimekei) and black tetras (Gymnocorymbus ternetii) which are laterally compressed, and when observed from their anterior or posterior end it is possible to measure very accurately the angle which the fish makes to g (von Hoist 1950).

It can be assumed that in each case for fish in balance the angle measured represents a condition of equilibrium in the central nervous system between the information coming from the eyes and the information coming from the utricular statoliths. Therefore, torque resulting from stimulation of the eye is equal to that resulting from stimulation of the statoliths, but of opposite sign. If in such experiments the angle of light entry into the fish eye and the light intensity are kept constant (Fig. 3) while g is increased, then one finds that g times sine \( \alpha \) = constant (the sine rule referred to below). The stimulus coming from the sensory epithelium of the utriculi must remain unchanged in the measured position of the fish, for otherwise the fish would be off balance. The component equal to g times sine \( \alpha \), which is the effective shear component, remains constant with an increase in g, although the pressure component increases. Maintaining a constant optical situation while increasing the weight of the statoliths causes the tilted fish to orient in such a way that the shearing portion remains constant. Thus it is the shear component and not the pressure component which is the physiologically important sensory input.

Let us put this sine rule to use in the normal field of gravity (g). In the upright position of a “normal” fish the shearing force component is zero (Fig. 4). If the fish tips to one side the stimulus to restore

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**Fig. 4.** Sketch to explain the function of the sensory input, depending on the position of the utricular statoliths. \( \alpha \) = angle between dorsoventral axis and vertical. The solid line represents the effective shearing component (sine function); the dotted line represents the ineffective pressure component while the fish is turned around its long axis in the normal field of gravity (1g) (after von Holst 1950).
the normal position increases with the sine of the angle of inclination. Accordingly the stimulus reaches its maximum value with a 90° inclination to the vertical. As the angle is further increased, the stimulus is decreased with the sine of the angle (Braem 1957). As a result of this relationship the stimulus increases at a maximal rate with a small deviation from the normal vertical position. Thus the fish is able to regulate its position in a very precise way, when near its normal posture.

In experiments conducted by Lowenstein and Roberts (1950), unit responses of the utriculus macula were obtained at intervals throughout a complete revolution about the longitudinal axis in the elasmobranch Raja clavata. The discharge frequency shows a maximum near a position in which the labyrinth under observation lies uppermost, but a minimum near the spatially opposite position. Besides units which have static discharge rates strictly corresponding to certain spatial positions of the labyrinth (position receptors), there are other end organs in the macula which react by a change in their discharge rate to the movement as such, irrespective to the direction of change, returning to a basic discharge rate whenever the head has come to rest in a new position (out-of-position receptors).

C. Fish with a non-horizontal position

We have raised the question as to how those fish in which the normal position deviates from the horizontal, by rotation about the transverse axis, use these sensory organs. There are two possibilities (Fig. 5): (1) the utricular statoliths may lie in a horizontal plane when these fish are in their characteristic position, or (2) the plane of these statoliths may not be horizontal in the normal position of the fish. In the first case artificially raising the gravitational force will only increase the ineffective pressure component, while the shearing on the sensory hairs will not be increased. In other words this procedure would not re-

![Fig. 5. Possible position of utricular statoliths in fishes with slanted normal position. A. tail-stander. B. headstander.](image_url)
FIG. 6. Experimental apparatus. A. longitudinal section. The plexiglas container for the free-swimming fish has roughened walls and is surrounded by a white screen to make the light diffuse from all sides. B. cross section. If the scaled ring is turned so that the threads are parallel to the fish the hand points on the angle of inclination.

FIG. 7. Drawing of the centrifuge in operation. In the left gondola shaped container is the observer with the experimental apparatus. The right container serves as counterweight.
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Fig. 8.  a. The angle of inclination of Thayeria Boehlkei Weitzmann against the "horizontal" is independent of g. The three points in each curve are average values of at least 10 single recordings for a single fish.  b. Horizontal position of the utricular statolith in the head of Thayeria from measurements in fishes made transparent.

In experiments designed to test these possibilities, fish were placed in a chamber illuminated from all sides by diffuse light (Fig. 6). With the fish in this chamber the angle of deviation from the direction of g could be measured. This simple apparatus, along with the observer, was placed in a centrifuge (Fig. 7) in which forces up to 2.2 g could be obtained.

After these experiments some fishes were killed and treated to make them transparent (Ahrens 1950). The position of the statoliths in the fish was determined in the following way: the transparent fishes were photographed under the binocular microscope and the angle which the statolith of the utriculus made with the longitudinal axis of the fish was measured.

In systematic series the species under study were photographed with a flash bulb in complete darkness with a robot camera, in order to find out the swimming angle of the fishes under these conditions.

D. Quantitative experiments on three species

1. Thayeria Boehlkei Weitzmann (formerly Th. obliqua Eigenmann) (penguin fish) normally swims at an angle of 25° off horizontal during both day and night. When g is increased, this angle does not change. This means that that aspect of the weight of the utricular statoliths which is physiologically important (shearing force) cannot be increased by centrifuging. The theory predicts that the utricular statoliths lie horizontally on the sensory epithelium while the fish is in its normal posture. This conclusion was verified by direct observation of the utricular statoliths in cleared preparations (Figs. 8a and 8b).

2. Poecilobrycon (Nannobrycon) eques Steind (pencil fish) swims on more of a

3 In the experiments with the centrifuge, the "horizontal" is perpendicular to g. The centrifuge was designed by Dr. E. von Holst.

4 The taxonomy of the species is not clear. We followed the helpful advice of Dr. Werner Ladiges, Hamburg, Germany.
slant during the day than at night (Fig. 9). This was demonstrated to be due to the presence of light during the day. Three age groups were studied since younger stages swim at more of a slant than older ones. When centrifuged in uniform diffuse light, the angle which the fish makes to the horizontal is reduced (Fig. 10). Therefore the statoliths of the utriculi cannot be horizontal while these fish are in their normal daytime posture.

It should be remembered that the optical conditions remained constant in the above experiments. The fish were exposed to diffuse light from all directions. Immediately following the measurements made with the increased weight, the fish again swam at the same angle as before the experiment. We assume therefore that the condition of the central nervous system is not changed. Therefore, since it has also been shown that the adequate stimulus is the shearing force

![Fig. 9](image_url) Position and coloration of different sized specimens of Poecilobrycon (Nannobrycon) egues during day and night. The lines over the individual animals indicate the position of the utricular statoliths. At night the fish swim close to the surface with the statoliths approximately horizontal.

![Fig. 10](image_url) Angle of inclination of Poecilobrycon (Nannobrycon) egues against the “horizontal” as a function of g in different sized specimens (small sm., medium med., large la.). Data are average values of many individual recordings with ten animals in each set. The thin curves indicate how the fish would behave if the utricular statoliths were arranged parallel to the long axis of the fish. The thick curves fit the actual statolith inclination best.

![Fig. 11](image_url) Sketch to explain the behavior when g is doubled. The dashed line is the continuation of the long axis of the fish. The angle between the dashed line and the solid line is the calculated angle of the utricular statolith in the fish. The angle of inclination of the utricular statolith is so changed that the shearing force (s) acting vertically to the sensory hairs remains constant. The pressure component (d) may increase considerably.
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Fig. 12. Angle of inclination against the “horizontal” as a function of g. 1) Average curve from five intact specimens of Poecilobrycon. 2) Same fish as in 1), one statolith removed. 3) Expected behavior of animals in 1), after removing one statolith with linear stimulus evaluation and addition of the torque caused by both statoliths (theoretical curve). 4) Five intact Chilodus. The scattered field includes the extreme measured values. 5) Average curve for one Chilodus after removal of one utricular statolith. The individual points give the extreme values. 6) Expected behavior of animals in 4) after removing one utricular statolith with linear stimulus evaluation and addition of the torque caused by both statoliths (theoretical field). 7) Curve indicates how intact Chilodus would behave if the utricular statoliths were arranged parallel to the long axis of the fish.

(von Holst 1950), it is easy to calculate just how the statolith of the utriculus must be positioned in the fish (Fig. 11). Direct measurements with cleared specimen confirmed this conclusion. On this basis it was also determined that the angle of the utricular statoliths to the long axis of the fish must be reduced in the course of its life. We have already stated that these fish swim at less of a slant during the night than in the daytime. We have taken photographs of a large number of fish during the night. In this way we determined that the position of the fish at night is such that their utricular statoliths lie approximately horizontally (Fig. 9).

3. Chilodus punctatus (headstander) is the third species we have investigated. Only five of these animals were available. They swim with their heads downward at an angle
of 45–50° during both day and night. In the centrifuge this angle is reduced (Fig. 12, Curve 4). We assumed therefore, as in the case of the pencil fish, that in this animal the statoliths of the utriculi must lie at a slight angle from the long axis of the fish, but in the opposite sense to the one found in Poecilobrycon and Thayeria. The cleared preparation of only one fish, however, did not confirm this conclusion. In this case the morphological angle of the statoliths deviated by 20° from the calculated value (Fig. 13). This discrepancy is discussed later.

E. Relations between central nervous system and receptor

We should like now specifically to consider the relation between the equilibrium receptors and the central nervous system. This relation is especially clear in the behavior of Chilodus and Poecilobrycon. As we have seen, the normal position is not necessarily the position in which the statoliths lie horizontally. From simple observation we know that all animals, including man, are able to maintain positions which deviate from the normal equilibrium position. For example fish can assume a vertical position, and man also changes his normal position when swimming under water. We are accustomed to say in these cases that the “righting reflexes” have been inhibited, but this is not the case. For in these positions there is a constant orientation to gravity which is lacking if the organs of equilibrium are destroyed. These positions are maintained by means of the same “reflexes” which operate in keeping the animal in its normal position relative to gravity. This means, however, that there is not simply a righting reflex controlled by the organs of equilibrium alone, but that the equilibrium function is a “feedback” process of peripheral and central factors, with the sensory receptor built into the system as the external control element.

Impulses are sent from the equilibrium center to the effectors, which, in turn, cause the animal to rotate. This produces an excitation in the static organs. If the impulses from the central nervous system and the sensations coming from the statoliths are equal in intensity but opposite in sign, the animal will be in equilibrium. This mechanism enables the animal to keep each position, dictated by the central nervous system through the same “reflexes” even against mechanical disturbances (von Holst and Mittelstaedt 1950, Schoene 1957, Braemer and Braemer 1958). This will also be demonstrated in the next example.

Von Holst determined the manner in which the left and right statolith of the utriculus work together. A fish with one utricular statolith removed tilts much more strongly toward a horizontal light beam than before the operation. Von Holst obtained an equal mechanical balance component whether he applied a certain shearing force to both statoliths, or doubled the shearing component after removal of one statolith. The obvious conclusion is that the impulses coming from the left statolith of the utriculus are simply added to the impulses coming from the right side.

F. Experiments after removal of one utricular statolith

We have also studied the interrelationship of the right and left statolith in orientation of our fishes about the transverse axis. According to the studies of von Holst, removing one of them should reduce the
static equilibrium component to one-half its normal value. Therefore, we expected that following the destruction of half the sensory cells half the afferent impulses would be removed. A fish lacking one utricular statolith will attempt to achieve an equilibrium position with the remaining statolith according to the consideration given above. In this condition the last two species discussed should show considerably larger angles of inclination to the horizontal, since they should attempt to double the shearing force of the single remaining utricular statolith. Consequently by applying 2 g we should obtain the same angle as that produced by 1 g before the operation.

We found in both cases a marked weakening of the static equilibrium component (Fig. 12, Curves 2 and 6), but these results are not in quantitative agreement with the expected result. This is the present stage of our investigations.

One particular feature of Poecilobrycon and Chilodus as compared with other species is that their normal position does not conform to the zero position of their statoliths. So far as is known in other species the statolith is imbedded in the body so that it lies horizontal or nearly so in the normal position, as for example in Thayeria. Upon deviation from this zero position the excitation rises sharply (sine rule Fig. 4). This causes a high accuracy in balancing when the fish is near its normal position. In Poecilobrycon and Chilodus, however, the normal position deviates from this zero position of the statoliths. As a consequence the stimulus will not be as strong when deviations occur. We think that there might exist a relation between the behavior of animals with one statolith removed and this phenomenon. In Chilodus the morphological angle of the statoliths deviated also from the calculated value. We assume that one of the other statoliths may be acting in maintaining the equilibrium position of these two species. The advantages of cooperation between the utricular statoliths and those in the lagenae or in the saccules are evident. The precision of adjustment would be improved. Our studies will continue in this direction.

**SUMMARY**

The equilibrium-position about the transverse axis was studied in three species of Characinoidei, following the original work of von Holst.

A. *Thayeria Boehlkei* Weitzmann (penguin fish) normally swims 25° off horizontal, during both day and night. Increasing its weight does not change this angle. This means that the shearing component of the utricular statoliths, which is physiologically effective, is not increased by centrifuging. This, in turn, is only possible if the statoliths lie horizontally on the sensory epithelium while the fish is in its normal posture. This conclusion was verified by direct observation of the utricular statoliths in cleared preparations.

B. *Poecilobrycon (Nannobrycon) eques* Steind (pencil fish) swims on more of a slant during the day than at night. This proved to be due to the presence of light during the day. Three age groups of the animals were studied since younger animals swim at more of a slant than older ones.

When centrifuged in uniform diffuse light, the angle the fish takes to the horizontal is reduced. This indicates that during the day the utricular statoliths lie at a definite angle to the horizontal. This angle decreases as the fish becomes older. Direct observations of cleared preparations of the three age groups confirm this conclusion.

At night *Poecilobrycon* lies at such an angle that the utricular statoliths are approximately horizontal.

Removing one utricular statolith does not result in reducing the equilibrium response by exactly one half, as would be expected on the basis of earlier studies.

C. *Chilodus punctatus* (headstander) directs its head downward at an angle of 50° during both day and night.

In the centrifuge this angle is reduced. It was calculated that in this animal the utricular statoliths must lie at a slight angle from the long axis of the fish, but in the opposite sense from the angle found in *Poecilobrycon* and *Thayeria*. The cleared preparation did not confirm this conclusion.

Removing the utricular statoliths on one side resulted in a marked weakening of the
peripheral equilibrium component. But again in this fish the equilibrium response was not reduced by exactly one half.

The functions of the gravitational sense organs in these fishes and their connections with the central nervous system, as described, are supported by the results of other experiments. The incomplete halving of the peripheral equilibrium component, following the removal of one utricular statolith, suggests that other statoliths are involved, as does the fact that in two species (Poecilobrycon and Chilodus) they do not lie horizontally in the normal position.

REFERENCES


