THE REACTION OF BLINDED GOLDFISH TO ROTATION IN A CENTRIFUGE*

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INTRODUCTION

Blinded goldfish are known to respond to absolute rotation about the vertical axis by swimming so as to counteract the imposed rotation (Harden Jones, 1957). This reaction has also been found in blind cave fish, Anoptichthys jordani, and in normal goldfish in visual and absolute darkness (Howland, 1958).

The experiments of Harden Jones in which the fish and the bowl containing the fish were rotated about an axis which was displaced laterally by several bowl radii gave rise to the same counter-rotational swimming behaviour as when the bowl was centred over the axis of rotation. The fish in this situation were evidently unaffected by the additional cyclic translational accelerations, and maintained their orientation as before.

The relative sophistication of the inertial guidance system possessed by fish, which the foregoing experiments imply, can best be appreciated if we compare the performance of the fish with that of various known mechanisms for the detection of rotation. In Table 1 we have listed some common devices which detect rotation and their characteristics.

<table>
<thead>
<tr>
<th>System</th>
<th>Axis about which rotation is detected</th>
<th>Primarily sensitive to</th>
<th>Indicates direction of rotation or acceleration</th>
<th>No. of sensitive axes</th>
<th>Responds to force of gravity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Centrifugal governor</td>
<td>Fixed to frame</td>
<td>Yes</td>
<td>—</td>
<td>1</td>
<td>—</td>
</tr>
<tr>
<td>Torsional pendulum</td>
<td>Fixed to frame</td>
<td>Yes</td>
<td>No</td>
<td>1</td>
<td>No</td>
</tr>
<tr>
<td>Foucault pendulum</td>
<td>Vertical</td>
<td>Yes</td>
<td>Yes</td>
<td>1</td>
<td>Yes</td>
</tr>
<tr>
<td>Vibratory rate gyro</td>
<td>Fixed to frame</td>
<td>Yes</td>
<td>Yes</td>
<td>1</td>
<td>No</td>
</tr>
<tr>
<td>Single axis rate gyro</td>
<td>Fixed to frame</td>
<td>Yes</td>
<td>—</td>
<td>1</td>
<td>No</td>
</tr>
<tr>
<td>Free gyro (2 gimbal)</td>
<td>Fixed in inertial space</td>
<td>Yes</td>
<td>Yes</td>
<td>2</td>
<td>No</td>
</tr>
<tr>
<td>Stabilized platform</td>
<td>Fixed in inertial space</td>
<td>Yes</td>
<td>Yes</td>
<td>3</td>
<td>No</td>
</tr>
</tbody>
</table>

We may inquire which of these devices in its behaviour (but not necessarily in its design) most closely approximates to the orientation system of the fish. We may rule out the centrifugal governor as a model for the fish’s behaviour because it is incapable of indicating the direction of the imposed rotation. We reject the possibility of detecting

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rates of prolonged rotation with a fixed torsional pendulum (e.g., a semicircular canal), as this device detects angular accelerations, and the time integration of angular acceleration always involves the uncertainty of the constant of integration.

Only with the last five devices, the Foucault pendulum (the first instrument to give direct indication of the rotation of the earth), a vibratory rate gyro (patterned after the haltere of a fly), or the various conventional gyroscopes do we have the possibility of indicating absolute rotations without ambiguity as to direction or uncertainty as to the long-term stability of the indication. (Fish have been observed to swim with the same counter-rotation for a period of as long as a day.)

With the elimination of the first two possibilities, we are faced with a selection of four or more devices which are possible analogues to the fish's mechanism. We wish, accordingly, to devise experiments to choose from among these the best analogue. An experimental situation which differentiates between two of these devices is well known. If a Foucault pendulum and a gyroscope are set in motion at a point on the earth's surface of any latitude \( \eta < 90^\circ \) their rates of precession will differ. The gyroscope, properly mounted, will indicate the true rate of rotation, \( \omega_0 \), and the pendulum will precess at the slower rate \( \omega_0 \sin \eta \). An analogous experiment with the fish has in fact already been performed (though not with this purpose in mind). For by displacement of the axis of rotation of the bowl by a substantial amount there results an inclination of the apparent vertical which is determined by the resultant of the centrifugal force and the force due to gravity. In the experiment of Harden Jones the centripetal acceleration at the greatest displacement was approximately \( 0.022 g \), corresponding to an angle of inclination of \( \eta = 88.7 \) degrees, for which \( \sin \eta = 0.9997 \).

Clearly, in this situation we cannot hope to differentiate between these two analogues by means of measurements of the fish's rate of compensation. The rates will in fact be at variance with one another only if the resultant of total acceleration is substantially different from that of gravity, which is to say that the centripetal acceleration must be of the same order as the acceleration due to gravity. In terms of apparatus some form of centrifuge is required to perform these tests.

Preliminary experiments on an open-air carnival centrifuge indicated that Anoptichthys jordani could swim more or less normally under increased accelerations. However, these experiments failed to show clearly in which plane and with what speed the fish swam. It was thus decided to try again with blinded goldfish (which we hoped would be less excitable) and with more controllable centrifuge conditions.

**MATERIAL AND APPARATUS**

(1) *Fish.* Three goldfish, *Carassius auratus*, averaging 7 cm. in body length were blinded by tying off the eyestalk and cutting out the bulb of the eye. A 5% urethane solution was employed as the anaesthetic, and an interval of 1 or 2 days was allowed between excisions. All operated fish survived and were still healthy after 4 months. As reported by Harden Jones (1957) such fish require no special care and can be kept in a tank together with normal goldfish.

(2) *The centrifuge.* This apparatus was built by von Holst and Göldner (von Holst, 1950) for experiments on the dorsal light reactions of fish. With their arrangement, in which the cabin and counterweight hang as opposed symmetrical rotating pendula.
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The direction of apparent vertical at the centre of the cabin remains sensibly the same relative to the cabin for all rates of rotation. A driving mechanism of variable speed provided a speed range of 10–19 r.p.m. corresponding to a range of accelerations of 1.1–2.5 g, measured at the centre of the cabin.

The volume and payload of the cabin were such as easily to accommodate the fish, fishbowl and ancillary apparatus, and an observer. In operation over the full speed range an observer in the light-tight cabin experienced little apparent sensation of motion. This would not have been the case had the acceleration and deceleration been uneven, or had the apparent direction of the vertical not remained constant with varying rates of rotation. Such indication of motion as did exist was provided by small noises and periodic vibrations generated by the gear train, which always appeared to come from the same direction relative to the interior of the cabin.

(3) The fishbowl. Inside the cabin of the centrifuge was installed apparatus whose function was to contain the fish while providing a minimum of tactile cues as to orientation, and to permit rotation of the fishbowl and its contents relative to the cabin about an axis parallel with that of the centrifuge. The fish was placed in a water-filled, air-saturated 2 l. spherical Florence flask. This flask was, in turn, contained in a rectangular water-filled chamber, constructed of thick plexi-glass. On to the bottom of the flask was cemented a conical brass teat, which rested in a stainless steel ball-bearing recessed into the floor of the plastic box. The top of the flask was positioned by a rubber cork, through the centre of which passed a drive shaft, colinear with the teat and bearing. This shaft was mounted in a bearing holder attached to the top of the plastic box and driven via a pulley and belt by a second idler shaft which was in turn coupled to a variable speed, reversible d.c. motor. Considerable care was taken to isolate the vibrations of the idler shaft from the flask holding the fish. This was accomplished with shock mounts and flexible rubber couplings.

The floor of the plastic box was a false bottom underneath which was placed a mirror; this permitted viewing the fish from below and from the side simultaneously. The purpose of the plastic box was, of course, to eliminate refraction at the face of the spherical flask.

This arrangement of flask, shafts and box allowed easy access to the contents of these vessels and to the fish, together with the possibility of rotating the same at a very uniform rate; the whole arrangement acted as a fluid clutch to integrate the effects of any residual unevenness in the drive mechanism.

Any rotations imparted to the flask must be about the same axis as that of the centrifuge; otherwise very complex convection currents would be generated inside the flask, and the physical environment of the fish would be almost impossible to specify. Since the cabin tips relative to the axis of the centrifuge, provision was made for tipping the entire apparatus relative to the cab by an equal amount in the opposite direction. For this reason the entire apparatus, together with lights and camera, was mounted on a hinged board with detents corresponding to the commonly used accelerations. The angle of tip was preset by the calculated amount, and rotation or counter-rotation of the bowl was initiated only after the centrifuge had attained operational speed. The cabin of the centrifuge was upholstered for an observer in the prone position and was provided with telephone and telegraph communication with the ground. The telegraph was employed when there was a possibility of sonic cues to the fish. A 16 mm.
cine camera, capable of remote or local operation, with lenses imaging bottom, side, or both views of the bowl, was used to obtain data as to the plane in which the fish swam.

**CALIBRATION OF THE CENTRIFUGE AND FISH**

Because of the constructional features of the centrifuge, in particular the pendulous mounting of the counterweight, the relation between total acceleration at any given point inside the cabin and the absolute rate of rotation of the assembly has to be taken into account. Since such a calculation required certain assumptions as to the distribution of mass in the cabin and its supporting structure, an experimental calibration was also thought to be desirable. To this effect, a short plumb bob, which we may term a Foucault pendulum, was installed in the cabin, the mean position of the bob being approximately the centre of the fishbowl. With the centrifuge rotating at a given rate, measurements were made of the period of this pendulum, \( t \), and the rate of precession, \( Q \), measured in revolutions per minute by an observer inside the rotating cabin of the centrifuge. This gave in effect two independent checks on the acceleration versus rate of rotation graph, since we have

\[
a = \left( \frac{t_0}{t} \right)^2 g, \quad (1)
\]

and

\[
a = Y/Q \cdot g, \quad (2)
\]

where \( a \) is the total acceleration, \( g \) is the acceleration due to gravity, \( t_0 \) is the period of the pendulum with no rotation, and \( Y \) is the rate of rotation of the centrifuge.

These calibration data are plotted in Figs. 1 and 2. The calculated points of these two figures were obtained by a method of successive approximations of the radius arm at the point of measurement. It is seen that the values of \( g \) and \( Q \) agree with the expected values to within a few per cent; the deviations may be due to the fact that the length of the experimental pendulum, about 40 cm., was not inappreciable compared with the relevant dimensions of the centrifuge.

The ability of the blinded fish to swim against rotation was tested 'on the ground',
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both before and after centrifugation. For this experiment the flask and the fish were rotated about the vertical axis at varying rates and the net algebraic change of the orientation angle of the fish for a specified interval was measured. These data for the three fish on five occasions are plotted in Fig. 3 with the rate of rotation of the fish relative to the flask as the ordinate, and the rate of rotation of the flask as the abscissa. Two regression lines have been drawn according to the method of least squares. Inspection of these lines shows that there is no significant change in the performance of the fish as a result of centrifuging.

![Graph showing effect of centrifuging on the compensation reaction of the fish.](image)

**Fig. 3.** Effect of centrifuging on the compensation reaction of the fish.

**THE SIMPLE EXPERIMENT**

The experiment in its elementary form consisted in placing the fish in the flask, the flask in the box, the box in the cab with an observer, and centrifuging all with total accelerations varying from 1.1 to 2.0 g. When the fish advanced one revolution relative to the box, the observer depressed a telegraph key, and the time was then noted by the operator in the control shack. After starting the centrifuge and after each change in speed we customarily waited 4–5 min. to allow the fish to accommodate before taking data. Since large changes in acceleration were found to be disturbing to the fish, the rate of rotation was increased very gradually and in small steps till the maximum value was attained and then it was similarly reduced. Points were taken at intervals of 0.1 or 0.2 g on the way up and down. At each acceleration setting the fish was timed for twenty revolutions relative to the cabin, or for about 2 min. of swimming. If its behaviour was inconsistent, as for example when the fish nibbled at particles on the bottom of the flask, a second twenty revolutions would be timed at the same setting and the data averaged.

The data are shown in Fig. 4 for the three fish on six occasions. The averaged data
for all points at each acceleration are shown in Fig. 5. The following points should be noted:

(1) Individual fish do not always swim consistently from one day to another.

(2) In three experiments the rate at which the fish swims relative to the cab decreases with increasing rate of rotation of the centrifuge, in two it remains about the same, and in one it increases slightly.

(3) The averaged data indicate that the fish do not compensate for the absolute rate of rotation of the centrifuge, but rather swim against the rotation of the centrifuge at a slower rate.

(4) The data are not inconsistent with the hypothesis that the fish swims counter to the imposed rotation at a rate approximately equal to the rate of precession of a Foucault pendulum.

![Fig. 4](image1.png)
**Fig. 4** Response of three fish in rotating centrifuge. Fish A: open triangles, open squares. Fish B: crosses. Fish C: solid triangles, solid squares, solid circles. Different symbols indicate experiments performed on different days. The curved line indicates the precession of a Foucault pendulum (see Fig. 2).

**Fig. 5** The data of Fig. 4 averaged at each value of acceleration.

**COUNTER-ROTATION AND THE NULL EXPERIMENT**

By tilting the apparatus relative to the cab of the centrifuge it was possible to bring the axis of the flask parallel to that of the centrifuge for any given acceleration. By rotating the flask relative to the box we could adjust the absolute rate of rotation of the flask, and thus of the water in which the fish swam, to any desired value. In particular we could completely compensate the rotation of the centrifuge by counter-rotating the flask at the same rate (complete counter-rotation). In this situation the flask containing the fish is not rotated at all; however, the apparent direction of gravity (i.e. the vertical) is made to describe a cone underneath the fish. At this point in our argument one can see more clearly the physiological meaning of this experiment: complete counter-rotation allows us to stimulate the otolithic apparatus of the free-swimming fish without stimulating the semicircular canals.

For each run of the experiment the centrifuge was brought to $1.3g$ ($13.15$ r.p.m.) and the absolute rate of rotation of the flask was varied. The rate of rotation of the fish
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was measured in the usual way. The data are plotted in Fig. 6. Note that here both the ordinate and the abscissa represent absolute rates of rotation.

For points on the left side of the line \( x = y \), the fish swam, on the average, against the rotation of the water. On the line \( x = y \) the fish need not have swum at all. Had the fish always compensated for the entire absolute rotation all points would lie on the abscissa. Had the fish behaved as if oriented by a Foucault pendulum all points would lie on the line \( pp' \). On the average, the fish rotated more slowly than the pendulum by 2.5 r.p.m. The line \( rr' \) is the regression of fish rates of rotation on water rates of rotation fitted by the method of least squares.

The points at the extreme left of Fig. 6 represent zero counter-rotation and were taken under conditions identical to the points at \( 1.3 \, g \) in the simple experiment, though they show the fish swimming somewhat slower by about 1.6 r.p.m. For all points to the right of these (i.e. for rates of rotation of the water greater than \( -13.15 \, r.p.m. \) the fish was being counter-rotated.

![Fig. 6](image)

**Fig. 6.** Results of the counter-rotation experiment. Note that ordinate and abscissa indicate absolute rates of rotation. \( \circ \), Fish: (a), 1st trial; \( \bigcirc \), fish (a) 2nd trial; \( \bullet \), fish c.

**Fig. 7.** The data of Fig. 6 graphed to show the frequency of occurrence of each period. Solid area indicates trials when the fish was not counter-rotated. Shaded area indicates trials when fish was counter-rotated.

As we shall see, the rotated fish swam in a plane which deviated from the apparent horizontal by only 5° at \( 1.3 \, g \). If the counter-rotation is such that the fish is required to make no forward or rotational motion with respect to the water, the fish will swim in a plane close to the apparent horizontal. We were able to photograph fish A while taking data for the point in Fig. 6 which lies at the intersection of line \( pp' \) and line \( x = y \). This fish aligned itself radially with respect to the flask and swam neither forward nor backward nor around its long axis, but rather it pitched and rolled so that it tended always to keep the same orientation with respect to the apparent vertical.

We regard the counter-rotation experiment as lending further support to the hypo-
thesis that the fish behaves in the centrifuge as if oriented by a Foucault pendulum. This is shown by Fig. 6 and also by Fig. 7 where it may be seen that the most frequent period at which the fish swam was that of the pendulum.

THE PLANE IN WHICH THE FISH SWAM

The simple experiment was repeated three more times, once for each fish, and motion pictures were taken of the fish swimming at different accelerations. The pictures were then projected frame by frame and the positions of the fish at the far left and far right of the flask were recorded. A line was drawn through each pair of points so obtained and the angles, $\alpha$, which these lines made with the apparent horizontal were measured and averaged. These data are presented in Fig. 8a, b, c. The vertical lines through each point indicate plus and minus one standard error of the mean. The angle that the axis of the centrifuge made with the apparent vertical is indicated on the graphs as the curve $\theta \theta'$.

The three fish swam at different rates of rotation. Fish A swam with an average period during the entire experiment of 6.22 sec., fish B swam very regularly with an average period of 3.11 sec. and fish C with an average period of 4.62 sec.

Had the fish always swum in a plane orthogonal to the axis of rotation of the centrifuge all points in Fig. 8 would fall around the curve $\theta \theta'$. Had the fish swum in the plane orthogonal to the apparent vertical, all points would fall around the abscissa. The planes in which the fish swam are much closer to that of the apparent horizontal than to the plane orthogonal to the axis of rotation. However, the behaviour of fish C, and particularly that of fish B, show that at higher rates of rotation (both of the centrifuge and the fish relative to the cab) the axis about which the fish swims leans toward the axis of rotation. Fish B swam so regularly that it was possible to observe also the second angle, $\rho$, which was normal to the plane in which it swam made with the apparent vertical orthogonal to the direction recorded in Fig. 8. The angle $\rho$ for fish B is graphed in Fig. 10 together with another angle, $\gamma$, derived from the measurements of $\rho$ and $\alpha$. 

Fig. 8. Relationship between value of $g$ and $\alpha$, the angle between the axis about which each fish swam and the apparent vertical. The line $\theta \theta'$ indicates the value of $\alpha$ if the fish swam always about an axis parallel to the axis of rotation of the centrifuge.
At this point it may be helpful to summarize the geometry of the centrifuge, and this is done in Fig. 9. The three-dimensional co-ordinate system (co-ordinates \(x, y, z\)) is rigidly attached to the cab of the centrifuge and so swings out and rotates with the cab. Thus the \(x\)-axis is always parallel to the apparent vertical, the \(y\)-axis is always a tangent to the circle that the cab of the centrifuge is describing, and the \(x\)-axis is always in the plane of the apparent horizontal. At an acceleration of 1 \(g\) the axis of rotation lies parallel to the apparent vertical and the angle of \(\theta\) is zero. At higher accelerations the angle \(\theta\) becomes greater than 0 and the fish swims about some axis, say \(OG\).

In all experiments in which the fish was photographed, the cab rotated clockwise as viewed from a point above the ground; i.e. looking from point \(V\) to point \(O\) down the axis of rotation, the co-ordinate system would be seen to rotate clockwise.

DISCUSSION

The simple experiment shows that blinded goldfish behave in the centrifuge as if oriented by a Foucault pendulum. That is, they tend to compensate only the component of rotation about the apparent vertical.

The counter-rotation experiment shows that fish which are not rotated will swim in a plane orthogonal to the apparent vertical. In so doing they will swim with a rate of rotation of \(V_r\), where

\[
V_r = Y (1 - \cos \theta),
\]

and \(Y\) is the rate of rotation of the centrifuge.
Moving pictures of three fish during the simple experiment show that the fish did not always swim in a plane orthogonal to the apparent vertical, but rather that the axis about which the fish swam leaned slightly away from the apparent vertical towards the axis of rotation of the centrifuge by an amount which increases with increasing rates of rotation of the centrifuge, $Y$.

In both the simple and counter-rotation experiments the information supplied to the otocysts and the information supplied to the semicircular canals would be mutually contradictory in a non-rotating environment. In Fig. 9 let $\mathbf{OV}$ be the rotational velocity vector describing the absolute rate of rotation of the centrifuge cab. This vector may be regarded as the sum of two other vectors, one along the $x$-axis, the other along the $z$-axis in a direction opposite to the imposed rotational component with equal magnitude. This means that the fish is continually presenting a different set of semicircular canals to the rotational component along the $x$-axis. The fish must interpret the resulting sensations on its semicircular canals as pitching or rolling motions about an axis lying in the $x$-$y$ plane. (A human observer in the moving centrifuge experiences pitching or rolling sensations when shaking his head 'no' about any other axis than the axis of rotation of the centrifuge.)

It should be noted that, had the fish swum about the axis of rotation of the centrifuge with the same rate of rotation as the centrifuge but in the opposing sense, there would remain no uncompensated signal on the semicircular canals, but the apparent vertical would have described a cone underneath the fish.

The work of von Holst (von Holst, 1950) shows that the utricular otocysts of fish influence the orientation of fish in such a way that the shearing force on the utricular otocysts is reduced to a minimum. In our experiments, for low rates of rotation, the plane on which the fish swam is evidently dictated by the otocysts.

That the sensations arising from the semicircular canals play a role in the normal orientation of fish can best be seen from the work of F. R. Lee (Lee, 1894) in light of the work of Lowenstein & Sand (1940) and von Holst (1950). Lee found upon cutting the ampullary nerves of the anterior vertical semicircular canals that the fish stood head down with their eyes rotated so that their anterior poles were pointed ventrally (an eye position).

Lowenstein & Sand showed that under conditions of no rotation there is a resting discharge from the anterior semicircular canals of the elasmobranch labyrinth which is augmented by pitching the head forward and diminished by pitching it backwards.

It is thus a simple logical step to assume that the absence of discharge from the transected ampullary nerves is interpreted by the fish as a velocity of pitching backwards, and that the fish normally responds to this by pitching its head forwards and rotating the anterior poles of its eyes ventrally. We know from von Holst's work that this tendency to pitch forward would be countered by a restoring moment arising from the utricular otocysts, the shear in the otoliths being at a maximum in the head-down position.

All of the results of Lee's operations on pairs of semi-circular canals are consistent with the findings of Lowenstein & Sand and with the interpretation given here and by van Egmond Groen & Jonkees (1949) of the normal function of the semicircular canals.

Thus we interpret the deviations of the axes about which the fish swam from the
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apparent vertical at high rates of rotation as reflecting the compensatory motions of the fish that the signals from the semicircular canals would normally engender.*

The exact relationship between the influence of the statocysts and the influence of the semicircular canals can most easily be studied in a centrifuge with independent control of the radius. With such an apparatus one could obtain, for each value of \( g \), measurements with a series of rates of rotation. This is perhaps logically the next experiment to be performed.

Basic to all these experiments is the, as yet undiscovered, method by which the fish detects absolute rotation. That the fish does compensate absolute rotation (about the apparent vertical) is, of course, further substantiated by the experiments reported here. With respect to the elimination of external environmental cues, the present apparatus enjoys one advantage over previous experimental arrangements in that the sound from the motor and gears driving the centrifuge always entered at the same angle relative to the rotating bowl. Had this effect been noticed by the fish, it would presumably have acted to diminish the compensatory reaction.

SUMMARY

1. Blinded goldfish behave in a centrifuge as if they were orienting to absolute rotation by means of a Foucault pendulum. That is, they swim so as to compensate the rate of imposed rotation about the apparent vertical.

2. Blinded goldfish swim in the centrifuge in a plane essentially orthogonal to the apparent vertical at low accelerations and low rates of rotation. With higher rates of rotation the axis about which the fish swims leans away from the apparent vertical and towards the axis of rotation of the centrifuge.

3. Analysis of the physics of the centrifuge shows that if the fish rotates about any axis relative to the cab of the moving centrifuge with a rate of rotation within the physiological range of its semicircular canals it will receive signals from its otocysts and its semicircular canals which would reflect contradictory information in a non-rotating environment. This fact, together with the fish's response to absolute rotation, affords a method for quantitatively assessing the relative roles of the otocysts and the semicircular canals in orienting the free-swimming fish.

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* This discussion does not account for the magnitude and direction of the deviation angle, \( \rho \), observed in the very regular swimming of fish B. This deviation is probably a function of the fundamental period of the semicircular canals (which are torsional pendula) and the phase relations between the otocysts and the semicircular canals. Both these factors await investigation.
REFERENCES


