
Head Turning in Herring and Some other Fish

D. M. Rowe, E. J. Denton and R. S. Batty

Phil. Trans. R. Soc. Lond. B 1993 **341**, 141-148
doi: 10.1098/rstb.1993.0098

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

Head turning in herring and some other fish

D. M. ROWE¹, E. J. DENTON² AND R. S. BATTY³

¹ School of Computing, University of Plymouth, Drake Circus, Plymouth PL4 8AA, U.K.

² Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, U.K.

³ Dunstaffnage Marine Laboratory, PO Box 3, Oban, Argyll PA34 4AD, U.K.

SUMMARY

Herring (*Clupea harengus* L.), swimming freely, were recorded on high-speed video and the positions of their heads found at 5 ms intervals. The displacements, velocities and accelerations of various positions along the head were estimated. An analysis of this data showed that, with continuous swimming, the lateral motions of the head could be described reasonably well as the sum of side-slip movements (with equal lateral displacements for all points along the length of the head) and yawing movements around a pivoting position, P, on the mid-line of the head, about 16%–18% of the body length of the fish from the snout. The phases of the lateral *displacements* due to yaw were close to those of the lateral *velocities* at P; the lateral displacements and velocities, both being measured in a direction perpendicular to that in which the fish was moving. The lateral velocities were in good agreement with the products of the steady forward velocity of the fish U and the angle α (in radians) between the direction in which the head was pointing and the direction in which the fish was swimming. The angular velocity, Ω , of the turning of the head was close to being equal to $0.87A/U$, where A is the acceleration of the head at P in the direction perpendicular to that in which the head was pointing. Ω and A were in phase.

These facts give support to a theory described by Lighthill in the preceding paper on how clupeids might 'turn their heads' during swimming so as to swim more economically and diminish the large stimuli that a fish's own movements would otherwise give to the receptor organs of the lateral line system.

An analysis of data taken from earlier work on cod (*Gadus morhua*) by J. J. Videler and C. S. Wardle, and on bream (*Abramis brama*) by R. Bainbridge, showed that these fish probably make head movements with the same properties.

1. INTRODUCTION

This paper is mainly concerned with an attempt to see if a clupeid fish does make head movements of the kind described in the preceding paper by Lighthill (1993) as being ones that would make swimming more economical and, at the same time, diminish the stimuli that a fish's own movements give to the neuromasts of the lateral line system (see Denton and Gray (1993) for a discussion of this second problem). In this paper, we use the symbols given by Lighthill (1993); some of these are shown in figure 1.

Lighthill's ingenious hypothesis demands that the lateral motions of the head can be described as the sum of side-slip movements, with equal lateral displacements for all points along the length of the head, and yawing movements around a position, P, on the mid-line of the head, well forward of the fish's mass centre. It predicts that swimming will be economical, and stimulation of the neuromasts small, if the movements are such that the lateral velocity \dot{y}_0 at P is close in value to and, in action, out of phase with $U\alpha$, where U is the forward velocity of the fish in the overall direction in which the fish is swimming and α is the angle between the direction in which the head

is pointing and the direction in which the fish is swimming. If U is constant, then the *displacements* due to yaw, which are proportional to α , must be in phase with the lateral *velocities* at P. For sinusoidal changes in α , the displacements of yaw for positions rostral to P, must be 90° ahead of the displacements of side-slip. Taking Lighthill's constants k , k_1 and K as 1.6, 1.1 and 3 respectively, the stimulation of the neuromasts will be zero if $U\alpha = 0.87\dot{y}_0$. Alternative 'close to ideal' conditions are that Ω , the angular velocity of yaw $d\alpha/dt$, is: (i) in phase with A , the acceleration of the head at P in a direction perpendicular to the direction which the mid-line of the head is pointing; and (ii) equal to $0.87(A/U)$, where $A = dV/dt + U\Omega$, where V is the velocity of the head at P, again perpendicular to the direction in which the head is pointing.

We may note that, for the herring, the ideal condition (that which minimizes both the net flow in the subcerebral canal and cross flows within the boundary layer over the fish's head) is that dV/dt is small, being equal to about $0.15 U\Omega$.

We have, in the discussion of the results below, assumed that the constant 0.87 given above for the herring is appropriate for other species of fish. A fuller

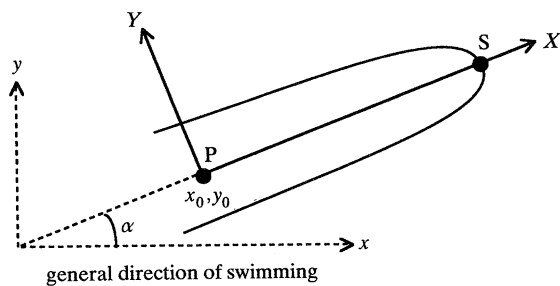


Figure 1. Motion of the head of the fish. x, y are axes for a frame of reference with x fixed in the overall direction in which the fish is swimming. X, Y are axes in which X points along the axis of symmetry of the fish's head. The point P (with coordinates x_0, y_0) is the point around which the head is pivoting. α is the angle of yaw. The point S is the snout of the fish.

analysis would require that the constant be calculated from the shape of the head for each species by the method given by Lighthill.

2. METHODS

Video recordings of swimming herring were made in Dunstaffnage with a NAC HSV 400 high-speed video-recording system, operating at 5 ms inter-frame interval and with strobed illumination.

The fish were in a 2 m \times 1 m tank containing sea water of depth 0.7 m and were at midwater, approximately 2.12 m from the camera (see figure 2). The fish were video-recorded from above through a Perspex window so as to prevent the image of the fish being disturbed by ripples on the sea water surface. The fish could be viewed through a side window so that we could confirm that they were swimming horizontally and at mid-water. The bottom of the tank was covered in Scotchlite, made by 3M.

In the analysis of the movements of a fish, for each frame of the video recording, the coordinates of three points were found: the tip of the snout, and two points

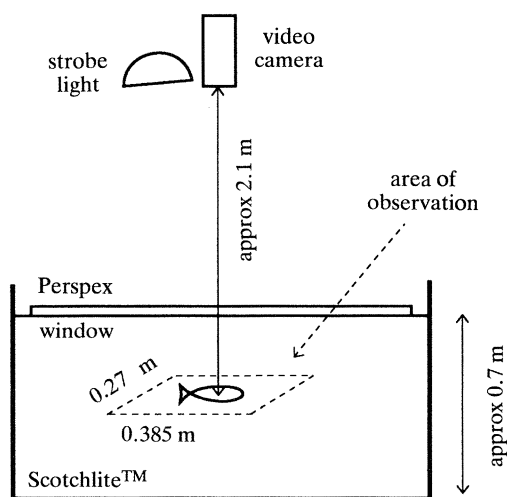


Figure 2. Scheme of the experimental system.

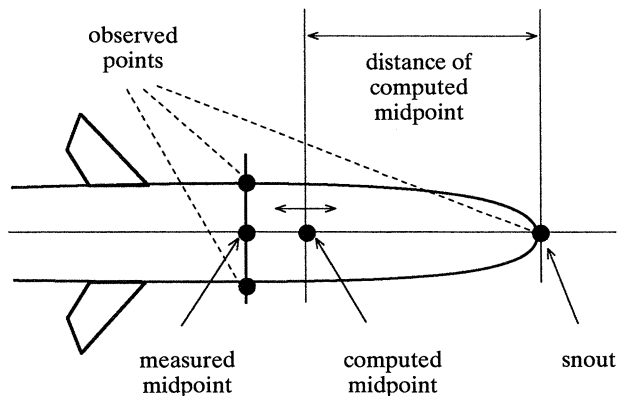


Figure 3. Scheme showing the position of various points on the head of the fish.

opposite to each other on the rigid part of the head (see figure 3). From the last two coordinates, the position of a 'measured mid-point' half way between the two was computed. A line joining the snout and this measured midpoint therefore formed the longitudinal axis of the head and this defined an angle relative to the frame of reference of the measurements. Knowing this angle and the position of the snout, the coordinates of points on the mid-line at various distances from the snout could be found; such points we shall name 'computed mid-points'. From the successive values of these various coordinates, the displacements, velocities and accelerations of the snout and these computed midpoints could be found.

The field of view observed by the video camera corresponded to an area 0.358 m by 0.27 m at the position of the fish, giving a maximum angular field of view of approximately 9° . The resolution of the image on the video screen was limited by the pixel size which corresponded to a distance of 0.65 mm at the point of observation. The small sudden discontinuities (see figure 4a) arising from this limit to resolution are not very disturbing when considering displacements, but become so on differentiating to give successively velocities and accelerations. Now these small discontinuities are clearly artefacts, mostly arising from a known source, the pixel size. They are not found in analyses of high-speed cine-recordings of fish swimming. It seems reasonable, therefore, to see if displacement curves such as those in figure 4a can be smoothed to a degree for which these discontinuities are greatly reduced without otherwise changing the curves appreciably.

The technique generally used for smoothing was a convolution method which fits a cubic to successive groups of 9 points with least squares difference (Savitzky & Golay 1964); this method was also used to compute the derivatives of the data, again smoothing over successive groups of 9 points. The effect of this smoothing can be seen in figure 4a; the root-mean-square difference between the observed values and the smoothed values being 0.28 mm for x values and 0.21 mm for y values, i.e. close to half the pixel size. The results obtained were consistent with other analyses using 3-point average smoothing: see figure

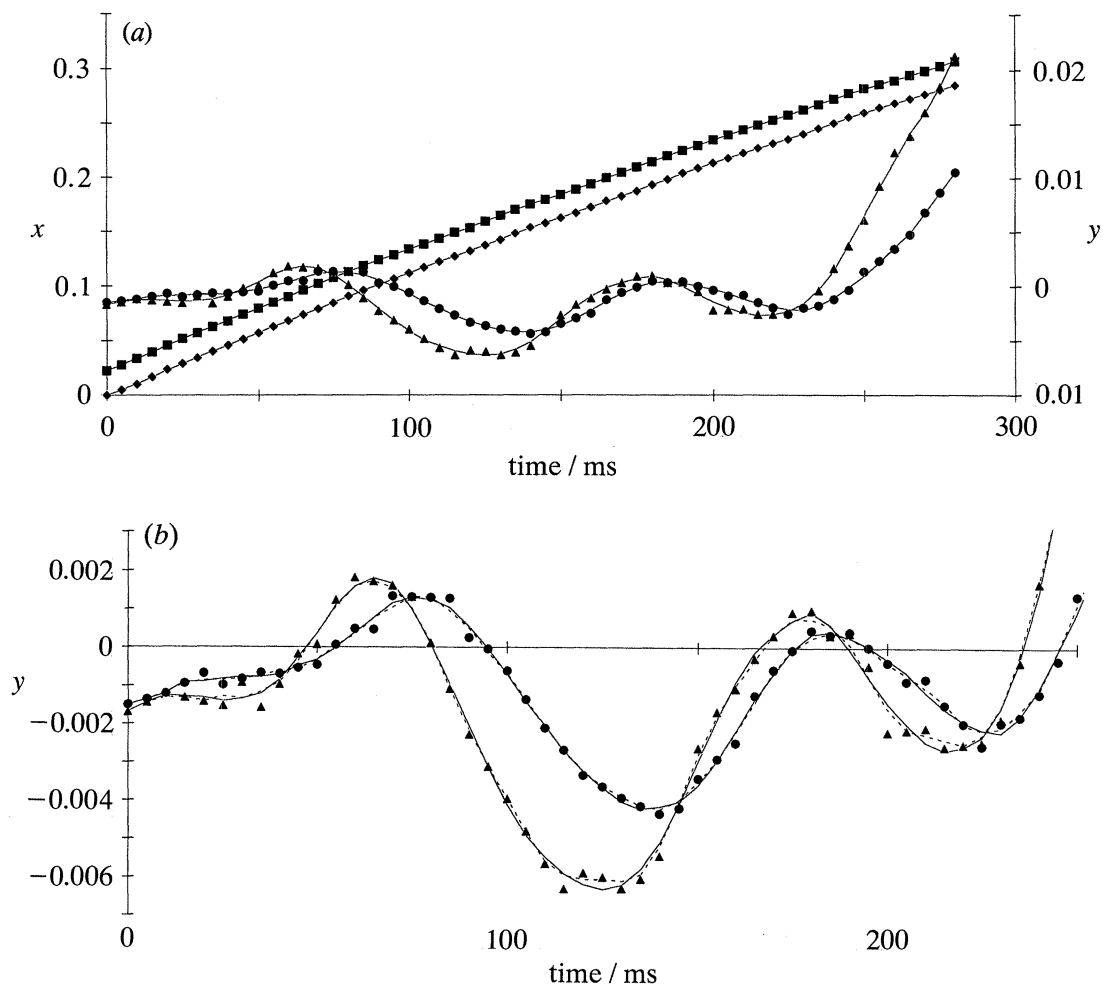


Figure 4. Coordinates of the snout and measured midpoint plotted against time, showing observed values, and values after smoothing. Distances are in metres. (a) Smoothing of the complete data set by the fitting of a cubic to 9-point groups of points using least squares difference. (b) Smoothing of y data by cubic fitting compared to 3-point averaging. Markers show observed values: squares, x snout; diamonds, x measured midpoint; triangles, y snout; circles, y measured midpoint. Solid lines show values after smoothing by cubic fitting; dotted lines show values after smoothing by 3-point averaging.

4b. In figures 4–10, the coordinate data has been rotated by $+33^\circ$ relative to the original observations to line up the x axis with the general direction of the fish's swimming. The zeros for the x and y axes are not particularly significant: they have in fact been adjusted so that the zero for x corresponds to the starting position for the measured mid point, and zero for y corresponds to the average value of y for all positions of the snout and measured mid-point.

One source of errors in making estimates of the angle α will be given by errors in the values found for measured mid-points caused by the head-rolling while swimming. We think that these errors will be small. The images of the fish on which measurements were made were, in effect, silhouettes of the fish against a bright background. When a fish rolls appreciably, as it does when making a sharp turn, the image can become markedly asymmetric. In particular, the image of one eye becomes more prominent and the other less so. No appreciable changes in the symmetry of the image of the head could be seen during the

swimming movements analysed here, which indicated that any rolls were not large. However, even for quite appreciable rolling of the head, the errors in estimating the measured midpoints will be small. We have made careful measurements of the shape of the head of a herring at various points along its length and some of these are reproduced in figure 4 of Lighthill's paper. From a cross section in the region of the lateral recess, it is easy to show that a roll as great as 25° about a point in the centre of the cross-section will, for a fish of length 10 cm, only produce an error in the estimate of the position of the measured midpoint of about 0.1 mm. As the distance between the lateral recess and the snout is about 18 mm, this will give a maximal error of about 0.3° .

Data for some other fish were taken from figures given by Videler & Wardle (1978) for the cod and for four freshwater fish by Bainbridge (1963). Measurements were made on these figures with a dissecting microscope at six times magnification against a micrometer eyepiece scale.

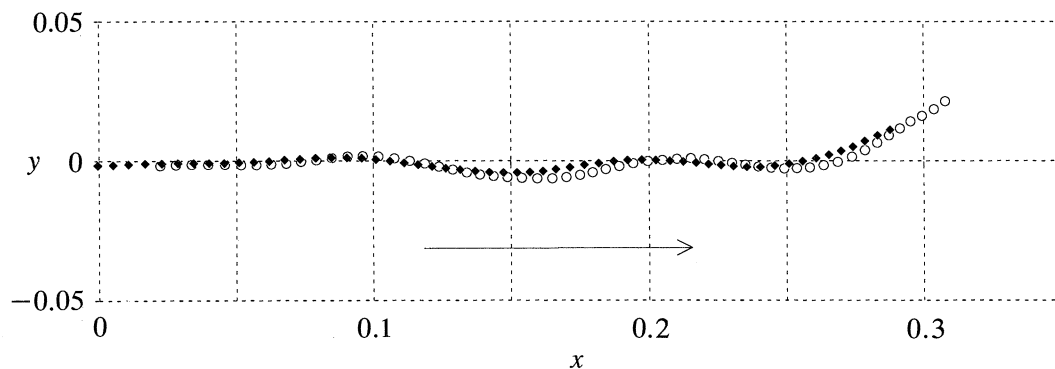


Figure 5. The track of the fish, showing the positions of the snout (open circles), and the positions of the computed mid-point (filled diamonds) at 5 ms intervals. Distances are in metres. The computed midpoint is at a distance of 16% of the fish's length from the snout.

3. RESULTS AND DISCUSSION

(a) *Herring (Clupea harengus L.)*

Photographs of swimming herring show definite pivoting of the head at positions that are about one-fifth of the body length of the fish from the tip of the snout.

Figures 4–10 are based on a recording of a herring, of length 14.3 cm, swimming continuously, but not regularly, at the fairly high speed of approximately 1 m s^{-1} and with a tail-beat frequency of about 10 Hz. Figure 5 shows successive positions of the tip of the snout and a position on the mid-line of the head about 16% of the body length behind the snout. It may be seen that the angles that the mid-line of the head makes with the direction of swimming are always small, varying from -9.5° to $+3.5^\circ$, except at the end where the fish is turning away to its left at an angle of $+26^\circ$.

If the lateral movements of the head are the sum of side-slip movements, these being the same for all positions along the length of the head, and yawing movements around a constant position P, then P will be the position for which the amplitude of lateral

displacements will be least. On figure 6, displacements of the head at various distances from the snout (position S) are plotted against time.

The minimum values of displacement are for a distance of about 16% of the length of the fish. If this is the true pivoting position, then the displacements here will be those of pure side-slip. If we subtract the displacements at P from those at S, the differences will be those due to yaw alone (figure 7).

Values for the angle α can be found by dividing the yaw displacements at S by the distance PS. Because the value for U is known, we can find the absolute value for $U\alpha$. In figure 8, the $U\alpha$ curve for yaw velocity is compared with the curve for 0.87 times the side-slip velocity, \dot{y}_0 , given by differentiating the curve for side-slip displacement (i.e. that at P) with respect to time. We see that the $U\alpha$ curve is close in amplitude and phase to that for $0.87\dot{y}_0$; a slightly better match is obtained if a small offset of 0.025 m s^{-1} is added to $U\alpha$ (see figure 8); this offset could arise from a number of causes; for example, a small transverse water current possibly caused by the motion of other fish in the tank. In figure 9, the Ω curve for angular velocity is

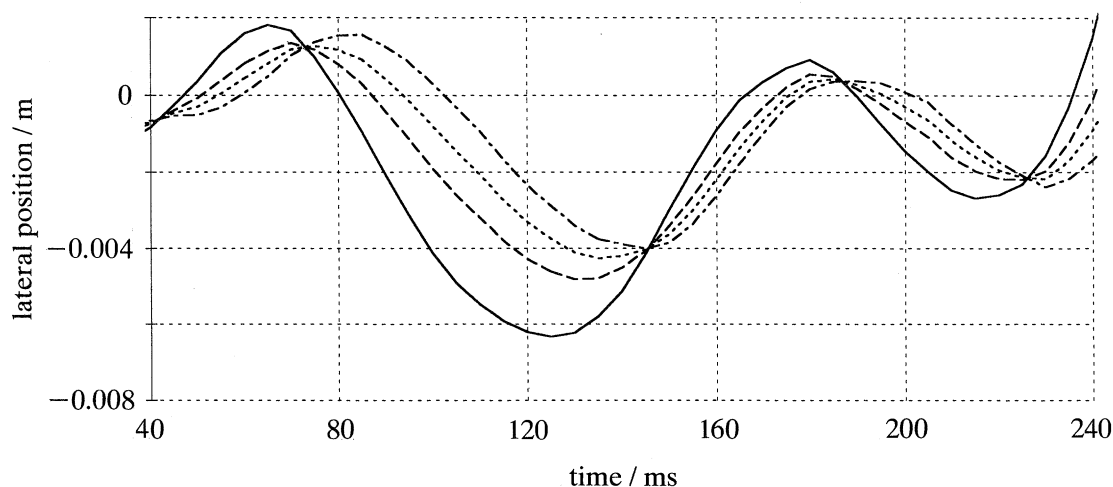


Figure 6. Lateral displacements (relative to fixed direction of swimming) of points on the head at different distances from the snout, plotted against time: snout at 0% (solid line), at 10% (dashed line), at 15% (dotted line), and at 20% (dot-dashed line) of the fish's length. The time frame has been restricted to the central period of the observations.

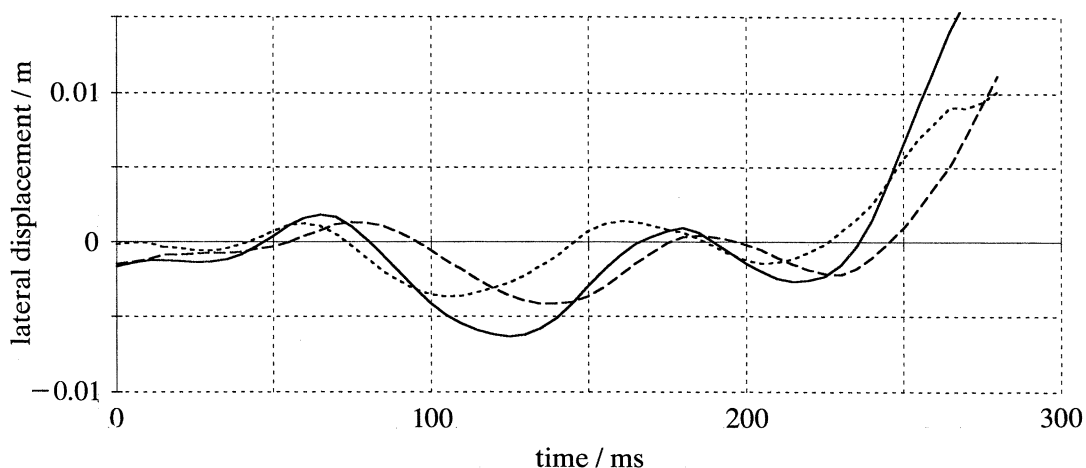


Figure 7. Lateral displacements (relative to fixed direction of heading) of the snout, the 16% midpoint, and the difference between them, plotted against time: solid line, snout; dashed line, 16% midpoint; dotted line, the difference between snout and the midpoint.

compared with the curve for $0.87 (A/U)$. Again, we find close agreement in both amplitude and timing. All this accords with predictions based on Lighthill's hypothesis.

We can check the agreement between hypothesis and experiment in another way, for if at a particular time $U\alpha$ had been almost equal to \dot{y}_0 , the direction in which the head pointed would have been almost parallel to the track of the head at P, the pivoting position. On figure 10, the curve gives the lateral displacements of the fish at P and the straight lines the directions in which the head was pointing, at 20 ms intervals. We see that, as the hypothesis predicts, the lines are close to being tangential to the curve. What is particularly significant is that this remains true for all the period shown, even though the swimming is not regular in amplitude and there is a change in the direction of swimming. We may note that on this figure, the lateral displacements have been magnified about five times relative to the displacements in the

direction of swimming and that the actual angles of yaw are everywhere small.

A mismatch of only one degree between the 'ideal' direction and the actual direction in which the head is pointing in a fish of length 14.3 cm swimming rapidly with a tail beat frequency of 10 Hz and a maximal angle of yaw of 5° would, from Lighthill's equations (4) and (30), and assuming dV/dt to remain constant and Ω to be four-fifths of the 'ideal' value, give effective pressure differences of up to about 6 Pa. This is about half of the value that would saturate the responses of the lateral line neuromasts close to the lateral recess at 10 Hz (see Denton and Gray 1993, table 1). A similar mismatch at the low frequency of 1 Hz and a forward velocity of 0.1 m s^{-1} instead of 1 m s^{-1} would give effective pressure differences of up to about 0.06 Pa. This is close to the threshold of the receptor organs at 1 Hz. This suggests that the properties of the receptor system are very close to those needed in a system 'designed' to

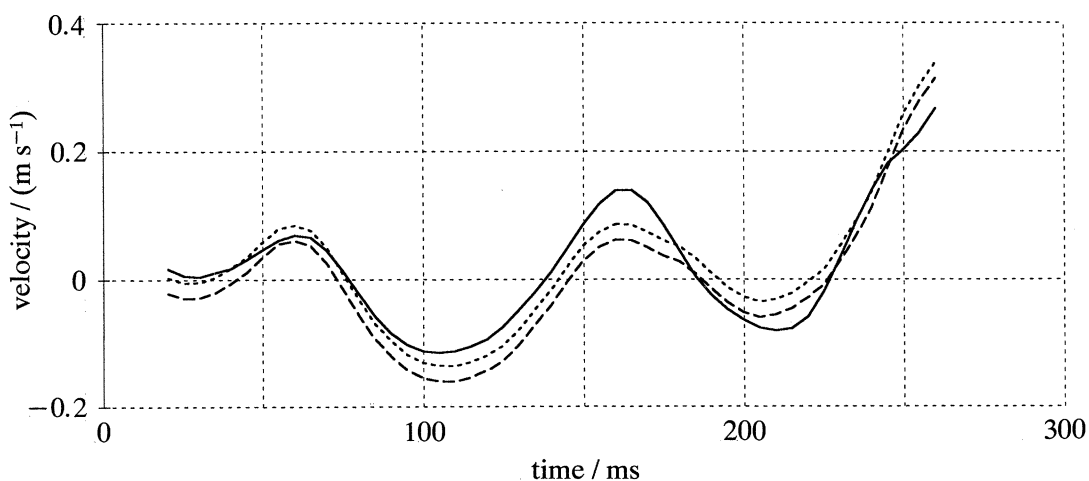


Figure 8. Showing the relationship, over time, between: $0.87\dot{y}_0$, solid line; $U\alpha$, dashed line; and $U\alpha + 0.025$, dotted line.

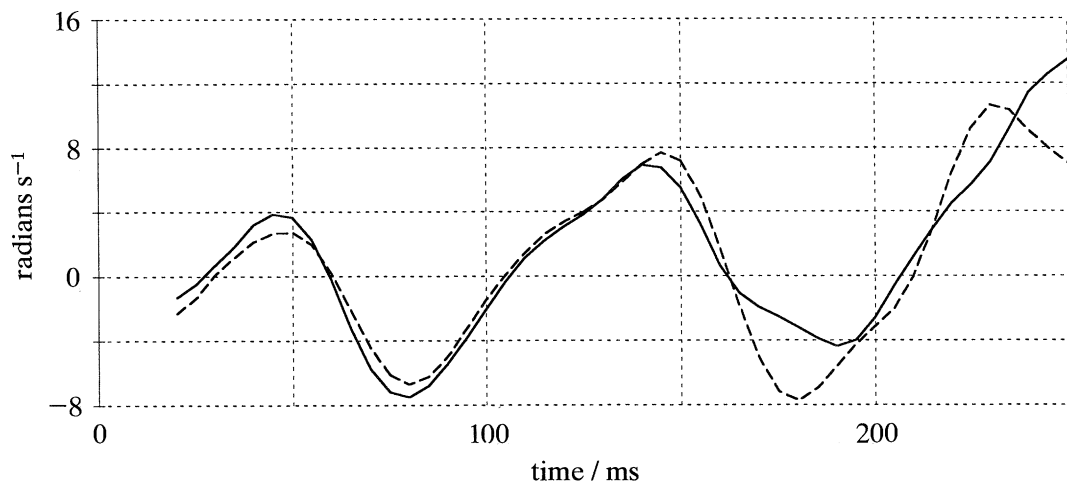


Figure 9. Showing the relationship over time between Ω (solid line) and $0.87A/U$ (dashed line).

hold the effective pressures between the lateral recesses (Lighthill's $[\Delta p]_{\text{eff}}$) close to zero over the usual working range of movements.

(b) *Cod (Gadus morhua)*

For the cod, we were able to draw on the very careful measurements made by Videler & Wardle (1978) from the high-speed cine-recordings shown on their figure 3. They give the amplitudes of tracks of seven points along the body of a cod. From measurements of these tracks, we deduced that the position P of minimum lateral displacement (i.e. that we take to be the position of pure side-slip) lay at a distance close to 11.5 cm from the snout for a fish that was 42 cm long. Here the amplitude of displacement from the mid line of displacements was 0.30 cm. At the snout, where we expect the displacements to be a combination of side-slip and yaw, the amplitude of displacement

was 0.75 cm. The displacements were clearly approximately sinusoidal, with a frequency close to 3 Hz. The phase advance of displacements at S before those at P we estimate to be about 65° (the mean of three estimates of 71° , 81° and 42° at different times during the period shown on the figure). Now if the yaw component had been phase advanced by 90° on the side-slip component, then the predicted phase advance of the displacements at S over those at P would be \cos^{-1} of the ratio of maximum amplitudes of displacements at P and S, i.e. $\cos^{-1}(0.3/0.75)$, which is 66° . This is in good agreement with the value measured. This leads to an amplitude of displacement for yaw of 0.69 cm.

From the amplitude of displacement at P, i.e. 0.30 cm, multiplied by 2π times the frequency, we have \dot{y}_0 the maximum side-slip velocity = 5.7 cm s^{-1} , so $0.87\dot{y}_0 = 5.0 \text{ cm s}^{-1}$. The maximum value for α is 0.69 cm divided by the distance PS of 11 cm, i.e. 0.06

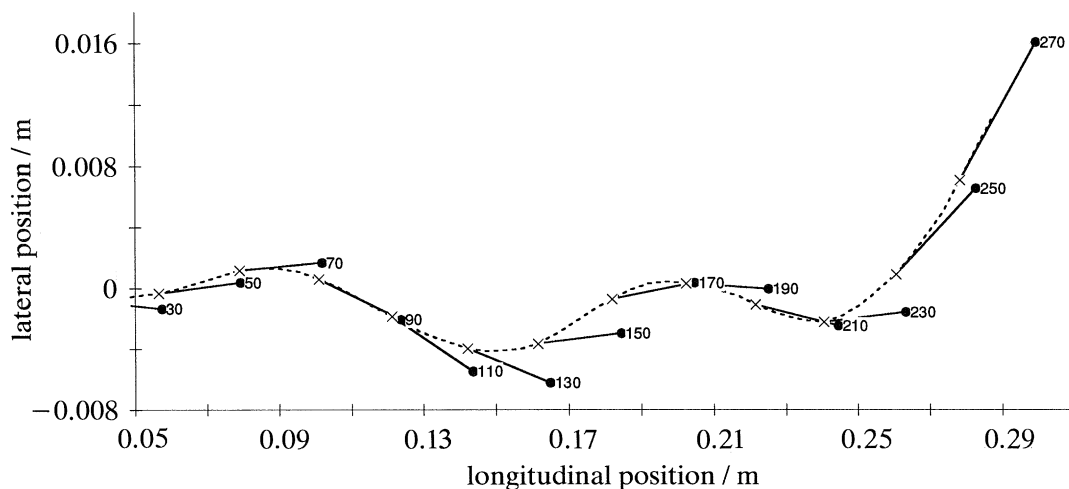


Figure 10. The dashed curve shows the motion of the point P the pivoting position on the fish, at 16% of the length of the fish from the snout. The straight lines represent the direction in which the fish was pointing at 20 ms intervals, with the circles indicating the position of the snout S, and the crosses indicating the position of the pivoting point P. Lateral distances have been exaggerated by a factor of approximately 5.

Table 1. *Some data for continuously swimming fish*
(The numbers given for $U\alpha$ and \dot{y}_0 are maximal values.)

| fish | Length (L) (cm) | SP (as % of L) | U (cm s ⁻¹) | α (radians) | $U\alpha$ (cm s ⁻¹) | \dot{y}_0 (cm s ⁻¹) | $U\alpha/0.87\dot{y}_0$ |
|----------------------|------------------------|----------------------|------------------------------|-----------------------|------------------------------------|--------------------------------------|-------------------------|
| herring ^a | 14 | 16 | 100 | 0.11 | 11.6 | 13.0 | 1.10 |
| cod | 42 | 26 | 91 | 0.06 | 5.4 | 5.7 | 1.08 |
| bream | 19 | 21 | 45 | 0.14 | 6.2 | 7.3 | 0.98 |
| goldfish | 16 | 31 | 46 | 0.13 | 6.0 | 9.5 | 0.72 |
| dace | 25 | 28 | 42 | 0.03 | 1.3 | 7.6 | 0.20 |

^a Values for time around 100 ms on abscissa of figure 8 and for curve with offset of 0.025 added.

radians. U is given as 91 cm s⁻¹, so $U\alpha$ is about 5.4 cm s⁻¹. The agreement between $0.87\dot{y}_0$ and $U\alpha$ and the fact that yaw displacements are approximately 90° phase advanced on side-slip displacements is what the hypothesis predicts.

(c) *Bream (Abramis brama)*

From data given by Bainbridge (1963) on his figure 13, we can make similar calculations to those made above for the cod. We arrive at the following values: $L=19.0$ cm; $U=45$ cm s⁻¹; $PS=4.0$ cm; maximum displacement at snout=0.61 cm; and maximum displacement at P (the pivoting position, taken as the position of least lateral displacements) is 0.26 cm.

From these values we deduce that $U\alpha=6.2$ cm s⁻¹. The value for \dot{y}_0 is about 7.3 cm s⁻¹ and $0.87\dot{y}_0=6.4$ cm s⁻¹. We have a less good estimate for the phase advance between the displacements at S and P than we had for the herring and cod, but it cannot be far from 90°, so again we find for continuous steady swimming a good agreement between the predictions of the hypothesis and experiment.

(d) *Goldfish (Carassius auratus) and dace (Leusiscus leusiscus)*

From data given by Bainbridge, similar calculations to those made above for bream were made. For these two species, the agreements between $0.87\dot{y}_0$ and $U\alpha$ were not close (see table 1).

4. SOME GENERAL CONSIDERATIONS

The results given above and in table 1 on the herring strongly support the hypothesis which Lighthill has made on the way in which clupeid fish might 'turn' their heads so as to swim more economically and remain sensitive to external stimuli. The results on the cod and the bream suggest that the same mechanism may exist in other fish. It is true that the anatomy of the lateral line system of the clupeid seems to be particularly well adapted for 'measuring' the effective pressure across the head, but it may well be that other fish have channels across the head between the left and right lateral line systems. It would certainly be worth looking for such channels. Even in their absence, the very common arrangement of the lateral

lines on the head, with major canals oriented in a dorso-ventral direction behind the eye, is admirably suited to detect cross-head flows at a position close to that at which the head will pivot—the sensory information that they give helping the fish to swim economically and quietly. This may indeed be a function of lateral lines in other fishes, although Dijksgraaf (1989) has argued against the lateral line being used by a fish to regulate its own locomotions. He draws a sharp distinction between water displacements produced by the fish's own muscle actions, which the animal knows when to 'expect', and those arising from forces unknown to the fish: reactions to the first kind being usually suppressed, either through efferent nerve impulses or centrally.

It is evidently of interest to consider the stimulus given by the swimming movements to the otolith organs which in the herring, as in all fish, act as a system of extremely sensitive accelerometers (see, for example, Sand & Enger 1973; Sand & Hawkins 1973; Chapman & Sand 1974; Karlsen 1992a,b). Professor J. H. S. Blaxter has kindly given us permission to reproduce some unpublished results of X-Ray measurements that he has made on the position of the saccular otoliths of herring from the same school as those used in our experiments. These results are given in table 2. They show that the otoliths lie very close to the pivoting points around which the head turns. However, although they are placed where they will be least stimulated by the lateral movements of a fish that is swimming steadily, the minima are not very sharp. Thus, for the lateral excursions of the head shown in figure 6, the minimum displacements (i.e. those at points lying around 16%–18% of the body length from the tip of the snout) are still about two-thirds of those found at the tip of the snout. If there is one sensory feedback system regulating the swimming movements of the herring it therefore seems that the receptors involved are more likely to be those of the lateral-line neuromasts. However, it is certainly possible that the otolith organs, together with the semi-circular canals, play a role. They could well provide an alternative, complementary, or auxiliary source of useful information for the regulation of swimming movements. They are placed where they could measure pure side-slip accelerations, while the semi-circular canals 'measure' yaw. The side-slip accelerations could by integration give velocities. Karlsen

Table 2. *Position of saccular otolith of herring along the length of the fish, measured by Professor J. H. S. Blaxter*

| total length of fish (L) / cm | distance from snout to midpoint of sagitta (d) / cm | d/L as a percentage |
|-----------------------------------|---|-----------------------|
| 15.0 | 2.6 | 17.3 |
| 18.7 | 3.2 | 17.1 |
| 15.0 | 2.6 | 17.3 |
| 15.6 | 2.8 | 17.9 |
| 16.6 | 2.9 | 17.5 |

(1992*b*) has shown that the otolith organs are in some fish very sensitive to very low frequencies (less than 0.1 Hz in the plaice) and he suggests that they might be useful in inertial navigation. There can, however be no doubt that the otolith organs are placed where the masking of signals from external sources of vibration by self-generated stimuli will be least troublesome. In unpublished experiments, we have shown that this advantage is very much greater for more vigorous movements, e.g. making sharp turns.

We may note that the peak pressure that would exist across the head of the herring when swimming like the herring to which table 1 relates would, if there had been no yaw component, have been about 200 Pa. For the tail-beat frequency which was about 10 Hz, Denton and Gray give the pressure which would saturate the neuromasts of the lateral line close to the lateral recess as 10 Pa. If the tail beat frequency had been 3 Hz, the corresponding figures would be about 10 and 18 Pa. We therefore see how necessary the balancing effects of the yawing motions are if these neuromasts are to be useful.

Denton and Gray have drawn attention to the relative ineffectiveness of pressure fields arising from external sources of vibration in stimulating these neuromasts. This is because these fields will, with respect to lateral y_0 accelerations, accelerate the water around the fish's head in much the same way as the head itself. However, if the disturbance is fairly local, with components whose dimensions are appreciably less than the length of the fish (e.g. in the wake of a fish in a school of fish) it could have an appreciable effect by changing the angle α . Indeed, one of the merits of the mechanism we discuss in this paper for fish living in streams may well lie in the sensitivity of the system to changes in α . For a fish swimming into a region in which α is varying, the stimulus given to the system we are discussing will be proportional to the fish's forward velocity, U . Thus the stimulus given by the change in α will rise approximately in proportion to the background stimulation likely to arise from the fish's own activity.

We are very grateful to Professor J. H. S. Blaxter, Professor A. D. Hawkins and Sir James Lighthill F.R.S. for advice and help. One of us (E.J.D.) is an Honorary Fellow of the Marine Biological Association of the U.K. and received a generous grant from the National Environmental Research Council. The work would not have been possible without the splendid facilities of the Dunstaffnage Marine Laboratory and we warmly thank its Director and staff.

REFERENCES

- Bainbridge, R. 1963 Caudal fin and body movement in the propulsion of some fish. *J. exp. Biol.* **40**, 23–56.
- Chapman, C.J. & Sand, O. 1974 Field studies of hearing in two species of flatfish *Pleuronectes platessa* (L.) and *Limanda limanda* (L.) (Family Pleuronectidae). *Comp. Biochem. Physiol.* **47A**, 371–385.
- Denton, E.J. & Gray, J.A.B. 1993 Stimulation of the acoustico-lateralis of clupeid fish by external sources and their own movements. *Phil. Trans. R. Soc. Lond. B* **341**, 113–127. (This volume.)
- Dijkgraaf, A.S. 1989 A short personal view of the history of lateral line research. In *The mechanosensory lateral line: neurobiology and evolution* (ed. S. Coombs *et al.*), pp. 7–16. New York: Springer Verlag.
- Karlsen, H.E. 1992*a* The inner ear is responsible for detection of infrasound in the perch (*Perca fluviatilis*). *J. exp. Biol.* **171**, 163–172.
- Karlsen, H.E. 1992*b* Infrasound sensitivity in the plaice (*Pleuronectes platessa*). *J. exp. Biol.* **171**, 173–187.
- Lighthill, J. 1993 Estimates of pressure differences across the head of a swimming clupeid fish. *Phil. Trans. R. Soc. Lond. B* **341**, 129–140. (Preceding paper.)
- Sand, O. & Enger, P.S. 1973 Functioning of the swimbladder in fish hearing. In *Basic mechanisms in hearing* (ed. A. R. Møller), pp. 893–910. New York: Academic Press.
- Sand, O. & Hawkins, A.D. 1973 Acoustic properties of the cod swimbladder. *J. exp. Biol.* **58**, 797–820.
- Savitsky, A. & Golay, M.J.E. 1964 Smoothing and differentiation of data by simplified least squares procedures. *Analyt. Chem.* **36**, 1627–1639.
- Videler, J.J. & Wardle, C.S. 1978 New kinematic data from high speed cine film recording of swimming cod (*Gadus morhua*). *Netherl. J. Zool.* **28**, 465–84.

Received 17 September 1992; revised and accepted 26 February 1993