Drag force acting on a neuromast in the fish lateral line trunk canal. I. Numerical modelling of external–internal flow coupling

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Fishes use a complex, multi-branched, mechanoreceptive organ called the lateral line to detect the motion of water in their immediate surroundings. This study is concerned with a subset of that organ referred to as the lateral line trunk canal (LLTC). The LLTC consists of a long tube no more than a few millimetres in diameter embedded immediately under the skin of the fish on each side of its body. In most fishes, pore-like openings are regularly distributed along the LLTC, and a minute sensor enveloped in a gelatinous cupula, referred to as a neuromast, is located between each pair of pores. Drag forces resulting from fluid motions induced inside the LLTC by pressure fluctuations in the external flow stimulate the neuromasts. This study, Part I of a two-part sequence, investigates the motion-sensing characteristics of the LLTC and how it may be used by fishes to detect wakes. To this end, an idealized geometrical/dynamical situation is examined that retains the essential problem physics. A two-level numerical model is developed that couples the vortical flow outside the LLTC to the flow stimulating the neuromasts within it. First, using a Navier–Stokes solver, we calculate the unsteady flow past an elongated rectangular prism and a fish downstream of it, with both objects moving at the same speed. By construction, the prism generates a clean, periodic vortex street in its wake. Then, also using the Navier–Stokes solver, the pressure field associated with this external flow is used to calculate the unsteady flow inside the LLTC of the fish, which creates the drag forces acting on the neuromast cupula. Although idealized, this external–internal coupled flow model allows an investigation of the filtering properties and performance characteristics of the LLTC for a range of frequencies of biological interest. The results obtained here and in Part II show that the LLTC acts as a low-pass filter, preferentially damping high-frequency pressure gradient oscillations, and hence high-frequency accelerations, associated with the external flow.

Keywords: fish lateral line; wake vortices; mathematical modelling

1. INTRODUCTION

1.1. Problem of interest and prior work

Fishes can detect water motions in their immediate surroundings through minute sensors referred to as neuromasts. A neuromast consists of a number of directionally sensitive hair cells enveloped by a protective gelatinous cupula, the unit being highly sensitive to extremely small displacements. The neuromasts may be located superficially all over the fish skin (superficial neuromasts) or just under the skin in interconnected fluid-filled canals distributed over the head and along the length of the body of the animal (canal neuromasts). Electrophysiological measurements of the neural responses of these two types of neuromasts in trout show that superficial neuromasts respond to changes in external flow velocity, while canal neuromasts respond

to changes in external flow acceleration (associated with corresponding changes in external flow pressure) around the fish (Kroese *et al.* 1978; Kroese & Schellart 1992). Electrophysiological measurements taken from the anterior lateral line nerve of the goldfish *Carassius auratus* show the capability of this fish to detect low-frequency vortices shed by a cylinder upstream of the fish (Chagnaud *et al.* 2007).

This study is concerned with the neuromasts embedded in the lateral line trunk canal (LLTC), a long tube-like organ on either side of the fish (figure 1), often with secondary canals linked to it. The LLTC is itself embedded just under the skin of the fish and has pore-like openings periodically distributed along its length. Each neuromast inside the LLTC is contained between a pair of pores. Disturbances in the external flow near to the fish (due to other fishes, prey and predators, vegetation or a variety of other underwater objects) produce pressure variations along the LLTC that act on the pore openings and induce motion of the fluid inside the canal. Drag forces created by the

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Figure 1. Schematics of a typical LLTC on the side of a fish and of the motion-sensing neuromast between a pair of pores inside the canal.

moving fluid in the canal act upon the neuromast cupulae,¹ which, even though displaced only by a few tens to hundreds of nanometres, is sufficient to generate graded potentials from the hair cells (sensory neurons) embedded in them. The information so generated is transmitted to the animal's brain to inform on the external fluid motion. Of special interest is the animal's ability to distinguish meaningful external signals in the presence of background noise and/or fluid motions induced by its own body motions. The LLTC has recently inspired the design and fabrication of arrays of artificial motion sensors embodying some of its principles (Fan *et al.* 2002).

The LLTC has been extensively investigated by many biologists (see Bleckmann 1993, 1994; Coombs & Montgomery 1999; van Netten 2006; Chagnaud *et al.* 2008 and numerous references therein). Fishes use this organ to detect other fishes (conspecifics, prey and predators), to swim in schools and to sense the presence of other underwater objects, in all cases via changes induced in the flow fields around their bodies and often in the presence of background noise. For instance, the piscivorous catfish is able to track wakes up to 10 s old and over distances up to 55 prey body lengths with its lateral line alone (Pohlmann *et al.* 2001, 2004). Several hydrodynamic models have been developed to describe the flow inside the LLTC and its performance characteristics, notably by Denton & Gray (1983, 1988, 1989) and van Netten (2006). In the study by van Netten (2006), the viscous forces acting on a neuromast are estimated by approximating the neuromast as a sphere exposed to a low-Reynolds-number Stokes flow (Stokes 1851). The model results obtained by van Netten (2006) have been compared with corresponding experimental observations of neuromast displacements measured via a laser interferometry technique. In the experiments, a vibrating sphere

located very near an opening in the LLTC was used to induce the flow dragging on a neuromast. The combined experimental and model results in van Netten (2006) show that the neuromast cupula responds to the flow in the canal at low frequencies, and then has an enhanced response at the resonance frequency of 120 Hz for the case of the ruffe. At this resonance frequency, the canal acts as a low-pass filter, reducing the velocity of the flow past the cupula. The combined properties of the canal and the enhanced response of the cupula at resonance give canal neuromasts the characteristics of a flat low-pass filter with a larger flat frequency response range than is simply explained by the low-pass filtering of the canal (see fig. 7 in van Netten 2006). As a consequence, it appears that there is little, if any, suppression of low-frequency information, the high-frequency information being what is mainly filtered out by the combined system. These observations are supported by the numerical results of the present study, and the analytical and numerical results presented in Part II (Humphrey 2009).

1.2. Objectives of this study

To our knowledge, no physical–mathematical model has yet been developed to calculate the flow inside the LLTC for the case of a fish sensing a wake. This is undoubtedly due to the complexity of the problem. Many previous investigations have used a vibrating sphere (modelled as a dipole) as an external flow stimulus, keeping the sphere oscillation amplitude constant while varying its oscillation frequency and other parameters such as the distance between the sphere and the fish skin and the angle between the axis of vibration of the sphere and the fish skin. In the case of the flow induced by a dipole of constant oscillation amplitude, the amplitude of the resulting pressure gradient increases with increasing dipole oscillation frequency with two possible consequences: (i) this condition may not be representative of the biological flows arising in nature, and (ii) an experiment

¹The drag force of interest acts on the neuromast cupula, that part of the neuromast exposed to the pressure and shear forces induced by the flow past it. In this work, we simply refer to the 'neuromast', having removed any ambiguity concerning where the drag force is applied.

conducted in this way will, most probably, generate results that are biased towards high oscillation frequencies. As explained below, in this study, we seek to investigate the response of the LLTC of a fish to pressure variations induced by a more natural stimulus, due to the vortex street in a wake flow.

The present study is strongly motivated by the experimental investigation of Chagnaud *et al.* (2007) who pointed out that the natural stimuli of the lateral line of river fishes include: (i) vortex motions in the wakes of inanimate objects, which, for example, trout can use for station holding, and (ii) vortex motions in the wakes of undulatory swimming fishes, which some piscivorous fishes can detect and follow. Anaesthetized goldfish (*C. auratus*) were held in a stationary position in a water flume with their heads facing the approaching flow. A cylinder placed upstream of a fish was used to generate a Kármán vortex street of known average frequency. In the experiments, cylinder diameter and cylinder location with respect to the fish, and water flow speed, were varied. For sets of such conditions, electrophysiological recordings were made of single unit activity from anterior lateral line nerve fibres of the fish. The frequencies obtained from spike train power spectra showed reproducible peaks at the cylinder vortex-shedding frequencies (less than 2 Hz). The authors pointed out that by using the information coming from several hundred primary lateral line afferent fibres, the fish may be able to detect and determine vortex-shedding frequency from the passage of just a few vortices.

To render this type of wake-sensing problem theoretically tractable and numerically predictable, it is convenient, and to a large extent necessary, to make certain simplifications while retaining the essential physics. To this end, we first idealize the flow configuration by considering a fish coasting behind an elongated prism-like object, both moving at the same speed. (This is precisely the case investigated by Chagnaud *et al.* (2007) using a cylindrically shaped prism, wherein both the fish and the cylinder are stationary relative to the flow going past them in a water tank.) The leading edge of the elongated prism of this study is streamlined and the trailing edge is rectangular with two well-defined right angle corners. By construction, for the flow Reynolds numbers of interest, the vortices shed from the trailing edge of an elongated prism are very clean and periodic. This is because: (i) the two downstream corners of an elongated rectangular prism fix the locations of vortex shedding, and (ii) the streamlined nature of the leading edge suppresses vortex shedding at that location, thus suppressing any possible cross-talk between the flows at the leading and trailing edges. In the case of a circular cylinder at Reynolds numbers greater than 80 (based on the cylinder diameter and the speed of the approaching flow), the vortex street shed by the cylinder induces the vortices forming on either side of it to break off alternately (Kundu & Cohen 2004). The same mechanism applies to a streamlined prism with end corners, but, because in the case of the circular cylinder the vortex-shedding locations are not defined by such sharp geometrical discontinuities, the vortex flow separation points jitter around average locations on

either side of the cylinder. Jitter increases with increasing flow Reynolds number and contributes to the early two-dimensional to three-dimensional breakdown and turbulent-like nature of the flow in the wake of the cylinder. In this regard, the Reynolds number of the cylinder generating the wake flow of Chagnaud *et al.* (2007) was 2540, approximately, for a 2.5 cm diameter cylinder in water moving past it at 0.1 m s^{-1} . Inspection of their fig. 2 for these conditions shows that the flow in the wake of the cylinder contained a wide range of energetic frequencies in addition to that associated with the purely two-dimensional Kármán vortex street. That rectangular prisms with streamlined leading edges generate well-defined, clean, wake flows of a highly two-dimensional nature has been well established in the literature (e.g. Okajima *et al.* 1992; Hourigan *et al.* 2001). Also, because, in the present study, the fish coasts behind the prism there are no body motions to deal with and, therefore, the periodically oscillating pressure signals arriving at the surface of the fish are due solely to the prism wake. Although the vortices that are alternately shed from the downstream corners of a rectangular prism (or from a cylinder) rotate counter to those in the wake of a fish swimming by undulating its body and caudal fin, the resulting spatial and temporal characteristics of the induced pressure oscillations in the prism wake (and arriving at the fish surface) are quite similar. Thus, for the purposes of this investigation, the much simpler model presented for analysis is an especially useful surrogate.

Second, we recognize that the disparity in length scales between the flows external and internal to the LLTC would require such refined grids and small time steps to calculate them simultaneously as to render the exercise impracticable with the computational resources available. The problem is overcome by recognizing that the two flow fields are one-way coupled, meaning that the flow external to the fish drives the flow internal to the LLTC, with no feedback from the internal flow to the external flow that would alter the external flow. Therefore, using a Navier–Stokes solver, we first calculate the unsteady two-dimensional flow past the prism–fish pair. The pressure field associated with this flow is then used as the boundary condition to calculate the flow inside the LLTC, with the neuromasts present, using the same Navier–Stokes solver. Finally, the flow in the LLTC is used to calculate the drag forces acting on the neuromasts. This numerical calculation approach allows an in-depth study of the hydrodynamic performance characteristics of the LLTC. Note that while for a coasting fish the unsteady external flow over the LLTC is well approximated as being two-dimensional, owing to the presence of the neuromasts in the LLTC, the flow inside it is three-dimensional as well as unsteady.

While physically rigorous and accurate, the numerical approach used in this study is tedious, as well as inefficient, since it does not readily reveal the parameter dependencies of the drag force. In Part II of this work, we present an analytically based physical–mathematical model for rapidly calculating the drag force acting on a neuromast cupula, and it is found that the analytical model results are in good agreement with the Navier–Stokes based solutions of the present study.

2. CALCULATION OF THE TWO-DIMENSIONAL FLOW AROUND A PRISM–FISH PAIR

The flow fields created by swimming fishes have been the subject of previous research (e.g. [McCutchen 1977](#); [Blickhan et al. 1990, 1992](#); [Bleckmann et al. 1991](#); [Müller et al. 2000](#)). The complex structure of the wake of a swimming fish contains information concerning the speed, direction and size of the animal ([Bleckmann et al. 1991](#); [Hanke et al. 2000](#)). Such information is of considerable value to a piscivorous fish, which may even be able to estimate the age of a prey's wake ([Hanke et al. 2000](#)). By contrast, very little is known about the pressure and velocity distributions inside the fish LLTC. The strategy pursued in this study is to numerically generate simplified yet physically realistic unsteady two-dimensional external flows representative of a fish coasting in the wake of a vortex-shedding object moving at the same speed, and to use this information to calculate the unsteady three-dimensional flows and associated drag forces acting on the neuromasts inside the LLTC of the fish. Aside from its computational convenience, the simplified external flow retains all the essential physics of the problem of interest, and the two-dimensional assumption is partly justified by the fact that the diameter of the LLTC is much smaller than the height or length of a fish.

2.1. Numerical approach

The numerical calculations presented here were performed with the computer code flow and heat transfer solver (FAHTSO). FAHTSO is a custom written Navier–Stokes solver, which has been extensively tested and applied to a number of complex flows by, among others, [Rosales et al. \(2000, 2001\)](#), [Barbier \(2006\)](#) and [Humphrey et al. \(2008\)](#). The code solves discretized forms of the momentum and energy equations for three-dimensional, unsteady, constant property flows using an adaptation of the SIMPLE algorithm described by [Patankar \(1980\)](#). Finite-difference equations for velocity components and scalar quantities are derived using a staggered grid, control-volume formulation. A third-order quadratic upwind interpolation scheme is used to represent the convection terms and a central differencing scheme to represent the diffusion terms. The use of these two schemes ensures local second-order calculation accuracy for both high and low Reynolds number flows. A fully implicit, second-order, three-level time algorithm is incorporated. Full details concerning the code are provided in [Rosales et al. \(2000, 2001\)](#).

The differential forms of the mass and momentum conservation equations in vector notation for a constant property fluid are

$$\nabla \cdot \mathbf{U} = 0, \quad (2.1a)$$

$$\frac{\partial \mathbf{U}}{\partial t} + \mathbf{U} \cdot \nabla \mathbf{U} = -\frac{1}{\rho} \nabla P + \nu \nabla^2 \mathbf{U}, \quad (2.1b)$$

where ρ and ν are, respectively, the density and kinematic viscosity of water; $\mathbf{U}$ is the vector velocity; P is the modified pressure; and t is the time. Subject to appropriately specified boundary conditions discussed below, the numerical procedure solves these equations

Figure 2. Plan view profiles (shown to scale) for the elongated (a) prism and (b) the pikeperch used in the external flow calculations. For reference, the length and thickness of the prism are 5 and 0.6 cm, and the length and maximum thickness of the fish are 20 and 2.5 cm, respectively.

in component form in terms of the primitive variables velocity and pressure.

As explained above, we are concerned here with modelling the unsteady two-dimensional flow generated by an elongated prism and a coasting fish behind it moving at the same speed. Plan outline profiles for these two objects are shown to scale in [figure 2](#). The one for the fish, corresponding to the pikeperch (*Sander lucioperca*), was provided by H. Bleckmann (2006, personal communication). The LLTC of the fish is aligned along the length of its body and its diameter is taken to be 250 μm , in keeping with fish of this size. Invoking Galilean invariance, rather than calculate water motions generated by a prism–fish pair moving through water, we calculate the motions of water past a stationary prism–fish pair with respect to a coordinate system fixed to them. Characteristic values of the Reynolds numbers based on the approaching flow velocity and the widths of the prism and of the fish are 180 and 760, respectively. These relatively low values allow a direct numerical simulation calculation approach.

Owing to the highly streamlined shapes of the two bodies, and owing to the highly refined grid made possible by the two-dimensional flow assumption in this study, we have chosen to approximate the curved surfaces defining the fish on a Cartesian grid as opposed to using curvilinear or body-fitted coordinates ([figure 2](#)). The calculation domain and its relative dimensions are shown in [figure 3](#). A non-uniform grid consisting of 228×202 (x, y) nodes, especially refined near the surfaces defining the prism and the fish, was used with a time step $\Delta t = 0.25 \times 10^{-3}$ s. A grid independence investigation justifying these values is provided in appendix A. The boundary conditions used for the calculations are shown in [figure 3](#) and were (i) uniform, constant velocity $U = 0.03 \text{ m s}^{-1}$ at the inlet plane, (ii) non-reflective wave boundary condition ('wave BC') at the exit plane ([Li & Humphrey 1995](#)), (iii) top and bottom surfaces of the domain treated as symmetry planes, and (iv) impermeable, no-slip velocity conditions on the prism and fish surfaces. The profile outlines of the two bodies are approximated on a highly refined Cartesian grid by blocking off the grid cells corresponding to the bodies. In this way, the surface contours of the fish and of the leading edge of the prism are represented in a stair-step fashion. It has previously been shown that this method efficiently calculates the flow around complex bodies ([Najjar & Mittal 2003](#)).

2.2. Results and discussion

Calculations of the external two-dimensional flow were performed until it converged to a steady–periodic state. Contours of instantaneous vorticity, provided in

Figure 4. Field values of (a) instantaneous vorticity, Ω_z (s^{-1}), and (b) pressure, $P_{\text{inst}} - P_{\text{mean}}$ (Pa), for the two-dimensional external flow past a prism–fish pair. Positive (anticlockwise) vortices are shed from the bottom of the prism, while negative (clockwise) vortices are shed from the top. The mean pressure field is subtracted from the instantaneous one to show the pressure wave clearly.

Figure 5. Comparison between two-dimensional numerical (solid curves) and wave model (triangles) calculations of the relative pressure $P - P_{\infty}$ (Pa) for three consecutive pores ($n-1$, n and $n+1$) located approximately one-quarter of the way along the length of the side surface of the fish starting from the nose.

typically approximately the diameter of the LLTC. As shown in figure 6, two finite segments of the LLTC are modelled, which consist of three and five consecutive pores, respectively. The same pressure wave is applied to both segments to reveal possible differences arising from the different number of pore openings (figure 6). Non-uniform grids consisting of 666×52 and 998×52 (x, y) nodes are used, with 28 (x) nodes defining each pore opening and 16×30 (x, y) nodes defining each neuromast. As above, the FAHTSO code was used to solve the Navier–Stokes equations. Impermeable, no-slip boundary conditions are imposed at the ends of each segment and at all inner surfaces. (The goodness of the segment end boundary conditions is discussed

further below.) The dimensions specified for the calculations are as follows: canal diameter, $250 \mu\text{m}$; pore opening, $250 \mu\text{m}$; length between consecutive pores, 4 mm ; neuromast height, $150 \mu\text{m}$; neuromast width, $150 \mu\text{m}$. For simplicity, the neuromasts between pores are represented by rectangles instead of semicircles and, owing to the very small value of the Reynolds number of the flow inside the LLTC, this should have little if any serious consequence on the accuracy of the results obtained. Because any deformations or translations of the neuromasts due to the drag forces acting on them are extremely small (nanometre range), their effects on the local flow can be neglected.

3.2. Results and discussion

Figure 7 shows contours of the instantaneous velocity magnitude inside the segments of the LLTC with three and five pores, respectively. For the conditions plotted, a net background positive pressure gradient is established between pores that, on average, drives the bulk of the flow inside the LLTC from right to left. Close inspection of the streamlines in the vicinity of the centre pore, also shown in figure 7, reveals a weak flow entering and leaving the centre pore. The flow in the segment accelerates right over the neuromasts, attaining a local velocity up to $35 \mu\text{m s}^{-1}$, approximately. Figure 8 shows two pressure profiles inside the LLTC plotted along the y -coordinate (normal to the LLTC) at locations ‘a’ and ‘b’ in the vicinity of the central pore. The profiles show that pressure does not vary with the transverse y -coordinate, and this finding is used to simplify the three-dimensional LLTC flow calculations. The results presented in figure 8 strongly suggest that, to calculate the flow inside the LLTC, it is only necessary to specify the external pressure at the pore locations, and that the value of pressure along the y -coordinate direction inside the LLTC at a pore location is essentially the external pressure at the pore. The combined pressure and viscous drag forces on neuromasts N_2 and N_3 for the segment calculations with three and five pores are shown in figure 9. No differences are observed for the N_2 neuromast and those observed for N_3 are less than 1 per cent. This insensitivity to the end segment locations confirms the goodness of the boundary conditions imposed there. Since the wavelength (approx. 31.4 mm) of the pressure wave is approximately eight times larger than the distance between two consecutive pores (4 mm), the drag force on a neuromast depends primarily on the pressure differences between the pores in its vicinity. As shown in figure 10, it is clear that the neuromast drag force time records contain the necessary information from which to determine the frequency and wavelength of the external pressure wave.

4. CALCULATION OF THE THREE-DIMENSIONAL FLOW INSIDE THE LLTC

4.1. Method and numerical approach

The unsteady three-dimensional pressure-driven flow between a pair of planes passing through a pair of

Figure 6. Geometrical layout for the numerical calculations inside a two-dimensional segment of the fish LLTC. Calculations were performed for (a) three pores and (b) five pores labelled L_i . The neuromasts, labelled N_i , are approximated as rectangles. Note that the drawing is not to scale as the $y : x$ ratio is actually 5.

Figure 7. (a) Contours of instantaneous velocity magnitude, V_{mag} (m s^{-1}), for a segment of the fish LLTC with three and five pores. (b) Detail of the two-dimensional grid and selected flow streamlines around pore L_3 for the case of five pores.

adjacent pores in a tube-shaped segment of the LLTC has also been calculated using a non-uniform Cartesian grid with $122 \times 54 \times 56$ (x, y, z) nodes, x being the coordinate direction along the length of the tube. As shown in appendix A, this level of grid refinement is found to be quite adequate for the purposes of this study. The use of a Cartesian grid as opposed to a cylindrical grid allows implementing larger calculation time steps because no special treatment is required to obtain the velocity at the tube centreline. A neuromast located between the pair of planes is approximated as a cube of dimensions $150 \mu\text{m} \times 150 \mu\text{m} \times 150 \mu\text{m}$. The cube is fixed to the bottom of the canal and is typically defined by $40 \times 35 \times 30$ (x, y, z) grid nodes. As for the two-dimensional canal case, because the Reynolds number of the three-dimensional flow inside the LLTC is very small ($Re=0.0035$), the sharp edges of the neuromast should have a minimal effect on the accuracy of the calculated flow. Therefore, the geometrical approximation should provide a good basis for estimating the combined pressure and viscous drag forces acting on a neuromast. Since the external flow remains the same, the wave model (equation (3.1)) used for the two-dimensional LLTC flow calculations is again used to specify the spatial and temporal variations of pressure at the planes delimiting the tube segment in the three-dimensional calculations.

Although the basic pressure oscillation frequency investigated, $f=0.7$ Hz, corresponds to the external flow generated by the prism-fish pair, we are also interested in the response of the LLTC flow to higher frequencies corresponding to other external flow conditions. This is for three reasons, which are as follows.

Figure 8. (a) Contours of instantaneous pressure (Pa) and (b) pressure profiles plotted as a function of y at two locations 'a' (red line) and 'b' (blue line) near pore L_3 .

(i) A predator fish pursuing a prey fish at a positive relative velocity with respect to it should perceive higher, Doppler-shifted frequencies associated with the vortices shed by the prey fish. (ii) The flow in the wake of a swimming fish is three-dimensional and multiscale and, therefore, contains higher frequencies associated with the pressure oscillations (Bleckmann *et al.* 1991; Bleckmann 1994; Hanke & Bleckmann 1999; Hanke *et al.* 2000; Brucker & Bleckmann 2007). (iii) The environment surrounding a fish may be noisy (turbulent) for a variety of reasons and, as a consequence, may contain higher frequency components also associated with pressure oscillations. Therefore, in order to better understand

Figure 9. Drag force per unit length ($\mu\text{N m}^{-1}$) acting on neuromasts (a) N_2 and (b) N_3 in a two-dimensional segment of the fish LLTC with three (solid curve) and five pores (dashed curve), respectively.

how a fish uses its LLTC as an external fluid motion-sensing organ, we investigate a biologically meaningful range of frequencies f extending from 0.7 to 200 Hz.

To this end, we first perform a calculation to determine the steady mean flow field inside the LLTC. This flow field corresponds to that which the neuromasts inside the LLTC of a coasting fish would sense in the absence of disturbances produced by an object in the water.² As a consequence, a fish can only perceive a wake if it can detect fluctuations about this mean background force. Then, using this mean flow field as an initial condition, we perform an unsteady flow calculation over several cycles to obtain the steady-periodic state. For the range of conditions examined, the flow was found to be quasi-steady after two to three oscillation cycles.

In addition to the neuromast discussed above for which results are presented here, Navier–Stokes-based calculations were performed for a second neuromast of base dimensions $50\text{ }\mu\text{m} \times 50\text{ }\mu\text{m}$ and height $100\text{ }\mu\text{m}$. These results are presented and discussed in Part II (Humphrey 2009) of this two-part study. In this regard, we note that canal neuromast sizes and shapes vary, depending on the fish species as well as the diameter and length of the LLTC. Generally, however, canal neuromasts tend to have length/width base aspect ratios of order 1, and rarely much larger than 2. The height/width ratio of a neuromast is more difficult to determine experimentally but can be expected to range between 1 and 10, approximately. These ratios follow from limited data provided to the authors by S. Coombs for *Trematopus bernacchii* and by H. Bleckmann for *C. auratus*, *Rhodeus sericeus* and *Gobio gobio* (2008, personal communications). In Part II of this two-part study, a detailed analysis is provided, showing the analytical dependence of the drag force acting on a canal neuromast on the neuromast size, the canal length and the flow oscillation frequency.

Figure 10. Drag force per unit length ($\mu\text{N m}^{-1}$) acting on neuromasts N_2 (red), N_3 (orange), N_4 (green) and N_5 (blue) in a two-dimensional segment of the fish LLTC with five pores.

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Figure 11 shows the total absolute value of the drag force acting on the neuromast investigated ($150\text{ }\mu\text{m} \times 150\text{ }\mu\text{m} \times 150\text{ }\mu\text{m}$) for various external flow pressure gradient oscillation frequencies. The data clearly show a decrease in the drag force amplitude with increasing pressure gradient oscillation frequency, and this correlates with a reduction in the mean velocity of the flow past the neuromast with increasing frequency (discussed below) shown in figure 12. Also noticeable is the shift of the drag force maxima towards larger dimensionless times with increasing frequency. The same variation with frequency, but corresponding to smaller magnitudes of the drag force and velocity, is observed for the smaller neuromast of dimensions $50\text{ }\mu\text{m} \times 50\text{ }\mu\text{m}$ (discussed in Part II).

The theoretical analysis provided in Part II based on limiting forms of eqn (15.87) in Schlichting (1968) shows that the shape and characteristic magnitude of the velocity profile of an oscillating pressure-driven laminar flow in a tube depends on the kinetic Reynolds number, $\omega_D^* = \omega(D/2)^2/\nu$, where D is the tube diameter; $\omega = 2\pi f$ is the oscillation angular frequency; $\nu = \mu/\rho$ is the fluid kinematic viscosity; and μ and ρ are the dynamic viscosity and density, respectively. The kinetic Reynolds number is a dimensionless frequency, and, as it increases, the parabolic shape of the velocity profile transforms into a flatter, plug-like shape.

²The hair cells in a neuromast respond to nanometre-scale displacements of the neuromast-cupula unit caused by the fluid drag forces acting upon the cupula. Because we do not model neuromast-cupula unit displacements in this work, we use the drag force itself as a surrogate measure of the effects of the flow on the unit.

Figure 11. Cyclic variation of the total absolute drag force acting on a neuromast for different flow oscillation frequencies for the three-dimensional model of the flow in the fish LLTC segment. Time is normalized by the oscillation period. Solid curves: blue, 0.7 Hz; cyan, 25 Hz; green, 75 Hz; orange, 125 Hz; red, 200 Hz. Dashed curves: blue, 5 Hz; cyan, 50 Hz; green, 100 Hz; orange, 150 Hz.

Figure 12. Cyclic variation of the average velocity (left ordinate) in the middle of the three-dimensional model of the fish LLTC segment with a neuromast present, and the pressure gradient (right ordinate) applied at the ends of the canal segment for different flow oscillation frequencies. Dashed curves: blue, 0.7 Hz; cyan, 25 Hz; green, 75 Hz; orange, 125 Hz. Solid curves: blue, 5 Hz; cyan, 50 Hz; green, 100 Hz; orange, 150 Hz; red, 200 Hz; black, dP/dx .

The analysis shows that for a relatively large range of canal and neuromast dimensions (including those of this study) at frequencies $f < 40$ Hz, approximately, the water flow in a tube-shaped canal is primarily viscous dominated, whereas, for $f > 40$ Hz, it is primarily inertia dominated. In the viscous-dominated regime, the velocity in the tube and hence the drag force acting on the neuromast are relatively independent of frequency. However, for frequencies larger than 40 Hz, both the velocity and the drag force decrease with increasing frequency. The same observations apply to the tube-shaped segment of the LLTC under consideration here. The decrease in the mean velocity past the neuromast with increasing frequency results in a

Figure 13. Definition of the phase shift, Φ , between the pressure gradient (dashed curve) applied at the ends of the LLTC segment and the drag force (solid curve) experienced by the neuromast. Data shown correspond to the case with $f = 125$ Hz.

corresponding decrease in the drag force acting on the neuromast. To show this, from numerical calculations of the flow field, we obtain the surface-average velocity, $\langle U \rangle$, past the neuromast at the segment mid-length ($x = 2$ mm) where the neuromast is located. This quantity is given by

$$\langle U \rangle = \frac{1}{S} \int_S |\mathbf{u}_x \cdot \mathbf{e}_x| dS, \quad (4.1)$$

where S is the tube cross-section surface available to the flow past the neuromast and $\mathbf{e}_x$ is the unit vector in the x -coordinate direction (along the length of the tube). Figure 12 shows that $\langle U \rangle$ varies over an oscillation cycle and that its maximum value decreases with increasing frequency. The theoretical analysis in Part II of this study supports this finding.

We call Φ the phase shift between the pressure gradient applied at the ends of the LLTC segment and the drag force experienced by the neuromast (figure 13). Values of Φ can be obtained relative to the viscous drag, the pressure drag and the total drag. This quantity is used for analysing the frequency filtering characteristics of the fish LLTC. Values of Φ as a function of the flow oscillation frequency are plotted in figure 14, where the drag forces are considered separately and combined. Also shown are the variations of the drag force (viscous, pressure and combined) amplitude with frequency. The behaviour exhibited by the drag force and the phase shift as a low-pass filter agrees with various physiological experiments (Kroese & Schellart 1992; van Netten 2006), as well as with the model of van Netten (2006). (However, it is important to keep in mind that the current model does not account for the additional filtering inherent to the neuromast/cupula unit itself.) These results show that for oscillation frequencies $f > 40$ Hz, approximately, the canal–neuromast system starts damping higher frequency contributions to the motion of fluid in the canal.

Figure 15 shows instantaneous profiles of the vector velocity at different longitudinal locations in the symmetry plane passing through both the LLTC tube

Figure 14. (a) Drag force amplitude and (b) the corresponding phase lag for the oscillating flow past a neuromast in the canal segment at different frequencies. Red, total drag; blue, viscous drag; green, pressure drag.

segment and the neuromast in it. The parabolic shape of the flow approaching the neuromast is quickly recovered downstream of it. The instantaneous pressure field in the same plane with selected streamlines is shown in figure 16a. The longitudinal variation in pressure at $y=200\text{ }\mu\text{m}$ from the bottom of the tube (dashed line) in the same plane is plotted in figure 16b. The pressure profile can be divided into three constant pressure gradient segments. Thus, the flow in the canal away from the neuromast is similar to a Poiseuille flow as observed in figure 15. This supports the fact that the pressure force represents approximately two-thirds of the total drag force acting on the neuromast.

In order to gain further insight into the external flow pressure gradient filtering characteristics of the LLTC, three-dimensional calculations of the LLTC flow were performed for a time-varying pressure gradient with white noise (WN) superimposed. This was done for a base flow with $f=5\text{ Hz}$ using the following prescription for pressure:

$$P(x, t) = 3.24x + 7.5 \times 10^{-4} \sin(2\pi ft - 250x) + \text{WN}, \quad (4.2a)$$

$$P(x=0, t) = 7.5 \times 10^{-4} \sin(2\pi ft) + \frac{6.48 \times 10^{-4}\alpha}{2}, \quad (4.2b)$$

$$P(x=L, t) = 0.01296 + 7.5 \times 10^{-4} \sin(2\pi ft - 1.0) - \frac{6.48 \times 10^{-4}\alpha}{2}, \quad (4.2c)$$

where α is a random number between -1 and 1 . For an interpore distance $L=4\text{ mm}$, the difference between equations (4.2b) and (4.2c) results in the following pressure gradient:

$$-\frac{dP}{dx}(t) = -3.24 + 0.1875 \times (\sin(2\pi ft) - \sin(2\pi ft - 1.0)) + 0.162\alpha. \quad (4.3)$$

In this way, random values ranging from -5 to $+5$ per cent of the total mean pressure gradient (-3.24 Pa m^{-1}) are added to the instantaneous quantity. Figure 17 shows the variation of the pressure gradient with time as well as the corresponding drag force acting on the neuromast. Two observations are noteworthy: (i) the amplitudes of the noise-induced components of the drag force are relatively small, being

Figure 15. Instantaneous velocity profiles for the flow around the neuromast in the vertical mid-plane of the fish LLTC at $t/T_{\text{per}}=5$ with $f=5\text{ Hz}$. Note that, in this case, the flow goes from right to left because the gradient of pressure applied at the extremities of the canal is positive.

± 3 per cent of the instantaneous mean value, and (ii) the time variation of the noise-contaminated drag force is much smoother than that of the noise-contaminated pressure gradient. The second finding is reflected in the spectra shown in figure 18. These data show that, for the conditions explored, the LLTC acts as a low-pass filter with respect to the external flow oscillating pressure gradient, a finding also obtained in Part II. These fluid mechanic results are in general agreement with corresponding physical and electrophysiological observations made by various biologists (see van Netten 2006 and numerous references therein).

5. CONCLUSIONS

This numerical investigation demonstrates the capability of the fish LLTC to filter out high values of pressure gradient oscillation frequencies arising from the flow external to the fish. Damping is primarily due to inertial effects inside the canal and, for the conditions of this study, becomes significant above 40 Hz , approximately. The same result is found in Part II of the two-part study. Because, ignoring viscous effects, $\partial U/\partial t \sim \partial P/\partial x$ in the external flow, damping of the high-frequency motion induced by $\partial P/\partial x$ inside the LLTC corresponds to a loss of information concerning this quantity or, equivalently, of the high-frequency accelerations of the external flow. This finding partly explains the capability of fish in noisy water environments to detect low-frequency pressure gradient oscillations associated with accelerations of the water medium due to the relative motions of other fishes, predators, prey and other underwater objects.

Figure 16. (a) Instantaneous pressure contours with selected streamlines superimposed for the flow around the neuromast in the vertical mid-plane of the fish LLTC. (b) Pressure profile at $y=200\ \mu\text{m}$ (dashed line in (a)) and $t/T_{\text{per}}=5$ with $f=5\ \text{Hz}$.

Figure 17. (a) Time variation of the pressure gradient applied along the fish LLTC segment with WN superimposed. (b) Time variation of the resulting absolute drag force acting on the neuromast.

To our knowledge, these are the first unsteady three-dimensional flow calculations using a full Navier–Stokes solver of the time-resolved drag forces acting on a simulated neuromast inside a fish LLTC. The one-way coupled external-to-internal flow calculation approach employed should be of special interest to biologists, since the method directly links the flow field external to a fish to the flow field internal to the LLTC where drag-induced stimulation of the neuromasts takes place. However, and in spite of its physical and numerical accuracy, because it is computationally intensive, the Navier–Stokes-based solution approach is not well suited for repeated calculations aimed at elucidating the parameter dependencies of the drag force acting on a neuromast in the LLTC. Such an effort has been undertaken in Part II, where (i) it is shown theoretically that the dimensionless drag force due to an oscillating

flow acting on a neuromast of characteristic length scale d in a tube segment of length L_t and diameter D depends on three dimensionless parameters (d/D , L_t/D and ω_D^*), and (ii) a fast and relatively accurate analytical model is provided for calculating this force.

The LLTC sensory organ is a remarkable example of an exquisitely sensitive and specific motion-sensing system, capable of inspiring the design of corresponding synthetic motion-sensing devices. In this regard, much work remains to be done to fully understand how fishes process the information received from numerous neuromasts inside the LLTC, by means of which they track prey, flee from predators, swim in schools and avoid obstacles.

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Figure 18. Power spectrum of the drag force acting on the neuromast in the presence of WN superimposed on a 5 Hz flow oscillation frequency.

Figure 19. The x -coordinate locations at which the mean and r.m.s. velocity profiles in figures 20 and 21 are plotted. The locations are shown to scale in the first two-thirds of the calculation domain.

defining the profile shape of the pikeperch used in the calculations. J.A.C.H. expresses his sincere appreciation to the University of Virginia for a one-year sabbatical leave, and to the University of Vienna for a most stimulating Guest Professorship in the Department of Neurobiology and Cognition Research, both of which allowed him the quality time needed to focus on this work. This study was performed under a DARPA BioSenSE Award via AFOSR grant no. FA9550-05-1-0459.

APPENDIX A. GRID INDEPENDENCE OF THE NUMERICAL CALCULATIONS

Grid independence studies were performed for the calculations of the two-dimensional flow around a prism–fish pair and of the three-dimensional flow inside the LLTC of the fish. While the two-dimensional flow inside the LLTC was calculated on a very refined grid, a grid independence study was not performed for this case because the results obtained were used only to guide the three-dimensional flow calculations in the LLTC.

A.1. Two-dimensional flow around a prism–fish pair

For guidance in setting the initial grid used for the external prism–fish flow, we have looked to the grid studies in Rosales *et al.* (2000, 2001), who calculated the

unsteady two-dimensional flow around a pair of rectangular prisms, oriented in tandem in a channel, using the same boundary conditions and very similar dynamic conditions as implemented in the present study. After some preliminary testing to get the near-surface grid distributions required to solve the boundary layers in the present flow, calculations were performed on a non-uniform grid consisting of 228×202 (x, y) nodes, especially refined near the surfaces defining the prism and the fish, using a time step $\Delta t = 0.25 \times 10^{-3}$ s. The adequacy of this grid was verified by reference to a second set of calculations performed on a more refined non-uniform grid consisting of 332×202 (x, y) nodes using a smaller time step $\Delta t = 0.125 \times 10^{-3}$ s. Values of the two velocity components were extracted from the field calculations along the transverse y -coordinate direction at the x -coordinate locations denoted by A, B and C in figure 19, and plots of the x -directed streamwise mean and r.m.s. velocity components at these three locations are shown in figures 20 and 21, respectively. For the mean velocity profiles, differences between the two grids are negligible at all three locations. For the r.m.s. velocity profiles, negligible differences arise between the grids at locations A and B. At location C, the r.m.s. maxima in the wake of the prism are slightly better resolved on the more refined grid. (Owing to its streamlined shape, the fish does not contribute to the wake r.m.s.) However, it is clear from the agreement between grids observed at location B that location C is sufficiently removed downstream of the fish so as to have little influence on the flow around it. The conclusion is that the two-dimensional external flow results obtained on the 228×202 grid are essentially grid independent and sufficiently accurate for the purposes of this study, where the main objective is to obtain a physically realistic pressure waveform to drive the flow in the LLTC.

A.2. Three-dimensional flow inside the fish LLTC

The LLTC calculation approach was first validated with reference to the time-oscillating Poiseuille flow in a tube of diameter $250 \mu\text{m}$ and length $500 \mu\text{m}$. The pressure gradient applied along the tube length was specified according to the function

$$\frac{dP}{dx}(t) = 1.79 \times 10^{-4} \sin(2\pi ft), \quad (\text{A } 1)$$

with $f = 0.7$ Hz. A uniform grid consisting of $50 \times 50 \times 50$ (x, y, z) nodes was used with a time step $\Delta t = 5 \times 10^{-5}$ s. As shown in figure 22 for $t = 1$ s, an excellent agreement was found between the numerical results and the analytical solution in Schlichting (1968) for the mean velocity.

Following this, a more refined non-uniform grid consisting of $122 \times 56 \times 54$ (x, y, z) nodes was carefully designed for the three-dimensional calculations inside the LLTC with a neuromast present. The goodness of this grid was checked by reference to an even finer grid consisting of $147 \times 72 \times 67$ (x, y, z) nodes. Calculations of the drag force acting on the neuromast were derived

Figure 20. Transverse (y -directed) profiles of the mean streamwise (x -directed) component of velocity plotted for two grid refinements (a) 228×202 and (b) 332×202 at x -coordinate locations A (solid line), B (dashed line) and C (dotted line) shown in figure 19.

Figure 21. Transverse (y -directed) profiles of the r.m.s. streamwise (x -directed) component of velocity plotted for two grid refinements (a) 228×202 and (b) 332×202 at x -locations A (solid line), B (dashed line) and C (dotted line) shown in figure 19.

Figure 22. Comparison at $t=1$ s between calculated (squares) and analytical (solid line) profiles of the longitudinal (streamwise) velocity component for a fluid oscillating in a tube at 0.7 Hz.

from the field distributions of pressure and viscous shear on both grids. The comparison was performed for the LLTC and neuromast dimensions ($150 \mu\text{m} \times 150 \mu\text{m} \times 150 \mu\text{m}$) provided in the text for a flow oscillating at 150 Hz. The results obtained (figure 23)

Figure 23. Grid comparison of calculated viscous, pressure and total drag forces acting on a neuromast of dimensions $150 \mu\text{m} \times 150 \mu\text{m} \times 150 \mu\text{m}$ for the flow in the LLTC oscillating at 150 Hz. Results are plotted for one oscillation cycle after establishing steady-periodic flow. Solid line, $122 \times 56 \times 54$; dashed line, $147 \times 72 \times 67$.

show negligible differences between the two grids. The conclusion is that the three-dimensional LLTC flow results obtained on the $122 \times 56 \times 54$ grid are essentially grid independent.

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