Morphological Intelligence Mechanisms in Biological and Biomimetic Flow Sensing

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Many aquatic and aerial animals have evolved highly sensitive flow receptors to help them survive in challenging environments. The biological flow receptors, such as filiform hairs, lateral lines, and seal whiskers, are elegantly designed with interesting biomechanical processing principles for extreme sensitivity, exhibiting obvious morphological intelligence. For instance, superficial neuromasts on the surface of fish body have an elongated cupula to enhance flow detection with a magnified drag. The flow-induced mechanical information is transferred to arrayed hair bundles in the neuromasts, which show spontaneous oscillation and mechanical coupling effects for a high mechanical sensitivity. In this review, the biomechanical principles of morphological intelligence in biological flow field receptors are discussed, with an emphasis on the functions of stimulus enhancement, noise reduction, and nonlinear oscillation. In addition, the recent achievements in flow sensors with morphological intelligence are summarized in this article. Though there is still a big gap in principle discovery and practical application of morphological intelligence in engineered sensors, it can be anticipated that the field of intelligent flow sensing will be significantly promoted by the establishment of morphological intelligence models.

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1. Introduction

Flow stimulus provides an important source of external information for aquatic, semiaquatic, and aerial animals in a wide variety of functions, including navigation, prey or predator detection, and other social behaviors. It is no wonder that these animals have evolved with highly sensitive flow sensory organs, such as sensory hairs of insects, lateral lines of fish, and whiskers of many mammals. Filiform hairs in insects, trichobothria in arthropods, and flow sensilla in crustaceans are among the most sensitive sensory organ for flow detection in the animal world.^[1] Cricket filiform hairs can detect airflow as low as $0.03 \text{ mm s}^{-1[2]}$ and the minimum work to elicit an action potential is merely 10^{-20} J. Fish perceive hydrodynamic information with their lateral line neuromasts, which can be divided into pressure gradient sensitive canal neuromasts (CNs) and flow-velocity sensitive superficial neuromasts (SNs).^[3-5] In the case of Ruffe, the

pressure detection threshold is lower than 1 mPa and the flow velocity detection threshold is as low as $10 \,\mu m \, s^{-1}$.^[6] Harbor seal whiskers with exquisite undulated surface morphology show superior sensitivity to vortices by suppressing self-induced stimulus.^[7] Adapting to diverse living environments and social functions, biological flow sensory organs show significant differences in biomechanical mechanism, morphology, and arrangement.

The mechanosensory organs turn the flow stimuli into neural signals and transfer them to the central nervous system (CNS) for data processing. To prevent CNS from being overwhelmed by complex processing tasks, the sensory organs show remarkable intelligence in mechanics and informatics. Barth proposed that non-nervous auxiliary structures play a significant role in sensory biology, and they employed "simple mechanics" to preprocess information for the fine-tuning of mechanoreceptors.^[8] Sane and McHenry discussed the biomechanical filtering characteristics of sensory organs and pointed out that the physical properties of the sensory organs play a central role in determining the signals received by the nervous system.^[9] A variety of flow sensory organs can filter out unnecessary noise while enhancing useful information from their surroundings.^[10,11] As this kind of intelligence originates from the morphologies of sensory organs and even animal bodies, facilitating perception and offloading



computation from the brain to the body, it can be named as "morphological intelligence" in biological sensing or engineered sensor fields.^[12–18]

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Previous reviews on biomechanical filtering and information preprocessing have focused on the morphological intelligence in auxiliary structures of sensory organs.^[8,19] However, the influence of body shape on sensing performance and biological intelligence in sensor placement has never been addressed. In addition, the mechanoelectrical characteristics of hair cells, hair bundles, and their coupling were seldom discussed. In this review, the morphological intelligence in biological and biomimetic flow sensing is described with an emphasis on filiform hairs, lateral lines, seal whiskers, and hair cells. A few well-established models will be reviewed to highlight the relevant arguments and backgrounds. The review is organized in the essential functions of various morphological intelligent principles such as stimulus enhancement, noise reduction, and nonlinear oscillation for extreme sensitivity (Figure 1). Finally, the technological challenges and prospects of morphological intelligence for modeling and application in artificial sensors or sensing systems will be discussed.

2. Morphological Intelligence for Stimulus Enhancement

2.1. Drag-Enhancing Structures

2.1.1. Drag Enhancement in Lateral Line Neuromasts

Both superficial neuromast and canal neuromast consist of a group of hair cells embedded within a gelatinous cupula. As the cupula is directly subjected to flow forming the fluid–receptor interface, it can significantly increase viscous and pressure drags generated by hydrodynamic stimuli.

The fish body usually attenuates the flow stimulation due to the existence of a boundary layer.^[20,21] The height of the superficial cupula is related to the boundary layer thickness, which can be 4 times as high as the base diameter of the cupula.^[22] McHenry and van Netten proposed a structural mechanical model of SNs^[23,24] as schematically illustrated in **Figure 2**a,b. The cupula appears as a beam fixed to a hair bundle, and the proximal region of the cupula has a flexural stiffness proportional to the number of the hair bundles. This stiff region extends to the



Figure 1. Schematic diagram of morphological intelligence concept and sensing application based on biological structure (Reproduced with permission.^[27] Copyright 2020, International Society of Zoological Sciences, Institute of Zoology/Chinese Academy of Sciences and John Wiley & Sons Australia, Ltd. Reproduced with permission.^[40] Copyright 2019, AIP Publishing; Reproduced with permission.^[49] Copyright 2022, Springer Nature; Reproduced with permission.^[53] Copyright 2016, Elsevier; Reproduced with permission.^[72] Copyright 2015, Royal Society; Reproduced with permission.^[82] Copyright 2010, Company of Biologists Ltd.; Reproduced with permission.^[83] Copyright 2023, Mary Ann Liebert, Inc.; Reproduced under the terms of the CC-BY license.^[89] Copyright 2014, The Authors. Published by National Academy of Sciences USA; Reproduced with permission.^[120] Copyright 2016, AIP Publishing; Reproduced with permission.^[121] Copyright 2013, Springer Nature).

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Figure 2. Models of the lateral line neuromasts and lateral line inspired flow sensors: a) the major morphological features of SN (Reproduced with permission.^[24] Copyright 2007, Company of Biologists Ltd.); b) the fluid–structure interaction model of SN. The cupula is modeled as a two-part beam and coupled to a linear pivotal spring at its base and excited by a pressure-driven oscillating boundary layer (Reproduced with permission.^[24] Copyright 2007, Company of Biologists Ltd.); c) frequency responses of SN calculated for different aspect ratios of cupula (Reproduced with permission.^[5] Copyright 2019, IOP Publishing); d) flow sensor with biomimetic cupula developed by McConney et al. in 2009 (Reproduced with permission.^[29] Copyright 2009, Royal Society of Chemistry); e) artificial SN sensor based on the high aspect ratio Si-60 hair cell and PZT piezoelectric film (Reproduced with permission.^[20] Copyright 2016, Springer Nature); and f) cantilever beam flow sensor based on variable volume hydrogel (Reproduced with permission.^[30] Copyright 2021, John Wiley and Sons).

height of the kinocilia, and the rest of the cupula height provides a compliant tip. To deal with the fluid–structure interaction between the cupula and the freestream flow based on consideration of the boundary layer, many attempts have been done to build an elaborated model by McHenry and van Netten.^[22,23] They defined the mechanical sensitivity S_f of a superficial neuromast as the ratio of hair bundle deflection to stimulus velocity. They considered the mechanics of cupula and hair bundles that resist the flow resistance and produced an analytical model by the following equation^[22]

$$S_{\rm f} = K_{\rm low} K_{\rm comp} \frac{\sqrt{2if}}{1 + (K_{\rm low}/K_{\rm high})\sqrt{2if}} \tag{1}$$

where f is the stimulus frequency; K_{comp} , K_{low} , and K_{high} are the compliance parameter, low-frequency parameter, and high-frequency parameter, respectively. These parameters can be defined by **Equation (2–4)**.

$$K_{\rm comp} = \frac{2.37\sqrt{\rho}}{nk} \tag{2}$$

$$K_{\rm low} = h_{\rm c}^2 \sqrt{\mu} \tag{3}$$

$$K_{\rm high} = \frac{1}{4} w^2 \sqrt{E} \tag{4}$$

Here, ρ is the density of water and the cupula, *n* is the number of hair cells, *k* is the spring stiffness of the hair bundle, μ is the dynamic viscosity of water, and h_c , *w*, and *E* are the height, width, and Young's modulus of the cupula, respectively. It indicates that the mechanical sensitivity increases by increasing the dimensions (h_c , *w*) of the cupula.

Using sensitivity analysis, we assessed the effect of the parameters of SNs on the frequency response,^[5] and found that the sensitivity increased by increasing the aspect ratio of the cupula $\alpha = h_c/w$ (Figure 2c). Cupula consists mainly of a soft gelatinous glycoprotein material with a density close to that of water.^[25] Besides the large surface area of cupula enhances the drag force exerted by flow, its permeability and porosity may result in coupling interaction between the fluidic flow and the fluid within the cupula,^[26] which also contribute to further enhance the sensitivity of the cell bundles. In addition, an increase in the number of hair cells n will reduce the mechanical sensitivity of SN. whereas more hair cells lead to greater neural sensitivity. We investigated the lateral line morphologies in Chinese cavefish eyeless Sinocyclocheilus tianlinensis and eyed Sinocyclocheilus Macrophthalmus, and found that the blind cavefish show larger cupula size and increased number of hair cells per neuromast, compared with eyed S. Macrophthalmus.^[27] Principally, the larger superficial neuromast of blind cavefish is more sensitive than that of the eved counterpart.

Since the invention of the biomimetic flow sensor in 2002,^[28] employing a high-aspect ratio biomimetic cupula became a common design strategy to increase the sensor sensitivity. By introducing a hydrogel-based cupula into the cantilevered flow sensor, the fluidic drag force can be greatly enhanced. For example, an extreme detection threshold of $2.5 \,\mu m \, s^{-1}$ was achieved by Liu and Coombs^[29] with a silicon piezoresistive cantilever, on the apex of which a hydrogel was used to cap a SU-8 pillar (Figure 2d). Kottapalli et al. developed a MEMS artificial SN sensor,^[26] which consists of a PZT piezoelectric film and a Si-60 microhair cell with a high aspect ratio of 7.7 (Figure 2e). In 2020, Jiang et al. employed a thermoresponsive hydrogel as the artificial cupula as shown in Figure 2f. They used a

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microheater to modify the size of the cupula to achieve a tunable sensitivity and a wide detection range. $^{[30]}$

2.1.2. Drag Enhancement in Filiform Hairs

The arthropod filiform hairs, working as an air-motion detector, are essential for the survival of many arthropods. Among them, spider trichobothria and cricket cercal systems have been extensively studied with respect to morphology, physiology, and biomechanics. Despite many morphological differences between the two types of sensory hairs, both of them comprise a cup-like socket and a suspended hair (**Figure 3a**).^[31,32] The dynamic model of an individual hair was well established as Equation (5)

$$I\theta + R\theta + S\theta(t) = \tau(t) \tag{5}$$

where *I* is the moment of inertia of the hair, θ is the angular displacement, *R* is the resistance within the hair base, *S* is the torsional restoring constant of the spring diaphragm, and $\tau(t)$ is the driving torque acting on the hair. The driving torque on the hair can be expressed as the drag force distribution, *F*, along the hair times the lever arm integrated over the length of the hair

$$\tau(t) = \int_0^L F(\nu, r, \gamma, t) \gamma d\gamma$$
(6)

Here, ν is the local flow velocity, r is the radius of the hair shaft at position γ ($\gamma = 0$ at hair base). The drag force acting on the hair can be calculated by Oseen's method which is originally an approximation for steady flow past a cylinder.^[33] From

Equation (6), we can see that longer hairs lead to larger drag force and driving torque because of their large interaction surface with the airflow. Bathelier et al. suggested that the limit for transmitted energy increases with hair length.^[34] The sensory hairs show obvious length gradation in a group such as those typical of spiders like *Cupiennius salei* (Figure 3b),^[31] and the group of hairs will cover a larger frequency range with high sensitivity as compared to a single hair.

The filiform hairs of arthropods can be considered as a first-order lever system with pivots located between dynamics (force) and load (resistance), and between long lever arms and short lever arms, respectively.^[35] Typically, the length of the short arm (the distance between the base of the hair and the surface of the exoskeleton) is just 1 μ m, which is coupled to the sensory neurons. As the outer lever arm is much longer than the inner one, the force is scaled up with the level ratio to stimulate the sensory neurons.

The flow-sensing hairs of wandering spider *C. salei* exhibit elaborate feathered structures as shown in Figure 3c.^[36,37] The cuticular protuberances are up to 5 μ m in length and 1 μ m in diameter, arranged in high density parallel to the shaft axis. As the flow around a filiform hair is at Reynolds numbers of about 10⁻², the drag force is dominated by viscous force. Due to the small distance between neighboring protuberances, the strong viscous force can effectively stop any air movement in the spaces between the protuberances.^[38,39] Therefore, the feathered structures can increase the drag exerted by the moving air relative to a smooth cylinder surface thus enhancing the sensitivity. The smart surface design can significantly increase the effective diameter of the hair to airflow while retaining a small inertial mass. This kind of fluid-mediated coupling plays an



Figure 3. Mechanical model of the filiform hair and the biomimetic airflow sensors: a) general mechanical model of the filiform hair (Reproduced with permission.^[31] Copyright 2007, Elsevier); b) spiders trichobothria (*C. salei*) showing differences in hair length to measure larger frequency range (Reproduced with permission.^[31] Copyright 2007, Elsevier); c) the feathery surface structure of hair shaft from base to tip (Reproduced with permission.^[36] Copyright 1993, Royal Society); d) design of hair flow-sensor with leverage effect (Reproduced with permission.^[43] Copyright 2006, IOP Publishing); e) flow sensor array with long SU-8 hair structure (Reproduced with permission.^[46] Copyright 2013, Royal Society); and f) cantilever-based differential pressure sensor with a bio-inspired bristled configuration (Reproduced with permission.^[50] Copyright 2021, IOP Publishing).



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important role in drag enhancement. This design principle can also be found in the bristled wing of thrips and tiny wasps,^[40,41] even if they are not flow receptors.

Inspired by the sensing structure of the filiform hairs, researchers have developed a series of biomimetic flow sensors.^[42–50] Krijnen et al. proposed a capacitive-type flow sensor (Figure 3d), which used the lever effect to convert the flow-induced torque on a long SU-8 hair into the capacitance variation of base membrane.^[43] They also designed a hair sensor array to locate the dipole flow sources (Figure 3e).^[46] Shen et al. developed a flexible flow sensor based on microhairs.^[49] They employed a self-bending process to convert a flat polyimide cantilever beam into 3D curved hair to increase the flow sensitivity. Zhao et al. designed a bristled cantilever-based differential pressure sensor as shown in Figure 3f.^[50] The drag enhancement effect based on fluid-mediated coupling allows the sensor to maintain a high sensitivity at low differential pressures while achieving a large detection range.

2.2. Maximized Flow Stimulus Strategy

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Fish can perceive the ambient flow and resolve spatial and temporal variations in hydrodynamic signals with their lateral line systems. The distribution of lateral lines diversifies among different fish species. However, a basic layout is common to many fishes: the pressure-sensitive canal lateral line system extends over much of the body but is concentrated in the first 20% of the body length.^[51] Windsor et al. utilized particle image velocimetry and computational fluid dynamic (CFD) models to analyze the kinematics of blind Mexican cave fish (*Astyanax mexicanus*), and found that the changes in the stimulus to the lateral line were confined to approximately the first 20% of the body when approaching a wall head-on.^[52] The distribution of the lateral line is closely related to the flow stimulus, and the lateral line may be located where the flow stimulation is the most significant.

Jiang et al. investigated the relationship between lateral line distribution and flow stimulus in blind cavefish *S. tianlinensis.*^[53] It possesses proliferated lateral lines to compensate for the lack of vision. Yang et al. performed CFD simulations using a high-fidelity model and found that the regions with the maximum flow stimuli were consistent with the lateral line distribution of *S. tianlinensis.*^[54] **Figure 4**a–c shows the correlation between lateral line distribution (Figure 4a) of *S. tianlinensis*, maximum pressure stimulus (Figure 4b), and maximum flow velocity stimulus (Figure 4c) on the fish body. The maximized hydrodynamic stimulation strategy, which is obviously followed by the biological world, can be applied to place sensors in robotic fish and other underwater vehicles.

The maximized flow stimulus strategy involves placing sensors where the hydrodynamic stimulation changes significantly on the surface of an underwater model. Yang et al. developed a



Figure 4. Sensory organs and flow field distribution of fish (Reproduced with permission.^[54] Copyright 2022, IEEE) and mosquitoes (Reproduced with permission.^[57] Copyright 2020, IEEE) and mosquitoes (Reproduced with permission.^[57] Copyright 2020, AAAS). a) SNs (blue circles), CNs (red circles), and lateral canals (red line) distribution of *S. tianlinensis*. b) Regions with maximum differential pressure variation (red) and lateral canals (black line). c) Regions with maximum wall shear stress variation (blue) and SNs (black circles). d) Head and antennae of male *Anopheles gambiae* mosquito with fibrillae extended, and schematic diagram of cross section of mosquito antenna. e) Front view of a mosquito hovering at different altitudes. f) Side view of a hovering mosquito and distribution of absolute wingbeat averaged mean difference in pressure relative to the infinite case measured in the sagittal plane; white crosses show monitoring location corresponding to the tip of the antenna.



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bionic fish model, utilizing differential pressure sensors and hotfilm flow velocity sensors to mimic CNs and SNs, respectively.^[54] Sensors were placed at the intersection of areas with significant parameter variations (differential pressure and wall shear stress) at different yaw angles. The artificial lateral line system with optimized sensor placement demonstrated an enhanced capability in wall detection, which was comparable to that of living blind cavefish.

Insects like mosquitoes have an array of chordotonal mechanoreceptors Johnston's organ (JO) to detect antennal motion and air flows.^[55,56] Nakata et al. studied the aerodynamic imaging of mosquitoes and they calculated the wingbeat^[56] averaged pressure deltas at different distances from the ground.^[57] They found that the zones with the largest pressure deltas were located below the thorax. However, there was also another area with significant pressure deltas above the head, where the antenna was located (Figure 4e–f). Therefore, though the antennas with sensitive JO are located at the farthest distance from the ground, they are well placed to sense the flow stimulus. By mimicking the function of the flow-sensitive antenna, they integrated pressure sensors into a quadrotor drone and demonstrated its obstacle avoidance capability.

3. Morphological Intelligence for Noise Reduction

3.1. Biomechanical Filter

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3.1.1. Biomechanical Filter in Canal Lateral Line

Unlike SNs distributed on the surface of the skin to feel the external flow velocity, CNs are located within subepidermal canals on the head and trunk of fish. The fluid-filled lateral line canals are connected to the ambient environment via canal pores.^[58,59] Previous studies have measured the dynamic behavior of the cupula in the Ruffe canal lateral line, and found that in response to external stimulus, the cupula can be regarded as a rigid half sphere that slides on a smooth epithelium which is coupled elastically (**Figure 5**a).^[6,24,60] When there is an external pressure difference across canal pores, the response of CN is proportional to the pressure difference between the two adjacent pores, which, in turn, is proportional to the acceleration between the fish and the surrounding water.^[10,61–64]

The canal can be regarded as a high-pass filter for external pressure stimulus. Denton and $\text{Gray}^{[10,63]}$ measured and modeled fluid motions inside actual lateral line canals and canal-like structures (e.g., capillary tubes) as a function of the frequency of sinusoidal water motions outside the canal. They calculated the flow impedance outside the canal relative to the impedance inside the canal, and related it to the water displacements inside the canal (X_{in}) to water displacements of frequency *f* outside the canal (X_{out}), expressed by the following equation^[65]

$$\frac{X_{\rm in}}{X_{\rm out}} = \frac{j\omega I_{\rm out}}{j\omega I_{\rm in} + R_{\rm in}} \tag{7}$$

where $\omega = 2\pi f$ and *j* are the complex operators. I_{out} and I_{in} are the inertial components outside and inside the canal, respectively. R_{in} represents the frictional (viscous) component inside the canal calculated for steady (Hagen–Poiseuille) flow conditions.

The filter characteristics of the canal lateral line system are influenced by the canal morphology. In general, lateral line canals vary in diameter from 0.1 to 7 mm. In several fish species,



Figure 5. Mechanical filtering model of the lateral line canal and artificial canal lateral line sensors: a) the cupula in canal is modeled as a rigid hemispherical body that is coupled to the hair bundles (Reproduced with permission.^[24] Copyright 2007, Company of Biologists Ltd.); b) schematic diagram of the lateral canal structure and simplified physical model; c) mechanical properties of the lateral line canals with various diameters (Reproduced with permission.^[5] Copyright 2019, IOP Publishing); d) an artificial canal lateral line developed by Yang et al. (Reproduced with permission.^[69] Copyright 2011, AIP Publishing); e) a schematic showing the arrangement of bioinspired artificial canal neuromast sensors (Reproduced with permission.^[71] Copyright 2014, IOP Publishing); and f) the schematic diagram of artificial canal lateral line with constriction structure. The white dash line illustrates the constriction in canal (Reproduced with permission.^[73] Copyright 2019, IOP Publishing).

the lateral line canal becomes narrow near CNs. For instance, Montgomery et al. reported that Antarctic notothenioid fish *Dissostichus mawsoni* had a constriction structure near CN.^[66] Jiang et al.^[53] and Ma et al.^[26] found a constriction structure near CN in Chinese cavefish *S. macrophthalmus, S. microphthalmus,* and *S. tianlinensis*. In this case, the lateral line canal is modeled as a tube with two sections: a wide circular section with a diameter a_w , for a given length, l_w , which contained a narrower circular section with a diameter a_n in the middle of the canal, for the length, l_n (Figure 5b). The inertance (*I*) and resistance (*R*) terms in **Equation (7)** can thus be written as

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$$I_{\rm out} = \frac{\rho(l_{\rm w} + l_n)}{a_n} \tag{8}$$

$$I_{\rm in} = \rho \left(\frac{l_{\rm w}}{a_{\rm w}} + \frac{l_n}{a_n} \right) \tag{9}$$

$$R_{\rm in} = 8\pi \mu \left(\frac{l_{\rm w}}{a_{\rm w}^2} + \frac{l_n}{a_n^2}\right) \tag{10}$$

where ρ is the density of the surrounding fluid and μ is the dynamic viscosity. We calculated the mechanical filter characteristics of the lateral line canals with various diameters using Equation (7–10), as the results are shown in Figure 5c.^[5] The cutoff frequency shifts upward as the diameter of the canal decreases, and the canal with a larger diameter exhibits higher sensitivity. For canals with constriction structures, the reduction of the narrow diameter means: 1) a further attenuation of response at low frequencies; 2) an upward shift in the cutoff frequency; and 3) response gain at higher frequencies.^[65,66]

Klein et al. found that the canal lateral lines of stichaeid *Xiphister atropurpureus* have a multitrunk and high-branched structure with wide-spaced lateral lines pores.^[67,68] By modeling the complicated canal structure in detail, they found that although the wide pores spacing lateral line showed lower spatial resolution to stimulus localization, the signal-to-noise ratio could be improved in highly turbulent environments. The high-branched structure with a complicated mechanical filter function makes it more suitable for living in noisy environments.

By mimicking the structure of the canal lateral line system and its high-pass filter function to surface flow, researchers have developed a variety of artificial CN sensors.^[69-73] Typically, CN sensors consist of a canal structure with a series of pores and flow-sensing elements arranged in an array within the canal. For instance, Yang et al.^[69] developed a lateral line canal system with piezoresistive biomimetic SN sensors and PDMS canals (Figure 5d), which significantly suppressed the background turbulent noise. Kottapalli et al.^[71] integrated LCP piezoresistive sensing membranes, high-aspect ratio Si60 pillars, and a PDMS canal to form an artificial canal lateral line (Figure 5e). The canal structure completely filters away the dc flow at flow velocities tested from 0 to 275 mm s^{-1} . Ma et al. developed an artificial canal lateral line consisting of a P(VDF-TrFE) cantilever and a PDMS microfluidic canal with a constriction structure (Figure 5f).^[73] Experimental results showed that the constriction in the canal nearby the sensing element could enhance the hydrodynamic pressure sensing performance and achieve a pressure gradient detection limit of $0.64 \text{ Pa} \text{ m}^{-1}$.

3.1.2. Biomechanical Filter in Filiform Hair

The morphological intelligence of arthropod filiform hairs is not only reflected in the mechanism of drag enhancement, but also as a biomechanical filter of oscillating airflow signals in a wide frequency range. Previous studies have described filiform hairs as an inverted pendulum model supported by a spring diaphragm on a cuticle base.^[74–76] The pendulum protrudes into the air and is driven by the viscous force of moving air. As the filiform hairs resemble a light shaft structure with a very flexible connection to the exoskeletal cuticle, it can still deflect effectively at airflow velocities as low as $1\,mm\,s^{-1}$ and frequency up to several hundred Hz. In addition, a distinctive feature of the sensory filiform hairs of arthropods is their varying length in the range of 100-2000 µm. While shorter hairs are sensitive to high-frequency airflow signals, longer hairs are sensitive to low-frequency airflow signals. This phenomenon was also found in the cercal filiform hairs of crickets.^[76,77] In addition, for the detection of fast flow, short hairs are more responsive than long hairs.^[78]

The filiform hair is a strongly damped second-order mechanical system like an inverted pendulum, which acts as a mechanical band-pass filter.^[11] A transfer function of the system is given in Equation (11).

$$F(f) = \frac{T(f)}{W(f)} \tag{11}$$

Hair deflection sensitivity F(f) is the ratio of hair deflection to air velocity as a function of frequency f. Hair deflection T(f) at frequency *f* can be derived by the Fourier transform of the linear kernel of angular deflection $\theta(t)$. W(f) is the air velocity at frequency f. Kumagai et al. calculated the sensitivity F(f) of filiform hairs with different lengths based on the measurements of T and W in the frequency range 2–500 Hz. The filiform hairs act as the mechanical band-pass filters whose gain first increased continuously with the increase of frequency until it reached the optimal frequency, and then decreased gradually. The best frequency of the second-order system may be characterized by the resonant frequency, $(S/I)^{1/2}$, where S is the spring stiffness and I is the moment of inertia. The length dependency of the best frequency is expected to be $L^{1.5}$ according to the research results of Humphrey et al.^[31] As a group of band-pass filters, a large number of filiform hairs with different lengths cover a wide frequency range, ensuring that arthropods that use filiform hairs to sense airflow changes have good sensitivity to different frequencies of oscillating airflow.

When exposed to the same far-field amplitude of velocity, equal length hairs operating in air and water show very different characteristics. Equation (5) and (6) give a dynamic model of a single filiform hair where the force F is closely related to the density and viscosity of the fluid.^[79] In addition, the density and viscosity of the fluid medium also have contributions to the rotational inertia and the damping constant of the hair. The difference in density and viscosity of these two oscillating mediums leads to the fact that for the same velocity amplitude, the maximum angular displacement resonance frequency of an equal length of hair in water is significantly smaller than that of the hair in air.^[31] In the water medium, hairs at the resonant

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frequency have a larger angular displacement than at other frequencies, exhibiting a similar frequency selectivity to that in the air medium.

3.2. VIV Noise Reduction via Undulated Morphology

Marine mammals such as harbor seals and sea lions use their whiskers to perceive ambient flow variations. However, when they swim in water, the whiskers suffer from vortex-induced vibrations (VIVs), which are a source of noise to flow signals. The VIV phenomenon is caused by the alternating shedding of vortices on both sides of the whisker cross section, which leads to strong periodic changes in the force in the cross-flow direction. If the natural frequency of the seal whisker undulated structure is excited by this periodic load, and the damping is low enough, the structure will experience significant vibration, resulting in VIVs. Biological observations showed that the seal whiskers have a complex 3D undulated structure (**Figure 6**a). The role of the undulated morphology is to reduce VIVs by suppressing the formation of Kármán vortex streets in the wake,^[80,81] and to increase the signal-to-noise ratio in wake detection.

To reveal the VIVs noise reduction mechanism of the undulated morphology, researchers investigated the detailed morphologies of seal whiskers. Hanke et al.^[82] measured the shape of the harbor seal whiskers, determined the four semiaxes (a, b, k, l), the distance between the two ellipses (M) and the angle of attack (α, β) of the two control ellipses, and obtained an idealized whisker surface model (Figure 6b). To further analyze the effect of whisker undulations on noise reduction, Lyons et al.^[83,84] defined the two main length parameterhs of the free incoming flow on the positive *x*-axis as the mean thickness *T* and the mean chord length C, respectively. Then the slenderness ratio of the geometry is defined as $\gamma = C/T$, and the amplitudes of undulations in its thickness and chord length are described by A_T ($A_T = |b - l|/T$) and $A_{\rm C}$ $(A_{\rm C} = |a \cdot \cos \alpha - k \cdot \cos \beta|/T)$, respectively, as shown in Figure 6b. The seal whiskers in the flow field are subjected to periodic fluid forces, mainly including the drag force $F_{\rm D}$ in the downstream direction (x-direction) and the lift force $F_{\rm L}$ in the cross-stream direction (y-direction). The lift coefficient $C_{\rm L}$, drag coefficient $C_{\rm D}$, and Strouhal number St related to the frequency of VIVs are used as standards to measure the noise reduction ability.^[85]

$$C_{\rm L} = \frac{2F_{\rm L}}{\rho U^2 A} \tag{12}$$

$$C_{\rm D} = \frac{2F_{\rm D}}{\rho U^2 A} \tag{13}$$

$$St = \frac{f_s D_h}{U}$$
(14)

where ρ is the fluid density, *U* is the free-stream velocity, *A* is the projected area in the direction of free flow, f_s is the frequency of the vortex shedding, and D_h is the hydraulic diameter. The changes in vortical shedding patterns directly affect the frequency distribution of the C_L signal.^[85] An analysis of the C_L frequency spectrum provides insight into the flow characteristics of each topography, and *St* is defined as the dimensionless frequency with the strongest response peak.

The effect of whisker morphology on the hydrodynamic response has been investigated by particle image velocimetry (PIV) and computational fluid dynamics (CFD) methods. Yoon et al.^[85] simulated seven whisker-inspired models and compared them with a smooth elliptical cylinder. At the same Reynolds number, the modified geometries based on the elliptical cylinder provide the reduction of $C_{\rm D}$ and the suppression of the fluctuation of $C_{\rm L}$. In addition, by assessing the effects of the presence of both undulations in the computational work, Yoon et al. concluded that nonzero values of both $A_{\rm C}$ and $A_{\rm T}$ are required for maximum reduction of drag and oscillating lift, and the introduction of A_C had a larger impact on the force reduction than the introduction of $A_{\rm T}$. Yuasa et al.^[84] further explored the effects of $A_{\rm C}$ on $C_{\rm D}$ and $C_{\rm I}$. As shown in Figure 6c, they controlled the geometric parameters of cylinder models with $A_{\rm T} = 0$ and $A_{\rm C}$ increasing through the values 0, 0.1, 0.2, and 0.3. The $C_{\rm D}$ and $C_{\rm L}$ showed a significant drop when $A_{\rm C}$ increased from 0.1 to 0.2 and there was no significant change when $A_{\rm C}$ increased from 0.2 to 0.3 This suggests that oscillation lift and drag reduction can be achieved by controlling the geometric parameters of the whisker-inspired model, but there may be a limiting threshold value for $A_{\rm C}$ and $A_{\rm T}$. Zheng et al.^[86] compared the VIVs of two types of seal whiskers (harbor seal and gray seal) and a smooth cylinder, and found that the vortex intensity of the smooth cylinder was significantly higher than that of the two types of seal whiskers, which suggested that the seal whiskers had a VIV suppression effect. Meanwhile, the vortex intensity of the harbor seal whiskers was higher than that of the gray seal whiskers because the geometry of the gray seal whiskers had a better ability to suppress the VIV.

The VIV reduction mechanism has been applied to the development of highly sensitive flow sensors. Beem et al.^[87] connected an enlarged rigid seal whisker model to bending sensors arranged in four different orientations and encapsulated them into a biomimetic whisker sensor, as shown in Figure 6d. This sensor can be used to extract the direction of the incoming flow from the difference in VIVs characteristics of the artificial seal whiskers. Liu et al.^[88] developed a piezoresistive biomimetic whisker sensor by using a micro 3D printing technology and a direct liquid spreading method as shown in Figure 6e. When the flow rate was increased by a factor of 5, the variations of the RMS amplitude of the whisker sensor were in the ranges of 0.024–0.043% and 0.411–0.687% for the angle of attack θ at 0° and 90°, respectively, which suggests that the undulated surface morphology of seal whiskers can significantly reduce drag and VIVs at small angles of attack (Figure 6f). The biomimetic whisker-related research further consolidated the morphological intelligence of harbor seal whiskers for flow perception.

4. Nonlinear Oscillation for Extreme Sensitivity

4.1. Spontaneous Oscillation of Active Hair Bundles

Hair bundle is the mechanosensitive organelle of hair cell, which exists in vestibular organs of inner ear, bullfrog sacculus, and lateral line neuromasts of fish. The human cochlea contains about 16 000 of these cells, and they use active processes to amplify weak signals. The hair bundle consists of 30-300 rod-like

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Figure 6. Undulated morphology of seal whiskers and biomimetic whisker sensors: a) close-up views of the side and top of harbor seal whiskers reveal that they are not circular, but undulated and elliptical (Reproduced with permission.^[82] Copyright 2010, Company of Biologists Ltd.); b) Hanke's idealized whisker surface model, where λ is the wavelength, ε is the undulated offset, and Φ is the undulation symmetry, which defines the steepness or bias of the undulation (Reproduced under the terms of the CC-BY license.^[83] Copyright 2020, The Authors. Published by PLoS One); c) results from a single simulation including mesh-morphing transitions between four models are shown. Plots of drag coefficient C_D (top) and lift coefficient C_L (bottom) show smooth mesh morphing transitions between each of the four geometric models (Reproduced with permission.^[87] Copyright 2022, Elsevier); d) scaled-up whisker-like directional flow sensors deployed in the ocean (Reproduced with permission.^[87] Copyright 2013, IOP Publishing); e) schematic structure of the seal whisker-inspired flow sensor (Reproduced with permission.^[88] Copyright 2023, Mary Ann Liebert, Inc.); and f) amplitude of whisker's VIV-induced oscillatory voltage output variation with the flow velocity (Reproduced with permission.^[88] Copyright 2023, Mary Ann Liebert, Inc.).

stereocilia connected by tip links (**Figure 7**a,b).^[89,90] The stereocilia contain mechanosensitive ion channels that open by tensing the gate springs. The hair bundles display spontaneous oscillation with a typical amplitude in the range of \approx 20–100 nm (Figure 7c).^[91] Spontaneous oscillation is originated from the fast adaptation process of the transduction channel and the negative stiffness of the hair bundle. The stiffness of the hair bundle depends on the state of the channel, which has been experimentally verified by Howard and Hudspeth in 1988 from an oscillatory hair bundle of the bullfrog sacculus.^[92] The

force–displacement curve shows a region of effective negative stiffness for a displacement less than 20 nm (Figure 7d), which is larger than the thermal fluctuations inherent in the system.^[93]

By taking into account the properties of mechanosensitive ion channels coupled to motor proteins which are regulated by inflowing Ca^{2+} ions, Jülicher et al. proposed a simple model to explain the dynamic behavior of the hair bundle by the following coupled functions^[94,95]

$$\lambda \dot{X} = -K_{\rm gs}(X - X_{\rm a} - DP_0) - K_{\rm sp}X + \eta \tag{16}$$





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Figure 7. a) SEM image of hair bundles in bullfrog sacculus (Reproduced under the terms of the CC-BY license.^[89] Copyright 2014, The Authors. Published by National Academy of Sciences USA); b) biological structure and corresponding model of hair bundles (Reproduced with permission.^[90] Copyright 2013, Company of Biologists Ltd.); c) hair bundles oscillate spontaneously with a typical amplitude in the range of $\approx 20-100$ nm (Reproduced with permission.^[91] Copyright 2001, National Academy of Sciences USA); d) the force–displacement curve exhibits a region of effective negative stiffness (Reproduced with permission.^[93] Copyright 2000, National Academy of Sciences USA); e) spontaneous oscillation of the hair bundles leads to nonlinear amplification and enhances its sensitivity and frequency selectivity (Reproduced under the terms of the CC-BY license.^[96] Copyright 1998, The Authors. Published by National Academy of Sciences USA): may a the ratio of the response's amplitude to that of the linear passive system, is greatest for stimuli near threshold; f) an active, artificial hair cell based on MEMS technology using self-sensing and self-actuated cantilevers with feedback (Reproduced with permission.^[100] Copyright 2016, American Vacuum Society); and g) the sensor resulted in an amplification up to 15 dB to the sound signal (Reproduced with permission.^[100] Copyright 2018, IEEE).

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$$\lambda_{a}X_{a} = K_{gs}(X - X_{a} - DP_{0}) - F_{max}(1 - SP_{0}) + \eta_{a}$$
(17)

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Each hair bundle is described by two variables *X* and *X*_a characterizing the stereociliary deflection and the state of motors, respectively. *K*_{gs} is the gating spring stiffness and *K*_{sp} is the pivotal stiffness. The displacement *D* is associated with channel gating. Calcium influx through open channels inhibits motors' activity and thus adjusts the force generated by the motors, where the strength of inhibition is *S* and the open probability of the ion channels is *P*₀. If all channels are closed, the maximum force is *F*_{max}. Various sources of fluctuations are taken into consideration, including Brownian motion of the surrounding fluid and channel clatter, with effects on stereocilia and motors denoted by η and η_a , respectively. Hair bundles oscillate spontaneously under the action of noise and biological mechanisms (Figure 7c).^[91]

As shown in Figure 7e,^[96] the active process of the hair bundles leads to nonlinear amplification of oscillatory force stimulus and enhances its sensitivity and frequency selectivity. It should be noted that the hair bundles operate in a highly viscous environment and its active process partially overcomes the dissipation of stimulus energy due to viscous drag, ensuring acuity to acoustical stimulation.^[97]

Hair cells respond to the deflection of their hair bundles to detect stimuli such as sound, force, and fluid flow. Asadnia et al.^[98] developed an artificial hair cell sensor that closely mimicked the biological hair bundle through MEMS fabrication and soft lithography, and the sensor reached a water flow detection threshold of $8 \,\mu m \, s^{-1}$. Inspired by the active process of hair bundles, various biomimetic sensors with active mechanisms have been proposed.^[99-109] Lenk et al.^[99,100] realized an active, artificial hair cell using self-sensing and self-actuated cantilevers with appropriate feedback (Figure 7f). The hair cell exhibited an amplification of the sound signal up to 15 dB (Figure 7g). Ahn's group proposed an electromechanical model mimicking the negative stiffness and adaption process of the auditory hair cell.^[102] Guided by the theoretical model, they developed an artificial hair bundle, which obtained a sharp frequency selectivity in water and a great force sensitivity of 2.9 nN.^[103] Joyce and Tarazaga proposed a piezoelectric cantilever beam using nonlinear velocity feedback control to mimic the nonlinear amplification of active hair bundle. By positioning the system close to Hopf bifurcation, the bioinspired sensor showed a one-third amplitude scaling near the resonance frequency.^[105,106] In our opinion, the interesting nonlinear amplification mechanism is worth being attempted in the field of liquid flow, pressure, and sound perception.

4.2. Mechanical Coupling of Active Hair Bundles

The ability of a single hair bundle to detect oscillatory stimulus by using critical oscillation is limited by fluctuations which conceal the critical point. This limitation could be overcome if an ensemble of hair cells with similar characteristic frequencies was mechanically coupled. Coupled noisy oscillators could approach the ideal case of a critical oscillator near a Hopf bifurcation. In the mammalian cochlea, the gain that characterizes amplification of basilar-membrane motion is up to 10³, whereas the gain is

only 10 for a single hair bundle in the bullfrog sacculus.^[110] This finding suggests that the fluctuations of individual hair cells could be reduced by the cooperative action of many oscillatory cells.

Spontaneously active hair bundles are synchronized by mechanical coupling with their neighbors. In the cochlea of mammals, outer hair cells are directly coupled to the tectorial membrane via their hair bundles and are stimulated by shear between the vibrating basilar membrane and the overlying tectorial membrane (Figure 8a).^[111] For the hair bundle of the bullfrog saccule, a hair bundle (blue) is connected to one neighbor on each side (orange and red) by identical springs of stiffness (Figure 8b).^[112] Jülicher's group^[95] developed a theoretical description for the mechanical coupling of hair bundles. Hair bundle oscillations are pairwise uncorrelated in the absence of coupling. Upon a sufficient increase of the coupling strength, oscillations progressively synchronize (Figure 8c).^[113] Coupled hair bundles exhibit a substantially enhanced amplification gain compared with a single hair bundle, up to a maximum of 400 for the 9×9 system (Figure 8d).^[95] Based on numerical simulation, they combined dynamic force clamp of a hair bundle from the bullfrog's saccule with real-time stochastic simulations of hair-bundle mechanics to assay the effects of mechanical coupling on the hair-bundle amplifier. This setup effectively overcame intrinsic noise limitations and achieved high sensitivity and sharp frequency selectivity.^[112] Mechanical coupling of active hair bundles provides an innovative approach to suppress noise and improve sensitivity for bionic engineering applications.

5. Discussions and Perspectives

We have analyzed the morphological intelligence with respect to stimulus enhancement, noise reduction, and extreme sensitivity based on nonlinear mechanics. Specialized mechanisms of morphological intelligence have been applied in the design of biomimetic flow sensors. It is undeniable that the successful application of morphological intelligence is still very limited in the field of MEMS sensors. The main challenges lie in the discovery and modeling of novel mechanisms, applicability assessment, and difficulty in sensor fabrication.

5.1. Modeling of New Morphological Intelligence Mechanisms

The morphological intelligence in lateral lines, filiform hairs, and mammal whiskers has been extensively studied and their biomechanical models have been well established. However, there is an ongoing debate on the sensing methodology of seal whiskers: slaloming or stick-slip.^[114] Moreover, there is no top-down design way for the biomimetic whisker morphology to achieve the optimization of VIV reduction and sensitivity enhancement, which is crucial for the design of the vortex sensor for source localization. In addition, it should be noted that the biological examples of morphological intelligence in flow sensing are still very limited; the discovery of novel intelligent sensing mechanisms is strongly demanded.







Figure 8. a) Hair bundles are coupled with their neighbors through tectorial membrane in the cochlea of mammals (Reproduced with permission.^[111] Copyright 2006, Springer Nature); b) coupled model of hair bundles of bullfrog saccule (Reproduced under the terms of the CC-BY license.^[112] Copyright 2010, The Authors. Published by National Academy of Sciences USA); c) mechanical coupling of active hair bundle leads to oscillations synchronization (Reproduced with permission.^[113] Copyright 2012, Springer Nature); and d) coupled hair bundles exhibit an enhanced amplification gain compared with a single hair bundle (Reproduced under the terms of the CC-BY license.^[95] Copyright 2008, The Authors. Published by National Academy of Sciences USA).

5.2. Biomimetics Challenge in Sensor Fabrication

Another technological challenge is how to transfer biological intelligence to the biomimetics of flow sensors by taking manufacturing complexity and performance superiority into consideration. For instance, the feathery structures of some sensory hairs can significantly increase the drag force while maintaining light weight, which tends to give the flow receptor a high sensi-tivity without reduction in dynamic range.^[41,50] However, it is difficult to use this intelligent structural design in engineered hairlike flow sensors due to the limitation of fabrication complexity. Though MEMS technologies are well established for the fabrication of intelligent sensors integrated with signal processing circuits, it is very challenging to reproduce the delicate 3D design of biological models. 3D printing technology has been applied to the rapid prototyping of sensing structures.^[115] However, the high precision of micro-nanostructures requires further improvement in the resolution and positioning accuracy of printing technology.^[116] In addition, the high sensitivity of biological receptors is closely related to their material properties. It is very important to adopt new materials (hydrogels, polymer composites, nanofibers, etc.) in the structural design to improve the sensitivity, which also poses a challenge for microfabrication technologies.

5.3. System-Level Application of Morphological Intelligence

In most cases, biological flow receptors are arrayed to achieve the function of directional sensing or a system-level function of target localization. For example, SNs and CNs of the lateral lines appear at locations with high flow stimuli to cope with complicated flow environments. Arrays of seal whiskers of different lengths and diameters exhibit a wide range of frequency responses, enhancing the overall perception capability. This inspires the optimized design of sensor arrangements for system-level applications. Many researchers have demonstrated the applications of flow sensor arrays in the estimation of flight parameters^[117] and altitude control of underwater robots.^[54,118,119] The application of mechanical intelligence in a system level is a very promising and interesting field which is seldomly explored.

5.4. Potential Future Research Directions of Flow Sensing

The underlying morphological intelligence of flow sensory organs can facilitate noise filtering and sensitivity enhancement, providing valuable references for the design of novel flow sensors. The research in morphological intelligence with interdisciplinary collaborations can provide broad implications in the field of both biology and engineering. Here, we try to point out the potential research directions in the field of flow sensing-related morphological intelligence. First, it is very important to investigate the morphological intelligence mechanism in a system level to consider the optimization principle of sensor placement and morphological adaptions of both sensory organs and body shapes. For example, the hydrodynamic enhancement perception mechanism of the head-horn morphology of eyeless cavefish^[54] has been discussed. Second, the development of animal wearable neural probes and sensors can provide tremendous support for further exploration of morphological intelligence in biology. Third, though the application of morphological intelligence in engineering is very limited, it is very promising to adapt this advanced design concept into the field of sensors, robots, and other engineering devices. We believe that interdisciplinary

collaborations in the fields of behavioral biology, neurophysiology, fluid dynamics, flexible electronics, and MEMS technology are required to advance the understanding and expand the application of morphological intelligence in the field of flow sensing.

6. Conclusions

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The highly sensitive flow receptors of aerial and aquatic animals help them effectively perceive their surroundings and play a vital role in predation, communication, and other social behaviors. In this article, we summarized the morphological intelligence mechanisms in biological flow perception, which includes stimulus enhancement, noise reduction, and nonlinear oscillation for extreme sensitivities. With the rapid progress of smart materials and microfabrication technology, many researchers have developed biomimetic flow sensors based on these morphological intelligence-related principles. Although artificial flow sensors cannot simply copy the morphologies and functions of the biological flow receptors, biomimetic principles can be considered in the process of sensor design. By exploring new biological sensing models with this inherent smartness, we can anticipate a new research area of biomimetic sensing with morphological intelligence for practical sensor applications.

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Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

D.Z., K.W., and Y.J. proposed the idea of the review. Y.J. conceived the structure of the review and guided the entire work. Z.G., Y.C., H.C., B.W., Z.Y., and X.K. wrote the manuscript. Z.G. and Y.C. prepared the figures and completed the rest of the work. All authors read and provided feedback on the manuscript.

Keywords

biomechanical filters, biomimetic sensors, flow sensing, morphological intelligence, nonlinear mechanics

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