

Abstracts

Keynote lectures

K1

Role of the lateral line in fish behavior

John Montgomery

University of Auckland, Auckland, New Zealand

Fish inhabit a complex hydrodynamic environment where flow sensing is 'of the essence'. Their principal flow sensor is the lateral line; a series of hair-cell based receptors, called neuromasts, which respond to relative movement between the fish's body and the surrounding water. These unidirectional, or oscillating, flows on the surface of the fish may be generated by other animals, inanimate sources such as water currents and waves, or by the animal's own movements. Clearly, flows of this nature provide critical information to the fish, and this talk will focus on the behavioral utility of flow information provided by these sensors. The detailed biomechanics of flow sensing, and the rich structural diversity of lateral line systems across fish species, will be covered by other speakers. However, to understand the roles of the lateral line in fish behavior, it is necessary to appreciate that there are two principal submodalities of the lateral line: superficial neuromasts (SNs) on the surface of the skin, and canal neuromasts (CNs) that occur within sub-dermal canals that open to the surface via pores. SNs respond to flow velocity and lower frequencies, whereas CNs respond to pressure differentials between the canal pores and higher frequencies. Water movements produced by other animals are of obvious behavioral relevance, and have been shown to mediate conspecific mating signals, schooling coordination, predator avoidance, and prey capture. CNs have been shown to play a particular role in localization of small prey. The orientation of fish to steady, and to turbulent flows has been extensively studied. Fish are able to use information from the SNs to orient to slow steady flows, a behavior known as rheotaxis. They are also able to position themselves in front, or behind obstructions in the flow, to reduce the cost of holding station in a current. When the obstruction is spinning off regular alternating vortices (Kàrmàn vortex street) the fish can also make energetic gains by adapting their swimming gait to match the vortex frequency. Experimental manipulation of the lateral line provides evidence for the use of both SN and CN information in these behaviors. Stimulation of the lateral line flow sensors by the animal's own movements provides the basis for hydrodynamic imaging of stationary objects in the fish's environment. However, self-stimulation also creates problems for lateral line sensing, resulting in specific saltatory search strategies for lateral line predators, division of labor between SN and CNs, active gain control of the sensors through efferent control from the brain, and adaptive cancelation of self-generated noise in the ascending sensory pathways. Conflicting evidence for a possible contribution of lateral line flow sensing for swimming efficiency may indicate that flow sensing makes an indirect contribution to motor control.

Flow sensing by pinniped vibrissae

Guido Dehnhardt

Institute for Biosciences and Marine Science Center, Rostock University, Rostock, Germany

In addition to active touch, seals and sea lions use their highly sensitive vibrissae for the detection of hydrodynamic events. In prey-predator interactions hydrodynamic information caused by swimming pelagic fish is of special importance for a seal. As the wakes of fishes persist for several minutes they represent hydrodynamic trails of considerable length, which might be detectable and trackable for a seal. In order to generate well controlled hydrodynamic trails, miniature submarines and conspecifics were used. These experiments demonstrated that blindfolded seals can use their mystacial vibrissae to detect and track hydrodynamic trails of considerable length. The arrangement of mystacial vibrissae allows a seal to perform simultaneous multiple-point velocity measurements in the wake of a swimming fish from which the three-dimensional vorticity and thus information on the moving direction as well as the size and shape of the trail generator can be derived. Hypothetically, hydrodynamic trail following can be considered to be never-ending, as long as a fish is swimming and natural hydrodynamic events such as currents do not disturb a trail. In general, hydrodynamic trail following provides an explanation for how pinnipeds may successfully hunt on pelagic fish in dark and murky waters and represents a new mechanism of spatial orientation in the aquatic environment. While scanning the water for hydrodynamic signals at an own high swimming speed, harbour seals keep their long and flexible whiskers in an abducted position, largely perpendicular to the swimming direction. Remarkably, the whiskers of harbour seals possess a specialized undulated surface structure, the function of which was, up to now, unknown. In different experimental approaches it could be shown that this structure effectively changes the vortex street behind the whiskers and reduces the vibrations that would otherwise be induced by the shedding of vortices from the whiskers (vortex-induced vibrations). Using force measurements, flow measurements and numerical simulations, it could be demonstrated that the dynamic forces on harbour seal whiskers are, by at least an order of magnitude, lower than those on sea lion whiskers, which do not share the undulated structure. The results are discussed in the light of pinniped sensory biology and potential biomimetic applications.

K3

Cricket flow sensing hairs are optimally tuned to the high frequency components of predator signals

Jérôme Casas

University of Tours, Institut de Recherche sur la Biologie de l'Insecte (IRBI)/CNRS,
Tours, France

Using Particle Image Velocimetry (PIV)-based measurements combined to a novel and compact theoretical framework to describe hair mechanics, we identified a yet overlooked broad frequency band where cricket air motion sensing hairs work close to the physical limit of sensitivity and energy transmission. While the magnitude of airborne signals produced by an approaching predator is known to broadly decrease with frequency, our results point toward the existence of spectral signatures in the higher frequency range that may be weak but are crucial for survival. We therefore modeled the air flow ahead of running spiders using Finite Element Models and approximations for the body and leg shapes and movements, as well as taking into account the ground effect. We end up the talk by quantifying the response of the hair canopy to such stimuli and by characterizing the sequential recruitment of hairs during an attack.

K4

Structural diversity in the lateral line system of fishes: Evolution, development and implications for function

Jacqueline F. Webb

Department of Biological Sciences, University of Rhode Island, Kingston, RI USA

The mechanosensory lateral line system, found in all 30,000+ species of living fishes (the jawless, cartilaginous and bony fishes), and in larval and adult aquatic amphibians, is composed of a spatial array of water flow detectors (neuromasts receptor organs) that play critical roles in prey detection, predator avoidance, communication, and navigation. The neuromasts that define the lateral line system are composed of directionally polarized sensory hair cells that are innervated by afferent sensory neurons (and efferent neurons), which comprise a series of cranial lateral line nerves. Structural variation in the lateral line system among bony and cartilaginous fishes can be defined with reference to the morphology and placement of the lateral line canals, and the morphology, distribution and orientation of two classes of neuromasts - those contained within canals (canal neuromasts) and those on the skin (superficial neuromasts) of the head, trunk and tail. In the bony fishes, in particular, the cranial lateral line canals may be narrow, branched, widened or reduced (with a proliferation of superficial neuromasts), and are contained in a remarkably consistent subset of dermal cranial bones (the „lateral line bones“). On the trunk, the canals are contained within a series of tubed „lateral line scales“, and vary in number, relative length, course, and dorso-ventral placement. The functional significance of these sorts of variation has been experimentally determined in only a few instances. Some bony fishes demonstrate novel specializations including mechanical linkages of the cranial lateral line canals to the swim bladder and/or the inner ear (e.g., in herrings and relatives, some catfishes, some butterflyfishes), which likely broaden the range of functional roles of the lateral line system. The development of the lateral line system provides an understanding of structure-function relationships in the context of the ontogeny of bony fishes, and also provides insights into patterns of evolutionary change in the lateral line system. Neuromasts differentiate from small populations of migrating cells derived from ectodermal thickenings on the head of embryos, a process that has been most intensely studied in select model species (e.g., zebrafish). In embryos and early stage larvae, the number of superficial neuromasts increases, then a subset of these increases in size (with an addition of hair cells), change shape, and become enclosed in the cranial and trunk canals (to become canal neuromasts) as the fish transforms to the juvenile stage. As superficial neuromasts become canal neuromasts, as canal diameter increases, and as locomotory capabilities improve with increasing fish size, the hydrodynamic context in which the lateral line system functions changes, providing another dimension to our understanding of its structure-function relationships in the lateral line system.

Supported by US NSF Grant # IOS-0843307.

K5

Central processing of lateral line information

Horst Bleckmann

Institute of Zoology, University of Bonn, Poppelsdorfer Schloss, 53115 Bonn, Germany

The lateral line is a sensory system that allows fishes to detect the hydrodynamic stimuli caused by predators, prey or conspecifics. Rheophilic fish in addition may use their lateral line for rheotaxis and for the detection of the vortices caused by submerged objects. Benthic and pelagic fish not only can sense the water motions caused by a dipole source, but in addition have the ability to localize the source. With aid of lateral line information fish can also determine the direction of a moving moving object as well as object velocity and object shape. Thus the lateral line is a sophisticated sensory system that provides fish with important information about their environment. In my talk I will focus on the central processing of lateral line information. Special attention will be given to the coding of simple and complex hydrodynamic stimuli in both, still- and running water. I will argue that in order to fully comprehend lateral line information processing it is imperative to do studies that take into account the ecology of fishes, meaning that natural stimulus and noise conditions have to be considered.

Flies, flow and flight control

Holger G. Krapp

Department of Bioengineering, Imperial College London, UK

In the air, flies arguably belong to the most manoeuvrable creatures on the planet. Some species may hover perfectly stable in one instant, and then dart off so fast that we can hardly see their trajectory. They can reach angular rotations in excess of 3000 degrees per second during their breathtaking chasing flights, do not normally collide with any obstacles, and manage to touch down accurately even at small landing sites. One of the reasons for their stunning aerial capabilities seems to be a contradiction in terms: flies are aerodynamically unstable. But how do these animals manage then to easily beat any man-made micro-air vehicle in terms of flight performance?

The secret is that aerodynamic instability, if combined with powerful feedback control, results in high manoeuvrability. Flies, therefore, employ a number of different sensor systems which together provide them with information about their orientation and movements no matter how slow or rapid any changes are. Once the signals from the different sensor systems are appropriately combined they are used directly to maintain the flies' aerodynamic stability.

In my presentation I will give an introduction to fly motion vision which turns out to play a key role for successful flight control: When moving relative to the surroundings, the entire world is shifted across the fly's eyes - a phenomenon called 'optic flow'. Optic flow fields describe the direction and speed of such relative motions occurring at different locations over the entire eyes. The global appearance of an optic flow field depends on the rotations and translations the fly combines during its flight manoeuvres and provides valuable information for the animal to stay stable in the air.

I will also present contributions of other fly sensor systems to maintaining aerodynamic stability and will point out the significance of the animal's gaze stabilization system for high-performance flight control. Along my presentation I will argue in favour of an integrated neuroscience approach that studies the behavioural limits, structural adaptations, and neuronal mechanisms underlying insect flight control. Finally, I will give an example of how principles of biological control design may be applied to terrestrial and aerial robotic systems.

K7

The biomechanics of superficial neuromasts and their role in behavior

Matt McHenry

Ecology & Evolutionary Biology, University of California Irvine, USA

Investigators of the lateral line system have developed a strong understanding for the signals detected by canal neuromasts and how these signals inform behavior. This is in part because canal neuromasts detect pressure gradients that are easily modeled and largely unaltered by the presence of a fish's body. In contrast, superficial neuromasts are sensitive to viscous flows that are challenging to model and potentially vary with the size and shape of a fish's body. In order to understand the biomechanics and the behavioral role of superficial neuromasts, we have examined flow sensing in zebrafish larvae (*Danio rerio*), which have a lateral line system composed of a small number of superficial neuromasts. Using behavioral experiments, we learned that larvae rely on their lateral line system to evade fish predators. In order to simulate the stimulus generated by a predator, we developed a device to expose larvae to a computer-controlled pressure field that is similar to suction-feeding. Experiments using this device revealed that larvae exhibit a lateral-line mediated escape response that is rapid enough to evade a predator. In this pressure field, the signals detected by the superficial neuromasts depend on the flow velocity relative to the body. Generating this relative flow requires that the density of the larva's body differ from that of the surrounding water. Measurements of body density revealed that the relative flow that excites the superficial neuromasts is substantially reduced when a larva inflates its swim bladder and thereby achieves a density similar to water. We have used mathematical modeling and materials testing of individual neuromasts to examine how stimuli are further filtered at the receptor level. This work suggests that superficial neuromasts function as band-pass filters of flow signals due to the viscous boundary layer over the surface of the body and its interaction with the beam dynamics of the receptor. Therefore, flow sensing in superficial neuromasts may be critical to the survival of a larval fish and its sensitivity depends on fluid-structure interactions at both the level of a fish's body and the individual receptors.

How to catch the wind: Airflow sensing in arthropods

Friedrich G. Barth

University of Vienna, Life Sciences, Department for Neurobiology, Vienna, Austria

One of the reasons for the seeming contradiction between the smallness of the brain and the elaborate behavior of arthropods is the „cleverness“ of their sensory periphery. In many cases the sensory cells far outnumber the neurons in the central nervous system. More importantly, by proper filtering, highly selective sensory organs tuned to the specific needs of a particular behavior in a particular environment relieve the central nervous system from a lot of integration and decision making. A multifaceted approach is needed to understand the adaptedness of the sensors in this broad context.

Keeping this in mind, airflow sensing in arthropods will be introduced, largely referring to work on spiders, which has taught us a number of lessons of general significance. Basic principles of function are applicable to the different arthropod groups, which have evolved their medium flow sensors convergently, driven by the same physics of the stimulus.

(i) The lecture will first point to some basic working principles, „technical“ tricks and the outstanding performance of airflow-sensitive hair sensilla.

(ii) The focus will then be on illustrating the fact that the sensitivity and selectivity of the sensors to a surprisingly large extent reflect the properties of natural stimulus patterns.

(iii) Finally, the capture of flying prey by spiders and the guidance of this remarkable behavior by cues contained in the prey-generated airflow will serve to link the sensors to a natural stimulus and to behavior. Recent data on the demanding analysis of the airflow generated by a freely flying fly close to the sensors will be presented, showing both the necessity and virtues but also the difficulties of a proper analysis of biologically relevant flow patterns.

The big question of course is: „How does it all fit together?“ The path we are going is still winding and mountainous, but now and then it already offers glimpses of the panoramic views we are striving for on the way to the goal.

K9

**Hydrodynamic object formation:
Neuronal representation, multimodal integration, and biomimetics**

J. Leo van Hemmen

Physik Department T35, Technical University of Munich, 85747 Garching bei München,
Germany

Perception of a sensory 'object' is generated by physical stimuli impinging upon a field of corresponding detectors. Each sensory modality uses a different physical mechanism such as audible sound for hearing, a portion of the electromagnetic wave spectrum for normal or infrared vision (e.g., snakes), and water waves for the lateral line of fish and some amphibia, most notably *Xenopus*. In this talk three things are done. First, we turn to a review of recent results for an exact computation of the range of the lateral line as it observes the animal's surroundings through direct interaction. In the context of a multipole expansion we discuss the lateral line's capacity to recognize object shapes and the influence of fish length as a bound to resolving the outside world. We also focus on the dipole approximation and why it is so useful for both surface and canal neuromasts. Second, we consider how a lateral-line map can arise and how neuronal object formation of the immediate environment may look, in particular, through a map as a neuronal representation of the outside world. Of special interest here is the lateral line's vortex tracking as a way of following persistent traces of a swim trail of fish, a kind of indirect interaction with fish in motion. Wake tracking is a consequence of conservation of angular momentum in whirling vortices of water, whereas a direct map is due to momentum transfer from objects in the immediate environment to the lateral-line neuromasts on the animal's surface. We will discuss how the lateral-line map of the direct environment may be neurally integrated with the maps from other modalities such as vision (fish-eye camera). Third, we will present an artificial underwater vehicle (*Snookie*) that uses its lateral-line system to observe its direct surroundings as a biomimetic demonstration of the sensory capabilities of blind Mexican cavefish.

Oral presentations

Behaviour

O1

Hydrodynamic imaging by blind cave fish

Shane Windsor¹⁾, James Paris¹⁾, Gesche Neusel²⁾, Theresa Burt de Perera¹⁾

¹⁾ Department of Zoology, University of Oxford, UK

²⁾ Institute of Zoology, University of Bonn, Germany

Blind Mexican cave fish (*Astyanax fasciatus*) are able to sense their surroundings by using their lateral line to detect the changes that nearby objects cause in the flow field around their body; this behaviour is known as hydrodynamic imaging. Using a combination of flow measurement techniques and behavioural experiments we have been able to explore the mechanics and behaviour involved with this remarkable sensory modality.

We used particle image velocimetry (PIV) to measure the flow fields around gliding blind cave fish as they moved through open water and when heading towards, or following along, a wall. These measurements, combined with computational fluid dynamics (CFD) models, were used to estimate the stimulus to the lateral line system of the fish. We have also used a number of different behavioural experimental setups to measure the distances at which fish react to walls, the impact of hydrodynamic noise on the fish's ability to detect walls, and the relative contributions of hydrodynamic and tactile information during wall following.

Our results show that hydrodynamic imaging is a short range sense, with fish only reacting to the presence of a wall when approximately 10% of their body length away. This short range appears to be due to the nature of the flow field around the fish. Contrary to previous expectation it was found that swimming faster did not increase the distance at which fish detected walls, in fact modelling showed that swimming at higher speeds actually slightly reduced the distance at which a fish could detect a wall. However, when the effects of environmental noise are considered, swimming at higher speed may theoretically improve the signal to noise ratio of the stimulus to the lateral line. To test this prediction we measured the distance at which fish acted to avoid a head-on collision with a wall under different levels of background hydrodynamic noise. Surprisingly, at the levels of noise used we found that the distance at which the fish reacted to the wall and their ability to avoid collision were constant, illustrating the fish's remarkable ability to distinguish signal from noise.

When swimming alongside walls blind cave fish frequently touch them with their pectoral fins, possibly providing them with both tactile and hydrodynamic information. Using a wall with a netted region in its centre, which provided tactile information, but was undetectable hydrodynamically, we were able to measure the relative contributions of these two senses. We found that the fish used hydrodynamic information in preference to tactile information, swimming significantly closer to and colliding more frequently with the netted region of the wall.

Overall, the combination of behavioural and flow measurement techniques has revealed hydrodynamic imaging to be a robust and highly sensitive short range sensory modality which blind cave fish rely on to sense their surroundings.

Flow sensing in sharks: lateral line contributions to navigation and prey capture

Jayne M. Gardiner¹⁾, Jelle Atema²⁾, Robert E. Hueter³⁾ and Philip J. Motta¹⁾

¹⁾ University of South Florida, Dept of Integrative Biology, Tampa FL, USA

²⁾ Boston University Marine Program, Boston MA, USA

³⁾ Mote Marine Laboratory, Center for Shark Research, Sarasota FL, USA

The lateral line system of bony fishes has been shown to function in several behaviors, e.g. schooling, predator avoidance, rheotaxis, obstacle avoidance, and prey capture. Few studies to date, however, have examined the role of this system in elasmobranchs. We conducted studies on the function of the lateral line system in the feeding behavior of sharks, under controlled conditions in a flume. Individual animals were held in a downstream pen while odor plumes were established, generated from an upstream source (live food in 1) tethered prey experiment or squid rinse in 2) artificial stimulus experiment). Animal behavior was examined intact, with vision blocked, with the lateral line disabled using streptomycin, and with simultaneous vision/lateral line blocks. Upon release from the pen, sharks were filmed from overhead, laterally at the target, and for live prey experiments, laterally with a high-speed camera to record capture kinematics. Blacktip sharks, a coastal, midwater-swimming species, normally capture live tethered prey with rapid, visually mediated ram-suction strikes (prey overtaken and engulfed), executed from several meters. They can capture prey without vision, but strikes are slower and initiated from a closer proximity. With only the lateral line blocked, the frequency of misses and ram-bites (prey captured in the jaws) increased, and they showed a greater variation in capture angles. Simultaneous lateral line/vision blocks impaired their ability to navigate through their environment and avoid obstacles, and they could not locate prey. Benthic, suction-feeding nurse sharks successfully captured prey with both the lateral line and vision blocked but took a significantly longer time, travelled a longer path to reach the prey, and had impaired obstacle avoidance. This species often maintains contact with the substrate while swimming and may be using tactile cues to orient to the flow in the tank. In the artificial stimulus experiment, smooth dogfish, an epibenthic species, were simultaneously presented with two turbulent plumes (one plain seawater, one with food odor), each with spatially separate sources of odor (or seawater) and coincident odor (or seawater) and turbulence, for a total of four targets. Animals, with and without vision, struck preferentially on the odor/turbulence target. With only the lateral line blocked, they navigated upstream using vision, but struck equally on the odor and odor/turbulence targets. With both lateral line and vision blocked, they could not locate any targets. This research demonstrates that sharks use the lateral line for: 1) large-scale orientation to the mean flow (rheotaxis); 2) navigation and obstacle avoidance; and 3) efficient odor plume tracking, all with little need for visual information; and that they require lateral line information for 4) fine-scale turbulence detection, which contributes to target localization and, in ram-feeding species, precisely directs their rapid strikes.

Disrupted flow sensing impairs hydrodynamic performance in the Yellowtail Kingfish, *Seriola lalandi*

Kazutaka Yanase, Neill Herbert and John Montgomery

Leigh Marine Laboratory, The University of Auckland, Auckland, New Zealand

In the control and optimization of fish swimming performance, a role for flow sensing has long been proposed (reviewed by Dijkgraaf, 1963), but direct experimental demonstration has proved elusive (Ayali et al. 2009; McHenry et al. 2010). Using 2 independent measures of swimming performance in the yellowtail kingfish, *Seriola lalandi*, (FL \pm S.D. = 27.7 \pm 3.4 cm; $N = 36$; 18 degree Celsius), we have examined the effects of unilateral ablation of the trunk superficial neuromasts.

Trunk superficial neuromasts (SN) on one side of the fish body were removed by freezing with a probe cooled by liquid nitrogen. The mean critical swimming speed ($U_{crit} \pm$ S.D.) for the unilaterally SN ablated fish was 2.11 \pm 0.96 L/s ($N = 12$), which was significantly slower than the 3.66 \pm 0.19 L/s ($N = 12$) U_{crit} of sham-treated fish ($P < 0.01$). The oxygen consumption (in mgO₂/kg/h) of the unilaterally SN ablated fish in a speed range of 0.7 - 2.2 L/s was significantly greater than that of the sham-treated fish ($P < 0.01$). The optimal swimming speed, at which the cost of swimming as work per metre was minimal, was 2.73 L/s for the unilaterally SN ablated fish while it was 2.00 L/s for the sham-treated fish. Thus, unilateral ablation of the SN compromises swimming efficiency in this highly active pelagic species within the constraints of flume swimming. Swimming efficiency is likely to be more important in active species, so the use of kingfish, and unilateral disruption of lateral line input may explain the difference between the strong result obtained here, and previous experimental attempts to demonstrate a role for the lateral line in swimming. Further work is needed to understand the manner in which flow information contributes to control of swimming within the flume, or central pattern generation and hence to swimming efficiency. However, the results of this experiment suggest that bilateral comparison of flow information plays a significant role in swimming efficiency under the conditions of this experiment.

Evolution of a behavior and the superficial neuromast adapts *Astyanax* cavefish to life in darkness

Masato Yoshizawa and William R. Jeffery

Laboratory for Evolutionary Developmental Biology, Department of Biology, University of Maryland, College Park, USA

Acquiring better behavioral response to flow stimuli would be beneficial in the dark cave environment. Here we describe studies designed to reveal the sensory base of vibration attraction behavior in *Astyanax mexicanus*, which has an eyed surface (surface fish) and a blind cave (cavefish) dwelling forms. Vibration attraction behavior (VAB) is the ability of fish to swim toward the source of a water disturbance in darkness. Quantitative laboratory assays indicate that VAB is common in cavefish but rarely observed and much less robust in surface fish. In competitive prey-capture experiments, surface fish with VAB predominated over those without VAB in darkness but not in light, showing that VAB is beneficial for feeding in the dark. The frequency analysis in the range of 5 Hz to 500 Hz vibration stimuli revealed that VAB peaked at 35 Hz, which was in the best sensing range of the superficial neuromasts in cavefish. The following studies were to test the involvement of the superficial neuromasts in VAB. First, the pharmacological assays showed that VAB was blocked by the lateral line inhibitors cobalt and gentamicin. Ontogeny and ablation studies indicated that VAB appeared after a numerical increase in superficial neuromast (SN) during development, and was significantly reduced by bilateral SN ablation. The significant correlation between VAB and the number of SN supports the conclusion that enhanced SN mediated the evolution of VAB. These results provide a basic for future understandings in the evolution of the lateral line-neural processing.

Positive rheotaxis or directed random walks? Anuran tadpoles exhibit different positioning behaviors in weak water currents

Andrea M. Simmons, Jeffrey M. Knowles, Brian P. Schmidt, Kwanghoon Lee

Cognitive, Linguistic & Psychological Sciences, Brown University, Providence, USA

Current flow is an important biological stimulus for larval anuran amphibians, but little is known about how it is perceived in this biologically diverse group of animals. We quantified positioning and orientation behaviors of the bullfrog (*Rana catesbeiana*) tadpole in controlled water flow, and compared these behaviors with those exhibited by similar-aged *Xenopus laevis* tadpoles tested in the same flow tank. The dynamics of the flow field were varied in two different configurations by changing the size and position of the water intake tube. Flow fields were calibrated by digital particle image velocimetry and tadpole positioning and orientation were automatically tracked by a custom-written MATLAB routine. In response to both kinds of flow fields, bullfrog tadpoles actively swam towards the back of the tank. The latency and strength of this downstream positioning behavior differed in the two different flow fields, but was consistent across 3 flow rates. Bullfrog tadpoles tended to remain in areas of reduced flow, but, in contrast to *Xenopus* tadpoles, did not exhibit positive rheotaxis towards the source of the current in any condition at any flow rate. Analysis of swimming behavior showed that bullfrog tadpoles were not merely passively pushed by the current, but instead actively locomoted towards the back. Their movements under flow are consistent with a model of locomotion based on a directed random walk. The morphological basis for these species differences in flow behavior are currently under investigation.

Finding the right food: Developmental regulation of prey sensing

Cynthia M. Harley and Daniel A Wagenaar

Division of Biology, Broad Fellows Program, California Institute of Technology.
Pasadena, CA, USA

Medicinal leeches, like many aquatic animals, use water disturbances to localize their prey, so they need to be able to determine if a wave disturbance is created by prey or by another source. Many aquatic predators perform this separation by responding only to those wave frequencies representing their prey. Since leeches' prey preference changes over the course of development, we examined their responses at three different life stages. We found that juveniles more readily localize wave sources of lower frequencies (2 Hz) than their adult counterparts (8-12 Hz), and that adolescents exhibited elements of both juvenile and adult behavior, readily localizing sources of both low and mid-range frequencies.

Leeches are known to be able to localize the source of waves through the use of either mechanical or visual information. We separately characterized their ability to localize various frequencies of stimuli using unimodal cues. For visual or mechanical unimodal stimuli, the frequency response curves of adults and juveniles were virtually indistinguishable. However, the visual and mechanical curves were different from each other: the optimal visual stimulus had a much lower frequency (2 Hz) than the optimal mechanical stimulus (12 Hz), frequencies that matched, respectively, the juvenile and the adult preferred frequency for multimodally sensed waves. This suggests that in the multimodal condition, adult behavior is driven more by mechanosensory information and juvenile behavior more by visual. Indeed, when stimuli of the two modalities were placed in conflict with one another, adult leeches, unlike juveniles, were attracted to the mechanical stimulus much more strongly than to the visual stimulus.

Bat wing sensors support flight maneuverability

S.J. Sterbing-D'Angelo³⁾, M. Chadha^{1,2)}, C. Chiu²⁾, B. Falk²⁾, W. Xian²⁾, J. Barcelo²⁾,
J.M. Zook⁴⁾, and C.F. Moss^{1,2,3)}

¹⁾ Program in Neuroscience and Cognitive Science, ²⁾ Department of Psychology, ³⁾ Institute For Systems Research, University of Maryland, College Park MD, ⁴⁾ Department of Biological Sciences, Ohio University, Athens OH

Bats are the only mammals capable of powered flight, and can perform complicated flight maneuvers like tight turns, hovering or perching upside-down. The bat wing membrane is covered with microscopically small hairs, and we hypothesized that these hairs may be involved in sensorimotor flight control by providing aerodynamic feedback. While the existence of these wing hairs has been known for a long time, their actual function during flight has not been experimentally addressed. Here, we present electrophysiological and behavioral data concerning the hairs' functional role as revealed by experiments conducted before and after hair removal. We found that neurons in the primary somatosensory cortex of the anesthetized Big Brown Bat, *Eptesicus fuscus*, respond with directional sensitivity to stimulation of the wing hairs with low-speed air flow. Wing hairs, especially those along the trailing edge, mostly preferred reversed airflow, which occurs under flight conditions when the air flow separates and vortices form. This finding suggests that the hairs act as an array of sensors to monitor flight speed and/or air flow conditions that indicate stall. We recorded the flight paths during obstacle avoidance tasks in two bat species with different flight behavior: *Eptesicus fuscus* is an insectivorous bat, and *Carollia perspicillata*, a frugi- and nectarivorous species that hovers frequently. Analysis of the high-speed camera recordings revealed that the flight performance was altered after depilation of different functional regions of the bats' wing membrane. Aerial maneuverability was clearly decreased, as indicated by decreased turning angles between video frames, i.e., the bats made wider turns, and by increased flight speed. Our findings provide insights for the development of biomimetic adaptations of such sensors to improve flight vehicles.

Sponsored by the US Air Force Office of Scientific Research Multidisciplinary Research Program of the University Research Initiative (MURI) "Biologically Inspired Flight for Micro-Air Vehicles."

Morphology

O8

Development of hair cell polarity and properly connecting them to the brain: Ears and lateral line compared

Bernd Fritzschn

Department of Biology, University of Iowa, Iowa City, USA

The evolution of mechanosensory hair cells and the known genetic pathways that generate the directional sensitive hair cell will be reviewed in the context of ear and lateral line development and evolution.

This presentation will highlight the molecular basis of placode formation, including the common molecular basis of ear and lateral line placode development, will discuss the evolution of placodes as a localized developmental program to generate various cranial tissues, including hair cells and will move on to present some of the basic features of sensory epithelia formation in the ear and the molecular conservation in the mechanosensory lateral line development. Further discussions will focus on the evolutionary diversification of the lateral line system, including formation of electroreceptive organs out of the lateral line anlage and evolutionary and developmental loss of the entire system. The presentation will also briefly describe some strange organs found in elasmobranchs (Savi's vesicle) and the some tetrapod ears (Vitalli's organ) and the spiracle of elasmobranchs (spiracle organ) and relate that to lateral line placode development and evolution.

Beyond this overview, the presentation will focus on the mechanosensory hair cell polarity as it relates to the neuronal connections of this polarity to the brain. Specifically, the differences between sensory organs with opposing polarities (utricle, saccule) and identical polarities (canal cristae, cochlea) will be presented and their central representation will be discussed in the context of information processing. Data on various polarity defected mouse mutants will be presented with some preliminary data on their aberration of central connections. Overall, development requires a segregation, predominantly by molecular means, of the central projection of afferents mediating opposing information to avoid that movements perceived by hair cells with a different polarity do not cancel each other.

Building and breaking symmetry in a mechanosensory system

Hernan Lopez-Schier

Centre for Genomic Regulation (CRG), Barcelona, Spain

The development of peripheral sensory receptors and the neuronal pathways that communicate them with the brain are often coupled. The assembly of neuronal first-order projections is important because it forms the basis of a basic neuroanatomical code that relay sensory information to higher brain areas to create a central representation of the peripheral sensory field. We have been investigating the nature of this coupling using the superficial lateral-line system of the zebrafish larva. I shall describe our recent results that indicate the predominant role of developmental timing in ensuring a coherent assembly of the topographic mapping of the lateral line in the hindbrain of the zebrafish.

Patterning the posterior lateral line in teleosts

Alain Ghysen

INSERM, Université Montpellier, France

The pattern of the embryonic posterior lateral line system (PLL) is remarkably conserved from basal zebrafish to highly derived tunafish. The adult patterns, however, are very different:

- adult zebrafish have four antero-posterior lines that extend at dorsal, dorso-lateral, lateral and ventral levels along the body. Three of them display dorso-ventral polarization whereas the fourth, the ventral one, is (mostly) antero-posteriorly polarized.
- adult tuna display a single arcuate line with neuromasts of various polarities.

We explored the larval development of the PLL in these two species to understand how dissimilar patterns are generated from a common foundation. We will describe how the large difference in adult PLL can be traced back to a single difference that occurs during the first day after hatching.

We also show that, whereas the zebrafish line grows through the continuous addition of new neuromasts during larval life, the development of the tunafish line is highly discontinuous. We speculate that this discontinuity may correspond to a major change in PLL function between the very early larva, and the juvenile.

Lateral line architecture and function in larval zebrafish

James C. Liao and Melanie Haehnel

The Whitney Lab for Marine Bioscience, Department of Biology, University of Florida, USA

Afferent neurons of the lateral line system sense flow along the body with neuromasts and relay this information to hindbrain processing centers. We looked at the number of afferents innervating specific neuromasts to see if regions of the body are more represented than others. Early in development, the afferent: neuromast ratio is higher in the anterior lateral line compared to the posterior lateral line. Later in development this pattern reverses, suggesting that there is more redundancy in representing flow at the head early on while later on there is more representation of the body. Although afferents in the ganglion as well as neuromasts proliferate as the animal develops, we found that in general the ratio of afferent: neuromast does not change with age.

Within the posterior lateral line, electroporation of individual afferents using Alexa 647 in HUC-Kaede fish, a transgenic line expressing a photo-convertible protein under control of a pan-neuronal promoter, suggests that single and multiple-neuromast afferents correspond to later and early-born cells, respectively. Whole-cell patch clamp recordings of afferent neurons show an inverse relationship between soma area and input resistance, where input resistance is a proxy for excitability. In addition, larger, early born cells have a lower spontaneous spiking frequency than smaller, later born cells. Taken together, a picture is emerging that large, early-born cells are less excitable and may therefore fire only to strong hydrodynamic stimuli across the whole body, while small, later-born cells that are more excitable sense local flows. We hypothesize that large, coarse coding afferents innervating multiple hair cells are critical for initiating powerful escape responses while small, fine coding afferents are responsible for modulating routine motor behaviors such as swimming.

**Innervation, orientation, and homology of the cephalic neuromasts
in gobies: Patterns and interpretation based on new keys from
“Evo-Devo” studies**

Jiakun Song

Institute for Marine Biosystem & Neurosciences, Shanghai Ocean University, Shanghai, China
Dept. of Biology, University of Maryland College Park, MD 20742
Div. of Fishes, NMNH Smithsonian Institution, Washington DC 20013-7012

Patterns of the lateral line neuromast (“sensory papillae”) are important morphological characters in gobioid taxonomy. Complexity of the pattern, makes the phylogenetic interpretation of this character in systematic analysis of gobies difficult (Miller 2005). Recently, studies on gene expression, embryonic genes and postembryonic growth of the lateral line system reveal some mechanisms of the pattern formation. The new knowledge on the primordial migration, neuromast deposition, and the “love affair” of the glia-axon-lateral line precursors during the development that brings us to a new dimension of understanding the innervation and homology of the lateral line patterns. This study is following the timing and sequence of the lateral line nerve branching and the distribution/orientation of the neuromast pattern formation, to analyze their adult patterns in thirteen species of gobioid fish (from five groups: Rhyacichthyidae, Odontobutidae, Butinae, Eleotridinae, and Gobiinae). The results lead to a new proposal of homology of the mixed, reduced, longitudinal, and transversal patterns. A phylogenetic interpretation of the “sensory papillae” pattern in gobioid systematics is proposed. However, what are the functional significant differences between the two types of superficial neuromasts that still need further discussion.

Filter properties of superficial neuromasts in the lateral line organ of the zebrafish (*Danio rerio*)

Gaston Sendin, Primož Pirih, Theo Dinklo and Sietse van Netten

Department of Neurobiophysics & Department of Artificial Intelligence, Rijksuniversiteit Groningen, The Netherlands

The lateral line organ endows aquatic vertebrates with the ability to localize underwater moving sources in the near range. In the zebrafish, this organ consists of arrays of elementary functional units, called neuromasts (NM). Neuromasts are distributed along the trunk, tail and the head and can be either exposed on the skin surface, protruding into the surrounding aquatic medium (superficial neuromasts or SN) or embedded in subcutaneous canals (canal neuromasts or CN). While the filtering characteristics of CNs have been extensively investigated, the dynamics of superficial neuromasts (SNs) is less well understood. Electrophysiologically, SNs have been described as velocity detectors, best transmitting fluid motion in the range of 10-70 Hz (Kroese et al., 1978; Kroese et al., 1980; Kroese and Schellart, 1992; Coombs & Montgomery, 1994; Kroese & Schellart, 1992). Here we report the use of a microscope-based interferometer to measure cupular motion in SNs of the zebrafish lateral line in response to fluid-jet stimulation with well defined properties (see van Netten 1988; Dinklo et al., 2007). Amplitudes of cupular responses had maxima spanning a 200-fold range and the great majority of them followed a bandpass behaviour with cut-off frequencies (f_c) in the range between 4-100 Hz (mean= 25 Hz) and a slope (n) of ~ 1 . Attenuation of responses at higher frequencies occurred with a slope of 20db/decade. A small proportion, however, did not show any clear cut-off frequency. We were also able to simultaneously monitor the motion of a single SN cupula at three positions, located at 8 μm , 28 μm and 38 μm above the fish skin. We observed that the lowermost position had a more restricted movement at lower frequencies and its phase shift was more positive than for distally located regions. In addition, microphonic potentials evoked by stimulation at varying frequencies were tuned at ~ 30 -50 Hz, and agreed well with the mechanical data. Our recordings suggest that SNs can be best described as first-order low-pass filters with a cut-off frequency of about 25 Hz. It is interesting to speculate on the function of the cupula in extracting information from the free stream via the boundary layer in which it is situated. Especially at high frequencies, the tips benefit from the larger amplitude in the free stream to which they are exposed. At low frequencies, however, also the cupular tip is within the boundary layer, but it might profit from higher amplitudes than experienced at the level of the hair bundles and may therefore transfer the signal to these lower cupular levels. The role that the relative stiff kinocilia play in the cupular matrix (McHenry & van Netten, 2007), extending to roughly halfway up the cupular height, may therefore be an important one. It may facilitate the transfer of mechanical flow signals downwards to the sensory hair cells, that otherwise would have received a significantly smaller stimulus.

Effects of surface wave frequencies on spatially selective responses of lateral line neurones in the midbrain of the African Clawed Frog

Francisco Branoner^{1,3)}, Zhivko Zhivkov³⁾, Ulrike Ziehm³⁾ and Oliver Behrend^{2,3)}

¹⁾ Ludwig-Maximilians-Universität, Department Biology II, Neurobiology Division, Martinsried, Germany

²⁾ Ludwig-Maximilians-Universität, Munich Center for Neurosciences, Martinsried, Germany

³⁾ Humboldt Universität zu Berlin, Department of Biology, Aquatic Bioacoustics, Berlin, Germany

Xenopus laevis uses mechanosensory lateral lines (LL) to identify and localise objects on the water surface (e.g. potential prey) based on incoming surface wave signals. To illuminate central representations of wave emitting objects, we recorded extracellular responses to concentric waves in the animal's CNS. Wave signals were varied in frequency from 10-40 Hz and amplitude from 3.9-27.8 μm . Source locations covered 3 distances from 4-10 cm, and 6 different angles from 30-180°. 339 units showed significantly altered response rates during the presentation of water waves ($p < 0.05$, Wilcoxon), and were classified as LL-units. 153 LL-units were recorded in the Torus Semicircularis (TS), 79 of those in the laminar nucleus of the TS (TL) that is mainly known for its strong acoustic input. Indeed, 69.2% of 39 LL-units in the TL showed bimodal responses when stimulated with acoustic signals indicating multimodal processing is frequent in the TL. In the majority of the tested LL-units the evoked spike rates varied with changing wave parameters ($p < 0.05$; ANOVA; amplitude: 76.3% of $N=160$; frequency: 74.4% of $N=270$; source angle: 93.6% of $N=79$; source distance: 63.7% of $N=213$). Potentially functional specialisations across midbrain areas were suggested by three observations: 1. The ratio of best neuronal responses to signal frequency classes ≤ 25 versus > 25 Hz increased from caudal to rostral midbrain sections ($p=0.001$; Chi^2 ; $N=81$) and differed between the TS and the Optic Tectum (OT; Chi^2 ; $p < 0.05$). 2. The ratio of units spatially tuned to 30° versus 120° rose from superficial to ventral midbrain layers ($p=0.05$; Chi^2 ; $N=26$). 3. The relation of LL-units that selectively responded to either frequency-modulated ($N=27$), or non-modulated waves ($N=62$), respectively, deviated across the TS and OT ($p < 0.05$; Chi^2). Many LL-units responded well to particular combinations of spatial and temporal wave parameters not unlike those caused by prey objects on the water surface. In subsequent recordings, significant response rate changes to both source angle, and wave frequency variation were observed in 82.5% of 80 units. Response rate changes to both source distance, and wave frequency variation were registered in 49.3% of 213 units. However, in a combined test paradigm only 7 of 21 tested angle-sensitive units showed robust best responses across 6 source angles when wave frequencies were varied. In that case, also only 6 of 20 tested distance-sensitive units showed robust best responses across 3 source distances. That is, spatially selective responses seemed instable across different wave frequencies ($p > 0.05$; Chi^2). Conversely, population responses to frequencies remained robust independently from source angle or distance, respectively ($p < 0.001$; Chi^2 ; $N=26$, and $N=36$, respectively). We propose further studies on the frequency dependent occurrence of spatially selective responses in the CNS that might reflect temporal integration processes in central map formation.

Information processing in the mechanosensory and electrosensory lateral line systems

Michael H. Hofmann¹⁾, Lon A. Wilkens²⁾, Horst Bleckmann¹⁾, and Boris P. Chagnaud³⁾

¹⁾ Institute for Zoology, University of Bonn, Germany

²⁾ Department of Biology, University of Missouri, St. Louis, USA

³⁾ Division of Neurobiology, Department Biology II, University of Munich, Germany

The electrosensory system responds to electric fields that are quite different in nature from mechanosensory systems that detect water movements. There are, however a number of similarities. The electrosensory (eLL) and mechanosensory lateral line (mLL) systems have the same ontogenetic origin. Functionally, both systems respond to flow fields. Both systems consist of receptors distributed all over the skin surface and central information processing most likely involves computations based on receptor array information. The hindbrain centers processing these modalities are quite similar in cytoarchitecture and in both systems, secondary neurons receive massive input from the cerebellum. We have investigated some aspects of central information processing in the mLL and eLL systems in the goldfish and the paddlefish, respectively. In the mLL, primary afferents respond to flow fluctuations, but do not appear to code flow direction and speed directly. Instead of coding water velocity, their response follows a fractional derivative in time and space. Electrosensory primary afferents are even more uniform and all follow a temporal derivative of the stimulus. Very important in both systems is the propagation of the stimulus along the receptor array. In the mLL, cross correlation of the responses of two or more neuromasts in a row could give accurate information of the relative speed, as it is the case in the eLL. In the latter, a frequency analysis gives further information on source location. In the mLL, a frequency analysis of the response of primary afferents revealed that the vortex shedding frequency of a Kármán vortex street is coded in the spike train. Thus, both systems respond to a derivative of the stimulus, the propagation of the stimulus along the receptor array allows to determine speed and direction, and a frequency analysis reveals further properties of the stimulus. Although the physical nature of the stimuli are very different, the information processing may be more similar and common principles may be employed in both, the mLL and eLL.

Analysing Kármán vortex streets from a situated perspective

Otar Akanyeti¹⁾, Maarja Kruusmaa²⁾, William M. Megill³⁾ and Paolo Fiorini¹⁾

¹⁾ Department of Computer Science, University of Verona, Italy

²⁾ Center for Biorobotics, Tallinn University of Technology, Estonia

³⁾ Department of Mechanical Engineering, University of Bath, UK

Kármán vortex streets form due to the presence of objects in the flow and appear as a columnar array of vortices, shed alternately in a periodic fashion. In underwater locomotion studies, Kármán vortex streets offer benchmark hydrodynamic challenges as they provide energy saving opportunities and they can be realized in laboratory conditions. On one hand, biologists are interested in understanding the underlying principles that enable fish to turn the oncoming vortices into external propellers to possibly minimize their energy consumption. On the other hand, roboticists are keen to apply these principles to develop underwater technologies with higher efficiency, maneuverability and autonomy as well as stability in the presence of turbulent events in the flow.

It is suggested here that the key requirements for technological success are i) a body that allows life-like interactions with the flow, ii) a sensing mechanism that keeps track of how flow is reconfigured around the body and iii) real-time processing methods that elaborate the available information for control in finite time. Differentiating the relevant from non-relevant information and fast decision making are desired abilities when reacting to perturbations in the flow.

Up until now, as an external observer, our understanding of a Kármán street is achieved by describing it with a few hydro-dynamically significant features such as vortex size, shedding frequency and wake wavelength. Because of the complex nature of Kármán streets and non-linear scaling laws, these features can only be estimated from data sets that have a sufficiently large observation window (both in time and in space). Zooming in the flow to gain an insight on "how it feels to be in the flow", we might need to reevaluate some of these measures as they are perceived differently from a situated perspective. We also need to introduce new measures to obtain a more comprehensive picture of local fluid-body interactions.

In this study, we generate a Kármán street by placing a cylinder in uniform flow. We first quantify the flow with digital particle image velocimetry. After ensuring the presence of a vortex street, we analyze its global features. We then observe the turbulence within the flow by placing an array of pressure sensors in the wake of the cylinder. We present methods to recover features of interest from local sensing picture of the flow. We also evaluate the minimum requirements of these methods. With an eye on extracting control relevant information, we extend our analysis by highlighting changes in the flow and distinguishing vortex streets from other flow regimes. During our analysis we focus on two points: i) requirement of real-time processing to facilitate the integration of our methods to real-world applications and ii) addressing the question of "what kind of information in a vortex street is available to flow sensing?" that may provide useful insights to biological studies on lateral line sensing.

O17

A dynamic model for information transmission in fish schools

Amanda Chicoli and Derek Paley

Department of Aerospace Engineering, University of Maryland, College Park MD, USA

Information transmission in schooling fish is thought to underlie rapid decision-making, including the collective response to a predation threat that results from individuals reacting to changes in the relative position and velocity of their neighbors. In this manner, fish schools can be thought of as an interacting network where signals are emitted through motion and sensed by neighboring individuals through visual and lateral line sensing. Here, we present a model of threat detection in schooling fish that represents the school as a one dimensional kinetic interaction network. Startle responses are incorporated in the model as instantaneous changes in the velocity that result from neighboring masses exceeding thresholds for relative position and relative velocity. We use this model of network analysis to analyze optimal performance in threat detection as well as to predict the number of fish responding to a predation threat. This model contributes to the understanding information transmission within fish schools.

Natural hydrodynamic stimuli

Wolf Hanke

Institute for Biosciences and Marine Science Center, Rostock University, Rostock, Germany

The aquatic environment is rich of information transferred through water motions, or hydrodynamic stimuli. Hydrodynamic stimuli are all kinds of water motions that can act on the sensory receptor systems of an animal. In a narrower sense, water motions that propagate through the water by compression and decompression in the form of acoustic waves, or that propagate on the water surface as surface waves, are often excluded from the definition of hydrodynamic stimuli, leaving mainly flow events in the near field of the object that generates the stimulus.

An important class of stimulus generating objects are of course moving organisms such as predators, conspecifics or prey. Our studies focused on swimming fish and the water movements that they leave behind, so-called hydrodynamic trails. These hydrodynamic stimuli have the potential to play a crucial role in predator-prey interactions in dark or turbid waters. They gain in importance through the fact that although they originally spread only in the near field of the stimulus-generating fish, the distance to the fish increases by the fish swimming away. The water movements that it leaves behind can remain in the water for 5 minutes or more for example in 10 cm goldfish, and can show a clear vortex structure for 1 minute or more. The structure of the hydrodynamic trails can differ significantly between fish species. Recently it was discovered that harbour seals (*Phoca vitulina*) can discriminate the wakes of different sized and shaped objects, presumably enabling them to decide which fish is worth hunting (Wieskotten et al, J. Exp. Biol., doi:10.1242/jeb.053926).

Escaping fish can produce even stronger water movements. In a C-start response, two to three characteristic jets containing vortex rings are produced that contain at least some information about the escape direction of the fish. Extrapolation from our measurements indicates that these hydrodynamic stimuli can still be detectable after 20 minutes and more (Niesterek et al., in preparation).

Another kind of hydrodynamic stimuli that fish produce originates from their respiration. We investigated the breathing currents, that is the water expelled through the gill openings, of three fish species, namely flounder (*Platichthys flesus*), eel (*Anguilla anguilla*) and trout (*Oncorhynchus mykiss*) and found highly significant differences in the strength and the direction of the water flow (Bublitz et al., in preparation). Most striking was the strong breathing current in flounders, that reaches more than ten times the maximum velocity of that in trout, relative to body weight. We conclude that breathing currents can play an important role in the detection of cryptic prey.

Beside predator-prey interactions, also intraspecific communication and the detection of conspecifics are tasks where hydrodynamic stimuli can play a role. We found that blindfolded harbour seals are able to follow the paths of conspecific harbour seals, and therefore measured the water movements left behind by a swimming harbour seal. These hydrodynamic trails grow to a width of 2 m or more and contain high water velocities that can still be about 30 mm/s after 30 s (Schulte-Pelkum et al., J. Exp. Biol., doi:10.1242/jeb.02708). Following the trails of conspecifics is believed to aid the animals in finding feeding grounds or other locations of interest.

Response to coise – Coding at high precision in the velocity-regime

Julie Goulet¹⁾, J. Leo van Hemmen¹⁾, Nicola Jung²⁾, Boris Chagnaud³⁾, Björn Scholze⁴⁾
and Jacob Engelmann⁵⁾

¹⁾Physik Department T35, TU München & BCCN - Munich, Garching, Germany

²⁾Max Planck Institute for Neuroscience and BCCN - Munich, Martinsried, Germany

³⁾BioZentrum der Ludwig-Maximilians Universität, Martinsried, Germany

⁴⁾Institut für Zoologie, Universität Bonn, Bonn, Germany

⁵⁾University of Bielefeld - Active Sensing, Bielefeld, Germany

The mechanosensory lateral line system, unique to aquatic vertebrates, is characterized by two types of sensory unit, superficial neuromasts (SN) and canal neuromasts (CN). Anatomical differences between both are linked to various physiological differences; most importantly, the canals render CNs unresponsive to flow perturbations as long as their scale is smaller than the inter-pore distance. SNs are affected by the rapid change of water velocity in a small layer of fluid around the fish (the *boundary-layer*, BL). Previous studies (Coombs, Hastings et al. 1996; Goulet, Engelmann et al. 2008), comparing the neuronal activity of the afferent nerve to the water velocity, concluded that the most efficient SN stimulus is the water velocity outside the BL. An influential theoretical analysis (Kalmijn 1988) and some recent 3D flow-field work (Rapo, Jiang et al. 2009) proposed a frequency dependency of the SNs, such that SNs should respond to the acceleration of the water outside the BL for low frequencies, when viscosity is dominant. At higher frequencies, however, SNs should respond to the velocity outside the BL.

Here, for the first time, we employ an information-theoretical analysis to study tuning and encoding of SNs and show that for all frequencies from 10-150Hz the water velocity *outside* the BL predicts the response. All SN afferents responded robustly to white-noise stimuli, revealing that an optimal decoder would need to rely on a temporal code. The correlation between the stimuli and their reconstructions was high and, depended on the stimulus intensity, reached up to 70%. Covariance analysis of the neuronal activity and coherence analysis between the neuronal response and the water displacement outside the boundary layer consistently showed that encoding is sufficiently described as a linear, velocity-sensitive mechanism.

In summary, we confirm the velocity sensitivity of SNs over a wide frequency range and show that the hypothesis of the SNs being sensitive to a *fractional* derivative of the water motion, i.e., changing from acceleration to velocity sensitivity with increasing frequency, is irrelevant to the SNs' encoding capability.

Coombs, S., M. Hastings, et al. (1996). "Modeling and measuring lateral line excitation patterns to changing dipole source locations." *J Comp Physiol [A]* 178(3): 359-371.

Goulet, J., J. Engelmann, et al. (2008). "Object localization through the lateral line system of fish: theory and experiment." *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 194(1): 1-17.

Kalmijn, A. J. (1988). "Hydrodynamic and acoustic field detection." *Sensory Biology of Aquatic Animals*, Springer, New York: 151-186.

Rapo, M. A., H. Jiang, et al. (2009). "Using computational fluid dynamics to calculate the stimulus to the lateral line of a fish in still water." *The Journal of experimental biology* 212(Pt 10): 1494-1505.

Impact of the aerodynamical signature of attacking spiders on the sensory performance of prey

Thomas Steinmann and Jérôme Casas

University of Tours, Institut de Recherche sur la Biologie de l'Insecte (IRBI)/CNRS, France

Predatory arthropods running on the ground are perceived by their prey using array of filiform hairs sensitive to the slightest air movement. Many studies focused on the coding of air flows by filiform hairs sensory systems, and the determination of how parameters like frequency, direction, or velocity can be implemented at different levels of the prey sensory system. In all these neurophysiological or computational study, the real nature of the input signal to be processed is rarely taking into account. The aim of this study was the identification of the elements composing the aerodynamical signature of an attacking predator and the determination of their impact on the sensory performance of a prey. This work was conducted in three steps, (i) the computation of the flow produced by a running spider, (ii) the time frequency analysis of the flow, (iii) and the computation of the incremental response of hairs of different sizes.

The development of a computational model of the previously reported air flow velocity upstream of a running spider was conducted using an iterative process starting with simple analytical approximations of a sphere and ending with a finite element model of intermediate geometric complexity. The Stokes, Oseen and potential flow analytical approximations as well as a computational finite element model of a sphere of the size of the spiders fitted the flow velocities poorly. The incorporation of the ground effect and the further addition of two small spheres acting as front legs gave a satisfactory fit. When considering the flow upstream of a running arthropod, both viscous forces and inertia must therefore be taken into account, as well as the ground effect and the kinematics of the appendages. Indeed, leg movements, despite their smaller contribution to the flow velocity, introduce characteristic high frequencies in the aerodynamical signature of incoming predators, which are picked up by prey.

In order to prove this statement, we analysed the time frequency characteristics of these signals using Fast Fourier Transform and Wavelets. It appears that the flow generated by a moving body will result in a broadband signal, with low frequencies appearing first, and higher frequencies appearing later. Taking individually, the different components, legs movement, body to ground distance, will lead to the timing of appearance and increase of specific frequencies, establishing a specific "spider attack signature", conspicuous for the prey.

The last part of the study was the establishment of the prey hair canopy perception of these broadband signals. We combined the individual hair flow velocity thresholds at a given frequency and the time frequency signature of the spider attack to determine the specific time frequency response of individual hairs. Long hairs fire first, at lowest frequencies, and small hairs are recruited later. This dynamical recruitment of hairs of different sizes could be the first step of coding of such a complex signal essential for the survival of prey. It also highlights an adaptation of the structural, external complexity of the sensory organs to a specific time frequency pattern of those signals. This approach, which consisted in investing ramp signals rather than oscillatory flows, allows us to revisit the question of the large spectrum of hair sizes within cercal sensory organs. Having such a broad range of hair sizes offer the cricket the possibility to generate an impulse pattern at the primary level of the signal transduction that truthfully characterizes the complexity of the flow generated by the predator.

O21

Differentiation of submerged objects by means of unsteady flow signatures: a study of the fish lateral line

Adrian Klein, Maximilian Bothe, Simon Kranz, Jan Winkelkemper, Horst Bleckmann

Institut für Zoologie, Universität Bonn, 53115 Bonn, Germany

Inanimate objects exposed to running water as well as objects moving through the water cause hydrodynamic perturbations. With aid of the mechanosensory lateral line fish can detect weak water motions and pressure gradients. Fish use lateral line information for predator avoidance, prey capture, schooling and schooling, rheotaxis and energy efficient locomotion in unsteady flow. The differentiation of inanimate and animate objects is crucial for the survival of animals. The neuronal mechanisms used by fish to analyze hydrodynamic perturbations may be useful for the implementation of smart algorithms in autonomous submarines. Our work focuses on the lateral line organ of fish and the neuronal coding of hydrodynamic perturbations with respect to object recognition. To uncover possible neuronal algorithms for object identification we exposed fish to the water motions caused by upstream objects. The activity of neurons recorded in the medulla (MON) and midbrain (TS) of fish was recorded. Electrophysiological data were compared with the data obtained from the artificial lateral line. To do so the artificial lateral line was exposed to the same upstream objects as the experimental fish. Several parameters were used to express the data obtained from the artificial lateral line in multidimensional space. We found that different objects cluster in distinct regions of the multidimensional space even if object position and/or flow velocity is altered, i.e. object differentiation is possible with artificial lateral lines. Flow fields obtained from particle image velocimetry were compared with data of the artificial lateral line.

Supported by the DFG (GRK1572)

Arrays of biomimetic hair flow-sensor dedicated for measuring flow patterns

A.M.K. Dagamseh and G.J.M. Krijnen

Transducers Science and Technology group (TST group), MESA⁺ Research Institute, University of Twente, Enschede, The Netherlands

Flow sensor arrays can be used to extract features from flow fields providing local measurements, rather than averaged signals, provided the sensors in the array structure can be interrogated individually. This paper addresses the latest developments in fabrication and array interfacing of biomimetic artificial air-flow sensors. Hair flow sensors in wafer-scale arrays have been successfully fabricated using SOI wafers with deep trench isolation structures. The current fabrication process differs from the previous process [1] in a redesign of the sensor electrodes enabling wafer-level array fabrication and individual array element interfacing.

Using Frequency Division Multiplexing (FDM) technique, we were able to simultaneously measure flow signals at multiple sensor positions. To employ FDM a bank of oscillators is used to feed different carrier signals to array columns. The amplitude modulated (AM) signals are collected per row of the array and fed into a single charge amplifier and further to synchronous demodulator to eventually extract the actual flow-velocity signals. Reconstruction of the flow fields by the array, while employing FDM, is demonstrated by localizing position of the sphere along the array using beamforming techniques. The results show a successful imaging of the sphere as detected by different hairs along the array while using array signal processing (i.e. Beamforming) techniques. The estimated separation distances between the hairs perfectly matches the measured distance. This verifies the capability of artificial hair arrays in imaging flow patterns.

With virtue of array signal processing techniques and FDM, once signals are retrieved from all individual array hairs, spatio-temporal flow patterns can be reconstructed while few system interconnects are required. This adds new dimensions to 3D imaging of the surrounding environment.

References

- [1] C. Bruinink et al., Proc. MEMS 2009, pp. 152-155.

Spatially segmented imaging of artificial hair arrays for on-line detection of characteristic near-wall flow signatures

Christoph Brücker

Technical University Bergakademie Freiberg, Germany

Signal detection of the flow near the surface of animals in nature is often not only based on single sensors but on arrays with characteristic spatial distribution. It has been shown that arrays are useful for spatio-temporal detection of bulk flow, source position detection and frequency discrimination (Van Netten 2004, Casas et al. 2010, Bleckmann et al. 2010). However, processing of the neural information on the sensor may be partially pre-conditioned on a low level by delay lines (Mulder-Rosi et al. 2010) or correlation of neighboring signals (Chagnaud et al. 2008). However in highly turbulent flows it is not understood how complex flow signals are separated from each other. This is also depending on the typical signal structure of the environment of the living animal and adaptation to typical prey / predator footprints. So, presumably not the whole spectrum of spatial and temporal resolution needs to be detected for survival. Near wall flow sensing by dense artificial sensory hair arrays is documented by Brücker (2011). Therein all information is obtained simultaneously on larger surfaces with sufficient high spatial and temporal resolution. On the other hand, the processing of this information still needs a large image processing overhead including the upload and storage of the recordings. As a counterpart of the adaptation of natural sensory systems to prey / predator signals, flow control mechanisms are often also highly adapted to the characteristic flow patterns to achieve maximum efficiency. With the knowledge of such typical near-wall structures in turbulent flows such as hairpin vortices travelling along the wall with a certain size and spatial pattern, processing needs could possibly be largely reduced. Instead of using the whole sensor format for image processing, we apply a spatially segmented imaging of the hairs which is implemented by the method of using a lens system with distributed micro-lenses (Bauer et al 2009). The lens system we used in the recent study is arranged in form of a streamwise oriented wedge similar to the expected size and shape of larger hairpin vortices. Recent developments in high-speed and on-line processing of images using FPGA sensors (Field Programmable Gate Arrays) allow us to tune the processing such that the event of passage of a hairpin-type structure over the segmented image region is documented simply by tracking the mean average intensity of all segments in the micro-lens arrangements. This can be done on-line up to frequencies up to 1kHz. Further arrangements will be shown which could be tuned to other specific flow signatures.

- Chagnaud BP, Brücker Ch, Hofmann MH, Bleckmann H (2008) Measuring Flow Velocity and Flow Direction by Spatial and Temporal Analysis of Flow Fluctuations. *J Neurosci* 28, 1-15.
- Casas J, Steinmann T, Krjinen G (2010) Why do insects have such a high density of flow-sensing hairs? Insights from the hydromechanics of biomimetic MEMS sensors. *J R Soc Interface* 7(51), 1487-1495
- Mulder-Rosi J, Graham I, Cummins GI, and John P. Miller JP (2010) The Cricket Cercal System Implements Delay-Line Processing. *J Neurophysiol* 103: 1823–1832
- van Netten S (2004) Hydrodynamic detection by cupulae in a lateral line canal: functional relations between physics and physiology. *Biological Cybernetics* 94, 67-85.
- Bauer D, Chaves H, Brücker Ch (2009) A multiple-segment long-distance microscope for flow visualization and measurements. *Measurement Science and Technology*

Stress-driven artificial hair cell for flow sensing

Francesco Rizzi¹⁾, Antonio Qualtieri¹⁾, Lily Chambers²⁾, William Megill²⁾,
and Massimo De Vittorio¹⁾

¹⁾ Center for Biomolecular Nanotechnologies @UNILE, Istituto Italiano di Tecnologia, Via Barsanti, 73010 Arnesano (LE), Italy

²⁾ Ocean Technologies Laboratory, Department Mechanical Engineering, University of Bath, BA2 7AY, UK

In some harsh environments vision can be limited and cannot always be used. Nature has evolved other sensory mechanisms such as fluid flow sensing: hair cells on skin are natural mechanoreceptors transducing motion into signal and providing velocity and pressure gradient information to the animal. The lateral line system of a fish is one example of such a modified receptor array. This kind of sensor could be a key feature for underwater vehicles navigating through complex environments.

Several approaches to a biomimetic design of an Artificial Hair Cell-based (AHC) flow sensor have been proposed and are based on different sensing principles. A new biomimetic micro-electromechanical system (MEMS) has been realized based on exploiting a stress-driven geometry. We outline here the design and development of a Si/SiN multilayered cantilever (2 μm overall thickness, 100 μm wide and 1.5 mm long) where the internal stress gradient bends the beam out of plane allowing for surface flow velocity detection. A Nichrome-based (50 nm thick) strain gauge along the beam senses the deformation. A Wheatstone Bridge circuitry has been integrated on the sensor device. This configuration eases the microfabrication process and allows a tip height greater than 500 μm . Finally, a water resistant coating allows the device to be able to sense underwater. A set-up for applying up to 50 cm/sec water flow velocity demonstrated initial sensing capabilities. An optical inspection guaranteed a mechanical resistance of the flow sensors in this velocity range.

The stress-driven geometry, in tandem with various surface-coating material properties (SiN, SU8, Parylene), can be optimized to design the best cantilever flexural stiffness to adapt to external environment. Flow sensitivity in one direction, along the length of the cantilever beam, and a stiffness value closer to the natural cupula mimics the directionality and sensitivity of a biological lateral line neuromast.

This is a promising bio-mimetic approach to an artificial hair cell to allow for adaptation to changing environments. This technology paves the way for the fabrication of sensors with a small footprint and high integration density to be implemented in a variety of fields, such as bio-medical, oceanographic and automotive industries.

This work is carried out under the robotic Fish Locomotion and Sensing (FILOSE) project, supported by the European Union, seventh framework programme (FP7-ICT-2007-3).

Snookie - An autonomous underwater vehicle with artificial lateral line system

Andreas N. Vollmayr¹⁾ and Stefan Sosnowski²⁾

¹⁾ Lehrstuhl für theoretische Biophysik T35, Physik Department, TU München, Germany

²⁾ Lehrstuhl für Steuerungs- und Regeltechnik (LSR), TU München, Germany

Snookie is a project of the Excellence Cluster Cognition for Technical Systems (CoTeSys), aimed at designing and building an autonomous underwater vehicle with artificial lateral line system integrated with other sensory modalities.

The submarine is approximately 75 cm long and 40 cm in diameter. The control and sensor unit of a quadcopter is combined with six thrusters for good manoeuvring capabilities. An on-board pc allows us to perform high level navigation tasks, processing of measurement data from the artificial lateral line system and decision making.

The artificial lateral line system consists of an array of low cost hot thermistors integrated in the nozzle. The thermistors are run at constant temperature by means of an analogue control circuit.

Thermal dissipation at the sensor surface is a function of fluid velocity and thus can be measured via the power consumption of the sensor.

The talk will describe the design, the fluid mechanics and the resulting technical realization of the robot Snookie and it's artificial lateral line system.

Posters

Behaviour

P1

Influence of food availability on the station holding behavior of trout (*Oncorhynchus mykiss*) exposed to turbulent flow

Bernd Baier, Anja Przybilla, Ilka Niemeyer and Horst Bleckmann

Institut für Zoologie, Universität Bonn, 53115 Bonn, Germany

Trout (*Oncorhynchus mykiss*) are able to exploit flow fluctuations reducing their swimming effort. To do so they may hold station in the bow wake zone in front of a stationary object (e.g. a cylinder), they entrain (i.e. they hold station downstream of, and next to, the cylinder), or they show Kármán gaiting (i.e. for station holding they exploit vortices shed behind the cylinder). These behaviors are not only characterized by the position trout take with respect to the cylinder but also by different swimming kinematics. What behavior an individual fish shows in a given situation is not predictable, that means the integration of information about the flow conditions and intrinsic motivation of fish are not yet understood. Feeding motivation probably effects the position preferences of trout, so we tested whether food availability alters the preference of trout to swim in the hydrodynamic flow environment established around a stationary cylinder placed in uniform water flow. If no food was available, trout preferred entraining ($65.7 \pm 27\%$) over swimming in the bow wake zone ($3.3 \pm 8.2\%$) or Kármán gaiting ($3.2 \pm 6.3\%$). When food pellets were dropped upstream to the trout in the flow tank (water velocity 42 cm/s), the time trout entrained decreased to $42.7 \pm 29.2\%$. In contrast, trout now spent $26.2 \pm 30.4\%$ of the time in the bow wake zone. If trout were retested on 4 consecutive days they did not alter their station holding preference as a result of prior exposure.

The influence of the lateral line and visual system on station holding in trout

Anja Przybilla and Horst Bleckmann

Institut für Zoologie, Universität Bonn, 53115 Bonn, Germany

The most simplified experimental situation to study fishes in turbulent flow is to consider a fish in the hydrodynamic environment established around a stationary D-shaped cylinder placed in laminar water flow. This cylinder generates a staggered array of discrete, periodically shed, columnar vortices of alternating sign in the wake downstream of it, called a Kármán vortex street. Using this model system it has been shown that rainbow trout, *Oncorhynchus mykiss*, hold station relative to a stationary D-shaped cylinder by either swimming with undulating motions in the region of reduced flow in the wake behind it (drafting) or by swimming in the Kármán vortex street synchronising their axial swimming kinematics with the shed vortices (tuning, Kármán gait). For station holding, trout also use the high-pressure, reduced-flow bow wake zone in front of the stationary D-shaped cylinder. Trout also entrain downstream of, and next to, the stationary D-shaped cylinder and angle their bodies away from it and the main flow direction.

The Kármán vortex street is probably predictable by trout and lacks the complexity often found in natural aquatic environments. To address the issue of complexity, a motor-controlled system moved the D-shaped cylinder transversally to the mean water flow direction across the width of the flow tank. This allowed us to observe the behaviour of trout exposed to more unpredictable flow conditions and to assess the relative roles of the mechanosensory lateral line (LLS) and the visual system on the station holding behaviour. Vision and LLS information were restricted temporally by using infrared illumination (IR) and by pharmacologically/surgically blocking the LLS. In trout, like in many other fish, the peripheral lateral line consists of two receptor classes, superficial neuromasts (SN) freestanding on the skin and canal neuromasts (CN) embedded in subepidermal canals, situated on the head and trunk. SN and CN are sensitive to different flow characteristics. In experimental group I the posterior lateral line nerves were cut bilaterally behind the cleithrum. In experimental group II, streptomycin was used to block the whole LLS. In experimental group III the CNs were selectively blocked with gentamicin. Compared with the control group (vision and LLS intact) and with trout of group I and III, trout treated with streptomycin (group II) no longer followed the cylinder movement across the width of the flow tank. Our data suggest that only the SNs of the anterior lateral line are important for station holding and the responses to destabilizing flows.

Supported by the DFG

The effect of group size on rheotactic performance in schooling Giant Danio

Joseph Coleman¹⁾, Sachit Butail²⁾, Derek Paley²⁾, Sheryl Coombs¹⁾

¹⁾ Biological Sciences and J.P. Scott Center for Neuroscience, Mind and Behavior, Bowling Green State University OH, USA

²⁾ Department of Aerospace Engineering, University of Maryland, College Park MD, USA

When placed in a unidirectional flow field, many fish exhibit positive rheotaxis, a tendency to swim upstream. Positive rheotaxis confers many potential benefits, including the interception of downstream prey and energetic cost savings. Although rheotactic performance of individual fish has been characterized as a function of flow speed, little is known about rheotactic performance of schooling fish and how nearby conspecifics affect rheotactic performance. In this study, we examine the effects of group size (N= 1, 2, 4 and 8) and flow speed (0 to 1 BL/s) on rheotactic performance of giant danio (*Devario aequipinnatus*), a stream-dwelling, strongly schooling species. In a visually-impooverished flow tank, flow speed had little effect on rheotactic performance for group sizes smaller than 4, for which the mean % of time spent within +/- 45 deg of upstream was less than chance (25%) at all flow speeds. In contrast, the mean % of time spent upstream for the larger groups increased from near chance levels to over 60%. Furthermore, the mean distance from the downstream end of the tank was significantly correlated with the degree of upstream orientation and larger groups of fish were significantly more likely to maintain an upstream position at higher flow speeds than smaller groups. These results indicate that rheotactic performance is enhanced in larger groups of schooling fish. Future experiments will determine whether the apparent enhancement is due to a hydrodynamic benefit, sensory cues provided by nearby conspecifics or other factors.

Orientation behavior of the Suckermouth Catfish, *Hypostomus plecostomus*, in artificial stream flows

Neva Wood, Christina Howard and Randy Zelick

Department of Biology, Portland State University, Portland OR, USA

We describe an inexpensive laminar flow flume for behavioral experiments with fish up to 25 cm in length and for flow up to 40 cm s⁻¹. The flume (0.4 m dia. x 2.5 m long, 286 l filled volume) was constructed from standard plumbing pipe and supported with a simple welded steel frame, inspired by a well-considered published design^{1,2}. A fisherman's trolling motor (Minnekota Endura) was used to provide nearly silent flow.

The flume was used to analyze the behavior of *Hypostomus plecostomus*, a species of suckermouth catfish (Loricariidae). These fish are ideal subjects for flow studies because they maintain a fixed position by latching onto the substrate unless motivated to move. Fish attached in an energetically unfavorable orientation will predictably shift orientation as flow speed increases. One fish at a time was tested in a 1.9 x 0.37 x 0.1 m (L x W x H) portion of the flume (21 l volume), constrained by a collimator on the flow source side and netting on the downstream side. Two video cameras recorded fish position (overhead, side views). Eleven small *H. plecostomus* (5.5 - 13 cm) were tested. One fish was non-responsive to any flow change and excluded from analysis. We confirm results of Gerstner³ that fish began shuffling their position at approximately 8 cm s⁻¹ (n=10). They oriented (criterion of 30° for 80% of the duration of a given flow speed) to the flow at approximately 17 cm s⁻¹.

When averaged across all fish (n=10) for flows of 16 cm s⁻¹ or less, fish could maintain angles (long body axis) to flow between 20° and 80°. At flows of 18 cm s⁻¹ or more, the greatest maintained angle to flow dropped from 60° to 40°, with a mean of 20°.

To determine if the lateral line is required for flow-dependent orientation, in one set of experiments we mechanically abraded the surface of the fish to disrupt free-standing neuromasts. Fish were lightly anesthetized (0.02% MS-222) and neuromasts damaged using a scalpel to lightly scrape the fish's skin, similar to the procedure successfully used by Baker & Montgomery⁴. The fish's skin was minimally affected and the fish remained healthy and exhibited no signs of distress following the procedure. Fish were tested prior to scraping and again 24 hours after scraping. Comparison of control fish with those treated by abrasion showed that damage to neuromasts reduced the ability of fish to orient in the flow stream. Control fish maintained a mean angle to flow of 38° (n=6) at a flow of 17.5 cm s⁻¹ but after neuromast disruption the same individuals yielded an average angle of 60°, i.e., often remaining broadside to the flow. This implies that a functional lateral line is necessary for flow angle and/or velocity determination in *H. plecostomus*.

The design of the laminar flume with the use of this hardy species is a useful setup for studying how the lateral line processes bulk water flow information.

References

1. Vogel, S „Making Flow Tanks“ www.sicb.org/dl/serve.php3?file=11.1.rtf
2. Vogel S (1978) Simple Flow Tanks for Research and Teaching. *BioSci* 28:638
3. Gerstner CL (2007) Effect of oral suction and other friction-enhancing behaviors on the station-holding performance of suckermouth catfish (*Hypostomus* spp.). *Can J Zool* 85: 133-140.
4. Baker & Montgomery (1999) The sensory basis of rheotaxis in the blind Mexican cave fish *Astyanax fasciatus*. *J. Comp. Physiol. A* 184:519-527

Discrimination of spatial parameters in hydrodynamic trails
Daniela Haas, André Steiner and Horst Bleckmann
Institute of Zoology, Poppelsdorfer Schloß, University of Bonn, Germany
<p>There is high interspecific diversity in the morphology of the mechanosensory lateral line system of fishes. However, a clear systematic relationship between lateral line morphology and the systematic group of a fish species, or the habitat it prefers (e.g., limnophilic / reophilic), or its lifestyle, or feeding habit has never been shown. Anyhow, many previous studies have demonstrated that the lateral line is used by fishes to capture prey (e.g., Hoekstra and Janssen 1985). Moreover, it has been suggested, that fish can follow the hydrodynamic trails generated by moving prey using sensory input from the lateral line (Pohlmann et al. 2001; Pohlmann et al. 2004).</p> <p>In the present study we investigated whether European perch (<i>Perca fluviatilis</i>) can be conditioned to a hydrodynamic trail generated by an artificial rubber-fish (6 cm length). Two series of experiments were conducted using two-alternative forced-choice tasks. In the first series, perch were trained to follow the hydrodynamic trail generated by the rubber-fish into one of two goal compartments that were located side by side in an experimental tank. In the second series, perch had to intercept the hydrodynamic trail generated by the rubber fish in a T-maze and discriminate between two alternative motion directions (from left to right or opposite) of the rubber-fish.</p> <p>During pre-training, perch were allowed to follow the rubber-fish using visual in addition to other sensory information. Under these conditions, all individuals (N = 4) learned to follow and find the rubber-fish. In successive experiments, perch were prevented from seeing the rubber-fish moving by introducing a blind between their start compartment and that part of the tank that contained the rubber fish. They were released only after the movement of the rubber fish had ended. 3 out of 4 individuals learned to find the goal location to which the rubber fish was moved and discriminate it from the other goal location at which an identical rubber fish, that was not previously moved, was presented. We hypothesize that in order to perform this task perch used the hydrodynamic trail produced by the rubber-fish. In the second series of experiments, perch were able to discriminate between the two possible motion directions of the rubber-fish by intercepting and following its hydrodynamic trail, suggesting that they were able to extract directional information from the hydrodynamic trail.</p> <p>Particle Image Velocimetry (PIV) revealed that the hydrodynamic trail of the rubber-fish was similar to the hydrodynamic trails of living fish. Thus, our results indicate that European perch (<i>Perca fluviatilis</i>) can detect and follow hydrodynamic trails generated by swimming fish. Although the involvement of other sensory systems cannot be completely ruled out in our experiment, most likely the perception of the information that is contained in a hydrodynamic trail is achieved with the lateral line.</p> <p>References: Hoekstra, D., Janssen, J. (1985): Non-visual feeding behavior of the mottled sculpin, <i>Cottus bairdi</i>, in Lake Michigan. <i>Environmental Biology of fishes</i> 12 (2): 111-117. Pohlmann, K., Atema, J., Breithaupt, T. (2004): The importance of the lateral line in nocturnal predation in piscivorous catfish. <i>The Journal of Experimental Biology</i> 207: 2971-2978. Pohlmann, K., Grasso, F. W., Breithaupt, T. (2001): The nocturnal predatory strategy of piscivorous catfish. <i>Proceedings of the National Academy of Sciences</i> 98 (13): 7371- 7374.</p>

Detection of complex hydrodynamic stimuli by the fish lateral line

André Steiner and Horst Bleckmann

Institut für Zoologie, Universität Bonn, 53115 Bonn, Germany

Hydrodynamic stimuli, local water movements and pressure gradients, provide important information about the aquatic habitat of fish. They are generated by conspecifics, predators, prey or by objects in running water. Fish perceive hydrodynamic stimuli with the mechanosensory lateral line. Lateral line information can be used for orientation, prey detection, predator avoidance, schooling and for inner-specific communication. In addition, Kármán vortex streets, emerging behind objects in running water, can be used to save locomotive energy during station holding. We do not know whether and to which precision fish can detect and discriminate vortex streets. Here we investigated the perception of Kármán vortex streets in roach (*Rutilus rutilus*) in a two alternative forced choice task. Roach were trained to enter the compartment of a flow tank in which a vortex street was generated both with and without visual cues. Whereas three out of five roach learned the task under daylight conditions, only two roach then relearned the task under infrared illumination. Since the hydrodynamic stimulus required a certain time to build up, response times were determined to uncover responses to non-hydrodynamic cues. In both roach that learned the task under infrared illumination, response times positively correlated with the performance, indicating the use of hydrodynamic information.

Feeding in the dark: Peacock cichlids detect prey using the lateral line system

Margot A. Bergstrom and Jacqueline F. Webb

Department of Biological Sciences, University of Rhode Island, Kingston RI, USA

Among fishes, only a small number of taxa have been experimentally determined to use their mechanosensory lateral line system to detect their prey. Among teleost fishes, there are four lateral line canal morphologies: narrow, branched, reduced and widened. Widened canals, characterized by reduced ossification, large neuromasts, and large pores in the canal bone covered by epithelia pierced by small pores, are quite obvious on the head of fishes. Widened canals have evolved convergently in fishes living in habitats with relatively low levels of hydrodynamic noise and/or in light-limited (e.g., turbid) environments where non-visual senses are likely to be more important. First described in the Eurasian ruffe, *Gymnocephalus cernuus*, widened canals are common among mesopelagic and bathypelagic and some bottom dwelling marine fishes and a small number of freshwater taxa that tend to live in turbid waters or over sand. Widened canals are suggested to be an adaptation for prey detection, but there is little direct experimental evidence. The exception is work on the freshwater Eurasian ruffe (*Gymnocephalus cernuus*) that demonstrates its superior capabilities in detecting prey in the water column, especially in low light, when compared to yellow perch (*Perca*), a species with narrow canals. Cichlid fishes are known for their explosive adaptive radiations in the African Rift Lakes, generally have narrow lateral line canals, and are considered to be visual predators. However, peacock cichlids (*Aulonocara* spp.) of Lake Malawi are reported to use their widened lateral line canals for the detection of hydrodynamic stimuli generated by their benthic invertebrate prey. We tested the hypotheses that these fishes are able to detect live invertebrate prey using their lateral line system. We allowed individual *A. stuartgranti* to feed on live and dead tethered brine shrimp, under light and dark (with IR illumination) conditions. Prey detection behavior (time to first strike, # prey strikes, detection distance and angle, strike order [live/dead]) was analyzed using HD digital video recordings from above a behavioral arena. Cobalt chloride was used to temporarily inactivate the lateral line system and these same parameters were measured in trials before treatment with cobalt, with cobalt treatment, and then after several weeks of „recovery“ from cobalt treatment. We have demonstrated that *Aulonocara* can successfully feed in the dark using its lateral line system, that it uses different strategies in the light and in the dark, and may in addition, rely on input from other non-visual sensory systems for prey detection. This work demonstrates the role of widened lateral line canals in prey detection, establishes a new system in which to study lateral line-mediated feeding behavior on benthic prey in fishes, and provides insights into the ecological and evolutionary significance of non-visual feeding behavior in cichlid fishes.

Supported by NSF grant IOS-0843307 to JFW.

The contribution of vision and lateral line information to prey capture behavior in three species of fish

Judith Meyer-Schwickerath, Bernd Baier and Joachim Mogdans

Institut für Zoologie, Universität Bonn, 53115 Bonn, Germany

Animal behavior is guided by multiple sensory inputs. However, studies on the relative contributions of different senses to particular behaviors are scarce. We studied the relative contributions of the visual and the lateral line sense for the catching of live prey (*Gammarus pulex*) in a perciform fish, the pumpkinseed (*Lepomis gibbosus*), and in two cyprinid species, minnow (*Phoxinus phoxinus*) and gudgeon (*Gobio gobio*).

Quantification of the 3D swimming paths showed that in all species swimming behavior critically depended on the available visual information. Swimming distance of fish and prey as well as the distance between fish and prey were significantly smaller under infrared illumination compared to room light conditions. Moreover, while fish showed an increase in swimming distance just before snapping the prey in room light, this was not the case under infrared illumination.

At least in pumpkinseed and minnow, the lateral line played an important role for catching prey in the dark. In these species but not in gudgeon, prey capture success decreased under infrared illumination and in complete darkness. However, all fish were able to capture prey in darkness suggesting that sensory information other than vision was used.

Inactivation of the lateral line with the antibiotic streptomycin caused a further decrease in prey capture success in pumpkinseed and minnow but not in gudgeon, suggesting that these two species used lateral line information for prey catching in the dark. Surprisingly, under infrared light, streptomycin treated pumpkinseed performed as well as untreated pumpkinseed, raising the possibility that this species is sensitive to near infrared wavelengths.

Sensitivity of crocodiles (*Crocodylus niloticus*) to water surface waves

Marcel Gerson, Tobias Kohl, Guido Westhoff and Horst Bleckmann

Institute of Zoology, Poppelsdorfer Schloß, University of Bonn, Germany

We determined the behavioral thresholds of juvenile crocodiles (*Crocodylus niloticus*) to water surface waves. Stimuli were produced by blowing a sinusoidal air stream (23 Hz, 200 ms duration) onto the water surface. If a crocodile (N=2) orientated towards the stimulus source (positive reaction) it was rewarded. Each trial was digitally recorded and analyzed with the commercial software Vidana. Due to the attenuation of water surface waves the percentage of positive responses decreased with increasing distance from the stimulus source. The distance where the crocodiles responded in 50% of the cases defined the behavioral threshold. At this distance the peak-to-peak amplitude of the surface wave was 63 µm. Our study shows that Nile crocodiles, like alligators (Soares 2002), are sensitive to water surface waves. Whether the behavioral responses are mediated by the integumentary sensory organs found in morphological studies (Jackson 1996; von Düring 1973) remains to be shown.

References:

- Jackson K, Butler DG and Youson JH (1996) Morphology and Ultrastructure of Possible Integumentary Sense Organs in the Estuarine Crocodile (*Crocodylus porosus*). *Journal of Morphology* 229: 315-324.
Soares D (2002) An ancient sensory organ in crocodylians, *Nature* 417: 241-242.
Von Düring M (1973) The ultrastructure of lamelled mechanoreceptors in the skin of reptiles. *Z. Anat. Entwickl.-Gesch.* 143: 81-94.

Perception of vortex rings by stationary Harbour Seals (*Phoca vitulina*)

Yvonne Krüger, Sven Wieskotten, Lars Miersch, Guido Dehnhardt, Wolf Hanke

Institute for Biosciences and Marine Science Center, Rostock University, Rostock, Germany

Seals often hunt in dark and murky waters, where vision is impaired. While odontocetes can rely on echolocation under such conditions, several experiments have shown that harbour seals (*Phoca vitulina*) rely on a quite different sensory system. The mystacial vibrissae or whiskers of harbour seals represent highly sensitive hydrodynamic sensors allowing the animals to detect and track hydrodynamic trails left by prey fish. A hydrodynamic trail left behind a swimming fish propelled by continuous beating of the caudal fin contains vortex rings with a median jet flow. In this study, single vortex rings with predefined sizes, velocities and accelerations, similar to those produced by swimming fish, were generated by vortex ring generators. The vortex ring generators consisted of 20*20*20 cm cubes with a 2 cm circular opening on one side. On top of the cube, a 10 cm diameter vertical pipe was mounted in which a plunger was moved by a linear motor to expel water through the circular opening. Particle Image Velocimetry (PIV) was used to quantify the parameters of the generated vortex rings. In a psychophysical experiment with harbour seals, two vortex ring generators were fixed on two semicircular horizontal profiles on either side of a point directly ahead of the animal's snout. In a first step, the ability of blindfolded stationary harbour seals to perceive and detect the direction of single vortex rings was investigated. For every trial, one of the two generators was oriented towards the animal in order to produce a vortex ring that travelled to the seal's vibrissal pad (the second vortex ring generator produced a vortex ring that travelled away from the seal and was used to avoid acoustical directional cues). The blindfolded seals were able to perceive vortex rings and detect their direction, either coming from the right or the left side at an angle of 60° to the midline of the animal, over a range of various moderate maximum velocities in the median jet flow. In the course of the experiments, one of the seals developed a head movement strategy which enabled the perception of vortex rings with maximum velocities that were only about one third as high. In a second step, a reliably perceivable vortex ring was used to find a minimum angle from which the direction of the vortex ring is still detectable by the vibrissal system. This angle, termed the 'minimum hydrodynamically perceivable angle' (MHPA), was experimentally investigated in accordance to the underwater minimum audible angle (MAA) of harbour seals. A preliminary upper bound of the MHPA was assessed. The tested harbour seal was able to detect the direction of a vortex ring coming from an angle of +20° or -20° to the midline of the animal if the head movement strategy was applied. Preliminary results indicate that the animal is able to perceive the direction of the vortex ring even at significantly smaller angles.

Supported by the DFG (Ha4411/8 and De538/9, priority program SPP1207)

Hydrodynamic discrimination of wakes generated by objects of different size or shape in a Harbour Seal (*Phoca vitulina*)

Sven Wieskotten¹, Björn Mauck², Lars Miersch¹, Guido Dehnhardt¹, Wolf Hanke¹

¹ Institute for Biosciences and Marine Science Center, Rostock University, Rostock, Germany

² Institute of Biology, University of Southern Denmark, Odense, Denmark

Harbour seals (*Phoca vitulina*) cannot rely on their visual system only when foraging in dark or murky waters. Consequently, a high selection pressure on the development of sensory systems suitable to support or even substitute vision under such conditions can be assumed. While toothed whales possess a sonar system, corresponding sensory abilities are not known in pinnipeds. In this respect it has been shown for blindfolded harbour seals that they can use their whiskers to detect and follow hydrodynamic trails left by different kind of moving objects, such as miniature submarines, conspecifics or even skin divers. To be able to adapt their foraging tactics and thus optimise hunting success, it might be crucial for a seal to recognise different parameters of a fish trail even before other sensory modalities play a role. Therefore we investigated the ability of a harbour seal to discriminate objects of different size or shape by their hydrodynamic signature only. Particle Image Velocimetry (PIV) was used to identify the hydrodynamic parameters that a seal may be using to do so. Hydrodynamic trails were generated by different sized or shaped paddles, which were moved in the calm water of an experimental box to generate a characteristic hydrodynamic signal. A two-alternative forced-choice procedure was used. The seal was blindfolded and supplied with headphones for acoustical masking. It stationed in front of the box while a hydrodynamic trail was generated inside the box by moving one of the objects through the water. After a delay of 3 s, the headphones were removed and the animal entered the box to decide whether the hydrodynamic trail had been generated by a standard or an alternative object. The seal indicated its decision by choosing one of two response targets at the front side of the box. The tested seal was able to discriminate object size differences of down to 3.6 cm (Weber fraction 0.6) when paddles were moved at the same speed. In the second experiment the seal was able to distinguish hydrodynamic trails generated by flat vs. cylindrical, triangular and undulated paddles of the same width. PIV measurements demonstrated that the seal could have used more than one hydrodynamic parameter to discriminate object size. Beside the highest velocities and the steepness of the gradients within the wake, the size of counter-rotating vortices and the spatial extension of a wake were typical for the different sized objects and were in the sensory range of the seal. To discriminate different shaped objects the tested seal could have used two hydrodynamic parameters within the wake: the spatial extension of the whole wake and the arrangement of the vortices. In an additional set of experiments we tested whether the seal used highest velocities or the steepness of the gradients to discriminate object size and whether it used the spatial extension of the wake for shape discrimination by varying moving speed and paddle size, respectively. The tested seal was still able to discriminate between the respective object sizes. However, the minimum size difference the seal needed to distinguish between different sized objects increased slightly to 4.4 cm (Weber fraction 0.73). For the shape discrimination task, the seal was then only able to distinguish the flat from the triangular paddles. Our results indicate that the discrimination abilities of the tested seal depend, similar to what was found in fish, on more than one hydrodynamic parameter, and that the size of single vortices or the whole wake seem to play a major role.

Supported by the Volkswagenstiftung and the DFG (Ha4411/8 and De538/9, priority program SPP1207)

Morphology of the peripheral lateral line in two cypriniform fish

Johanna Franken, Anke Schmitz and Joachim Mogdans

Institut für Zoologie, Universität Bonn, Germany

The fish lateral line consists of superficial neuromasts (SN), which are freestanding on the skin, and canal neuromasts (CN), which are embedded in lateral line canals. We investigated the morphology of the lateral line in two Cypriniform species, the Silver Shark (*Balantiocheilos melanopterus*, Cyprinidae) and the Siamese Algae Eater (*Gyrinocheilus aymonieri*, Gyrinocheilidae). We used vital stains (methylene blue and DASPEI) to determine neuromast number and location and, in *Gyrinocheilus*, scanning electron microscopy to determine SN orientation.

Balantiocheilos (n=6, average fish length 5.1 ± 0.2 cm) had more than 3000 SN on each body side, of which 42% were on the head, 48% on the trunk and 10% on the tail fin. On the trunk, SN were found along the entire rostro-caudal extent but not on back and belly.

Gyrinocheilus (n=6, average fish length 3.8 ± 0.3 cm) had about 300 SN per body side, of which 35% were on the head, 45% on the trunk and 20% on the tail fin. On the trunk, SN were found only on scales along the trunk canal and on the back just below the dorsal fin. SN on the trunk and tail fin were oriented with their axis of preferred sensitivity predominantly parallel to the longitudinal axis of the fish, whereas SN on the head had various orientations.

Both species had lateral line canals on the head and on the trunk, typically with one CN between adjacent canal pores. In *Gyrinocheilus*, the head canal system was incomplete and differed between individuals, i.e. it was not yet fully developed.

The differences in SN number and distribution between *Balantiocheilos* and *Gyrinocheilus* coincide with differences in body form and, at least as adults, in life style. *Balantiocheilos* has a slender body, occurs in midwater depths in large and medium-sized rivers and lakes, and feeds mostly on small crustaceans, rotifers as well as insects and their larvae. *Gyrinocheilus* has a more compact body, occurs in medium to large-sized rivers, may enter flooded fields, is found predominantly on solid surfaces and grazes algae. The individuals studied here were not full-grown and thus may have different life styles compared to adults. Thus, functional relationships between lateral line design and body form and/or life style in these two species as well as in other fish remain to be determined.

How is coding of stimulus orientation and position wired?

Jesús Pujol-Martí, Adèle Faucherre, Jean-Pierre Baudoin and Hernán López-Schier

Laboratory of Sensory Cell Biology and Organogenesis, Centre de Regulacion Genomica,
Barcelona, Spain

Sensory perception is a complex process that allows organisms to sample the environment and to react appropriately. A serious obstacle in research on sensory systems is that their constituent cells perform their main physiological function of transmitting environmental stimuli to the brain only in their native context. Many vertebrate sensory neurons are very difficult to access even in newborn animals, precluding circuit observation, mapping or manipulation. By contrast, fishes and amphibians have a superficial and accessible mechanosensory organ called lateral line. The lateral-line system serves to detect hydromechanical variations around the animal's body. The functional units of the lateral line are called neuromasts, which occur freestanding on the surface of the animal. Each neuromast contains 20 to 30 mechanosensory hair cells organized in two population of opposite polarity. Sensory information gathered by hair cells is collected by afferent neurons and sent to the hindbrain. The distribution of neuromasts along the animal's body is represented by a dorsoventral organization (somatotopy) of the afferent neurons' first order projections within the hindbrain. The organization of hair cells in two opposite polarities in the neuromast, and the somatotopic representation of the lateral line in the brain indicate that this sensory system may be able to localize mechanical signals along the animal's body and discriminate the signal's vectorial component. Our strategy is to use this sensory system to study sensory neuron projections and connectivity with peripheral and central targets. So far, we have shown that lateral-line afferent neurons can recognize the orientation of hair cells to form synapses with hair cells of identical polarity, dividing the neuromast into functional plane-polarized compartments. In addition, we have shown that the patterning of both central and peripheral projections of the lateral line afferent neurons depends on the timing of neuronal differentiation.

**Looking at owls from two angles; A study of wing anatomy of the barn owl
Tyto alba with two different multi camera systems**

Thomas Erlinghagen¹⁾, Thomas Wolf²⁾, Robert Konrath²⁾, Hermann Wagner¹⁾ and
Werner Baumgartner¹⁾

¹⁾RWTH Aachen University, Institute of Zoology, 52074 Aachen, Germany,

²⁾Deutsches Zentrum für Luft- und Raumfahrttechnik e.V., Institut für Aerodynamik
und Strömungsmechanik, Abt. EV Bunsenstr. 10, 37073 Göttingen

Barn owls have undergone many adaptations to optimize flight behaviour for catching small rodents in environments where visibility is impaired. These birds have, for example, developed structures that reduce noise production during flight and they have adapted wing form to slow flight. For such reasons, the wing of the barn owl serves – in a biomimetic sense - as a role model for the construction of airplane wings. The biological part of such a project is to exactly measure wing form. Measuring under life conditions has turned out to be a difficult problem, because wing form in bird flight is not constant. The DLR Göttingen and the RWTH Aachen have developed two different systems which allow high precision measurements of the owl wings during free flight. Both systems rely on multiple cameras that record the barn owl during flight. The first system uses a fine random pattern of light points which is projected onto the wing surfaces. Each surface is being recorded by two synchronised high speed cameras. By correlating the dot patterns recorded by the two cameras a 3D model can be generated. The second approach uses a number of laser sheets, to create cross sections of the wing. Line lasers are affixed to a frame so that unbroken laser lines are projected onto the wing surface perpendicular to the flight path. The shape of the laser lines on the wing surface is recorded with single-lense reflex cameras, and three-dimensional shape of the upper and lower side of the wing is reconstructed. The weaknesses and the strengths of both approaches will be discussed and compared.

Responses of toral lateral line units to laminar flow and artificial turbulence

Jens Hellinger and Horst Bleckmann

Institut für Zoologie, Universität Bonn, 53115 Bonn, Germany

Fish use the mechanosensory lateral line to detect weak water motions. Although fish can detect the direction and velocity of bulk water flow the peripheral lateral line neither encodes bulk flow velocity nor bulk flow direction. Instead the peripheral lateral line responds in proportion to the micro-fluctuations that are superimposed on the flow. Simultaneous recordings from two lateral line afferents that innervated different neuromasts revealed that a cross-correlation analysis of the spatial temporal flow fluctuations experienced by a fish can be used to determine bulk flow velocity and bulk flow direction. Assuming that a cross-correlation mechanism is implemented in the central lateral line pathway some central units should be sensitive to bulk flow velocity and bulk flow direction but not to the fluctuations superimposed on the flow. To test this we recorded toral lateral line units from goldfish (*Carassius auratus auratus* Linne, 1758) while stimulating the animal with artificially induced turbulences superimposed on the flow. 90% of all units responded only to high water velocities (10 cm s^{-1} - 12 cm s^{-1}) and units were (30%) or were not directionally sensitive. If bulk flow velocity was kept constant only 20% of the flow sensitive toral lateral line units were not sensitive to flow fluctuations.

Sensing of bulk flow velocity and bulk flow direction in rheophilic fish

Hendrik Herzog, Adrian Klein and Horst Bleckmann

Institut für Zoologie, Universität Bonn, 53115 Bonn, Germany

Fish can sense water motions with their mechanosensory lateral line. This sensory modality is required for prey detection, predator avoidance, schooling, intraspecific communication, rheotaxis and station holding. Previous studies have shown that lateral line afferents of goldfish (*Carassius auratus*) neither encode bulk flow direction nor bulk flow velocity. Instead they respond in proportion to the micro-fluctuations that are even present in quasi laminar flow. Simultaneous recordings from two lateral line afferents that innervate different neuromasts revealed that a specific analysis of spatial temporal flow fluctuations can be used to determine flow velocity and flow direction without measuring the DC component of the flow. However these studies were done with goldfish that naturally live in small ponds and therefore are not exposed to bulk water flow. In the present study we investigated the flow sensing capabilities of the golden ide (*Leuciscus idus*). This cyprinid fish is classified as rheophilic and behavioral and anatomical studies suggest that the ide is adapted to running water conditions. Our physiological data suggest that the ide uses the same flow sensing mechanism as suggested for goldfish. Thus the proposed mechanism may be a general principle used by fish to measure bulk water flow. Our study in addition shows that higher brain centers may use further cues (e.g. spectral composition) to estimate flow velocity.

Supported by the BMBF (Biona project 01RB0902A)

Responses of midbrain lateral line units in the goldfish can be used to determine flow velocity

Volker Hofmann¹⁾, Randy Zelick²⁾ and Horst Bleckmann³⁾

¹⁾ University of Bielefeld - Active Sensing, Bielefeld, Germany

²⁾ Department of Biology, Portland State University, Portland OR, USA

²⁾ Institute for Zoology, University of Bonn, Bonn, Germany

Fish use their mechanosensory lateral line to detect weak water motions and pressure fluctuations as they occur in running water. These provide a potential source of information in the aquatic world and are used, e.g. for alteration of locomotory body kinematics in relation to stream characteristics.

In previous studies in the lateral line periphery, a delay line like model was supposed to cross correlate turbulence travelling along the array of lateral line sensors on the body surface determining bulk water flow velocity. Coincidence detectors of such a delay line should therefore be found in higher ordered lateral line nuclei. However recordings in the first order lateral line nucleus (medial octavolateralis nucleus, MON) did not affirm this.

We investigated the responses of midbrain lateral line units in the torus semicircularis of the goldfish, *Carassius auratus*, to unidirectional water flow. Recordings were made while the fish was stimulated in an oval flow tank with water velocities between 0 to 13 cm · s⁻¹.

Toral units (n = 19) increased their discharge rate in response to bulk water flow, irrespective of flow direction. Ongoing activities, maximum response frequencies, response strengths and discharge patterns differed. A burst like discharge behavior was more or less noticeable in all cases. In no case adaptation to constant water flow was apparent. In 12 of 14 units the responses were coincident with increased amplitudes of flow fluctuations, i.e. superimposed turbulence. These response properties were consistent with earlier reported responses of afferent fibers and MON units, suggesting that the lateral line responded in proportion to superimposed turbulence but not to the bulk water flow directly.

One unit responded to intermediate flow velocities exclusively, i.e. showed velocity tuning. The responses of this unit were not directionally selective and not relying on the presence of increased turbulence amplitudes. Therefore it is unlikely that it is an output neuron in a delay line array.

The majority of units (9 of 14) gradually increased their discharge rate with gradually increasing flow velocity. Velocity thresholds, response slopes and the encoded velocity range differed. The rate code of averaged responses of a small population of units however imaged the turbulence characteristics quite well.

Subtracting velocity response functions (VRFs), which imaged the dynamic range of response of units, from one another resulted in tuned output functions. These computed output functions were similar to the VRFs determined for the tuned unit recorded. Therefore it is more likely that the output of the tuned unit is a result as a similar rate code comparison. A neuronal subtraction mechanism may enable the fish to determine flow velocity this way.

Neural mechanisms of multisensory behavior in larval zebrafish

Pablo Oteiza, Ruben Portugues, Misha Ahrens and Florian Engert

Department of Molecular and Cellular Biology, Harvard University, Cambridge, USA

Animal behavior has evolved in a stimulus-rich environment, in which multiple sensory modalities are combined to produce behavior. However, the neural mechanisms underlying this integration are still poorly understood. Here, we have started to characterize these mechanisms using the larval zebrafish as a model system. Using a combination of video-projected visual stimulation and motor-induced water flow, we have found that the zebrafish larvae integrates both visual and mechanical information to determine its position in space and modulate its motor activity accordingly. In addition, we have translated this assay into a fictive environment setup in which visuo-mechanical stimuli are presented to the paralyzed larvae while performing whole-brain 2-photon calcium imaging. These experiments represent the starting point for analyzing the basic mechanisms by which the vertebrate central nervous system integrates composed sensory information and translates it into behavior.

The mechanism by which water movement receptors fine tune non-giant escape swimming in crayfish

David L. Macmillan

Department of Zoology, University of Melbourne, Australia

Crayfish swim using „non-giant tail-flips“: a series of rhythmic alternating abdominal flexions and extensions. The swimming can be triggered by water movement or touch receptors on the abdomen. These cuticular afferents excite, among other neurons, the motor neurons innervating the muscles of the abdominal stretch receptor organ. The forces generated by the flexions are directional and the initial direction is predicted by the location of the triggering stimulus. The trajectory is determined mechanically by the positioning of the tail fan. The water movement receptors are a long way from the tail fan but efficient escape requires that its shape is adjusted rapidly and cyclically. Evidence from my research group and that of others suggests that the axons of the large abdominal stretch receptor organs provide the link for the rapid transmission of information from the water movement receptors to the tail fan. Using intracellular staining, electrical recording and ablation we have shown that: the muscle receptor organs receive input from water movement receptors located on the anterior abdomen; they fire cyclically during non-giant swimming; their projections in the tail fan ganglion are somatotopic and the synaptic strength graded. We propose that the muscle receptor organs transmit fast. Labeled-line information from the water and touch receptors on the anterior abdomen to the tail fan. This information critically and cyclically adjusts the tail fan for efficient directional escape.

DPIV analysis to investigate turbulent fluid-structure interactions

Jennifer Brown, Lily Chambers and William Megill

Ocean Technologies Lab, Dept. of Mechanical Engineering, University of Bath, UK

Understanding what is available, from a hydrodynamic point of view, for fish to interact with in their environment is a key area to investigate. It will allow for a better awareness of fish behaviour and increase the ability to mimic it. The high manoeuvrability and efficiencies of fish are of interest for the biologically inspired design of submersible craft. A way in which it is useful to mimic fish is to investigate their hydrodynamic sensing systems, mainly the lateral line, and to use a similar system on a submersible. For any mechanical sensor to be useful for navigation a better understanding of the real world turbulent flows is required.

Our study used digital particle image velocimetry (DPIV) to visualise uniform flow and turbulent flow with a measure of predictability (the Kármán vortex street) in a flow channel (90 x 40 x 36 cm). The Kármán vortex street was generated by a cylinder (45 mm diameter) and was characterised by mapping the velocity magnitude and position of vortices in the tank. The influence of a rigid model and a flexible silicone rubber model with biomimetic stiffness on the re-distribution of the flow and the vortex street was then analysed. Preliminary results have shown that a rigid object will tend to destroy the vortex street when placed in the centre, whilst a flexible object can destroy the street, but it can also interact so that the vortex street is maintained in the wake of the model.

This step by step approach has led to a better understanding of the position of forms in the flow for altering the vortices present; namely their trajectory and their intensity. Finally an initial investigation of a swimming trout in the same flows provides an illustration of a complex fluid-structure interaction. A high speed camera (100Hz) was used to record the kinematics of a rainbow trout (*Oncorhynchus mykiss*) in a hydrodynamic environment with a cylinder to body length ratio of around 1:5. Although this study is preliminary, it highlights issues such as self-generated wakes and turbulent event interaction from a fluids perspective. This research contributes to the development and use of flow sensors in turbulent environments as well as to behavioural analysis of fish swimming in complex environments.

When size matters: extracting distance and shape information through the passive electrosensory and mechanosensory lateral-line system of fish

J. Engelmann¹⁾, J. Goulet³⁾, S. Gertz^{1,2)} and J.L. van Hemmen³⁾

¹⁾ Department of Biology - Active Sensing, 33501 Bielefeld, Germany

²⁾ Department of Neuroethology/Sensory Ecology, Bonn, Germany

³⁾ Physik Department T35, TU München & BCCN - Munich, 85747 Garching, Germany

The passive electrosensory system and the mechanosensory lateral line of fish share several anatomical similarities and need to extract information under comparable constraints. For both modalities, a simple dipole field suffices to describe moving objects sensed at a certain distance from the fish. Moreover, the action range – see below – extends to one fish length. That is, provided the water flow fulfills the Euler equation, both the electric potential and the velocity field share the same mathematical characteristics.

Sichert et al. (2009) have already shown that the degree of shape information the lateral line can extract from an object depends on both the object's size and distance to the sensory array; see also Goulet et al. (2008). For distances exceeding a fish length, the stimulus is nearly a perfect dipole. Thus only within the near range can fish extract shape-related multipole information from the flow field.

Here we extend the above approach to the passive electrosensory system by showing that, for the latter, stimuli can also be regarded as perfect dipoles. Accordingly, shape information is only available within a prey-fish or object length. In both sensory systems, distance-related cues are available at behaviorally relevant distances whereas shape information is severely limited by the distance to the receiver.

References

- A.B. Sichert, R. Bamler, and J.L. van Hemmen (2009) Hydrodynamic object recognition: When multipoles count. *Phys. Rev. Lett.* 102: 058104
- J. Goulet et al. (2008) Object localization through the lateral line system of fish: theory and experiment. *J. Comp. Physiol. A* 194: 1-17

Measurement techniques for studies of zebrafish lateral line neuromasts

Primož Pirih, Gaston C. Sendin and Sietse M. van Netten

Artificial Intelligence Department, University of Groningen, The Netherlands

We present techniques used for fluid flow stimulation and mechanical measurements of lateral line neuromasts.

Water flow can be generated by a stimulus ball or by a fluid jet. A vibrating stimulus ball produces a dipole flow field with a sharp intensity fall-off ($1/r^3$) and may be too bulky for microscopic studies. We therefore preferred the smaller piezoelectric fluid-jet device, which generates the flow through a pulled micropipette. We used tip sizes between 10 and 20 μm . In this range, the device has an almost constant velocity response (Dinklo et al. 2007). The jet divergence angle was similar to the pipette tip angle. We have observed that the flow in the jet centre is following almost linear trajectories, while the jet sides produced elliptical flow trajectories.

We measured the electro-mechanical cross-talk into the measurement of extracellular receptor potential (ERP). Careful grounding was essential for reducing the electrical pick-up, which is characteristically stronger at higher frequencies. When the ERP electrode is very close to the tip of the fluid jet, mechanical pick-up can produce a spurious second harmonic component, resembling the neuromast ERP response.

A straightforward method for measuring mechanical motion is using transillumination differential interference contrast (DIC) microscopy with a differential photodiode (DPD, Kros et al., 1992, Martin and Hudspeth 1999). As this technique relies on DIC, it cannot be used on thick tissue. In zebrafish, it can be used on neuromasts of young larvae ($< P10$), possibly in combination with enhancing the contrast by using small (100 nm) polystyrene beads (McHenry et al. 2007).

In order to be able to measure from thicker tissue, we used two epi-illumination measurement techniques where backscattered light was provided by bigger polystyrene beads (1 μm) stuck to the cupulae. The first technique was based on a position-sensitive detector (PSD). Reflections of the objective lens (40x0.8) were reduced by using spatial filtering. The sensitivity of the system was $< 100 \text{ nm}/\sqrt{\text{Hz}}$. The sensitivity might be further improved by using a DPD or a line-scan camera.

For more accurate measurements, we used a laser interferometric microscope (LIM) with a Leitz 25x NA 0.50 water objective. In combination with a custom water-immersion condenser and crossed polarizers, it was possible to visualize neuromasts in up to 1 month old zebrafish. LIM was implemented by modulating the laser half-beams with Bragg cells. The beams were combined in the focal plane and interfered in the detection volume ($\varnothing \sim 5 \mu\text{m}$). The light reflected from the bead was detected with a PMT. Bead movement was detected as the modulation of 400 kHz carrier. Velocity was extracted by a FM demodulator and displacement by a phase demodulator.

We stimulated the motion of the neuromasts by a sinusoidal jet flow at frequencies from 2 to 500 Hz. At each frequency, the measurement signals were sampled using 16 cycles per 512 samples. The stimulus was repeated continuously and the signals were averaged on-line. The discrete samples/cycles ratio kept the signal energies in single Fourier components, simplifying the neuromast frequency response analysis. We found that the velocity measurement was generally more accurate above 10 Hz. The displacement measurement suffered from losses of tracking due to fish movement. This could be enhanced by selecting the reliable signal parts off-line.

Theory of reconstructing stationary objects by the blind mexican cave fish through flow sensing

Sebastian Urban, Andreas N. Vollmayr and J. Leo van Hemmen

Physik Department T35, Technische Universität München, Garching, Germany

The blind Mexican cave fish uses its lateral line organ to sense and navigate through its surroundings. By gliding through water the blind cave fish creates a flow field which is disturbed by objects around it. By sensing these disturbances the cave fish can map its surroundings and avoid obstacles. For the case of a fish swimming along a stationary object with an arbitrary form we present a mathematical method based on a novel explicit solution of the Euler equations in Fourier space for calculating the stimulus to the lateral-line organ. The method is verified by flow simulations using the boundary element method. We present calculated stimuli for various distances so as to show how the hydrodynamic image of the object is damped as the distance increases. The functional dependence of a lateral-line stimulus given the object form is invertible. Accordingly an approximate reconstruction of the object form and the flow field can be calculated given only the flow velocities at the lateral line. Even the complete flow field around a fish can be calculated online and in real time by convolution of the lateral line stimulus with an appropriate kernel. This operation can be performed by a neur(on)al net and is therefore a biologically plausible reconstruction mechanism. Plots of simulated flow field reconstructions are shown. The dependence of the reconstruction quality on the distance to the object is analyzed. This method can also be used by underwater vehicles, e.g., the AUV Snookie from TU Munich, to passively sense obstacles and avoid collisions with them. Implementation efforts are in progress.

Hydrodynamics of fast starts in teleost fish and their possible meaning for predator-prey interactions

Benedikt Niesterok, Guido Dehnhardt and Wolf Hanke

Institute for Biosciences and Marine Science Center, Rostock University, Rostock, Germany

C-starts are brief fast starts of high acceleration distributed over a wide phylogenetic range of fish. In this study we first investigated the variability of the C-start movement, which in general is divided into two major stages, using the example of the rainbow trout (*Oncorhynchus mykiss*). The second aspect of this study concerned the hydrodynamics of C-starts as this might be of great impact for potential piscivorous predators. The following questions concerning the hydrodynamics of C-starts were investigated:

- (1) How large is the temporal and spatial extension of the C-start flow pattern?
- (2) How long do water movements generated by C-Starts last?
- (3) Can the fish's movements and escape direction be derived from the flow patterns?

C-start measurements were conducted in an experimental basin using Particle Image Velocimetry (PIV) based on a 10 W OPSSL laser (530 nm) and a Phantom V12 high speed CMOS camera.

The kinematic evaluation of the C-start recordings showed a wide range in terms of total angle, escape angle, angular speed and duration of the two phases of the C-start. The angular movement during the first stage of a C-start covered angles from 40° up to 220°, in case of stage 2 the angles reached from 5° up to 80°. The maximum angular velocity found was 4053 deg/sec, the axial component of the C-start movement reached speeds of about 1.28 m/s and an acceleration of up to 46.68 m/s².

The hydrodynamic evaluation revealed a temporal extension of up to 25.5 ms (extrapolated) and a spatial extension of up to 1.53 m (extrapolated) for a certain flow structure called jet 1, that is the flow produced by the tail fin. Duration and spatial extension of jet 2, the flow produced by the body, tended to be lower.

The direction of the fish movement could be shown to be in a certain range of angles in relation to the flow direction of jet 1 and 2 at the end of the C-start and up to at least 500 ms after the onset of the C-start.

Funded by the DFG (HA4411-8, SPP1207)

Different mechanisms for the detection of hydrodynamic events in seals and sea lion

Lars Miersch¹⁾, Johannes Oeffner²⁾, Wolf Hanke¹⁾, Sven Wieskotten¹⁾, Guido Dehnhardt¹⁾

¹⁾ Institute for Biosciences and Marine Science Center, Rostock University, Rostock, Germany

²⁾ Institute of Animal Physiology, Westfälische Wilhelms-Universität Münster, Münster, Germany

In terrestrial mammals a typical vibrissal hair-shaft is round in cross-section, while those of eared seals and walruses as well as those of some phocid species like the bearded seal are oval. As in terrestrial mammals, vibrissal hair-shafts of all eared seals, walruses, the bearded seal, and Monk seals are smooth in outline. In contrast, those of all other phocid species are extremely flattened and have waved surfaces. Here we show that unlike as in cylindrical structures the undulatory shape of harbor seal whiskers does not cause a flow generated Karman vortex street, so that the noise usually caused by this vortex shedding is minimized. This noise reducing effect leads to a high signal to noise ratio (SNR) which makes seal vibrissae an optimized hydrodynamic sensor. Smooth sea lion whiskers produce a vortex street, which masks signal detection by a relatively high noise level. If signal processing in both animals would be identical seal whiskers show a much better SNR. However, sea lions might use a detection mechanism different from seals. A hydrodynamic event may disturb the eigenfrequency caused by vortex shedding, which may represent useful information. Taking this into account, calculated SNRs were within the same range for seal and sea lion whiskers. The quantitative comparison of seal and sea lion whiskers regarding the sensory efficiency reveals the evolutionary development of two different working principles for the detection of hydrodynamic stimuli.

Comparison of the bending behaviour of barn owl feather vane with the bending behaviour of single feather barbs

Stefan Blazek¹⁾, Thomas Bachmann²⁾, and Hermann Wagner¹⁾

¹⁾ RWTH Aachen University, Institute for Biology II, Aachen, Germany

²⁾ TU Darmstadt, Institute for Fluid Mechanics and Aerodynamics, Griesheim, Germany

The barn owl flight is not only a model for silent flight but also for highly efficient cruise-flight aerodynamics. Compared to an air plane foil the owl wing shows a very flexible bending behaviour. The bird wing consists of bones, muscles and feathers. For a better understanding how flexibility might affect the aerodynamic performance of the owl wing, a closer description of the passive elements, the feathers, is required. In preliminary work single barbs of the barn owl feather vane were tested in a 2-point bending test. In a further step we want to understand how these subunits behave in a bending test when they work as an array, as they are arranged in the vane.

Thus, we investigate arrays of barbs and their behaviour under load. As a comparison we perform a 2-point bending test with a single barb of the same piece of the feather vane. A 3 cm piece of the feather vane is fixed to a micromanipulator with the rachis part. The tips of barbs are positioned on a support (thin metal membrane) of a digital balance. The second moment of area is determined by scanning the vane specimen with a microcomputer tomograph and by reconstructing the three-dimensional structure by assembling the image stacks. The second moment of area is determined by analysing the cross section of barbs. Afterwards the length of the barbs and the measured loads together with the second moment of area are used to calculate the Young's modulus for the array of barbs. To determine the influence of the barb interactions in the vane on the bending behaviour, the Young's modulus of the vane and the Young's modulus of the single barb were compared.

We will present preliminary data on the influence of barb interaction on the bending behaviour of the feather vane.

UV-B-radiation induced ageing of barn owl feathers and their effect on the bending stiffness

Franziska Oschmann, Stefan Blazek, and Hermann Wagner

RWTH Aachen University, Institute for Biology II, 52074 Aachen, Germany

The barn owl (*Tyto alba*) is an crepuscular animal and is characterized by its slow and silent flight. Several anatomical adaptations of the wing enable this animal to fly slowly and silently.

The profile and the surface of the wing and the material properties of the feathers have been implicated to play a role in the silent flight. If so, the ageing of the feathers may influence noise production during flight. It is known that birds of the same weight category as the barn owl moult once a year. By contrast, the barn owl has a moulting cycle of three years. Thus, it seems that the feathers of the barn owl show late-ageing appearance, maybe due to quite robust feather material. The feathers of the barn owl consist essentially of α -keratin, which is a very complex and fibrillar protein. An analysis of the amino acid composition has shown that the amino acid cysteine has a large share in the amino acid composition of α -keratin. The amino acid cysteine includes sulfur and is able to build disulfide bonds which underlie the high stability of the protein. Cysteine has a peak in the absorption spectrum for wave lengths ranging from 280 to 310 nm. Thus, UV-B-radiation destroys the disulfide-bonds and leads to a lower stability of the protein.

It was the aim of this study to determine whether and how barn owl feathers age. Ageing was induced by UV-radiation. The change in bending stiffness of the feather barbs was investigated. The dosage of UV-B radiation corresponded to the annual UV-B-exposition in Germany. The bending resistance was measured before, during and after the UV-B treatment. We shall present preliminary data on the influence of UV-radiation on bending stiffness.

On the use of various oscillatory air flow fields for characterization of biomimetic hair flow sensors

H. Droogendijk, A.M.K. Dagamseh, D.R. Yntema, R.G.P. Sanders, G.J.M. Krijnen

Transducers Science and Technology group (TST group), MESA+ Research Institute,
University of Twente, Enschede, The Netherlands

To determine the characteristics of flow sensors, a suitable source for flow generation is required. We discuss three different sources for oscillating air flow, by considering their acoustic impedance, frequency range, velocity and ability to distinguish between flow and pressure. We discuss the impact of these sources on characterization of our biomimetic hair flow sensors, which operate at flow velocities from 1-100 mm/s within a frequency range from 10-1000 Hz.

First, a loudspeaker was used as source. Its frequency range is in the order of 10-1000 Hz, capable of generating high flow velocities (up to 1 m/s) The distance of the loudspeaker to the sensor is of importance, since the typically small acoustic impedance (the ratio of flow to pressure) decreases with distance to the loudspeaker. Using this source, we determined the sensor's mechanical transfer (both magnitude and phase) using laser vibrometry. Also, a clear directivity profile was observed, indicating that the sensor is mainly responsive towards flow.

Another used source is a vibrating sphere, which behaves more like a monopole than a dipole source in the near field compared to a loudspeaker. The vibrating sphere is typically used for frequencies in the range of 10-100 Hz. A property of the vibrating sphere's near field is that for measuring right below the sphere its acoustical impedance is theoretically zero, meaning no pressure fluctuations and thus only flow. We used this source for realizing a nearly incompressible flow field for lateral line experiments. Measurements with a reference flow sensor and our flow sensors showed both a flow profile in close resemblance with the theoretical predictions for dipole source flows.

The third type of source used is a standing wave tube. Inside, well-defined patterns of standing waves occur at frequencies depending on the tube geometry. Advantages are the range of frequencies (10-4000 Hz) together with high flow velocities (up to 1 m/s). The acoustic impedance varies with frequency and depends on the position in the tube. Another advantage is the ability to distinguish between pressure and particle velocity (i.e. flow), since for standing waves there is a 90 degrees phase difference between pressure and particle velocity. Exploiting this property, we learned that our flow sensor has finite pressure sensitivity. However, directivity measurements using a loudspeaker showed almost exclusively sensitivity to flow. This is explained by the acoustic impedance at the sensor's position, which was much smaller in case of the loudspeaker. Therefore, the acoustic impedance matters for measurement quality on our flow sensors.

In conclusion, depending on the design and application of flow sensors, a suitable source is required to determine the sensor properties. For our sensors, the combination of three different flow sources gave good insights in the behavior of our flow sensory system.

Scene reconstruction for dipole sources in motion

Maria-Camilla Fiazza

University of Verona, Department of Computer Science, Verona, Italy

In developing underwater vehicles with flow-sensing capabilities, a fundamental question concerns the design of contextual locomotor strategies, informed by data gathered through an array of flow or pressure sensors. This sensing concept is gaining interest as means to emulate the key aspects of a biological solution: lateral line sensing in fish. Strategies for navigation, approach or obstacle avoidance based on flow sensing depend critically on the ability to extract conclusive information on source types and positions, in addition to discriminating size and direction of motion (if any) of each source.

Scenarios involving hydrodynamic dipole sources in still water have been widely used to investigate signal patterns in distributed flow sensing, with the typical target of performing source localization. A range of techniques is available and their evaluation has shown that the problem of localizing a dipole source, steadily vibrating with an arbitrary orientation and within the "field of view" of the sensing system, has been solved with error margins below 5%.

What has yet to be addressed is the problem of how to derive an image of the environment in the presence of multiple signal sources. Multiple sources can shadow each other, in the sense that they make critical signal features (peaks or phase shifts) very hard to detect, if they can be detected at all. This "partial visibility problem" is further aggravated in environments that differ from still water.

In this work, we address issues related to ambiguity and partial visibility in scenarios with multiple dipole-sources; the proposed approach is based on resolving ambiguity by integrating continuity constraints related to source motion. Sources can move by moving along a straight line or (an arc of) circumference, by rotating in place or by a combination of the two. Changes in the source configuration are highlighted through novelty-filtering, which we prefer to comparing consecutive scene estimates.

Snookie - An autonomous underwater vehicle with artificial lateral line system

Stefan Sosnowski¹⁾, Andreas N. Vollmayr¹⁾, Kolja Kühnlenz²⁾, Sandra Hirche²⁾ and Leo van Hemmen¹⁾

¹⁾ Lehrstuhl für theoretische Biophysik T35, Physik Department, TU Muenchen, Germany

²⁾ Lehrstuhl für Steuerungs- und Regeltechnik (LSR), TU München, Germany

Snookie is a project of the TUM Excellence Cluster 'Cognition in Technical Systems' (CoTeSys). It is meant to be for designing and building an autonomous underwater vehicle with an artificial lateral-line system\nintegrated with other sensory modalities.

'Snookie' should function as a test bed for new, passively functioning, detector systems such as the lateral line. We aim at utilizing this sensory system for object avoidance in situations where existing sensors provide insufficient results; e.g., poor vision or too short a distance.

We achieve the robotic system's autonomy to independently explore ist environment by using a small-scale, self-sufficient design, embedding the necessary computational power, energy supply, and actuators into a cylindrical robot of 0.75m length and 0.25m diameter

The poster will focus on the technical details of the robot and particularly on the measurement system designed for the artificial lateral-line system. Proof of concepts and first measurements are shown.