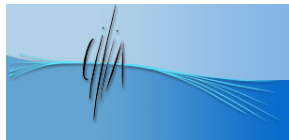# Flow Around a Hair

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Collaborators: J.-M. P. Franosch, J. Diepenbrock,
A. Vollmayr

More than half of the vertebrates perform stimulus detection in fluids. A detailed analysis of the hydrodynamics envolved in the detection process is essential in understanding the ensuing neuronal information processing.

Here we analyze three systems:

- Frog (*Xenopus*) – superficial lateral-line system
- Fish – superficial and canal lateral-line system
- Cricket – cercal system consisting of two cerci sparsely covered by hairs
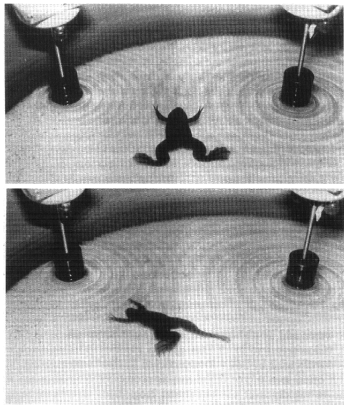
- has superficial neuromasts ***only***
- lives in still, turbid ponds
- hunts insects that have fallen onto the water surface
- localizes its prey by means of its lateral line and determines its edibility
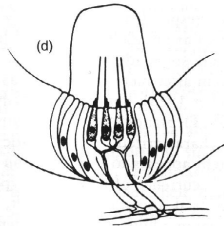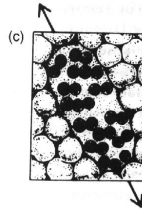
... determine local water velocity.

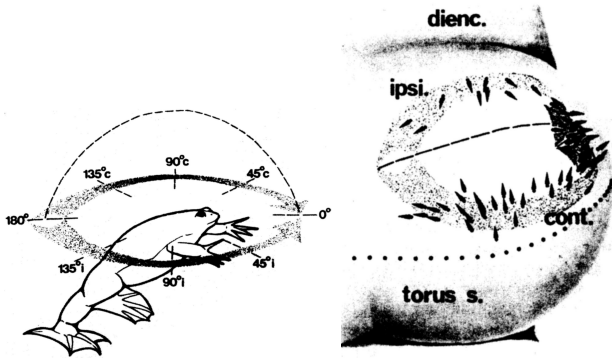The frog turns to the 'tasty' wave source on the left.

Figure: Zittlau, K. E., Claas, B. & Münz, H. (1986) *J. Comp. Physiol. A* **158**, 469–477.

Left: The frog's coordinate system.
Right: A neuronal map of directions in the frog's brain.
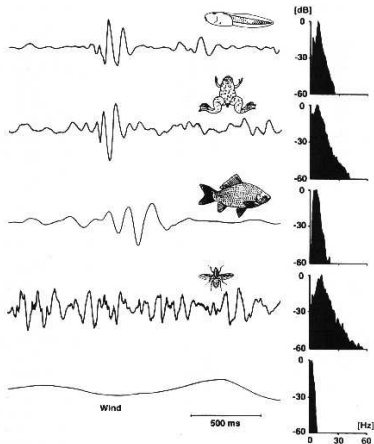
The frog does

- stimulus localization
- stimulus recognition
- robust with respect to noise

Let us therefore hypothesize: The frog *reconstructs* the wave form at the *source* position on the basis of its hydrodynamic input.

Examples of natural stimuli from Bleckmann (1994).

→ The frog performs wave form reconstruction!

The water surface modeled as a *linear* system is described by

$$y(t) \quad = \quad \int_{-\infty}^{+\infty} h(t - \tau, \mathbf{r})\, x(\tau) d\tau \qquad (1)$$

$$Y(\omega) \quad = \quad H(\omega, \mathbf{r})\, X(\omega) \qquad (2)$$

with the transfer function

$$H(\omega, \mathbf{r}) \quad = \quad \sqrt{\frac{r_0}{r}}\; 10^{-2|\Delta\varphi|/\pi} \times$$

$$\exp\left[-\frac{4\nu k^3}{3\,\omega}\,(r - r_0) - kd - ik\,(r - r_0) \right] \qquad (3)$$

$$\omega^2(k) \quad = \quad \left(gk + \frac{Tk^3}{\rho} \right) \tanh(Dk) \qquad (4)$$

Create an estimator $\hat{x}^{\mathbf{p}}(t)$ for the original wave form $x^{\mathbf{p}}(t)$ at source position $\mathbf{p}$ by minimizing expectation of the error

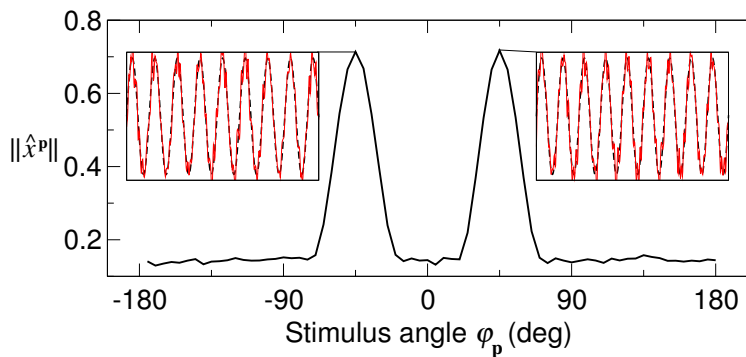$$E = \left\langle \int [\hat{x}^{\mathbf{p}}(t) - x^{\mathbf{p}}(t)]^2 \, \mathrm{d}t \right\rangle , \tag{5}$$

where $\hat{x}^{\mathbf{p}}$ can be written as

$$\hat{x}^{\mathbf{p}} = \sum_j s_j^{\mathbf{p}} \star y_j , \tag{6}$$

$$y_j = h_j^{\mathbf{p}} \star x^{\mathbf{p}} + n_j . \tag{7}$$

The reverse transfer function $s_j^{\mathbf{p}}$ contains adjustable parameters that can be chosen so that reconstruction of $x^{\mathbf{p}}$ in (6) occurs, giving the ideal model.

Performance of a linear model of a map provided by 180 lateral-line neurons with angular preference plotted on the x-axis. Two sources of 17 and 18 Hz are discerned. The inserts show the reconstruction in comparison with the true wave form.
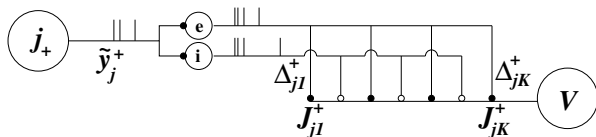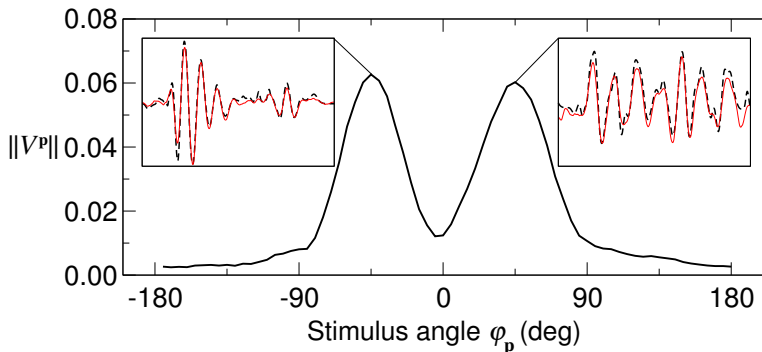
$$\tilde{y}_j^+(t) := \sum_{f^+} \delta(t - t_j^{f^+}) \ , \qquad \tilde{y}_j^-(t) := \sum_{f^-} \delta(t - t_j^{f^-}) \qquad (8)$$
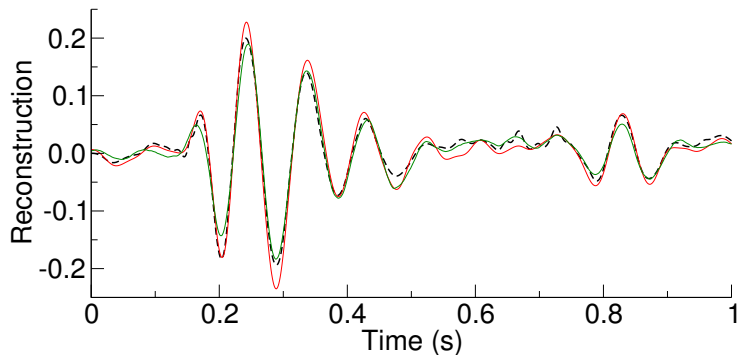
$$V(t) = \sum_j \left[\sum_{k=1}^{K_+} J_{jk}^{\ +} \left(\tilde{y}_j^+ \star \varepsilon \right)(t - \Delta_{jk}^+) - \sum_{k=1}^{K_-} J_{jk}^{\ -} \left(\tilde{y}_j^- \star \varepsilon \right)(t - \Delta_{jk}^-) \right]$$
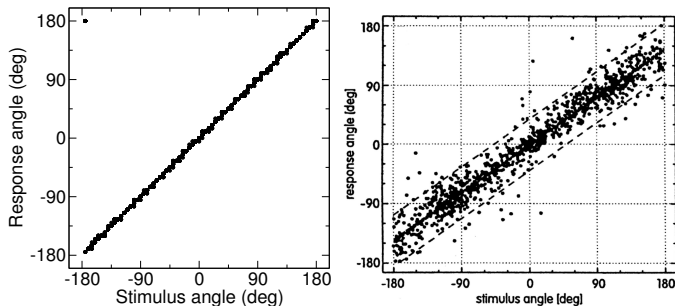
$$(9)$$

The (model) frog can discern two different natural stimuli presented *at the same time* without any problem.

Reconstructing a Natural Stimulus

Reconstruction of a natural stimulus with full sampling and synapses with randomly distributed delays.
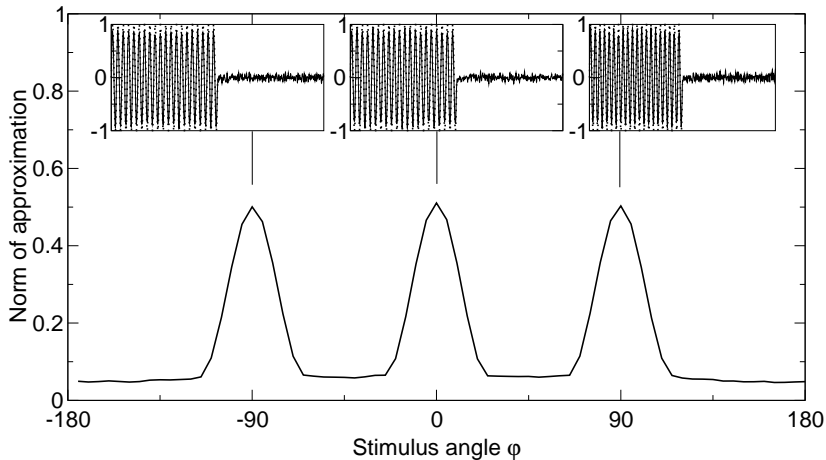
Left: The frog's response according to the neuronal model.
Right: Behavioral experiment [Claas & Münz, J. Comp.
Physiol. 178(1996) 253].
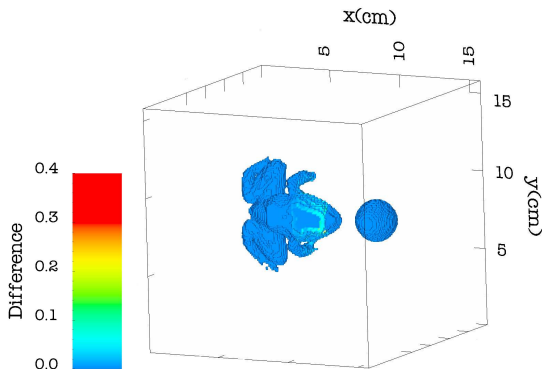→ The neuronal model is even better :-)

Map for *three* 20 Hz wave sources.

The relative difference between the projection of the water velocity caused by a moving sphere *without frog* onto a frog's skin and the numerically calculated velocity at the frog's body is color-coded. The differences are small.

3D frog data taken from "The Whole Frog Project" http://froggy.lbl.gov/.

How to get the appropriate synaptic strengths and hence a map?
How to coordinate *different* modalities?
Is there a teacher and, if so, who?

- The visual system is a candidate.
- There is a visual map in the *tectum opticum* as well as a lateral line map.
- Barn owl calibrates auditory system using the visual one (Miller & Knudsen, J. Neurosc. 1999; Gutfreund, Zheng & Knudsen, Science 2002).
- We assume the teacher system provides reference input about the signal at $\mathbf{p}$ to a lateral line unit with preferred direction $\mathbf{p}$.

Window of Reference

The learning equation becomes

$$\Delta J_{ik}^{\mathbf{q}} = -2\eta \int\int_{-\infty}^{\infty} [V^{\mathbf{q}}(t) - F(\mathbf{p}, \mathbf{q})x^{\mathbf{p}}(t-T)]$$
$$\times \, y_{ik}^{\mathbf{q}}(\tau)\,\varepsilon(t-\tau)\,\mathrm{d}\tau\,\mathrm{d}t \tag{13}$$

The figure shows how the neuronal circuit provides the *feedback* $F(\mathbf{p}, \mathbf{q})x^{\mathbf{p}}(t-T)$.
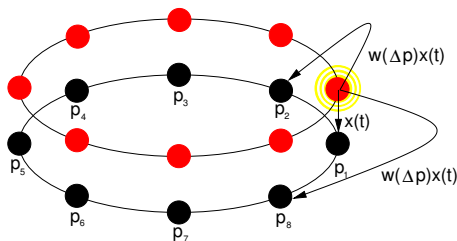
Realization Through Neuronal Minimization Principle

Define the expected neuronal error (with the teacher signal) by

$$E = \left\langle \int \left[V^{\mathbf{p}}(t) - \left(\tilde{x}^{\mathbf{p}} \star \varepsilon \right)(t) \right]^2 \mathrm{d}t \right\rangle \tag{14}$$

and minimize it by adjusting the synaptic strengths by

$$\Delta J_{jl}^{\mathbf{p}} = -2\eta \, \frac{\partial E_{\mathsf{n}}}{\partial J_{jl}^{\mathbf{p}}} = -2\eta \int \sum_{t_{jl}^{\mathbf{p}}} \varepsilon(t - t_{jl}^{\mathbf{p}}) \left[V^{\mathbf{p}}(t) - \left(\tilde{x}^{\mathbf{p}} \star \varepsilon \right)(t) \right] \mathrm{d}t \ .$$

$$\tag{15}$$

The times $t_{jl}^{\mathbf{p}}$ are the arrival times of a spike from lateral-line nerve j to synapse l at the reconstruction neuron for position $\mathbf{p}$. Eq. (15) gives rise to a supervised spike-timing-dependent plasticity (SSTDP) algorithm, here with learning window $W(t) = -\varepsilon(-t)$.

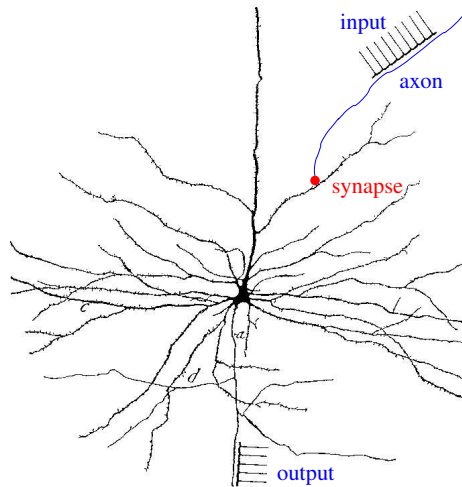# Anti-Hebbian Learning Window
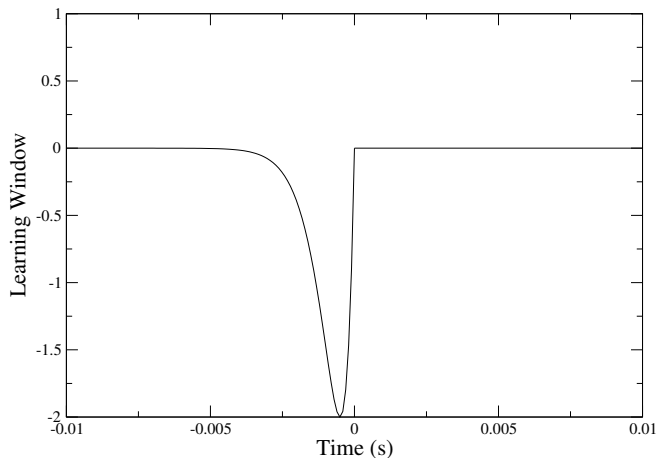
Change of synaptic strength in dependence of the arrival time of the input spike.
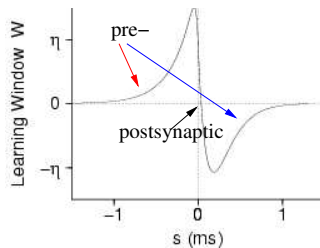
Result of Learning
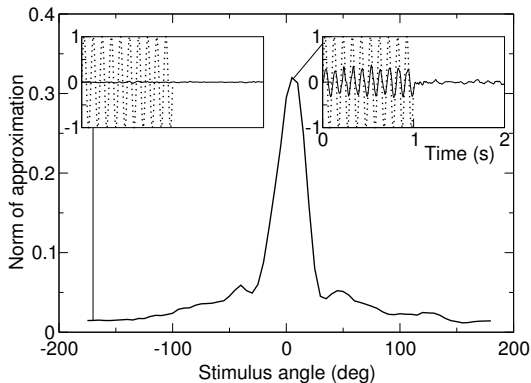
Neuronal map after learning. Reconstruction (solid in the insets) of a sinusoidal stimulus (dotted) in front of the frog. Parameters are reconstruction parameter $\sigma = 0.1$, and synaptic time constant $\tau = 5\,\text{ms}$.
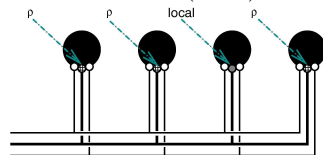
Neuron

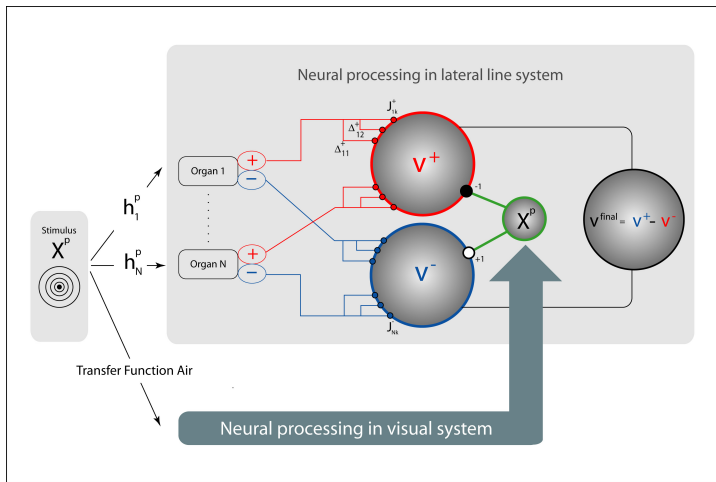Pyramidal neuron (after Ramon y Cajal 1898).

STDP

W. Gerstner, R. Kempter, J.L. van Hemmen, H. Wagner Nature **383**(1996) 76-78
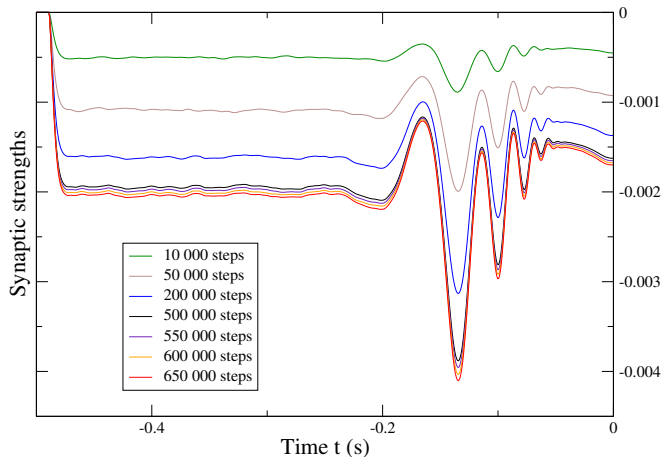
Axon-mediated synaptic learning (AMSL).

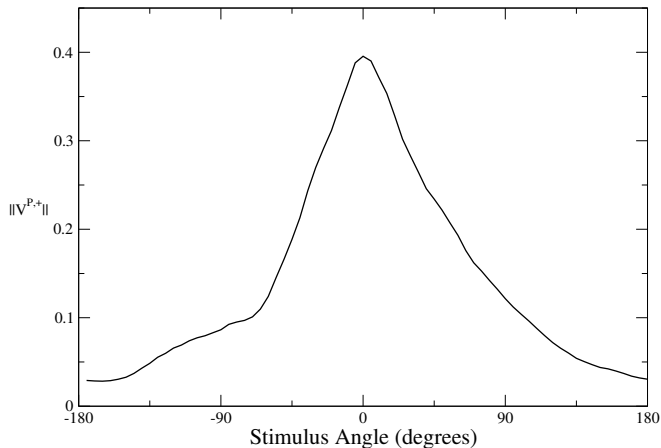# Learning by Supervised STDP with Spike-Time Differences

The "negative" and the "positive" afferents connect to separate localizing neurons.

Learning by Supervised STDP with Spike-Time Differences
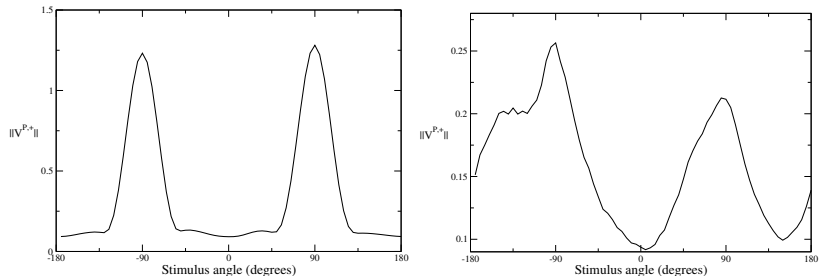

Supervised STDP with spike-time differences seems to converge to synaptic strengths, but there is not convergence theorem (yet).

Learning by Supervised STDP with Spike-Time Differences

Neuronal map through supervised STDP learning with spike-time differences.

Learning by Supervised STDP

Neuronal map (two stimuli) through supervised STDP learning
with membrane potential (left) and spike-time differences
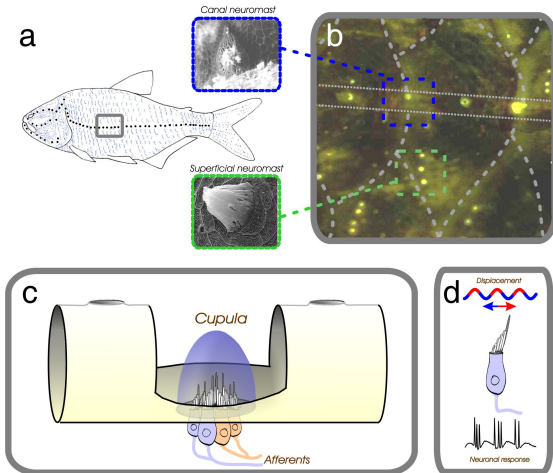(right).

Do crocodilians use a similar mechanism for prey localization?

Crocodilians hunt at night, waiting half-submerged for land-bound prey to disturb the water surface. They have specialized sensory organs that can detect small disruptions in the surface of the surrounding water (Soares 2002), just as *Xenopus*.
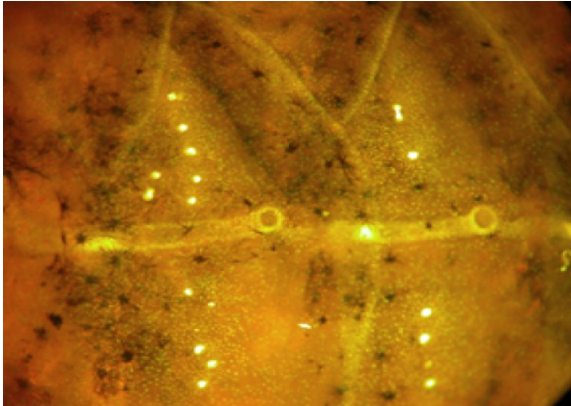
Pictures from D. Soares, Nature **417** (2002) 241-242.

The hydrodynamic pressure difference between two pores evokes fluid motion in the subepidermal canal resulting in a neuronal signal. By using its lateral line only, fish can track the hydrodynamic "pathway" of other fish.
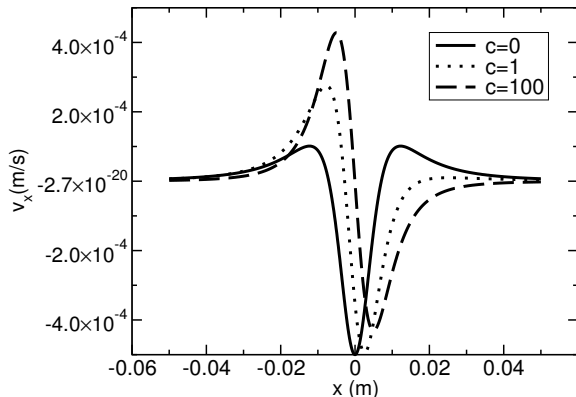
Canal lateral-line organs (Horst Bleckmann, Bonn).

Fish Use Their Lateral-Line System, e.g., for Orientation in a Swarm

Photograph taken from http://www.seafriends.org.nz/enviro/Fish/jack/FA005312lr.jpg.
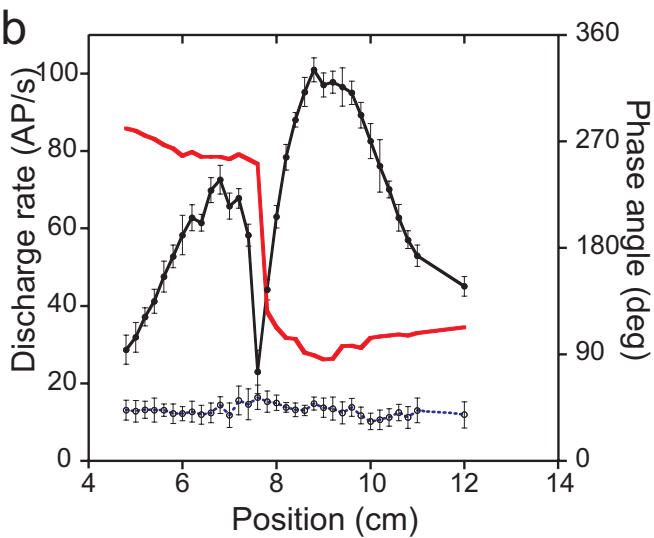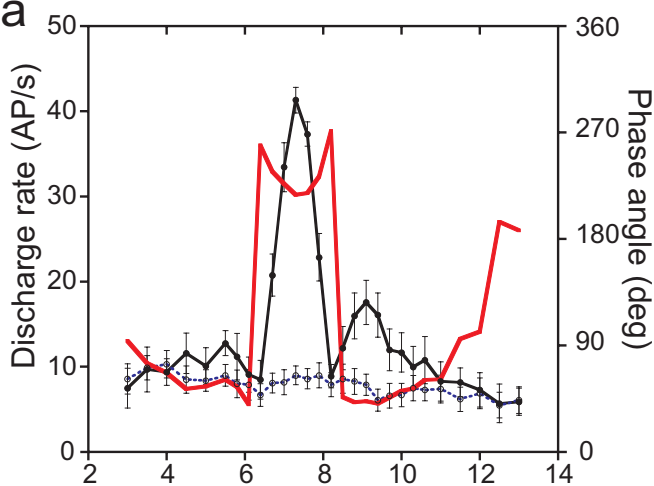
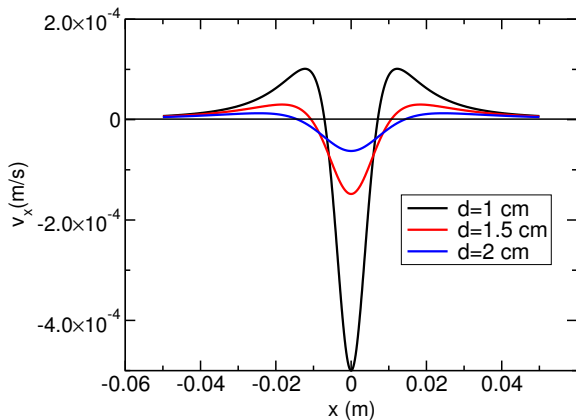# Sensory Input at a Lateral Line

The velocity v_x of the water along the line of lateral-line organs for a prey with radius $a = 1\,\text{mm}$, distance $d = 1\,\text{cm}$, position $x_0 = 0$ and prey velocity $w = 0.1\,\text{m/s}$ for different values of $c := \tan\varphi = w_y/w_x$.

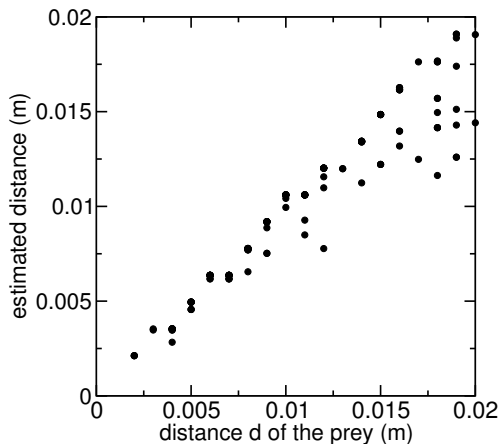# Sensory Input at a Lateral Line

The distance of the zeros is proportional to the distance d of the prey.

Neuronal Model

The distance estimated by the neuronal model versus the true distance of the prey during 10 trials for each distance.

The model parameters are $\varphi = 0°$, $w = 10 \, \text{cm/s}$, and $a = 1 \, \text{mm}$, which is small. Water velocity, however, is proportional to a^3.
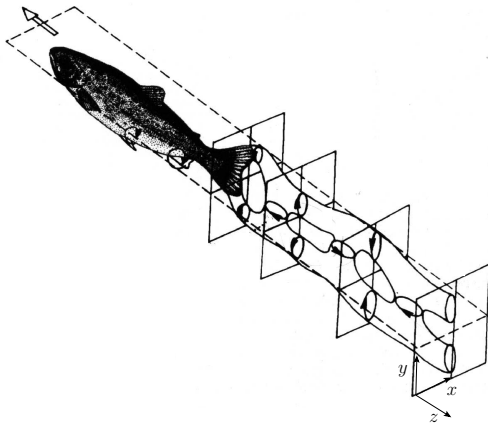
Wake structure generated by an undulatory swimmer (Blickhan et al. 1992). The vortex tubes in z direction are tail-tip vortices arising from the fish's displacement. The vortices in the horizontal plane are generated by the tail beat.
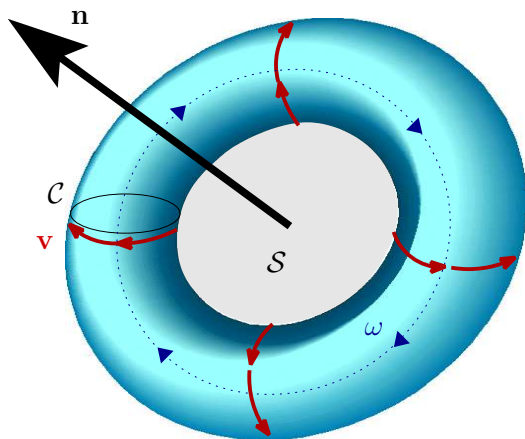
Velocity $\boldsymbol{v}$ and vorticity $\boldsymbol{\omega} = \text{rot}\,\boldsymbol{v}$ are orthogonal. Vortex lines that go through a closed curve $\mathcal{C}$ set up a vortex tube. The corresponding vortex filament (dotted arrows) encloses area $\mathcal{S}$. The ring's orientation $\boldsymbol{n}$ is perpendicular to $\mathcal{S}$. The ring moves in the direction opposite to $\boldsymbol{n}$.

The vortex ring has orientation γ.

The body surface $\partial\mathcal{B}$ is rotationally symmetric with maximum radius ϵ BL. A continuous distribution of hydrodynamic poles $g(z, \epsilon)$ on the axis of the fish body is chosen such that the flow through the surface $\partial\mathcal{B}$ is zero (Geer 1975). This distribution of poles is used to calculate the stimulus on the skin of the fish.

Under negligible viscosity, vortices are *persistent* due to the conservation of angular momentum. We model a vortex tube by a infinitely thin vortex filament that encloses the circular area $\mathcal{S}$. Outside a vortex filament the flow is irrotational so that a flow potential exists.

$$\phi_0(\mathbf{x}) = \frac{\Gamma}{4\pi} \iint_{\mathcal{S}} \left(n_x \frac{\partial}{\partial x'} + n_y \frac{\partial}{\partial y'} + n_z \frac{\partial}{\partial z'} \right) \frac{1}{|\mathbf{x} - \mathbf{x}'|} \, dS' \quad (10)$$

By comparison with a dipole potential $\nabla|\mathbf{x}|^{-1}$ we see that the potential of a vortex ring is equivalent to that of a uniform distribution of dipoles lying in $\mathcal{S}$.

We use an additional potential ϕ_{b} to model alteration of the vortex flow due to the presence of the fish body. The source strength distributions along the axis of the fish are to be determined in such a way that the resulting overall potential satisfies the Euler boundary condition

$$\frac{\partial}{\partial \mathbf{n}} \left(\phi_0 + \phi_{\mathrm{b}} \right) \Big|_{\partial \mathcal{B}} = 0 \, . \quad (11)$$

We can neglect viscosity here because viscosity only alters the flow field in a so-called boundary layer near the fish's body surface. The boundary layer does not alter the lateral line stimulus since pressure is about constant in any cross section of the boundary layer that is orthogonal to the flow and to the surface.

We use the Bernoulli equation

$$p - p_0 = -\varrho \, \frac{\partial \phi}{\partial t} - \frac{1}{2} \, \varrho \, \mathbf{v}^2 \qquad (12)$$
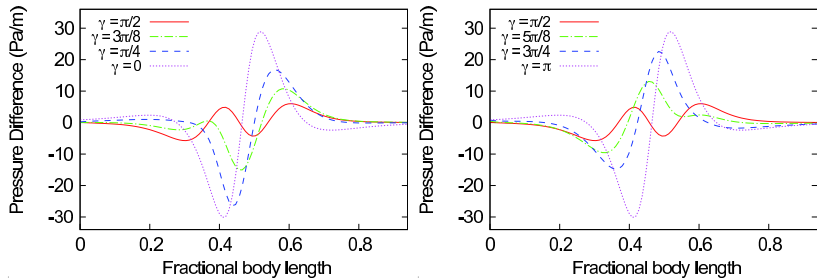
with $\phi = \phi_0 + \phi_b$ and $\mathbf{v} = \nabla \phi$ to determine the pressure distribution p at the lateral line.
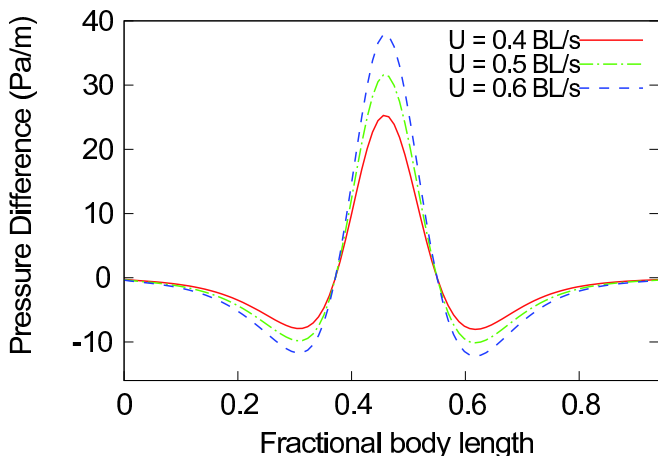
The relative velocity U between fish and vortex leaves the pressure excitation *pattern* practically unaffected. The most important parameter for wake tracking, the *orientation* of wakes, can therefore be extracted from the excitation pattern, independently of the other parameters.

For a *fixed* fish, which is a setup that can be realized experimentally, a vortex ring that moves in the x-z plane generates excitation patterns that depend on vortex orientation γ. There is *no* one-to-one relation between orientation γ and stimulus pattern. That is, a theory of vortex ring detection cannot be based solely on the currently experimentally verifiable case.
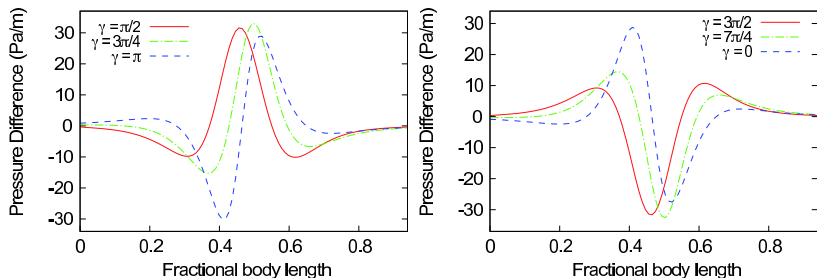
Vortices with different orientations γ that move in z direction relatively to the fish occur during wake tracking and thus represent a natural stimulus condition. Any such vortex generates an excitation pattern *specific* to its orientation angle γ. Patterns corresponding to orientations that differ by $\gamma = \pi/2$ are orthogonal functions so that the orientation of a vortex ring can be determined by projecting the stimulus pattern onto a given basis function. Fish can thus determine the direction they must follow to track their target.
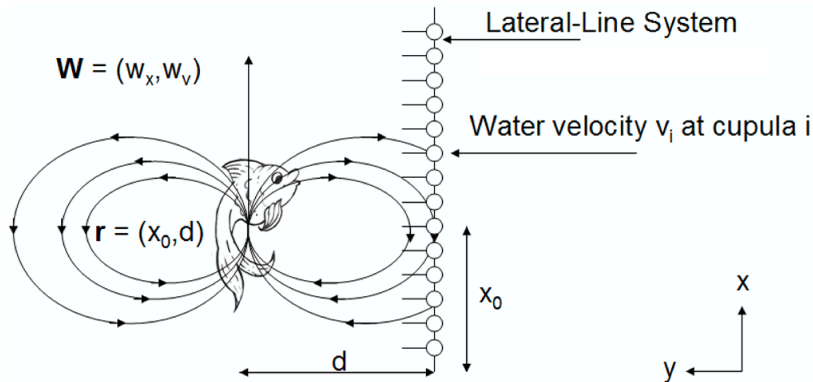
Lateral-line organs are arranged parallel to the x-axis. A prey at position (x_0, d) is moving with velocity $\boldsymbol{w} = (w \cos \varphi, w \sin \varphi) = (w_x, w_y)$ at distance d.

Why do *canal* and *superficial* lateral-line system receive the same stimulus pattern?

Canal lateral-line organs of fish are sensitive to pressure differences between the pores but insensitive to the fish eigenmotion.

In terms of the velocity potential ϕ, the pressure p is given by the Bernoulli equation

$$p = \varrho \frac{v^2}{2} + \varrho g z + \frac{\partial \phi}{\partial t} \qquad (13)$$

where the term ϱv^2 is negligible. Therefore, the pressure difference between two pores at distance δ follows from

$$p(x + \delta) - p(x) \approx \delta \frac{\partial p}{\partial x} = \delta \frac{\partial^2 \phi}{\partial t \partial x} = \delta \frac{\partial v_x}{\partial t} \, . \qquad (14)$$

Thus, for a *vibrating* sphere as "prey", the stimulus to the canal lateral-line system is proportional to that of the external lateral-line system for a *moving* sphere and **exactly the same theory holds**.
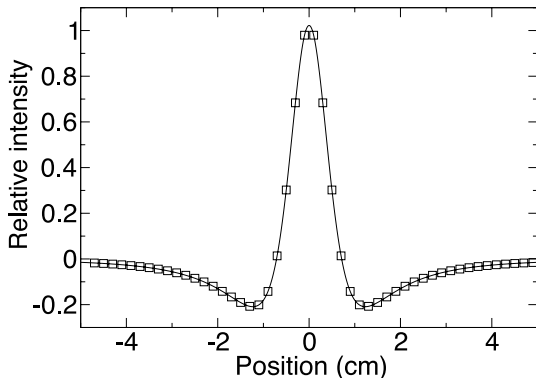
Pressure-difference (squares) and velocity distribution (solid line) coincide.

The spider *Cupiennius salei* can localize a fly by the air flow
caused by the prey through thousands of hairs on its skin.
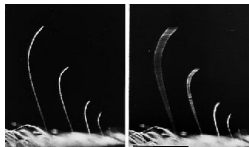
Future work is planned how information is processed on a
neuronal level allowing e.g. the spider to determine the position
of prey in *three*-dimensional space.

Barth F.G. (2000) How to catch the wind: spider hairs specialized for sensing the
movement of air. *Naturwiss.* **87**(2): 5158

Barth F.G. (2004) Spider mechanoreceptors. *Curr. Opin. in Neurobiol.*
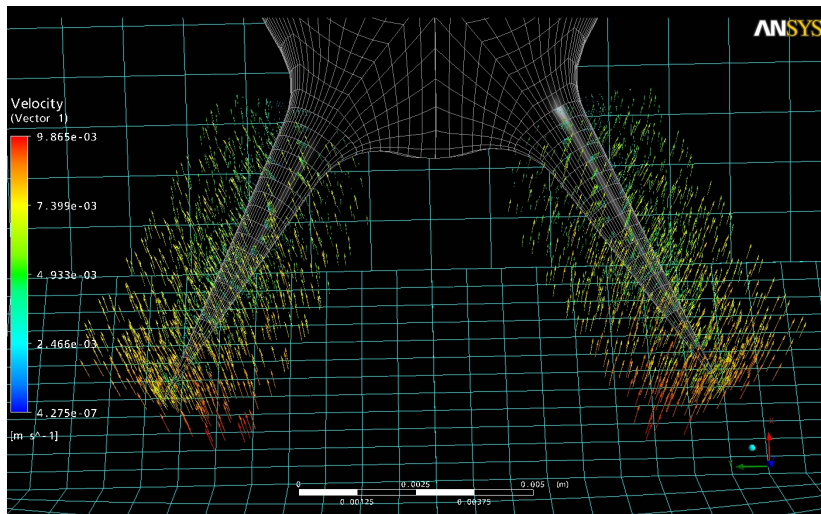**14**:415422
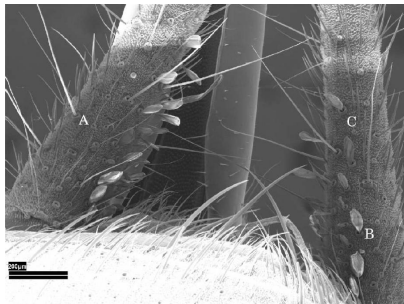
Crickets can *detect* an attacking spider and can *determine the direction* of attack through air currents along mechanoreceptor hairs on the two cerci.
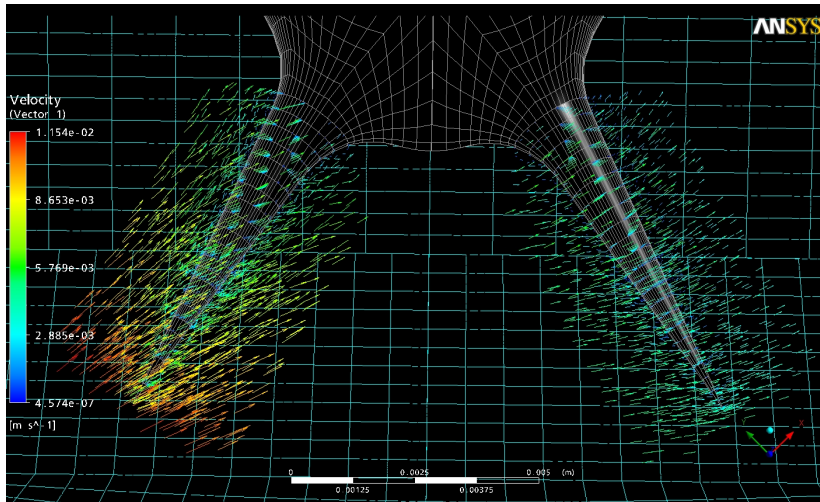
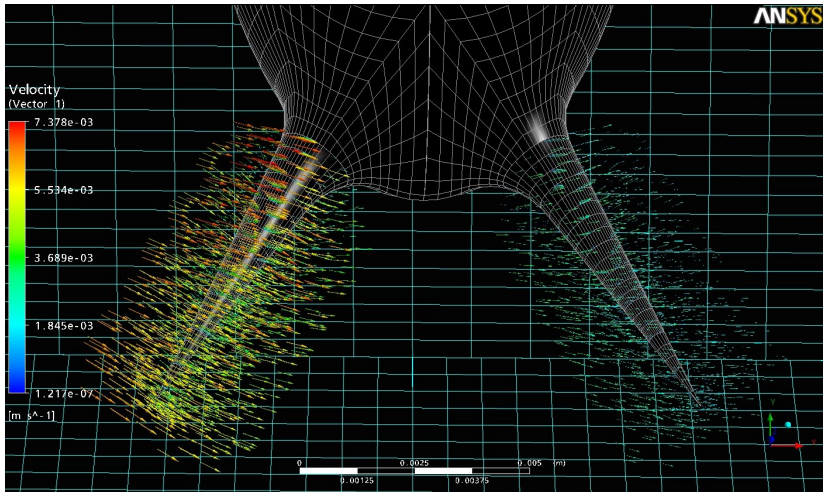Pictures: O. Dangles et al. (2005), M. Seidel (2006)

- The clawed frog, as well as the neuronal model, can discern several $n \geq 3$ *identical* stimuli presented simultaneously.
- Fish can determine the orientation of a vortex ring through its lateral-line input as the only cue and in this way perform the tracking of wakes.
- Other animals, such as crocodilians, spiders and crickets, also use hydrodynamic information to localize prey or predators.