

Becoming a Killer

A model of prey localisation and recognition
by means of the lateral line

Martin Lingenheil

Physik Department
TU München

July 8, 2004



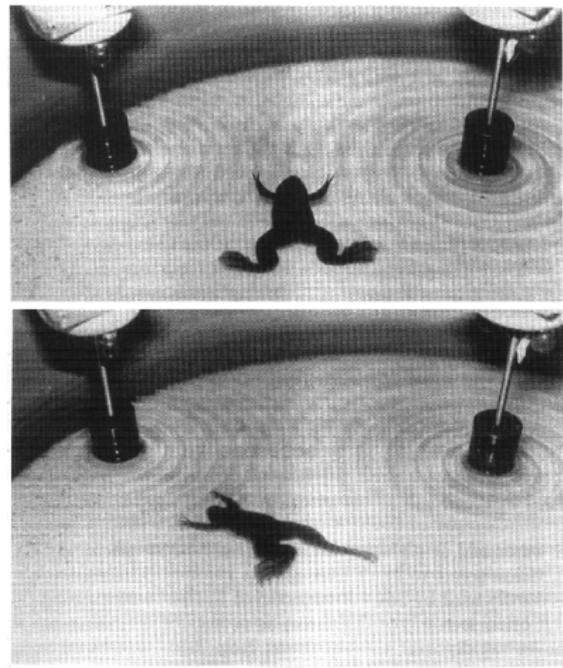
- 1 Introduction
 - Xenopus and its Lateral Line
 - Water Waves
- 2 Minimal Model
 - Reconstruction of the Wave Form
 - Performance of the Minimal Model
 - Learning
- 3 Field Reconstruction
 - Full-Field Reconstruction
 - Window of Reference
- 4 Neuronal Implementation of the Model
 - Implementing a Convolution
 - Learning a Neuronal Model
 - Performance of a Neuronal Model

Xenopus laevis laevis

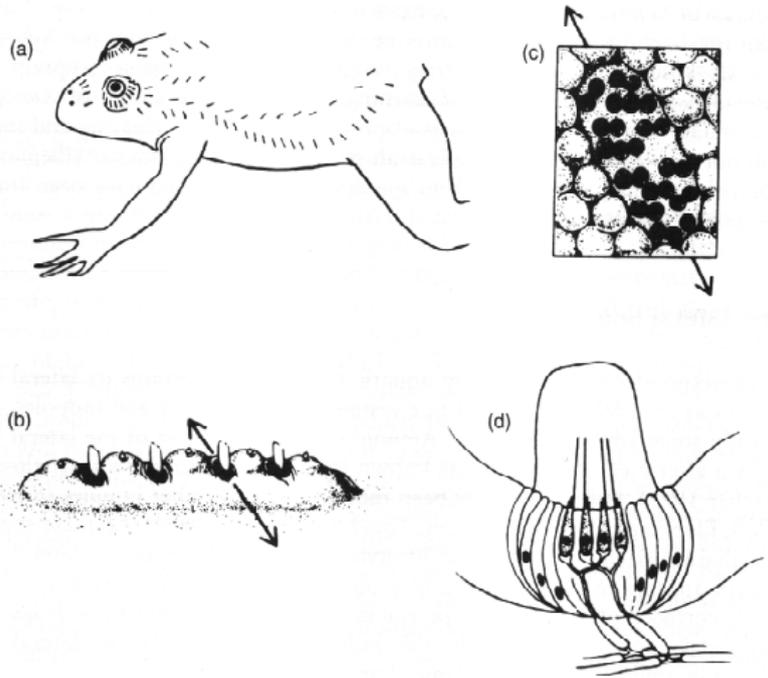


- completely aquatic
- carnivorous
- nocturnal
- lives in turbid waters
- prey localisation by means of the lateral line

Behavioural Experiments



Lateral Line System



Performance

- robust with respect to most lesions

Performance

- robust with respect to most lesions
- robust with respect to body position

Performance

- robust with respect to most lesions
- robust with respect to body position
- wave source localisation ($\geq 5^\circ$ accuracy)

Performance

- robust with respect to most lesions
- robust with respect to body position
- wave source localisation ($\geq 5^\circ$ accuracy)
- frequency discrimination and recognition (approx. 4% discrimination threshold)

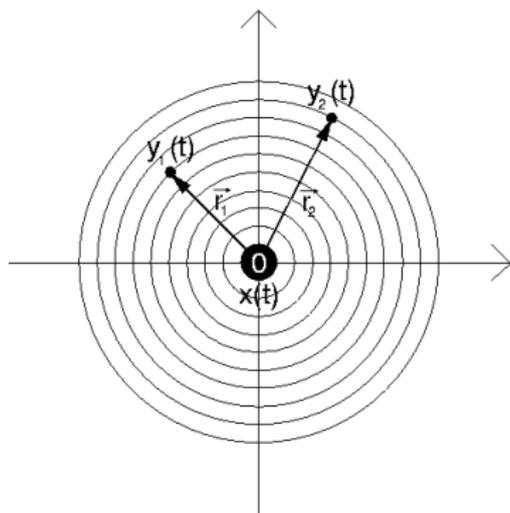
Performance

- robust with respect to most lesions
- robust with respect to body position
- wave source localisation ($\geq 5^\circ$ accuracy)
- frequency discrimination and recognition (approx. 4% discrimination threshold)
- discrimination of the superposition of both waves

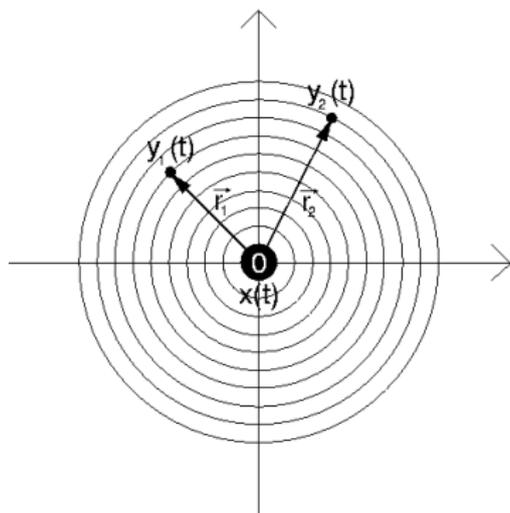
Performance

- robust with respect to most lesions
- robust with respect to body position
- wave source localisation ($\geq 5^\circ$ accuracy)
- frequency discrimination and recognition (approx. 4% discrimination threshold)
- discrimination of the superposition of both waves
- normal operating range: ≤ 30 Hz

Water Waves I



Water Waves I



$$y_{1,2}(t) = \int_{-\infty}^{+\infty} h(t - \tau, \mathbf{r}_{1,2}) x(\tau) d\tau \quad (1)$$

Water Waves II

Fourier transformed with respect to time the equation looks like this

$$Y_{1,2}(\omega) = H(\omega, \mathbf{r}_{1,2})X(\omega) , \quad (2)$$

with the transfer function

$$H(\omega, \mathbf{r}) = \sqrt{\frac{r_0}{r}} 10^{-2|\Delta\varphi|/\pi} \times \exp\left[-\frac{4\nu k^3}{3\omega}(r - r_0) - kd - ik(r - r_0)\right] \quad (3)$$

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

Impulse Response

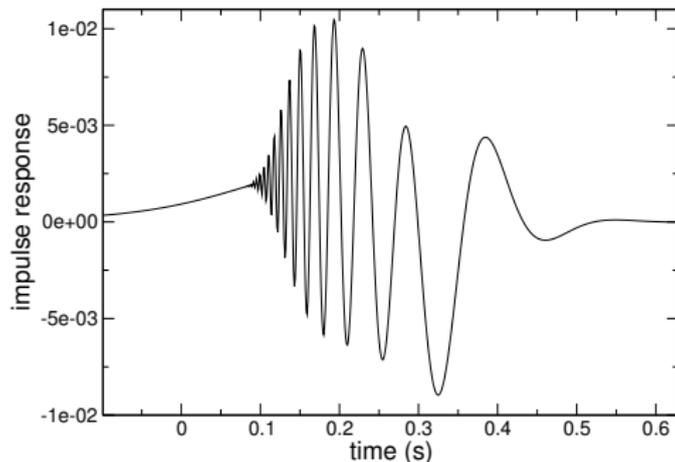


Figure: Impulse response at the position of an organ at 8 cm distance from the source.

Transfer Function

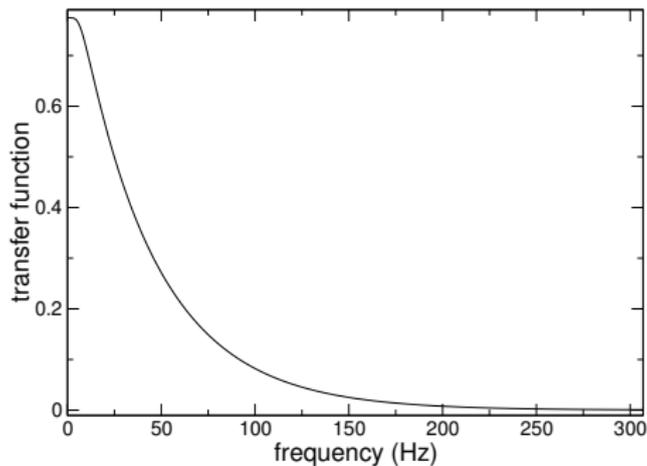


Figure: Same situation as on the last slide: Transfer function.

- 1 Introduction
 - Xenopus and its Lateral Line
 - Water Waves
- 2 Minimal Model
 - Reconstruction of the Wave Form
 - Performance of the Minimal Model
 - Learning
- 3 Field Reconstruction
 - Full-Field Reconstruction
 - Window of Reference
- 4 Neuronal Implementation of the Model
 - Implementing a Convolution
 - Learning a Neuronal Model
 - Performance of a Neuronal Model

Outline of the Model

- stimulus localisation

Outline of the Model

- stimulus localisation
- hypothesis: reconstruction of the wave form

Outline of the Model

- stimulus localisation
- hypothesis: reconstruction of the wave form
- robust with respect to noise

Outline of the Model

- stimulus localisation
- hypothesis: reconstruction of the wave form
- robust with respect to noise

⇒ Construct a maximum-likelihood estimator for the original wave form!

Wave Form Reconstruction I

Create an estimator $\hat{x}(t)$ for the original wave form $x(t)$ by minimizing expectation of the error

$$\bar{E} = \left\langle \int [\hat{x}(t) - x(t)]^2 dt \right\rangle, \quad (5)$$

where \hat{x} can be written as

$$\hat{x} = \sum_j s_j \star y_j, \quad (6)$$

$$y_j = h_j \star x. \quad (7)$$

Wave Form Reconstruction II

Find the minimum of \bar{E} with respect to the model parameters

$$\frac{\delta \bar{E}}{\delta s_j(\tau)} = 2 \left\langle \int \left\{ \sum_i [s_i \star y_i](t) - x(t) \right\} y_j(t - \tau) dt \right\rangle \stackrel{!}{=} 0, \quad (8)$$

Wave Form Reconstruction II

Find the minimum of \bar{E} with respect to the model parameters

$$\frac{\delta \bar{E}}{\delta s_j(\tau)} = 2 \left\langle \int \left\{ \sum_i [s_i \star y_i](t) - x(t) \right\} y_j(t - \tau) dt \right\rangle \stackrel{!}{=} 0, \quad (8)$$

which looks quite plain if Fourier transformed

$$0 = \left\langle \left(\sum_i s_i Y_i - X \right) Y_j^* \right\rangle. \quad (9)$$

Wave Form Reconstruction II

Find the minimum of \bar{E} with respect to the model parameters

$$\frac{\delta \bar{E}}{\delta s_j(\tau)} = 2 \left\langle \int \left\{ \sum_i [s_i \star y_i](t) - x(t) \right\} y_j(t - \tau) dt \right\rangle \stackrel{!}{=} 0, \quad (8)$$

which looks quite plain if Fourier transformed

$$0 = \left\langle \left(\sum_i s_i Y_i - X \right) Y_j^* \right\rangle. \quad (9)$$

Assuming the noise to be Gaussian and with $\sigma := \frac{\sigma_n}{\sigma_x}$ this Eq. is solved by

$$s_j = \frac{H_j^*}{\sum_i |H_i|^2 + \sigma^2}. \quad (10)$$

Reverse Transfer Function I

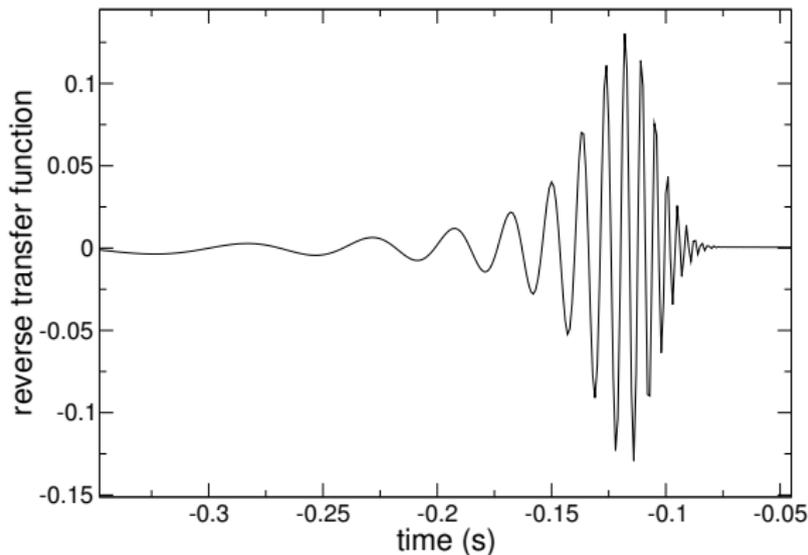


Figure: Reverse transfer function for an organ at 8 cm from the source (time domain).

Reverse Transfer Function II

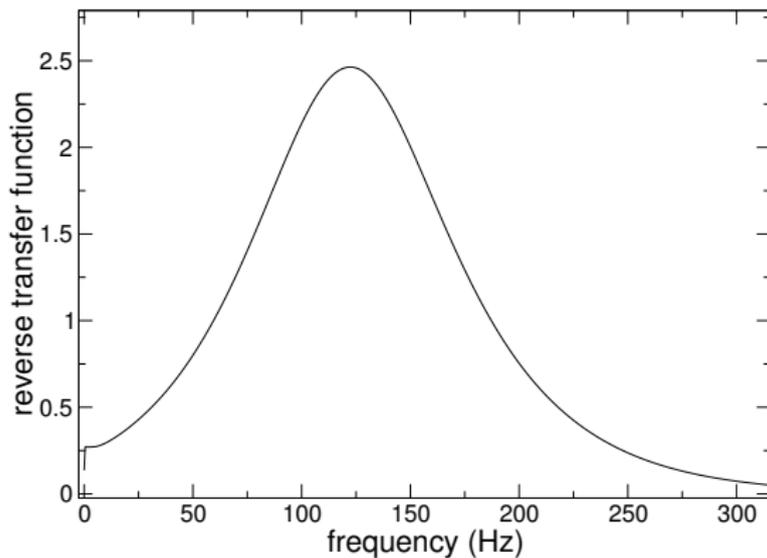


Figure: Same as the last slide: frequency domain.

Reconstruction of a Monofrequent Stimulus

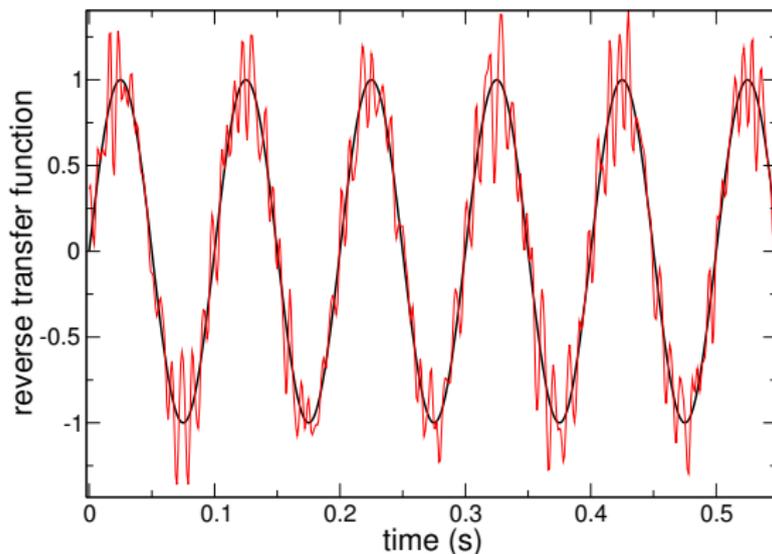


Figure: **Reconstruction** of the wave form using equation (7) ($f = 10$ Hz, $\sigma_x = 1$, $\sigma_n = 0.1$).

Reconstruction of a Complex Stimulus

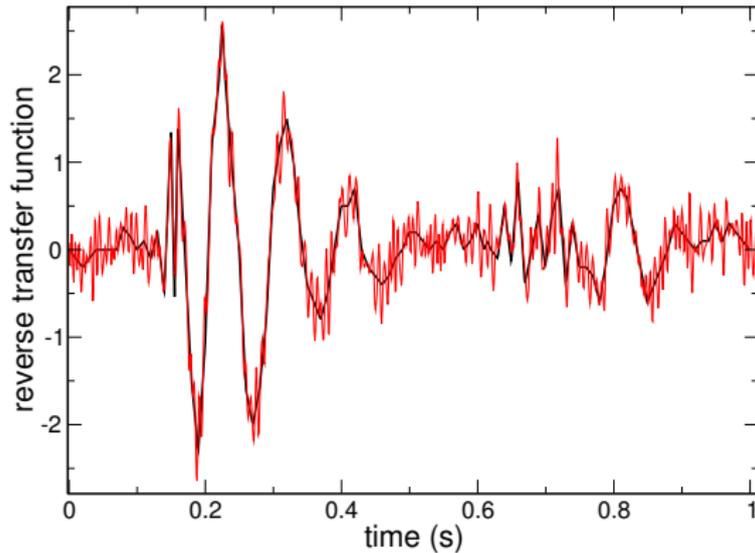


Figure: Same as on the last slide, but the stimulus is more realistic.

Localisation I

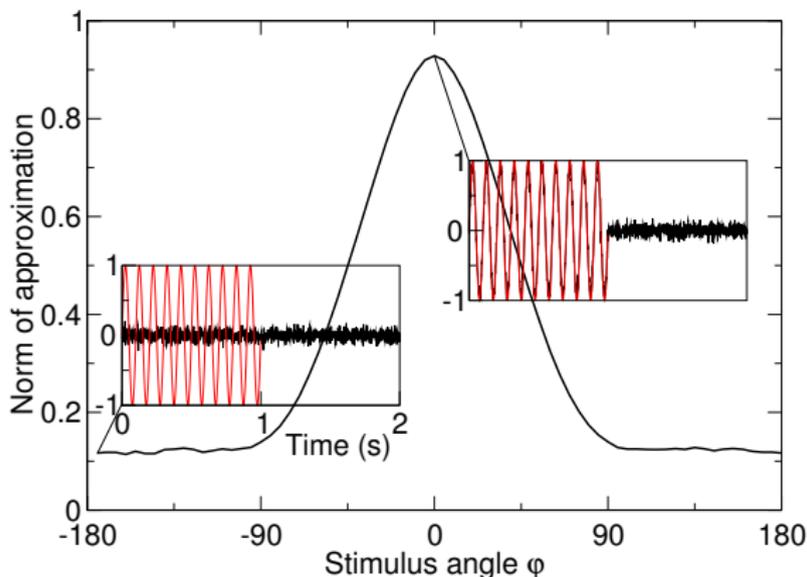


Figure: Map of reconstruction norms for various assumed source angles ($f = 10$ Hz, $\sigma_x = 0.5$, $\sigma_n = 0.1$)

Localisation II

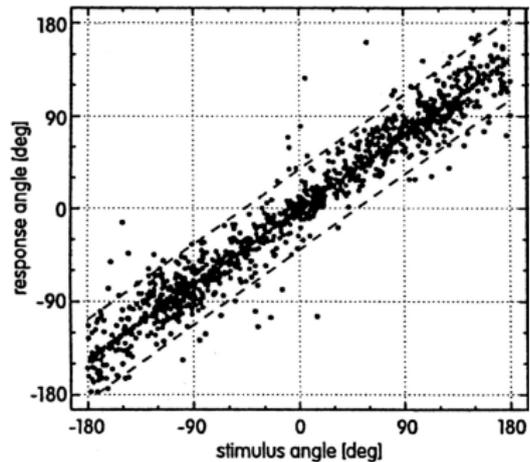
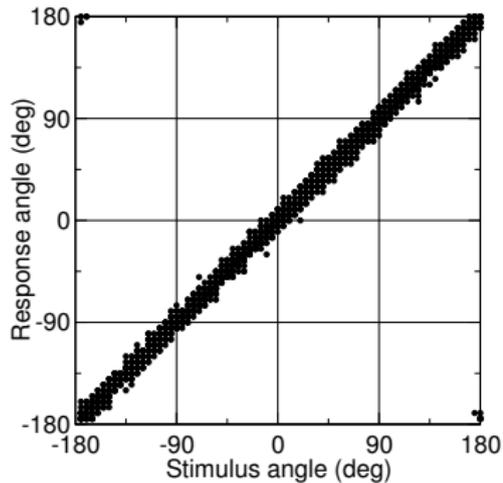


Figure: Localisation in model and experiment.

Wave Source Discrimination

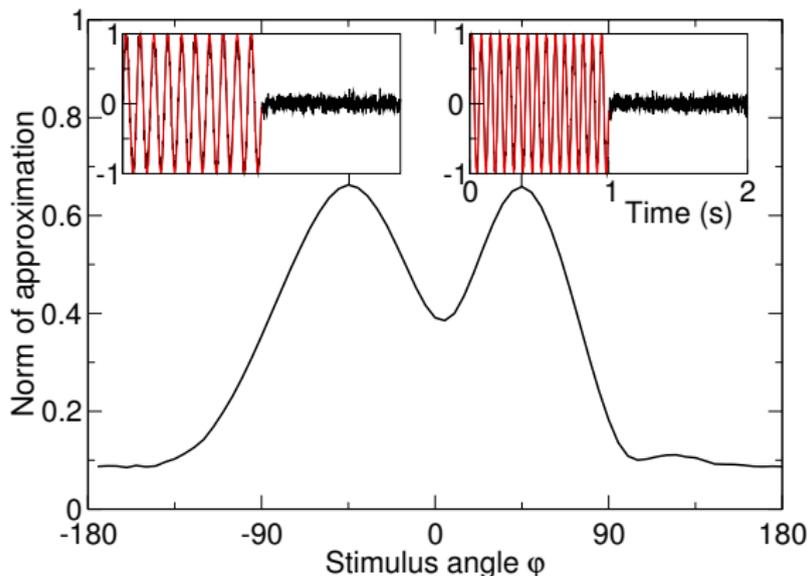


Figure: Two sources of 10 and 15 Hz, respectively, can be clearly discriminated.

Learning Algorithm

- return to the generalised gradient of the expected error (equ. (8))
- online learning rule to find the minimum: descent along the gradient

$$\Delta s_j(\tau) = -\eta \frac{\delta E}{\delta s_j(\tau)} \quad (11)$$

$$= \mathcal{F}^{-1} \left[-2\eta \left(\sum_i S_i Y_i - X \right) Y_j^* \right] \quad (12)$$

Results I

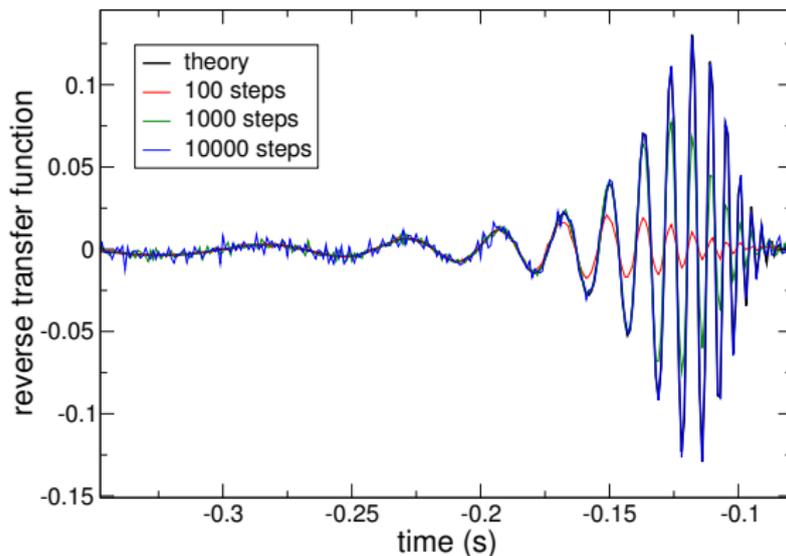


Figure: Linear learning: convergence ($\sigma = 0.1$, $\sigma_n = 0.1$, $\eta = 10^{-5}$).

Results II

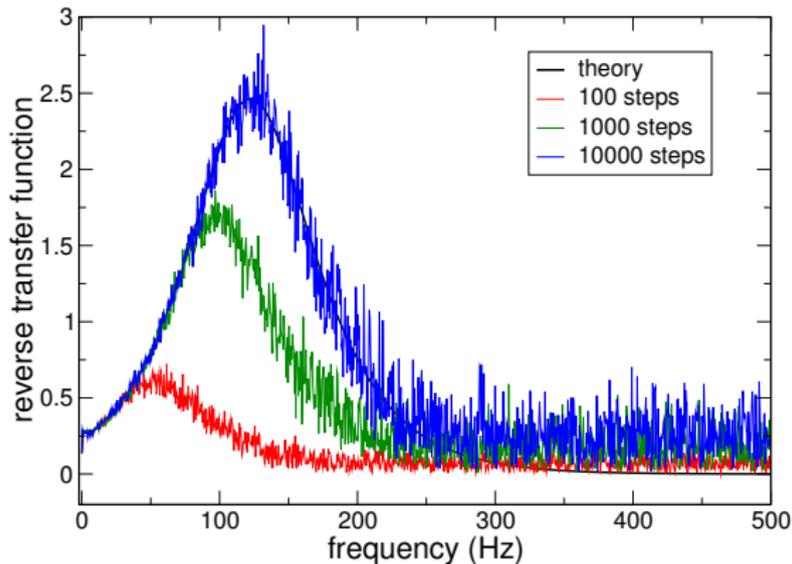


Figure: Convergence in frequency space.

- 1 Introduction
 - Xenopus and its Lateral Line
 - Water Waves
- 2 Minimal Model
 - Reconstruction of the Wave Form
 - Performance of the Minimal Model
 - Learning
- 3 **Field Reconstruction**
 - Full-Field Reconstruction
 - Window of Reference
- 4 Neuronal Implementation of the Model
 - Implementing a Convolution
 - Learning a Neuronal Model
 - Performance of a Neuronal Model

Full-Field Theory I

We want to

- improve the localisation performance,

Full-Field Theory I

We want to

- improve the localisation performance,
- simplify the implementation of the learning process.

Full-Field Theory I

We want to

- improve the localisation performance,
- simplify the implementation of the learning process.

⇒ Find the maximum likelihood reconstruction with respect to the whole field!

$$0 \stackrel{!}{=} \frac{\delta \bar{E}_{\text{ff}}}{\delta s_j^{\mathbf{P}}(\tau)} \quad (13)$$

$$\bar{E}_{\text{ff}} = \left\langle \sum_{\mathbf{P}} \int_{-\infty}^{+\infty} [x^{\mathbf{P}}(t) - \hat{x}^{\mathbf{P}}(t)]^2 dt \right\rangle \quad (14)$$

Full-Field Theory II

It can be shown that $\hat{x}^{\mathbf{P}}$ is again found by convolution of the signal coming from the organs with reverse transfer functions

$$\hat{x}^{\mathbf{P}} = \sum_i s_i^{\mathbf{P}} \star y_i . \quad (15)$$

\bar{E}_{ff} is minimised if $S_j^{\mathbf{P}}(\omega)$ solves the following system of linear equations:

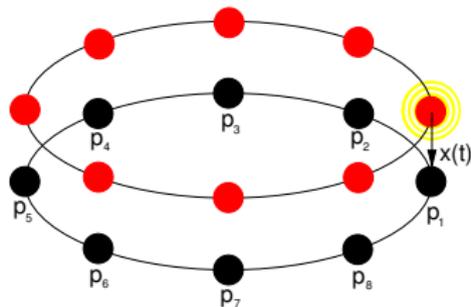
$$\sum_{\mathbf{p}} \left[\sum_i H_i^{\mathbf{q}*}(\omega) H_i^{\mathbf{p}}(\omega) + \sigma^2 \delta_{\mathbf{qp}} \right] S_j^{\mathbf{p}}(\omega) = H_j^{\mathbf{q}*}(\omega) . \quad (16)$$

Full-Field Learning

To learn this, we can use something like equation (12) again

$$\Delta s_j^{\mathbf{p}'}(\tau) = -\eta \frac{\delta E_{\text{ff}}}{\delta s_j^{\mathbf{p}'}(\tau)} \quad (17)$$

$$= \mathcal{F}^{-1} \left[-2\eta \left(\sum_i S_i^{\mathbf{p}'} Y_i - \delta_{\mathbf{p}, \mathbf{p}'} X^{\mathbf{p}} \right) Y_j^* \right] \quad (18)$$



Full-Field Calculation

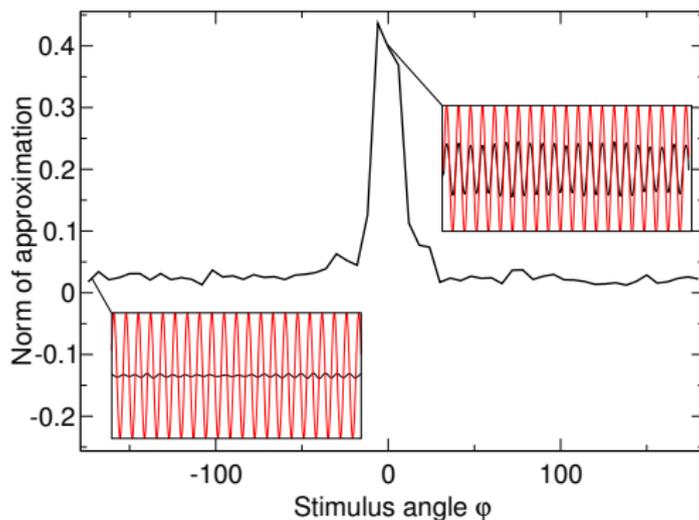


Figure: Map of reconstructions with a learned model (60 organs, 200000 steps).

Convergence

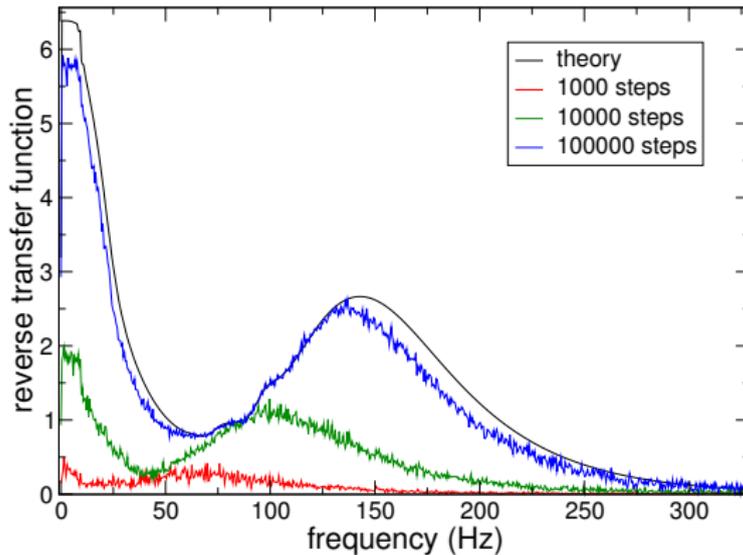


Figure: Full-field learning session (60 units).

Problems with Full-Field Learning

- very slow convergence

Problems with Full-Field Learning

- very slow convergence
- individual reconstruction norm strongly influenced by stochastic inhomogeneities during learning

Problems with Full-Field Learning

- very slow convergence
- individual reconstruction norm strongly influenced by stochastic inhomogeneities during learning
- improvement of localisation at the expense of reconstruction quality

Problems with Full-Field Learning

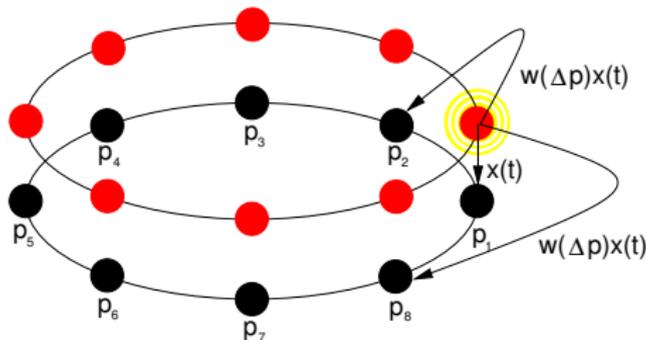
- very slow convergence
- individual reconstruction norm strongly influenced by stochastic inhomogeneities during learning
- improvement of localisation at the expense of reconstruction quality

⇒ Find a compromise between single position and full-field reconstruction!

Window of Reference I

The idea is to give reference input $x^{\mathbf{p}}(t)$ to a unit assuming input at position \mathbf{p}' weighted by the window of reference:

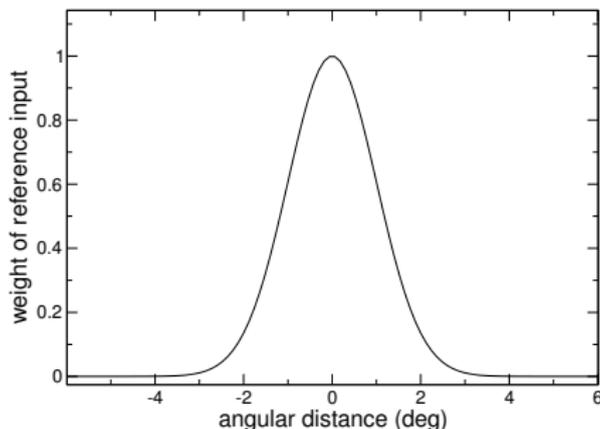
$$\Delta s_j^{\mathbf{p}'}(\tau) = \mathcal{F}^{-1} \left[-2\eta \left(\sum_i S_i^{\mathbf{p}'} Y_i - W(\Delta \mathbf{p}) X^{\mathbf{p}} \right) Y_j^* \right] \quad (19)$$



Window of Reference II

An example is be the gaussian function:

$$W(\mathbf{p}' - \mathbf{p}) = e^{-\frac{1}{2} \frac{\Delta\varphi^2}{\sigma_\varphi^2}} \quad (20)$$



Learning a WOR model

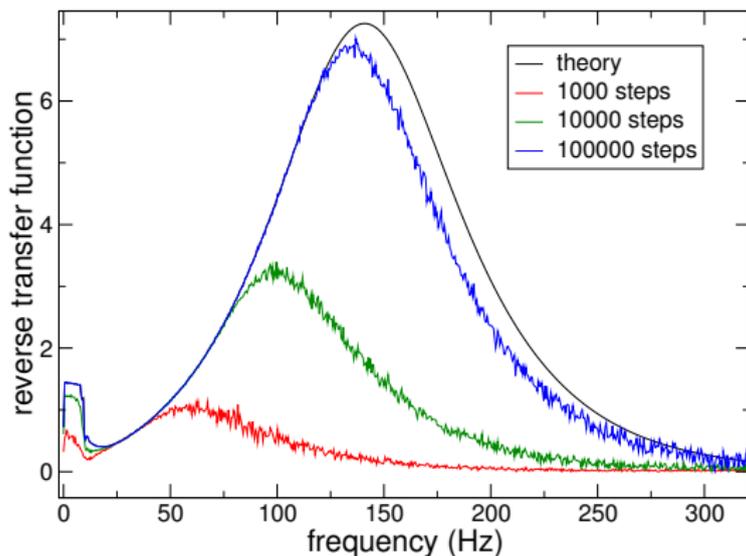


Figure: Convergence of a WOR model ($\sigma_\varphi = 12^\circ$).

Performance of a WOR Model

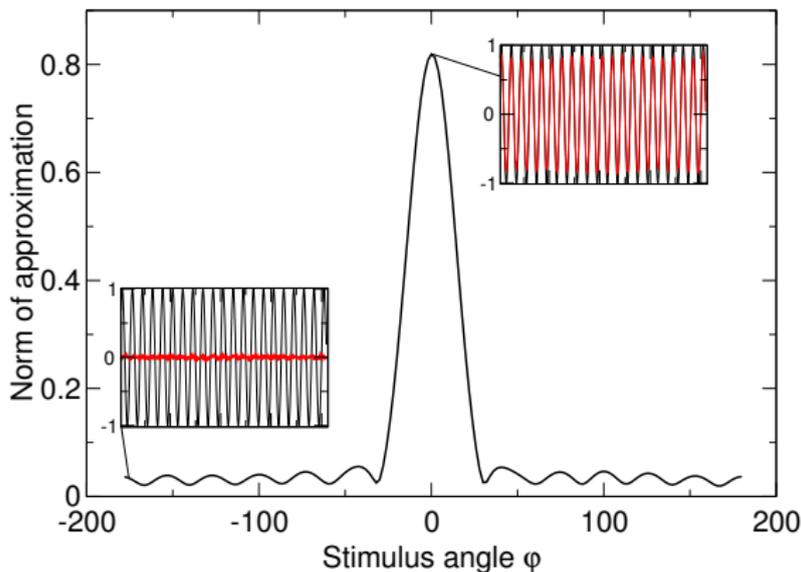
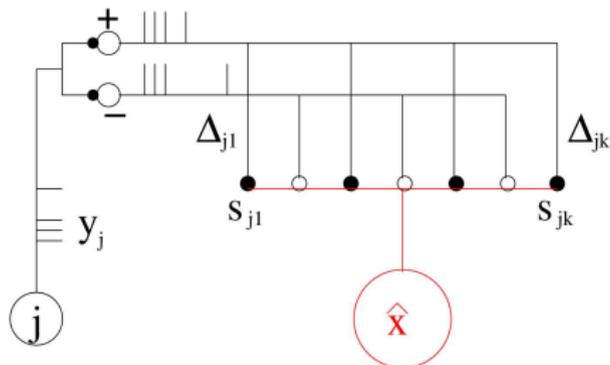


Figure: Localisation performance of a WOR model ($\sigma_\varphi = 10^\circ$).

- 1 Introduction
 - Xenopus and its Lateral Line
 - Water Waves
- 2 Minimal Model
 - Reconstruction of the Wave Form
 - Performance of the Minimal Model
 - Learning
- 3 Field Reconstruction
 - Full-Field Reconstruction
 - Window of Reference
- 4 **Neuronal Implementation of the Model**
 - **Implementing a Convolution**
 - **Learning a Neuronal Model**
 - **Performance of a Neuronal Model**

Neuronal Implementation of a Convolution

$$\hat{x}(t - T) = \sum_{jk} s_{jk} y_i(t - \Delta_{jk}) \quad (21)$$



Basic Learning Equation

Synaptic learning with a learning window $W(t_2 - t_1)$:

$$\Delta J_{ik} = \eta \int dt_1 \int dt_2 W(t_2 - t_1) \Sigma_{ik}^{\text{in}}(t_2) \Sigma^{\text{out}}(t_1) . \quad (22)$$

Choose $W(t) = -2\epsilon(-t)$ and make sure that $\Sigma^{\text{out}} = \hat{x}(t) - x(t)$ by giving $x(t)$ as additional inhibitory input to ensure equivalence to our learning equation

$$\Delta s_{ik} = \mathcal{F}^{-1} \left[-2\eta \left(\hat{X} - X \right) Y_i^* \right] . \quad (23)$$

Reverse Transfer Functions I

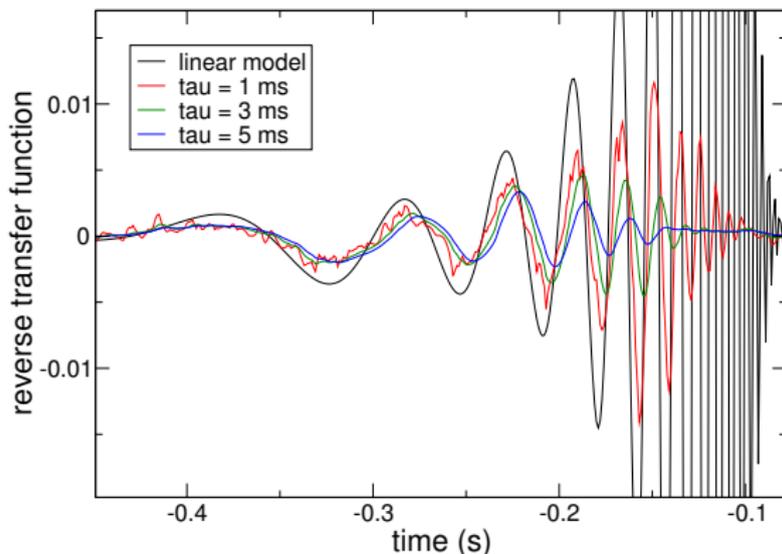


Figure: Reverse transfer functions implemented in neuronal hardware. The linear model can only provide rough comparison.

Reverse Transfer Functions I

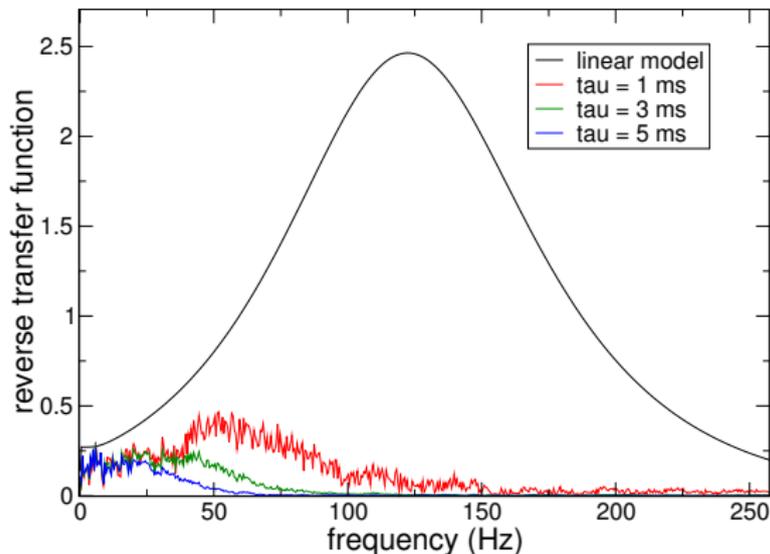


Figure: Same as the last slide in frequency space. The broadening of a spike in the PSPs acts as a low pass filter.

Localisation

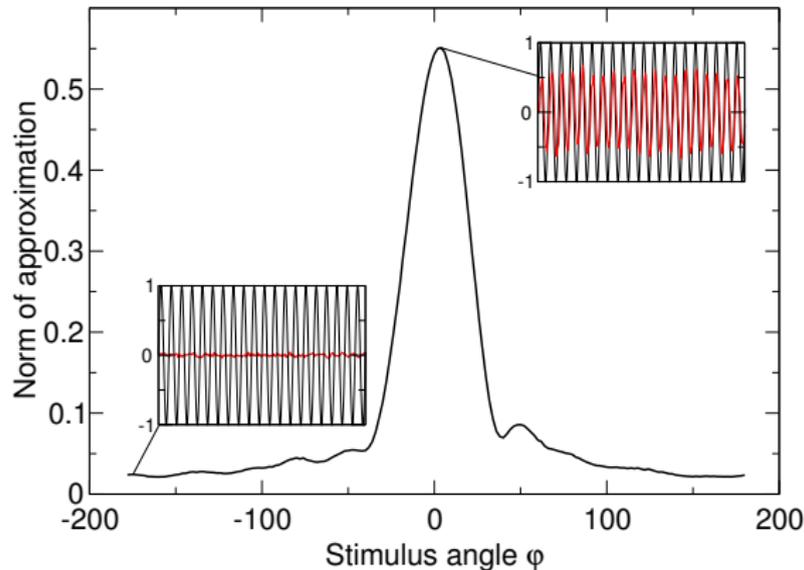


Figure: Localisation performance of a field of 180 neurons after 25000 learning steps.

Outlook

What still has to be done:

- convergence of the neuronal model

Outlook

What still has to be done:

- convergence of the neuronal model
- distance learning

Outlook

What still has to be done:

- convergence of the neuronal model
- distance learning
- underwater detection

Outlook

What still has to be done:

- convergence of the neuronal model
- distance learning
- underwater detection
- reference input

Bibliography



A. Elefandt and L. Wiedemer.

Lateral-line responses to water surface waves in the clawed frog, *Xenopus laevis*.

J. Comp. Physiol. A, 160:667–682, 1987.



B. Claas and H. Münz.

Analysis of surface wave direction by the lateral line system of *Xenopus*.

J. Comp. Physiol., 178(2):253–268, 1996.



J. M. P. Franosch, M. C. Sobotka, A. Elefandt, and J. L. van Hemmen.

Minimal model of prey localization through the lateral-line system.

Physical Review Letters, 91(15), October 2003.