

How a Frog Can Learn What Is Where in the Dark

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During the night 180 lateral-line organs allow the clawed frog *Xenopus* to localize prey by detecting water waves emanating from insects floundering on the water surface. Not only can the frog localize prey but it can also determine its character. This suggests waveform reconstruction, and a key question is how the frog can establish the appropriate neuronal hardware. Detecting time differences arising from the input on the skin is a key to neuronal information processing, and spike-timing-dependent synaptic plasticity (STDP) therefore seems to be the natural tool. We show how supervised STDP allows a frog to learn what is where in the dark. Learning can also be derived from a minimization principle.

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In nature animals interact with their surroundings, and, conversely, their surroundings influence the way in which their brain and, hence, their handling of sensory data develop. In so doing they “learn,” and questions that have tantalized learning theory for so long are whether or not a neuronal system needs a teacher and, if so, who is teaching and how?

Sensory input arrives as a *spatiotemporal* activity pattern. Learning happens in general at the level of synapses, and there is a detailed biophysical theory describing how synapses learn as they are driven by their presynaptic and postsynaptic neurons. Here we study the clawed frog *Xenopus laevis laevis*, an aquatic animal living in ponds and hunting at night for insects floundering at the water surface. This prey generates surface waves that activate about 180 receptor organs on the frog’s skin and, hence, the underlying lateral-line system [1] in the frog’s brain.

Not only can the frog determine a prey direction but it can also determine its character, say, edible or not. How does it do so? We have shown [2] that neurons can perform a waveform reconstruction, which solves the problem—except for the key question of how a frog *attains* the neuronal “hardware” needed to do the waveform reconstruction job. Here we suggest a solution to this problem by indicating how this can be done through supervised learning with, e.g., the visual system of a young frog as teacher. Learning now means *supervised* spike-timing-dependent synaptic plasticity handling input patterns as they evolve in space *and* time.

The lateral-line system of *Xenopus* has 180 sensory units measuring the local water velocity. Each receptor projects to afferent fibers that lead to the medulla in the central nervous system. All fibers possess identical response characteristics. For comparison, the visual system [3] of a human has millions of light-sensitive receptors with different characteristics, and in the human ear [4] there are about 3500 inner hair cells sensitive to different frequencies and levels of loudness. In contrast, the lateral-line system has relatively few organs of only one type. Their anatomy [1] is relatively simple.

The sensory organs project to the medulla, and from there via the torus semicircularis to the optical tectum. Here the visual and the lateral-line systems “meet” and form maps [5] in register with each other [6]. There we also find bimodal neurons that react to a visual as well as a lateral-line stimulus [6]. The neuronal model presented here reveals how the two simplest tasks of a remote sensory system, namely, to determine *what* happens *where*, may be performed and *learned* by a single neuronal circuit. Computer simulations support the underlying ideas and show that the learning algorithms are feasible, given the known constraints of neuronal hardware.

Each of the 180 lateral-line organs on the skin of *Xenopus*’ body consists of 4–8 cupulae [1] being deflected proportionally to the local water velocity [7]. This deflection is transferred into action potentials (spikes) in the nerve fibers attached to the lateral-line organs.

The deflection $y_i(t)$ of the cupulae of lateral-line organ i at time t is taken proportional to the local water velocity and thus a linear function of the stimulus $x^{\mathbf{p}}$ at direction \mathbf{p} on the water surface. We therefore write

$$y_i(t) = (h_i^{\mathbf{p}} \star x^{\mathbf{p}})(t) = \int_{-\infty}^{\infty} h_i^{\mathbf{p}}(\tau) x^{\mathbf{p}}(t - \tau) d\tau, \quad (1)$$

where $h_i^{\mathbf{p}}$ is the impulse response at cupula i while being stimulated by a Dirac delta impulse at direction \mathbf{p} on the water surface, the star \star denoting convolution. The Fourier transformation of the impulse response $h_i^{\mathbf{p}}$ is the transfer function [2] $H_i^{\mathbf{p}}(\omega) = \int h_i^{\mathbf{p}}(t) \exp(-i\omega t) dt$. For the sake of simplicity we *discretize* the directions \mathbf{p} , here 180 altogether.

Xenopus is able to distinguish different wave sources, say, 17 and 18 Hz, presented *simultaneously* at different positions on the water surface so that they impinge on the frog in an overlapping fashion. In principle, it can reconstruct [2] the waveform *at its origin* through neuronal hardware by minimizing the expectation value of the quadratic error $\int [\hat{x}^{\mathbf{p}}(t) - x^{\mathbf{p}}(t)]^2 dt$ between the true waveform $x^{\mathbf{p}}$ of the source and its estimate $\hat{x}^{\mathbf{p}}$. With σ_x denoting the standard deviations of Gaussian wave source noise and

σ_n of additional Gaussian white noise added to the deflections of the receptor organs and $\sigma := \sigma_n/\sigma_x$, the solution is [2]

$$\hat{x}^{\mathbf{p}} = \sum_j s_j^{\mathbf{p}} \star y_j, \quad S_j^{\mathbf{p}}(\omega) = \frac{H_j^{\mathbf{p}*}(\omega)}{\sum_i |H_i^{\mathbf{p}}(\omega)|^2 + \sigma^2}. \quad (2)$$

A reverse impulse response $s_j^{\mathbf{p}}$ may be computed from its given Fourier transformations $S_j^{\mathbf{p}}$, the reverse transfer function. The transfer function $H_i^{\mathbf{p}}$, as given in [2], as well as its complex conjugate $H_i^{\mathbf{p}*}$, depend on the position \mathbf{p} an animal is interested in.

Say a prey has position \mathbf{p} . The Kronecker delta $\delta_{\mathbf{p},\mathbf{p}'} = 1$ if $\mathbf{p} = \mathbf{p}'$, otherwise 0. To learn where the prey is as well as what waveform $x^{\mathbf{p}}$ it generates, let us assume that *Xenopus* somehow minimizes the expectation value of

$$E = \sum_{\mathbf{p}'} \int [\hat{x}^{\mathbf{p}'}(t) - \delta_{\mathbf{p},\mathbf{p}'} x^{\mathbf{p}}(t)]^2 dt, \quad (3)$$

where the sum is over all different directions \mathbf{p}' on the water surface. This minimization ensures that, first, the reconstruction $\hat{x}^{\mathbf{p}'}$ resembles the source $x^{\mathbf{p}}$ as closely as possible if $\mathbf{p}' = \mathbf{p}$ and, second, when reconstructing at the wrong position $\mathbf{p}' \neq \mathbf{p}$, it is as close to zero as possible. The source can therefore be localized by calculating $\hat{x}^{\mathbf{p}'}$ for every position, choosing position \mathbf{p} where the norm $\|\hat{x}^{\mathbf{p}}\|$ of the reconstruction is maximal.

Let us suppose a learning neuronal system uses the simplest optimization procedure, a “steepest descent.” It is, for the moment, learning by adapting the reverse impulse responses $s_j^{\mathbf{p}}$ in the direction of the negative functional derivative of the error E of (3),

$$\Delta s_j^{\mathbf{p}'}(\tau) = -\eta \delta E / \delta s_j^{\mathbf{p}'}(\tau), \quad (4)$$

where η is a (small) learning parameter. Using the expression for $\hat{x}^{\mathbf{p}}$ from (2) we find

$$\frac{\delta E}{\delta s_j^{\mathbf{p}'}(\tau)} = 2 \int \left[\sum_i (s_i^{\mathbf{p}'} \star y_i)(t) - \delta_{\mathbf{p},\mathbf{p}'} x^{\mathbf{p}}(t) \right] y_j(t - \tau) dt. \quad (5)$$

The solutions $s_j^{\mathbf{p}'}$ of the minimization problem can also be computed by solving (5) for $\delta E / \delta s_j^{\mathbf{p}'}(\tau) = 0$ directly, which leads, after Fourier transformation, to the linear system of equations

$$\sum_i \left[\sum_{\mathbf{p}} H_j^{\mathbf{p}*} H_i^{\mathbf{p}} + \sigma^2 \delta_{ij} \right] S_i^{\mathbf{p}'} = \sum_{\mathbf{p}} \delta_{\mathbf{p},\mathbf{p}'} H_j^{\mathbf{p}*}. \quad (6)$$

Figure 1 shows a comparison between the power spectrum $|S^{\mathbf{p}}(\omega)|$ of a theoretical reverse impulse response $s^{\mathbf{p}}$ and that of the numerically learned one after different numbers of learning steps.

Convergence of the model based on (5) is very slow. Furthermore, according to the authors’ experience, a “map” of reconstruction norms as suggested above still

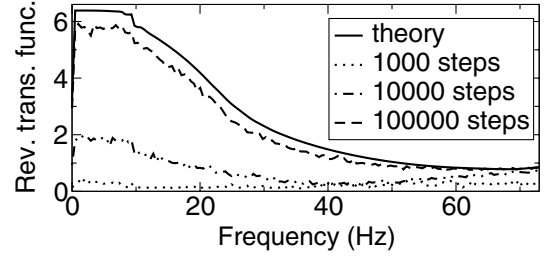


FIG. 1. Power spectrum $|S^{\mathbf{p}}(\omega)|$ of a theoretical reverse transfer function computed from (6) (solid line) and power spectra of learned reverse transfer functions according to (4) after different numbers of learning steps (see legend, $\eta = 10^{-5}$). White noise ($\sigma_x = 1$) at random angles 10 cm away from the frog was used as learning stimulus. As the number of learning steps increases, the learned transfer functions converge to the theoretical result.

contains a good deal of randomness, which depends on the specific learning procedure. Reconstruction quality is strongly influenced by noise. Hence we suggest to replace the “sharp” δ expression $\delta_{\mathbf{p},\mathbf{p}'}$ in (3) and thus in Eqs. (5) and (6) by a larger *window of reference* $F(\mathbf{p}, \mathbf{p}')$, e.g., the Gaussian

$$F(\mathbf{p}, \mathbf{p}') = \exp\{-[\varphi(\mathbf{p}) - \varphi(\mathbf{p}')]^2 / [2\sigma_\varphi^2]\}, \quad (7)$$

which depends on the angular difference $\varphi(\mathbf{p}) - \varphi(\mathbf{p}')$ between the actual position \mathbf{p} of a prey and the reconstruction position \mathbf{p}' .

The underlying idea is the following and is, in fact, biological. We cannot expect the error E of (3) to become exactly zero because the norm $\|\hat{x}^{\mathbf{p}}\|$ is a smooth function of \mathbf{p} so that at neighboring positions the reconstructions are bound to “look” similar. So for discrete directions we replace the Kronecker delta by a finite window $F(\mathbf{p}, \mathbf{p}')$ and minimize

$$E_W = \sum_{\mathbf{p}'} \int [\hat{x}^{\mathbf{p}'}(t) - F(\mathbf{p}, \mathbf{p}') x^{\mathbf{p}}(t)]^2 dt. \quad (8)$$

Figure 2 shows the result of a numerical simulation with a window of reference.

A neuronal implementation of the model developed above has to solve two problems. First, how is the wave source reconstruction $\hat{x}^{\mathbf{p}}$ computed according to (2), *given* the functions $s_i^{\mathbf{p}}$? Second, how are the latter found through a *learning process*?

A neuron whose membrane potential approximates the convolution of (2) is depicted in Fig. 3. We denote the so-called “spike train” by $y_{ik}^{\mathbf{p}}$. This is the sequence of spikes that arrive from lateral-line nerve fiber i at synapse k of the neuron that is responsible for a reconstruction of the wave source at position \mathbf{p} . The spike train is the same as that coming from the lateral-line nerve, only *delayed* by a time $\Delta_{ik}^{\mathbf{p}}$. If f_i denotes times when spikes are generated in lateral-line nerve i , then

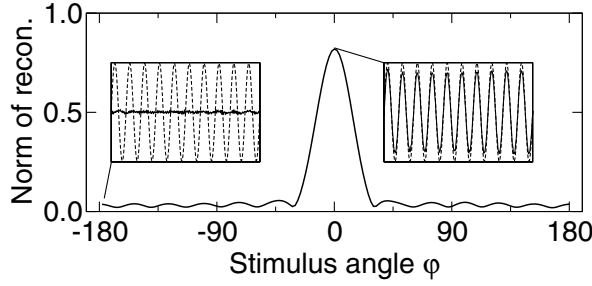


FIG. 2. A model minimizing the error E_W from (8) has been learned applying the method of Fig. 1 with the window of reference ($\sigma_\varphi = 14^\circ$) of (7) for 200 000 times. The figure shows a map of norms of reconstructions $\|\hat{x}^{\mathbf{p}}\|$ (thick solid line) at different angles $\varphi(\mathbf{p})$ around *Xenopus*. As expected, the norm is maximal where the actual test stimulus is, viz., at 0° , 10 cm right in front of *Xenopus*. Moreover, at 0° the model reconstructs (solid line in the inset on the right) the given test stimulus (sinusoidal with amplitude 1, dashed line in the inset) quite well. At angles far off (-180° in the inset on the left), the reconstruction is basically noisy with a low amplitude. The Gaussian white noise added to the deflections y_i of the lateral-line organs has a standard deviation of $\sigma_n = 0.01$.

$$y_{ik}^{\mathbf{p}}(t) = \sum_{f_i} \delta(t - f_i - \Delta_{ik}^{\mathbf{p}}), \quad (9)$$

where δ denotes the Dirac delta function describing an action potential. Each spike arriving at a synapse generates a membrane potential $\varepsilon(t)$. Denoting synaptic strengths by $J_{ik}^{\mathbf{p}}$, we can compute the membrane potential $V^{\mathbf{p}}$ of a neuron, modeled as a spike-response neuron [8],

$$V^{\mathbf{p}}(t) = \sum_{ik} \int_{-\infty}^{\infty} J_{ik}^{\mathbf{p}} \varepsilon(t - \tau) y_{ik}^{\mathbf{p}}(\tau) d\tau. \quad (10)$$

For simulations, we take $\varepsilon(t) = t/\tau_s^2 \exp(-t/\tau_s)$ for $t \geq 0$ and $\varepsilon(t) = 0$ for $t < 0$, with a synaptic time constant $\tau_s = 10$ ms. The membrane potential $V^{\mathbf{p}}(t)$ of our neuron at time t should closely resemble the deflection $x^{\mathbf{p}}(t - T)$ of the source at a time $t - T$ in the *past* so that we are able to construct a *causal* system with $\Delta_{ik}^{\mathbf{p}} \geq 0$. Accordingly, the neuronal learning process should minimize the error,

$$E_N = \sum_{\mathbf{p}'} \int [V^{\mathbf{p}'}(t) - F(\mathbf{p}, \mathbf{p}') x^{\mathbf{p}}(t - T)]^2 dt.$$

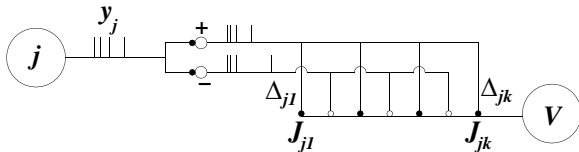


FIG. 3. Circuit diagram of a neuron with membrane potential V that is connected to lateral-line nerve fiber j by excitatory (full circles) and inhibitory (open circles) synapses with synaptic strengths J_{jk} and delays Δ_{jk} . The neurons labeled by “+” and “-” signs accommodate the observation that a single fiber can have synapses of only one type, excitatory or inhibitory.

After substituting $V^{\mathbf{p}'}$ from (10), minimization with respect to $J_{ik}^{\mathbf{p}'}$ leads to the learning equation

$$\Delta J_{ik}^{\mathbf{p}'} = -2\eta \iint_{-\infty}^{\infty} [V^{\mathbf{p}'}(t) - F(\mathbf{p}, \mathbf{p}') x^{\mathbf{p}}(t - T)] y_{ik}^{\mathbf{p}'}(\tau) \times \varepsilon(t - \tau) d\tau dt. \quad (11)$$

The “teacher’s” feedback $F(\mathbf{p}, \mathbf{p}') x^{\mathbf{p}}(t - T)$ is provided through synapses with strengths $F(\mathbf{p}, \mathbf{p}')$ and projecting from the visual system to the lateral-line “map.” Equation (11) is similar to a more general learning rule [8],

$$\Delta J = \eta \iint_{-\infty}^{\infty} y_{\text{out}}(t) y_{\text{in}}(\tau) W(\tau - t) d\tau dt, \quad (12)$$

where y_{in} is the input spike train as in (9), y_{out} the output spike train, and W the *learning window*. If we identify y_{in} with $y_{ik}^{\mathbf{p}'}$ and set $W(t) = -2\varepsilon(-t)$, Eqs. (11) and (12) match. We just have to give the original stimulus $x^{\mathbf{p}}$ as additional inhibitory input to our neuron, delayed by T and weighted by the window of reference so that its output spike train y_{out} approximates the function $V^{\mathbf{p}'}(t) - F(\mathbf{p}, \mathbf{p}') x^{\mathbf{p}}(t - T)$. As it is not known yet for sure which learning rule real neurons implement, the authors have used the more exact (11) for the simulations.

In experiments [9], the frog turns into the direction of a wave caused by a moving plunger. In Fig. 4, the model frog can even discern two *simultaneous* stimuli, just as in experiment [10]. The *Xenopus* model of Fig. 5 learns to localize the prey with high accuracy after 50 000 learning steps (about one day of practice).

Action potentials in the lateral-line nerves are generated by an inhomogeneous Poisson process approximating the real input-output characteristics [11] of the lateral-line organ. Nerve i generates an action potential in the time

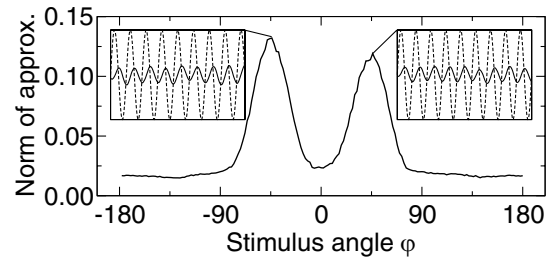


FIG. 4. A map of 180 neurons learned to reconstruct the source at 180 positions arranged in a circle with radius 10 cm around *Xenopus*. After 50 000 learning steps, i.e., presentations of Gaussian white-noise stimuli during 2 s, performed according to (11), the map is able to accurately *localize* both of two *simultaneous* wave sources at $\varphi = -45^\circ$ (17 Hz) and 45° (18 Hz). In addition, the neurons indicating the respective angles *reconstruct* the wave source (solid lines in the insets). The delays $\Delta_{ik}^{\mathbf{p}}$, $k = 1, \dots, 100$, of (9) are randomly distributed in an interval of 500 ms. In this way the animal could easily distinguish position and waveform of the sources. As σ_φ (here 14°) becomes larger, the two “hills” become broader and the discrimination ability of *Xenopus* decreases accordingly.

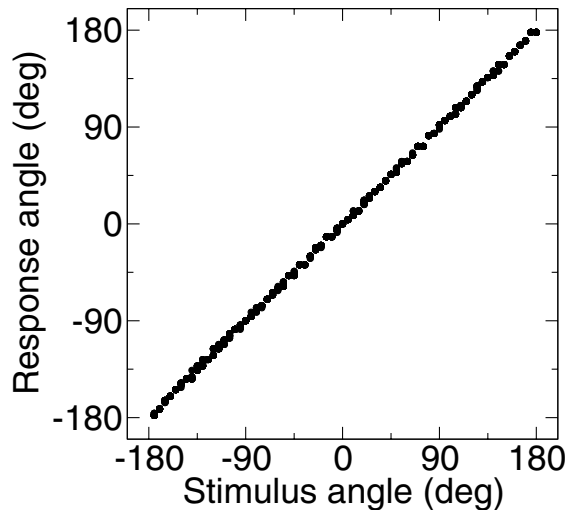


FIG. 5. *Xenopus*' simulated response angle versus stimulus angle φ during 25 trials at angle $\varphi = n \times 5^\circ$, $-36 < n \leq 36$. *Xenopus* was assumed to turn into the direction $\varphi(\mathbf{p})$, such that the model response $\|\mathbf{VP}\|$ of the neuron reconstructing the stimulus at position \mathbf{p} is maximal. The neuronal system has learned as in Fig. 4. The frog's performance is excellent.

interval $[t, t + dt)$ with a probability of $[\pm R y_i(t) + R_s] dt$, $R = 300$ Hz, giving realistic spike rates lower than about 150 Hz and spontaneous rates $R_s = 10$ Hz [12]. The negative sign is for nerves that are excited by negative deflections $y_i(t) < 0$. Action potentials generated by Gaussian random noise produce the feedback $F(\mathbf{p}, \mathbf{p}') x^{\mathbf{p}}(t - T)$ in (11). The postsynaptic potential ε for the feedback is the same as above.

The model presented here shows how *Xenopus* can learn how to localize prey. It is based on realistic properties of a neuronal system. Moreover, it also learns an internal representation of the wave source *at its origin* that would allow the frog to discern different kinds of prey. The model, based on a minimization principle, is so general that it can learn any linear relationship between a reference input and sensory input. It solves the problem of determining *what* is going on *where* through a map of neurons indicating by their *activity* where the source is and by their *activity pattern* what kind of stimulus it is, independently of its origin.

The model may well be applicable to other animals, such as crocodylians that use about 2000 dome pressure receptors on their face to localize prey [13]. Fish use canal organs to measure water accelerations [14]. The barn owl uses visual feedback to match its auditory prey localization [15] to its visual system [16]. Many animals use independent sensory systems like vision, audition, the equilibrium sense, and tactile senses that have to work together to form some representation or "picture" of the outer world in the animal's brain.

The exact kind of feedback *Xenopus* needs to calibrate its neuronal system is not known yet. One possibility is that

its eyes are designed to view accurately in air, i.e., above the water surface [1]. In the barn owl, visual input guides auditory plasticity. The visual activity that results from a bimodal stimulation encodes the *mismatch* between spatial representations of auditory and visual stimuli [16] in the nucleus where learning takes place, just as what we assume here for *Xenopus*.

It would suffice if *Xenopus* were able to see the prey moving only during the learning phase. There is no need to observe the water surface at the wave's origin directly as we can assume a linear coupling between the prey's movements and the waveform of the source. If so, just the prey's movements as being observed by the eyes would be matched with the lateral-line input, which would be perfectly adequate to distinguish different kinds of prey.

Finally, the present model suggests that experimentally observed and theoretically analyzed learning "rules" [8] like Eq. (12) might be derived from an error minimization principle. The minimization procedure leads to an exact learning window that can be used in the learning rule but also in applications, whenever two sensory modalities, such as a visual and mechanosensory one, shall be matched or in underwater localization.

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