The leaky integrator with recurrent inhibition is a predictor

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Abstract: It is shown that the leaky integrator, the basis for many neuronal models, possesses a negative group delay when a time-delayed recurrent inhibition is added to it. By means of this negative group delay, the leaky integrator becomes a predictor for low-frequency components of the integrated signal. The prediction properties are derived analytically and an application to a local field potential is provided.

Running Title: The leaky integrator as a predictor

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In "How delays affect neural dynamics and learning" 1, Baldi and Atiya state that "Integration and communication delays are ubiquitous, both in biological and man-made neural systems ... Indeed, delays should be considered as an additional media through which evolution, or skilled engineers, can achieve particular dynamical effects." In fact, time delays have an impact on the dynamics of neuronal networks, for example by their ability to cause oscillations and waves 2. In this Note I would like to point out how time delays added to leaky integrators are defining predictors for smooth but otherwise arbitrary input signals. The underlying mechanism, negative group delay, is known from simple electronic circuits 3, 4, but to the best of my knowledge has not been used in the neurosciences so far.

The basic model is a leaky integrator with a recurrent, time-delayed inhibition. The leaky integrator is defined as usual as a capacitance, the integrator, in parallel to a resistance, the leak 5. The recurrent inhibition is modelled following Plant 6 as a linear time-delayed feedback term with negative gain. Then, the leaky integrator with recurrent inhibition follows as

\[ \dot{y}(t) = -a y(t) + b x(t) - c y(t - \tau), \]  

(1)

where \(a \geq 0\) is the leakage coefficient, \(x(t)\) the input signal (zero-mean, stationary), \(b > 0\), \(c \geq 0\) the (inhibitory) feedback gain, and \(\tau > 0\) a time delay. For \(c = 0\), Eq. (1) would simply be a leaky integrator, but for \(c > 0\) it has an inhibitory feedback that enters the model as a delayed leak. Therefore, model (1) is referred to as a "delayed-leak integrator" (DLI). For \(a = 0\) and \(c > 0\), it describes a pure DLI without a conventional leak, which would have similar properties as the DLI with \(a > 0\) but is not further considered here.

Equation (1) is linear and thus can be described by its frequency response function
\[ H(\omega) = \frac{b}{a + i\omega + ce^{-i\omega\tau}} = \frac{b}{\beta}(h_1 + ih_2), \]  

with \( h_1 = a + c \cos(\omega \tau), \ h_2 = c \sin(\omega \tau) - \omega, \ \beta = h_1^2 + h_2^2 \). It defines the steady-state input-output relationship between \( x \) and \( y \) in Fourier space as \( Y(\omega) = H(\omega)X(\omega) \), where \( f \) is frequency, \( \omega = 2\pi f \), \( x(t) = \int X(\omega)e^{i\omega t}d\omega \), and \( y(t) = \int Y(\omega)e^{i\omega t}d\omega \). If written as \( H(\omega) = G(\omega)e^{i\phi(\omega)} \), its gain is \( G(\omega) = b/\sqrt{\beta} \), and its phase is \( \Phi(\omega) = \arg(h_1 + ih_2) \). The frequency dependent group delay is

\[
\delta(\omega) = -\frac{d\Phi(\omega)}{d\omega} = \frac{c \cos(\omega \tau) - c^2 \tau - a(c \tau \cos(\omega \tau) - 1) + c\tau \omega \sin(\omega \tau)}{\beta}.
\]  

Negative group delay in general means a group advance \cite{3,4}, or real-time prediction of the input signal \( x \). For the prediction of smooth, i.e., band limited signals, of particular interest is the value of \( \delta(\omega) \) for small \( \omega \): Expansion of \( \delta(\omega) \) for small \( \omega \) shows that there are no linear terms in \( \omega \) remaining. If quadratic and higher order terms in the counter and denominator of Eq. (3) are neglected, it follows

\[
\delta_{\text{small } \omega} \approx \frac{1 - c \tau}{a + c}.
\]  

This main result has two important consequences for input signal components with small \( \omega \):

(i) For \( c\tau > 1 \), the group delay is negative, a necessary condition for prediction.

(ii) The group delay is approximately independent of \( \omega \), a necessary condition for distortion-free signal transfer \cite{4,9}.

The figure shows a numeric simulation of the DLI (1) with input \( x \) consisting of the first 6.25 s of a local field potential (LFP) from the left hippocampus (CA1) of a rat ("hc-5" data from CRCNS.org \cite{10}). Specifically, \( x \) is the average over all electrodes, Butterworth low-pass filtered with a cutoff at 10 Hz, then transformed to zero mean and unit standard deviation. The parameters were manually optimized to cause real-time prediction, as \( a = 0.600 \text{ ms}^{-1}, \ b = 0.480 \text{ ms}^{-1}, \ c = 0.432 \text{ ms}^{-1} \), and \( \tau = 40.0 \text{ ms} \). Equation (1) was solved with a Runge-Kutta scheme of 4th order with \( y(0) = x(0) \) and \( y(t) = 0 \) for \( t \in [-\tau, 0] \). All computations were performed with MATLAB R2015a (The MathWorks, Inc., Natick, MA).

In Figure (a) the first quarter of the input \( x \) and the output \( y \) are shown. **It is evident that the DLI output \( y \) at time \( t \) (red) predicts the LFP input \( x \) at a time \( t + \delta \) (black) on average.** More specifically, the cross-correlation function (CCF) between \( x \) and \( y \) (c) has a global maximum of 0.96 at \( \delta = -12.0 \text{ ms} \). Further, the group delay \( \delta_{\text{small } \omega} \) is -15.8 ms (Figure (b), red dashed line shows 10\( \delta_{\text{small } \omega} \)). Figure (b) also depicts the estimated and analytic phase and gain of the frequency response function. It has a frequency band with negative group delay followed by a band with positive group delay. Therefore, low frequency components of \( x \) are predicted, some higher components are lagged by \( y \). Figure (d) shows the same simulation with an unfiltered input signal, and (e) its CCF with global maximum of 0.72 at -6.4 ms.
A discussion concludes this Note: The DLI (1) performs a real-time prediction of the LFP. Although counterintuitive, it does not violate causality and is a special case of anticipatory relaxation dynamics. Its performance depends on the choice of parameters and the data; for improperly chosen parameters it might not predict or cause oscillatory instabilities. Very recently it has been emphasized that anticipatory systems can defy the inference of the direction of information flow from data. It would be interesting if this holds true for negative group delay systems, too, which would render this task even more difficult. Further, DLIs might augment the related concept of neuronal anticipatory synchronization, which recently has been used to explain observations in brain data. Note that DLIs, in contrast to most other prediction schemes, do not require a memory of past signal values, only of past predicted, already internalized, states, as Eq. (1) does not contain delayed inputs. It would be worth investigating how negative group delay systems fit into general theories of prediction or if they can be used as predictive components in artificial neuronal networks. It is an open question if nature uses DLI-like systems for real-time prediction. However, due to the ease with which negative group delay can be achieved, namely by just a simple time delayed feedback, it is quite conceivable that Baldi and Atiya’s insights would be corroborated once again.

Figure: Simulation of the DLI system with experimental input data. Please refer to text for detailed description.
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