

## S8 First Order Temporal Low-Pass Filter (Equation 4)

This section derives equation (4) from the differential equation of a leaky integrator. Let  $x$  be the state variable of the leaky integrator which, for example, may represent the firing rate of a neuron:

$$\tau_m \frac{dx(t)}{dt} = -x(t) + z(t) \quad (\text{S27})$$

The last equation integrates the input  $z(t)$  with time constant  $\tau_m$  (which may represent the membrane time constant of a neuron). If  $\tau_m$  is sufficiently small, then past inputs are quickly discarded, and the filter response  $x(t)$  (“output variable”) eventually follows the input  $z(t)$ . In other words, few low-pass filtering of  $z(t)$  occurs, and the filter is said to have a short memory.

If  $\tau_m$  is very big, then the opposite will occur: The filter gets very sluggish, and eventually sums up all inputs  $z(t)$ . This means that the filter output  $x(t)$  is a strongly low-pass filtered version of the input  $z(t)$ , and the filter is said to have a long memory.

The just described behavior is readily seen when we consider a discretized version of the last equation. For discretization, we assume that time  $t$  increases in steps of  $\Delta t$  (“sampling interval” or “integration time step”). We have two possibilities for implementing discretization: *Forward differencing* and *backward differencing*. Both differencing schemes will be considered in turn.

### S8.1 Forward Differencing (“Forward Euler”)

Here, the right hand side depends on  $t$  (i.e., only on past terms):

$$\tau_m \frac{x(t + \Delta t) - x(t)}{\Delta t} = -x(t) + z(t) \quad (\text{S28})$$

By Rearranging terms we obtain:

$$x(t + \Delta t) = \left[ 1 - \frac{\Delta t}{\tau_m} \right] x(t) + \frac{\Delta t}{\tau_m} z(t) \quad (\text{S29})$$

Now let  $\xi \equiv \Delta t/\tau_m$ , and  $0 \leq \xi \leq 1$ . Then, we readily obtain equation (4) by defining the memory constants as  $\zeta_i \equiv 1 - \xi$  with  $i = 1, 2$ . A big time constant  $\tau_m \gg \Delta t$  implies  $\zeta_i \rightarrow 1$ . This would endow the filter with an infinite memory – it will never change its initial value, because the input  $z(t)$  will be multiplied by zero.

The other limit case is defined by  $\tau_m = \Delta t$  (“small  $\tau_m$ ”), and thus  $\zeta_i = 0$ . Then,  $x(t + \Delta t) = z(t)$ , meaning that the filter has no memory on past inputs. In other words, no lowpass filtering takes place – the filter output  $x$  follows the input signal  $z$ .

### S8.2 Backward Differencing (“Backward Euler”)

Here, the right hand side depends on  $t + \Delta t$  (i.e., on future terms):

$$\tau_m \frac{x(t + \Delta t) - x(t)}{\Delta t} = -x(t + \Delta t) + z(t + \Delta t) \quad (\text{S30})$$

A more compact notation can be obtained by substituting  $\tilde{t} \equiv t + \Delta t$  in the last equation (and omit the tilde in what follows):

$$\tau_m \frac{x(t) - x(t - \Delta t)}{\Delta t} = -x(t) + z(t) \quad (\text{S31})$$

By Rearranging terms we obtain:

$$x(t) = \frac{\tau_m}{\tau_m + \Delta t} x(t - \Delta t) + \frac{\Delta t}{\tau_m + \Delta t} z(t) \quad (\text{S32})$$

For backward differencing, the filter memory constants  $\zeta_i$  ( $i = 1, 2$ ) from equation (4) are defined by  $\zeta_i \equiv \tau_m / (\tau_m + \Delta t)$ . Notice that  $1 - \zeta_i = \Delta t / (\tau_m + \Delta t)$ , which is the factor associated with the input  $z$ . For big time constants  $\tau_m \gg \Delta t$  we get  $\zeta_i \rightarrow 1$ , meaning that our filter would approach an infinite memory (strong lowpass filtering).

For small values  $\tau_m = 0$ , we obtain  $\zeta_i = 0$  and thus  $x(t) = z(t)$  – the filter has no memory on past inputs, and consequently no lowpass filtering will take place.