

**Appendix for Hooper chapter in Temporal Patterns in the Nervous System, E. Covey, ed.**

To show that, when temporal summation has stabilized,  $V_{ave} = I \times R \times \text{duty cycle}$ , first remember that the average of a function  $f(x)$  is given by  $ave_{f(x)} = \frac{1}{b-a} \int_a^b f(x)dx$ . When

temporal summation has stabilized, the function to be averaged has two parts, the charging curve from  $V_{min}$  to  $V_{max}$  that occurs during the current pulse, and the relaxation curve from  $V_{max}$  to  $V_{min}$  that occurs during the interpulse interval (Fig. 1). Since current pulse duration ( $PD$ ) plus interpulse interval ( $IPI$ ) equals cycle period ( $per$ ), it follows that

$$\text{the average is given by } ave = \frac{1}{per} \left( \int_0^{PD} rise(t)dt + \int_0^{IPI} relax(t)dt \right). \quad (1)$$

The functions  $rise(t)$  and  $relax(t)$  can be determined as follows. For  $rise(t)$ , first note that if there were no charge on the capacitor when the current was turned on,  $V$  would increase according to  $IR(1 - e^{-t/RC})$ . However, in the case at hand when the current pulse begins, there is already a charge ( $V_{min}$ ) on the capacitor. It is therefore necessary to re-integrate the differential equation that describes an RC circuit not from  $V$  to 0, but instead from  $V$  to  $V_{min}$ .

$$I_{inj} = I_R + I_C = V/R + CdV/dt$$

Rearranging gives

$$\frac{dV}{IR - V} = \frac{dt}{RC}$$

We now integrate the  $V$  side of the equation from  $V$  to  $V_{min}$ , and the  $time$  side of the equation from  $t$  to 0 (because, once the temporal stabilization is over, the charging curve exactly repeats each cycle). This gives

$$\int_{V_{\min}}^V \frac{dV}{IR - V} = \int_0^t \frac{dt}{RC}$$

$$-\left[\ln(IR - V)\right]_{V_{\min}}^V = \left[\frac{t}{RC}\right]_0^t$$

$$\ln(IR - V) - \ln(IR - V_{\min}) = -t / RC$$

$$\ln\left(\frac{IR - V}{IR - V_{\min}}\right) = -t / RC$$

$$\frac{IR - V}{IR - V_{\min}} = e^{-t / RC}$$

$$V = IR(1 - e^{-t / RC}) + V_{\min} e^{-t / RC} \quad (2)$$

This is how  $V$  changes during the current pulse, and is therefore the  $rise(t)$  function needed in equation 1. The  $relax(t)$  function is simple exponential relaxation from  $V_{max}$ ,

$$V = V_{\max} (e^{-t / RC}). \quad (3)$$

Substitution into equation 1 gives

$$ave = \frac{1}{per} \left( \int_0^{PD} IR(1 - e^{-t / RC}) dt + \int_0^{PD} V_{\min} e^{-t / RC} dt + \int_0^{IPI} V_{\max} e^{-t / RC} dt \right).$$

Integrating gives

$$ave = \frac{1}{per} \left( IR \cdot PD + IR \cdot RC(e^{-PD / RC} - 1) - V_{\min} RC(e^{-PD / RC} - 1) - V_{\max} RC(e^{-IPI / RC} - 1) \right)$$

Since  $PD/per$  is duty cycle, it follows that if

$$IR \cdot RC(e^{-PD / RC} - 1) - V_{\min} RC(e^{-PD / RC} - 1) - V_{\max} RC(e^{-IPI / RC} - 1) = 0$$

then

$$ave = IR \cdot \text{duty cycle}$$

which is our goal. Factoring out the common RC term gives

$$IR \cdot (e^{-PD/RC} - 1) - V_{\min} (e^{-PD/RC} - 1) - V_{\max} (e^{-IPI/RC} - 1) = 0 \quad (4)$$

as what needs to be shown. To do this requires expressing  $V_{\min}$  and  $V_{\max}$  in terms of the circuit's and pattern's fundamental constituents,  $I$ ,  $R$ ,  $C$ ,  $PD$ ,  $per$ , and  $IPI$ . This can be done by noting that, when temporal summation is finished, the change in amplitude as the circuit rises from  $V_{\min}$  to  $V_{\max}$  equals the change in amplitude as the circuit relaxes from  $V_{\max}$  to  $V_{\min}$ . For the rise,  $V_{\max}$  is reached at time  $PD$ , and thus by equation 2,

$$V_{\max} = IR(1 - e^{-PD/RC}) + V_{\min} e^{-PD/RC}.$$

The rise amplitude ( $? V_{rise}$ ) is  $V_{\max} - V_{\min}$ , or

$$\Delta V_{rise} = IR(1 - e^{-PD/RC}) + V_{\min} e^{-PD/RC} - V_{\min} = (IR - V_{\min})(1 - e^{-PD/RC}).$$

Turning to the relaxation amplitude change, the relaxation occurs for the duration of the interpulse interval ( $IPI$ ). Substituting into equation 3 gives  $V_{\min} = V_{\max} e^{-IPI/RC}$ .

Therefore,

$$\Delta V_{relax} = V_{\max} - V_{\max} e^{-IPI/RC} = V_{\max} (1 - e^{-IPI/RC}).$$

Setting  $\Delta V_{rise} = \Delta V_{relax}$  gives

$$(IR - V_{\min})(1 - e^{-PD/RC}) = V_{\max} (1 - e^{-IPI/RC})$$

Noting again that  $V_{\min} = V_{\max} e^{-IPI/RC}$  and substituting gives,

$$(IR - V_{\max} e^{-IPI/RC})(1 - e^{-PD/RC}) = V_{\max} (1 - e^{-IPI/RC}).$$

Solving for  $V_{\max}$ ,

$$V_{\max} = \frac{IR(1 - e^{-PD/RC})}{1 - e^{-IPI/RC} e^{-PD/RC}}$$

Remembering the law of exponents ( $e^a e^b = e^{a+b}$ ) and noting that  $IPI + PD = per$  gives

$$V_{\max} = \frac{IR(1 - e^{-PD/RC})}{1 - e^{-per/RC}}. \quad (5)$$

Substituting this expression into  $V_{\min} = V_{\max} e^{-IPI/RC}$  and again using the law of exponents

and  $IBI + PD = per$  gives

$$V_{\min} = \frac{IR(e^{-IBI/RC} - e^{-per/RC})}{1 - e^{-per/RC}}. \quad (6)$$

Substituting equations 5 and 6 into equation 4 gives

$$IR \cdot e^{-PD/RC} - IR - \frac{IR(e^{-IPI/RC} - e^{-per/RC})}{1 - e^{-per/RC}}(e^{-PD/RC} - 1) - \frac{IR(1 - e^{-PD/RC})}{1 - e^{-per/RC}}(e^{-IPI/RC} - 1) = 0$$

. Factoring out the common  $IR$  term, multiplying both sides of the equation with

$1 - e^{-per/RC}$ , and multiplying through gives

$$(e^{-PD/RC} - e^{(-PD-per)/RC} - 1 + e^{-per/RC}) - (e^{(-IPI-PD)/RC} - e^{-IPI/RC} - e^{(-per-PD)/RC} + e^{-per/RC}) - (e^{-IPI/RC} - 1 - e^{(-PD-IPI)/RC} + e^{-PD/RC}) = 0$$

Gathering like terms gives

$$e^{-PD/RC} - e^{-PD/RC} - e^{(-PD-per)/RC} + e^{(-per-PD)/RC} - 1 + 1 + e^{-per/RC} - e^{-per/RC} - e^{(-IPI-PD)/RC} + e^{(-PD-IPI)/RC} + e^{-IPI/RC} - e^{-IPI/RC} = 0$$

and thus  $ave = IR \cdot duty\ cycle$ .

**Figure 1**

