APPENDIX

The equations describing the HVC_X neuron dynamics are taken from the work of Daou [1]. That paper 1

also has an extensive account of his experiments on the other two major classes of neurons in HVC. The 2 equations are of Hodgkin-Huxley (HH) form for a neuron without spatial extent; this is called a one-3

compartment model. It is meant to apply to neurons in isolation of the network, here HVC, in which they sit 4

in vivo. The dynamical variables include the observable quantities: voltage across the cell membrane, V(t)5

and the intracellular concentration of $[Ca^{2+}]_{in}(t) = C(t)$. V(t) is directly connected to action potentials 6 7 or voltage spikes that communicate among cells in a network; the time scale of these spikes is a few ms.

C(t) provides a slow background modulation that raises the cells potential (depolarizes the cell) or lowers 8

9 it (hyperpolarizes the cell) on time scales as long as 10's of ms.

The voltage equation, conservation of charge, relates the capacitance of the cell membrane C_m as it 10

separates concentrations of ions within and without the cells to the various currents which contain the 11

nonlinear voltage dependence of the permeability of ions to passing into and out of the cell. The model 12

represents these ion currents: $\{Na, K, Ca\}$ in several different ways. 13

14 The general form of an HH current is

$$I_{ion}(t) = g_{ion} m_{ion}^{integer1}(t) h_{ion}^{integer2}(t) (E_{rev-ion} - V(t)),$$

$$\tag{1}$$

where the reversal potential is the equilibrium Nernst potential [2, 3]. The gating variables $\{m(t), h(t)\}$ lie 15

between zero and one and represent the amount the ion channel is open relative to the maximum opening it 16

17 may have. The maximal conductance g_{ion} represent the number or density of ion channels in the neuron

model. This form of ion current applies when the concentrations of the ion are not significantly different 18

outside and inside the cell. This is not so for Ca^{2+} ions, so there we use the Goldman-Hodgkin-Katz 19 (GHK) form of the current [4].

20

$$I_a(t) = -P_a z_a^2 F^2 \left(\frac{[ion]_{in}(t) - [ion]_{out} e^{-z_a FV(t)/RT}}{1 - e^{-z_a FV(t)/RT}} \right),$$
(2)

for iona. z_a is the charge on the ion, F the Faraday constant, R the gas constant, T the temperature, and P_a 21 the permeability of the cell membrane to ion a. 22

23 We use an approximation to the GHK equations for the two types of Calcium currents selected in [1]

$$I_{CaL}(t) = g_{CaL} V s_{\infty}^{2}(V(t)) \left(\frac{[Ca]_{out}}{e^{2FV(t)/RT} - 1} \right)$$

$$I_{CaT}(t) = g_{CaT} V(t) [a_{T}]_{\infty}^{3}(V) [b_{T}]_{\infty}^{3}(r_{T}^{A}) \left(\frac{[Ca]_{out}}{e^{2FV(t)/RT} - 1} \right)$$

$$b_{T_{\infty}}(r_{T}) = \frac{1}{1 + e^{\left(\frac{r_{T} - \theta_{b}}{\sigma_{b}}\right)}} - \frac{1}{1 + e^{\left(\frac{-\theta_{b}}{\sigma_{b}}\right)}}$$
(3)

24 a_T and b_T are instantaneous activating and inactivating gating variables, respectively. r_T is a slow gating variable which takes the same functional form as a_T and other gating variables m(t) and h(t). These gating 25

variables w(t) satisfy a first order kinetic equation 26

$$\frac{dw(t)}{dt} = \frac{w_{\infty}(V(t)) - w(t))}{\tau_w(V(t))},$$
(4)

in which 27

$$w_{\infty}(V) = \frac{1}{2} \left[1 - \tanh\left(\frac{V - \theta_w}{2\sigma_w}\right) \right],\tag{5}$$

for all gating variables except $h_{\infty}(V)$ appearing in $I_{Na}(t)$ [1]. θ_w is the half-activation voltage and σ_w 28 controls the slope of the activation function. For fast gating variables, such as m of I_{Na} , and s of I_{CaL} we 29 30 replace the time dependence by $W_{\infty}(V)$.

 $\tau_w(V)$ is the time constant of each gating variable. Time constants for the n and hp gating variables 31 (these names refer to [1]) are given below, where $\bar{\tau}_w$ is an average time constant. Our model differs from [1] 32 by one time constant. Instead, $\tau_{rs}(V)$ takes the form presented here: 33

$$\tau_w(V) = \frac{\tau_w}{\cosh\left(\frac{V - \theta_w}{2\sigma_w}\right)}$$

for n or hp

$$\tau_{rs}(V) = 0.1 + 193.0 \left(1 - \tanh^2 \left(\frac{V(t) + 80}{-21} \right) \right)$$

$$\tau_{rf} = \frac{p_{r_f}}{\frac{-7.4(V+70)}{e^{\frac{V+70}{-0.8}} - 1} + 65e^{\frac{V+56}{-23}}} \quad \tau_{r_T}(V) = \tau_{r_0} + \frac{\tau_{r_1}}{1 + e^{\left(\frac{V-\theta_{r_T}}{\sigma_{r_T}}\right)}}$$

For our choice of ion currents we follow the results of experimental data [5, 6, 7] and generally reproduce 34 the model listed in [1]. HVC_X spiking properties include fast rectifying current, sag in response to 35 36 hyperpolarizing current, and spike frequency adaption in response to depolarizing current.

$$C\frac{dV(t)}{dt} = I_{Na}(t) + I_{K}(t) + I_{L}(t) + I_{CaT}(t) + I_{CaL}(t) + I_{A}(t) + I_{SK}(t) + I_{h}(t) + I_{Nap}(t) + I_{injected}(t)$$
(6)

 $I_{Na}(t)$ and $I_K(t)$ are the standard HH currents. They produce fast spiking in response to injected currents. 37 $I_L(t)$ is a leak current meant to capture all linear currents of the neuron. $I_{CaT}(t)$ is a low threshold T-type 38 calcium current that causes rebound depolarization in cooperation with $I_h(t)$. $I_{CaL}(t)$ is a high threshold 39 L-type calcium current. $I_{CaL}(t)$ works in conjunction with $I_{SK}(t)$, a calcium concentration dependent 40 potassium current, to create frequency adaptation in neuron spiking. $I_A(t)$ is an A-type potassium current. 41 $I_{Nap}(t)$ is a persistent sodium current. From the model presented in [1], we eliminate $I_{KNa}(t)$, a sodium 42 dependent potassium current, and rewrite all sigmoidal functions as hyperbolic tangents. 43

The mass conservation equation for Ca^{2+} is written as 44

$$\frac{dC(t)}{dt} = \epsilon (I_{CaT}(t) + I_{CaL}(t)) + k_{Ca}(b_{Ca} - C(t)),$$
(7)

again following [1]. 45

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