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COMMENT
A "simple" implementation of the Izhikevich neuron with AMPA, NMDA,
GABA_A, and GABA_B receptor dynamics. Equations and parameter values are taken from
Izhikevich EM (2007).
"Dynamical systems in neuroscience"
MIT Press

Equation for synaptic inputs taken from
Izhikevich EM, Edelman GM (2008).
"Large-scale model of mammalian thalamocortical systems."
PNAS 105(9) 3593-3598.

Example usage (in Python):
from neuron import h
dummycell = h.Section() # Since Izhi is a point process, it needs to be in a section
izhl = [h.Izhi2007(0.5) for i in range(2)] # Create two new Izhikevich cells
connection = h.NetCon(izhl[0], izhl[1]) # Connect them
izhl[0].Iin = 70 # activate 1 cell

Cell types available are based on Izhikevich, 2007 book:
1. RS - Layer 5 regular spiking pyramidal cell (fig 8.12 from 2007 book)
2. IB - Layer 5 intrinsically bursting cell (fig 8.19 from 2007 book)
3. CH - Cat primary visual cortex chattering cell (fig 8.23 from 2007 book)
4. LTS - Rat barrel cortex Low-threshold spiking interneuron (fig 8.25 from 2007
book)
5. FS - Rat visual cortex layer 5 fast-spiking interneuron (fig 8.27 from 2007
book)
6. TC - Cat dorsal LGN thalamocortical (TC) cell (fig 8.31 from 2007 book)
7. RTN - Rat reticular thalamic nucleus (RTN) cell (fig 8.32 from 2007 book)
ENDCOMMENT

: Declare name of object and variables
NEURON {
    POINT_PROCESS Izhi2007a
    RANGE C, k, vr, vt, vpeak, a, b, c, d, Iin, tauAMPA, tauNMDA, tauGABAA, tauGABAB,
tauOpsin, celltype, alive, cellid, verbose
    RANGE V, u, gAMPA, gNMDA, gGABAA, gGABAB, gOpsin, I
    RANGE factor, eventflag, delta, t0
}

: Specify units that have physiological interpretations (NB: ms is already declared)
UNITS {
    (mV) = (millivolt)
    (uM) = (micrometer)
}

: Parameters from Izhikevich 2007, MIT Press for regular spiking pyramidal cell
PARAMETER {
    C = 1 : Capacitance
    k = 0.7
    vr = -60 (mV) : Resting membrane potential
    vt = -40 (mV) : Membrane threshold
    vpeak = 35 (mV) : Peak voltage
    a = 0.03
    b = -2
    c = -50

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d = 100
Iin = 0
Vpre = 0
tauAMPA = 5 (ms) : Receptor time constant, AMPA
tauNMDA = 150 (ms) : Receptor time constant, NMDA
tauGABAA = 6 (ms) : Receptor time constant, GABAA
tauGABAB = 150 (ms) : Receptor time constant, GABAB
tauOpsin = 50 (ms) : Receptor time constant, opsin, from Mattis et al. (2011)
celltype = 1 : A flag for indicating what kind of cell it is, used for changing the
dynamics slightly (see list of cell types in initial comment).
alive = 1 : A flag for deciding whether or not the cell is alive -- if it's dead,
acts normally except it doesn't fire spikes
cellid = -1 : A parameter for storing the cell ID, if required (useful for
diagnostic information)
verbose = 0 : Whether or not to print diagnostic information to file -- WARNING, do
not modify this manually -- it's set by useverbose()
}
: Variables used for internal calculations
ASSIGNED {
factor : Voltage factor used for calculating the current
eventflag : For diagnostic information
V (mV) : Membrane voltage
u (mV) : Slow current/recovery variable
gAMPA : AMPA conductance
gNMDA : NMDA conductance
gGABAA : GABAA conductance
gGABAB : GABAB conductance
gOpsin : Opsin conductance
I : Total current
delta : Time step
t0 : Previous time
}
: Initial conditions
INITIAL {
V = vr
u = 0.0
t0 = t
gAMPA = 0
gNMDA = 0
gGABAA = 0
gGABAB = 0
gOpsin = 0
I = 0
delta = 0
net_send(0,1) : Required for the WATCH statement to be active
}
: Function for printing diagnostic information to a file -- usage example:
cell.useverbose(2,"logfile.txt")
VERBATIM
char filename[1000]; // Allocate some memory for the filename
ENDVERBATIM
PROCEDURE useverbose() { : Create user-accessible function
VERBATIM
#include<stdio.h> // Basic input-output
verbose = (float) *getarg(1); // Set verbosity -- 0 = none, 1 = events, 2 = events +
timesteps
strcpy(filename, gargstr(2)); // Copy input filename into memory

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ENDVERBATIM
}
: Define neuron dynamics
BREAKPOINT {
    delta = t-t0 : Find time difference
    : Receptor dynamics -- the correct form is gAMPA = gAMPA*exp(-delta/tauAMPA), but
this is 30% slower and, in the end, not really any more physiologically realistic
    gAMPA = gAMPA - delta*gAMPA/tauAMPA : "Exponential" decays -- fast excitatory (AMPA)
    gNMDA = gNMDA - delta*gNMDA/tauNMDA : Slow excitatory (NMDA)
    gGABAA = gGABAA - delta*gGABAA/tauGABAA : Fast inhibitory (GABA_A)
    gGABAB = gGABAB - delta*gGABAB/tauGABAB : Slow inhibitory (GABA_B)
    gOpsin = gOpsin - delta*gOpsin/tauOpsin : Optogenetic (opsin)

    : Calculate current
    factor = ((V+80)/60)*((V+80)/60)
    I = gAMPA*(V-0) + gNMDA*factor/(1+factor)*(V-0) + gGABAA*(V+70) + gGABAB*(V+90) +
gOpsin*(V-0) : Treat the opsin channel like an AMPA channel

    : Calculate neuronal dynamics; -I since I = -I_{syn}, which is really what I is as
I've defined it above
    Vpre = V
    V = V + delta*(k*(V-vr)*(V-vt) - u - I + Iin)/C : Calculate voltage

    if (Vpre<=c && V>vpeak) {V=c+1} : if just spiked, wait at least 1 timestep before
increasing V>vpeak again, so V reset value takes effect; WATCH statement requires V to
cross the vpeak threshod)

    : Cell-type specific dynamics
    if (celltype<5) {
        u = u + delta*a*(b*(V-vr)-u) : Calculate recovery variable
    }
    else {
        : For FS neurons, include nonlinear U(v): U(v) = 0 when v<vb ; U(v) = 0.025(v-vb)
when v>=vb (d=vb=-55)
        if (celltype==5) {
            if (V<d) {
                u = u + delta*a*(0-u)
            }
            else {
                u = u + delta*a*((0.025*(V-d)^3)-u)
            }
        }

        : For TC neurons, reset b
        if (celltype==6) {
            if (V>-65) {b=0}
            else {b=15}
            u = u + delta*a*(b*(V-vr)-u) : Calculate recovery variable
        }

        : For TRN neurons, reset b
        if (celltype==7) {
            if (V>-65) {b=2}
            else {b=10}
            u = u + delta*a*(b*(V-vr)-u) : Calculate recovery variable
        }
    }
}

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t0=t : Reset last time so delta can be calculated in the next time step

: Print diagnostic information to a file

if (verbose>1) { : Verbose turned on?

VERBATIM

FILE *outfile; // Declare file object

outfile=fopen(filename,"a"); // Open file for appending

fprintf(outfile,"%8.2f cell=%6.0f delta=%8.2f gAMPA=%8.2f gNMDA=%8.2f

gGABAA=%8.2f gGABAB=%8.2f gOpsin=%8.2f factor=%8.2f I=%8.2f V=%8.2f

u=%8.2f (timestep)\n",t,cellid,delta,gAMPA,gNMDA,gGABAA,gGABAB,gOpsin,factor,I,V,u);

fclose(outfile); // Close file

ENDVERBATIM

}

}

: Input received

NET_RECEIVE (wAMPA, wNMDA, wGABAA, wGABAB, wOpsin) {

INITIAL { wAMPA=wAMPA wNMDA=wNMDA wGABAA=wGABAA wGABAB=wGABAB wOpsin=wOpsin} :

Insanely stupid but required, otherwise reset to 0,

: Check if spike occurred

if (flag == 1) { : Fake event from INITIAL block

if (celltype < 4 || celltype == 5 || celltype == 7) { : default

WATCH (V>vpeak) 2 : Check if threshold has been crossed, and if so, set flag=2

}

else if (celltype == 4) { : LTS cell

WATCH (V>(vpeak-0.1*u)) 2 : Check if threshold has been crossed, and if so, set

flag=2

}

else if (celltype == 6) { : TC cell

WATCH (V>(vpeak+0.1*u)) 2 : Check if threshold has been crossed, and if so, set

flag=2

}

}

: Event created by WATCH statement -- i.e. threshold crossed

else if (flag == 2) {

if (alive) {net_event(t)} : Send spike event if the cell is alive

: For RS, IB and CH neurons, and RTN

if (celltype < 4 || celltype == 7) {

V = c : Reset voltage

u = u+d : Reset recovery variable

}

: For LTS neurons

else if (celltype == 4) {

V = c+0.04*u : Reset voltage

if ((u+d)<670) {u=u+d} : Reset recovery variable

else {u=670}

}

: For FS neurons (only update v)

else if (celltype == 5) {

V = c : Reset voltage

}

: For TC neurons (only update v)

else if (celltype == 6) {

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    V = c-0.1*u : Reset voltage
    u = u+d : Reset recovery variable
}

    gAMPA = 0 : Reset conductances -- not mentioned in Izhikevich's paper but
necessary to stop things from exploding!
    gNMDA = 0
    gGABAA = 0
    gGABAB = 0
    gOpsin = 0
}

: Actual input, calculate receptor dynamics
else {
    gAMPA = gAMPA + wAMPA
    gNMDA = gNMDA + wNMDA
    gGABAA = gGABAA + wGABAA
    gGABAB = gGABAB + wGABAB
    gOpsin = gOpsin + wOpsin
}

: Print diagnostic information to a file
if (verbose>0) { : Verbose turned on?
    eventflag = flag
    VERBATIM
    FILE *outfile; // Declare file object
//if(cellid>=0 && cellid < 300) {
    outfile=fopen(filename,"a"); // Open file for appending
    fprintf(outfile,"t=%8.2f   cell=%6.0f   flag=%1.0f   gAMPA=%8.2f   gNMDA=%8.2f
gGABAA=%8.2f   gGABAB=%8.2f   gOpsin=%8.2f   V=%8.2f   u=%8.2f (event)\n",t,
cellid,eventflag,gAMPA,gNMDA,gGABAA,gGABAB,gOpsin,V,u);
    fclose(outfile); // Close file
//}
    ENDVERBATIM
}

}

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