Lecture 5: Oscillators and Pattern Generation

I. Oscillators

A. Oscillators generate repeating cycles of neural activity

1. Periods can vary greatly

a) The circuits responsible for flying in insects can oscillate at over 50 Hz

b) Most animals have circadian rhythms

c) Some animals breed only at a certain time of year

B. There are three basic ways to make an oscillator which appear to have biological significance - maybe only true for short period oscillators

1. The three mechanisms can be combined in some oscillators

a) Special synaptic properties may be important in mechanism of oscillation

2. Half-center model

a) AKA "reciprocal inhibition" or "mutually depressing inhibition" (m-d-i is the terminology used in SWIMMY)

b) Two neurons (or pool of neurons) are connected with reciprocal inhibitory synapses

c) Both neurons receive tonic excitatory drive to activate them

(1) Or the cells could be tonically active by themselves

d) When the excitatory drive is turned on, one of the cells will end up inhibiting the other

(1) There must be a way for the inhibited cell to escape from the inhibition or the cells will not oscillate

(a) There are two ways this could come about

(i) Inhibition from the active member could decline with time (a presynaptic effect)

(a) *For example, less transmitter could be released with time*

(b) *Could be produced by reduced spiking frequency*

(ii) The inhibited cell could possess voltage-dependent conductance mechanisms that cause it to respond to inhibition by depolarizing (a postsynaptic effect)

(a) *i.e., hyperpolarizing the cell turns on a depolarizing current*

(iii) These two general mechanism are not mutually exclusive & have been seen together

II. Closed-loop model

A. ***Also called "recurrent cyclic inhibition" or a "ring oscillator" (ring oscillator is terminology used in SWIMMY)***

B. ***One limitation of half-center circuits is that they can have only 2 phases - on or off***

C. ***Many real world behaviors have more than just two phases***

1. **Go through mechanism of oscillation**

a) ***Note that the oscillation precedes in a clockwise direction (opposite of direction of connections)***

D. ***One advantage of closed loop circuits is that the neurons don't need any special properties like we needed for the half-center***

1. **i.e., the ability to escape from inhibition**

E. ***However, you do need an odd number of cells to make it oscillate if you assume no special properties in the cells***

1. **If you have an even number of cells you end up with the circuit behaving as a half-center model**

F. ***Last type of oscillator is the*** *pacemaker model*

1. **Called a endogenous burster model in SWIMMY**

2. **Here one cell has membrane properties which produce rhythmic excitation**

3. **Some cells have a current similar to I_h, that produces the pacemaker potential in cardiac muscle cells**

    a) ***This current produces a ramp of depolarization***

4. **Eventually threshold is reached and the cell spikes**

    a) ***There may be other special conductances to produce a plateau of excitation***

5. **The excitation eventually terminates (example of calcium-activated potassium current) and the cell hyperpolarizes**

6. **This then reactivates the current producing the ramp depolarization**

7. **Pacemaker cells can be integrated into either half-center or closed loop circuits**

III. How are motor behaviors controlled?

A. The most complete picture of a neuronal pathway which controls and generates a rhythmic behavior is that of swimming in the leech (Fig. 1)

1. **The behavior (swimming) can be elicited by touching the animal**

    a) ***Swimming consists of dorsal-ventral undulations of the body wall***

        (1) The animal is generating **oscillations**

2. **The circuitry which controls and generates swimming can be broken down into 5 functional levels**

    a) ***The first level is that of the*** *sensory neurons*

        (1) Sensory neurons are activated by touching body wall

    b) ***Sensory neurons then excite*** *trigger neurons*

        (1) Trigger neurons, when stimulated briefly, cause a prolonged swim episode which outlasts activity in the trigger neurons

c) ***Trigger neurons then excite*** *gating neurons*

(1) Gating neurons cause swimming for as long as the gating neuron is depolarized

(a) Swimming does <u>not</u> outlast activity in the gating neurons

d) ***Gating neurons then drive the*** *oscillator neurons*

(1) Through their interconnections, oscillator neurons generate phasic activity

e) The oscillator neurons excite and inhibit the motor neurons which control the muscles

(1) In any particular region of the body the excitatory dorsal motor neurons are receiving input of opposite sign from the ventral excitatory motor neurons

IV. A more complex oscillator- *Tritonia* swimming (Fig. 2 & movies)

How the circuit works

1. Sensory input activates DRI (dorsal ramp interneuron)

a) Cell Tr1 acts as a trigger neuron

2. DRI excites DSI (dorsal swim interneuron)

a) DRI acts as a gating neuron

3. DSI excites C2

4. C2 feeds back and excites DRI, further exciting DSI via a positive feedback loop

5. C2 excites VSI, which inhibits DSI and C2, thereby momentarily interrupting the positive feedback loop