Neural Circuit for Cricket Mating

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[1] Cricket mating

(1) Song type

-**calling song**: attract female
-courtship song: facilitate copulation
-aggressive song (rivalry song): territorial, male-male fight
Only the males sing.

(2) Behavior
Males sing, females try to locate males based on song.

Q: How do you show that this behavior is purely auditory?
Str: Use telephone! (Johann Regen, 1913)
Res: females approached the telephone ear piece

This is called **positive phonotaxis** (cf klinotaxis of a fly larva)

(3) Song terminology
-chirps (4 syllables)
-syllables (5kHz carrier frequency)

[draw song pattern]

[slides: song example]

[2] Phonotaxis in the female

(1) Measuring phonotaxis in the lab

Q: What song features are important for the female cricket?
Str: female on a trackball, manipulate different parts of the song systematically
(+) crickets can be tested for hours, yet remain constant distance from the song!
Res: most important feature is the syllable rate of 30/s (syllable duration, duty cycle, number of syllables don't matter), band-pass filter characteristic

Q: How does the sensory system filter the relevant info?

(2) cricket auditory system
-eardrums are located on the cricket's front legs!
-connected to **spiracles** via tracheal tube
-pressure-difference receiver
-left eardrum responds maximally to sounds coming directly from the left and vice versa (at 5kHz)
-Interaural time difference (ITD) is two small given cricket's size

[draw figure]
[slides: trackball, auditory system]

(3) Sensory neurons
-about 60 auditory neurons
-project to the auditory neuropile in the prothoracic ganglion on the ipsilateral side

(4) Omega interneurons
-a pair of auditory interneuron @ prothoracic ganglion
-morphology looks like an Omega

[draw figure]

Q: Is there a connection between Omega neurons on both sides? (Selverston ... Huber, 1985)
Str1: paired intracellular recording
Res1: Spike in one Omega neuron leads to an IPSP in the other one
Str2: killing one Omega neuron while recording from the other one
Res2: inhibition goes away
-**reciprocal inhibition (mutual inhibition)** increases direction sensitivity (eigenvector for this weight matrix is [1,-1])

(5) Ascending neuron and its role in phonotaxis

-excitatory input from auditory afferents
-inhibition from contralateral omega neuron

Q: Role of ascending interneuron (AN1) on phonotaxis?
Str: intracellular recording & current injection during phonotaxis
Res:
(1) AN1 responds more strongly to ipsilateral sound stimulus.
(2) Hyperpolarizing AN1 on one side was sufficient to reverse the direction of the animal!
Int: Bilateral AN1 feed into a comparator that determines the direction of walking.

[slides: auditory neurons]

(6) Mechanism of phonotaxis: localization vs recognition (Poulet & Hedwig)

Q: Localization vs recognition? (Poulet & Hedwig, PNAS 2005)
Str: compare attractive (species-specific) vs non-attractive sounds
Res:
(1) Even non-attractive sounds produce small steering response
(2) If you present the non-attractive song immediately after the attractive song, the steering response remains high
Int: Pattern recognition (slow, several seconds) modulates the gain of reactive steering (rapid)

[slides: recent phonotaxis studies]
[draw interpretation of gain modulation]

[3] Song production in the male

(1) Song production mechanism
-Song is produced by rubbing one forewing against the other (stridulation)
-**Scraper** at the tip of the wing slides against the **file** on the other wing. This determines the carrier frequency.
-Sound is produces during **closing**.

[draw figure]

(2) Neural circuit for song production

Q: Singing is a rhythmic movement. Mechanism for rhythm generation?
Hyp1: chain reflex
Hyp2: CPG
Str: **deafferentiation** (Bentley)
Res: CNS could still generate song like pattern
Int: CPG

Q: How to identify neurons that are part of the CPG? (Schoeneich & Hedwig, 2012)
Str: **intracellular recording + staining during fictive singing**
Criteria (1): the neuron exhibit rhythmic activity
Criteria (2): the neuron passes the reset test
Res: fictive singing is associated with rhythmic activation of wing-closer motor neuron and wing-open motor neuron
found opening interneuron, closing interneuron in the thoracic and abdominal ganglia
Int: **mutual inhibiting interneurons that respond with post-inhibitory rebound?**
* no paired recording to demonstrate the synaptic connectivity

(3) command neurons for singing (Hedwig, 2000)

Q: Is there a command neuron for singing?
Hyp: in the brain (electrical stimulation produced singing)

Str: intracellular recording from several hundred neurons!
Res: Found a paired neuron in the brain (soma at the protocerebrum, descending fiber to thoracic ganglia)
Activation of this neuron by intracellular current injection triggered singing.
Inactivation of this neuron by intracellular current injection stopped the song.
*downstream connections are not identified

[slides: sound production mechanism, CPG, command neuron]

(4) collorary discharge interneurons

Q: How does a male cricket prevent himself from deafening, or desensitization? (Poulet & Hedwig, 2002)
Hyp: cricket inhibits his own auditory system during singing using **corollary discharge**
Str: record auditory response during singing and outside singing
Res: auditory response in ON1 is indeed inhibited

Q: Which neuron is responsible for the inhibition? (Poulet & Hedwig, 2006)
Str: paired recording between auditory neurons and neuron in the thoracic ganglia
Res: Found a pair of corollary discharge neuron (CDI)
(1) CDI was active during singing
(2) CDI did not pass the reset test (CDI is not part of the song CPG)
(3) CDI was not active during flight, nor active to song playback

Q: Interaction between CDI and auditory neurons?
Str: paired recording
Res:
(1) CDI spike lead to a primary afferent depolarization (PAD) in the auditory afferent.
(2) CDI spike lead to an IPSP in the ON1.
Int: CDI inhibits auditory response during singing by both presynaptic inhibition of the affererent, and by postsynaptic inhibition of ON1.

Q: Is CDI the only neuron providing the inhibition of auditory response? (sufficiency)
Str: inactivate CDI and see if there are still inhibition
*CDI is a bilateral pair, so the authors needed to cut the connective on the other side.
Res: Inhibition is not present if CDI is prevented from spiking by hyperpolarizing current.
Int: CDI is the only neuron that mediates the inhibition.

[slides: corollary discharge interneuron]