How do animals perform the right behaviors at the right time? In the right context?
• Active at night only
• What if conflicting signals?

• Magnetic cues are always present
• But migrate only during specific seasons

• **Not** simply stimulus → response
• Temporal organization
  – Across day
  – Across year
• Prioritize
  – Avoid incompatible behaviors
Outline

• Neural “Command Centers”

• Behavioral Schedules
  – Daily rhythms: internal and external factors
  – Long-term rhythms: internal and external factors

• Priorities & the Social Environment
  – Hormones & parental behavior
  – Hormones & reproductive behavior
  – Hormones & aggressive behavior
“Command Centers”

- Although specific behaviors may be controlled by specific groups of cells, there must be cross-talk to organize the activities of different cell groups
  - “decision” about what to do at any given time
  - external stimuli might indicate that several behaviors are appropriate, but the animal has to “choose”

- Command centers often exert their control by inhibiting other cell groups until it is appropriate to release a particular behavioral pattern

- Synapses can be excitatory or inhibitory
Inhibitory control

- If you isolate the brain (protocerebral ganglion) from the rest of the nervous system, then the animal will try to walk and grasp simultaneously.

- Excitatory messages (for grasping) come from another ganglion in the head (the subesophageal ganglion), just below the brain, so the brain inhibits this excitatory ganglion until certain behaviors are appropriate.
Inhibitory control

• Remove the whole head (both the brain and subesophageal ganglion) and the mantis won’t do much…except mate!

• Males have their heads eaten during copulation (a nutritious gift to the female), which actually elicits vigorous sexual behavior from the headless male body

• What hypothesis does this raise regarding subesophageal ganglion control of mating?

http://ca.youtube.com/watch?v=KYp_Xi4AtAQ
• Neural “Command Centers”

• Behavioral Schedules
  – Daily rhythms: internal and external factors
  – Long-term rhythms: internal and external factors

• Priorities & the Social Environment
  – Hormones & parental behavior
  – Hormones & reproductive behavior
  – Hormones & aggressive behavior

An organism must “choose” what to do at any given time, and that decision often depends upon the time of day or season.
Daily rhythms

- Many behaviors are organized on a 24 hour cycle – e.g., heliotropic plants

- Are such rhythms generated only by external stimuli (e.g., light) or is there an internal clock?

- If external stimuli are the sole source of timing, then removal of external stimuli should remove the daily patterning of behavior – how to achieve this?
DeMairan (1729)
Temporal organization

• Crickets are active at night and males begin calling at dusk – inhibitory control varies across day
• If external stimuli are the sole source of timing, then removal of external stimuli should remove the daily patterning of behavior.
Rhythms in cricket calling behavior

- Crickets in constant light (LL) exhibit a free-running cycle that is about 26 hours.
- Crickets in a 12:12 light-dark cycle (LD) show an entrained cycle that is exactly 24 hours.
Rhythms in cricket calling behavior

- These results demonstrate that the cricket has an internal clock that is capable of keeping time without any information from external stimuli.

- Free-running period of the internal clock is not exactly 24 hours

- Internal clock needs to be set (entrained) by an external stimulus (light)

<table>
<thead>
<tr>
<th>Rhythm type</th>
<th>Environmental cycle</th>
<th>Period length</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Entrained</td>
</tr>
<tr>
<td>Circadian</td>
<td>Revolution of earth</td>
<td>24 hours</td>
</tr>
<tr>
<td>Circa tidal</td>
<td>Tides</td>
<td>12.4 hours</td>
</tr>
<tr>
<td>Circa lunar</td>
<td>Phases of moon</td>
<td>29.5 days</td>
</tr>
<tr>
<td>Circa annual</td>
<td>Seasons of the year</td>
<td>365.25 days</td>
</tr>
</tbody>
</table>
5.7 The cricket nervous system
Rhythms in cricket calling behavior

- What happens if you maintain cricket in 12L:12D and cut connections between retina and optic lobes of brain?
Rhythms in cricket calling behavior

• What happens if you maintain cricket in constant light and cut connections between optic lobes and rest of brain?

• Cricket still calls but no circadian rhythm!

• Cricket will call with equal probability at any time of day (arrhythmic)
In transgenic crickets without a functional retina, you notice that their calling is free-running under 12L:12D. Which segment of the following pathway has been disrupted?
Suprachiasmatic Nucleus (SCN) of the hypothalamus

- Nucleus is a cluster of cells (part of a bigger structure). The hypothalamus (major brain region) regulates many behaviors, and one cluster of cells in the hypothalamus, the suprachiasmatic nucleus (SCN) acts as a clock.
SCN

- Small electrolytic lesions of adult hamster SCN eliminate circadian rhythms.
- SCN tissue transplants reinstate rhythmicity.
- SCN cells in vitro.
How do clocks work?

Random mutagenesis & large behavioral “screens”
Konopka & Benzer
How to measure circadian rhythms in Drosophila

1) Eclosion assay

[Graph showing eclosion activity over time]

2) Activity assay

[Graph showing activity patterns over two days]

http://www.hhmi.org/biointeractive/media/activity_pattern-lg.mov
Identification of a biological clock gene

- EMS mutagenesis of Drosophila, allowed them to have offspring
- Housed offspring in complete darkness
- Screened for flies who deviated in eclosion timing
- Mapped 3 mutations to same gene; named the gene *per*

Konopka & Benzer, 1971
Single base pair mutations of the \textit{per} gene in fruit flies

- Wild-type
- Long-period mutant
- Arrhythmic mutant
- Short-period mutant

24 hours
Where is the PER protein?

• Created antibodies that bind to the PER protein
• Used these antibodies to label the PER protein in adult fruit flies
• Observed high levels of staining in photoreceptors in the eyes and some cells in the optic lobes (and elsewhere) of flies
• Observed intense staining of PER at night, but not during the day
Gene expression

Hypothesis from these data: Cycling of PER mRNA could be caused by negative-feedback by PER protein
Gene expression in biological clocks in fruit flies

http://www.hhmi.org/biointeractive/media/drosophila-lg.mov
PER protein in mammalian brain

A. $mPer1^{ldc}$

Clocks of mammals and flies are similar but not identical
• Human isolation experiments. Subjects placed in underground bunker and allowed to turn lights on or off at will (weeks to months).
• Tracked sleep-wake cycles, body temperature, etc.
• Humans have circadian cycles too.