

In the last unit, we introduced the concept of innate releasing mechanisms, “black boxes” that refer to the neural mechanisms that “link” sign stimuli (inputs) to fixed action patterns (outputs). In this unit, we’ll gain some insights into other neural mechanisms. We’ll still be “black boxing” to a large extent, but we’ll also see how careful and creative investigations can help us understand important features of the neural organization of behavior even if we don’t understand the specifics. The primary question we’ll be asking here is how, when animals are bombarded by simultaneous, often conflicting, and often changing stimuli, do they organize their behavioral responses in adaptive ways.

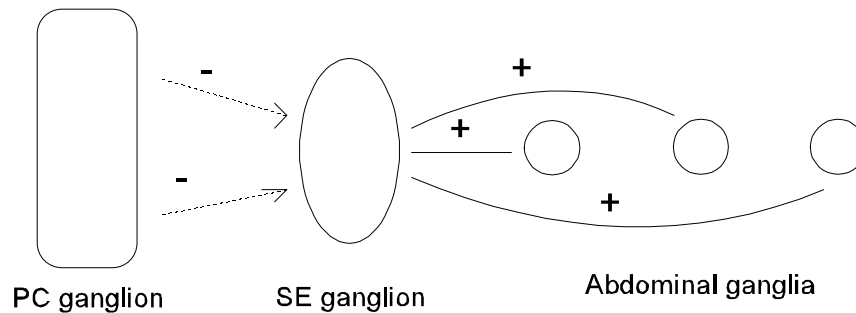
CHAPTER 6: THE ROLE OF BEHAVIOR – ORGANIZING MECHANISMS

A. In the most immediate level, how do animals avoid “trying to do 2 things at once” when they receive contradictory stimuli from the environment?

1. One major hypothesis is that animal nervous systems are organized into **command centers**
 - a. A command center = a unit of the nervous system that could include a variety of components, such as innate releasing mechanisms, pattern generators, song control systems, etc.
 - b. Command centers are interconnected via a hierarchy of inhibitory relationships: activating 1 inhibits the other
 - c. This would mean that an animal carrying out one behavior in response to one stimulus would be prevented from simultaneously trying to carry out another.
 - d. In general, this would be highly adaptive!
2. Decision-making in praying mantis – one example of using command center hypothesis to decipher organizing mechanisms
 - a. General behavior pattern = sit motionless until prey approaches, then make rapid, powerful grasping motions with forelimbs.
 - b. Roeder proposed that behavior organized by assortment of command centers:
 - i. Presence of ganglia (clusters of nerves) in each body segment suggested

that they controlled muscles of each segment – confirmed with experimental evidence from cutting connections, stimulating isolated ganglia

- ii. Proposed that some brain cells were responsible for inhibiting activity in abdominal ganglia – preventing muscles from acting until “ordered” to do so by other command centers in brain
 - a) hypothesized that protocerebral ganglion (brain) inhibited abdominal ganglia
 - 1) severed connection from PC ganglion to abdominal ganglia
 - 2) mantises tried to walk and grasp simultaneously – clearly not adaptive behavior
 - 3) confirms hypothesis
 - b) but, when he removed the entire head, mantis became immobile
 - 1) removing whole head removes subesophageal ganglion
 - 2) suggests that SE ganglion “turns on” abdominal ganglia (with details determined by which regions of the SE ganglion is active)
 - 3) also suggests that PC ganglion usually inhibits SE ganglion – preventing it from communicating with abdominal ganglia
- iii. Putting results together, suggests hierarchical organization:
 - c) PC ganglion typically inhibits SE ganglion, suppressing muscle activity
 - d) in response to specific stimuli, PC ganglion stops inhibiting specific cells of SE ganglion
 - e) “unblocked” SE cells turn on specific abdominal ganglia, inducing appropriate motor response



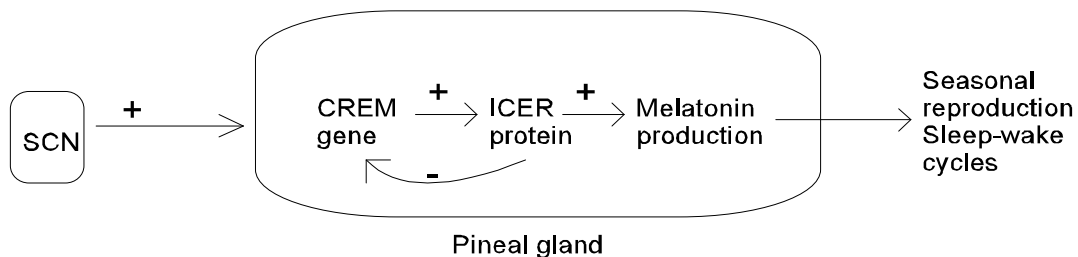
3. Control of feeding by foregut in blowflies – example 2 of command center function, this time including internal and external stimuli
 - a. Blowflies feed by sucking fluid in through proboscis
 - b. Rate of sucking determined by sugar concentration in fluids: rate of oral receptor firing is proportional to sugar concentration
 - i. So, at this level, the duration of feeding is determined by the sugar concentration (energy value) of the food – flies spend more time feeding on richer food
 - c. No matter how rich the food, sucking stops when crop is full
 - i. When crop is full, fluid forced into foregut
 - ii. As foregut stretches, stretch receptors associated with foregut fire
 - iii. Signal goes to brain via recurrent nerve, inhibiting feeding response
 - iv. If recurrent nerve severed, flies drink until body bursts!
 - d. This example, then, illustrates interaction among command centers (one controlling sucking rate, one controlling amount of food consumed) mediated by feedback among internal organs (vs. mantis e.g., where stimuli all external)
- B. Changes in the environment may require changes in the inhibitory relationships among command centers to compensate. Pacemaker or clock mechanisms

regulate nervous, hormonal systems in cycles, usually corresponding to days and/or years.

1. Because transition from day to night biologically significant for most species, common to see internal “clocks” cued to 24-hour = **circadian cycle**
2. Exploring circadian cycles using crickets as example
 - a. Typically, females active only after dusk; males start calling in evenings – can think of this as a cyclic change in behavioral priorities in males from hiding/resting to calling mates, back to hiding/resting
 - b. If command center model applies, then inhibitory relationship between “calling center” and centers regulating other activities must change over 24-hr cycle (i.e., calling center is inhibited for most of day, then “released” at appropriate time, then inhibited again etc.)
 - c. How does mechanism work? Two simple hypotheses to start:
 - i. Mechanism is completely intrinsic – behavioral priorities change over cycle independent of environmental cues
 - ii. Mechanism is environment-dependent, requiring appropriate environmental stimuli to activate appropriate behavioral responses
 - d. Test hypotheses in crickets
 - i. If environmental cue hypothesis is correct, and cue = light (pretty obvious choice) then crickets kept in lab conditions of constant light should show no cyclical pattern of calling
 - a) under these conditions, crickets **do** call regularly for limited blocks of time
 - b) but, each cycle begins 25-26 (not 24) hours after previous one
 - c) **free-running cycle** (cycle seen under constant lab conditions) greater than 24 hours strongly suggests internal mechanism
 - 1) if cycle were ~ 24 hours, could be keyed to some other cue from earth’s rotation
 - 2) deviation too great for that to be reasonable

- ii. If no environmental cue needed, then crickets kept under conditions of 12L:12D should show same pattern as crickets in constant light
 - a) under these conditions, crickets rapidly acquire regular 24-hour cycle – begin calling ~ 2 hrs before lights off (corresponding to dusk) and stop about 2.5 hrs before lights on (before dawn).
 - b) clearly, external cue has important role in setting starting/ending points for internal mechanism
 - c) say that light **entrains** the internal mechanism
 - iii. Conclusion: control system for crickets has two components:
 - a) environment-independent **biological clock** with intrinsic cycle of 25-26 hours
 - b) environment-dependent entrainment device for synchronizing clock with local conditions
 - c) clearly elegant and adaptive system:
 - 1) purely intrinsic would require different clock for different latitudes, seasons
 - 2) purely environment-dependent would require lots of processing power
 - e. Neural mechanisms underlying this system can be investigated using Roeder's methods of disconnecting parts of brain, sensory organs:
 - i. If nerve from eyes to optic lobes in males cut, free-running cycle begins
 - a) so visual signal needed for entrainment, but not for the biological clock itself
 - ii. if optic lobes severed from rest of brain, then free-running cycle breaks down
 - a) so clock must reside within the optic lobes
 - f. On your own, read experiments on emergence in silkworm moths (way cool!)
3. In mammals, central pacemaker for circadian rhythms seems to be the suprachiasmatic nucleus (SCN) of the hypothalamus

- a. In hamsters, Norway rats:
 - i. Destroying SCN cells leads to arrhythmic cycles of feeding, locomotion, hormone secretion
 - ii. If arrhythmic animals receive transplants of SCN tissue from fetal hamsters, normal rhythms restored in ~ 40%
 - iii. If arrhythmic animals receive transplants of other brain tissue, remain arrhythmic
- b. Mechanism appears to involve neural feedbacks between the SCN and the pineal gland:



- i. Signals from SCN stimulate CREM gene in pineal gland
- ii. CREM gene product = ICER protein, involved in stimulating melatonin production (melatonin involved in seasonal reproduction, sleep-wake cycles)
- iii. Negative feedback between ICER protein and CREM gene – as ICER levels build up, CREM gene inhibited
- iv. Inhibition pattern entrained by photoperiod = night length for preceding several days:
 - a) as nights grow longer, sensitivity to inhibition decreases and more ICER needed to turn off CREM
 - b) this means that, as nights grow longer, peak CREM activity occurs longer after dark:

- 1) animals exposed to 8-hr nights have peak activity ~ 6 hrs after dark
 - 2) animals exposed to 12-hr nights peak activity ~ 10 hrs after dark
- v. So, as with crickets, have biological clock entrained by environmental cue, allowing adjustment of activity levels to seasonal variation in photoperiod etc.!
- c. Note that this system very active area of research for shift workers, people with Seasonal Affective Disorder, and people with various sleep disorders
- C. Other patterns and mechanisms of behavioral organization (summarizing last part of chapter -- make sure you can provide one example of each, with evidence)
1. Circannual patterns also exist, but are harder to study (for obvious reasons) than circadian patterns). Work to date suggests that , like circadian patterns, at least some of these also involve interaction between biological clock and environmental entrainment.
 2. Photoperiod is not the only environmental variable that can affect cyclic behavior patterns:
 - a. Moonlight can be important factor for nocturnal animals –
 - i. e.g., many species of kangaroo rats limit above-ground foraging to times when moon not full
 - ii. For these animals, mechanism is probably ~ entirely environment-dependent
 - iii. Evidence includes fact that “aversion” to moonlight can be overcome when food is scarce
 - b. Temperature can be important factor –
 - i. In green anoles, reproduction is triggered by temperature
 - ii. Rising temps trigger release of GNRH and consequent gonad development
 - iii. Timing of emergence can be altered by cold spells, warm spells
 - c. In crossbills, food availability seems to be superimposed on cyclic changes regulated by photoperiod

- i. Males kept in constant lab conditions with abundant food show annual cycle of testicular development, with “lull” from October-December
 - ii. But, for rest of year, food availability seems to determine whether or not they breed
 - d. Social interactions – visual, mechanical, and/or acoustical signals associated with mating play important role in regulating reproductive status in many species
3. Not surprisingly, for many species coordinated behavioral responses to changing physical, social environment are mediated by hormones – but the precise roles of various hormones (testosterone in males, e.g.) are highly variable among species.

This ends our discussion of the proximal causes of behavior – for rest of semester, we’ll focus on ultimate causes, seeking to understand the adaptive value of behavior and how we can develop and test adaptive hypotheses. But remember that these proximate mechanisms are what selection is acting on during the evolution of behavior.