

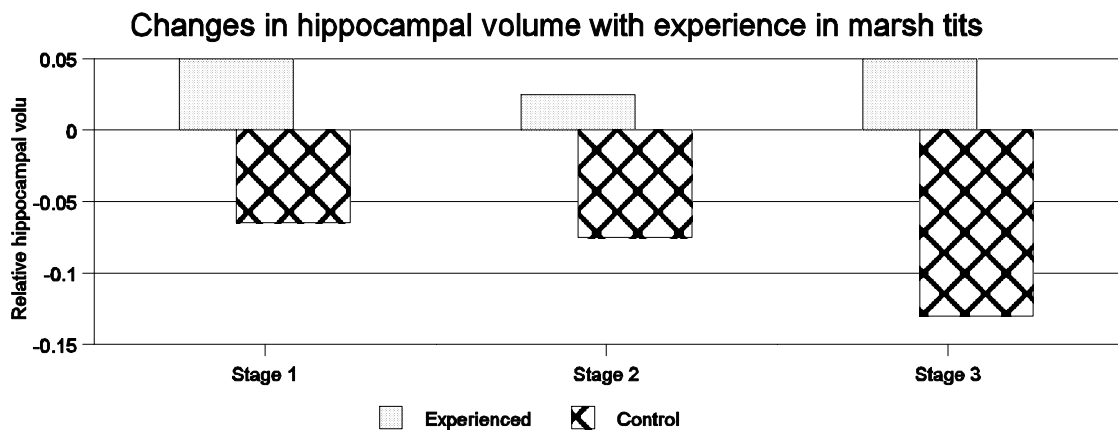
By now we are now very familiar with the fact that the development of behavior involves the interaction of genes with features of both the intrinsic (cellular, e.g.) and extrinsic environment. In this chapter, we'll look at the effects of a variety of extrinsic environmental factors on the development of behavior. Note that, because the development of behavior is a complex process, we'll be able to use some of the same behaviors to illustrate several different "lessons" about the role of the extrinsic environment in development. Note also that the effects of the environment are mediated via their effects on neuromuscular structure and function -- just as are the effects of genes!

CHAPTER 4: THE DEVELOPMENT OF BEHAVIOR -- THE ROLE OF THE ENVIRONMENT

A. A wide range of "material", sensory and social experiences can act as cues that can have long-term effects on the development of behavior. Examples (just to illustrate the range of possibilities) include:

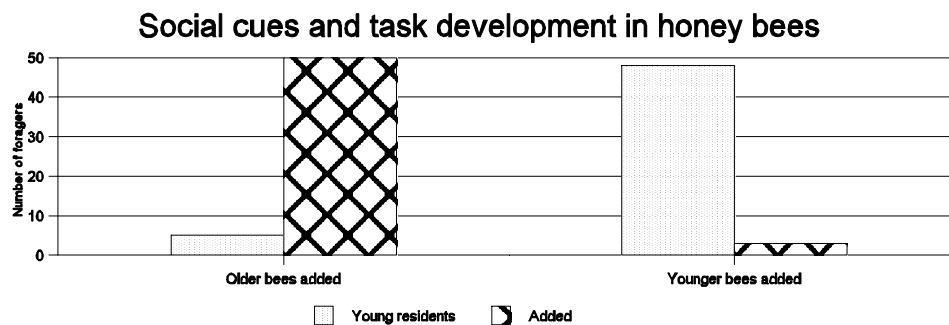
1. In honeybees, the kind of food consumed by larvae determines whether females will develop into workers or queens -- which differ both in morphology and behavior.
2. Environmental sex determination: In a number of reptiles (particularly turtles and crocodiles), incubation temperature, rather than genes or chromosomes, determines the sex of the offspring (with consequent behavioral differences)
3. In house mice, levels of sex hormones in the amniotic fluid influence the development of "male" behaviors (aggression and territoriality):
 - a. Because sex organs begin to develop fairly early, both male and female embryos secrete hormones into the amniotic fluid. Males gestating between two female embryos are exposed to more estradiol than are males gestating between males.
 - a. basic methods:
 - i. babies were delivered by C-section to determine position in utero
 - ii. compared 0M = between 2 females with 2M = between two males

- iii. males castrated at birth then later given testosterone to be sure only differences were due to effects of circulating hormones on brain development pre-birth (vs. postnatal effects of own testosterone)
- b. At 90 days, 2M males more than 2X as likely to attack strangers than 0M females
- c. In study of females in “natural” environment (highway cloverleaves), found that 2M females:
 - i. had significantly larger territories than 0M females (males have larger territories than females)
 - ii. are more aggressive than 0M females
 - iii. are less attractive to males than 0M littermates
- 4. In marsh tits, the experience of storing seeds is correlated with development of hippocampus (region of the brain associated with spatial learning) --
 - a. hand-reared individuals assigned to two behavioral categories
 - b. one group (“experienced”) were allowed to store sunflower seeds at three different stages of development; one group (control) was not
 - c. experienced group had larger hippocampal volume at every stage of development; controls actually appeared to lose cells.



B. Effects of environmental influences I: a variety of environmental cues seem to act as developmental “switches” between behavioral phenotypes. Phenotypes may be subtly or dramatically different; “switch” may be permanent or temporary. In any case, this type of effect maintains a degree of behavioral flexibility within individuals and species. Examples include:

1. Caste switching in honeybees: environmental cues alter timing of normal developmental sequence (minor morphological change; irreversible)
 - a. Normal developmental pattern = workers switch castes over time; switching is correlated with age and mediated by changes in hormone levels and brain anatomy.
 - i. first = “youngest” stages = “nurse” stage; behavior = cleaning cells, feeding broods
 - ii. last = “oldest” stage = forager
 - b. Interactions within the hive can change timing of behavior switches:
 - i. when all workers are same relatively young age, some remain nurses longer than normal while others become foragers earlier than normal
 - ii. when younger bees are added to young colony, young residents become precocious foragers
 - iii. when older foragers are added to young colony, young residents do not become precocious foragers



2. Cannibalism in salamander larvae: environmental cues produce alternate larval phenotype (major morphological change; irreversible)
 - a. In tiger salamanders (*Ambystoma tigrinum*), two larval morphs:
 - i. "normal" tadpole feeds on small pond invertebrates
 - ii. cannibal morph much larger with larger jaws, teeth; feeds on other salamander tadpoles
 - b. development into cannibalistic morph depends on environmental conditions: more common when
 - i. tadpole density is high
 - ii. substantial size difference exists among individuals (largest typically develop into cannibalistic form)
 - iii. population consists largely of unrelated individuals
 - c. note that, in this case, "switch" is actually a function of several environmental factors (all of which are somehow being monitored by individual tadpoles!)
3. Sequential hermaphroditism in fish (substantial change, irreversible)
 - a. Sequential hermaphroditism is fairly common in teleost fish -- normal pattern = sex change (either way) dependent on body size
 - b. in some species, developmental change triggered by social cues
 - i. in gobies, new pairs form as individuals move among coral heads -- change may occur based on relative size and sexes of new partners (usually smallest partner is or becomes female)
 - ii. in anemonefish, largest female dominates social group; when largest female is removed (by predation, e.g.), larger males switch to female. In this case, changing individuals begin to exhibit female pattern of aggression as soon as one day after the female is removed, long before any significant morphological change is evident!
 - c. changes are mediated by changes in hormonal status, brain structure

4. Satellite males in fish (substantial change; may or may not be reversible):
environmental cues trigger changes associated with switch from subordinate to dominant male status
 - a. We'll talk about satellite males in other contexts later in the course; for now, the general concept is this:
 - i. in many species, only dominant males acquire territories, mates
 - ii. subordinate males (which are often smaller and more similar to females in external morphology) may hang out on fringes of territories and use a variety of techniques to "sneak" mating opportunities from dominant's mate
 - b. Read about midshipman fish in readings text (don't worry about brain anatomy and biochemistry as much as general pattern of development -- what is/are the environmental cues; is the change in morphology reversible?)
 - c. In one species of African cichlid (OH), cue for switching is territorial status:
 - i. when territory becomes vacant, satellite males switch to dominant morph
 - ii. if territory owner defeated, switches to satellite morph
 - iii. switching is mediated by changes in testes, brain, and hormones that "communicate" between them:
territorial (dominant) morphs have larger GnRH neurons, which release hormones stimulating testicular growth, which promotes testosterone production, which stimulates aggressive behavior by altering activity of cells in other parts of the brain
5. Environmental "developmental switches" are not always so dramatic -- may involve relatively limited changes in behavior. For example:
 - a. in European wagtails, changes in food availability trigger changes back and forth from territorial to non-territorial behavior (when food is abundant, territories form -- we'll discuss why later!)

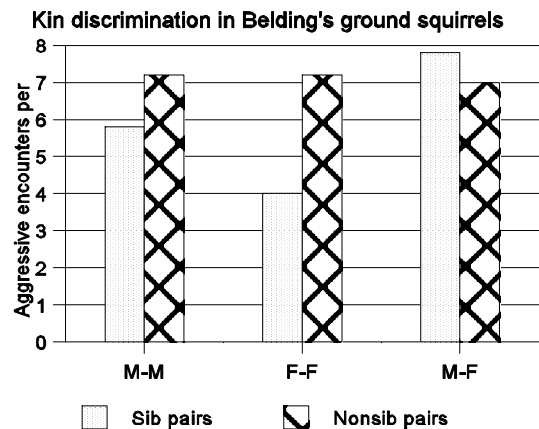
- b. In male meadow voles, spatial learning ability varies seasonally:
 - i. males have greater spatial learning ability and hippocampal size than females
 - ii. but difference only exists during summer, when males searching widely for mates -- in winter, difference disappears
 - c. Of course, seasonal changes in behavior are the norm for animals -- and all, if you think about it, represent this type of environmental effect on behavior!
- C. Effects of the environment II: for many kinds of animals, experiences with the environment lead to adaptive changes in behavior, or **learning**.
1. As we learn more about learning and about the kinds of “unlearned” responses to the environment discussed above, the distinction between “learned” and “unlearned” changes in behavior become less and less clear:
 - a. Learning is usually defined as a change in behavior based on experience.
 - b. “Experience” means interaction of the animal with its biotic and abiotic environment
 - c. In this sense, learning can legitimately be considered a “special case” of environmental factors acting as “developmental switches” -- the key differences perhaps are that
 - i. a learned response may require longer or more repeated interactions and
 - ii. the range of possible “learned phenotypes” may be greater
 - d. Those differences, though, are clearly not absolute.
 - e. Nonetheless, we (and ethologists generally) discuss learning separately simply because it’s been the focus of much study historically (especially by psychologists) and has achieved status as a large discipline on its own
 2. The most common type of learning that seems to exist (and that’s been the most studied) is **associative learning**, in which an animal makes associations between stimuli, its own behavior, and rewards or punishments. Is often broken down into sub-categories:

- a. **habituation**: repeated exposure to a stimulus with no reward or punishment leads to a reduction in response to the stimulus
 - i. e.g., clamworm (Nereis sp.) lives in burrows in mud or sand on the floor of estuaries; many stimuli result in retraction of worm into burrows. If stimuli repeated at one-minute intervals, worms stop responding
 - ii. this is a common and adaptive response -- it's a way for an animal to "filter" information from its environment, but more flexible than "hardwiring" the neuromuscular system to not respond
- b. **classical conditioning** = animals learn to associate a new stimulus with an existing reflex (Pavlov's dogs); unclear how important this is to animals in nature
- c. **operant conditioning** = "trial-and-error" learning: animals learn to associate a specific behavior with a punishment or reward; this is very important!
 - i. simple e.g. = toad on p. 114: one or two trials is sufficient for it to associate the behavior of "trying to eat a millipede" with the punishment of nasty taste
 - ii. this is the phenomenon that allows mimicry to work (predators associate a particular color pattern with distaste or illness; learn to avoid all individuals with that pattern)
 - iii. more complex example: prey handling in grasshopper mice (Onychomys)
 - a) insectivorous rodents common to great plains, southwest US
 - b) one prey species = "stink beetle" (squirts acetic acid from ducts in rear)
 - c) adult mice avoid being sprayed by sticking beetle's rear into ground, biting off head
 - d) young seem to have innate tendency to hold prey down on ground; need to learn which end is which!
 - iv. operant conditioning has been widely studied and we now know that it's a

very complex phenomenon, prone to a number of limits and biases
depending on the species -- e.g., fig 23 p. 117 (study on your own)

3. It's well-established that differences in learning ability among species (and among individuals within species) are due, at least in part, to genetic differences.
 - a. if heritable variation exists, then trait should be subject to natural selection
 - b. if that's true, then we should expect to see different kinds of associative learning in organisms with different "life styles"
4. Examples of "special learning"
 - a. **kin recognition**: for species with extended parental care and for social species, individuals may exhibit different behaviors when interacting with kin than with non-kin (we'll talk about the ultimate reasons for that later). So, those kinds of animals must have some mechanism for learning "who's kin".
 - i. **imprinting**
 - a) this is a special form of kin recognition can take two forms (not mutually exclusive):
 - 1- **filial attachment** = attachment to parents; common and well-studied in ducks and geese (e.g., Konrad Lorenz and his greylag geese)
 - 2- **sexual imprinting** = early experience determines objects of sexual attraction at physiological maturity
 - a- e.g.'s from Lorenz (read briefly)
 - b- e.g. Vos's work with albino zebra finches: males raised by parents with different bill colors preferred adults of same bill color as mother -- even if those adults were male
 - c- note that pattern may vary among the sexes: female albino zebra finches preferred adult males, apparently on the basis of behavior

- d- think about why this makes sense evolutionarily
- b) main characteristics of imprinting are that, in general (there are exceptions)
 - 1- recognition is learned rapidly
 - 2- imprinting is often only possible within brief critical learning period
 - 3- effects, while not irreversible, are difficult to reverse
- ii. recognition by association: young “pay attention” to sensory cues associated with early companions, who are most likely its littermates
 - a). spiny mice prefer to huddle with littermates, even when litters artificially created by combining offspring from multiple females
 - b) paper wasp queens tolerate nonkin if queens exposed to “nest scent” of nonkin workers shortly after birth
- iii. **phenotype matching** = special mechanism of kin recognition that seems to operate according to the rule “if it’s like me, it’s kin”
 - a) Sherman and Holmes studied Belding’s ground squirrels: two females gave birth at ~ same time; created four classes of juveniles:
 - 1) sibs reared apart
 - 2) sibs reared together
 - 3) nonsibs reared apart
 - 4) nonsibs reared together
 - b) after weaning, paired encounters staged:
 - 1) offspring reared together generally non-aggressive, even if non-kin (as above)
 - 2) animals reared apart generally aggressive, even if kin (as expected if kinship learned by association)
 - 3) major exception: female sibs reared apart showed significantly less



aggression to one another than non-sibs reared apart: (note that both sib and nonsib pairs were reared apart -- the "recognition by association" hypothesis predicts same levels of aggression for sibs and nonsibs)

- b. **spatial learning** is important for species who move extensively in order to store and retrieve food, seek mates, etc.; we see variation in spatial learning ability based on many different factors
 - i. in birds, many species store caches of food for later retrieval
 - a) black-capped chickadees remember several hundred cache sites for up to 28 days
 - b) Clark's nutcrackers can remember thousands of cache sites over large area for months
 - c) Olson et al. compared spatial vs. non-spatial learning in nutcrackers and three other jay species (fairly close relatives)
 - 1- comparing spatial learning demonstrated that nutcrackers had significantly greater ability than did other species
 - 2- but nutcrackers performed toward low end of range in non-spatial learning tests
 - 3- indicates that nutcrackers don't have better "general learning" ability, but greater ability with a fairly specific form of learning
 - ii. in voles, differences in spatial learning among and within species is correlated with differences in mating system, sex, season, and possibly levels of hormones during development:
 - a) spatial learning ability is correlated with mating system:
 - 1- in polygynous species, males have larger home ranges than females; each male's home range encompasses that of several females
 - 2- in monogamous species, male-female pairs occupy same home

range while rearing offspring

3- not surprisingly, males of polygynous (wide-ranging) species perform better in maze-running tests than do females

4- similarly, males and females of monogamous species perform at same level

b) males from litters with larger numbers of males perform better than do males from litters in which most offspring are female -- suggesting role of hormones on development of brain regions associated with spatial learning

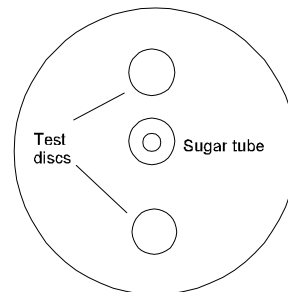
c) in wide-ranging species, differences in learning ability (and hippocampal size) are expressed only during the breeding season, while males are actively searching for mates

c. Honeybees learn to recognize and remember food sources based on flower color and scent

i. ability to associate color with food

tested using “artificial flowers” - table with three inset glass discs, each of which can be lit from below. Filters allow colors of light to be switched rapidly from yellow to blue. Central disc contains tube

with sugar solution for training; on return visits, central disc covered and bees given choice between yellow and blue discs. Because bees take time to feed, color of “artificial flower” can be changed while bee is feeding



- ii. Investigators found that period of association required for learning color very brief:
 - a) color had to be present ~3 seconds before bee landed; didn't matter if it changed as little as .5 s after start of sucking (bees would still prefer original color on return visit)
 - b) single experience of this type can be retained for several days; three experiences and association will be retained for rest of bee's life
 - iii. even cooler -- in nature, bees use both color and scent to trigger feeding:
 - a) color is good cue for early approach, but nectar load can vary among flowers, so scent is appropriate secondary cue
 - b) most flowers vary nectar production throughout day -- producing different amounts and different times
 - c) Bees can learn to associate specific scents with rewards at specific times of day -- up to 8 such associations! I.e., individuals can learn that "orange blossom = food at 11:00 but lavender = food at 1:00" and adjust foraging behavior appropriately!
- D. Although environmental factors clearly play important role in development of behavior, it's also clear that developmental processes can be buffered from the effects of abnormal environmental influences -- read section on developmental homeostasis just for background for this "take-home" message (see summary #4 p. 125).