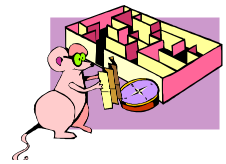
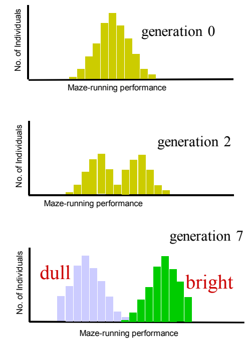
**Quiz #2**

1. Define the four (4) conditions required for natural selection to shape behavior.

2. What level of selection will we most often presume to be shaping behavior? Level of:
   a. Gene
   b. Individual
   c. Group
   d. Kin

## Artificial selection for maze-running performance in rats






Bidirectional selection

Clearly, variation in maze-running has a genetic component.

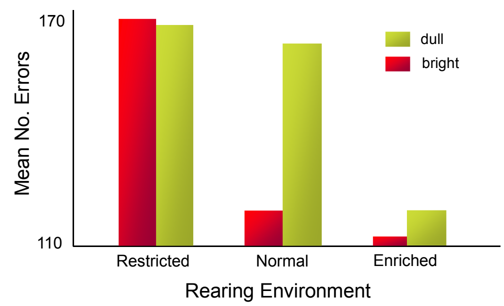
**Is environment also important?**

**Experiment**

Rear "bright" and "dull" rats in 3 kinds of environments:

- restricted (1/cage; no toys)
- normal (3/cage; no toys)
- enriched (12/large cage; 5-6 objects)

Measure maze running for each combination (3x2=6).




Effect of genotype depends on environment!

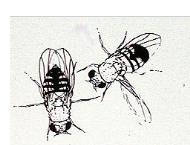
We call this a
**genotype x environment interaction**

**Rats in enriched environment treatment had:**

- thicker **cerebral cortex**
- more **synaptogenesis** (= more new synapses)

## Another Example of Role of Environment

Sex determination often genetic (e.g., *fru* locus in *Drosophila*).



Not so in many reptiles, including turtles, some lizards and all… **CROCODILES!**

## All crocodilians have TSD, or **temperature-dependent sex determination**

Sex depends on the temperature at which egg is incubated during a **sensitive period**.

**Nile Crocodile Data**

T ≤ 31.7°C ⇨ females

31.7 < T < 34.5°C ⇨ males

T ≥ 34.5°C ⇨ females

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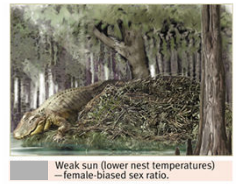


- **Sensitive period** is ~ 10 days long in middle third of embryonic development
- Involves activation of steroid-producing **enzymes** and **steroid receptors**
- Can lead to **biased sex ratios**
- Can be **disrupted by toxins** such as PCBs

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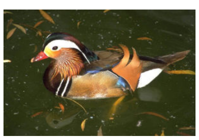
## Ontogeny (= Development) of Behavior

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## Behavior and Environment

**Two basic processes:**

**a. internal processes**

environment consists of an animal's own cells, tissues and organs.

**b. external processes**

environment is external to the animal.

---

## Internal Processes

**Case study**. Development of target neurons in tobacco hornworm, *Manduca sexta*

**Basic facts**

*M. sexta* males fly upwind in plume of **sex pheromone** produced by female.


Work by Anne Schneiderman, John Hildebrand and colleagues at UA

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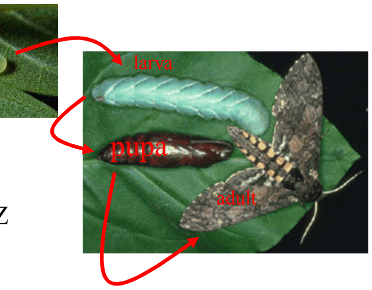
## *Manduca sexta* Life Cycle

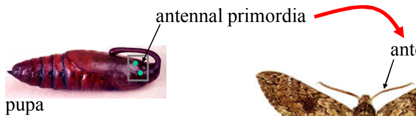



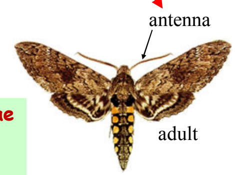

Males WW
Females WZ

**Basic facts (cont'd)**

Pupa has **antennal primordia** which develop into antennae.

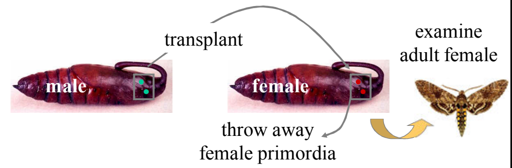
Developing primordia connect 'downstream' to **target neurons.**




**Target neurons and antennae look different in males and females.**

**Experiment**
Primordia transplanted during pupal development




**Results**
Antennae were male in appearance (as expected).

BUT… target neurons in female brain became male in appearance!

**Conclusion**

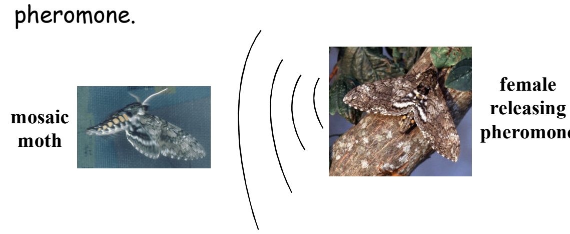
Despite being genetically female (WZ),

target neurons have potential to express either male or female morphology,

depending on input from antennal primordia.

target neuron development was affected by **internal environment**

**Experiment**
Place **'mosaic moths'** in wind tunnel with female pheromone.




**Results**
Mosaic moths moved upwind in response to pheromone, even though mostly female!

## Conclusion

complex interaction between gene expression in developing neurons

and the **internal environment** in which neurons develop.

## External Processes

**Case Study.** Harry Harlow and "The Nature of Love"

**Rhesus monkeys** deprived as infants of mother and other conspecifics develop social pathologies:

- **withdrawal** from social interactions
- self-clasping and other **self-directed behavior**
- **deficits in sex**ual behavior
- **failing to care** for own young, even abuse

Harlow set about to define the **maternal stimuli** to which a rhesus infant responded.

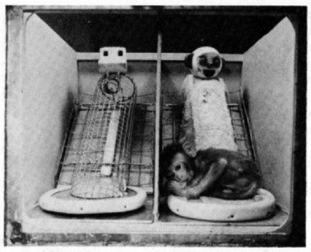


Figure 4. Wire and cloth mother surrogates.

Video

Figure 13. Typical fear stimulus.

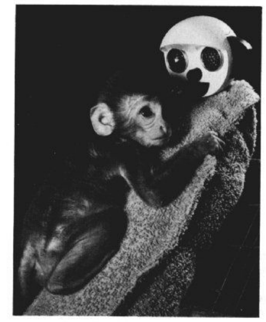
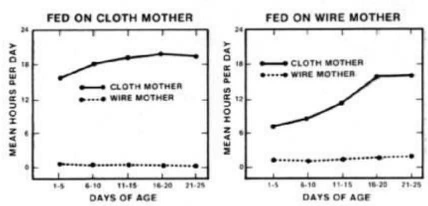


Figure 14. Typical response to cloth mother surrogate in fear test.

http://www.youtube.com/watch?v=hsA5Sec6dAI




Adding just a few stimuli, like cloth and a face,

had a profound effect on responses by infants.

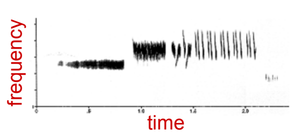
Harlow's monkey studies are examples of deprivation experiments.

**deprivation experiment**
experiment in which animal is deprived of particular environmental cues for particular periods of time

**Case Study.** Acoustic deprivation and song development in **white-crowned sparrow**

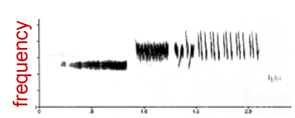
Male white-crowned sparrows sing a complex song.

**Sonogram** is shown below.

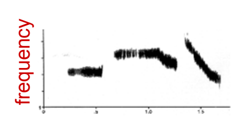



If a young wcs male is held in **acoustic isolation** from song of adult males,

The male eventually sings a less complex **isolate song**.




typical song




'isolate song'

**Conclusion:** To sing a species-typical song, young male must hear other males singing.

If a young male is actually **deafened** from hatch, he doesn't sing the isolate song.

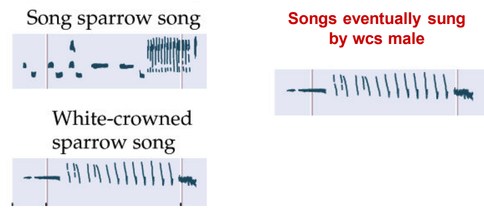
In fact, the male only **screeches**.

**Conclusion:** young male must hear himself practicing his own song.

## Song learning has a species bias

Songs presented to juvenile wcs male

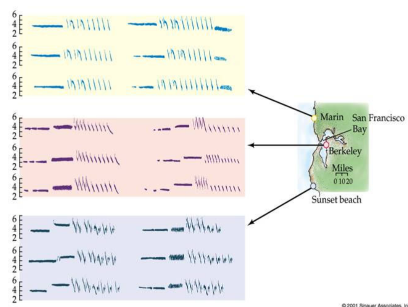
Songs eventually sung by wcs male




**Conclusion**: White-crowned sparrows are **'prepared to learn'** their own song.

Mountain subspecies and coastal subspecies prefer to learn their own song.

In other words, a sub-species bias in song learning.




Males from a given population learn a **local dialect** in nature,
But in lab will learn any dialect.

## Time Course of wcs Song Ontogeny

| When Song is Heard (Days) | Song Sung |
|---|---|
| 1 - 10 | isolate song |
| 10 - 50 | normal song |
| 50 - death | isolate song |

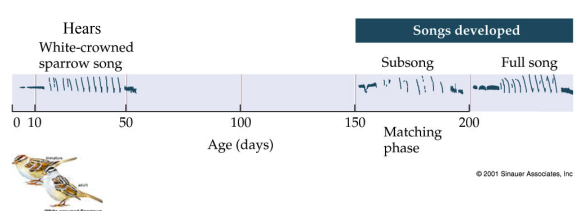
***sensitive phase***

Day of Life 0 10 50 150

Male begins to sing at ca. **Day 150**.

Young male first sings a **subsong**.

With practice, the song becomes a **full song** (= **crystallized song**).



## Template Model for WCS Song Ontogeny

SENSORY PHASE

crude template ↓ ← owns species' song heard

template matched to song heard ↓

exact template

- - - - - - - - - - - - - - - - - - - - - - - - -

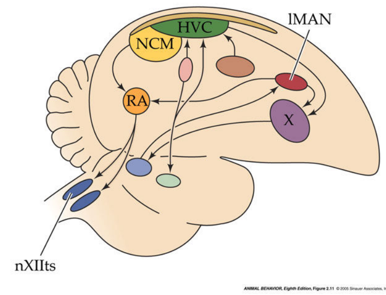
SENSORIMOTOR PHASE

↓ ← hears own song

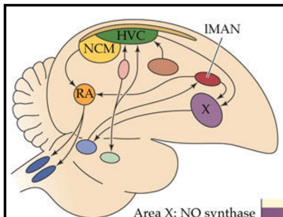
song matched to template ↓

sings copy of song heard

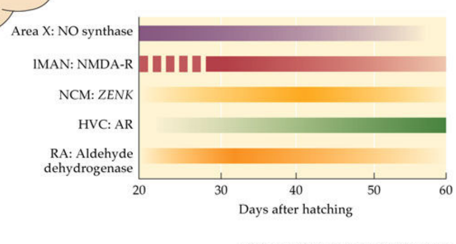
## Where's the template?




**Mostly based on zebra finch**




Gene expression varies in timing in different regions.



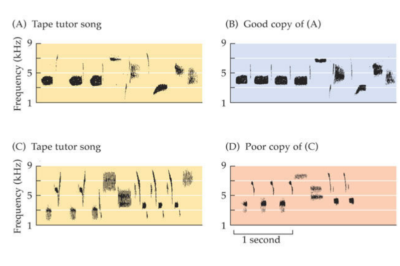

# Why learn song?

Video of bird song…. From The Life of Birds (Attenborough)

Luciano Pavarotti

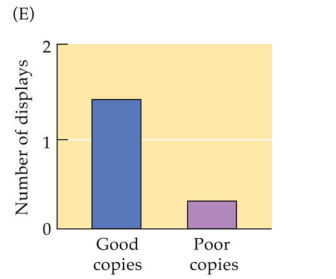
Don't always need to know what the song 'says' in order for song to have meaning

## Songs vary in quality




Song sparrow data

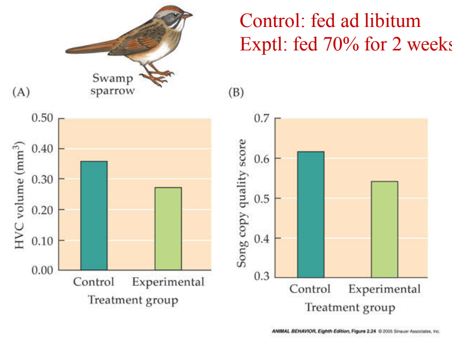
**Females song sparrows prefer better copies.**




**But… why?**

**Possibly… song copy quality indicates health of male.**

Control: fed ad libitum
Exptl: fed 70% for 2 weeks





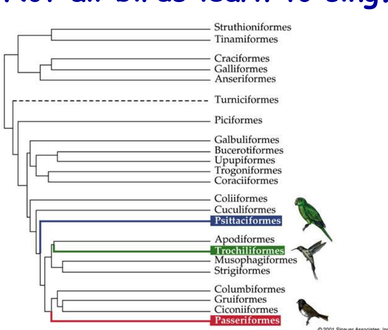
**The Model of Song Development?**

***There are issues!***

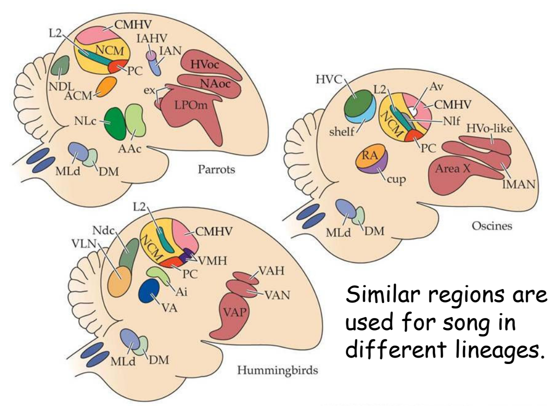
First, there are species differences in song learning.

1. Effect of early deafening
   *canaries* sing normally
2. Effect of acoustic isolation
   *cowbirds* sing normal song
3. Timing of memorization and motor phase
   *zebra finches* memorize other songs even as they are singing old ones
4. Kind of song learned
   *mockingbirds, parrots, mynahs* learn vocalizations of other species
5. Accuracy of copy
   *wcs* copy almost perfect; *song sparrow* copy poor

## Not all birds learn to sing.




Song learning apparently evolved or lost 3 separate times.



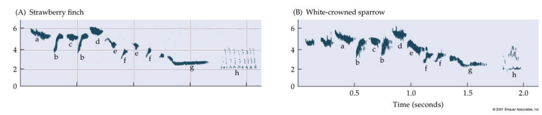

Similar regions are used for song in different lineages.

Second, there were problems with acoustic isolation experiment.

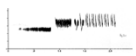
A young wcs allowed to hear song of other wcs, but held with a **strawberry finch**,

Sang the FINCH song!

Strawberry finch acted as **social tutor**.




'typical' wcs song:



The last issue is more worrisome.

**Three Problems With Deprivation Experiments**

Problem #1:

experiments frequently deprive animal of more than the factor intended.

**Example**

Acoustic isolation experiments deprive a songbird of more than sound.

also deprive visual and tactile input from other birds.

Problem #2 with deprivation experiments:

Environmental factor may be important even if deprivation does not affect behavior.

**Example**

Kittens deprived of mother express species-typical social behavior.

Is mother unimportant? **NO!!**

Rather, kittens deprived of mother play more with other kittens.

**Extra stimulation compensates**.

**Developmental homeostasis**

animals may all develop species-typical behavior through alternative routes

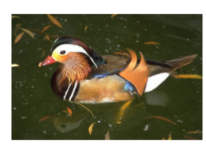
**Development is buffered** to some extent from the environment.

Problem #3 with deprivation experiments:

It can be challenging to deprive an animal of all possible environmental input.

**Example:**

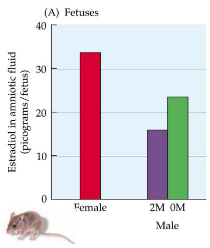
Ducklings isolated from mother at egg stage prefer own species' vocalizations.

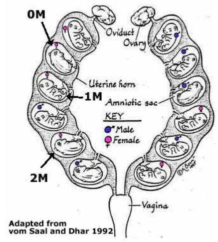


If isolated and devocalized at hatching, they still prefer own species call.

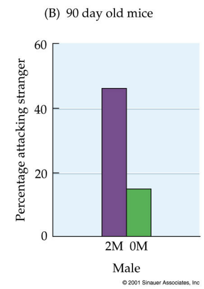
If devocalized **in the egg**, they fail to recognize own species' vocalizations.

## Neighbor effects in the mouse womb…



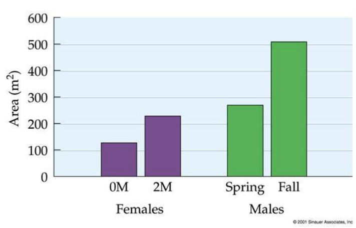




Being surrounded by 2 females in womb (= 0M) causes male to be bathed in amniotic fluid which is higher in **estradiol** than in male surrounded by 2 males (= 2M).




The '**feminized**' male mice are much less aggressive towards strangers at 90 days of age.

Female mice also show an effect of embryonic environment on behavior.




**Home ranges** of females surrounded in the womb by 2 males are larger (= more male-like).

**OLD VIEW:**

genes ⇨ development ⇨ innate behavior

environment ⇨ development ⇨ acquired behavior

**NEW IMPROVED VIEW:**

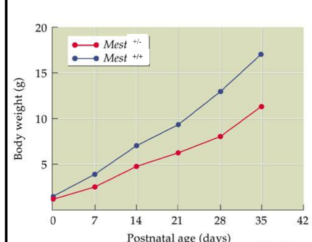
genes ⇘
development ⇨ **all behavior**
environment ⇗

## Genomic Imprinting: A Unique Type of Gene-Environment Interaction

**Genomic imprinting**
gamete-of-origin dependent modification of phenotype

Or, the phenotype elicited from a given allele depends on the sex of the parent contributing that particular allele

## Genomic imprinting of pup growth and maternal care in mice




Only paternal Mest gene active in normal Mest$^{+/+}$ mouse pup.

Knocking out the paternal copy (= Mest$^{+/-}$) **reduces pup growth**.

And… Mest$^{+/-}$ females **fail to care** for young.

**Why** does an allele from the ***father*** only promote increased pup growth and increased care by the daughter ***mother***?

**Because of a key tradeoff:**
Increased pup growth in current litter reduces number and fitness of future litters.

Since father of current litter might not sire future litters, father's genes favor investing more in growth of current litter (= the one he sired) than would mother's genes.

This is… **intragenomic conflict!**

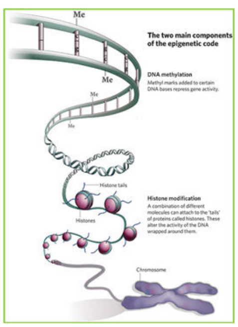
Genomic imprinting is an example of **epigenetics.**

**Epigenetics**
a stable alteration in gene expression *without* changes in DNA sequence

Regulates whether genes are expressed and proteins produced

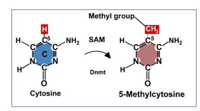
**Basic epigenetic processes:**

**DNA methylation** and **histone acetylation** alter gene expression by affecting how tightly coiled the DNA molecule is.

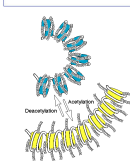


## DNA can be less or more tightly coiled

**DNA methylation** (adding a methyl group)
- Tightens coil
- Helps turn gene OFF




**Histone acetylation**
- Loosens coil
- Help turn gene ON



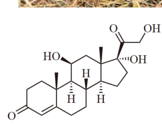
**Both processes are affected by environment**

## Epigenetics of stress response in Norway rats

Some Norway rat mothers nurture young more than other mothers

◊ **Pups of nurturing mothers tolerate stress better** than pups of neglectful mothers

◊ Stress tolerance a function of **glucocorticoid hormones**

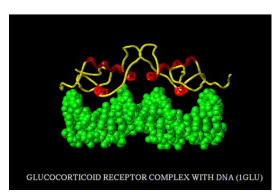


**cortisol is a glucocorticoid hormone**

Contact between mother and pups **increases expression of gene for glucocorticoid receptor** in pup's hippocampus.

More glucocorticoids are bound.

Pups are consequently **less fearful.**




very relaxed pups

**Process involves DNA methylation.**

At birth, promoter of glucocorticoid receptor gene is demethylated.

Over time, the promoter in pups of neglectful mothers becomes more methylated than in pups of nurturing mothers.

Receptor gene of neglected pups is expressed less, leading to more stress.


If stress reduces nurturing, this process can cause inheritance of stress which is epigenetic, not genetic.

## Epigenetic 'inheritance' of nurturing in Norway rats

Some Norway rat mothers nurture young more than other mothers

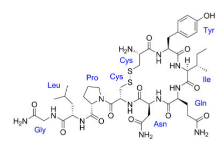
◊ well-nurtured pups become nurturing mothers

**Mother-daughter similarity in caring could be due to genetics… or social learning… or … EPIGENETICS.**

Nurturing **increases expression of ER $\alpha$ gene for estrogen receptor** in pup's preoptic area (POA) of hypothalamus,

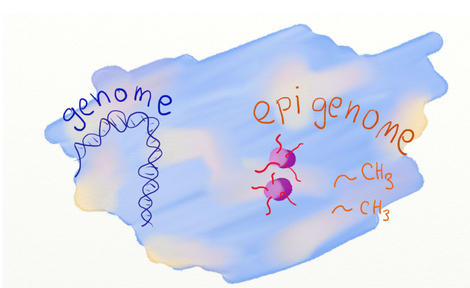
By **reducing degree of methylation of gene promoter.**

Influences response to **oxytocin**, a hormone critical for maternal care.



oxytocin

future nurturing mothers




This process can cause inheritance of nurturing which is epigenetic, not genetic.

**But inheritance not as fixed! Can be reversed!**