“An instinct, unlike learned behavior, is a behavior under genetic control.”

Discuss.

Behavior Genetics

a. Do genes encode behavior?
b. Do genes encode learning?
c. How many genes encode a behavior?
d. Can a gene have more than one effect?
e. Do individual differences in behavior in nature reflect genetic differences?
f. What is the role of genetic variation in evolution by natural selection?

a. Do genes encode behavior? Yes!

building a better honey bee

In late 1800’s, Austrian tried to breed hard-working but good-natured honey bee.

He crossed Italian strain (gentle) with German strain (hard-working) and...

...obtained an extremely aggressive bee!

Yes! Gregor Mendel!

Do genes encode behavior? YES!

Drosophila Mutants as a Case Study

Drosophila males 'sing' to females.
cac mutants sing poorly and shout to boot.

Some Drosophila behavior mutants

\begin{align*}
eag & \quad \text{ether-a-go-go} \\
kdn & \quad \text{knockdown} \\
per & \quad \text{period} \\
fru & \quad \text{fruitless} \\
qtc & \quad \text{quick to court} \\
spin & \quad \text{spinsters} \\
sk & \quad \text{stuck}
\end{align*}

obtained by 'forward genetics' in which mutants are screened in behavioral assays.

forward genetics
seeks to define genetic basis of a particular phenotype*

reverse genetics
seeks to define effect of a DNA sequence on the phenotype; newer approach

*phenotype = an observable property of an organism
Reverse Genetics: Knockout Technique

Use 'gene targeting' to knock out a specific gene, or even just one transcript of a gene.

Observe effect of knockout on animal’s behavior.

fosB+ mice show normal maternal care. fosB- mice are indifferent to pups.

A good introduction to the knockout technique:

http://www.bio.davidson.edu/Courses/genomics/method/homolrecomb.html#KO

Reverse Genetics: Viral Techniques

Prairie Vole
Males are monogamous, having a single partner

Meadow Vole
Males are polygynous, having multiple partners

Vasopressin is a hormone thought to promote pair bonds and social behavior in voles.

Prairie voles show greater levels of V1a vasopressin receptor in the ventral pallidum of brain.
(as indicated by large dark regions)
Viral vector-mediated gene transfer: Virus used to vector V1a gene of prairie vole to meadow voles.

Brain of engineered meadow vole shows strong expression of V1a vasopressin receptor.

Engineered meadow voles are more likely to interact with PARTNERS than wild type meadow voles.

b. Do genes encode learning? YES!

Partial list of Drosophila learning mutants

dnc  dunce
rut  rutabaga
rad  radish
amn  amnesiac
n^{ts1}  notch temperature-sensitive

1st 4 obtained by ‘forward genetics’ in which mutants were screened in learning assays.

c. How many genes encode behavior?

Drosophila learning mutants

Mutants have different effects on learning and/or memory.

In Drosophila, four kinds of memory have been described:

STM = Short Term Memory
ARM = Anesthesia-Resistant Memory
MTM = Medium Term Memory
LTM = Long Term Memory

<table>
<thead>
<tr>
<th>Mutation</th>
<th>Effect</th>
</tr>
</thead>
<tbody>
<tr>
<td>dnc</td>
<td>dunce Learning &amp; STM</td>
</tr>
<tr>
<td>rut</td>
<td>rutabaga Learning &amp; STM</td>
</tr>
<tr>
<td>rad</td>
<td>radish ARM</td>
</tr>
<tr>
<td>amn</td>
<td>amnesiac MTM</td>
</tr>
<tr>
<td>n^{ts1}</td>
<td>notch temperature-sensitive LTM</td>
</tr>
</tbody>
</table>
Mutations map to different sites in the fly genome.

Learning in fruit flies is therefore polygenic, meaning 'controlled by many genes'.

c. How many genes encode behavior?

Cricket Song

In crickets, often the male sings, attempting to attract a female.

Males make sounds by drawing a 'file' on one forewing across a 'scraper' on the other forewing.

In crickets, often the male sings, attempting to attract a female.

F1 songs:
1. Songs are a blend of parental songs
2. F1 song depends on what species contributes which parent.

Backcross songs:
1. Songs are blend of parental and F1 song.
2. If backcross repeatedly to parental species, song resembles parental species' song more and more.
All results together suggest that:

1. Song production is **polygenic**
2. Song production is **sex-linked**, meaning some genes for trait are on X chromosome

One final result:
If hybrid females are offered a choice between a hybrid male song and a parental species’ song,

**hybrid females prefer hybrid male song!**

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*Ormia* flies parasitize *Teleogryllus* crickets in Hawaii.

*Ormia* uses male's chirps to locate them and then lay eggs on the cricket.

Maggots cause the death of their host.

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In 2003, a mutation arose in Kauai population that rendered males mute!

Called flatwing (fw), the new form is protected from parasitism, but must use other cues to mate.

**Mutation increased from 0 to 90% in 30 generations!**

**Natural selection in the here and now!**
**New Approaches: Use of Gene Microarrays**

Honeybee workers start adult life out as nurses, caring for brood. After two weeks, they begin foraging for nectar and pollen.

Thousands of genes extracted from brains of honeybees of different ages, stamped onto glass slide, and their activity measured.

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**d. Can a gene have > 1 effect?**

Yes!!

**Example.** The period (per) mutant in *Drosophila*

*per* affects:
- time of day that pupa becomes adult
- daily activity rhythm
- male courtship song rhythm

**Pleiotropy**

the tendency for a gene to influence more than one trait

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**Obsessive grooming in mice**

- Results from knocking out the SASAP3 gene
- SASAP3 gene product strongly expressed in cortical striatum tissue
- Lentiviruses carrying SASAP3 restore normal grooming when micro-injected into striatum

**SASAP3 knockout affects multiple traits. Knockouts:**

- are less likely to move into the open
- take longer to enter a brightly-lit area

SASAP3 gene has pleiotropic effects on behavior
Food for Thought
Suppose that scientists find that alcoholics differ at a certain locus in the genome from other people.
Is that then the gene for alcoholism?
Is alcoholism then genetically-controlled?

The occurrence of types in nature is referred to as a polymorphism.

Genetic Polymorphisms

<table>
<thead>
<tr>
<th>Forms</th>
<th>Animal</th>
</tr>
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<tbody>
<tr>
<td>winged/wingless</td>
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</tr>
<tr>
<td>right-billed/left-billed</td>
<td>crossbill finches</td>
</tr>
<tr>
<td>slug-loving/slug-refusing</td>
<td>garter snakes</td>
</tr>
</tbody>
</table>

Example of genetic polymorphism (from Alcock text)

But usually, variation in nature is continuous...

Variation forms a 'bell curve', also called a normal distribution.

A naturally-occurring genetic polymorphism

<table>
<thead>
<tr>
<th>Phenotype</th>
<th>rover for(^a)</th>
<th>sitter for(^a)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larval movement</td>
<td>More</td>
<td>Less</td>
</tr>
<tr>
<td>Adult movement</td>
<td>More</td>
<td>Less</td>
</tr>
<tr>
<td>Pupation site</td>
<td>On and off fruit</td>
<td>On Fruit</td>
</tr>
<tr>
<td>Habituation - sucrose</td>
<td>Slower</td>
<td>Faster</td>
</tr>
<tr>
<td>Habituation - escape</td>
<td>Slower</td>
<td>Faster</td>
</tr>
<tr>
<td>Short-term learning*</td>
<td>Stronger</td>
<td>Weaker</td>
</tr>
<tr>
<td>Long-term memory*</td>
<td>Weaker</td>
<td>Stronger</td>
</tr>
</tbody>
</table>

All effects due to difference in one gene that encodes for a protein kinase.

* Mery et al., Proc Nat. Acad. Sci. 2007

Pleiotropy!
Is this variation genetically-based?
Or is variation due to environmental factors (nutrition, disease, etc.)?
Must ask where genetic relatives are found in the distribution.

If much of variation is genetically-based, then members of a family will cluster together.

If variation is not genetically-based, then families will show no such clustering.

Heritability
a measure of degree to which variation in a trait is genetically-based variation

\[ h^2 = \frac{\text{genetic variation} (V_G)}{\text{total variation} (V_G + V_E)} \]

Where \( V_E \) is amount of variation due to environmental influence

\( h^2 \) will vary between 0 and 1

Heritability is sometimes measured by comparing parents and offspring, using an offspring-parent regression.

Slope of line proportional to \( h^2 \)

Parent-offspring regression for plumage spottiness in the barn owl

Spottiness measured on breast, belly, flanks and underside of the wings
Parent-offspring regression for anti-predator behavior in Alpine swifts

Scoring of Anti-Predator Behavior at Nest

- 0 bird flushes upon approach
- 0.5 bird flushes as hand reaches out
- 1 individuals remain immobile during capture and test
- 1.5 bird aggressive as hand reaches out
- 2 bird aggressive on approach

Conclusions
Some suggestion that anti-predator behavior is heritable, but NO suggestion that social copying affects anti-predator behavior.*

* Whereas bird song often influenced strongly by social copying

Heritability Values for Behavior*

- phototaxis in flies 0.60
- cricket song characteristics 0.72 - 0.76
- social dominance in chickens 0.16 - 0.28
- honey bee learning abilities 0.39 - 0.54
- human IQ scores 0.70

** all values should be taken with a grain of salt.

Treatments:
Some chicks allowed to be raised by biological parents.
Some chicks transferred to nests and raised by foster parents.

Parent-offspring regressions done for both treatments.
Summary Message

Genetic differences in behavior in nature due to small differences at many loci.

The exception that proves the rule:
sexual differences in behavior

Males and females generally result from a genetic polymorphism.

Sometimes it has a simple genetic basis.

Example. fruitless (fru) locus in Drosophila

The original fru phenotype involve males courting other males, forming a chain.

Gene targeting used to generate:

1. female-type splicing in males (fru^F).
2. male-type splicing in females (fru^M).

Results:
fru^F males court females less and rarely mate.
fru^F males court males, forming chains.
fru^M females court females.

Conclusion: fru is a sexual behavior switch gene.
(sexual difference due to a single gene of large effect)
**f. Does genetic variation play a role in evolution by natural selection?**

**YES!**

Evolution = change in gene frequencies

Hence, evolution can only occur if there is genetic variation in a trait.

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Evolution by **natural selection** requires that:

1. individuals in a population vary with respect to some trait.
2. at least some variation is **genetically-based** (i.e., heritable).
3. certain genotypes reproduce more than others.
4. differences in reproduction are attributable to an **agent of selection**.

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**Three forms of natural selection**

- Directional
- Stabilizing
- Disruptive

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**The Starting Population**

Trait Distributed as a 'Bell Curve'

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**Directional Selection**

Genotypes at one end of the distribution do worse.

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**Directional selection for maze-running performance in rats**

<table>
<thead>
<tr>
<th>generation</th>
<th>No. of individuals</th>
<th>Maze-running performance</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>generation 0</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>generation 2</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>generation 7</td>
<td></td>
</tr>
</tbody>
</table>
Stabilizing Selection

The average genotype does best.

Disruptive Selection

Genotypes at both tails fare best.

Disruptive selection may result in two distinct kinds of individuals

Disruptive selection on bill size in African seedcracker finch

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<tr>
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<td>Drosophila melanogaster</td>
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Artificial Selection
a kind of selection in which humans are the agent of selection
E.g., animal breeding

Adaptation
A trait that serves a definable function and has evolved under natural selection