In this chapter, we’ll look at some of the techniques by which the role of genes in the development of behavior can be investigated. By doing so, we’ll also see that differences in many kinds of behavior can be explained at least in part by genetic differences.

CHAPTER 3 -- THE DEVELOPMENT OF BEHAVIOR: THE ROLE OF GENES

A. Genetic techniques can be used to identify and study “single-gene” behaviors

1. Basic techniques of Mendelian genetics demonstrate that “roving” behavior in fruit flies is controlled by a single gene:
   a. Sokolowski et al. created 2 uniform strains -- “rover” larvae covered 4 times as much distance while foraging than did “sitter” larvae
   b. When adults of the two lines were bred, all F1 were rovers
   c. When F1s were crossed, got 3:1 rover:sitter -- as would be expected if original “rover” parents were homozygous for dominant allele and sitters were homozygous recessive (F1 were heterozygous)
   d. note that, because they’re so well studied, we have many examples of “single-gene” behaviors in fruit flies -- but many of these are probably rare or nonexistent in nature!

2. Genetic manipulation demonstrates that a single gene underlies differences in maternal behavior in lab mice
   a. Single genes can be targetted for alteration so that they’re not transcribed (called “knockout” mice -- see handout)
   b. In one line, single gene = fosB knocked out, leading to substantial changes in maternal behavior:
      i. wild-type females homozygous for active fosB investigate newborns, gather pups together, crouch over them, and retrieve displaced pups
      ii. knockout females investigate newborns briefly, then ignore
   c. hypothesis for difference is that the two forms differ in the effects of stimuli from initial investigatory behavior on gene activation:
Chapter 3: The development of behavior -- the role of genes

Dr. Kilburn

i. in wild-type females, sensory stimuli trigger cascade of events resulting in \textit{fosB} transcription, which in turn promotes other changes to the neural circuitry of the brain and ultimately the maternal behaviors

ii. in knockout females, gene can't be transcribed, so genetic/developmental pathway “stops early”

3. “Take home” messages from these and similar studies:
   a. It is possible for differences in even complex behaviors to be the result of single-gene differences (although it’s probably pretty rare)
   b. This DOES NOT MEAN that there is a “gene for” the behaviors in question: genes code for mRNA, not behavior! -- Read fosB section detailing the complex interactions between genes, environment, brain neurology and chemistry, etc. to reiterate.
   c. New genetic techniques give us great tools for investigating relationships between genetic differences and behavioral differences
   d. As these techniques are applied to the study of human behaviors, we will be increasingly faced with several important issues:
      i. improving public understanding of the relationship between genes and behaviors (there is no “alcoholism gene”, e.g.)
      ii. variety of social/ethical issues that arise as genetic underpinnings of various behaviors are explored and clarified (or sensationalized, as is often the case initially)

B. Breeding experiments in uniform environments can be used to investigate the role of genes in complex natural behaviors -- especially when behavioral differences are also correlated with environmental differences

1. Hedrick and Reichert analyzed differences in response time of spiders to prey in webs
   a. spiders living in different environments had different response times:
      i. desert grassland individuals responded quickly to new prey in webs
ii. streamside individuals responded slowly

b. difference could be genetic, or could be environmental: streamside environments could have more prey, so spiders would be less hungry, e.g.

c. To test the hypothesis that the difference in behavior is largely genetic, reared offspring of both types under identical lab conditions (what are the predictions?

i. offspring of “slow” parents took, on average, 1 min to pursue cricket on web

ii. offspring of “fast “ parents took, on average, <3 seconds

iii. conclusion: much of the difference is hereditary -- due to differences in genes

d. Note that they didn’t look for Mendelian ratios in offspring -- why not?

2. Berthold and colleagues used similar kinds of techniques to study differences in migratory behavior in blackcap warblers:

a. Three “migratory phenotypes”

i. Birds wintering in Great Britain (“WIB”)

ii. German and Scandinavian birds that stop in Spain en route to E. Africa

iii. Hungarian birds that stop in Turkey en route to W. Africa (OH)

b. Identified several hypotheses for differences in behavior:

i. WIB birds have lost hereditary ability to migrate

ii. WIB birds are German birds with different genes

iii. WIB birds are Scandinavian birds that stop, rather than continuing to Africa

c. Used breeding experiments to study migratory behavior:

i. adults from different regions brought to lab, allowed to breed, offspring reared in lab

ii. study migratory behavior in lab-bred birds, with attention to 

a) “tendency” or “desire” to migrate manifested by specific kinds of
heightened activity in individuals

b) migratory orientation (manifested by direction of specific kinds of movements)

d. First set of tests: adult WIB birds brought to Germany from Britain; bred and offspring reared in Germany:
   i. in their first fall in Germany, both adults and offspring exhibited heightened activity = ready to migrate (so falsifies hypothesis #1)
   ii. direction of migratory orientation indicated that birds were originally from Germany (supports hypothesis #2; falsifies #3)

e. Second set of tests: could difference between German birds WIB and German birds WIA be environmental? Need to rear genetically different birds in same environment:
   i. brought birds from SW Germany (where presumably genetically different from originals)
   ii. reared in lab under ID conditions as first group
   iii. offspring oriented toward traditional wintering grounds, not Britain
   iv. supports hypothesis that difference genetic

3. Hybridization study supported general hypothesis that differences in blackcap migration largely genetic:
   a. general model = if phenotype largely genetic, then hybrid offspring should be phenotypically intermediate between parents
   b. Helbig tested by breeding parents migrating SW to W Africa with parents migrating to E Africa
   c. on average, migration orientation of offspring was intermediate between that of parents!
C. Comparisons among relatives can be used to study genetic influences on human behavior

1. Studies of twins and non-twin siblings, while not as powerful as controlled breeding studies, can provide good information about genetic vs. environmental influences on behavior
   a. Three types of sibs differ in genetic, environmental differences:

<table>
<thead>
<tr>
<th>Relationship</th>
<th>Genotype</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td>identical (monozygotic) twin</td>
<td>identical</td>
<td>developmental environment nearly identical; other environmental influences similar</td>
</tr>
<tr>
<td>fraternal (dizygotic) twin</td>
<td>50% similar</td>
<td>same as above</td>
</tr>
<tr>
<td>non-twin siblings</td>
<td>50% similar</td>
<td>developmental and other environmental influences most different</td>
</tr>
</tbody>
</table>

b. “Ideal” predictions for hypothesis that differences in behavior are the result of genetic differences would be
   i. identical twins will exhibit same behavior
   ii. fraternal twins and non-twin siblings will exhibit same behaviors about half the time

c. “Ideal” predictions for hypothesis that differences in behavior are the result of differences in environment would be
   i. identical and fraternal twins will exhibit greatest behavioral similarity
   ii. non-twin sibs will exhibit the least behavioral similarity

d. But, argument can be made that even for non-twin sibs, environment is similar enough to account for similarities in behavior -- so best possible situation is identical twins reared apart

e. Two long-term studies of twins, one in Minnesota and one in Sweden, provide evidence that many differences in personality traits have at least a partial genetic basis
2. Comparisons of twins, siblings and of parents to offspring can all be used to quantify genetic contributions to differences in behavior (and other traits) by measuring **heritability**

a. Most broadly defined, heritability is a measure of the similarity of parents to offspring; it is measured by analyzing the correlation between traits in individuals of known genetic relatedness (usually parents and offspring)

b. Heritability is always a number between 0 and 1:

i. 0 heritability occurs when either
   a) no variability exists in the first place (trivial)
   b) variation among individuals is due solely to environmental differences

ii. heritability of 1 occurs when either
   a) no environmental variability exists (trivial)
   b) variation among individuals is due solely to differences in genes

c. Heritabilities have been calculated (using a variety of techniques) for a number of human characteristics. E.g.’s from twin studies:

![Graph showing heritabilities for various human characteristics](image)

Note: thinking about these traits should help us understand what we mean when we talk about the genetic basis for behavior
Important note about heritability: this measure tells us only about within-population variation; it tells us NOTHING about the reasons for differences AMONG populations -- i.e., high heritability within two populations doesn’t mean that differences between the populations are due to genetic differences

i. thought experiment with clones (OH/OH):

a) asexually-reproducing individuals gathered from 8 populations
b) offspring from each reared together in two different environments (so we have two populations, each in a different environment, but each with the same overall genetic makeup)

Assume offspring in population 1 are, on average, larger than parents; offspring in population 2 are, on average, smaller than parents

d) Because conditions within each environment are identical for all individuals, differences among individuals within each environment can only be due to differences in genes: heritability = 1 for both

e) Knowing heritability within each population doesn’t tell us anything about why the two populations are, on average, different from one another (in fact, in this case, the difference between populations must be due to differences in the environment)

ii. This is one major fallacy in the “Bell Curve” -- ascribing differences in IQ scores between whites and blacks to genetic differences
D. Artificial selection experiments can demonstrate genetic basis for behavior
1. Reasoning follows from basic theory of natural selection: selection (natural or artificial) can only act on traits that are heritable. Consequently, if trait responds to selection (natural or artificial), it must have an underlying genetic basis.
2. E.g. Carol Lynch was able to select for mice that collected large and small amounts of cotton for nesting (read on your own).
3. E.g., William Cade was able to select for short- and long-calling crickets.

E. Selection experiments bring up important question: if behavior can evolve by natural selection, why do we see differences in behavior within species? Why doesn’t selection result in one “best phenotype” for everyone? Several mechanisms can act to maintain variation within and among populations (situation known as balanced polymorphism):

1. **Frequency-dependent selection**: if selection favors the rare phenotype, two or more phenotypes can be maintained over time -- e.g. scale-predator cichlids
   a. two phenotypes, “right-jawed” and “left-jawed”, differ in direction of “attack” on prey
   b. prey learn to be alert from attacks by whichever phenotype is most common
   c. so selection always favors the rare form: as the rare form increases in frequency, selection begins to favor the other one
   d. result is changing frequencies of both, but maintenance of both over time

2. **Multiple niche polymorphism**: different phenotypes are favored under different conditions that vary in space or time, within or among habitats.
   a. e.g., variation over time within a population: sand crickets
      i. two forms of males: short-winged, flightless and long-winged fliers
      ii. Short-winged males have greater mating success under normal environmental conditions
      iii. During periods of environmental stress, long-winged males are favored (presumably because of their ability to find new, favorable habitat).
iv. Consequence = as long as environmental stress occurs regularly, both forms will persist

b. e.g., variation among habitats in space: gopher snake food preferences
   i. two phenotypes: coastal snakes feed on banana slugs, inland snakes feed on fish, frogs, etc. in streams and ponds.
   ii. Stevan Arnold demonstrated that difference in preference for slugs was due largely to genetic differences (how?)
   iii. why would slug-eating be favored in coastal but not inland areas?
       a) in coastal areas, slugs = rich source of food
       b) but snakes that eat slugs also eat leeches, which are common in inland habitats (maladaptive consequence of otherwise adaptive behavior!) -- this could be detrimental, as leeches can live within the digestive tracts of the snakes

iv. Consequence is that slug-eating will be favored in one part of species' range and not in others

F. Take-home messages:

1. We have a wide variety of techniques that can be used to identify whether and the extent to which differences in behavior are caused by differences in genes.

2. However, many of those techniques are going to be unavailable or impractical for many species

3. From studies that have been done, we know that
   i. “single-gene” behaviors (differences among individuals are due to differences in single genes) do exist, although they are probably rare in nature
   ii. Genetic differences have been found to account for differences
       a) among species, populations, and individuals
       b) in many different kinds of behaviors (feeding, parental care, mate acquisition, etc.)
       c) in behaviors ranging from fairly simple to fairly complex