Notes on Genetics that are Relevant to Behavior

Eth. & Behav. Ecol.
Biology 287
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Question for the day: When do we say that a gene is involved in the production of a trait -- what do we really mean?

I. Behavior, Social Systems and Inheritance

A. In this section we will see how it is possible for behavior and even relatively complex social behavior to be inherited.

B. What are a couple of simple lines of evidence in favor of this? For the moment let's use the most difficult to fathom example -- the possibility that social systems are partially under genetic control.

1. In insect societies -- social groups can be very large (ranging from just a few individuals to over a million in different species), yet they often start with just a single individual, a founding queen. There is little opportunity to re-invent the species-specific culture by learning it. Further, as we will see, most the behaviors that are important to the society appear in individuals the first time that appropriate stimuli are presented. Thus, the behaviors that make the social order possible seem to be inherited and the society then springs from these behaviors.

? In what sense is this analogous to the unfolding of the genetic program?

2. Different species reliably exhibit differing societies and different enabling social behaviors. Thus, behaviors, just like morphologies can be species-specific and we will see behaviors are related to an organism's particular ecological niche.

Throughout this course we will make the argument that many behaviors are at least in part "inherited". If this is the case, then we will see that it is inevitable that behavior can evolve and in particular that it can be shaped by natural selection. Thus, one of the most important things that you will need to do is to learn how it is possible to inherit behavior and furthermore to review a number of features of genetics and reproduction that we will soon see are central to the study of animal behavior.

II. About Genes and Organisms:

A. Some definitions:

1. **Gene:** a portion of an hereditary molecule that possesses some discrete instruction -- for instance, the sequence of amino acids in a protein (in which case it is a ***structural gene***) or a code that works along with proteins or other substances (such as hormone-receptor complexes) to determine whether or not one or more genes will be transcribed. In this case, it is a ***regulatory gene***.
Since genes are physical locations on hereditary molecules, they are also often referred to as **LOCI** (plural) or as a **LOCUS** (singular).

2. **Allele**: a version of a gene -- in the strictest sense, any difference in the information contained in the sequence (for instance, two sequences that are identical

except for a single difference in a nitrogenous base) gives two different alleles of one gene.

More generally, alleles are only detected if they result in differences in the proteins the genes code for or if they change the way regulation occurs. This is the sense we will use when talking about alleles.

3. **Genotype**: the genes possessed by an organism -- this term is usually used in a limited sense (for example, which particular alleles of a single gene (e.g., at a single locus) are present in an individual) or more generally to indicate the entire complement of genes present in the individual. However, this latter sense is generally referred to by the term **GENOME**, that is, the total complement of genes present in an individual.

4. By contrast, we will also often refer to the **GENE POOL**. In this case, it refers to the genes and their alleles present in some population (either an entire species or some subset). Notice that this is a population concept while genome and genotype are concepts related to individuals

5. The **PHENOTYPE** refers to the actual structures, processes and behaviors of the organism.

a. Put another way, if we tend to think of the genotype as largely an information system. The phenotype is what emerges when the genome interacts with itself (the products of genes interacting with the products of other genes) and the environment and builds and organism. Thus, the phenotype is a physical manifestation of the interaction between the genetic information and its environment. However, it is more than that in that it also includes aspects that could not be reasonably be said to have arisen from such an interaction. Scars, adornments or learned behaviors are all parts of the phenotype.

b. As with the genotype, the phenotype can be seen as either limited to a single factor of interest (often referred to as a **TRAIT**) or it can refer to the entirety of an organism's characteristics.

c. As we will soon see, the phenotype is what selection "sees" -- what selection acts upon. Natural selection does no view genetic information (the genotype) directly. This is a very important point.

d. Note again that behavior is every bit as much a part of the phenotype as are physical structures. Behavior obviously is an important aspect of an organism's ability to survive and reproduce. Furthermore, behavior is produced by neural and chemical structures that in all cases are at least partially the result of the genes the individual possesses.

? Why do you think it is that people often do not think about behavior as part of the phenotype?

B. **A Digression: selfish genes and survival machines**: Here is another way of looking at the genome-phenotype duality of life (sounds very religious doesn't it!) that we will find useful at the start of the course:

1. The genome is made up of units called **Replicators**[1].

a. These are single genes or groups of genes.

b. The rationale is rather simple -- these are visualized as relatively independent entities whose entire "goal" is to replicate themselves as many times as possible. While we have not yet discussed natural selection, I am sure that you are aware that this is how the evolution game is played -- the more copies of yourself that are made, the more the next generation resembles you!

1. Thus, replicators are viewed as the smallest relatively indivisible (so they remain the same from one generation to the next) entities that are capable of replicating.

2. This will normally mean that a replicator will be either a single gene (since detectable crossovers within a gene are relatively uncommon -- more about this later) or in a physically joined block of genes (again, since crossovers are relatively uncommon between adjacent genes).

3. *Replicators are not chromosomes or single DNA or RNA molecules* -- these rather large structures usually never remain the same -- crossovers are virtually assured and therefore the particular genes (replicators) that make up a chromosome are constantly changing.

c. Anything that the replicators can do to increase their replication rate will be in their interest. They have two general strategies:

1. Cooperate with other replicators to create a phenotype (organism) that gives them a better chance for reproduction or

2. Be parasitic on other replicators and utilize the phenotype they produce to aid in reproduction. This may seem bizarre, but it has been seriously suggested and is yet in any way to be disproved that at least portions of the large amount of repetitive DNA found in eukaryotic organisms may in fact be such "Selfish DNA".

In fact, it would be argued that all genes or replicators are in fact "selfish" since they all must at least copy themselves in order to continue to exist (there is no logic other than this needed). Thus, if a certain replicator can pull replication off without doing anything else (coding for some useful thing) then it would seem that parasitism is inevitable since it will work under the right conditions -- there is no morality or conscious design needed -- it will simply happen by chance and under the right circumstances will continue.

? Defend and attack the previous argument with parasitism.

[1] This replicator/survival machine dichotomy was largely put forth by Richard Dawkins, a British evolutionary biologist and student of animal behavior in his very provocative and influential book, The Selfish Gene. Early in this course we will use this analysis, in part just to shake up your preconceptions on nature of organisms. We will also begin to question it rather soon after we have reviewed evolution. For the moment at least, try to take his ideas as far as you can. A lot of the fun and excitement (and frustration and danger) of sociobiology is that it is an emerging field and there are a lot of ideas out there -- many of which do not have good backing, others which on first examination seem absolutely crazy and yet on closer view in fact might be very valuable ways to look at things.

Do you think that: genes must be conscious to join with others to form an organism? Explain why this would not need to be the case.
Why might producing a phenotype be advantageous -- why is there an organism and not merely selfish genes?

2. The phenotype is the replicator's **Survival Machine**. In this view the organism is merely a lifeboat produced by replicators with the goal of protecting them and allowing them to reproduce themselves as much as possible.

a. This may seem like a totally bizarre idea, but I would urge you to consider that in fact the organism (phenotype) and its genome do not survive intact -- only the replicators (or some of them) manage to pull off this trick.

b. Thus, it can be argued that the replicators alone are somewhat "eternal". The organism merely appeared to increase the **fecundity** (reproduction) of the replicators.

? Do you know of any lines of evidence to suggest that groups of genes can in fact join together to produce organisms that are capable of doing different things than either could do by themselves?
How (in general terms) might such joining improve the reproduction of each of the "joining" groups of genes?
If we adopt the replicator/survival machine dichotomous view of life, then what is a family?
In the sacred Hindu text, the Bagawan Gita, Lord Krshna says to the young Prince Arjuna "He who thinks this Self to be a slayer, and he who thinks this Self to be slain, are both without discernment; the soul slays not, neither is it slain." E.O. Wilson used this quotation to introduce his monumental text Sociobiology in 1974 (in many ways the most important book dealing with evolutionary biology written this century). What is the analogy between the "soul" in Krshna's words and the "biological" soul that Wilson was thinking of?

II. How is a phenotype produced?

A. How does a complex phenotype appear given a start from a rather simple, generalized cell?

B. The classic discussion is that it is an "interaction between environment and genotype" but we will examine that in just a bit more detail, although unfortunately not in the detail that it deserves

C. The first thing is to try to get some conception of the possible interactions between the **product of a given gene** (usually a **protein**) and its environment. This environment will include:

1. Physical factors such as heat, pressure, light etc

2. Chemicals from both the environment and those produced within the organism. As you are well aware, many of these can cause general effects on a protein's exact shape, others have very specific effects and may actually serve to modulate the protein's shape in a controlled matter and thereby they all affect its ability to interact with other molecules to produce structures, catalyze reactions, transport substances or whatever.

Genes have evolved in situations where they unconsciously "expect" a certain environment. Any differences will to greater or lesser degrees affect the results they produce

D. **Proteins and the allele sequences have evolved in a situation where they unconsciously "expect" a certain environment** -- differences will to greater or lesser degrees affect how they behave. Let's consider this in a bit more detail.

1. A proteins function is dependent on its exact shape and the position of various side groups of amino acids.

2. Genes only directly specify the sequence of amino acids on a polypeptide chain (the **primary structure**)-- they do not directly specify the three dimensional shape of the final protein (the **tertiary structure**).

3. As of shortly after the polypeptide is produced during the translation process, the each amino acid side group interacts with its immediate environment. This includes both other amino acids on the polypeptide and just as importantly polar and non-polar molecules in the immediate vicinity of the molecule. The exact way the protein will fold is determined by these interactions.

4. Notice therefore that environment is adding important information that helps, to use information theory terminology, compute the final shape of the protein. **Information always comes from both the genes and from the environment.**

5. Thus, the genes do "expect" a certain environment and as long as it is there, a predictable version of a protein will result. But change the environment and you change the information used to compute the protein's shape and you probably get something different -- perhaps even non-functional! This is less of a problem in highly homeostatic organisms but it is nevertheless perhaps the main reason that physiological regulation processes evolved in the first place.

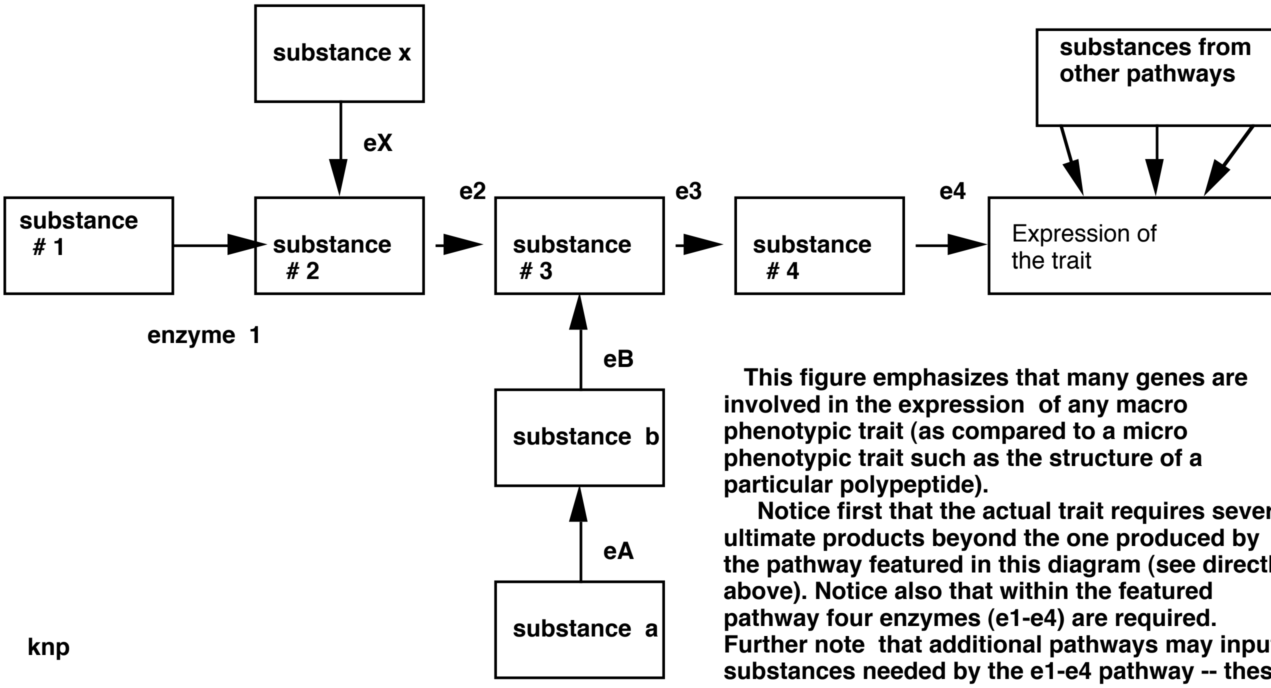
E. Moreover, we must also realize that the expression of the genetic program is strongly influenced by the environment, including other genes.

1. Chemical and physical events that affect regulatory genes and therefore induce or prevent transcription of particular genes or blocks of genes. Whether or not genes are transcribed can obviously be related also to whether or not certain products of other genes are present that enable signals to recognized by regulatory genes.

2. The interactions that occur between the protein products of different genes. Most proteins are used in either relatively complex structures or as part of a reaction pathway (sequences of linked reactions). In both cases, the proteins are mutually dependent on each other. The other proteins must be present in the proper amounts and must have the correct function.

3. Thus the phenotype is the result of complex interactions between the genes and their products. Most macro phenotypic traits (those apparent without delving into an organism's protein biochemistry) are **POLYGENIC.** This means that the trait is due to the interactions of a number of genes:

The Polygenic Nature of the Phenotype



This figure emphasizes that many genes are involved in the expression of any macro phenotypic trait (as compared to a micro phenotypic trait such as the structure of a particular polypeptide).

Notice first that the actual trait requires several ultimate products beyond the one produced by the pathway featured in this diagram (see directly above). Notice also that within the featured pathway four enzymes (e1-e4) are required. Further note that additional pathways may input substances needed by the e1-e4 pathway -- these could supply needed intermediates in large amounts (or even too large amounts) and make up for deficiencies of inputs to the e1-e4 pathway or for poorly functioning versions of any of the enzymes in e1 or e2.

Finally, be aware that substances produced by other proteins or patways may regulate the activity of any of the enzymes in these pathways, thus even more genes are potentially involved.

In class we will look at a model akin to the one above but that involves hormones. Be sure you understand the "pathway" model above. Be able to make the same sort of diagram for neural transmission or for synaptic transmission. I will probably ask about these in class.

We commonly think about single genes determining traits. Using the scheme above, explain how a change in a single locus (gene) could affect the expression of a trait.

In addition to polygeny there is another factor that must be considered -- **Pleiotropy**. This is a very important concept and it is basically defined as the tendency for a given gene to affect many traits. This is obviously not true of all genes, but many nevertheless exhibit pleiotropic effects. For example, the famous alternative alleles for sickle-cell anemia not only affect the shape of red blood cells but also a great number of behavioral traits (for instance, the ability to engage in highly levels of aerobic exercise for long periods of time). You should be able to think of many possible cases where genes are pleiotropic. Finally, keep in mind that not all pleiotropic effects are necessarily deleterious to an organism.

! Be sure that you have a good understanding of the differences between phenotype at the molecular level and at the organismal level; likewise; understand the differences between what would be considered a mutation at the genetic level and one that is evident at the easily observable external level.
? Are there any rules that would allow you to know if a random change would have significant phenotypic effects or not?

4. Don't get the idea that every change in the environment or genotype results in a noticeable change in phenotype. There are many mechanisms built into organisms that tend to cause them to reach the same phenotype even in the face of certain differences in environment. These mechanisms are ones that tend to produce a constant (homeostatic) environment over a range of environmental conditions. We often speak of **Developmental Homeostasis** where organisms with the same genotype reach an "expected" phenotype even though the environments they developed in were not all the same**.** We also sometimes say that development of the phenotype is **canalized** in that once developmental movement starts down a certain path it will tend to move a preferred "direction" and not take possible alternatives. The great developmental biologist Waddington viewed the development of the phenotype as a ball rolling from a hill down a complex landscape. Once a particular path was started down, mechanism ensured that a certain final result occurred -- it becomes increasingly difficult to achieve other results just as it is harder and harder for the rolling ball to change paths once it has started movement.

SOME QUESTIONS TO PONDER
? What genetic mechanisms would allow development to be canalized? Why does it seem to happen even when there are differences in environment that relatively similar products are produced by identical genomes?
? What are some of the ways that things genes can determine a trait -- why are some genes more important than others in terms of their apparent effect on the phenotype?

E. Molecules are fine, but how can molecules have anything to do with the determination of behavior?

1. Control of behavior patterns in higher organisms.

(a) Molecules (enzymes and their products) are too simple to perform any crucial function by themselves.

(b) Typical behaviors involve reasonably complex patterns of muscle contractions or glandular releases that are usually under a continuous feedback control. Fixed action patterns (FAPs) for instance, can be thought of as analogous to computer programs that control some sort of mechanical device. When activated, they cause the device to do one thing then another etc. In sophisticated programs, the progress of the behavior is monitored and adjustments are made as needed. In a computer, the instructions reside in some sort of memory.

(c) In the case of FAPs, the program is stored as a series of neural connections that are activated in a certain sequence; as they are activated, they activate appropriate muscles for an appropriate period of time.

Please note that while FAPs sometimes appear to produce highly stereotyped and even inappropriate behavior that ignores what is going on around the animal, this is not usually the case. The same can be said of computers (although it is perhaps far more common that they do act "stupidly"!). As we have gotten better at making machines that perform stereotyped behaviors with alteration according to the situation, we have come to understand better how a nervous system might to the same.

(d) How are the neural pathways in the brain created?

1. Obviously a number of different types of functional neurons with different properties must be created. The differences in these cells are nearly all due to differences in gene regulation between the different cell lines. Clearly the exact function of the members of a particular cell line will be determined by:

(a) The exact versions of each protein that are synthesized -- alternative versions coded by different alleles in different individuals could result in either minor or even major differences in cellular function.

(b) The extent to which each protein is expressed (how many copies). For example, it only a few hormone or neurotransmitter receptor proteins are put in the dendrites and cell body of a neuron, the cell will be relatively insensitive to these signals.

(c) The ways these cells interact.

2. Growth of cells: in many cases neurons apparently extend their axons following chemical trails left by other cells that lead them eventually to the correct target. However, if one considers the billions and billions (I sound like Carl Sagen) of connections in the nervous system, it is quite evident that many of the connections cannot be specified by unique chemical attractants formed by unique genes. There simply aren't enough genes! Instead, it appears that in many cases:

(a) The wiring is set up roughly at first where chemicals guide axons to the vicinity of their targets. Typically, a given cell will connect weakly to a very large number of cells.

(b) By a number of different mechanisms, the cells recognize which connections are correct. We'll talk about this in class but the result is that those connections are reinforced and others wither away. Over time the total number of connections generally reduces as wiring becomes more precise.

(c) The important thing to realize about point (b) is that what is happening is that the final wiring is not really being determined by genes in the usual sense (as in a) but instead by what are essentially environmental interactions; albeit ones that are either set up or expected by the genes.

Note that the final structure and behavior that results is highly polygenic in nature. However, also note that just as the diagram showed earlier, some genes certainly matter more than others if they redirect the ways neural computation occurs (e.g., by altering the number of receptors) or alter the wiring process.

2. So what do sociobiologists mean when they talk about genes for a behavior? Well, as Dawkins points out in **The Extended Phenotype**, they simply mean some inheritable unit that has a statistically predictable effect on behavior. They are not

at all necessarily implying some single locus always causes a certain behavior to appear (although they might). More often, they simply mean that that there is a heritable component to the behavior. The next set of notes will look into how we attempt to quantify how heritable a trait is.

So, try to visualize the "gene" for a complex yet innate behavior such as feeding young. How would it physically differ from the usual locus concept of a gene? Would there still be a role for the environment in an innate trait?

<u>Some more questions to ponder</u>:
Imagine a single replicator early in the history of a planet.
Why might it come to associate with other replicators?
Why might a phenotype (survival machine) beyond the actual replicator molecule evolve?
Why is possible for some replicators within one "survival machine" to become parasitic?
What is a parasite?
Is it possible to imagine an organism as being essentially a society of interacting genes, each of which is interested in only its own reproduction -- yet nevertheless the entire thing works well together to produce a functional survival machine?
Make an analogy between a complex organism that is the result of the interactions of a number of proteins all of which have rather simple functions, yet what **emerges** when they work together is great complexity and a society based on simple behaviors exhibited by different individuals. Does this help you better see how a social system might potentially emerge from a series of simple inherited behaviors?