

Notes on the Behavioral Continuum

Eth. & Behav. Ecol.
Biology 287
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I. The Behavioral Continuum:

A. Philosophical Introduction: The scientific view of the cause of all behavior springs from the philosophical stance of **materialism**. In materialism all actions are seen to arise from physical and chemical processes. All processes are, in principle, explainable through natural law. This contrasts with the common view, called **vitalism** where some non-material agent (such as a spirit) is in part responsible for the actions and processes within an organism.

1. A materialist framework allows one to test ideas about the nature of behavior. Explanatory hypotheses can potentially be falsified or supported through experimental observation. This is in contrast to supernatural explanations that always reserve the right to explain action as something beyond what is observable.

2. Thus, materialists posit that behavior in animals with nervous systems is the result of the ways that neurons behave individually and wired together into networks. They study how the actions of these cells and networks gather sensory information, store or recall information, make decisions, and direct behaviors.

3. The ways that this wiring is achieved (ontogeny) is a central problem to both ethologists and comparative psychologists and particularly to neuroethologists and (comparative and evolutionary neurophysiologists).

4. One of the most persistent issues in the study of behavior is the so-called **nature-nurture controversy**. It is the subject of these notes.

B. The Poles: Classically, behaviors were thought of falling under one of two categories that were entirely separate from each other:

1. **innate** (also often called **instinctual**) **behaviors**: species-specific stereotyped behaviors believed to be inherited and not learned. It is easy to see how such behaviors would be subject to natural selection. The first modern persons to study them systematically were the **ethologists** (biologists who studied the adaptive significance of natural behaviors -- famous names include Niko Tinbergen (Dutch), Konrad Lorenz and Karl Von Frisch (both German)). The classical criteria for referring to a behavior as innate included the following:

a. these behaviors were produced in a **fully functional form the first time an appropriate stimulus** was presented -- no learning was required for them to be performed correctly.

b. the behaviors were very stereotyped and were not changeable; they were not "**plastic**" (changeable).

c. the behaviors were often categorized as **species-specific** (this is true enough in some cases but in many other behaviors were species typical. Nevertheless, early ethologists often focused on species-specific behaviors).

d. The ethologists identified a series of components or events involved in these behaviors. These include the following:

1. **Sign-stimulus**: some environmental signal or signal given by a conspecific. A good example is the red patch on a parent gull's beak. It serves as a sign stimulus for a hungry gull chick to identify it as the place where food may be obtained.

2. **Releaser**: this term is shortened from the more correct "social releaser". Used most correctly, releasers are signals or stimuli given by conspecifics that elicit a fixed action pattern (see below). Note that many use releaser and sign-stimulus as synonyms.

3. **Innate-releasing mechanism** -- a neural mechanism that decides if the appropriate sign stimulus or releaser has been given and other criteria are present. If they are, it will activate the neural pathways that store the behavioral pattern (fixed action pattern). Classically, this is seen as removing inhibition so the action pattern can emerge.

4. **Fixed-Action Pattern (FAP):** the stereotyped behavior elicited by the sign-stimulus. In class we will discuss models of how the activation of FAPs are controlled – for instance, Konrad Lorenz's famous (or perhaps infamous) "toilet-flush" model which assumes that once the FAP pathway is activated the behavior continues more or less unabated until it is complete -- like flushing a toilet.

MAPs – modal action patterns. Ethologists have found many problems with the idea of a constant, fixed action pattern being elicited by a sign-stimulus or releaser. One problem is that the action patterns are often variable (not fixed) about some mean response. Thus, the suggestion that they are better termed modal action patterns.

5. According to ethologists, very complex behaviors can be produced by interlocking the sequences of one innate behavior with another; this was termed **CHAINING**.

! One unfortunate side effect of the ethologists work was to portray animals as lumbering automatons that are slaved to their innate behavioral patterns and are unable to modify them. We now know this to be incorrect -- more about this in class.
Note a shift of emphasis -- now we tend to talk about action patterns, not fixed action patterns.

One thing we will pursue early in this course will be seeing how a number of genes can interact to produce innate behaviors. We will see that specific neural wirings are created during development by chemical recognition signals or responses of cells to certain firing patterns by cells in the developing nervous system.

b. **Learned Behavior:** In learned behavior the connections are not inherited but instead are produced as the result of experience of the individual with its environment. Radical learning theorists believe that in appropriate circumstances nearly anything is learnable. On a cellular level, **these scientists believe that the nervous system is as easily capable of being wired in one manner as any other.** In this view, genes only matter in the sense that they are required to produce the nervous system. This includes setting some very basic rules as to the conditions under which connections between nerve cells are made, broken or maintained. And it is assumed by the more extreme students of behavior that all of these elements are the same in all animals except those with obvious diseases. General characteristics of learned behavior include:

1. **Learning involves linking stimuli with one or more responses that were not previously so linked.** Thus, experience is required. Repeated experience is often required to maintain what has been learned.

2. Learned behavior is therefore seen as being **plastic**, that is, modifiable.

3. Within the capabilities of an animal (for instance, its senses and the size of its nervous system), all things should in principle be learnable (an extreme view).

4. There are many forms of learning and a bit later this semester we will look at them in detail and also at what may fundamentally unite them at the cellular level. For the moment, two are particularly important: so called **classical and operant learning or conditioning.**

a. **Operant Learning** has been heavily studied by a branch of learning theory in psychology called **Behaviorism.**

i. It posits a central role of something called a **reinforcer** (a reward of some sort -- including the removal of something aversive) to link a particular stimulus with a response (the response may be built up and made more and more complex). In general, most experiments suggested that the reinforcer, stimulus and response all needed to be given very closely together in time for learning to occur. (This is an example of the limitations imposed on the learning by the architecture of the nervous system).

ii. In nearly all cases, operant learning involves the conditioning (learning) of so-called **voluntary responses**; that is, responses by muscles or related structures under the somatic nervous system that controls only skeletal muscles (it is also known as the voluntary nervous system).

iii. Operant learning is the most common type of learning for most animals -- they use it to learn about their environment or to improve the effects of their behaviors. More about it later in the course.

b. **Classical Learning** was studied scientifically before operant (thus the name) but is probably less important in terms of animal behavior.

i. In classical learning an involuntary response to a certain stimulus (called the **unconditioned response** and **unconditioned stimulus** respectively) becomes associated with a stimulus (neutral or "**to-be-conditioned stimulus**") that would not originally lead to the unconditioned response.

ii. The process requires close temporal pairing of the unconditioned stimulus with the to-be-conditioned stimulus. After a number of trials, if classical learning occurs the formerly neutral stimulus will elicit the response. At this point in time the formerly to-be-conditioned stimulus is known as the **conditioned stimulus** and the former unconditioned response is known as the **conditioned response** whenever it is given in response to the conditioned stimulus.

iii. An example of classical conditioning is pairing a siphon withdrawal reflex in *Aplysia* (a.k.a. sea slugs -- a shell-less marine mollusk) that can be conditioned to a change in lighting and touches to parts of the animal away from the siphon (initially the unconditioned stimulus is a touch to the siphon). I mention *Aplysia* since it is a major model for linked behavior/neurophysiology of learning studies.

C. Research in recent years has led to the view that the **Learned-Innate behavior dichotomy is artificial** -- it is far more of a continuum than two distinctly different mechanisms to produce behavior. In fact, close examination has shown that it is hard to find pure examples of either type of behavior.

1. On the poles -- it has been found that **learning is generally biased and heredity influenced** (some things are learned more easily than others and these may have survival value and furthermore definitely seem that such differences are influenced not only by differences in environment, but also by differences in genes. **Likewise, except in perhaps the simplest of organisms, all innate behaviors have been found to be modified by experience** -- the basic patterns may be laid down prior to birth, but these are then modified, often greatly after birth. Animals are not quite the automatons that early ethological work and biases suggested.

2. Between the poles are many examples of types of learning that are clearly biased or heredity influenced. Examples include:

a. **imprinting**: very early experiences of specific nature that are easily learned but thereafter difficult if not impossible to modify. The most famous example (but there are many) is the behavior of young birds that learn the way their species is supposed to look by seeing or following their parents -- if they are cross-fostered by other species, for instance the human ethologist Lorenz, they will tend to act towards that species throughout their lives as if it were their own.

b. **biased learning**: often seen as the ability of some animals with rather limited nervous systems to learn certain very specific types of knowledge very quickly (one trial, in just a few seconds) whereas other things that would seem easy but are not important to them, they seem totally incapable of learning. Tinbergen's beewolf experiments reveal an example of biased learning capabilities. Other examples include the biased learning seen in more complex species, such as was shown by Garcia in his work with learning in rats.

If a general rule can be made about the learned and innate behavior continuum it is that:

i. **behaviors towards the innate end tend to be behaviors of high survival value that are either very important early in life when there is no time to learn them** (for instance, sucking in mammal babies or pecking at appropriate objects in birds) **or where learning might well mean death** -- for instance, avoidance of dangerous animals, plants or environments. More on this later on.

ii. By contrast, **learning is more important when things that are likely to change are involved, especially if the first encounter is not critical to survival value.**

We will consider learned behavior in much more detail later in the course.
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Where we are going: Please think about the largely historical material given above when we begin to work our way through the ways that, over a lifetime, behavior develops and changes in tandem with changes in the nervous system.

The major basis for over-throwing the nature-nurture dichotomy however lies in a better appreciation of how development really works and in an understanding of the concept of heritability.

The present view, which we will explore in some depth, is that all behaviors spring from both genes and environment. At a mechanistic level, we will see that all behaviors are generated through roughly similar means. What will be of great interest to us is not the nature-nurture conflict or whether or not genes influence behavior. Instead, we will want to learn about the **extent to which variation in behaviors found in a population reflects genotypic variation and therefore the extent to which variation of behavior within a population can evolve via natural selection.**