Chapter 1: History & Philosophy of Behavioral Analysis
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Prehistory and Adaptive Perspectives on Behavior

The behavior of animals evolves and is shaped by natural selection. In a similar way our own behaviors and our understanding of how animals behave, was shaped by survival needs in the remote past. By better understanding the behaviors of animals, our hunter-gatherer ancestors more successfully caught and trapped game. There is of course no way to see direct evidence of such observational skills in prehistoric humans as they are no longer in existence. However, samples of Paleolithic art from 35,000+ years ago provide indirect evidence that primitive humans observed the animals that they hunted. Cave paintings often portray animals, which are naturally found in herds, grouped on the walls of the cave. Images seem to capture mass movement reminiscent of terrestrial migrations. These paintings show hyenas hunting in groups. Bears are portrayed as solitary. In some cases solitary animals are painted together, but they appear to interact and face off in ritualized contests.

By studying animal behavior primitive humans were able to exploit the differences in behaviors associated with solitary animals versus those living in herds. Their knowledge helped them capture prey more efficiently. They learned that animals traveling in herds could be driven over cliffs in large numbers, provided that lead animals were first driven over the precipice. Some aspects of human behavior and hunting were culturally transmitted. They learned to avoid risky situations where large predatory beasts could ambush them, or they died. Some human behavior with survival value became instinctive. Other behaviors like tool use and tool making was so complex it could not be re-discovered each generation by trial-and-error learning. These behaviors were undoubtedly culturally transmitted via teaching by the parental generation and learning by the progeny generation. This reflects the *vertical transmission* of ideas from one generation to the next. Culture can also be *transmitted horizontally*, from one distinct culture to another. In a curious way, our own initial ideas regarding behavior undoubtedly developed for the very reasons behaviors have arisen in all organisms -- behavior has adaptive value and is shaped by the force of natural selection. Even the process of learning behavior was shaped by natural selection. Those individuals or groups that transmitted knowledge with high fidelity had an edge in the “struggle for existence” compared to others that were less successful. Innovation was likewise favored. Insight and other higher-level cognitive functions were also refined over eons of selection.

Although the meaning of cave art is debatable, it is clear that humanities' appreciation of animals reaches back to the dawn of prehistory. In the modern day, if one is ever granted the opportunity to follow an aboriginal "tracker", one can learn an amazing amount about an animal's behavior from just a few signs in the sand, or a few indistinct bulges in the snow. A student of animal behavior uses similar skills of observation when they study their organism of choice. Many field biologists become extraordinary "trackers" because they must catch many animals repeatedly over the years. Many of these animals become incredibly difficult to catch as the animals themselves learn to predict the researcher's behavior. One might say that we are very adapted for the study of animal behavior owing to the force of past natural selection. Therefore, we have an intuition for the study of behavior that is shaped by generations of selection.

Despite this kind of intuitive sense of animal behavior, it is still a large leap from practical aspects of behavioral observation to the study of animal behavior as a discipline. What are the origins of modern ideas on animal behavior? The scientific study of animal behavior is founded on Darwin's ideas concerning evolution by the process of natural selection (Darwin, 1859). In treating the ideas in any field, one must consider the origin of those ideas. This appreciation of philosophy is essential for complete comprehension of important concepts. We could use Darwin's theory of evolution by the process of natural selection as a starting point for modern ideas on animal behavior, but realize that our understanding of animal behavior has very deep roots and undoubtedly arose during our own prehistory.

Typological Thinking and Classical Views of Species

Greeks philosophers were interested in describing the order of the world. They considered the origin of each animal species and the attributes that they exhibit unique. Embodied in the Greek version of species was the concept of type, or idea (ειδοζ). Underlying their concept is the notion that there is a perfect type for a species, much in the same way as each geometrical shape has an ideal. An equilateral triangle is the ideal form for all three-sided polygons that we call triangles. One of the obvious aspects that differentiates and typifies organic species is the kind of behaviors animals display when they interact with members of their own species

Classical Greek ideas on species and an underlying type that defined species persisted until the time of Darwin's formulation of the theory of evolution by the process of natural selection. Pre-Darwinian theologians and academics used classical Greek ideas in their formulation of the Ladder of Life or *Scalae Naturae*. For example, Carrolus Linneaus' ordering of organic forms in the volumes that comprise the *Systema Naturae* (1735) was developed in a large measure to categorize the types of animals. The Linnean system was meant to showcase the "Creator's" handiwork. How each set of types lead to higher and higher types (from slugs to man) in a ladder-like sense of perfection. Pre-Darwinian scholars defined species in a way that was closely linked to their theological views on the origin of the universe.

This type of thinking has been referred to as **typological thinking** by Ernst Mayr (1976), an evolutionary biologist who had tremendous influence on the development of modern views of organic evolution. By focusing on **type**, Greeks, theologians, and pre-Darwinian scholars ignored the interesting differences found among individuals of a single species. Such within-species variation was considered unimportant.

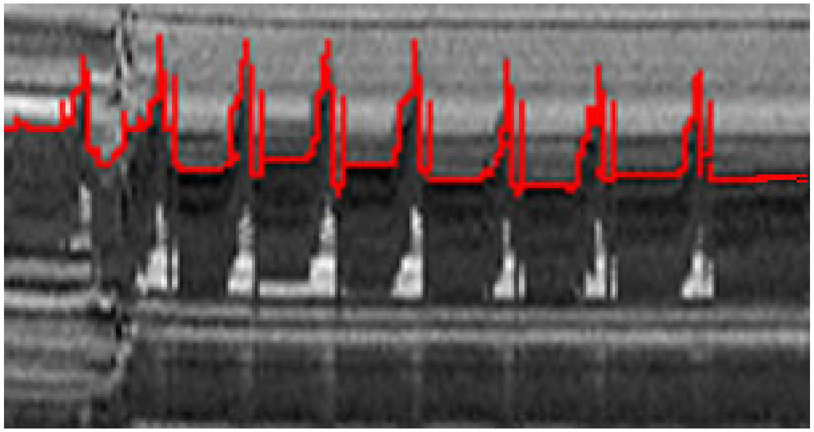


Figure 1. A sequence video of images was used to track the top of the lizard's head (outlined) over time (30 frames per s). The species typical bob is from a side blotched lizard (*Uta stansburiana*). Each horizontal slice is 1/30th of a sec.

Side Box 1.1: An Essay on Typological Thinking and Human Cognition

The concepts of typological thinking bring up an interesting diversion regarding our own curiosity about human thought. The field of animal behavior has a peculiar recursive quality to it (Hofstadster 1979). We attempt to study how animals think, perhaps to gain a better idea of what makes us think. The field is recursive, in that we are thinking about the mechanisms of thinking or meta-cognition. The study of behavior is one of the most interesting of the sciences because it addresses issues related to the origin and mechanisms of human thought and cognition.

Cognitive processes of humans and other animals may be structured in a way that is conducive to a form of stereotyping. While such stereotyping allows us to remember and order objects in the world around us, it may limit our ability to remember the subtle differences among objects. By categorizing objects and other organisms into types and sub-types, we would require less information to remember salient features that define a group of things. Rather than remember each and every object, categorizing objects in this manner takes advantage of the relationship among objects. Data storage mechanisms in the field of computing which use this kind of hierarchical relational storage are referred to as relational databases. This contrasts with an encyclopedic knowledge in which lots of detail is stored, but the relationships among objects are not used during information retrieval.

Sub-typing and typing in a relational style database would allow for efficient information retrieval. If a "label" were used as a handle to pull information out of long-term memory, fewer labels would be needed in the first round of information retrieval in a relational database. This model of information retrieval in human cognition and artificial intelligence is now being applied to more efficient algorithms that allow computers to rapidly sort and sift through vast amounts of data. In contrast, sifting through the information in a non-relational database is very slow. Rapid access to memory should have adaptive value under most circumstances in which a reaction to a current environmental condition requires information from past events (e.g., foraging). Stereotyping may provide us with a way to rapidly access that information.

Do we have personal experience with stereotyping? Obviously, we all engage in stereotyping all the time. Moreover, stereotyping appears to have a strong downside in modern society. Many people apply stereotypes to racial and ethnic groups, which, in most cases have negative effects on the workings of society. The application of stereotypes to one group ignores the fact that within that group you can find entirely unique individuals. We should recognize these differences among individuals and their importance. Unfortunately, these differences are often ignored.

Are our brains "wired" in a way that makes it natural for us to stereotype? Some might argue that posing such questions of **biological determinism** might cause problems. For example, it has been argued that if we are predisposed to certain behaviors because of biological causes, then we are not necessarily responsible for our actions. Elucidating such societal interpretations of human "free will" is not the aim of behavioral research. Such research looks for the cause of behavior and seeks to explain the way the world works. These questions explore the biological basis of our own species and this example is meant to illustrate how such study might me be powerful in explaining behavior patterns in our own species. Nevertheless, because behavior forms the foundation of human society and culture, the study of animal behavior has been, and will always be controversial. It is a subject that explores many "loaded questions" of biology.

Studying animal behavior allows us to ask questions of ourselves. This is a mind-bending concept if there ever was one. Are we constrained in our thinking? Has this limited the way we have developed ideas concerning our own human origins? Was it because of our propensity to stereotype or form typologies? As we shall see, Darwin's idea is so simple, and has such intuitive appeal that it is a wonder that no one thought of the theory before his time. If we are prone to typological thinking, does this limit our ability to grasp other patterns and processes in the world around us? The study of behavior and indeed the study of the brain, the source of most interesting behavior, is a field that challenges our minds to the utmost, for we use our own minds to fathom the origins of our own minds. [Don't think too hard about this one or it might start to hurt].

In retrospect, it is not surprising that typological thinking dominated our concept of species over the ages. Today we still talk about **species-typical behaviors**. We tend to see these behaviors during mating, which is an event that is highly ritualized and stereotyped in all animals. Insuring that an animal mates with a member of its own species is critical for propagation. Hybridization between species often leads to sterility and finding a mate of the right species is a fundamental behavior that evolves when new species arise. Animals also display other species typical behaviors during the activities of daily life such as foraging, preening, and social interactions.

A lizard's push-up display (Hunsaker, 1962) is a classic example of species-typical behavior. Male lizards display a series of push-ups in rapid succession. The pattern of head movement up and down over time is specific to each species. Some components of the songs of a songbird species provide other examples of species-typical behavior.

While species typical displays are prevalent in nature, this does not necessarily give us a historical account of why it took so long for us to uncover the theory of natural selection? It is tempting to speculate that the millennial-long hold of typological thought on our views of animal origins might actually have a reason that is rooted in our own human behaviors. Typological thinking may be related to human cognitive processes. Side box 1.1 provides a bit of self-reflection on human cognition and evolutionary history that is important to our understanding of behavior.

Variation and Darwinian Ideas on Evolution

For over two millennia, until the time of Darwin, typological thinking and theological views strongly influenced the study of the origin of species. While typological thinking provides order and pattern in our cataloging of species, it ignores the small intra-specific variation among individuals within a species that forms the basis for the processes by which evolution takes place. Natural selection acts on variation among individuals. Large differences between species arise by the process of natural selection. Thus, the typological mode of thought acted as a major stumbling block in understanding the origin of species. Darwin's contribution to scientific thought revolutionized the study of Biology. His written works also launched the discipline of Animal Behavior.

Darwin's interest in intra-specific variation was the key shift in **paradigm** that revolutionized thoughts concerning evolution (Kuhn, 1962; Gruber, 1974). A paradigm is a worldview or a theoretical basis for explaining many seemingly unrelated observations. Prior to Darwin's theory, the paradigm under which academics operated held that species arose by special creation and were immutable.

Certainly other people considered the theoretical possibility of evolution before Darwin. The most famous of these evolutionists was Lamarck. Lamarckian theories of species change have been caricatured in early textbooks on evolution, but it is important to realize that Lamarck was the champion of evolutionary thought. Lamarck just happened to mistake the mechanisms underlying evolutionary change. In Lamarck's theory, organisms **adapt** to their environment by acquiring changes in their lifetime and passing on such changes to their offspring. If such a theory operated in practice, then Arnold Schwartzenegger would tend to produce offspring with phenomenal or at least above average muscle development, largely because of the characters Arnold acquired during his own youth. This is the theory of evolution by the process of the inheritance of **acquired characters.**

Darwin's Theory of Evolution by Natural Selection

Darwin came up with a theory that had a non-Lamarckian basis for the variation that leads to adaptation. Let us consider Darwin's idea in greater detail. The following is a synopsis of Darwin's formulation of the theory of evolution by the process of natural selection (Darwin, 1859):

1. Darwin assumed that organisms naturally vary in almost every attribute that they display.
2. Such **variation** might lead to differences in survival or reproduction.
3. All organisms produce an excess number of progeny and this generates a competition to produce successful progeny. Darwin called this competition a "struggle for existence."
4. If the variation that leads to differences in survival or reproduction is heritable, then those individuals that produce the most progeny will also tend to have offspring that resemble the parents. The species will thus evolve by a process that Darwin referred to as **natural selection.**

5. New species arise from old species by slowly inheriting successful traits from their ancestors. The blind force of natural selection drives these changes.

The key to Darwin's argument is his idea that variations among individuals are heritable, and that such differences lead to heritable changes from generation to generation. These changes ultimately lead to the origin of an entirely new species. This view is dramatically different from typological thinking in which attention focuses on similarity among species. By focusing on the minute differences among individuals of a species Darwin came up with the mechanism of natural selection -- the driving force behind evolutionary change. However, evolution by natural selection is **blind**. At its core, the process of natural selection is stochastic or governed by the laws of chance. Individuals survive, reproduce, and die as a function of their traits, but the outcome is probabilistic (Dawkins, 1986).

The process of mutation is the ultimate source of all genetic variation, and mutations provide the raw material for natural selection. Mutations arise in a probabilistic fashion. Sometimes mutations are beneficial to the individual, but more often than not mutations are detrimental. Natural selection eliminates detrimental mutations and preserves those beneficial mutations that tend to arise only rarely in a population. However, even when a beneficial mutation arises in a population it will not necessarily be passed on to subsequent generations, owing to the probabilistic nature of segregation during meiosis (see next chapter).

Darwin formulated his ideas concerning natural selection over the course of many years. A key event in the development of the theory of evolution by the process of natural selection was his world tour on the H.M.S. Beagle. As the ship's naturalist, Darwin was in charge of collecting and cataloging every species he encountered. The observations he made on that voyage generated raw natural history observations on many different species. When Darwin returned to England, he began to formulate his ideas in several sketchbooks. Looking at his sketchbooks it is clear that Darwin cemented his theory of natural selection by 1838. For nearly 20 years Darwin held onto those ideas, and only fear of being scooped moved him to publish them. Alfred Russell Wallace had sent Darwin a manuscript to read and he asked Darwin’s advice on the content of the manuscript before he presented the ideas on natural selection to the scientific community. These ideas were very similar to Darwin's own theory.

Alfred Russell Wallace was, like Darwin, as superb naturalist. Wallace also voyaged around the world visiting exotic locales like the Amazon and the islands of Indonesia. There he collected specimens, shipped them back to Victorian England and sold them to wealthy “collectors”. He was instrumental in filling the curio cabinets of many a Victorian mansion. Prior to sending the shipment he would arrange these collections by species, and it was as he categorized the species that he discovered the fundamental nature of all species. Unity of type could not characterize the burgeoning variation that Wallace saw. A dazzling array of variants was displayed before Wallace each time he sorted a species. This variation had a profound effect on Wallace’s theory and it formed the core of his ideas on natural selection.

In 1858, Darwin and Wallace communicated a joint paper to the Royal Society's meetings in which they described the role of natural selection in evolution. Darwin (1859) then published his famous book "On the Origin of the Species," setting off a firestorm of controversy in the Victorian world of England.

Philosophical and Theological Objections to Darwin's Theory

By placing the study of human origins on par with the study of biological processes that govern evolution, Darwin's controversial idea stirred up the lay public, theologians, and even some scientists. Another controversial aspect of Darwin's Theory was the notion that evolution has no direction or progress; that natural selection is a purely **blind** and mechanical process. The relentless elimination of less fit variants ran against theological notions of **design** in nature. John Dewey (1909), a contemporary philosopher (Gruber, 1974) provides a wonderful summary of these philosophical objections:

> "The Darwinian principle of natural selection cut straight under this philosophy [that of design]. If all organic adaptations are due simply to constant variation and the elimination of those variations which are harmful in the struggle for existence that is brought

> about by excessive reproduction, there is no call for a prior intelligent causal force to plan and preordain them. Hostile critics charged Darwin with materialism and with making chance the cause of the universe."

The impact of Darwin's Theory of Evolution by Natural Selection on Society was immediate, dramatic, and long-lasting -- a few examples (Gruber, 1974)

1. Social Darwinism (1890's) was formulated in an attempt to link social change via competition, (e.g., Adam Smith) with evolution (Hofstadter, 1955). Darwin described such comparisons as foolish.

2. Karl Marx used Darwin's theory of the law of development of organic nature for his ideas on the law of development of human history (technological evolution). Marx dedicated a copy of *Das Kapital* to Darwin.

3. The notion of genetic fitness in humans was used to rationalize the eugenics movement, a field focused on the improvement of the human gene pool. The Nazi party in Germany during the 1930's is the most notorious example of the eugenics movement, which resulted in the death of millions of humans. The term genocide, the slaughter of one group of people by another differentiated group, was coined by historians to classify these incomprehensible acts. However, the eugenics movement was worldwide in scope. The United States had "feeble-mindedness" sterilization laws on the books in some states until the late 1950's.

4. In a reaction to Eugenics, *Lysenkoism* arose to prominence in the Soviet Union. Lysenko was an agricultural advisor of Stalin who had neo-Larmarkian views on the role of environment and species change. These views dominated Soviet agriculture through the 1950's. Many geneticists were imprisoned during Stalin's tenure of power as the field of genetics was denounced by communism.

5. Modern ideas arose concerning the "selfish gene" in human evolution and society (Dawkins, 1986). More recently, we have seen the emergence of the discipline of evolutionary psychology, which applies the ideas of behavioral ecology of animals to humans.

6. Ideas concerning cultural evolution arose in part as a reaction to the notion that not all of our human behaviors are genetically based. For example, human culture can evolve by non-genetic transmission of ideas (see above). Because culture forms the basis for many aspects of behavior, it is argued that environment plays a major role in shaping our (collective) psyches.

Darwin even placed the evolution of human mental powers, emotions, and ethics within the context of animal evolution. This application of evolutionary theory to human behavior still elicits controversy in the present day. T. H. Huxley, Darwin's close friend and champion of evolutionary theory, wrote an essay on "Evolution and Ethics" in 1893 that still has great relevance in present day debates.

> "There is another fallacy which appears to me to pervade the so-called 'ethics of evolution'. It is the notion that because, on the whole, animals and plants have advanced in perfection of organization by means of the struggle for existence and the consequent 'survival of the fittest'; therefore men in society, men as ethical beings, must look to the same process to help them towards perfection. I suspect this fallacy has arisen out of the unfortunate ambiguity of the phrase 'survival of the fittest'. 'Fittest' has a connotation of 'best'; and about 'best' there hangs a moral flavour. In cosmic nature, however, what is 'fittest' depends on conditions."

As we will find out in subsequent readings, natural selection could operate on aspects related to human morality, but the defining process underlying much of human behavioral evolution is that selection leads to patterns of behavior that benefit the individual or the "inclusive fitness of the individual", which includes the individual's closely related kin. The study of animal behavior has no room for value judgments regarding a particular behavior. We do not need to apply a moralistic thinking to behaviors exhibited by animals, humans included, even though the evolution of human morals is likely to have come about by the biological process of evolution. The scientific study of behavior delves into the roots of all kinds of topics that humans make moral decisions about on a daily basis including racism, sexism, altruism, etc. Any *ism* likely has a biological basis and this observation makes it useful to take a behavioral perspective to the study of humans.

Darwin Formulates a Theory of Sexual Selection

Darwin did not let the uproar die down for too long before he published yet another controversial book entitled "The Descent of Man and Selection in Relation to Sex" (Darwin, 1971). If Darwin's theory of evolution forms the core of evolutionary theory, we could consider Darwin's book on sexual selection to form the core of animal behavior because it is was the first scientific (i.e. hypothetico-deductive) attempt to explain sexual behaviors (aside from Sigmund Freud's views on the origin of human sexuality in psychology). This was the first book to treat animal behaviors within his evolutionary (Darwinian) framework. Darwin attempted to explain many curious puzzles regarding animal behavior and morphology in animals, in addition to the origin of emotions and thought in humans. Darwin realized that traits related directly to mate acquisition and mate choice, were distinctly different from other traits under natural selection (e.g., foraging ability). He coined the term sexual selection to emphasize the distinction between the two processes.

Figure 2. A bowerbird male displaying in front of the entrance to his bower or decorative nest.

The theory of sexual selection explained why certain traits that appeared to have little survival value, or that might even be **maladaptive**, could evolve. Why does a male peacock drag around an elaborate, energetically costly, expensive-to-produce tail, which might even lead to a higher risk of predation? Males of many other species carry costly structures or even engage in perplexing behavior. The bowerbird constructs an elaborate structure out of twigs called a bower and he decorates his bower with many flashy items. The sole function of this colorful, ornamented nest is to entice females into copulation. The bower is not used as a place to incubate eggs, although it superficially has qualities that are reminiscent of a nest. If such traits increase the number of mates that a male gets, then such **sexual selection** could overwhelm the force of natural selection and spread traits, which appear to be maladaptive throughout the population. We will consider Darwin's theory of sexual selection in greater detail in subsequent chapters. For the moment, we will consider sexual selection as variation in mating success among individuals in a population that arises from either the choices that females make regarding showy ornaments that males display, or male-male competition for females.

Darwin's theories of natural and sexual selection have stood the test of time. We use most of his ideas unaltered from the original text. We can credit Darwin for a starting a revolution, a shift in our paradigm of biology. Scientists fully accepted the occurrence of evolution. However, scientists did not accept the premise that evolution took place through the process of natural and sexual selection. This issue was not resolved during Darwin's lifetime. Resolution came with the Neo-Darwinian synthesis, which began in the early 1900's -- long after Darwin's death in 1893. In some areas, such as the Soviet Union, Lysenko's ideas persisted until the 1960's.

A historical footnote is necessary to understand the reasons that all biologists did not immediately accept Darwin's theory (Provine 1971). Darwin did not properly understand the mechanisms of inheritance. Darwin did not know that differences in the alleles at a genetic locus formed the basis for variation, a fact contemporaneously discovered by Gregor Mendel. Second, Darwin did not understand how new genetic variation arose. We now know that the ultimate source of all variation is mutation. A mutation at one copy of a gene (i.e., an *allele*) yields new genetic variation. Hugo de Vries is credited with formulating a theory of mutation, or "*mutationstheorie*." De Vries' theory along with theories based on a re-discovery of Mendel's Laws in the early 1900's began to compete with Darwin's theory of evolution by natural selection. In the *mutationstheorie*, evolution occurred by the force of mutants and large evolutionary jumps, which produced new variants or species. Because Darwin missed these key points, his theory of natural selection did not gain the widespread acceptance in the scientific community, which it now garners today.

The Neo-Darwinian Synthesis, which occurred after 1910, brought all the opposing views together into a single unified theory of evolution. Evolution occurs by natural selection. However, natural selection depletes genetic variation. New heritable variation, upon which natural selection can act, arises by the process of mutation. Major players in the neo-Darwinian synthesis include the theoreticians Sir Ronald Fisher, Sewall Wright and J. B. S. Haldane who developed a mathematical formulations for evolution that added much needed rigor to the arguments (Provine, 1971). Ronald Fisher also elaborated on Darwin's theory of sexual selection and illustrated the fundamental reason why natural selection should be thought of as distinct from sexual selection. We will consider the details of this theory later, but a synopsis of Fisher's ideas is that sexual selection can lead to a runaway process in which females choose ever more showy males, even if such choices have maladaptive consequences for the survival of their male progeny.

The Traditions of Animal Behavior: Nature versus Nurture

Ethology

Although Darwin shifted the way we view animal behavior, the discipline also has a tradition that stretches before the time of Darwin (Drickamer and Vessey, 1986). The field of ethology, which is the study of the evolution and functional significance of behavior, originated with C. O. Whitman in the 1800's. Whitman coined the term **instinct** to describe the display patterns of pigeons. The **ethogram,** a graph of the time course or switch points in a sequence of behaviors, became a way of categorizing species-typical behaviors. Many of these instincts are triggered by various environmental stimuli and von Uexkull termed such triggers of instinctive stereotyped behaviors **sign stimuli**. A classic sign stimulus triggers the courtship display of male three-spined sticklebacks fish. The enlarged belly of a female triggers the zigzag dance in male stickleback fish. The males use the dance to entice the female stickleback to enter the nest that the male has built.

Two Nobel Laureates, Niko Tinbergen and Konrad Lorenz synthesized much of the work of early ethologists. Lorenz is noted for his work on genetically programmed behaviors in young animals and for studies on **imprinting**, a critical developmental period in neonates during which maternal bonds are established. A classic example of imprinting occurs in young geese when they form an image of their mother just after hatching. If hatchlings first encounter a human such as Lorenz, they will imprint on him and follow him around as if he were their mother. A third Nobel Laureate, Karl von Frisch, pioneered studies in bee communication and he decoded the language of bees called the waggle dance.

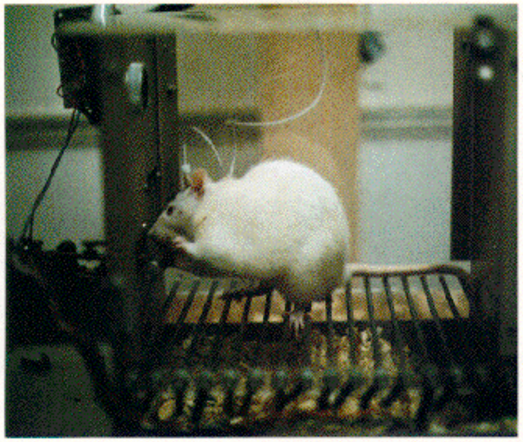


Figure 3. A rat learns to press a bar in a Skinner box. With each bar press the rat is rewarded with food.

One of Tinbergen's seminal contributions was the formulation of a method to study animal behavior (Tinbergen, 1963). This method forms the basis for how I have structured material in this text. These issues are central to developing a philosophical approach to animal behavior. The ethological approach had a strong Darwinian tradition underlying its development. Much of the work in ethology was aimed at understanding the ultimate evolutionary reasons for behavior. Tinbergen listed four areas of inquiry that could be used to understand issues of animal behavior. The following mnemonic can be used to remember these four areas ABCDEF [Lehrman, 1966]:

A -- Animal refers to the organisms.

B -- Behavior refers to the observable actions and reactions of the organism.

C -- Causation refers to the proximate causes of behavior such as genes, hormones, and nerve impulses that control, regulate, or generate the expression of behaviors.

D -- Development refers to the ontogeny of behaviors such as imprinting, or in the case of cognition, learning.

E -- Evolution refers to the phylogenetic context in which behaviors arise. For example, the prevalence of parental care in birds, but not reptiles (with some exceptions) is an example of the taxonomic affiliations of some behaviors.

F -- Function refers to the adaptive value or contribution that the behavior makes to fitness.

Psychology and Behaviorism

The ethological approach, typified by the research of Lorenz, Tinbergen, and von Frisch, was largely concerned with the behavior of organisms as it is expressed in their natural environment. Another large group of scientists focused on the mechanistic underpinnings of behavior. This research was on model organisms (e.g., Norway rat) in a controlled laboratory setting. Classic work by B. F. Skinner led to the development and use of learning paradigms. The **Skinner box** remains an important tool in the field of animal psychology.

Learning theorists sought to uncover similarities of learning mechanisms among all animals that allow them to respond to their environment. The field of comparative psychology included developments in the psychological sciences and spanned the following topical areas:

1. **Perceptual psychology** -- reception of environmental stimuli through the senses, and subjective perceptual interpretation of these sensory stimuli,
2. **Physiological psychology** -- an attempt to relate physiological properties within an organism to external behaviors (e.g., measuring nerve impulse transmission in sensory and motor nerves),
3. **Functionalism** -- the study of the mind (e.g., John Dewey 1909) and how the mind operates.
4. **Behaviorism** -- the study of how accumulated experiences shape the behavior of the organism. The idea that an organism is born a *tabula rasa* or (blank slate) upon which experiences accumulate and thereby shape subsequent behavior is central to behaviorism.
5. **Animal psychology** -- while initially related to the study of learning in model systems, the field of animal psychology in the present day encompasses a large body of work related to cognition in a diverse group of animals in semi-natural contexts.

The Debate on Nature versus Nurture

The field of Ethology typified by the work of Tinbergen, Lorenz, and von Frisch, and the broadly defined field of comparative psychology formed two drastically different schools of thought on the causes of behavior. We can compare and contrast their views to develop a deeper understanding behavioral analysis. The field of ethology, which originated in Europe, looked for the genetic underpinnings of behavior. In contrast the field of comparative psychology, which originated in America, viewed behaviors as largely the product of the environment. Differences between ethology and animal psychology led to a debate on the causes of behavior that has been captured in the often quoted question, "Is it nature or nurture"? What influences behavior -- genes or environment? The answer to this contentious debate cannot be put in terms of either genes or the environment, but must instead be looked at in terms of a more complex interaction between genes and the environment. This interaction forms a dominant them in my book.

Behavioral Ecology and Sociobiology

Students of **Behavioral Ecology** have attempted to synthesize both the evolutionary traditions of Ethology, and the mechanistic studies of Comparative Psychology. This is a relatively new movement compared to the traditions of ethology and psychology and has developed over the last five decades. The study of behavioral ecology looks at how organisms interact in their natural environments (Krebs and Davies, 1987). Researchers are interested in both the mechanistic underpinnings of behavior, as well as the fitness consequences of behavioral traits. This tradition can be traced back to Tinbergen and the four study areas (Causation, Development, Evolution and Function). Behavioral ecology is broader than just a study of behavior, but also draws in issues of energetics and physiology (e.g., Calow, 1987). Rather than measure differences in survival and reproduction of behavioral traits, behavioral ecologists estimate energy maximization or foraging success of behavioral traits, and use these as proxies for fitness. The development of optimal foraging during the 70's and 80's has added a distinct theoretical perspective to the field of Behavioral Ecology.

The newest approach to studying behavior involves a consideration of social systems in diverse groups of organisms. This field has taken off since the publication of **Sociobiology** by E. O. Wilson (1980). Because some of these ideas have been applied to humans, the theory has been the target of much controversy. Sociobiology has a strong Darwinian tradition because it attempts to develop rules that explain the evolution of social systems. Sociobiology has however, strong antecedents in the mathematical formulations of general theories of social selection by W. D. Hamilton. Hamilton came up with the key concept of **kin selection**. Hamilton generalized the ideas of genes helping genes that are present in another individual, even if these genes cause the death of helper. Our modern biological ideas of the evolution of altruism come from the idea of such genes, which Dawkin’s (1976) coined **greenbeards** in his influential book “*The selfish gene”*. We will find that greenbeards are everywhere in the animal kingdom. The idea of genes helping genes forms the core concept that underlies the evolution of cooperation.

More recently, the field of **Evolutionary Psychology** has co-opted the approaches of behavioral ecology and sociobiology in order to explain a diversity of human behaviors such as foraging, **siblicide**, and female choice. Humans are subject to the same "organic rules" that shape other organisms. Needless to say, this area is ripe for debate as researchers attempt to derive explanations for behaviors displayed by humans in modern society.

Ultimate versus Proximate Causes

The dichotomy between Ethology and Comparative Psychology with their focus on adaptation and mechanism respectively, can be succinctly described as a concern for **ultimate** versus **proximate causes**. Ernst Mayr (1961) described the pursuit of those ultimate causes as a concern for the "Why Questions." Why does a bird give parental care? Why is a bee brightly colored? In contrast, the pursuit of proximate causes is concerned with the way the world works or the "How Questions." How does a bat transmit echoes? How do nerves carry impulses? Where are memories stored?

Tinbergen's four study areas also block out into ultimate versus proximate causation. For example, Tinbergen's view of causation is concerned with Proximate Causation, or mechanism. Development is also considered to be in the category of proximate cause. However, *evolution* or phylogenetic context is squarely in the field of ultimate cause. Likewise the issue of *function*, which treats the adaptive value or fitness effects of a behavior, is directly related to evolutionary change (Curio 1994). Our study of animal behavior begins with a consideration of the ultimate causes of evolutionary change -- adaptation and natural selection.

Cause, Development, Evolution, and Function

Tinbergen's breakdown can be used as a summary of the material covered thus far. I prefer to make the breakdown a little more detailed to include other approaches that have been added more recently by Behavioral Ecologists and Sociobiologists**: Genes, Ecology, Physiology, Development and Learning, Evolution, and Sociality**. This categorization is slightly finer than Tinbergen's but it provides the structure for this text and a schema for understanding the process of adaptation in behaviors at a variety of temporal scales. Paul Sherman (1988) would add yet another category to the list -- **Cognition**. However, cognitive theories are an outgrowth of the fields that study development and learning, and cognition will be included in those categories. Behavioral Ecology is undergoing a large-scale renaissance as researchers attempt to generalize the classically developed ideas of Psychology and Cognitive Processes into wild populations (Real, 1994).

The first two subjects, **Genes** and **Ecology**, will cover the basics of Darwinian natural and sexual selection as they apply to animal behavior. To cope with environmental variation, the organism evolves adaptations of **physiology** that promote successful survival or reproduction. Such physiological change could act at the level of endocrinology, neurophysiology, metabolism, or any of the myriad proximate mechanisms that operate in an organism. These proximate mechanisms are used to help the organism cope with both **abiotic** (e.g., the extremes of weather, navigation, etc.) and **biotic** environmental factors (e.g., the social environment, predation, etc.). Additional components to an organism's life history are the **developmental** changes and **learning** that are adaptations to changing environments. Whereas physiology operates in the very short term, development unfolds during the lifespan of an organism. With an understanding of these genetic, ecological, physiological, developmental and cognitive processes in our intellectual arsenal, we will be ready to tackle the concepts of behavioral evolution.

Phylogeny and Constraints on the Evolution of Behavior

Up to this point, I have operated under the premise that adaptation is the sole process that governs the evolution of behavior. However, in recent years, students of animal behavior have become more sensitive to the limitations of organic systems to change in response to selection. Organisms may be well adapted, but limitations in organismal design **constrain** adaptation. In addition, organisms are also constrained by the effects of history or their own **phylogeny**. During the evolution of a lineage, adaptations pile on top of one another. The net result is that closely related organisms share similar features, which further constrain the acquisition of new adaptations. Functional and structural constraints arise from the material properties of organisms and additional developmental constraints arise from how structures are built during embryogenesis. The constraints on organisms reside at the level of proximate causation, yet we resolve often constraints at the level of phylogenetic patterns.

Consider a simple phylogenetic example taken from two lineages of vertebrates -- birds and mammals. All birds lay eggs, undoubtedly because the common ancestor of birds, some reptile-like dinosaur, also laid eggs. However, most mammals bear live young because in the remote past a new kind of mammal-like reptile evolved a different mode of reproduction and passed this novel trait on to all subsequent species in the **lineage** or **phylogeny.** A famous exception to this mammalian generalization includes the monotreme mammals of Australia, the platypus and echidna. It is thought that the monotremes branched off from the main evolutionary branch of mammals so early that they retain the more ancestral mode of egg-laying reproduction.

Such differences in reproductive mode (egg-laying versus live-bearing) constrain both birds and mammals in terms of parental care behaviors that might evolve in each group. Additional adaptations in mammals may similarly constrain the evolution of parental care. Evolution of the mammary gland as the primary source of nutrition tends to lead to species of mammals that display a preponderance of maternal care. There are in fact few examples of male care in mammals compared to birds. In contrast, many bird species have evolved male and female parental care, which is termed **biparental care**, so that the costs of rearing the young can be distributed across two parents. Some species of birds provide a milky substance, which is secreted by part of their digestive system called the crop. Because both male and female birds have the crop, in theory both parents can evolve to produce a milky substance as a form of parental investment. The phylogenetic difference in the amount of male versus female care between mammals and birds leads to additional differences in how mating systems evolve in these two groups. To understand phylogenetic constraints that limit the design of other traits, we need a working knowledge of the proximate mechanisms, as well as the process of natural selection. Accordingly, I leave the discussion of such higher-level macroevolutionary process for later chapters, but I distribute the discussion of selection and behavioral mechanisms throughout all the chapters.

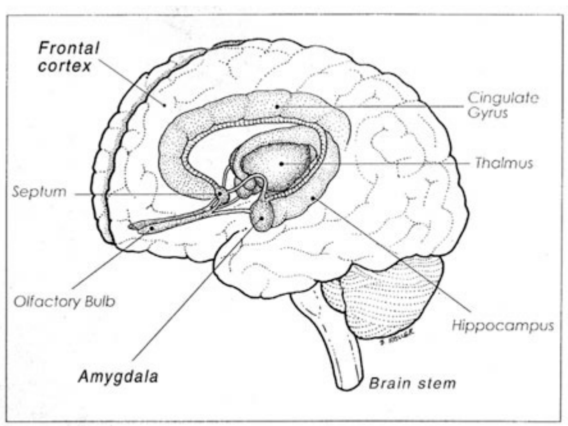
Societal and Cultural Evolution

Finally, I leave the discussion of sociality until the very end, because it includes even more complex interactions that occur between organisms such as learning and communication. The added complexity of sociality makes the study of behavior very rich indeed. A simple example will suffice. In developing our paradigm for animal behavior, I have thus far assumed that all changes, which are passed on between generations are largely genetic and that populations evolve and genes change by the process of natural and sexual selection.

Social evolution and the advent of **culture** introduce another mode of transmission of behavioral traits between generations. One need only walk into the nearest library to realize the impact of mass storage of human culture. Libraries serve as a vehicle for passing information from one generation to the next. There is no genetic basis to the information in libraries. The theory of cultural evolution holds that many behavioral changes in humans might have a largely non-genetic component arising from such **cultural transmission** of information. Your reading of this book forms a kind of cultural inheritance. Cultures are likewise important in many other animals besides humans.

An example using the amygdala

Where do stereotypes come from? We can ask this at a proximate level by studying the brain regions responsible for the formation of fear responses. Deep in the recesses of our brains lies the amygdala, a walnut sized organ responsible for codifying fear. In primates, there are genetically programmed responses for fear. Macaque monkeys will instinctively show a fear response to a snake-like object and brain scans show that this response arises in the amygdala (Amaral 2002). Snake toys presented to monkey subjects with an intact amygdala is strong compared to one with an ablated amygdala (lesioned by surgery).



How do humans respond to ingroup racial versus outgroup racial images? Amygdalae have been intensively researched for the past 10 years. A functional Magnetic Resonance Imaging (fMRI) scan shows that the amygdalae light up strongly (indicative of the influx and oxygen metabolism of sugar, which the fMRI is picking up).

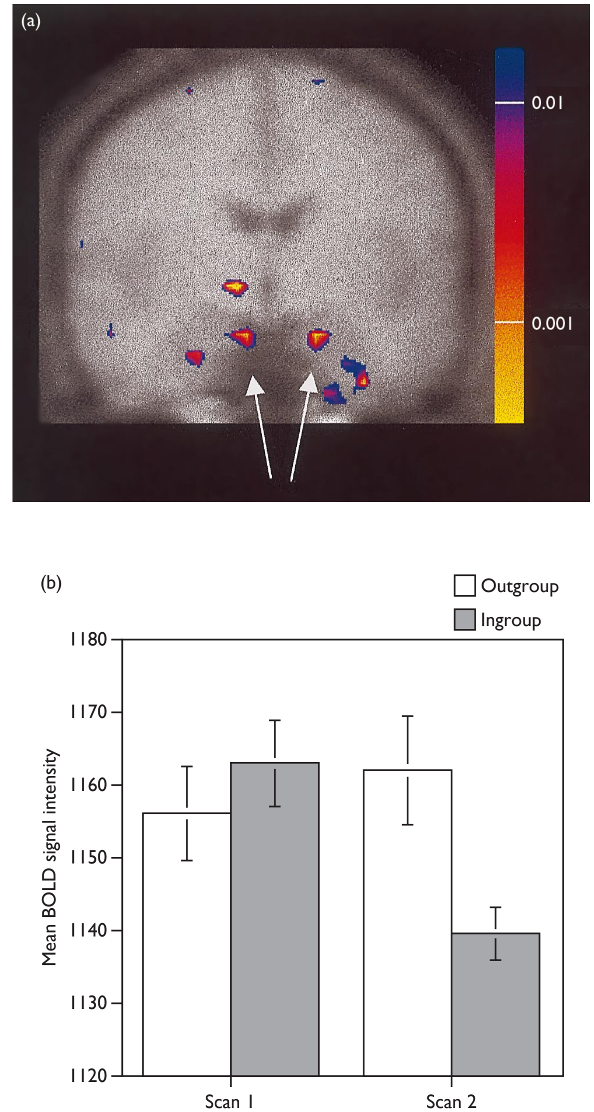


Fig.4. Differntial response of a humans, shown an outgroup racial image versus ingroup image. However, this response is only apparent on Scan 2. Subjects habituate to ingroup faces more rapidly while outgroup response remains high.

The twin amygdalae are the pair of structures to either side of the brain (with a bright influx of sugar metabolism) (Fig. 4). The differential and heightened amygdala response to outgroup facial images remains high over time, in contrast to the response to ingroup faces, which decays rapidly. This is indicative of habituation. This result implies biological (neuronal) bases to racial responses but does not reveal whether it is culturally or genetically programmed. Returning to the Macaque example, Amaral (2002) suggests that the development of fear in social context might arise from different regions of the brain than the response to an inanimate object like the rubber snake. This suggests an important role of non-genetic cultural or ontogenetic forces in shaping the development of fear.

Moreover, the response does not get at the potential adaptive or evolutionary history of the racial response. We evolved pigment differences among the races only recently (Chapter 20). However, all of these subjects will be addressed in subsequent lectures, including the most interesting subject of group selection (Chapter 4) and strategic interaction (Chapters 7 and 8). I welcome you on this journey of you inner self and hope that you come away from the course understanding yourselves, others, as well as the behavior of animals.

Study Questions for Chapter 1

1. Why did typological thinking act as a stumbling block for the understanding and acceptance of evolution by natural selection?

2. Explain the process of natural selection and why it is considered a "blind" process.

3. How might an organism be evolutionarily constrained? Can natural selection evolve any behavior imaginable?

4. What are the four questions that Tinbergen asked about Animal Behavior, and explain the gist of each question?

5. What is a species typical behavior? What is the utility of a species typical behavior?

6. What are proximate questions? What are ultimate questions? Ask a proximate and an ultimate question regarding an animal that you observed today.

7. What are the fields of Behavioral Ecology, Ethology, and Animal Psychology? How would you differentiate these fields?

7. How would you resolve the old question of is it nurture or nature?

8. A useful and lively discussion topic would be to discuss *isms* in humans and potential biological bases for the evolution of *isms*. Why should we keep moral judgment out of a study of behavior?

9. Describe a potential biological basis to racial profiling.

10. How might you control your own “ism” responses? Biologically speaking that is, how can you attenuate your own proclivity to react differentially to others of a different “type”.