Integration of Proximate and Ultimate Causes

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Introduction

A discussion of proximate and ultimate causation in relation to animal behavior must begin with some definitions. Proximate causation refers to the underlying endocrine system, nervous system, immune system, and developmental processes that result in observed behavior patterns. Ultimate causation refers to the effects of behavior on fitness, through an understanding of the ecology of the organism and its evolution. Consequently, the integration of these two concepts would involve an examination of the ways in which evolutionary selection pressures shape the various internal mechanisms that regulate behavior.

These terms, and their definitions, should not be confused with the nature–nurture debates. The observed behavior, part of the organism's phenotype, is a product of its genetic blueprint unfolding under the influence of all the experiences and environmental effects beginning from fertilization. In this way, we perceive genetics as setting up limits for potential phenotypic traits and the experiences as shaping the actual phenotype. For example, feeding behavior is constrained genetically by several traits, including the ability to forage for and ingest certain foods, the digestion of those foods in terms of enzymes and other features of the digestive tract, and the capacity of the animal to shift its diet seasonally whenever that is necessary. The actual, phenotypic, food preferences are shaped by where the animal lives, the foods that are available, and the experiences that it has had with different foods.

Our purpose in this article is to provide a historical perspective on the ideas behind proximate and ultimate causation to give the reader some context for where we are today. As discussed in another article on the future of animal behavior, scientists are moving forward with studies that integrate the proximate and ultimate causation concepts. The link between these two major ideas is, of course, genetics. For evolution to occur, via differential reproductive success, there must be changes in the genetics of the organism. Each organism 'faces' the world with its phenotype as its set of tools. The success of the organism depends on how its internal mechanisms meet the ecological challenges it faces on a daily basis; that is, how well the animal functions can be measured in terms of the number of progeny, which is a dual product of genetics and environmental influences. Studies of both proximate and ultimate causation occur in the context of the interaction of the genetics and environment of the organism. The article concludes with an up-to-date coverage of the ongoing integration of proximate and ultimate causation.

One term in particular, mechanism, is typically defined in one way by those who study primarily proximate mechanisms, and in another way by those who study ultimate mechanisms. For those who explore proximate causation, the meaning of mechanism incorporates the animal's physiology, immunology, endocrinology, nervous system, and development. These are basically internal processes. To an individual examining ultimate causation of behavior, mechanism generally refers to the ways in which an animal's phenotype functions in its ecological context. These are usually considered as traits best studied in a natural or wild setting. We attempt to be explicit when we use the term 'mechanism' in this essay.

Ultimate Causation: Historical Perspective

The easiest way to distinguish between proximate and ultimate causation is to consider the answers one might get when asking *why* a particular behavior pattern occurs. For instance, when asked why dogs wag their tails, we might give an answer based on proximate causation, in terms of the nerves and muscles involved, the role of the central nervous system, and so on. Alternatively, we might answer that it is based on ultimate causation, in terms of the function of the pattern (communicating aggression perhaps) and the evolutionary history of the pattern.

A second example is to ask why male rhesus monkeys invariably leave their natal social group around the time of puberty (4 years) and join a new social group. The transition process can be difficult, as they are likely to be rejected by members of any different group. While in their natal group, they share their mother's social rank, but in the new group they assume the lowest dominance rank, where rank is based on group tenure. Why would an adolescent male give up the security and status of his mother's group and risk rejection and possible injury by joining a new group? The proximate causes of this behavior are not clearly understood, but are manifested as an incest taboo, as is seen in human cultures. Either the males are somehow repulsed by the proximity of their mothers and other female relatives, or they are rejected by them as possible mates. The male sex hormone testosterone is likely involved because the departure occurs during the mating season and castrated males do not emigrate. The ultimate causes are likely the avoidance of inbreeding and its resulting accumulation of deleterious recessive genes. A male that fails to emigrate potentially could mate with the large number female relatives of his mother and thus could have inbred offspring of lower fitness.

In this section, we focus on the study of ultimate causation, that is, the evolutionary forces responsible for behavior patterns. Ultimate causation of behavior is mediated by the environment, through such negative pressures as climate, predators, and competitors, as well as through positive opportunities such as new food sources or new habitats. These environmental variables create pressures for genetic evolution by means of natural selection. In responding to these pressures, the species is constrained by the amount of genetic variability present in a population and the existence of mutations that might increase fitness. This process of adaptation takes many generations.

One of the earliest experimental studies exploring ultimate causation of behavior was Tinbergen's observations of black-headed gulls removing the eggshells from around the nest after their young hatched. Tinbergen wondered what the function of such behavior was, given the apparent cost of such a behavior pattern. Although the eggs are mottled-brown colored on the outside, inside they are bright white and highly visible, suggesting that egg predators might cue in on broken egg shells. Tinbergen tested this notion by placing broken eggs at varying distance from intact eggs. As predicted, the closer the intact eggs were to the shells, the more likely they were to be taken by predators. From this manipulation, Tinbergen inferred that the tendency to remove egg shells was a heritable trait that had become typical of this and other gull species through natural selection.

Tinbergen's approach to questions of ultimate causation derives directly from Darwin's theory of evolution by means of natural selection, whereby members of a species differ in characteristics, some of which increase survival and reproduction. Although Darwin did not understand the mechanism of inheritance, he realized that these traits tended to be passed on to offspring, so individuals with such traits tended to increase in the population from one generation to the next. In the gull example, if an individual happened to remove eggs shells from the vicinity of the nest, its chicks would be more likely to survive. If the tendency were heritable, their chicks in turn would be more likely to show that behavior pattern, and egg shell removal would spread throughout the population.

Study of the evolution of behavior patterns by means of natural selection had received relatively little attention up to this point, in spite of much progress being made on the role of genetics in animal behavior. A series of publications in the 1960s and 1970s focused attention on the level, individual versus group, that natural selection acts on. Darwin had argued that selection acts at the level of the individual, since the individual is what natural selection 'sees' in terms of survival and offspring production. He was troubled by instances of seemingly altruistic behavior in social insects, where workers sacrifice their reproductive interests to help the queen raise more offspring. His way around this problem was to consider the colony or hive a 'superorganism,' such that selection would act on the colony as a whole.

In the early twentieth century, many, if not most, biologists accepted the notion that traits could evolve for the good of the group or species and paid little attention to the level upon which selection was supposed to act. Survival of individuals and groups was thought to increase as a function of the degree to which they harmoniously adjusted themselves to their physical and social environment. This line of thinking was especially prevalent among many plant ecologists, who spoke of plant 'sociology.' Studies of overcrowding and stress in animal populations revealed that hormonal changes can lead to reduced reproductive activity and increased morbidity. It was argued that this behavioral-endocrine feedback loop serves as a group-level adaptation for regulating population density; as populations reach the carrying capacity of the environment, aggression increases, followed by increases in stress hormones and the associated loss of fitness. Once the population declines, aggression declines and individual fitness increases.

The idea that individuals sacrifice reproduction for the good of the group was expounded in two books by Wynne-Edwards. He argued that many species have evolved behavior patterns he called epideictic displays that function to tune the birth rate to the available resources. Groups or populations that lack such patterns are more likely to exceed the carrying capacity of the habitat and potentially go extinct. If the unit of selection were the population, then selection might occur for individuals that sacrifice their own reproductive interests for the good of the group. In other words, groups that avoid overexploiting the environment are more likely to survive and may later colonize habitats left vacant by imprudent groups that have become extinct.

This train of thought was vigorously challenged by George C. Williams, who argued (as had Darwin) that group selection, as proposed by Wynne-Edwards and others, was much less likely than individual selection to be a potent force for evolutionary change. He pointed out that the conditions necessary for group selection to override selection at the individual level were stringent, given that groups must maintain their integrity for relatively long periods, that groups must differ genetically for traits that affect the groups' survival, and that group extinction rates must be relatively high. In most cases, traits that lower fitness of individuals will be selected against, even if they favor group survival. Williams argued that selection at higher levels should be invoked only if lower-level selection, that is, the individual and its offspring, cannot explain the evolution of the observed traits. This view has dominated the thinking of most behavioral ecologists as they explore the ultimate causes of behavior, and group selection, although considered theoretically possible, is generally discounted or ignored altogether.

In the meantime, several other ideas of how altruistic behavior could evolve were put forth that were argued not to involve group selection. One is the concept of inclusive fitness, that is, the sum of an individual's direct fitness, as measured by the reproductive success of one's own offspring, and indirect fitness, as measured by the reproductive success of one's nondescendent relatives, for example, siblings or cousins. For instance, in the classic study of prairie dogs by Sherman, he argued that although individuals risked their own lives by giving alarm calls, thus revealing their whereabouts to predators, they increased their inclusive fitness by warning close relatives, a process referred to as kin selection. Other models based on games theory were developed, such as reciprocal altruism, where one individual performs an altruistic act with the expectation of being repaid, with interest, at a later time.

In 1975, E. O. Wilson published his compendium entitled *Sociobiology, The New Synthesis*. Wilson drew heavily on population biology in shaping the emerging fields of sociobiology and behavioral ecology. Evolutionary history and environmental factors that determine the ecological niche affect population growth and dispersal rates, the focus of evolutionary ecology. Behavioral and population parameters, such as birth and death schedules and gene flow between populations feed into the theory of sociobiology. This theory's goal is to enable predictions of behavior from knowledge of population parameters and the behavioral constraints imposed by the gene pool. Although several models of group selection were presented in the book, it was generally assumed by Wilson that individual selection is main force for behavioral evolution.

The year after the publication of Wilson's tome, Richard Dawkins published *The Selfish Gene*. The basic argument was that the unit of selection is the gene, rather than the individual organism or group. Genes are referred to as replicators that typically help their temporary host, the organism, survive, and reproduce, thus improving the gene's own chances of being passed on. In some instances, however, the gene's interests may not coincide with the host's, and hence the term selfish gene.

Most biologists still think of the organism, or phenotype, as the main unit of selection because that is what natural selection 'sees.' Genes can perhaps be better thought of as the unit of evolution, since evolution results from changes in gene frequency. Thinking of genes as replicators makes it somewhat easier to understand how altruistic traits might be maintained in a population via kin selection: Organisms might act against their individual interests to help related organisms reproduce because genes set 'helping' copies of themselves in other bodies to replicate. Thus, the 'selfish' actions of genes might lead to unselfish actions by organisms.

The study of ultimate causation in behavioral ecology and sociobiology mushroomed in the 1970s and continues to this day, testing the fitness consequences of behavior patterns and social groupings. The vast majority of these studies follows Williams's law of parsimony and assumes that selection occurs at the level of the individual and no higher. Most instances of helping behavior or other potentially altruistic acts not explained by classic Darwinian selection are explained by kin selection, reciprocal altruism, or some other model not involving selection above the level of the individual.

Although group selection was dismissed by most behavioral ecologists, as noted earlier, new modeling techniques and empirical data suggest that it may play a more important role than previously thought. D. S. Wilson has argued that adaptations can potentially evolve at any level, from genes to ecosystems. In a joint paper with E. O. Wilson, they dismiss what they call the naïve group selection arguments of early workers, including Wynne-Edwards, who assumed that group selection would easily prevail over selection at the individual level. But Wilson and Wilson go on to argue that the theoretical foundation of sociobiology needs to be reformulated to include multilevel selection, including selection at the level of the group. Whether theoretical and empirical evidence will continue to build in support of higher-level selection remains to be seen.

Proximate Causation: Historical Perspective

The study of proximate mechanisms dates back to antiquity, in a general sense, with initial interest in the 'how' questions of animal behavior with regard to potential food sources and predators. In the first millennium, anatomists learned a great deal about animal structure through their extensive dissections. When, after stagnation during the Middle Ages, scientific inquiry resumed in the sixteenth and seventeenth centuries, new discoveries were made. These included Harvey's findings on circulation and Borelli's contributions on form, function, and muscular physiology. These works and others provided the basis for the emergence of studies of how internal and developmental processes influence behavior.

One important distinction between studies of ultimate and proximate causation of behavior involves the ability to 'see' the subject matter. Generally, as covered in the previous section, behavior in the functional and evolutionary sense can be observed directly, whether in a field or laboratory environment. On the other hand, mechanisms that involve the nervous system, endocrine system, and underlying genetics and development, all take place away from our normal visual world. To be sure, these events can be observed with a variety of techniques, but most people do not see behavior in this way. This distinction could be a partial reason for the divergence between those who study proximate mechanisms and those who explore ultimate causation.

In a modern sense, the investigation of proximate causes of behavior begins with three threads, all of which emerged in the latter half of the nineteenth century and continued into the first half of the twentieth century. First, psychologists, primarily in North America, explored the possible relationships between human and non-humans in terms of their mental processes. This progressively led to interest in species-specific behavior and the functional aspects of observed phenomena. Second, American zoologists began formulating explanations about behavior mechanisms on the basis of both natural history and physiology. Early writings in natural history by colonists and later explorations westward provided information that led to questions about how the behavior patterns were controlled and concerning their functions. During the first half of the twentieth century, this blossomed into studies relating physiological mechanisms to observed behavior. Last, the ethology tradition in Europe was initiated with studies of natural history and attempts to explain, via models, the internal processes underlying behavior. So, for example, Lorenz and others developed terminology including 'innate releasing mechanism' and 'sign stimulus' to explain behavior that was under significant genetic control. European work also included aspects of physiology, such as the studies by von Holst, bridging ethology and emerging neurobiology.

During the last half of the twentieth century, several individuals provided overall schemes for categorizing the way scientists posed questions about animal behavior. Niko Tinbergen's 1963 paper 'On the Aims and Methods of Ethology,' provided such a scheme, one that is used even today. He proposed four types of questions: two concerning proximate mechanisms and two about ultimate mechanisms. His scheme involved causation (control), ontogeny (development), survival value (function), and evolution. Frank Beach provided a similar scheme, which included historical determinants, direct and indirect determinants, and organismal determinants. More recently, Donald Dewsbury proposed a structure involving three categories of questions: the genesis of the behavior, its control, and the consequences of the actions. The common elements in these schemes, from a proximate causation perspective, encompass physiological mechanisms and development.

Physiological studies of the neural bases for behavior, and explorations of endocrine functions and behavior have their roots in early American comparative psychology, augmented into the mid-twentieth century by work in zoology. Karl Lashley was a key pioneer in the exploration of the neural bases for behavior, sensory systems, and brain function. Others who made significant contributions to this emerging field were Hermann von Helmholtz for work on visual systems; Donald O. Hebb, who worked on connections between the brain and learning; James Olds, who co-discovered the pleasure centers in the brain; and Rita Levi-Montalcini, who discovered the nerve growth factor. Signaling the growing importance of neurobiology in relation to behavior, Nobel Prizes for Physiology or Medicine were awarded to Roger Sperry, David Hubel, Torsten Wiesel, and Eric Kandel for their research and findings on vision and cognitive neuroscience.

Many journals involving various aspects of neurobiology began publication during the decades of the 1970s and 1980s as the field expanded and diversified. Until the past few years, there were almost no papers published in *Animal Behaviour*, the primary journal in this field, with neural aspects of behavior as a major focus. Even now, the vast majority of papers are concerned with ultimate causation issues. This decades-long emphasis in the journal no doubt was a significant stimulus for the many neurobiology journals that emerged.

Frank Beach was an early proponent of examining the endocrine bases for behavior. His work on hormones and reproduction served as the primary basis for launching a number of careers and lines of inquiry. One key principle Beach championed was that the endocrine-behavior link worked both ways. That is, hormones can affect behavior, but also behavior can influence hormone levels.

Both field and laboratory environments are used for investigations of endocrines and behavior. Much of the work on female sexual receptivity in birds and mammals, maternal and paternal behavior, male aggression, and the interplay between behavior and endocrine systems has been laboratory-based research. Lehrman's elegant work on coordinated activities and hormones in the breeding cycle of the ring dove is particularly fascinating in this regard.

Field studies have involved the use of artificial hormone doses to test effects in wild or free-living animals. Collection of blood, urine, or feces provides a way to measure various hormone levels. However, the stress associated with capture and restraint, or even just being in a laboratory setting, can compromise hormonal information gathered in this manner. With the advent of new hormone assay technologies, investigators can now gather samples of urine or feces without the necessity of capturing the animal and providing a picture of hormone levels based not on a point in time, but representative of a longer period, up to a day or more. Monitoring hormone levels in wild animals makes it possible to examine variations in both sex steroids and stress hormones for animals under different conditions and in different social situations.

Research on hormones and behavior led to its inclusion in classes and textbooks in physiological psychology by the 1950s. Further growth in this arena spawned a new journal, *Hormones and Behavior.* There have been at least three textbooks devoted to the subject of endocrines and behavior.

In the last three decades, a new horizon has emerged: the investigation of relationships between the immune system and behavior. This topic was addressed by Hamilton and Zuk in their work on blood parasites in birds. Work on the Major Histocompatibility Complex (MHC) in mice and its role in odor preference and mate choice also relate to the role of the immune system in affecting behavior. More recent work by Wingfield draws connections between stress, sickness, and immune system function in birds and mammals. Though the interplay between an animal's immune system and behavior has received modest attention for several decades, this relationship is currently being more thoroughly investigated.

The interrelationships among neural, hormonal, and immunological systems provide a stimulus for future exploration of the two-way roles between these systems and behavior. The key to understanding the connections between proximate mechanisms of behavior and the functional or ultimate causation is genetics. This is a key theme in the section on integration at the conclusion of this article.

Behavior development received considerable attention in the early days of comparative psychology, probably because of the connections drawn between human and non-human animal learning during growth and maturation. The processes of behavior development are often divided along a chronological timeline beginning with prenatal or prehatching events, followed by early postnatal considerations, and aspects of behavior during juvenile stages. Play behavior is often considered as part of the investigation of behavior development.

Prenatal influences on behavior include such things as exposure to hormones in utero, effects of stress on the mother on later offspring behavior, and ways in which both external and internal stimulation contribute to the maturation and refinement of the brain, sensory systems, and motor development. Early postnatal events include imprinting, emergence of food preferences, and the beginning of some forms of play behavior. Among the extensive investigations of juvenile and adolescent behavior are those on bird song, the form and functions of play behavior, sexual maturation and changes in behavior, and connections between early behavior actions, prior to birth or hatching and the period immediately following those events with later behavior.

Imprinting refers to the formation of either filial ties involving formation of an attachment to a parent or object, or the establishment of strong tendencies to court and mate with individuals of the same kind. The phenomena associated with imprinting encompass many subtopics among which are the notions of critical and sensitive periods, the importance of different sensory modalities, and variations in the timing and strength of the imprinting experience.

A favorite procedure for the early investigators of behavior development was the isolation (deprivation) experiment. Can we isolate an organism from particular sorts of stimulation and discover specific deficits in later actions? These studies provided useful information, but various confounds rendered them less important as the field progressed. The opposite manipulation, providing and enriched environment with added stimulation, sometimes specific and other times general, was used to explore ways in which environmental impacts enhanced the learning of various organisms. Many of these studies were, of course, directed at understanding the processes occurring in human development. Relating differences in environment to learning and other endpoints served as the basis for changes in such areas as early childhood education and orphanages.

Synthesis and Integration

Categorization of causes of behavior patterns as either proximate or ultimate is an arbitrary distinction, though convenient at some levels. The term 'ultimate' is also problematic in this context, since it conveys the notion of an absolute end point; 'proximate,' on the other hand, is a relative term. A more appropriate antonym for 'proximate' is 'distal.' Consider the study of the role of natural selection by observing behavior in the field, as Tinbergen did with the egg shell removal experiment, versus documenting changes in gene frequencies due to selection using new molecular and statistical techniques. Both approaches ask evolutionary questions, but the latter is clearly getting at proximate causes of evolution. The same can, no doubt, be said for examples of proximate causation discussed earlier: some are more proximal than others. A full understanding of any behavior pattern requires study at all levels, from its selective advantage or disadvantage in the field, that is, how and why it affects fitness, through all levels of organization down to the mechanisms of gene action. This line of thinking might predict a trend toward studies taking a multilevel approach to causation, but this has not always been the case.

In his 1975 treatise on sociobiology, E. O. Wilson depicted the relative sizes of the different fields dealing with animal behavior in 1950, 1975, and 2000. On the left, or proximal end, was neurophysiology and its close connections with cellular biology. On the right, or ultimate end, were behavioral ecology and sociobiology, with connections to population biology. In 1950, connecting the two ends of this 'dumbbell' were the two large traditional branches of animal behavior, ethology and comparative psychology. Wilson predicted that, rather than the expansion of these connecting disciplines to unify the ends, neurophysiology would cannibalize ethology and comparative psychology from one end, and behavioral ecology would cannibalize them from the other. To some extent this has come true, given the explosion of research in both cellular/molecular biology at one end and in population biology/behavioral ecology at the other.

Countering the trend toward increasing dichotomy between proximate and ultimate causation is the appearance of a number of academic departments dedicated to integrative biology. Many of these, however, incorporate evolution and ecology to the extent that they deal mainly with ultimate causation, leaving proximate causation to departments of cellular and molecular biology. Funding agencies tend to follow the same pattern.

Perhaps more important than names for channeling academic programs and grant proposals, however, is the increasing number of research projects in animal behavior that span many levels of causation. For example, the study of mating systems in rodents has been approached at a number of levels, from the environmental conditions favoring the evolution of monogamy versus polygamy in field experiments to the differences in the DNA that regulate these mating systems. At the proximal level, not only have researchers identified a gene that controls the number of hormone receptors in the forebrain of the polygynous meadow vole, but they have also been able to transfer extra copies of this gene into the brain and cause meadow voles to behave like monogamous prairie voles. At the same time, others are exploring the long-term fitness consequences of these manipulated animals in seminatural field enclosures.

A number of other research teams are studying behavior at multiple levels of causation, including those of both Ketterson and Wingfield on bird physiology, Houck on salamander mating pheromones, Robinson on honeybee genomics and social behavior, and Strassmann and Queller on genomics and the evolution of slime mold sociality. Although much of this research gets published in specialized journals, the teams work at multiple levels and ask questions about both proximate and ultimate causation. The success of such efforts to demonstrate how evolutionary selection pressures shape the various internal mechanisms that regulate behavior depends in no small part on project leaders that have a broad vision and the ability to coordinate the activities of researchers with different specializations.

See also: Behavioral Ecology and Sociobiology; Comparative Animal Behavior – 1920–1973; Ethology in Europe; Future of Animal Behavior: Predicting Trends; Neurobiology, Endocrinology and Behavior; Psychology of Animals.

Further Reading

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Relevant Websites

http://findarticles.com/p/articles/mi_qa3746/is_199802/ai_n8801814/ – A symposium on integration of proximate and ultimate causation.
http://www.ias.ac.in/currsci/oct102005/1180.pdf – An article exploring differences between those studying proximate and ultimate causation.
http://cas.bellarmine.edu/tietjen/Ethology/introduction_and_history_of_anim.htm – Historical perspective on many aspects of animal behavior.
http://www.sciencedirect.com/science?_ob=ArticleURL&_udi=B6VJ1-3Y86861-G&_user=109269&_rdoc=1&_fmt=&_orig=search&_sort=d&_docanchor=&view=c&_searchStrId=1012941289&_rerunOrigin=google&_acct=C000059546&_version=1&_urlVersion=0&_userid=109269&md5=7a129b63b5c0c3ee43d09427ee55dd53 – Examination of shifts toward studies of proximate mechanisms.