

Karl Ritter von Frisch (November 20, 1886 – June 12, 1982) was an [Austrian ethologist](#) who received the [Nobel Prize in Physiology or Medicine](#) in 1973, along with [Nikolaas Tinbergen](#) and [Konrad Lorenz](#). His work centered on investigations of the sensory perceptions of the [honey bee](#) and he was one of the first to translate the meaning of the [waggle dance](#). His theory was disputed by other scientists and greeted with skepticism at the time. Only recently was it definitively proved to be an accurate theoretical analysis (see Nature magazine reference).

Konrad Zacharias Lorenz (November 7, 1903 in [Vienna](#) – February 27, 1989 in [Vienna](#)) was an [Austrian zoologist](#), [animal psychologist](#), [ornithologist](#), and [Nobel Prize](#) winner. He is often regarded as one of the founders of modern [ethology](#), developing an approach that began with an earlier generation, including his teacher [Oskar Heinroth](#). Lorenz studied [instinctive behavior](#) in [animals](#), especially in [greylag geese](#) and [jackdaws](#). Working with geese, he rediscovered the principle of [imprinting](#) (originally described by [Douglas Spalding](#) in the 19th century) in the behavior of [nidifugous birds](#). He wrote numerous books, some of which, such as [King Solomon's Ring](#) and [On Aggression](#) became popular reading. In later life his interest shifted to the study of man in society.

Nikolaas "Niko" Tinbergen (15 April 1907 – 21 December 1988) was a [Dutch ethologist](#) and [ornithologist](#) who shared the 1973 [Nobel Prize in Physiology or Medicine](#) with [Karl von Frisch](#) and [Konrad Lorenz](#) for their discoveries concerning organization and elicitation of individual and social behaviour patterns in [animals](#). In the 1960s he collaborated with [filmmaker Hugh Falkus](#) on a series of wildlife films, including *The Riddle of the Rook* (1972) and *Signals for Survival* (1969), which won the Italia prize in that year and the American blue ribbon in 1971.

Eric Heinz Lenneberg (1921 - 1975) was a [linguist](#) and neurologist who pioneered ideas on [language acquisition](#) and [cognitive psychology](#), particularly in terms of the concept of innateness. He was born in [Düsseldorf](#), Germany. An ethnic [Jew](#), he left [Nazi Germany](#) because of rising [Nazi persecution](#). He initially fled to Brazil with his family and then to the United States where he attended the [University of Chicago](#) and [Harvard University](#). A professor of [psychology](#) and neurobiology, he taught at the Harvard Medical School, the [University of Michigan](#) in Ann Arbor and [Cornell University](#) and Medical School.

Lenneberg's 1964 paper "The Capacity of Language Acquisition," originally published in 1960, sets forth seminal arguments about the human-specific biological capacity for language, which were then being developed in his research and discussions with [George A. Miller](#), [Noam Chomsky](#), and others at Harvard and MIT, and popularized by Steven Pinker in his book, *The Language Instinct*. He presents four arguments for biological innateness of psychological capacities, parallel to arguments in biology for the innateness of physical traits:

- Universal appearance of a trait at a single time across a species. "Species typical" traits.
- Universal appearance across time for a group. Not just an artifact of cultural history. Again, "species typical" diagnostic feature.
- No learning of the trait is possible.
- Individual development of a trait rigidly follows a given schedule regardless of the particular experience of the organism.

In his publication *Biological Foundations of Language* he advanced the [hypothesis](#) of a [critical period](#) for language development; a topic which remains controversial and the subject of debate. Lenneberg's biological approach to language was related to developments such as the [motor theory of speech perception](#) developed by Alvin Liberman and colleagues at [Haskins Laboratories](#) and also provided historical antecedents to issues now emerging in [embodied philosophy](#) and [embodied cognition](#).

David Hunter Hubel (born February 27, 1926) was co-recipient with [Torsten Wiesel](#) of the 1981 [Nobel Prize in Physiology or Medicine](#), for their discoveries concerning information processing in the [visual system](#); the prize was shared with [Roger W. Sperry](#) for his independent research on the cerebral hemispheres. In 1978, Hubel and Wiesel were awarded the [Louisa Gross Horwitz Prize](#) from [Columbia University](#).

Torsten Nils Wiesel (born June 3, 1924) was a Swedish co-recipient with [David H. Hubel](#) of the 1981 [Nobel Prize in Physiology or Medicine](#), for their discoveries concerning information processing in the [visual system](#); the prize was shared with [Roger W. Sperry](#) for his independent research on the cerebral hemispheres.

Kittens open their [eyes](#) about seven to ten days following [birth](#). At first, the [retina](#) is poorly-developed and vision is poor. Kittens are not able to see as well as adult cats until about ten weeks after birth.

All kittens' eyes are blue, and will remain so for several weeks. Their vision will be blurred at first, and their pupils don't dilate and contract readily, so they should be protected from bright lights.

Clinton Richard Dawkins, [FRS](#), [FRSL](#) (born 26 March 1941) is a British [biological theorist](#) with a background in [ethology](#). He is a [popular science](#) author focusing on [evolution](#).

Dawkins is one of Britain's best-known academics. He came to prominence with his 1976 book *The Selfish Gene*, which popularised the [gene-centred view of evolution](#) and introduced the term *meme*. In 1982, he expanded the gene-centred view with his book *The Extended Phenotype: The Gene as the Unit of Selection*, emphasizing that the [phenotypic](#) effects of genes are not necessarily limited to an [organism's](#) body but can stretch via biochemistry and behaviour into other organisms and the environment. He is well-known as a presenter of the case for [rationalism](#) and [scientific thinking](#). His later works continued to expand upon these ideas and their implications.

Dawkins is one of the world's most widely publicised [atheists](#). He is a prominent critic of [religion](#), [creationism](#) and [pseudoscience](#). In his 1986 book *The Blind Watchmaker: Why the Evidence of Evolution Reveals a Universe Without Design*, he argued against the [watchmaker analogy](#), an argument for the existence of a [supernatural creator](#) based upon the complexity of living organisms. Instead, he described a [dysteleological](#) perspective on the process of [evolution by natural selection](#) as "blind", without a design or a goal. In his 2006 million-selling book *The God Delusion*, he contended that a supernatural creator almost certainly does not exist, writing that such beliefs, based on [faith](#) rather than on evidence, qualify as a [delusion](#). He was a co-founder of the [Out Campaign](#), as a means of advancing [atheism](#) and [freethought](#).

Dawkins retired from Oxford University in 2008 and remains a writer and public figure.

The Extended Phenotype (subtitled "The Gene as the Unit of Selection", and later, "The Long Reach of the Gene") is a 1982 book by [Richard Dawkins](#). A revised edition was published in 1999 with an afterword by the philosopher [Daniel Dennett](#). Dawkins considers the concept of the *Extended Phenotype* to be his principal contribution to [evolutionary theory](#).

Dawkins starts from the ideas of his 1976 book *The Selfish Gene*, which portrayed the [organism](#) as a survival machine constructed by its [genes](#) to maximize their chances of replicating. In a much more technical presentation than the earlier book, Dawkins devotes a significant portion of this work to an attempt to rebut criticism of *The Selfish Gene*.

In the main portion of the book, Dawkins argues that the only thing that genes control directly is the synthesis of [proteins](#). He points to the arbitrariness of restricting the idea of the [phenotype](#) to apply only to the phenotypic expression of an organism's genes in its own body.

Dawkins develops this idea by pointing to the effect that a gene may have on an organism's environment through that organism's behaviour, citing as examples [caddis houses](#) and [beaver dams](#). He then goes further to point to first animal [morphology](#) and ultimately animal behaviour, which can seem advantageous not to the animal itself, but rather to a [parasite](#) which afflicts it. Dawkins summarizes these ideas in what he terms the *Central Theorem of the Extended Phenotype*:

“ An animal's behaviour tends to maximize the survival of the genes "for" that behaviour, whether or not those genes happen to be in the body of the particular animal performing it.

In conducting this argument, Dawkins aims to strengthen the case for a [gene-centric](#) view of life, to the point where it is recognized that the organism itself needs to be explained. This is the challenge which he takes up in the final chapter entitled "Rediscovering the Organism."

Richard Charles "Dick" Lewontin (born March 29, 1929) is an [American evolutionary biologist](#), [geneticist](#) and [social commentator](#). A leader in developing the [mathematical](#) basis of [population genetics](#) and evolutionary theory, he pioneered the notion of using techniques from [molecular biology](#) such as [gel electrophoresis](#) to apply to questions of [genetic variation](#) and evolution.

In a pair of 1966 papers co-authored with [J.L. Hubby](#) in the journal *Genetics*, Lewontin helped set the stage for the modern field of [molecular evolution](#).

In 1979 he and [Stephen Jay Gould](#) introduced the term "[spandrel](#)" into [evolutionary theory](#). A spandrel is an evolved biological feature which arises as the result of the modification of another trait.

Lewontin strongly opposed [genetic determinism](#), especially as allegedly expressed by [sociobiology](#) and [evolutionary psychology](#).

In "Organism and Environment" in *Scientia*, and in more popular form in the last chapter of *Biology as Ideology*, Lewontin argued that while traditional [Darwinism](#) has portrayed the organism as passive recipient of environmental influences, a correct understanding should emphasize the organism as an active constructor of its own environment. [Niches](#) are not pre-formed, empty receptacles into which organisms are inserted, but are defined and created by organisms. The organism-environment relationship is reciprocal and [dialectical](#). [M.W. Feldman](#), [K.N. Laland](#), and [F.J. Odling-Smee](#) among others have developed Lewontin's conception in more detailed models.

Lewontin has long been a critic of traditional [neo-Darwinian](#) approaches to [adaptation](#). In his article "Adaptation" in the Italian [Encyclopedia Einaudi](#), and in a toned-down version in *Scientific American*, he emphasized the need to give an engineering characterization of adaptation separate from measurement of number of offspring, rather than simply assuming organs or organisms are at adaptive optima. Lewontin has claimed that his more general, technical criticism of [adaptationism](#) grew out of his recognition that the fallacies of [sociobiology](#) reflect fundamentally flawed assumptions of adaptiveness of all traits in much of the [modern evolutionary synthesis](#).

Lewontin accused Darwinists of telling "Just So" stories when they try to show how natural selection explains such novelties as long-necked giraffes.

Lewontin and his late [Harvard](#) colleague [Stephen Jay Gould](#) introduced the evolutionary term [spandrel](#), inspired by the [architectural](#) term "[spandrel](#)" and transferred the word to an evolutionary context, in an influential 1979 paper "The spandrels of [San Marco](#) and the [Panglossian paradigm](#): a critique of the adaptationist programme", using it for a feature of an [organism](#) that exists as a necessary consequence of other features and is not selected for directly. The relative frequency of spandrels, so defined, versus adaptive features in nature, remains a controversial topic in evolutionary biology.

Stephen Jay Gould (September 10, 1941 – May 20, 2002) was an American [paleontologist](#), [evolutionary biologist](#), and [historian of science](#). He was also one of the most influential and widely read writers of [popular science](#) of his generation. Gould spent most of his career teaching at [Harvard University](#) and working at the [American Museum of Natural History](#) in New York. In the latter years of his life, Gould also taught biology and evolution at [New York University](#) near his home in [SoHo](#).

Gould's greatest contribution to science was the theory of [punctuated equilibrium](#) which he developed with [Niles Eldredge](#) in 1972. The theory proposes that most evolution is marked by long periods of evolutionary stability, which is punctuated by rare instances of [branching evolution](#). The theory was contrasted against [phyletic gradualism](#), the popular idea that evolutionary change is marked by a pattern of smooth and continuous change in the fossil record.

Most of Gould's empirical research was based on the land snails *Poecilozonites* and *Cerion*. He also contributed to [evolutionary developmental biology](#), and has received wide praise for his book *Ontogeny and Phylogeny*. In evolutionary theory, he opposed strict selectionism, [sociobiology](#) as applied to humans, and [evolutionary psychology](#). He campaigned against [creationism](#) and proposed that [science](#) and [religion](#) should be considered two distinct fields, or "[magisteria](#)", whose authority does not overlap.

Many of Gould's *Natural History* essays were reprinted in collected volumes, such as *Ever Since Darwin* and *The Panda's Thumb*, while his popular treatises included books such as *The Mismeasure of Man*, *Wonderful Life* and *Full House*.

The **modern evolutionary synthesis** (also referred to as the **new synthesis**, the **modern synthesis**, the **evolutionary synthesis** and the **neo-darwinian synthesis**) is a union of ideas from several [biological](#) specialties which forms a logical account of [evolution](#). This synthesis has been accepted by nearly all working biologists. The synthesis was produced over about a decade (1936–1947), and the development of [population genetics](#) (1918–1932) was the stimulus. This showed that Mendelian [genetics](#) was consistent with [natural selection](#) and gradual evolution. The synthesis is still, to a large extent, the current paradigm in evolutionary biology.

[Julian Huxley](#) invented the term, when he produced his book, *Evolution: The Modern Synthesis* (1942). Other major figures in the modern synthesis include [R. A. Fisher](#), [Theodosius Dobzhansky](#), [J.B.S. Haldane](#), [Sewall Wright](#), [E.B. Ford](#), [Ernst Mayr](#), [Bernhard Rensch](#), [Sergei Chetverikov](#), [George Gaylord Simpson](#), and [G. Ledyard Stebbins](#).

The modern synthesis solved difficulties and confusions caused by the specialisation and poor communication between biologists in the early years of the 20th century. Discoveries of early geneticists were difficult to reconcile with gradual evolution and the mechanism of natural selection. The synthesis reconciled the two schools of thought, while providing evidence that studies of populations in the field were crucial to evolutionary theory. It drew together ideas from several branches of biology that had become separated, particularly genetics, cytology, systematics, botany, morphology, ecology and paleontology.

Adaptation is the evolutionary process whereby a population becomes better suited to its [habitat](#). This process takes place over many generations, and is one of the basic phenomena of biology.

Also, the term *adaptation* may refer to a feature which is especially important for an organism's survival. For example, the adaptation of horses' teeth to the grinding of grass, or their ability to run fast and escape predators. Such adaptations are produced in a variable population by the better suited forms reproducing more successfully, that is, by [natural selection](#).

The following definitions are mainly due to [Theodosius Dobzhansky](#).

1. *Adaptation* is the evolutionary process whereby an organism becomes better able to live in its [habitat](#) or habitats.
2. *Adaptedness* is the state of being adapted: the degree to which an organism is able to live and reproduce in a given set of habitats.
3. An *adaptive trait* is an aspect of the developmental pattern of the organism which enables or enhances the probability of that organism surviving and reproducing.

Exaptation, **cooption**, and **preadaptation** are related terms referring to shifts in the function of a trait during [evolution](#). For example, a trait can evolve because it served one particular function, but subsequently it may come to serve another. Exaptations are common in both anatomy and behavior. Bird feathers are a classic example: initially these evolved for temperature regulation, but later were adapted for flight. Interest in exaptation relates to both the process and product of evolution: the process that creates complex traits and the product that may be imperfectly designed.

Evolutionary developmental biology (**evolution of development** or informally, **evo-devo**) is a field of [biology](#) that compares the [developmental processes](#) of different [animals](#) and [plants](#) in an attempt to determine the ancestral relationship between [organisms](#) and how developmental processes [evolved](#). It addresses the origin and evolution of [embryonic development](#); how modifications of development and developmental processes lead to the production of novel features, such as the evolution of [feathers](#); the role of [developmental plasticity](#) in evolution; how [ecology](#) impacts in development and evolutionary change; and the developmental basis of [homoplasy](#) and [homology](#).

Although interest in the relationship between [ontogeny](#) and [phylogeny](#) extends back to the nineteenth century, the contemporary field of evo-devo has gained impetus from the discovery of [genes](#) regulating [embryonic](#) development in [model organisms](#). General [hypotheses](#) remain hard to test because organisms differ so much in [shape and form](#). Nevertheless, it now appears that just as

evolution tends to create new genes from parts of old genes (molecular economy), evo-devo demonstrates that evolution alters developmental processes (genes and gene networks) to create new and novel structures from the old gene networks (such as bone structures of the jaw deviating to the ossicles of the middle ear) or will conserve (molecular economy) a similar program in a host of organisms such as eye development genes in molluscs, insects, and vertebrates. Initially the major interest has been in the evidence of homology in the cellular and molecular mechanisms that regulate body plan and organ development. However more modern approaches include developmental changes associated with speciation.

[Charles Darwin](#)'s theory of [evolution](#) is based on three principles: [natural selection](#), [heredity](#), and [variation](#). At the time that Darwin wrote, the principles underlying heredity and variation were poorly understood. In the 1940s, however, biologists incorporated [Gregor Mendel](#)'s principles of [genetics](#) to explain both, resulting in the [modern synthesis](#). It was not until the 1980s and 1990s, however, when more comparative molecular [sequence](#) data between different kinds of organisms was amassed and detailed, that an understanding of the molecular basis of the [developmental](#) mechanisms has arisen. Currently, it is well understood how genetic mutation occurs. However, developmental mechanisms are not understood sufficiently to explain which kinds of [phenotypic](#) variation can arise in each generation from variation at the genetic level. Evolutionary developmental biology studies how the dynamics of development determine the phenotypic variation arising from genetic variation and how that affects phenotypic evolution (specially its direction). At the same time evolutionary developmental biology also studies how development itself evolves. Thus, the origins of evolutionary developmental biology come from both an improvement in molecular biology techniques as applied to development, and the full appreciation of the limitations of classic neo-Darwinism as applied to phenotypic evolution. Some evo-devo researchers see themselves as extending and enhancing the modern synthesis by incorporating into it findings of [molecular genetics](#) and [developmental biology](#). Others, drawing on findings of discordances between genotype and phenotype and [epigenetic](#) mechanisms of development, are mounting an explicit challenge to neo-Darwinism.

Evolutionary developmental biology is not yet a unified discipline, but can be distinguished from earlier approaches to evolutionary theory by its focus on a few crucial ideas. One of these is [modularity](#): as has been long recognized, plants and animal bodies are modular: they are organized into developmentally and anatomically distinct parts. Often these parts are repeated, such as fingers, ribs, and body segments. Evo-devo seeks the genetic and evolutionary basis for the division of the embryo into distinct modules, and for the partly independent development of such modules.

Another central idea is that some [gene](#) products function as switches whereas others act as diffusible signals. Genes specify [proteins](#), some of which act as structural components of [cells](#) and others as [enzymes](#) that regulate various biochemical pathways within an organism. Most biologists working within the modern synthesis assumed that an organism is a straightforward reflection of its component genes. The modification of existing, or evolution of new, biochemical pathways (and, ultimately, the evolution of new species of organisms) depended on specific genetic [mutations](#). In 1961, however, [Jacques Monod](#), [Jean-Pierre Changeux](#) and [François Jacob](#) discovered within the bacterium [Escherichia coli](#) a [gene](#) that functioned only when "switched on" by an environmental stimulus. Later, scientists discovered specific genes in animals, including a subgroup of the genes which contain the [homeobox](#) DNA motif, called Hox genes, that act as switches for other genes, and could be induced by other gene products, [morphogens](#), that act analogously to the external stimuli in bacteria. These discoveries drew biologists' attention to the fact that genes can be selectively turned on and off, rather than being always active, and that highly disparate organisms (for example, fruit flies and human beings) may use the same genes for [embryogenesis](#) (e.g., the genes of the "developmental-genetic toolkit", see below), just regulating them differently.

Similarly, organismal form can be influenced by mutations in [promoter](#) regions of [genes](#), those [DNA](#) sequences at which the products of some genes bind to and control the activity of the same or other genes, not only [protein](#)-specifying sequences. In addition to providing new support for Darwin's assertion that all organisms are descended from a common ancestor, this finding suggested that the crucial distinction between different species (even different orders or phyla) may be due less to differences in their content of gene products than to differences in spatial and temporal *expression* of [conserved](#) genes. The implication that [large evolutionary changes in body morphology](#) are associated with changes in gene regulation, rather than the evolution of new genes, suggested that the action of natural selection on promoters responsive to Hox and other "switch" genes may play a major role in evolution.

Another focus of evo-devo is [developmental plasticity](#), the basis of the recognition that organismal [phenotypes](#) are not uniquely determined by their [genotypes](#). If generation of phenotypes is conditional, and dependent on external or environmental inputs, evolution can proceed by a "phenotype-first" route, with genetic change following, rather than initiating, the formation of morphological and other phenotypic novelties. The case for this was argued for by [Mary Jane West-Eberhard](#) in her 2003 book *Developmental plasticity and evolution*.

An early version of [recapitulation theory](#), also called the *biogenetic law* or *embryological parallelism*, was put forward by [Étienne Serres](#) in 1824–26 as what became known as the "Meckel-Serres Law" which attempted to provide a link between comparative [embryology](#) and a "pattern of unification" in the organic world. It was supported by [Étienne Geoffroy Saint-Hilaire](#) as part of his ideas of [idealism](#), and became a prominent part of his version of [Lamarckism](#) leading to disagreements with [Georges Cuvier](#). It was widely supported in the [Edinburgh](#) and [London](#) schools of higher anatomy around 1830, notably by [Robert Edmond Grant](#), but was opposed by [Karl Ernst von Baer](#)'s embryology of divergence in which embryonic parallels only applied to early stages where the embryo took a general form, after which more specialised forms diverged from this shared unity in a branching pattern. The anatomist [Richard Owen](#) used this to support his idealist concept of species as showing the unrolling of a divine plan from an [archetype](#), and in the 1830s attacked the [transmutation of species](#) proposed by Lamarck, Geoffroy and Grant. In the 1850s Owen began to support an evolutionary view that the history of life was the gradual unfolding of a [teleological](#) divine plan, in a continuous "ordained becoming", with new species appearing by natural birth.

In *On the Origin of Species* (1859), [Charles Darwin](#) proposed evolution through natural selection, a theory central to modern biology. Darwin recognised the importance of embryonic development in the understanding of evolution, and the way in which von Baer's branching pattern matched his own idea of descent with modification:

“ We can see why characters derived from the embryo should be of equal importance with those derived from the adult, for a natural classification of course includes all ages. ”

[Ernst Haeckel](#) (1866), in his endeavour to produce a synthesis of Darwin's theory with Lamarckism and [Naturphilosophie](#), proposed that "[ontogeny](#) recapitulates [phylogeny](#)," that is, the development of the embryo of every species (ontogeny) fully repeats the evolutionary development of that species (phylogeny), in Geoffroy's linear model rather than Darwin's idea of branching evolution. Haeckel's concept explained, for example, why humans, and indeed all vertebrates, have gill slits and tails early in embryonic development. His theory has since been discredited. However, it served as a backdrop for a renewed interest in the evolution of development after the [modern evolutionary synthesis](#) was established (roughly 1936 to 1947).

[Stephen Jay Gould](#) called this approach to explaining evolution as *terminal addition*; as if every evolutionary advance was added as new stage by reducing the duration of the older stages. The idea was based on observations of [neoteny](#). This was extended by the more general idea of [heterochrony](#) (changes in timing of development) as a mechanism for evolutionary change.

[D'Arcy Thompson](#) postulated that differential growth rates could produce variations in form in his 1917 book *On Growth and Form*. He showed the underlying similarities in *body plans* and how geometric *transformations* could be used to explain the variations.

[Edward B. Lewis](#) discovered [homeotic](#) genes, rooting the emerging discipline of evo-devo in [molecular genetics](#). In 2000, a special section of the [Proceedings of the National Academy of Sciences](#) (PNAS) was devoted to "evo-devo", and an entire 2005 issue of the Journal of Experimental Zoology Part B: Molecular and Developmental Evolution was devoted to the key evo-devo topics of evolutionary innovation and morphological novelty.

Spandrel is a term used in [evolutionary biology](#) to describe a [phenotypic](#) characteristic that is a byproduct of the evolution of some other character, rather than a direct product of [adaptive selection](#). The term was coined by the [Harvard paleontologist Stephen Jay Gould](#) and [population geneticist Richard Lewontin](#) in their influential paper "The Spandrels of San Marco and the [Panglossian Paradigm: A Critique of the Adaptationist Programme](#)" (1979). In this paper [Gould](#) and [Lewontin](#) employed the analogy of [spandrels](#) in [Renaissance architecture](#): curved areas of masonry between arches supporting a dome that arise as a consequence of decisions about the shape of the arches and

the base of the dome, rather than being designed for the artistic purposes for which they were often employed. Properties that they singled out were the necessary number of four and their specific three-dimensional shape. In the biological sense, a 'spandrel' or 'exaptation' (as Gould and Lewontin referred to them) might be the result of an architectural requirement inherent in the [Bauplan](#) of an organism, or to some other constraint on [adaptive evolution](#).

Their suggestive proposal generated a large literature of critique, which Gould characterised (Gould 1997) as being grounded in two ways. First, a terminological claim was offered that the "spandrels" of [Basilica di San Marco](#) were not spandrels at all, but rather were [pendentives](#). Gould (1997) responded, "The term spandrel may be extended from its particular architectural use for two-dimensional byproducts to the generality of 'spaces left over', a definition that properly includes the San Marco pendentives." Other critics, such as [Daniel Dennett](#), further claimed that these pendentives are not merely architectural by-products as Gould and Lewontin supposed. Dennett argues that alternatives to pendentives, such as [corbels](#) or [squinches](#) would have served equally well from an architectural standpoint, but pendentives were deliberately selected due to their [aesthetic](#) value. Critics argue that Lewontin and Gould's oversight in this regard illustrates their underestimation of the pervasiveness of adaptations found in nature.

Gould responded that critics ignore that *later* selective value is a separate issue from *origination* as necessary [consequences](#) of structure; he summarised his use of the term 'spandrel' in 1997: "Evolutionary biology needs such an explicit term for features arising as byproducts, rather than adaptations, whatever their subsequent [exaptive utility](#).... Causes of historical origin must always be separated from current utilities; their conflation has seriously hampered the evolutionary analysis of form in the history of life." (Gould 1997:Abstract).

The linguist [Noam Chomsky](#) has argued that the '[language faculty](#)' that plays a central role in his theory of [Universal Grammar](#) may have evolved as a spandrel: in this view, human language originated as a by-product of the general [recursion](#) faculty of the human mind, which would have evolved without any evolutionary 'reasons'.

Tinbergen's four questions, named after [Nikolaas Tinbergen](#), are categories of explanations of animal behavior.

Elementary school children can answer that animals have vision to help them find food and avoid danger ([adaptation](#)). Biologists have three additional explanations: sight is caused by a particular series of evolutionary steps ([phylogeny](#)), the mechanics of the eye ([causation](#)), and even the process of an individual's development ([ontogeny](#)). Although these answers may be very different, they are consistent with each other. This idea was hashed out in the 1960s when Tinbergen delineated the **four questions** based on [Aristotle's four types of causes](#). This schema constitutes a basic framework of the overlapping behavioral fields of [ethology](#), [behavioral ecology](#), [sociobiology](#), [evolutionary psychology](#), and [comparative psychology](#).

Evolutionary (ultimate) explanations

1 Function ([adaptation](#))

Darwin's theory of [evolution](#) by natural selection is the only scientific explanation for why an animal's behavior is usually well adapted for survival and reproduction in its environment. The literature conceptualizes the relationship between function and evolution in two ways. On the one hand, function and evolution are often presented as separate and distinct explanations of behavior. ^[1] On the other hand, the definition of adaptation, a central concept in evolution, is a trait that is functional to the reproductive success of the organism and that is the result of natural selection; that is, function and evolution are inseparable. Given this, it is best to conceptualize function as an evolutionary explanation. The term "function" is preferable to "adaptation", because it is understandable to students prior to an explanation of evolution.</ref> Many examples are well-known. For instance, birds fly south in the winter to find food and warmth, and mammalian mothers nurture their young, thereby having more surviving offspring.

Ultimate function corresponds to [Aristotle's final cause](#).

2 Phylogeny (evolution)

“Phylogeny” captures all evolutionary explanations other than function/adaptation.^[2] There are several reasons why natural selection may fail to achieve optimal design (Mayr 2001:140-143; Buss et al. 1998). One entails random processes such as mutation and environmental events acting on small populations. Another entails the constraints resulting from early evolutionary development. As many characteristics are retained over the course of phylogeny, each organism harbors characteristics of various (phylogenetic) ages. This applies equally to anatomy and behavior. Reconstructing the phylogeny of a species often makes it possible to understand the "uniqueness" of recent characteristics: Earlier phylogenetic stages and (pre-) conditions which persist often also determine the form of more modern characteristics. For instance, the vertebrate eye (including the human eye) has a [blind spot](#), whereas octopus eyes do not. In those two lineages, the eye was originally constructed one way or the other. Once the vertebrate eye was constructed, there were no intermediate forms that were both adaptive and would have enabled it to evolve without a blind spot.

Proximate explanations

3 Causation (*proximate mechanisms or proximate cause effect relations*)

Here are several prominent classes of proximate mechanisms:

- [Brain](#): Broca's area, a small section of the human brain, is key to the use of grammar ([The Language Instinct](#)).
- [Hormones](#) are chemicals used to communicate among cells of an individual organism. Testosterone, for instance, stimulates aggressive behavior in a number of species.
- [Pheromones](#) are chemicals used to communicate among members of the same species. Some species (e.g., dogs and some moths) use pheromones to attract mates.

Proximate mechanisms correspond to [Aristotle's material cause](#).

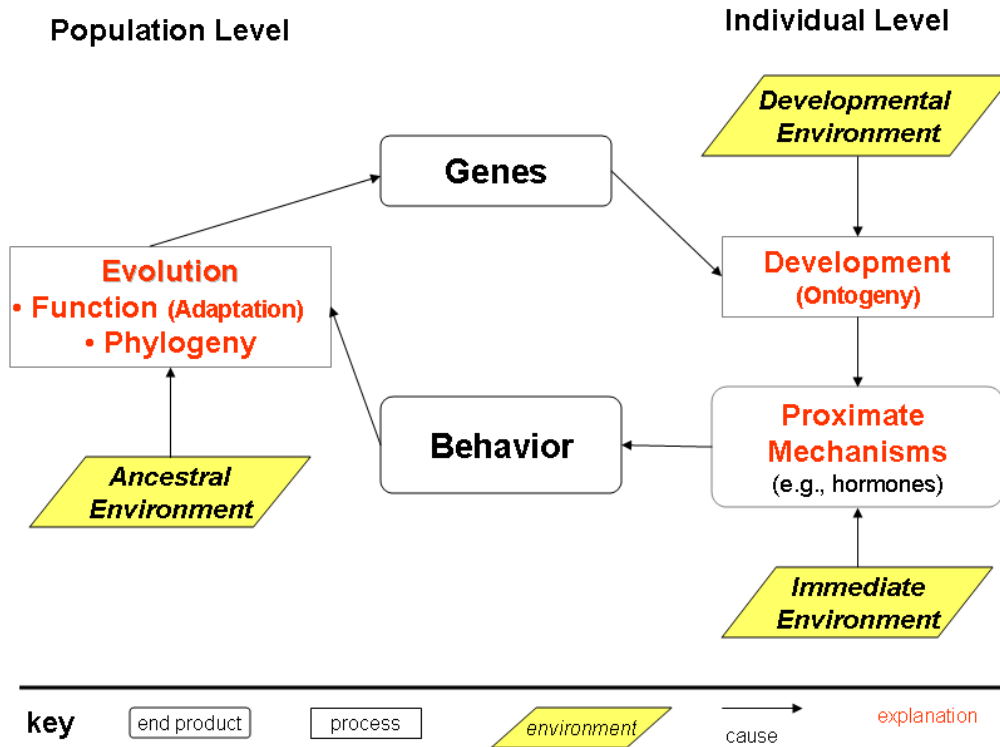
In examining living organisms biologists are confronted with diverse levels of complexity (e.g. the chemical level, the physiological level, the psychological level, the social level). Subject of investigation are **functional relations between cause and effect** within and between the levels. Within the scope of (behavioral) physiology they examine, inter alia, hormonal and neuronal aspects such as the influence of social and ecological conditions on the release of certain transmitters and hormones, and the effects of such releases on behavior. In mammals, stress during birth has a tokolytic (contraction-suppressing) effect. Findings regarding the basic levels are a (proximate) prerequisite for understanding superior levels. However, awareness of the chemical messengers of nerve cells (transmitters) is not enough to understand the superior levels of neuroanatomic circuit diagrams or behavior: "The whole is more than the mere sum of its parts." - All levels must be considered as being equally important (cf. "Laws about the Levels of Complexity" of [Nicolai Hartmann](#); see also [Transdisciplinarity](#)).

4 Development ([ontogeny](#))

In the later 20th century, social scientists debated whether human behavior was the product of nature (genes) or nurture (environment in the developmental period, including culture). The consensus among biologists now is that behavior is the product of [gene-environment interaction](#), in which the whole can be more than the sum of the parts, that is, the genetic and environmental components. By way of contrast, tallness may simply be the sum of “tall genes” and an environment rich in food.

An example of interaction (as distinct from the sum of the components) involves familiarity from childhood. In a number of species, individuals prefer to associate with familiar individuals but prefer to mate with unfamiliar ones (Alcock 2001:85-89, [Incest taboo](#), [Incest](#)). By inference, genes affecting living together interact with the environment differently from genes affecting mating behavior. A homely example of interaction involves plants: Some plants grow toward the light ([phototropism](#)) and some away from gravity ([gravitropism](#)). Such species react differently to the same environment because of different genes.

Many forms of developmental learning have a [critical period](#), for instance, for [imprinting](#) among geese and [language acquisition](#) among humans. In such cases, genes determine the timing of the environmental impact.



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Recursion, in [mathematics](#) and [computer science](#), is a method of defining [functions](#) in which the function being defined is applied within its own definition; specifically it is defining an infinite statement using finite components. The term is also used more generally to describe a process of repeating objects in a self-similar way. For instance, when the surfaces of two mirrors are exactly parallel with each other the nested images that occur are a form of infinite recursion.

In [mathematics](#) and [computer science](#), a class of objects or methods defined by a simple base case (or cases) and rules to reduce all other cases toward the base case.

For example, the following is a recursive definition of a person's ancestors:

- One's [parents](#) are one's [ancestors](#) (*base case*).
- The parents of one's ancestors are also one's ancestors (*recursion step*).

The [Fibonacci sequence](#) is a classic example of recursion:

- Fib(0) is 0 [base case]
- Fib(1) is 1 [base case]
- For all integers $n > 1$: Fib(n) is (Fib(n-1) + Fib(n-2)) [recursive definition]

Although many mathematical functions can be expressed recursively, the overhead of actually applying the recursive definition may be prohibitive. For example:

- Factorial(1) is 1 [base case]
- For all integers $n > 1$: Factorial(n) is ($n * \text{Factorial}(n-1)$) [recursive definition]

A convenient mental model is that a recursive definition defines objects in terms of "previously defined" objects of the class to define. For example: How do you move a stack of 100 boxes? Answer: you move one box, remember where you put it, and then solve the smaller problem: how do you move a stack of 99 boxes? Eventually, you're left with the problem of how to move a single box, which you know how to do.

Definitions such as these are often found in mathematics. For example, the formal definition of [natural numbers](#) in set theory is: 1 is a natural number, and each natural number has a successor, which is also a natural number.

Here is another, perhaps simpler way to understand recursive processes:

1. Are we done yet? If so, return the results. Without such a *termination condition* a recursion would go on forever.
2. If not, *simplify* the problem, solve the simpler problem(s), and assemble the results into a solution for the original problem. Then return that solution.

A more humorous illustration goes: "To understand recursion, one must first understand recursion." Or perhaps more accurate is the following, from [Andrew Plotkin](#): "If you already know what recursion is, just remember the answer. Otherwise, find someone who is standing closer to [Douglas Hofstadter](#) than you are; then ask him or her what recursion is."

Examples of mathematical objects often defined recursively are [functions](#), [sets](#), and especially [fractals](#).

A **finite state machine (FSM)** or **finite state automaton** (plural: *automata*), or simply a **state machine**, is a model of behavior composed of a finite number of [states](#), transitions between those states, and actions. It is similar to a "flow graph" where we can inspect the way in which the logic runs when certain conditions are met. A finite state machine is an abstract model of a machine with a primitive (sometimes read-only) internal memory.

A current *state* is determined by past states of the system. As such, it can be said to record information about the past, i.e., it reflects the input changes from the system start to the present moment. A *transition* indicates a state change and is described by a condition that would need to be fulfilled to enable the transition. An *action* is a description of an activity that is to be performed at a given moment. There are several action types:

Entry action

which is performed *when entering* the state

Exit action

which is performed *when exiting* the state

Input action

which is performed depending on present state and input conditions

Transition action

which is performed when performing a certain transition

A FSM can be represented using a [state diagram](#) (or state transition diagram) as in figure 1 above. Besides this, several [state transition table](#) types are used. The most common representation is shown below: the combination of current state (B) and condition (Y) shows the next state (C). The complete actions information can be added only using footnotes. An FSM definition including the full actions information is possible using [state tables](#) (see also [VFSM](#)).

A **Turing machine** is a theoretical device that manipulates symbols contained on a strip of tape. Despite its simplicity, a Turing machine can be adapted to simulate the logic of any [computer](#) algorithm, and is particularly useful in explaining the functions of a [CPU](#) inside of a computer. The "Turing" machine (its author called his machine an "*a*(utomatic)-machine") was described by [Alan Turing](#) in 1937.^[1] Turing machines are not intended as a practical computing technology, but rather as a [thought experiment](#) representing a computing machine. They help computer scientists understand the limits of mechanical computation.

A succinct definition of the thought experiment was given by Turing in his 1948 essay, "Intelligent Machinery". Referring back to his 1936 publication, Turing writes that the Turing machine, here called a Logical Computing Machine, consisted of:

...an infinite memory capacity obtained in the form of an infinite tape marked out into squares on each of which a symbol could be printed. At any moment there is one symbol in the machine; it is called the scanned symbol. The machine can alter the scanned symbol and its behavior is in part determined by that symbol, but the symbols on the tape elsewhere do not affect the behavior of the machine. However, the tape can be moved back and forth through the machine, this being one of the elementary operations of the machine. Any symbol on the tape may therefore eventually have an innings^[2]. (Turing 1948, p. 61)

A Turing machine that is able to simulate any other Turing machine is called a [Universal Turing machine](#) (UTM, or simply a **universal machine**). A more mathematically-oriented definition with a similar "universal" nature was introduced by [Alonzo Church](#), whose work on [lambda calculus](#) intertwined with Turing's in a formal theory of [computation](#) known as the [Church–Turing thesis](#). The thesis states that Turing machines indeed capture the informal notion of effective method in [logic](#) and [mathematics](#), and provide a precise definition of an [algorithm](#) or 'mechanical procedure'.

Studying their [abstract properties](#) yields many insights into [computer science](#) and [complexity theory](#).

A **hidden Markov model (HMM)** is a [statistical model](#) in which the system being modeled is assumed to be a [Markov process](#) with unobserved state. An HMM can be considered as the simplest [dynamic Bayesian network](#).

In a regular [Markov model](#), the state is directly visible to the observer, and therefore the state transition probabilities are the only parameters. In a *hidden* Markov model, the state is not directly visible, but output dependent on the state is visible. Each state has a probability distribution over the possible output tokens. Therefore the sequence of tokens generated by a HMM gives some information about the sequence of states. Note that the adjective 'hidden' refers to the state sequence through which the model passes, not to the parameters of the model; even if the model parameters are known exactly, the model is still 'hidden'.

Hidden Markov models are especially known for their application in [temporal](#) pattern recognition such as [speech](#), [handwriting](#), [gesture recognition](#), [part-of-speech tagging](#), [musical score](#) following, [partial discharges](#) and [bioinformatics](#).

In [automata theory](#), a **pushdown automaton (PDA)** is a [finite automaton](#) that can make use of a [stack](#) containing data.

Pushdown automata differ from finite state machines in two ways:

1. They can use the top of the stack to decide which transition to take.
2. They can manipulate the stack as part of performing a transition.

Pushdown automata choose a transition by indexing a table by input signal, current state, and the symbol at the top of the stack. This means that those three parameters completely determine the transition path that is chosen. Finite state machines just look at the input signal and the current state: they have no stack to work with. Pushdown automata add the stack as a parameter for choice.

Pushdown automata can also manipulate the stack, as part of performing a transition. Finite state machines choose a new state, the result of following the transition. The manipulation can be to push a particular symbol to the top of the stack, or to pop off the top of the stack. The automaton can alternatively ignore the stack, and leave it as it is. The choice of manipulation (or no manipulation) is determined by the transition table.

Put together: Given an input signal, current state, and stack symbol, the automaton can follow a transition to another state, and optionally manipulate (push or pop) the stack.

In general pushdown automata may have several computations on a given input string, some of which may be halting in accepting configurations while others are not. Thus we have a model which is technically known as a "nondeterministic pushdown automaton" (NPDA). Nondeterminism means that there may be more than just one transition available to follow, given an input signal, state, and stack symbol. If in every situation only one transition is available as continuation of the computation, then the result is a [deterministic pushdown automaton](#) (DPDA), a strictly weaker device.

If we allow a finite automaton access to two stacks instead of just one, we obtain a more powerful device, equivalent in power to a [Turing machine](#). A [linear bounded automaton](#) is a device which is more powerful than a pushdown automaton but less so than a Turing machine.

Pushdown automata are equivalent to [context-free grammars](#): for every context-free grammar, there exists a pushdown automaton such that the language generated by the grammar is identical with the language generated by the automaton, which is easy to prove. The reverse is true, though harder to prove: for every pushdown automaton there exists a context-free grammar such that the language generated by the automaton is identical with the language generated by the grammar.

In [formal language theory](#), a **context-free grammar (CFG)**, sometimes also called a [phrase structure grammar](#) is a [grammar](#) which naturally generates a [formal language](#) in which clauses can be nested inside clauses arbitrarily deeply, but where grammatical structures are not allowed to overlap.

The canonical example is matching parentheses: parentheses of different types must open and close correctly inside each other, like this:

([[(([]]) (]))

like any context free grammars, the logical units, the contents of corresponding matched parentheses, nest cleanly.

A language which is *not* context free is that of two different types of parentheses, each separately balanced disregarding the other, but where the two types don't nest inside one another, for example:

[[[[((((]]]]))) (() () () ()]]]]

The logical units in this language overlap.

In terms of [production rules](#), every production of a context free grammar is of the form

$$V \rightarrow w$$

where V is a single [nonterminal](#) symbol, and w is a string of [terminals](#) and/or nonterminals (w can be empty). These rewriting rules applied successively produce a [parse tree](#), where the nonterminal symbols are nodes, the leaves are the terminal symbols, and each node expands by the production into the next level of the tree. The tree describes the nesting structure of the expression.

In a context free grammar the left hand side of a production rule is always a single nonterminal symbol. In a general grammar, it could be a string of terminal and/or nonterminal symbols. The term "context-free" means that the rules by which nonterminals are rewritten do not depend on the surrounding symbols, the context.

[Context-free languages](#) are exactly those which can be understood by a finite state computer with a single [infinite stack](#). In order to keep track of nested units, one pushes the current parsing state at the start of the unit, and one recovers it at the end.

Context-free grammars play a central role in the description and design of [programming languages](#) and [compilers](#). They are also used for analyzing the [syntax](#) of [natural languages](#). [Noam Chomsky](#) has posited that all human languages are based on context free grammars at their core, with additional processes that can manipulate the output context free component (the transformations of early Chomskyan theory).

Early information theoretic approaches natural language assumed that the processes that limit the speaker's choice were local. That is, natural languages were hypothesized to be stationary in the sense that statistical effects on choice would be restricted to a relatively small window that could be modeled by digrams (pairs of words) or trigrams (triples of words) ! Hidden Markov Models. Chomsky (1956), however, argued persuasively that natural languages are not stationary; indeed, languages could contain unbounded nested dependencies, as witnessed by the relationship between pairs like *both...and...* and *either...or....* [Chomsky, Noam. 1956. Three models for the description of language. *IRE Transactions on Information Theory* 2, 113–124.]