What is the Unit of Natural Selection?

Is the Gene's Eye View of Evolution Unacceptably Reductionist?

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The gene as the solution to the debate over the level at which natural selection acts has often been termed as too reductionist, but is this a valid criticism? Exploring this question in the context of nonlinearity illuminates not only the debate over the unit of natural selection but also the broader debate on reductionism versus holism in science.

"It's the genes that, for their own good, are manipulating the bodies they ride about in. The individual organism is a survival machine for its genes": Richard Dawkins

"…natural selection works on a hierarchy of levels simultaneously, of which genes are one and organisms are another, and…you also have higher units, such as populations and species, at which selection is very effective": Stephen Jay Gould

"What doesn't come out clearly in Darwinism is the notion that what happens in evolution is that organisms express their own natures, so that they are to be valued for their being rather than for their function": Brian Goodwin

The above quotes [1] represent the different extremes of the intellectual arena spanned by the debate over the unit of natural selection or 'optimon'. At one level, the resolution of this dispute lies in the domain of biology, and the outcome is important to the way biologists think about living organisms. But more broadly, the disagreement expressed above reflects a philosophical dispute to do with reductionism and holism as different scientific approaches to a particular question. While reductionists think that a natural system is best understood by breaking it down into smaller parts and studying those smaller parts, holists believe that key features of a system's behaviour are destroyed when it is

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broken down, and that it hence cannot be reconstructed by studying the smaller parts. The reductionism-holism debate is one that affects how *all* scientists tackle the questions they ask about nature, but is apparently further from being resolved than the optimon debate. The optimon debate has been influenced by the reductionism-holism debate to the extent that different points of view in the former have been labelled as reductionist or holist, but can examining the optimon debate throw light on the broader philosophical controversy?

Our understanding of evolution by natural selection has come a long way since 1859 when Darwin first described his observations of how living organisms survive and reproduce and showed that natural selection could explain these observations. His observations and subsequent deductions (*emphasized*) were:

- The reproductive potential of living organisms is immense; in principle, with unlimited resources, populations would tend to grow exponentially.

- This reproductive potential, however, is not attained – the size of a population tends to remain approximately constant, or in any case, rarely displays exponential growth.

- *There is therefore a struggle for existence – not all individuals survive.*

- Individuals vary considerably and variants have offspring with similar variations.

- *Individuals with favourable variations will survive and reproduce better than those lacking these variations.*

Darwin saw natural selection as the outcome of this differential survival and reproduction, which leads to an increase in the proportion of organisms possessing these favourable traits within a population. The evolution of any trait is a result of the degree to which possessing this trait helps an individual to survive and reproduce. Favourable traits, which enable an organism to perform better some task that affects its survival or reproduction, are expected to flourish and spread within a population while deleterious traits are expected to be eliminated (see *Box* 1).

Darwin realized that in order for 'winners' to emerge in the struggle for existence, the competitors in this struggle must vary in their traits, and that success or failure at surviving or reproducing must depend on this variation. Moreover, variation must be heritable if natural selection is to result in a change that lasts longer than a generation. But because Darwin did not know the mechanism of inheritance, he did not understand the precise mechanism of natural selection. He realized that natural selection results in the optimization of the survival and reproduction of *something* – he assumed that this something is the individual organism. After the discovery that genes are responsible for the inheritance of traits, biologists, most importantly George Williams, William Hamilton and Robert Trivers, put forward the idea that

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Box 1. The Evolution of Beak Dimension in Darwin's Finches

The Galapagos archipelago is home to fourteen species of finches, each characterized in part by the dimensions of its members' beaks. A thirty year long study on the island of Daphne Major has shown how natural selection results in the adaptation of beak dimensions to available food [2]. Daphne Major is home to a population of medium ground finches, which, at the start of the study, contained both large finches with larger blunt beaks and small finches with smaller pointed beaks. The occurrence of a drought, however, led to changes in the type of food available on Daphne Major, which in turn altered the frequency of long- and short-beaked finches on the island. During the drought, small seeds became scarce while large hard seeds were abundant. Large birds with blunt beaks that had the strength and appropriate beak shape to crack open and eat the hard seeds continued to enjoy a supply of food, but the small birds with pointed beaks died from starvation. Large blunt-beaked birds survived the drought and were able to breed, so the next generation of medium ground finches had a much higher proportion of large birds with large blunt beaks.

Implicit in the last sentence is the assumption that beak dimensions are heritable, allowing one to recast the above scenario in terms of the selection of alleles. If beak size and shape are heritable, there are genes or groups of genes that affect beak – the presence of a certain allele or set of alleles is correlated with increased beak size or blunt beaks, while other alleles decrease beak size and make beaks thinner or sharper, this variation being created by random mutations. At the time of drought, finches that possess the alleles that increase beak size are more likely to survive. Consequently, these alleles will, as a result of their phenotypic effect, be more likely to be passed on to the next generation of finches. The alleles for large beaks would therefore have higher frequencies in the next generation than in the present generation and would gradually replace other competing alleles in the population.

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evolution is a result of the natural selection of genes. This 'gene's eye view' of evolution was popularized by Richard Dawkins in his books *The Selfish Gene* and *The Extended Phenotype*.

The gene's eye view added a new dimension to the optimon debate. While Darwin himself believed that natural selection acts upon individual organisms, the opinion that populations or species are the unit of natural selection had since gained ground. Scientists' acceptance of the gene's eye view meant that the debate now spanned the hierarchy of levels of organisation of living organisms – from genes to individuals to populations and species. But it also came to span the entire range of the contemporary dispute between reductionism and holism.

In this article, I try to make sense of the question of what the unit of natural selection, or optimon, is. But beyond that, I ask how the optimon debate can influence the philosophical discussion of whether nature is explained better by a reductionist or a holist approach to science. I first discuss what is meant by reductionism and holism in the context of the mathematical idea of nonlinearity, examine the optimon debate from the perspective of nonlinearity, and finally discuss the implications of nonlinearity for both the optimon debate and the reductionism-holism debate.

Reductionism and Nonlinearity

Reductionism can loosely be defined as an approach to science that studies the parts making up a system to understand the behaviour of the whole system. A system is therefore 'reduced' to the smaller parts that make it up. Holism can, even more loosely, be defined as an 'anti-reductionist' approach to science, and holists believe that looking at smaller parts making up a system cannot explain the behaviour of the whole system.

At the outset, it is important to distinguish between reductionism that is compatible with nonlinearity and reductionism that is not. Some reductionists claim that systems can be studied and understood *in their entirety* by looking *only* at the smallest parts that make up the system and then extrapolating from their behaviour to deduce the behaviour of the rest of the system. Such a reductionist is what I call a 'linear reductionist' (Dawkins calls this a "greedy reductionist" [3]), because systems that can be explored by looking only at their smallest parts are necessarily linear.

To see why, consider the structure of systems studied within the framework of science. Even the simplest of these systems is built up of many layers, with building blocks starting as small as subatomic particles and systems ending up as large as galaxies, or as complex as the brain. The behaviour of parts constituting one layer and the relationship between layers are what that determine whether a system is linear or nonlinear. If the behaviour or relationship is defined by a function or operator 'f' such that $f(a + b) = f(a) + f(b)$, it is linear.

The essence of a linear system is its additive nature – it allows the superposition of states of a system by simple addition. For instance, two forces can be combined by vector addition because the underlying equations of motion are linear. The additive nature of linear systems ensures that the behaviour of the lowest layers and the relationships between layers can be used to predict features of higher layers. Similar extrapolation in nonlinear systems is difficult because of two features of nonlinear systems – sensitive dependence on initial conditions and emergence. Sensitive dependence on initial conditions, or the 'butterfly effect', implies that even a small change in the initial conditions of a nonlinear system has profound effects on its final state. Emergent properties are characteristics of higher levels of the system that arise as a result of the nonlinear behaviour of lower levels. For instance, the overall behaviour of the atmosphere emerges from the nonlinear interaction of the billions of gaseous molecules that it is made up of, and the weather is so sensitive to initial conditions that meteorologist Edward Lorenz has said that a butterfly flapping its wings can "cause" a storm thousands of kilometres away [4].

For centuries, scientists have studied linear approximations of natural systems despite the fact that most natural systems are nonlinear. While it is no doubt illuminating to study linear

approximations, their accuracy is limited and they cannot explain features of the system arising from nonlinearity. But since nonlinearity is difficult to handle mathematically, scientists stuck to tractable linear models of nature. With the advent of computers in the 1960–70's allowing for complex and rapid computation, a large number of scientists from various disciplines, recognizing that science had been neglecting the nonlinearity of natural systems [4], began to explain phenomena in nonlinear terms. They soon realized that nonlinearity captured the essence of the behaviour of natural systems in a way that linearity could not.

The effectiveness of nonlinearity in uncovering essential features of a system often depends on it forcing one to study higher levels of organization together with lower levels, because nonlinear relationships, the butterfly effect, and emergence link different layers inextricably. But this appears to imply that exploring the lower levels of a nonlinear system is never, or rarely, fruitful simply because nonlinearity results in quantitatively unpredictable higher level behaviour.

The rationale of the gene's eye view of evolution stems from recognizing nonlinearity, but also acknowledging that nonlinearity does not warrant always looking at a system from the perspective of higher levels of organization. When studying any system, there are certain features or properties of the system that are particularly relevant to the phenomenon or aspect of the system being studied. In a nonlinear system, these features 'emerge' at a certain level and it might become appropriate to study the phenomenon at the level at which these features emerge. If key features emerge at relatively low level, and one views the system from this low level, the approach could be called a reductionist one. However, this 'nonlinear reductionism' is distinct from linear reductionism; far from ignoring the nonlinearity of the system, it *follows* from it. Approaching the optimon debate in the context of nonlinearity clarifies the issue of whether the gene solution is unacceptably reductionist or not.

The Unit of Natural Selection

Without putting it in precisely these terms, Richard Dawkins, in his book *The Extended Phenotype*, uses a method of reasoning that involves locating the level in a nonlinear system at which key features emerge to investigate the issue of the unit of natural selection. He begins by rephrasing Darwin's observations and deductions in an abstract sense that makes no reference to life on earth, recognizing that the essential phenomena involved in natural selection are survival and reproduction. Any entity that survives and replicates in an environment in which it struggles for existence and competes with similar entities for resources, can undergo natural selection. Translated into the terminology of abstract replicators, the prerequisites for natural selection to occur become:

- Replicators must exist.

- There must be variation in the structure of these replicators and in their effects; the variations in effects must cause differential replicator survival and replication.

- The differences between and changes in the replicators must be heritable (passed on to copies of the replicator).

The resultant change in the frequency of replicators in a population results in evolution by natural selection [3].

Further dissection of the prerequisites for natural selection shows that, in order for a replicator to undergo natural selection, it must be an active, germ-line replicator. An active replicator is one whose nature (form, structure, effect on the surroundings, etc.) influences the likelihood of it being copied, and a germ-line replicator is potentially an ancestor of an infinite number of replicators. As Dawkins puts it, "If replicators exist that are active, variants of them with certain phenotypic effects tend to out-replicate those with other phenotypic effects. If they are also germ-line replicators, these changes in relative frequency can have a long term evolutionary impact." [3]

The question now becomes one of locating the level in the hierarchy of living systems at which the properties of the active germ-line replicator emerge. Individuals, groups of individuals and species can immediately be ruled out because they do not replicate. A replicator reproduces the changes or mutations that happen to it; an organism cannot transmit its acquired characteristics in a Lamarckian fashion because there is no causal arrow that leads from organism to genes. For instance, a mouse whose tail is cut off does not subsequently have tailless offspring. Organisms, groups of organisms and species are 'vehicles' [3] that carry replicators made up of the molecule DNA, and are not replicators themselves (*Figure* 1).

In other respects, however, individuals seem to fit the role of the optimon very well – individuals are subject to the selection pressures exerted by the environment, and, as Stephen Jay Gould puts it, "organisms are doing the struggling out there" [1]. Consequently, it appears that natural selection depends on the *individual's* survival and reproduction. But why do some individuals survive and reproduce better than others? Because they possess traits that enable them to do so – these traits are in fact the *means* by which the replicators responsible for creating the traits propagate themselves. Considering the traits as all-important suggests that the organism is central to natural selection, but separating the features essential to the optimon from characteristics of individual organisms immediately shows that the individual cannot be the optimon because it cannot replicate.

In fact, the replicators exist *within* individual organisms and are made up of the information-

bearing molecule, DNA, which satisfies the most important conditions for being the unit of natural selection. DNA replicates, making any information it encodes heritable and DNA is translated into proteins, the building blocks of life, implying that its information is expressed phenotypically. Variation in DNA can therefore result in phenotypic variation, on which natural selection can act. No other component of living organisms satisfies these properties and it seems clear that DNA constitutes the optimon to some extent.

But how much? DNA is made up of nucleotides, which are organised into genes, chromosomes, genomes and gene pools, and each of these levels could, based on the criterion of replication, be the optimon. The question of which level of organisation of the hierarchy is the optimon is resolved by recognizing further characteristics required of the optimon, and locating the level at which these characteristics emerge. In the following discussion, I first use characteristics of the optimon to explain why all levels in the DNA hierarchy other than the gene are *not* the optimon. Two such characteristics, frequency and phenotypic expression, rule out higher (chromosomes, genomes) and lower (nucleotides, codons) levels of the DNA hierarchy respectively.

It is the *change in frequency* of replicators in a population relative to their alternatives that results in evolution. Consider a single chromosome (other than sex-specific chromosomes such as the Y chromosome in humans) or the entire genome of a sexually reproducing organism; at the time of gamete formation, crossing over in meiosis results in the creation of a unique chromosome, and the fusion of two gametes at fertilization creates a unique genome. In sexually reproducing organisms, chromosomes and genomes do not remain intact for longer than a generation, and their selection cannot have the long term impact essential for the gradual evolution of the complex features of life on earth. In asexually reproducing organisms, whose genome remains unchanged for generations except by mutations, genome selection is plausible. Since a large number of organisms reproduce asexually, genome selection is probably a widespread phenomenon, but the genome cannot be the optimon in sexually reproducing organisms.

Phenotypic expression is relevant to the possibility that a single nucleotide is the optimon. It is important in the context of natural selection because the features of the replicator that are subject to the external environment, which is the framework within which the replicators survive and reproduce, are those that arise from the phenotypic expression of the replicator. Nucleotides replicate and cannot be fragmented as chromosomes can, but a nucleotide exerts a phenotypic effect *only* in the context of a codon. For instance, the nucleotide sequence CUA codes for the amino acid leucine. CCA, however, codes for proline. The position of adenine is the same in both triplets, but since the effect it has depends upon the other nucleotides in the

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Box 2. Glossary

Chromosome: A long chain of DNA plus associated proteins. Most organisms have two sets of chromosomes in each cell, with two chromosomes corresponding to form a pair.

Meiosis: Cell division resulting in four daughter cells with half the number of chromosomes of the parent cell. The process is a prerequisite for sexual reproduction and involves exchange of genetic information between chromosomes of a pair in the process of crossing over.

Gamete: The cell that forms after meiosis, with half the number of chromosomes; two gametes fuse at the fertilization stage of sexual reproduction, regaining the original chromosome number.

Gene pool: The collective genetic information contained within a population or species of sexually reproducing organisms. For a species it remains isolated from other gene pools since members of two species cannot interbreed.

Nucleotide: In this context, the building block of DNA comprising of the sugar ribose, a phosphate group and a nitrogenous base, one of adenine, guanine, thymine or cytosine. Nucleotides also can be made of other sugars and bases and make up RNA, energy storing molecules such as ATP, etc.

Codon: A sequence of three nucleotides that translates into one amino acid.

Cistron: A sequence of codons that translates into a protein.

*Allele*: One of a number of alternative forms of the same gene.
Phenotype: the expression and impact of a replicator on its surroundings. For instance, in living organisms, the information stored in the genes of an organism is manifest as traits or features of the organism, such as eye colour, leaf shape, etc.

El Nino: An oscillation or disruption in the ocean-atmosphere system of the Tropical Pacific affecting global weather, usually causing excessive rainfall and flooding.

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triplet, it has different effects in different contexts. The properties of a codon, the smallest unit of DNA that is expressed phenotypically, emerge at the level of three nucleotides, but even the phenotypic expression of a codon is not consistent – the same amino acid has different functions in different proteins. A protein, however, is an entity with a specific function or role and can be selected for or against by natural selection. A cistron, which codes for a protein, is therefore the smallest stretch of DNA with a consistent phenotypic effect.

Having eliminated nucleotides, codons, chromosomes, and genomes from the role of the optimon, we are left to consider genes and gene pools (*Figure* 1). Gene pools are replicators and, due to the reproductive isolation of species, are stable entities not subject to fragmentation. For selection to occur between gene pools there must be many gene pools to choose from. According to Eldredge and Gould's theory of Punctuated Equilibrium, many new species arise at
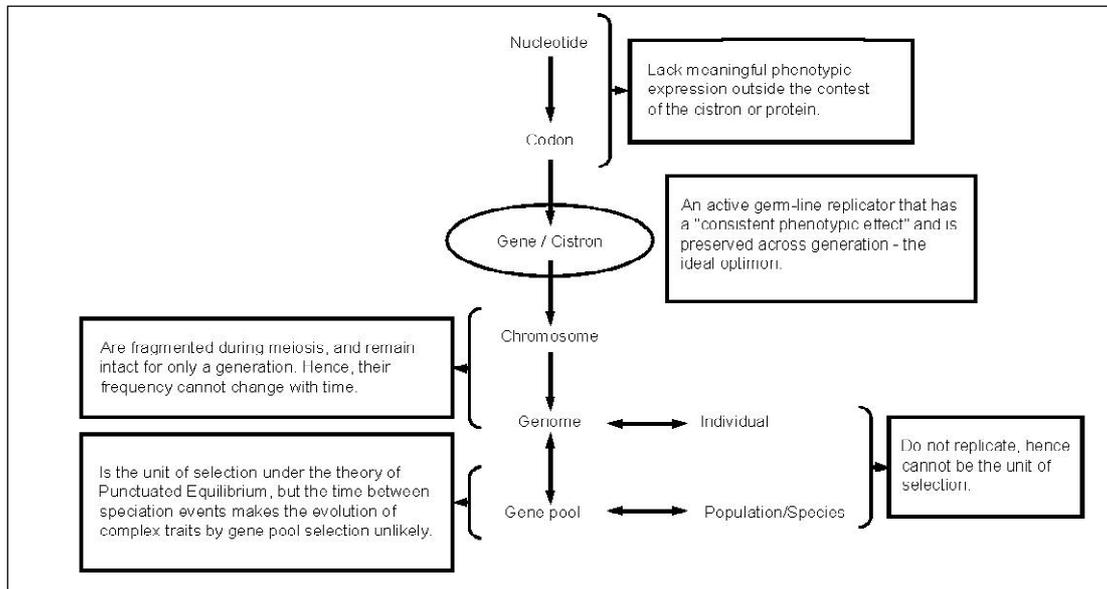
Figure 1. A schematic representation of the levels of the hierarchy of living organisms and their genetic material spanned by the debate over the unit of natural selection. Each layer is accompanied by an explanation of why the particular layer is or is not the optimon.

'speciation events' – relatively short periods of time where species rapidly diverge to form new species, interspersed with relatively long periods of inactivity or stasis. Also, according to Wright's Rule [3], the formation of new species is not a directed phenomenon – with respect to any trait, a new species is equally likely to display any of the alternatives of the trait (analogous to random mutations in DNA). The theory of Punctuated Equilibrium proposes that these 'mutations' happen relatively close together at speciation events, thus allowing for gene pool selection.

The objection to gene pool selection is that the time between speciation events is too long to allow for complex adaptations to arise. It takes between some minutes and some decades for a gene to be copied into a new organism; the time between speciation events is millions of times longer. Because speciation events are relatively so rare, for complex adaptations to develop by gene pool selection, it is essential, but also extremely unlikely, that different traits beneficial to the survival of the gene pool arise simultaneously. While gene pool selection may occur, it cannot be the main force behind the evolution of complex adaptations.

We have now seen that selection cannot occur at the level of a single nucleotide or, for sexually reproducing organisms, of a chromosome or genome, and the optimon must therefore lie in between the two (*Figure* 1). It is here that the features of longevity, fecundity and fidelity are

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Box 3. Explaining Segregation Distorters

'Segregation distorters' or 'meiotic drive genes' – alleles that bias the process of meiosis so that over fifty percent of the gametes produced by an organism contain this allele – are explicable only under the gene's eye view of selection [3]. Segregation distorters bias meiosis by the destruction of gametes that do not contain this allele. If evolution did proceed by the natural selection of individual organisms, the presence of such alleles would be hard to explain: the allele reduces the gamete count of the organism, thus reducing the organism's chances of reproducing successfully. From the standpoint of genome or chromosome selection also this event is incomprehensible, since the chromosome and the genome are split up and recombined during meiosis and fertilization, so parts of the old chromosome or genome may benefit from the presence of the segregation distorter, if they ride along with it, while others will lose out if they are present in the gametes that get destroyed by the segregation distorter. In a gene pool, too, part of the gene pool will benefit on some occasions and part will be at a disadvantage; on an average, in chromosome, genome or gene pool selection, no part is benefited consistently by the segregation distorter allele.

However, recognizing the gene as the optimon, this phenomenon becomes explicable – a segregation distorter has the ability to survive and spread within a population and is a successful allele, when compared with alleles that are not segregation distorters. Its nature as a segregation distorter definitely benefits its own survival and replication, even though it does not benefit the survival and replication of other genes. Segregation distorters cannot overrun the entire gene pool, however, since in a homozygous condition segregation distorters would cause the destruction of all gametes, rendering organisms sterile, to the detriment of all genes including segregation distorters. The frequency of segregation distorters within the gene pool reaches an optimum, largely due to the effects of 'modifier genes' at other loci which act to reduce the effect of the segregation distorter alleles. This conflict *between* genes is just one instance of the broader phenomenon of 'intragenomic conflict' that can be explained only by considering the gene to be the optimon.

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important. D L Hull has said (quoted in [3]), "Replicators need not last forever. They only need to last long enough to produce additional replicators [fecundity] that retain their structure largely intact [fidelity]. The relevant longevity concerns the retention of structure through descent." The optimon is therefore a length of DNA that replicates sufficiently frequently in a largely error-free manner for many generations. The exact length of the optimon is not universal, and depends on, in addition to longevity, fecundity, and fidelity of the stretch of DNA in question, the selection pressure on the phenotype of that DNA (e.g., a larger bit of DNA that is vitally important to the survival of the organism is as likely to be an optimon as a smaller bit of DNA that is not as important). This definition of the optimon might correspond with other definitions of the gene – the unit of natural selection might, but need not, be exactly the section of DNA that is translated into a protein. However, the very term optimon (following muton, cistron, and other such terms) is meant to suggest that the gene can be *defined* as that unit of DNA that is the unit of natural selection.

Is the Gene's Eye View of Evolution Unacceptably Reductionist?

Having looked at reductionism and nonlinearity and examined the logic behind the proposal that the gene is the unit of natural selection, I turn to the question of whether the gene's eye view of evolution is unacceptably reductionist. While no clear definition of 'unacceptably reductionist' is available, criticism of the gene's eye view of the optimon problem as well as more general criticisms of reductionism suggest that an 'unacceptable reductionist' is the linear reductionist described earlier. Critics of the notion of 'reductionism' point to the immense complexity of natural systems and declare that reductionism is just too simple an approach to describing such complexity. This is captured in the oft-quoted holist maxim "the whole is greater than the sum of its parts" – the reference to addition makes it almost certain that it is linear reductionism that is being criticized. But a linear reductionist is merely a straw man; in practice, nowadays scarcely anyone believes that natural systems are linear. In fact, most reductionists are nonlinear reductionists, and would even agree with the holist maxim, but would go on to say that despite the whole being greater than the sum of its parts, one can comprehend aspects of the whole by studying its parts while keeping in mind the relationships between parts and acknowledging the nonlinearity of these relationships.

Building on this general criticism, most critics of the gene's eye view say, and rightly, that the development of an organism from the genetic information stored in its DNA is a nonlinear process, but deduce, wrongly, that because it is the organism that finally experiences the selection pressures of the environment and due to the apparently unbridgeable nonlinear 'gap' between DNA and organism, natural selection cannot act on genes. As Gould says,

"If organisms could be described as the additive accumulation of what their genes do, then you could say that organisms are representing the genes, but they're not. Organisms have hosts of emergent characteristics. In other words, genes interact in a nonlinear way. It is the interaction that defines the organism, and if those interactions, in a technical sense, are nonadditive…then you cannot reduce the interaction to the gene. This is a technical philosophical point. As soon as you have emergent characteristics due to nonadditive interaction among lower-level entities, then you can't reduce to the lower-level entities, because the nonadditive features have emerged. These features don't get you into the higher level. His [Dawkins'] argument is wrong." [1]

Gould defends individual selection by sheltering behind the complexity that arises from the nonlinearity of the development of organisms, and the nonlinear way in which genes affect this development. Gould is right about this nonlinearity, but it does not affect the optimon debate – the gene's eye view depends on the *consistent effects* that genes have, which lead to the

differential survival and replication of genes. It does not depend on *how* these effects are caused.

Some think that Hamilton, Williams, Trivers, and Dawkins are unacceptable linear reductionists because they seem to be denying the nonlinearity of living systems. Dawkins counters this by pointing out the distinction between development and natural selection: while the development of an organism from a single cell definitely is a nonlinear process, it is not the same as natural selection. This counters objections like those raised by Gould, but does this mean that natural selection *is* a linear process?

Dawkins frames his argument in a way that only implicitly recognizes the nonlinearity inherent in the hierarchy of nucleotides, genes, gene pools and in their relationship with the organism. Consequently, one may finish reading Dawkins' account and not be entirely sure if he sees this as a linear or nonlinear hierarchy. However, it is not difficult to see that the process of the natural selection of genes not only does not conflict with the nonlinearity of living systems but that Dawkins' description of the process implicitly *depends* on nonlinearity.

How does the reasoning here recognize nonlinearity explicitly? Essentially, it involves identifying the features of the ideal optimon and then *locating the level at which these properties emerge*. Features like phenotypic expression simply do not exist at the level of the nucleotide – they emerge only at the codon level as a result of the organization of nucleotides. Processes such as meiosis act at even higher levels to cause events like the fragmentation of a chromosome, an event that does not affect lower levels such as nucleotides. Every time we speak of hierarchies where layers are related to each other in complex ways, of levels that have properties that preceding levels do not, every time we talk of emergence, we acknowledge the nonlinearity of the system in question. The "gene as the unit of natural selection" is not a *linear* solution to the optimon problem and is therefore not unacceptably reductionist.

The existence of a divide between reductionism and holism hinges on an apparent dichotomy between the two approaches, implying that they are mutually exclusive of each other. But this dichotomy is false – nonlinear reductionism and holism are both built upon foundations of nonlinearity and hence form part of a continuum. The optimon debate has a solution that lies closer to the apparently reductionist side of the continuum, but since the approach used to tackle the problem depends on the nonlinearity of the system being studied, it ensures that the answer indeed lies somewhere on the continuum and not in the domain of linear reductionism. A broader inference to draw from the optimon debate is that there is no definite solution to the reductionism-holism debate, or that there ought not to be a debate at all; instead, each system, or each problem related to a given system, occupies a position somewhere along the spectrum

between nonlinear reductionism and holism and what approach one uses to tackle the problem or the system will depend on where along this spectrum it lies.

It is extremely likely that the authors of the three quotes this essay begins with agree that living systems are nonlinear. Similarly, nobody involved in the reductionism–holism debate denies that the most fascinating natural systems are nonlinear. What remains is to examine the extent to which nonlinearity can be used to scale the gap between the reductionists and the holists, given that it essential to bridging that aspect of the divide that is manifest in the optimon debate.

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Suggested Reading

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[5]   Richard Dawkins, *The Selfish Gene,* Oxford University Press, 1976.
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