Darwinism and Selectionist Theories

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Technical Report 070618A

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Abstract-Darwin's natural selection theory of evolution to explain the origin of species is the archetype selectionist theory that inspired Jerne and Burnet's clonal selection theory of antibody diversity in immunology and various selectionist theories neurology such as Edelman's neuronal group selection theory. This work reviews these three seminal selectionist theories, and some general comments on universal selectionbased theories and frameworks.

Keywords-Natural Selection, Clonal Selection, Neuronal Selection, Darwinism, Selectionism

I. SELECTION THEORIES

Darwin's theory of natural selection is the archetype selectionist theory, which inspired the later theories of clonal selection in immunology and neuronal selection in neurology. These are perhaps the three more widely known selectionist theories [13,20], the first two of which are accepted as fact given the amount of supporting scientific evidence. This section briefly introduces each theory in turn, highlighting the principle aspects of each.

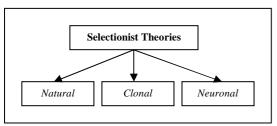


Figure 1 - Depiction of selectionist theories

A. Natural Selection Theory

What is the origin of species, the diversity and variety in form of living things? Darwin provided illumination of this problem in his renowned theory of natural selection [2].

A standard view to this general problem before Darwin's work was that species were created independently and positioned on earth in an immutable (unchangeable) form. Alternative and perspectives to this common view which contributed to Darwin's theory was (not limited to) the work of his grandfather (naturalist Erasmus Darwin), and the French naturalist Lamarck (both referenced highlighted by Darwin at the beginning of his abstract). Lamarck's theory of evolution 'hereditary of acquired characteristics' (Lamarckism [11]) proposed adaptations

to an organism are acquired by that organism over its lifetime and then passed to its offspring. Adaptation was defined by 'use and disuse' in the context of the environment (habitat and habit) where those physiological traits that are used are reinforced, and those that are disused atrophy, the characteristics of which are inherited.

Darwin proposed his 'natural selection' theory (Darwinism) of adaptation to explain the origin of species in which a selection process operates upon the accumulation of slight, successive, favourable variations over long periods of time. Darwin suggests that a given species is capable of creating far more progeny than can be supported for the species environment, thus there is a continual competition for survival in the context of limited resources. An inherited variation (born with, rather than acquired over the organisms lifetime) that results in a slight increase in chance of survival of the organism in its local environment (and subsequent reproduction) is a benefit, thus the organism is *naturally* selected in the face of competition. Darwin's decent with modification requires a strong principle of inheritance where slight variations that are selected for are propagated to progeny. Those variations that lead to less well-adapted organisms become extinct.

Reproduction: Individual growth with reproduction **Inheritance**: Inheritance implied by reproduction

Variation: Variation from the direct and indirect action of the external conditions of life, and from use and disuse

Competition: Rate of increase (reproduction) high enough (with regard to the environment) that it facilitates competition for survival (superfecundity or struggle for existence)

Natural Selection: Natural selection leading to the divergence of character and the extinction of less-improved forms

Figure 2 - Darwin's laws of evolution

The specific mechanisms of variation in organisms was not specified by Darwin, not ruling out 'use and disuse' and errors in the reproductive process. A modern evolutionary synthesis (neo-Darwinism) was achieved of Mendelian inheritance the integration (Mendelism) with Darwin's natural selection theory and the emerging field of genetics (DNA) [26] (major contributions not limited to [25,27]). Genetics provided the basis for inheritance (the genome), and mechanisms of variation (not limited to mutations to the genome and recombination of the genome in sexual reproduction).

B. Clonal Selection Theory

How can the immune system, specifically antibodies

be produced in response to practically any (even man made) antigens, and why does the response improve with subsequent exposures? This problem from immunology on the generation and diversity of antibodies was illumination by Burnet in his renowned theory of clonal selection based on Darwinian principles [8].

The popular theory for antibody diversity before the work of Jerne, Burnet, and Talmage was the 'template' theory of acquired immunity, outlined succinctly by Pauling [21]. The theory proposed that all antibody molecules were the same, and that through interaction with antigen inside antibody producing cells, antibody are instructed of the antigenic form, in effect cells using antigen as a template for antibody configuration. Jerne proposed a Darwinian-inspired 'natural selection' theory to address the list of growing problems with the template theory [22]. Jerne's theory suggested that a host possesses an innate diverse population of antibody molecules that compete for selection by antigen. The antigen-antibody complex triggers the production of more of the same selected antibody, with slight variations. Those antibodies that are selected for by selfantigens (autoimmune) are negatively selected, removed from the population.

Burnet extended Jerne's selectionist theory in his 'clonal selection' theory which proposed the lymphocyte (immune cell), rather than the antibody molecule was the unit of selection by antigen, resulting in the activation (release of antibody with the same specificity as the cells reactive site), and proliferation of the cell, with variation ([8] and elaborated in [9]). The same modification to Jerne's theory was proposed at the same time by Talmage ([3,4]), although Burnet took priority for the theory.

Initial Repertoire: Randomly generated initial population of antibody producing immune cells

One-to-one: An immune cell can detect and release antibody of one specificity, which is passed on to descendent cells

Elimination: Those initial cells that are reactive to self-tissues are selected against (killed)

Proliferation: Generation of antibody and the proliferators of the cell after contact (selection) with antigen

Forbidden: The elimination of progeny that can select for self tissues

Figure 3 - Summary of the characteristics of clonal selection (taken from [10])

Although the theory was proposed to explain the diversity of antibodies, the applicability of the theory has expanded with the developments of immunology. It applies both to B-lymphocytes (antibody producing), and T-lymphocytes (responsible for helping B cells and in killing infected cells). The specific mechanisms of variation were not specified by Burnet (or Talmage), although were later discovered by Tonegawa and colleagues to be genetic-based hypermutation (high-rate mutation) of progeny cells [24].

C. Neuronal Selection Theory

How does the brain increase efficiency in processing a given type of signal. How does it address new signals that have not been seen before, and how does it refine a response pattern when it receives repeats of the same signal? Edelman provided illumination on these problems with his 'group-selection theory of higher brain function' inspired by Darwinian principles [16].

There are many theories of brain function, including many selectionist theories, too many to compare and contrast (for example see Changeux [18]). Edelman's theory [16] ('Neural Darwinism' or 'theory of neuronal group selection' [15,17]), inspired by natural selection theory and clonal selection, suggests that pre-existing structural differences in multiply connected and distributed groups of neurons (brain cells) in the brain provide the basis for selection of groups based on function, and subsequent adaptation. Edelman describes how the nervous system is able to self-organise to store information and create new behavioural patterns.

Localisation: Groups of neurons are arranged into localised functional areas. The groups have similar or identical functions, although different internal connective structure (isofunctional and non-isomorphic providing degeneracy for selection to operate)

Neural Representation or Coding: Not specific to any neural representation, thus the theory assumes groups receive and respond to patterns of activity from other groups of neurons, although does not specify the nature of the spatiotemporal patterns

Synaptic Plasticity: the theory does not specify the mechanism for variation after selection (for example molecular synaptic), the theory does suggest that repeated selection alters their response and chance for further selection

Figure 4 - Summary of the principles of Neural Darwinism (from [12])

An evolved form of the theory is proposed with three primary tenants [15]: (1) developmental selection, (2) experimental selection, and (3) re-entrant mapping. Developmental selection is the physical process of cell organisation and connection, the development of the anatomy of the neural network (primary repertoire). The experimental selection is the modification of connection weights in the network with usage (secondary repertoire). Groups of neurons, and groups of groups of neurons form maps, which are interconnected with other maps. Re-entrant mapping is the indirect selection (stimulation) of maps by other connected maps.

D. Summary

Selection-based methodologies appear to be employed by nature to address problems with an unknown future. In evolution, the theory addresses species survival via adaptation to unknown changes in an environment. In immunology, the theory addresses detection and neutralisation of pathogen, given unknown changes encountered in a pathogenic environment. In neuroscience the theory addresses organisation, connectivity, and functionality of neuronal structures in response to unknown and changing sensory signals from an environment.

Theory	Environmental Challenge
Natural selection	Adaptations to changes in the habitat
Clonal Selection	Adaptations to pathogen exposure types and frequencies
Neuronal Selection	Adaptations to sensory stimuli types and frequencies

Table 1 - Summary of the environmental challenges for each theory

In each system, the proposed unit of selection is different from that which is inherited and varied. In evolution selection occurs against an organisms phenotype whereas inheritance and variation occurs in the genotype. Clonal selection has a similar relationship where the phenotype is the conformation and composition of the cells surface bound protein molecule, defined and manufactured from the cells genetic composition. In neuronal selection, a group of neurons and related structural and behavioural characteristics defines the phenotype (unit of selection), where as the chemical properties defines the substrate for variation. In effect, the genotype in each theory is implicitly selected when the expressed phenotype is selected, as there is a one-to-one causal relationship between the two.

Theory	Unit of selection	Unit of inheritance and variation
		variation
Natural selection	Genome (DNA)	Phenotype (structural and
		function behavioural
		characteristic)
Clonal Selection	Genetics of the cell	Surface-bound antibody
		molecule
Neuronal Selection	Synapses	Connectivity within a group
		of neurons

Table 2 - Summary of the units of selection and variation for each theory

II. DISCUSSION

The natural selection theory of evolution is easily underestimated. The theory not only subsumes the within-host nervous system and the immune system, but also the tools that facilitate variation and reproduction (the genome, sexual reproduction, and copying errors). This section discusses the selectionist theories from a sample of perspectives.

A. Adaptationism

An adaptation under a selectionist theory is a trait that has evolved over a period of time that provides a statistically improved chance of reproductive success (improves fitness in the face of competition for survival and reproduction) [14,19]. An adaptation (adaptationist) perspective considers the product of a process (like a selectionist theory) to an accumulation of adaptive traits, perhaps to an adaptive optimum such that the product is optimised to an environment. The perspective typically makes use of mathematical tools from engineering and economics such as control theory, dynamic programming and game theory.

Phenotype: Assumptions about the types of phenotypes that are possible **Fitness:** Assumptions about what is being maximised in an individual **Inheritance:** Assumptions about the methods of inheritance and population structure

Figure 5 - Three assumptions required for the adaptationist perspective of evolution (taken from [19])

Some problems with this perspective of selectionist theories (like natural selection) is the power of the selection process is over-emphasised, potentially ignoring constraints (such as developmental) in which adaptations are made. Natural selection may result in optimal adaptations, as well as adaptations that are suboptimal such as neural and maladaptations [23]. Natural selection suggests that traits need only be sufficient to provide an improved relative chance for survival and reproduction, not optimal with regard to the environment.

Perspective	Summary

Selectionist	Focus on the process of continuous change that shapes a
	product in an environment
Adaptationist	Focus on the product that is adapted by an process in the
	context of a problem

Table 3 - Comparison between the selectionist and the adaptationist perspectives

B. Towards Universal Selection

In his book on selectionist theories, Cziko [13] propose the a universal Darwinian (selectionist) theory, drawing strongly from natural selection, clonal selection and neuronal selection. In the formative chapters of the book, he focuses on the functional fit of variations as adaptations and contrasts the selectionist perspective with the instructionist and creationist (providence) perspectives.

Perspective	Summary
Creationist	Fit by providence or foresight of future needs (Designer)
Instructionalist	Fit instructed from an external source (Lamarkism)
Selectionist	Fit selected from among variations (Darwinism)

Table 4 - Three process perspectives on describing functional fit of adaptations in an environment

The ubiquity of selectionism is discussed in phrasing many complex learning problems of multiple scale in a selectionist framework. Selectionism is reduced to (1) variation, (2) selection, and (3) transmission. Three flavours of knowledge acquisition selection-based processes are discussed, taking into consideration generative versus non-generative forms, and single-step versus cumulative. The most powerful form of the selection processes is clamed to 'constructive-cumulative selection' (or 'generative-cumulative selection').

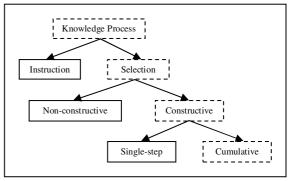


Figure 6 - Depiction of the flavours of selection processes (taken from [13])

Selection process is compared to generate-and-test, where the important distinction is made between constructed (generated) trials and those trials that may be generated although have not (thus remain potential trials). The gamble of the generate-and-test process is that the future will be much like the past, which is hedged with the potential for the gable to be wrong with the chance of larger changes.

Waste: Variations are new trials, and almost all blindly proposed trials are ignored and dead ends, representing wasted effort. Waste is the trade-off of the acquisition of information without insight (providence) or supervisory guidance (instruction).

Time: Selection processes are slow, requiring the proposal of many trials (manifest variations) which must be relatively assessed and evaluated.

Figure 7 - Example of some criticisms of selections theories

Darden and Cain [20] propose a general abstraction of selection type theories, initially modelling the Darwinian (simplified) natural selection theory, and extending the model in applying it the clonal and neuronal selection theories.

- **(A) Preconditions**: Aspects required before a selection interaction such as a set of individuals that vary among themselves in an environment that provides a context for interaction (spatiotemporal localised entities)
- (B) Selection: Interaction between individuals and the environment, different individuals interact differently (common causal influence)
- (C) Short-Range Effects: Individuals benefit or suffer (positive and negative feedback) as a result of the interaction (differential survival and reproduction), if the individual exists within a hierarchy then there may be short-range effects of sorting at other scales
- **(D) Medium-Range Effects:** Longer range effects of the interaction such as increased numbers (reproduction) of individuals with a specific characteristic
- (E) Long-Range Effects: Very long-range effects of an interaction such as the accumulation of traits over generations of individuals

Figure 8 - Abstraction of natural selection theory, and basis for the abstraction of immunological and neuronal selection theories (from [20])

Immunological example: (A) a population of lymphocyte cells each with a reactive site. (B) Cells interact with antigen at their reactive sites. (C) Selected cells are activated. (D) Activated cells proliferate, maturate, and differentiate. (E) Cell densities are adjusted and reactive sites refined such that it results in an improved secondary response to the antigen.

Neurological example: (A) a localised population of degenerate (isofunctional and non-isomorphic) groups of neurons exist which can respond to the same stimuli. (B) Neuron groups interact and respond differently to a given sensory signal. (C) Selected groups of cells are stimulated, and non-selected groups are somehow inhibited. (D) Stimulation of neuron groups causes reinforcement to those selected groups. (E) Stimulated groups of cells respond more efficiently to similar signals to those originally encountered.

C. Units of Adaptation (levels of selection)

Another important debate in selectionist-based biology is the identification of the level or scale at which selection takes place [7]. For example does selection occur on the phenotype of the individual organism, thus implicitly on the genotype, or does it occur on the genes themselves, or perhaps the species?

One of the instigators of the debate was Lewontin [1], who emphasised the general applicability of the Darwinian (simplified) theory of natural selection beyond that of an individual to that of multiple scales: molecules, cells, populations, species, and communities.

- 1) Different individuals in population have different morphologies, physiologies, and behaviors (phenotypic variation)
- 2) Different phenotypes have different rates of survival and reproduction in different environments (differential fitness)
- 3) There is a correlation between parents and offspring in the contribution of each to future generations (fitness is inheritable)

Figure 9 - Principles of Darwinian (simplified) evolution by natural selection proposed by Lewontin ([1])

Lloyd [5] provides an insightful four-question framework in which to consider the units of adaptation, as follows:

Interactor: The unit and the selection process: what are the units that are being actively selected in a process of natural selection? Traits mediate the interaction between the interactor and the environment to adjust survival and reproduction potentials.

Replicators: The unit that passes on its structure in replication – what are the organic units that are performing replication?

Beneficiary: Who benefits from the process of evolution by selection? Who benefits in the long run, and who benefits from possessing the adaptations as a result of the selection process?

Owner-of-Adaptations: At what level do the adaptations occur? What is the unit that is adapted in a process of natural selection?

Figure 10 - Summary of the four big questions in the 'unit of adaptation' debate (from [5])

ACKNOWLEDGMENTS

Tim Hendtlass for his patience and for providing useful feedback on drafts of this paper

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