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# THE EVOLUTION OF GENETIC COGNITION

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**Abstract:** As well as discovering and optimizing adaptations, natural selection acting on a genetic system will also discover and optimize processes which discover and optimize adaptations. However, attempts to account for the evolution of processes such as mutation, recombination, and sexual reproduction on this basis have encountered a fundamental difficulty—these processes will be selected against during periods in which there is little benefit in testing alternatives and in discovering new adaptations, e.g., when environmental conditions are constant. This difficulty will be overcome by processes which are able to survive these periods despite any selective disadvantage. This can be achieved by processes in which the rate of production of variation, and therefore the rate at which the process is removed from the population during these periods, is sufficiently low. Selection will favor processes of this type which are best at cost-effectively discovering new adaptations when there is advantage in testing alternatives, e.g., when circumstances change sufficiently. Selection will enhance this ability by optimizing the frequency and the content of the variation which is produced, and will organize the genetic system hierarchically. This hierarchic organization will reduce the amount of trial and error needed to discover adaptations, and will tend to preserve general, “default” adaptations. Genetic systems which include recombination will be superior at discovering adaptations than systems which do not, providing an advantage to sexual reproduction in widely applicable circumstances.

## 1. INTRODUCTION

The cognitive ability of a genetic system is its capacity to discover and perpetuate beneficial adaptations. In a typical genetic system, this will include the ability to accurately reproduce the best genetic arrangements that have been discovered in the past, and the ability to discover new and better genetic arrangements through the testing of variants by trial and error.

Cognitive ability will be influenced by genetic arrangements which affect the range and types of variant genotypes which are produced and trialled within the genetic system. For example, such a genetic arrangement might enhance the efficiency of the search for beneficial adaptations by reducing the amount of trial and error necessary to discover adaptations e.g. it may cause the production of variation which has an increased probability of being beneficial because the content of the variation is more likely to match likely environmental changes; or it may vary the frequency of testing of variation across the genome in proportion to the likelihood that variation in relation to each character will pay off.

A genetic arrangement which enhances cognitive ability will be selected within a population where the arrangement captures sufficient of the fitness benefits which it produces through the discovery of successful variants. Unlike other genetic arrangements, the cognitive arrangements are not selected because they directly produce phenotypic effects which increase the fitness of individuals which carry the arrangements. Instead, cognitive arrangements succeed through their association with successful variants which have been produced as a result of the effects of the cognitive arrangements (e.g. through the hitch-hiking effect modelled by Kojima and Schaffer, 1967).

However, as shall be discussed in detail below, the evolution of cognitive arrangements faces a fundamental difficulty. Arrangements which continually incur the cost of searching for beneficial adaptation by trial and error can be favoured only while there are beneficial adaptations to be discovered. During any period in which beneficial adaptations cannot be discovered (e.g. because the population is optimally adapted to a stable environment), such a cognitive arrangement will be out-competed by arrangements which reproduce the optimum genotype without testing variants.

Issues which will be investigated in this article through the application of the cognitive perspective to the evolution of the genetic system include: to what extent are genetic cognitive arrangements able to overcome this difficulty and evolve? to what extent have key features of the genetic system been shaped by selection for enhanced cognitive ability? what genetic cognitive abilities can be expected to have evolved? and, in particular, are there likely to be cognitive processes within the genetic system which are predicted by the cognitive perspective but which have not yet been recognised by current perspectives?

In addressing these issues, the article focuses primarily on processes internal to the genetic system which shape the production and testing of variation, rather than on processes in which behaviour plays a significant role in doing so e.g. by its impact on mate choice, the propensity to inbreed, and on population structure.

We begin in Section 2 by identifying the impediments which are suggested by current theory to limit the extent to which genetic arrangements will be shaped by selection for cognitive ability. This is followed in Section 3 by consideration of the types processes which might emerge in the genetic system to overcome these impediments. Section 4 explores the consequences of this analysis for the evolution of mutational systems, and Section 5 does the same for genetic systems which include recombination. This is followed in Section 6 by consideration of the extent to which selection which enhances cognitive ability will favour the hierarchical organisation of the adaptive processes of the genetic system. Section 7 applies the cognitive perspective developed in the article to the explanation of the evolution and maintenance of sexual reproduction - an issue which current evolutionary theory has had difficulty in resolving.

## **2. IMPEDIMENTS TO THE EVOLUTION OF GENETIC COGNITION**

Theory had little difficulty in acknowledging and explaining the evolution of arrangements which enhance genetic cognition while it was accepted that processes could be selected for 'the good of the species'. The production of variation through mutation, recombination, and sexual reproduction could be readily explained as enabling a species to adapt to changing circumstances - species which failed to produce this variation would be unable to adapt and would be out-competed by those which could (e.g. see Mather, 1943; and Kimura, 1967).

However, this form of explanation was largely discredited from the early 1960's through the work of theorists such as Hamilton (e.g. 1964), Williams (e.g. 1966) and Maynard Smith (e.g. 1971). These theorists emphasised that in most circumstances a character would not prevail in a population unless it benefits the individuals exhibiting the character, no matter how much the character benefits the population as a whole. This observation pointed to particular difficulties in the evolution of both cognitive arrangements and cooperation: although both cognition and cooperation could clearly be beneficial to the population, in many circumstances individuals which initiate cooperative behaviour or which produce the variation which underpins cognition would not capture these benefits.

In the case of cognition, this is because the need to adapt is not likely to be continuous, and therefore will not provide continual benefits to individuals which initiate cognitive processes. Over the longer term, enormous advantages may accrue to populations which include cognitive mechanisms where, for example, occasional environmental change provides strong selection in favour of the production of variants. However, these benefits will not be captured by the individuals who incur the costs of producing variants during periods when no change arises e.g. during periods in which the population is well adapted to a stable environment. Under constant conditions, arrangements which reproduce the optimal genotype without variation will be favoured. The capacity to provide future cognitive benefits will not assist shorter term competitive ability. Similarly, in the case of cooperation, individuals which direct cooperation toward others without capturing any of the benefits themselves (e.g. altruists) are likely to be out-competed no matter how beneficial the cooperation is to the population as a whole.

Since the 1960's, the consequences of this individual-focused perspective have been worked out in detail for the key processes of the genetic system which are involved in the maintenance and production of variation. For example, in relation to the accumulation and maintenance of variation within the gene pool, theory predicts that under constant conditions, the optimal genotype will prevail and all other variation will be removed (e.g. Wright 1935; and Lewontin, 1974); in relation to the production of new variation by mutation or by recombination, theory predicts that under constant conditions mutation and recombination rates will evolve to zero across the genome (e.g. see Karlin and McGregor, 1974; Maynard Smith, 1978; and Lieberman and Feldman, 1986); and if sexual reproduction is to be maintained in a population, there must be a short term advantage to sex over asex (however, this advantage must outweigh not only the cost of producing variation, but also the additional 'two fold' cost of sex identified by Maynard Smith, 1971).

But these clear and unequivocal conclusions have created other difficulties for theory: if cognitive mechanisms are continuously costly but provide fitness benefits only intermittently, what accounts for the evolution of the processes which maintain and produce variation? In particular, why is sex almost ubiquitous, why is recombination and mutation prevalent across the genome, and why is genetic variation found almost wherever it has been looked for by artificial selection experiments? These difficulties have been particularly resistant: Roughgarden (1991) describes the difficulty in accounting for the evolution of sexual reproduction as the major unsolved problem of biology today, and Barton and Turelli (1989) describe as a central paradox the maintenance of abundant polygenic variation in the face of stabilising selection which is expected to eliminate the variation.

Numerous attempts have been made to explain within the individual-focused approach the evolution of these processes which appear at first glance to have evolved on account of their capacity to enhance the ability of the genetic system to adaptively respond to selection. From the cognitive perspective being developed here, it is useful to divide models which attempt to overcome this difficulty into two categories: those which accept that the variation which underpins the

adaptive response is generally sub-optimal, but which explain the maintenance of the variation as an unavoidable side effect of some other process; and models which explain the maintenance and production of variation on the basis that it enhances the discovery of beneficial adaptation (these will be referred to here as 'cognitive' models).

Examples of 'side effect' models are: the mutation/selection balance theory which suggests that the accumulation and maintenance of variation found in most quantitative characters is the result of a balance between the continual creation of variation through mutation and the removal by selection of these mutations which are in most cases sub-optimal and deleterious (e.g. Wright, 1935; and Lande, 1975); pleiotropy theory which suggests that much of the variation associated with quantitative characters is due to the deleterious pleiotropic effects of genes which are nonetheless maintained because they have other beneficial effects on the organism, or are maintained for some other reason (e.g. Hill and Keightley, 1988; and Barton, 1990); and theories which explain the continual production of deleterious mutation across the genome on the basis that its suppression would be too expensive (e.g. Leigh, 1973; and Kondrashov, 1988).

Wright's 'shifting balance' theory which is directed at explaining how the structure and dynamics of populations may be able to enhance the capacity to discover adaptations is probably also best categorised as a 'side effect' model - the particular population structures and dynamics which enhance cognition are not themselves selected because of their cognitive contribution (Wright, 1977; and Schull, 1990).

The main 'cognitive' models usually rely on some form of environmental heterogeneity which prevents any single genotype from being optimal through time in all circumstances. The basis of the heterogeneity may be biotic or abiotic, spatial (e.g. Ghiselin, 1974; Williams, 1975; Maynard Smith 1978; Slatkin, 1987; and Gillespie and Turelli, 1989) or temporal (e.g. Van Valen, 1971; Williams, 1975; Hamilton 1980; and Hamilton *et al.*, 1990), and may be frequency dependent (e.g. the impact of the heterogeneity may be affected by the proportion of the population with a genotype which best exploits a particular part of the environment [Roughgarden, 1972]).

Some approaches have both a 'side-effect' as well as a 'cognitive' component. For example, the explanation of the maintenance of sex and recombination provided by Kondrashov (1988) relies on unavoidable mutation, much of which is deleterious, which is shed through the capacity of recombination to produce variants which do not include the deleterious genes.

The central difficulty encountered by all side effect models is the necessity to demonstrate that the maintenance of the sub-optimal variation as a side effect is indeed unavoidable, particularly given that selection would strongly favour the establishment of arrangements which would remove deleterious side effects. Under the Neo-Darwinian adaptationist program, any proposition that a significant characteristic of many organisms is sub-optimal and maintained as an unavoidable side effect of features that are advantageous will generally be viewed with suspicion and seen as an absolute last resort for evolutionary theory. On this basis, the mutation balance theory has a heavy onus to demonstrate that selection is unable to establish arrangements which prevent the production of deleterious mutations (proponents of the theory generally argue that this mutation is unavoidable because its prevention would not be cost-effective); and the pleiotropy theory must demonstrate that beneficial genotypes without detrimental pleiotropic effects are unable to be established either directly or by combinations of genes which suppress the side effects. No side effect model has yet discharged this onus sufficiently to gain wide-spread acceptance as a comprehensive explanation of the maintenance and production of variation.

The two main limitations of the cognitive models are: first, the selection they postulate to favour the maintenance and production of variation seems unlikely to be sufficiently general in its effects across the genome to maintain variation for all characters in which variation is found; and second, selection will favour the maintenance and production of the variation only while the circumstances which produce the selection continues.

Of course, this second difficulty dissolves if the selection for cognitive capacities is unending - i.e. if cognition is always beneficial because the population is continually in a state of dis-adaptation, ensuring that the production of a variety of genotypes continually pays off. However, it has not yet been convincingly demonstrated that this condition would hold for all populations of all organisms that appear to have genetic systems which exhibit cognitive capacities, particularly given that any relaxation of the condition would have to be limited because it would immediately result in selection against the cognitive capacity.

These difficulties in demonstrating how cognitive mechanisms could be established where they provide only intermittent benefits appear to have been the major impediment to the development and acceptance of a general cognitive approach to the evolution of the genetic system.

### **3. OVERCOMING IMPEDIMENTS TO THE EVOLUTION OF GENETIC COGNITION**

To what extent have the evolution of cognitive arrangements within the genetic system been impeded by the difficulties identified by the individual-focused perspective?

Stewart (1995 and 1997) has identified arrangements which can comprehensively overcome this cognitive limitation and the closely related limitation applying to the evolution of cooperative organisation amongst individuals (the cooperative limitation arises where the co-operator is unable to capture the benefits of its cooperative actions, and may therefore be out-competed, just as a cognitive arrangement may also be out-competed because its capacity to provide future cognitive benefits will not assist its shorter term competitive ability). The arrangements outlined by Stewart overcome these limitations by the formation of higher level organisations. These organisations each comprise a group of individuals which are managed and controlled by other individuals which are in hierarchical relationship with the original group. The hierarchical individuals manage the organisation by feeding back to members of the group the consequences to the organisation of the cooperative actions of the members (thereby overcoming the cooperative limitation), and by feeding back to members the expected future benefits of their actions (including their cognitive actions), thereby overcoming the cognitive limitation. As a result, cognitive arrangements which produce only future benefits will also be competitive in the shorter term. For example, a human government may intervene in an economic system to sustain research which would not otherwise be undertaken because it will pay off only in the long term.

The emergence of hierarchical individuals which are able to manage a group in this way will be favoured by selection because the individuals will be able to harvest some of the additional benefits produced by their promotion of cooperation and effective cognition, and will be able to use these resources for management and for their own reproduction. Examples of higher level organisations which are formed in this way are groups of molecular processes managed by RNA to form early cells, and groups of humans managed by rulers or governments to form human societies.

However, the task here is to explore the evolution of cognitive capacities within the typical genetic system, and most organisms are not organised into higher level organisations in the way

described by Stewart. We will therefore now turn to identifying circumstances and arrangements which could go at least some way to overcoming the cognitive limitation without the formation of higher level organisations:

We begin by noting that cognitive mechanisms which produce intermittent benefits will be out-competed under constant conditions only to the extent that they incur a cost. For example, during any period when the impact of a cognitive mechanism on fitness is neutral because it does not produce variants, it will not be at a competitive disadvantage to alternatives which merely reproduce the optimal genotype. Furthermore, the less frequently that variants are produced by a mechanism, the lower the competitive disadvantage over any given period, and the more likely that it will encounter changing conditions which provide it with a selective advantage before it is eliminated from the population due to competition.

This is a critical point in understanding the evolution of cognitive capacities in genetic systems: selection will favour the evolution of cognitive processes which are able to survive periods in which there is little benefit in the testing of alternative variation. Processes will be able to achieve this where the rate of production of variation, and therefore the rate at which the process is removed from the population during these periods, is sufficiently low. Selection will favour processes of this type which are best at cost-effectively discovering new beneficial adaptations when there is benefit in doing so - e.g. when circumstances change. Processes with the highest cognitive ability will out-compete less effective cognitive arrangements, and, in suitable circumstances, will out-compete alternative arrangements which merely reproduce the genotype which is optimal under most conditions, without testing variants.

Are genetic arrangements which have these features feasible? What kinds of cognitive processes might arise in response to this selection?

#### **4. THE EVOLUTION OF MUTATIONAL SYSTEMS**

##### **4.1 What circumstances will favour on-going mutation?**

We will proceed by considering a simple case: the production of genetic variation by mutation in a population of haploid asexuals. Theoretical work on the evolution of such a system predicts non-zero mutation rates for certain genes in an environment which cycles between two states (e.g. Leigh, 1970; and Ishii *et al.*, 1989). Mutation is favoured in genes which are optimal in one state of the environment, are able to mutate to a form which is optimal in the alternative state of the fluctuating environment, and are able to be restored by a reverse mutation. Leigh (1970) and Ishii *et al.*, (1989) demonstrate that the optimal mutation rate in such a system where selection is strong is  $1/n$ , where  $n$  is the average duration of each environmental state, expressed as the number of generations. The optimal mutation rate maximises the capacity of a mutator to produce the particular mutation(s) which will spread through the population when the environment enters the state favourable to the mutations.

This work is very limited in its ability to account for the evolution of the observed pattern of mutation in organisms. It can account only for the maintenance of mutation which produces variants each of which is beneficial in a recurring state of the environment. In contrast, the evidence suggests that the overwhelming majority of mutations are deleterious under all environmental conditions. These models would therefore not even be able to account for the more general pattern of mutation which presumably would be necessary for the initial discovery of the specific mutational systems

which are favoured in a cycling environment - the work can account only for the persistence of these specific mutational systems once they have been discovered.

However, an examination of the work from the perspective being developed here will assist the development of a theory of the evolution of mutation which is more generally applicable. A key point illustrated by the models is that a mutator can be maintained in a population no matter how infrequently the environment favours the mutant it produces, provided the mutation rate is sufficiently low - this is because the rate at which the mutator is removed from the population during a period in which the mutation is non-optimal depends on the rate at which it produces mutations; if the mutation rate is sufficiently low, it will survive until the environment changes to a state which favours its mutations, no matter how long this period is. In this way, mutators are able to persist away from equilibrium during constant conditions until conditions change and cognition is beneficial.

These considerations point to a solution to the more general problem of how selection might favour mutators which produces a variety of mutations, the majority of which are deleterious. The success of such a mutator within a population will be impaired only when an instance of the mutator cause an unsuccessful mutation, and then only if the mutator faces competition from an alternative which produces fewer unsuccessful mutations. Such a mutator will persist provided it produces a successful mutant before its production of deleterious mutants removes it from the population. When it produces a favourable mutation, it will increase again to fixation. If the probability that a favourable mutant will be produced increases to unity with sufficient time, this condition will be met provided the mutation rate is sufficiently low - with a sufficiently low mutation rate, the mutator will maintain its presence in the population until a favourable mutant is produced. As for the case studied by Leigh and by Ishii *et al.*, the optimal mutation rate will be the rate which maximises the capacity of a mutator to produce the mutation(s) which will spread through the population when favourable circumstances arise. And the optimal rate will be lower the longer it takes for the probability of the production of a favourable mutation to increase to unity.

But how plausible is this requirement that the probability of the production of a favourable mutation increases to unity with sufficient time? Will this requirement be sufficiently widely met to explain the ubiquity of mutation?

The probability that a random mutation in an organism will be favourable is likely to increase significantly with time. This is because the probability that a random change will be beneficial will increase as the adaptedness of the organism to its environment decreases. And given sufficient time, the adaptedness of a population can be expected to decline as changes in the biotic and abiotic environment accumulate. The probability that a mutation will be successful will also increase with time because new opportunities for adaptation will open up due to internal changes in the genetic system itself. For example, there will be advantage in masking sub-optimal mutation, and in contributing to optimising other successful genetic change in the population. On a long enough time scale, increasing change is inevitable, and increasing maladaptation is also therefore inevitable. Opportunities for successful mutation will therefore continue to increase through time. This is a general consideration which should apply ubiquitously. Consequently, if a mutator causes a sufficiently low mutation rate, it can survive until the rising level of maladaptation sufficiently increases the probability that mutation will be successful. Because there will be differences between characters in the rate at which environmental and other changes produce maladaptation, the optimal mutation rate will vary across the genome.

Other factors will also contribute to this evolution of non-zero mutation rates. For example: the optimal mutation rate will generally be greater than otherwise if the suppression of mutation incurs a fitness cost which increases as the magnitude of the suppression increases (Ishii, 1989); and at lower rates of mutation, mutators will experience longer periods during which they do not encounter competition from alleles which further suppress or prevent mutation (this is because these alleles can be generated only by mutations, and the lower the mutation rate, the lower the rate at which such alleles will be discovered - cognition is essential to the discovery of adaptations which reduce cognitive ability).

## 4.2 Enhancement of cognitive ability

The selection which arises under the circumstances which have been described will not only favour non-zero mutation rates, it will also favour mutators which produce a pattern of mutations which have a higher probability of including beneficial mutations. All other things being equal, mutators which produce such a pattern of mutations will out-compete mutators with a lower probability of producing beneficial mutations. Alternative mutators will therefore compete on the basis of the content of the pattern of mutations they produce, as well as on the frequency of the production of mutations. This competition will produce intense selection - a mutator which fails to discover adaptations because alternative mutators do so first will be removed from the population - it will not be able to recoup the cost of producing variation.

For example, selection acting on this basis would favour a variant mutator which generates a higher proportion of mutations which have a greater chance of success because they are phenotypically meaningful e.g. because they produce phenotypic changes which are at least consistent with the functional organisation of the organism, and are not lethal during development. In this way, selection will increase the probability of successful mutation by tuning the manner in which genotypic variation maps onto phenotypic variation (this relationship is termed the genotype-phenotype map by Wagner and Altenberg, 1996). By way of further example, selection can also be expected to tune the pattern of variation so that it is more likely to include mutation which will be successful given recurring environmental fluctuations. The specialised mutation systems analysed by Ishii *et al.* are an example of such highly targeted mutation: each mutator produces a single mutation which is beneficial under particular recurring conditions - no mutation is produced which is unconditionally deleterious.

The evolutionary improvement of cognitive ability within and between populations will create conditions which will favour the further evolution of cognitive arrangements: as evolution produces mutators which are able to discover beneficial mutation with less trial and error, higher mutation rates will be favoured because mutation is likely to be successful at lower levels of maladaptation; as a population adapts more closely to prevailing environmental conditions, the rate at which the population becomes maladapted due to environmental changes will increase; the higher the rate of successful mutation in one part of the genome, the greater the opportunities for complementary adaptation in other parts; and species will be maladapted sooner as their environment changes more rapidly due to the more frequent adaptation of other species (Glesener and Tilman, 1978 make a similar point in relation to the evolution of sexual reproduction).

If selection favouring enhanced cognitive ability is to be effective, there has to be heritable variation in the cognitive ability of mutational systems. At least some variation of this kind is likely to arise readily. For example, mutators which cause mutations in different sub-sets of the genome (e.g.



in different regions of a particular chromosome) are likely to differ in this respect, if only because the content of their mutational patterns will differ by chance. Selection will operate on any bias which arises in the content of the pattern of mutation, whatever its cause or origin. To the extent that suitable variation arises, selection will establish a pattern of mutation across the genome whose frequency and content is non-random relative to the past selective pressures encountered by the population. And it will be non-random relative to future pressures to the extent that future environmental conditions (including changes in conditions) are similar to past conditions (and past changes). In this respect, the evolved pattern of mutation will be like any other adaptation which is established through natural selection - the adaptations which exist at any time are those which are selected by past circumstance, and they will be relevant to future conditions only to the extent that the future resembles the past.

### **4.3 Tracking an environmental variable**

How effective is such a mutational system in a population of haploid asexuals likely to be at responding to a typical adaptive challenge encountered by the population? A common adaptive challenge would be to adapt the population to an environmental variable which is relatively constant on the time scale of the life of the organism, but which varies over a wide range on longer time scales. How effectively would a mutational system adjust a phenotypic character which has the potential to adapt the population if the character is adjusted appropriately as the variable changes?

The genetic system would adjust the character through the production of mutations. Mutations would be selected where they better adapt the character to the state of the variable which prevails at the time. As the environmental variable changes, successful mutation will adjust the character by moving the genetic system from one genetic arrangement to another. Given the nature of genetic action, it is highly unlikely that these various genetic arrangements would be able to be achieved entirely by a sequence of mutations of one gene which determines the character. Instead, tracking of the environmental variable is likely to also necessitate changes to other genes so that they modify the effect of the original gene, with each new modifier contributing to moving the character from one adaptive state to another. When the variable changes, the character will respond as a result of changes to genes which already affect the character and/or as a result of the establishment of new modifiers through changes to other genes. As more genes affecting the character are accumulated, it would become more probable that a given change in the character could be achieved by a mutation which changes an existing modifier gene (e.g. by disabling the gene or by reversing the disablement), rather than by the establishment of a new modifier gene (disabling or re-enabling an existing modifier is likely to move the character in a direction which has previously proved to be beneficial). In principle, the variety of genetic responses which are necessary to match the variety of the environmental variable could be produced by appropriate combinations of mutations which switch genes on or off, switch genes between other useful states, and produce new modifier genes. It is important to note that as these arrangements evolve, there are likely to be many different ways in which a particular state of the phenotypic character can be produced genetically. For example, various combinations of active and disabled modifiers will produce the same phenotypic effects. Selection will not distinguish between or favour these alternatives. For this reason, in a large population the genetic arrangements which determine a character are likely to differ significantly across the population even though the arrangements produce the same phenotypic effect, and once lineages diverge in this way, they are unlikely to converge again.

In this way the characteristic genetic architecture of characters which are polygenically determined is likely to arise. The architecture arises through the accumulation of genes and mutators which are each selected because they contribute to the tracking of an environmental variable. The emergence of the architecture improves the capacity of mutation to adjust the relevant phenotypic character to track the variable. The evolution of these cooperative and coadapted assemblages of genes is not impeded by any cooperative limitation - linkage ensures that individual genes capture the full benefit of any effects they have on other genes which increase the success of the assemblage as a whole.

The efficiency of such a system in tracking the environmental variable will depend in large part on the extent of trial and error needed to discover the mutations which adjust the character so that it continues to be optimal. The extent of trial and error would be substantially reduced where the only mutations which are produced are ones which move the character between states which are all optimal for some particular value of the environmental variable. This might be achieved within such a polygenic system by, for example, mutators which produce only mutations which disable or reverse the disablement of modifier genes, or which switch the directional effect of modifiers on the character (the simple two state mutation system examined by Leigh and Ishii *et al.* is a single-locus counterpart of such a polygenic arrangement). As the environmental variable changes, selection would operate on the variation produced by such a targeted mutational system, selecting the particular variants most adapted to the prevailing value of the variable.

Selection would favour mutators which produce patterns of mutations which improve the efficiency of the system in this way. However, the discovery of mutators with such narrow and precise effects would be likely to necessitate considerable trial and error which itself would be costly and prolonged. This process of discovery would need to be repeated for each and every character of the organism, and would also need to be repeated whenever there was a change in the range over which an environmental variable typically moved.

Arrangements which are able to produce such a beneficial pattern of variation for all characters immediately, without the need for the costly process of discovery, would have a substantial cognitive advantage, and be strongly favoured by selection.

## **5. EVOLUTION OF GENETIC SYSTEMS WHICH INCLUDE RECOMBINATION**

Such a pattern of targeted variation would tend to be produced as a matter of course where genetic material is exchanged between homologous chromosomes which include polygenic arrangements and originate from different individuals in the population (e.g. through the process of recombination associated with sexual reproduction or related arrangements such as conjugation). If the corresponding parts of homologous chromosomes which are exchanged contain different genetic arrangements, the resulting recombinant chromosomes will constitute variant genotypes. Importantly, this exchange process will produce variants even where selection has imposed a single optimal phenotype throughout the population. As we have noted, such a population is likely to be genotypically varied even though it is phenotypically uniform, because there are likely to be many different ways in which a particular state of a phenotypic character can be produced genetically by polygenic arrangements. Selection will not distinguish between or favour these alternatives, and a population is likely to accumulate greater genetic diversity of this type through time. Recombination between these phenotypically equivalent but genotypically diverse chromosomes has the potential to produce new chromosomes which are both phenotypically and genotypically variant. The rate at

which this variation is produced within the population will depend on the frequency of recombination. When there is no recombination, the genotypic diversity will be retained without cost to fitness. The capacity of such a system to produce variation will not diminish as the optimal phenotype changes through time because recombination is likely to continue to create a diversity of polygenic arrangements which produce the particular phenotype which is favoured at any particular time. And stabilising selection will tend to maintain the linkage disequilibrium which is necessary if recombination is to continue to produce variation (Wimsatt, 1981 discusses the capacity of linkage and selection to maintain this linkage disequilibrium).

Returning to the example of adaptation tracking a changing environmental variable, it is significant that the variants produced through recombination will comprise different combinations of the accumulated modifier genes which each tend to move the state of the character in a direction which previously has proved beneficial. The presence or absence of a particular gene in a combination will have a similar effect to a mutation which enables or disables the gene - the state of the character will be moved to a state which has previously been optimal. The variants will therefore tend to produce states of the character which are all optimal for some particular value of the environmental variable. In contrast, mutational systems which are not able to precisely target mutations in the way discussed above will tend to produce mutations which lie outside this range of states and have little chance of producing beneficial adaptation.

This points to the key cognitive advantage of recombinational over mutational systems: recombination operating on polygenic arrangements generates variation in a way which increases the chances that the variation will include beneficial variants. It does this by combining in different ways genetic elements which have proven beneficial under particular conditions in the past. This will ensure, as we have seen, that the variation is more likely to move characters to states which have been beneficial in the past and which may recur in the future. In the same way, it will produce variation which is more likely to map into meaningful phenotypic change - this is because the variation will comprise various combinations of genes which selection has accumulated over time and which are therefore likely to have proved to be phenotypically meaningful in the past. Thus, for example, if the accumulated genes tend to be modular in their phenotypic effects, variants produced by recombination will also tend to exhibit modularity of genetic effects (modularity is used here in the sense developed by Wagner and Altenberg, 1996 which refers to a genotype-phenotype map in which there are few pleiotropic effects amongst characters which serve different functions - pleiotropic effects fall mainly among characters which are part of a single functional complex). In contrast, un-targeted mutational systems acting on the same genetic arrangements will not exhibit any such fundamental tendency to produce variation which exhibits modularity, and modularity will be maintained only by selection.

The capacity of a system which generates variation by recombination to persist through time and to be selected on the basis of its cognitive ability will encounter the impediments identified by the individual-focused perspective - individuals which carry the arrangements will be selected against during constant conditions, no matter how beneficial recombination is over the longer term. But these impediments will be overcome in the same way as for mutational systems: selection will favour the evolution of arrangements which produce variation at a rate which is sufficiently low to enable the arrangements to survive periods of constant conditions, and which are best at discovering new adaptations when there is benefit in doing so. As we have seen, the production of variants can be reasonably expected to pay off eventually for all characters as the adaptiveness of characters diminishes over time due to environmental change and due to changes within the genetic system itself (including due to the production of deleterious variation [see Kondrashov, 1988]). And

no matter how long it typically takes for the adaptiveness of a character to diminish sufficiently, the optimal rate for the production of variation in the character will be non-zero. The capacity of recombination to produce better-targeted variation means that these optimal variation rates will be higher than otherwise, and the magnitude of maladaptation needed to ensure that the variation will be successful will be lower.

A number of factors in a recombination system will influence the rate at which variation is produced for a particular character which is polygenically determined. These include: the frequency and timing of sexual reproduction or conjugation; the rate at which particular segments of chromosomes are exchanged; the location on the chromosomes of these exchanges; and the genetic constitution of the segments which are exchanged (e.g. if the segments which are exchanged have identical phenotypic effects and epistatic effects are not significant, the exchange will not produce variation, no matter how frequently it occurs). Selection can be expected to tune these factors to optimise variation rates for each character. Furthermore, these factors could themselves be determined and adapted by polygenic arrangements, with the result that variation rates would respond readily and effectively to selection, and the production of variation in particular characters would increase or decrease as circumstances demand. Observed patterns of recombination rates are consistent with these expectations, varying widely across the genome, and responding readily to artificial selection (e.g. see Brooks, 1988; and Lichten and Goldman, 1995 for reviews).

Selection could be expected to tune not only the frequency of variation, but also its content - it will favour the further enhancement of the cognitive ability of a recombination system to generate patterns of variation which are more likely to produce beneficial adaptation. For example, selection could be expected to tune factors such as the location of crossing over and the genetic constitution of the segments which are exchanged. These can influence the content of the variation which is produced by, for example, affecting the extent to which variants are likely to deviate significantly from the parental genotypes. Furthermore, polygenic arrangements which track environmental variables are likely to be subject to selection which favours the production of patterns of variation which are centred on the mid-range of the variable and which provide for flexibility about the mid-range.

Together, these various selective pressures will result in the differentiation of variation across the genome in relation to its frequency and its content. This selection favouring differentiation will in turn favour the production of variation whose phenotypic effects impact only on the particular adaptations for which it is specialised - in this way, modularity of effects will be further favoured.

As for mutational systems, the pattern of variation produced across the genome by a recombination system can be expected to be highly non-random relative to the selective history of the population, and highly adaptive to the extent that future environmental and other changes are correlated with past changes.

Although cognitively superior in a number of respects, recombination systems cannot fully replace mutational systems. A recombination system needs to be complemented by mutational arrangements which will coevolve with it. Selection will favour mutational systems which establish new genes which might enhance the capacity of the recombination system to produce adaptation to both recurring and new environmental challenges, and which replace genes which are lost from the system where, for example, the flexibility of the recombination system is overtaxed by environmental change.

The analysis presented here arrives at a similar picture of the functioning of the typical recombining eukaryote genome to that presented by Mather (1943). Mather developed a comprehensive understanding of how recombination operating on polygenic arrangements can produce patterns of variation across the genome which enable populations to respond quickly and effectively to selection. His account provides a more detailed exposition than that presented here of the way in which such a system will produce and structure variation. However, widespread acceptance of Mather's scheme has been hindered because he relied primarily on selection operating at the level of the species to account for the continual production of variation. Unwillingness to seriously consider his proposals has been particularly marked since the rise of the individual-focused perspective. The analysis presented here rescues Mather's conclusions from their suspect evolutionary basis and integrates them with current mainstream evolutionary theory by accounting for the continual maintenance and production of variation on the basis of selection operating at the level of the individual.

## **6. THE EVOLUTION OF ADAPTIVE HIERARCHIES WITHIN GENETIC SYSTEMS**

The conclusion that fundamental aspects of the genetic system are shaped by selection favouring cognitive ability suggests that it may be worthwhile to examine whether key features of other cognitive systems are also found in genetic systems. A prime candidate for this type of analysis is the hierarchical organisation of adaptations which is characteristic of cognitive systems which accumulate adaptations by trial and error in a dynamic environment. We will proceed by briefly examining three examples of such adaptive systems:

Bateson (1963) and Slobodkin and Rapoport (1974) have described this hierarchical form of organisation and considered its cognitive significance in relation to physiological adaptation. Bateson notes that when an environmental challenge is encountered, the features of the physiological system which can adapt the organism to the challenge typically respond on different time scales. For example, an immediate response in humans to altitude is panting and a racing heart, but in the longer term, adaptation will be achieved by the deeper and more complex physiological changes associated with acclimation. If acclimation does not adequately provide adaptation, further adaptation resulting from longer-term genetic changes in the population is likely to follow. Slobodkin and Rapoport explain the evolution of this hierarchical structure on the basis that it achieves adaptation more economically - environmental perturbations are first met by short-term responses involving relatively minor commitments on the part of the organism which, if successful, make the longer-term, more major commitments unnecessary.

Rappaport (1979) suggests that the belief systems which underpin the adaptations of human organisations such as the New Guinea tribes he studied are also ordered hierarchically. Lower level beliefs change rapidly and continuously in response to environmental challenges, and relate to goals and concerns which are highly specific and concrete. In contrast, higher order beliefs change slowly in response to environmental perturbations (sanctification preserves the highest level beliefs from change), and relate to more general and less concrete goals. The result is that when a tribe is confronted with environmental challenges, changes in lower order beliefs and behaviour patterns are tested first, and only where these fail to adequately deal with the challenge are higher order changes tested.

The learning classifier system of Holland *et al.* (1986) is a machine learning system that uses a genetic algorithm to search for sets of rules which provide solutions to particular problem situations.

The sets of rules discovered by the system are often found to be organised as a default hierarchy. These are rule sets which allow the errors of imperfect default rules (rules that are correct for some situations, but incorrect for others) to be handled by exception rules. The exception rules produce a correct solution by shielding the default from errors. An exception rule can be imperfect as well, and multiple layers of exceptions can be used to further refine performance. This hierarchical structure allows for more parsimonious rule sets, expansion of the solution space, and graceful refinement of rule sets through incremental modification e.g. by the layered addition of exception rules (e.g. see Holland *et al.*, 1986; Goldberg, 1989; and Smith and Goldberg, 1992).

The hierarchical structure of adaptive processes which is illustrated in various forms by these three adaptive systems has the advantage of enabling adaptation to be achieved more efficiently. This advantage is most clearly demonstrated by considering an ideal adaptive system in which both the adaptations and the rate of trialling of alternative adaptations are capable of evolving. As we shall see below, such an ideal system will adapt efficiently by reducing the extent of trial and error needed to discover new beneficial adaptations, and by reducing the extent to which the adaptations accumulated by the system over time are changed in discovering new adaptations. This is the case both for adaptation to changing circumstances and for better adaptation to existing circumstances.

The way in which this is achieved can be demonstrated by examining how such an ideal adaptive system which combines the most effective features of the three examples would adapt through time in the face of environmental challenges. When environmental change is encountered, tactical changes in more specific and specialised adaptations would be trialled first. If these do not adapt the system, or if they do so only with significant stress, strategic changes in more general features of the system would be trialled. These more general features would usually be of larger scale within the system, and create the systemic context within which the more specific and specialised adaptations are optimised. The trialling of change would be repeated at progressively higher hierarchical levels until the environmental challenge is adequately met. Successful meeting of the challenge at a particular level would remove stress from lower levels and restore their adaptive flexibility.

In this way, costly trialling of change in higher level default adaptations which have stood the tests of time and which are also likely to be appropriate in the changed environment would be undertaken only if adaptation of more specific features at lower levels fails. The default hierarchy efficiently prioritises the order in which adaptations are reconsidered and trialled for change when environmental challenges are encountered. As well as minimising costly trial and error, this ensures that general defaults which have provided a good strategic base for lower level adaptations would be changed only as a last resort. Adaptation at lower levels shields the defaults from change by modifying the effects of the defaults to meet whatever circumstances arise (although this runs the risk of protecting inappropriate higher level adaptations from reconsideration). In contrast, an adaptive system which is not organised hierarchically in this way would test alternatives in all accumulated adaptations at once. This would be comparatively wasteful, and might result in inappropriate change to accumulated strategic adaptations in circumstances where effective adaptation might have been better achieved through tactical changes.

To what extent are the adaptive processes of the genetic system likely to be organised hierarchically in response to selection for enhanced cognitive ability?

A number of features of the evolution and the organisation of organisms are likely to encourage the emergence of hierarchical structure: As demonstrated by Holland's classifier system, the first adaptations which are discovered by a trial and error evolutionary system are likely to be simple, general rather than specialised, and of larger scale within the system of adaptive processes. As

organisms evolve, further adaptation can occur by changes to these existing adaptations, or through the addition of new adaptations which build on and modify the existing adaptations by refining them or by adapting them to new circumstances. The later adaptations which modify and build on the earlier adaptations in this way will generally be relatively more specialised and of smaller scale - a number of specific adaptations will usually modify each earlier adaptation. The likelihood that the effect of an adaptation will be changed by new modifying adaptations rather than by innovation in the adaptation itself will increase over time, as pointed out by Wimsatt (1986). This is because the more an adaptation is entrenched by being built on and modified by later adaptations, the more likely that trial and error change in the earlier adaptation will be deleterious because it disrupts the beneficial effects of later adaptation. This achievement of adaptation by changes to later adaptations or by new modifying adaptations will also tend to shield earlier adaptations from pressure to change.

This hierarchic differentiation of adaptive processes and their adaptations will be further enhanced by a complementary hierarchic differentiation of the rates at which the genetic system trials variation. As we have seen, the optimal rate of variation in a character depends on how long it will be before it becomes highly probable that variation in the character will be beneficial. Optimal variation rates can therefore be expected to be lower the more entrenched an adaptation, and the more it is shielded by later adaptation. This hierarchic differentiation of variation rates can also be expected to be reflected in a similar differentiation in the rates at which variation in variation rates are trialled and respond to selection - this is because it will be optimal for metavariation to be trialled at a lower rate than the variation it controls (this form of relationship between variation and metavariation will itself result in some hierarchic differentiation within a genetic system).

The way in which organisms are organised functionally will also contribute to the emergence of hierarchies in the genetic system. Functionally, organisms are typically organised hierarchically (e.g. organ systems, which are comprised of organs, which are in turn made up of tissues, which are in turn comprised of cells). This form of functional organisation is favoured by selection in part because it enhances the ability of the individual organism to adapt effectively during its life (Stewart, 1995). The critical point here is that the relationship between the larger scale, higher level adaptations and the lower level, more specific adaptations in these functional hierarchies is likely to produce the same selective effects as the relationship between entrenched adaptations and the later adaptations which modify them in the evolution of organisms. This is because the higher an adaptation in the functional hierarchy, the more its effects will be modified by lower level adaptations, and the less likely that trial and error change in the higher level adaptation will be beneficial because it is likely to disrupt the beneficial effects of lower level adaptation. Again, adaptation at lower levels will shield higher levels from change, and the rates at which variation in underlying genetic arrangements is trialled will also form a complementary hierarchy.

On this basis, many of the adaptive processes which comprise the genetic system of a population can be expected to be organised hierarchically. This hierarchic organisation would minimise the costly testing of variation by prioritising the rate at which variation in adaptations is trialled, and the rate at which changes in these rates are trialled. This prioritisation would complement and reinforce the tendency of the hierarchic organisation of adaptive processes to preserve larger scale, less specialised adaptations which are more likely to be beneficial across a wider range of environmental circumstances, and which would provide a useful fall-back position when the population encounters new circumstances - change to these more strategic default adaptations would be likely only where tactical change to more specialised adaptations fails.

This cognitive perspective adds to the explanation provided by Wimsatt (1986) of the relative stability over long evolutionary time scales of the fundamental body plans of the main lineages of animals: the cognitive perspective suggests that the fundamental body plans represent strategic adaptations of wide scale in the organisation which are trialled for change on a longer time scale than later, more specialised adaptations; and, in most circumstances, these adaptations at lower levels of the default hierarchy will change to meet changing conditions, preserving the strategic adaptations of the fundamental body plan (Stewart, 1995). The relative stability of adaptations at higher levels in the hierarchy also explains the observation of Simpson (1953) and Valentine (1969) that taxa of high rank tend to originate at earlier times in the fossil record than do taxa of lower rank - a constant proportion of new lower taxa will not be distinctive enough to form new higher taxa because it is more likely that they will differ in relation to adaptations at lower levels of their adaptive hierarchies, rather than at higher levels.

## **7. THE EVOLUTION OF SEXUAL REPRODUCTION**

Accounting for the evolution and maintenance of sexual reproduction has proved to be a particularly difficult challenge for evolutionary theory (e.g. see Maynard Smith, 1971 and 1978; Williams, 1975; and Bell, 1982).

However, the cognitive advantages of recombination which have been identified above go a long way towards accounting for the superiority of sex over asex in most circumstances. When confronted with a series of environmental challenges, a sexual population can be expected to be far superior to an asexual population at discovering appropriate adaptations.

This cognitive advantage will not, however, be sufficient to ensure that sex always beats asex. This is because asex has up to a two-fold advantage in fitness over asex in general circumstances (Maynard Smith, 1971). The two-fold cost of sex arises where half of the reproductive effort of sexuals goes into the production of males which do not themselves contribute anything other than genetic material to the next generation.

In what sort of circumstance might the two-fold advantage outweigh the benefits of greater cognitive ability? In addressing this issue it is useful to note that the two-fold advantage results in the production of greater numbers of female offspring, while improved cognitive ability has a greater capacity to produce higher quality young. As indicated by Stewart (1993), this is significant because during periods of 'r selection', fitness is likely to be influenced more by the number of female young produced than by their quality - improvements in quality achieved by superior cognition are unlikely to outweigh the advantage achieved by producing twice as many female offspring. In contrast, during periods of 'k selection', the best adapted individuals are likely to prevail - there is little benefit in producing greater numbers of lower quality females which will be out-competed.

On this basis, it can be expected that asex is more likely to be favoured over sex in populations which are continuously 'r selected'. The distribution of sex largely accords with this prediction (e.g. see Bell, 1982; and Bierzychudek, 1985).

In populations which cyclically alternate between periods of 'r' and 'k' selection, the two-fold cost of sex is more likely to outweigh the cognitive superiority of sex during 'r selection'. However, sexual reproduction can overcome this disadvantage in a manner which is similar to the way in which other cognitive arrangements survive periods in which cognition does not pay sufficiently: during periods



of 'r selection', individuals would avoid the two fold cost by reproducing asexually; and during periods of 'k selection' or in other circumstances where the quality of offspring is more important than the number, individuals would reproduce sexually. The ecological evidence seems consistent with this prediction e.g see Bell (1982).

However, a general difficulty remains: even under circumstances of 'k selection', sex would tend to be ousted by asex at any time that the cognitive superiority of sex does not provide sufficient fitness benefits to outweigh the two-fold cost. Would a population at k continuously encounter circumstances which provide sufficient benefits to cognition?

One response to this issue is to attempt to identify environmental circumstances which may continuously vary in ways which would provide continuous adaptive challenges for the population (e.g. the parasite/host coevolution theory of Jaenike, 1978; Hamilton, 1980; and Hamilton *et al.*, 1990). The weakness of such approaches is the implausibility that the continuous environmental variation on which they rely is as continuous and ubiquitous as sex.

The cognitive perspective developed here points to an alternative basis on which to suggest that populations are likely to be continually adapting, and therefore continually providing benefits to sexual reproduction. As we have briefly noted above, as cognition improves, the circumstances in which cognition is exercised and is likely to be beneficial will increase. This is because the population will be able to discover beneficial adaptation to environmental changes to which it previously did not adapt. Furthermore, the more closely the population adapts to circumstances as they arise, the more likely it is that there will be benefit in adapting as these circumstances change - members of populations with greater cognitive abilities will tend to be relatively more specialised to prevailing circumstances, and this relative specialisation will be maintained by further adaptation as circumstances change.

These same influences appear to result in the more or less continual adaptation to external and internal change exhibited by advanced physiological systems. It seems possible that these influences would produce the same outcome in genetic systems which have sufficient cognitive ability. The difference is that genetic adaptation responds to changes occurring on longer time scales (e.g. across generations) while physiological adaptation responds to changes occurring on shorter time scales within the life of individuals. The capacity of the physiological system to adapt individuals would not remove the selection pressures favouring adaptation by the genetic system to longer term changes. This is because selection operating on the genetic system will tune and specialise physiological adaptive mechanisms so that they deal optimally with the particular range of adaptive problems recently encountered by the population. On longer time scales this range will change, providing advantage to further genetic adaptation.

However, it is not possible without further evidence to determine whether these evolutionary processes will ensure that populations are continually adapting, providing continual advantages to sexual reproduction.

But there is a further mechanism which will overcome this difficulty and provide an advantage to sex in widely applicable circumstances as a result of the cognitive superiority of sex (Stewart, 1993). This advantage arises because the emergence of an asexual clone from a sexual population will cause environmental changes due to the clone's significantly higher per capita birth rate of females (the 'two fold' advantage). If the clone is to out-compete the sexual population, the impact of these changes must be sufficient to prevent the sexual population from reproducing through time. However, the cognitive superiority of the sexual population gives it a greater potential to adapt

to the changes and increase its fitness relative to the clone. The strength of the selection favouring the maintenance of sex should be stronger for specialised members of saturated stable communities where the emergence of a clone is likely to cause greater disruption to the adaptedness of itself and of the sexual population. This is consistent with the ecology of sex. Because this mechanism will operate whenever a sexual population is threatened by a clone, it does not need to rely on some independent source of incessant change which would continuously provide an advantage to sex.

## 8. CONCLUSION

Natural selection acting on a genetic system will not only discover adaptations, but will also discover more effective ways to discover adaptations. The result will be a genetic system which produces a pattern of variation which is highly differentiated and specialised across the genome. The variation will be hierarchically organised and will be tuned in relation to both frequency and content to enhance its ability to discover beneficial variants. The pattern of variation can be viewed as a set of hypotheses based on past experience about the likelihood that future change in particular characters will be worthwhile and about the type of changes which are likely to be beneficial. On a longer time scale, the pattern of variation will change dynamically, with the content and the rate of variation changing for particular characters in the light of experience.

This cognitive perspective provides a framework which appears to have the potential to resolve some of the most intractable problems confronting evolutionary theory: the maintenance of variation, the complex and prolonged response of populations to artificial selection, the ubiquity of sex, and the highly differentiated structure of mutation rates and recombination rates across the genome. In addition, it predicts phenomena not previously clearly recognised: the hierarchic organisation of the adaptive processes of the genetic system.

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