ON THE ORIGIN OF MODULAR VARIATION

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Abstract.—We study the dynamics of modularization in a minimal substrate. A module is a functional unit relatively separable from its surrounding structure. Although it is known that modularity is useful both for robustness and for evolvability (Wagner 1996), there is no quantitative model describing how such modularity might originally emerge. Here we suggest, using simple computer simulations, that modularity arises spontaneously in evolutionary systems in response to variation, and that the amount of modular separation is logarithmically proportional to the rate of variation. Consequently, we predict that modular architectures would appear in correlation with high environmental change rates. Because this quantitative model does not require any special substrate to occur, it may also shed light on the origin of modular variation in nature. This observed relationship also indicates that modular design is a generic phenomenon that might be applicable to other fields, such as engineering: Engineering design methods based on evolutionary simulation would benefit from evolving to variable, rather than stationary, fitness criteria, as a weak and problem-independent method for inducing modularity.

Key words.—Adaptation, development, evolvability, modularity, pleiotropy.

A common characteristic of both natural lifeforms and man-made products is their modular structure (Hartwell et al. 1999). It has long been recognized that architectures that exhibit functional separation into modules are more robust and amenable to design and adaptation. Modularity creates a separation that reduces the amount of coupling between internal and external changes, allowing evolution to rearrange inputs to modules without changing their intrinsic behaviors and so to reuse modules as high-level building blocks. In nature this idea is supported by theoretical arguments, such as that proteins are difficult to evolve once they are participating in many different interactions (Waxman 1998) and by observations of phenomena such as tight coordination of the expression of groups of genes functioning in a common process (Niehrs and Pollet 1999). Halder et al (1995) succeeded in sprouting extra functional eyes on the wings, legs and antennae of *Drosophila* by targeted misexpressions of *Drosophila* ''eyeless'' gene cDNA, suggesting the entire eye is represented as a modular unit. Conversely, there is evidence that proteins which interact with many other proteins, such as histones, actin and tubulin, have changed very little during evolution. In artificial systems modularity is critical too: Herbert Simon (1969) noted, in his famous ''Tempus and Hora'' fable, that the evolution of complex forms from simple elements depends critically on the numbers and distribution of potential stable intermediate forms. Modularity has also been recognized as a primary facilitating characteristic of system engineering (Steward 1981; Huang and Kusiak 1998), economics (Langlois 2001), and named as one of the principles of design (Suh 1990; Ulrich and Eppinger 2000). In our own preliminary experiments in the evolution of robotic lifeforms (Lipson and Pollack 2000), we reached a complexity barrier partially due to the lack of modularity and component reuse, and so the question of how modularity arises in nature has become a critical issue.

Although several mechanisms that can give rise to modularity have been suggested, such as symbiosis (Margulis and Fester 1991; Watson and Pollack 2000), developmental segmentation (Holland 1999), and connectivity-sensitive growth (Barabási and Albert 1999), these require advanced substrates to exist before they can be realized. Moreover, not enough is known yet to quantify the ''amount'' of modularity these mechanisms may introduce. Here we investigate the possibility that modularity arises in a natural system merely in response to variation in the conditions in which it evolves. This simple mechanism suggests a ''weak'' process that introduces modularity without relying on a particular representation or substrate. We thus argue that modularity is a fundamental consequence of variation and selection. Because modularity in turn affects the variability and evolvability of an individual, the proposed process sheds light on the question of the origin of variation (Levinton 1988) and the evolution of evolvability (Wagner and Altenberg 1996).
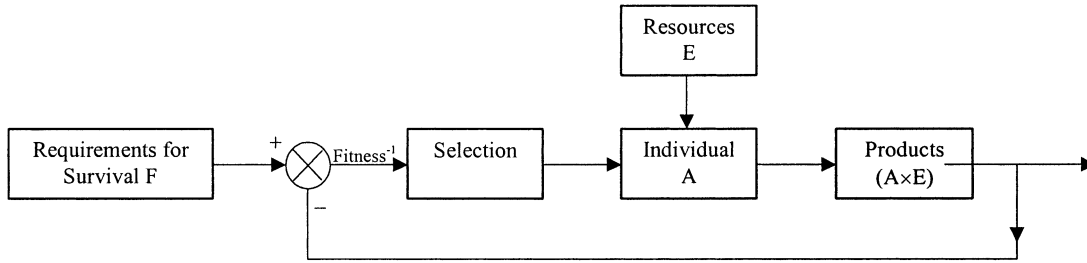
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FIG. 1. The model represents an individual, subject to selection, as a matrix A which transforms a set of environmental resources E into an arbitrary set of products $A \times E$. When compared to requirements F, the residual $|F - A \times E|$ determines the fitness of the individual, which in turn affects its selection. Variation and noise can be introduced at any point in this feedback loop, and the consequential effect on the structure of A is examined.

We have chosen to examine the evolution of modularity using a simple and abstract model of an adaptive system as a transformation of a set of resources into a set of arbitrary functional requirements for survival (exact formulation follows below). Although we realize that not all lifeforms can be abstracted in this way, and that naturally occurring systems are much more elaborate and nonlinear, we argue that this abstraction captures basic connectivity aspects that are necessary for the statistical quantification of the modularization process and for studying its dynamics. Furthermore, the simplification is necessary methodologically to keep the assumptions transparent and the simulation as unbiased as possible (Forbes 2000).

MODEL

We denote an individual as a matrix A, the environmental resources at its disposal as a vector E, and the set of arbitrary functional requirements it has to meet as a vector F. The feedback relationship between these elements is illustrated in Figure 1. In this model, the individual A transforms a set of environmental resources E into an arbitrary set of products $A \times E$. When compared to requirements F, the residual $|F - A \times E|$ determines the fitness of the individual which in turn affects its selection (Fitness is inversely proportional to the magnitude of the residual). We will introduce random variation into this feedback loop and investigate the consequence on the composition of A. Variation can be introduced at any point in this feedback loop, for example, we can vary resources E over time, we can vary the requirements F, we can vary the selection process, we can vary the way fitness is calculated or selection is performed, and we can arbitrarily put noise into the system. In the following experiments, however, we chose to introduce variation at E.

The representation of an individual as a matrix A can take on a variety of interpretations: For example, one interpretation would be where the resource vector E might represent availability or unavailability of a variety of chemicals, the target vector F might also represent a variety of chemicals that must be produced for survival. In this case A would be modeling the interdependencies of the chemical transformation processes that transform one set of chemicals, E, into the chemical set F. Another interpretation would be where E represents organic building blocks, the vector F represents some desired functionalities that must be carried out by the organism to survive, and A represents how building blocks

are composed to achieve this functionality; In this case the matrix would represent organismal structure. Yet another interpretation would be where the vector E represents genes, the vector F represents traits, and the transformation matrix A represents a pleiotropic relationships (Lande 1975). At an even higher level, the system might represent how individuals in an ecosystem cooperate to perform some tasks. Whatever the interpretation, the components can be understood as general units, thereby leaving open the hierarchical level at which the analysis is pitched. The units of F, E and A can also represent availability (binary), quantity (scalar), or any other metric. Although we have obtained results also with real-valued matrices, we present here results for binary/ternary matrices for simplicity. A variety of possible extensions are described in the concluding remarks of this paper.

As shown in Figure 2, an individual A needs to satisfy the following equality to survive, given E and F:

$$F - A \times E = 0 \qquad (1)$$

However, when an individual fails to fully satisfy the functional requirements, then there remains a residual term R:

$$F - A \times E = R \qquad (2)$$

The probability of survival of the individual (essentially, its fitness) is then inversely proportional to the magnitude of R. Note that the solution to the equation is not unique, and—as in real life—there are many different ways to carry out this transformation, some more successful than others. Even among successful solutions, some solutions exhibit more modularity, or less coupling, than other solutions. Here we study the amount of coupling in individuals that evolve under various conditions.

Quantifying Modularity

We represent an individual A as a ternary matrices consisting of elements $\{-1, 0, 1\}$. Such matrices are often used to describe dependencies among system components (Zero = independent, Nonzero = dependent, and the sign represents positive or negative feedback). Methods for improving design process and for identifying modules are based on reordering this matrix into near-block-diagonal form by swapping rows and columns (Warfield 1973). In this form, blocks on the diagonal represent modules, and nonzero elements outside the blocks represent sparse interactions between modules. Consider the systems described in Figure 3. Both matrices

$$F - A \times E = R$$

$$
\begin{bmatrix} -1 \\ +1 \\ +1 \\ -1 \\ +1 \\ -1 \\ -1 \\ +1 \end{bmatrix}
-
\begin{bmatrix}
+1 & 0 & -1 & -1 & 0 & 0 & -1 & 0 \\
0 & 0 & 0 & 0 & 0 & -1 & +1 & 0 \\
-1 & 0 & +1 & 0 & 0 & 0 & +1 & 0 \\
0 & -1 & 0 & 0 & +1 & 0 & 0 & 0 \\
-1 & 0 & 0 & +1 & 0 & 0 & 0 & -1 \\
0 & 0 & 0 & 0 & 0 & 0 & -1 & 0 \\
0 & 0 & +1 & -1 & 0 & 0 & -1 & 0 \\
+1 & 0 & 0 & 0 & 0 & 0 & -1 & 0
\end{bmatrix}
\times
\begin{bmatrix} +1 \\ -1 \\ +1 \\ +1 \\ -1 \\ +1 \\ +1 \\ -1 \end{bmatrix}
=
\begin{bmatrix} 1 \\ 1 \\ 0 \\ -1 \\ 0 \\ 0 \\ 0 \\ 1 \end{bmatrix}
$$

F — An arbitrary set of functional requirements for survival

A — An individual system transforming resources to meet requirements

E — An arbitrary set of resources available in the environment

R — Residual mismatch between actual and required

FIG. 2. The model represents a natural system as a matrix A which transforms a set of environmental resources E into an arbitrary set of requirements F, with unsatisfied requirements yielding a residual R. There are many A's (alternative systems) that solve this equation (yield R = 0), and many more that nearly solve it. The matrix above, for example, is not doing so well, with |R| = 2. Some of the matrices are more coupled (less modular) than others. Elements of F and E are random integers ±1, and elements of A evolve, and are either −1, 0, or +1.

(a)
$$
\begin{bmatrix} F1 \\ F2 \\ F3 \\ F4 \\ F5 \\ F6 \\ F7 \\ F8 \end{bmatrix}
=
\begin{bmatrix}
0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\
1 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
0 & 1 & 1 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 & 0
\end{bmatrix}
\times
\begin{bmatrix} E1 \\ E2 \\ E3 \\ E4 \\ E5 \\ E6 \\ E7 \\ E8 \end{bmatrix}
$$

(b)
$$
\begin{bmatrix} F3 \\ F5 \\ F7 \\ F8 \\ F1 \\ F2 \\ F4 \\ F6 \end{bmatrix}
=
\begin{bmatrix}
0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 1 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{bmatrix}
\times
\begin{bmatrix} E1 \\ E6 \\ E2 \\ E3 \\ E4 \\ E5 \\ E7 \\ E8 \end{bmatrix}
$$

(c)
$$
\begin{bmatrix} F1 \\ F2 \\ F3 \\ F4 \\ F5 \\ F6 \\ F7 \\ F8 \end{bmatrix}
=
\begin{bmatrix}
0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 & 1 \\
1 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 1 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 1 & 1 & 0 & 0
\end{bmatrix}
\times
\begin{bmatrix} E1 \\ E2 \\ E3 \\ E4 \\ E5 \\ E6 \\ E7 \\ E8 \end{bmatrix}
$$

(d)
$$
\begin{bmatrix} F1 \\ F2 \\ F4 \\ F5 \\ F3 \\ F6 \\ F7 \\ F8 \end{bmatrix}
=
\begin{bmatrix}
0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\
1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 1 & 0 & 0 & 1 \\
0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 1 & 1 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 1 & 1 & 0
\end{bmatrix}
\times
\begin{bmatrix} E1 \\ E2 \\ E4 \\ E7 \\ E3 \\ E5 \\ E6 \\ E8 \end{bmatrix}
$$

FIG. 3. Both matrices (a) and (b) represent exactly the same set of equations. However, in matrix (b), rows and columns have been swapped so as to group non-zero elements into blocks along the diagonal. This reordering does not change the equations, but reveals that the set of eight equations is really composed of six subsets of equations, and each subset can be solved and adapted independently of other subsets. Thus, we can say that the system described in (a) and (b) contains six modules. The system described in (c) also contains eight linear equations, but it can be rearranged into at most two blocks (d). Therefore, the system shown in (c) and (d) is less modular. Thus, the maximum number of blocks that a system can be rearranged into is a measure of its modularity.
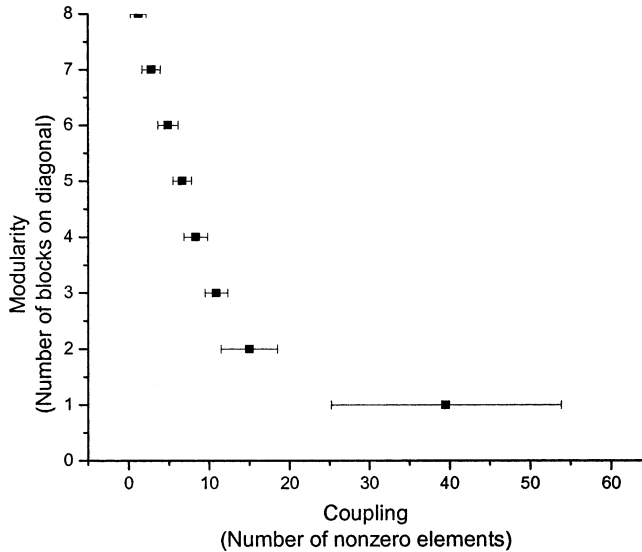
FIG. 4. The inverse correlation between the number of nonzero elements in an 8×8 matrix and the maximum number of blocks it can be rearranged into. Graph is based on 1000 samples uniformly distributed across the X-axis; error bars represent one standard deviation.

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The processes of rearranging a matrix into its block-diagonal form is computationally very expensive. Although a variety of approximation algorithms have been developed for

this purpose, the cost is still prohibitive for simulated evolutionary experiments that require analysis of billions of matrices, as we have conducted. The number of blocks is also a coarse-grained measure: Most of the matrices with higher than average density have a block count of 1, and are therefore indistinguishable (see Fig. 4). In some cases, some of these matrices can be rearranged into a near-block-diagonal form, where most of the nonzero elements are within blocks on the diagonal, except for a few off diagonal terms that represent sparse interaction among modules. A coarse-grained measure may have difficulty detecting such weak trends.

A possible alternative metric for measuring modularity is the number of nonzero elements in the matrix, corresponding to the amount of *coupling* in the system. As we shall show, this measure is inversely related to modularity, and therefore can be used to assess the modularity of a system. Because it is inexpensive to compute and offers a finer-grained resolution, it is also well suited for detecting weak trends in large samples.

In a system represented as a Ternary matrix A of size $N \times N,$ coupling C amounts to the fraction of nonzero elements:

$$C(A) = \frac{1}{N^2} \sum_{i,j=1}^{N} |A_{i,j}| \qquad (3)$$

An $N \times N$ matrix with B blocks on the diagonal, has at most C nonzero elements, depending on the distribution of the sizes of the blocks. In the optimal case, when the blocks are uniform in size, $C \approx N^2/B$ (if B is not a factor of N the formula is more complex but the order is the same). In the worst case (one large block and many unit ones), $C \approx (N - B + 1)^2 + B - 1$. In either case as B increases, C decreases. We confirmed this relationship empirically by generating random matrices whose sparseness is distributed uniformly from empty matrices to full matrices, and computing their optimal modular decomposition. Figure 4 confirms a clear inverse correlation.

Note that there may be occasional cases, such as the single-column system shown in Figure 5(a), where a matrix cannot be decomposed into blocks despite having low coupling.
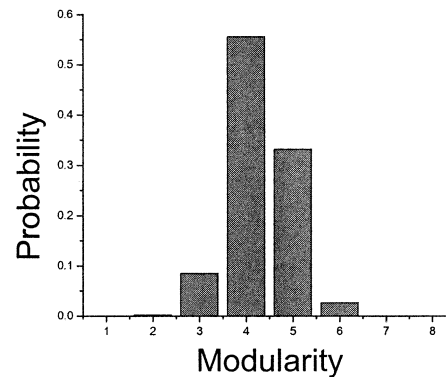
(a)

(b)

FIG. 5. Systems that are sparse yet have low decomposability, such as (a), are possible but exponentially unlikely. Figure (b) shows distribution of modularity for one thousand 8×8 matrices, each filled randomly with 8 nonzero elements.
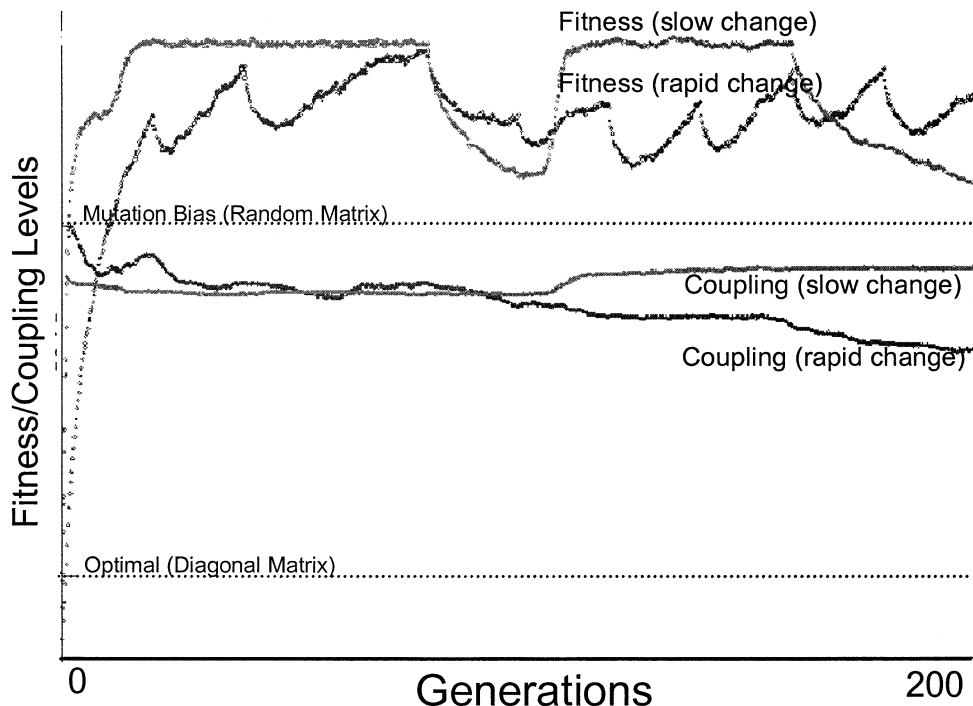
FIG. 6.   Two typical evolutionary runs subject to different environmental change rates: (darker) rapid change: environment changes every 20 generations, and (lighter) slow change: environment changes every 80 generations. For each of the two cases there are two curves: the top shows fitness on the scale of 0% to 100%, and the lower shows coupling on the scale of 0% to 100%. Note how under slow changing environment, solutions have higher average fitness but higher coupling, whereas under faster changing environment solutions have lower average fitness but decreasing coupling. Also note that when environment changes are introduced, the population with higher coupling suffers a harder blow and longer recovery time.

However, such matrix compositions are relatively rare; for example, the probability of N elements arranging into a single particular column is $p = N/N^2 \cdot (N - 1)/N^2 \cdot (N - 2)/N^2 \cdots 1/N^2 < 1/N^N$. Because there are N possible mutually exclusive column arrangements, the overall likelihood of any single-column arrangement is less than $p = 1/N^{N-1}$, which is exponentially unlikely (for example for $N = 8$, $p \sim 10^{-6}$). The bar chart in Figure 5 (b) shows the distribution of the number of blocks for randomly populated matrices with N elements. The distribution empirically confirms this result.

METHOD

We simulated a simple evolutionary process where a population of As was evolved for a given pair of F and E. We observed the dependency of the average coupling $C(A)$ on the rate of change dE/dt of the environment resources.

A basic evolutionary simulation process consists of a population of candidate individuals, selection criteria, a duplication and variation process, and replacement criteria. In a set of experiments, we used a simple genetic algorithm (Mitchell 1996, and details below) to evolve matrices with high fitness (low residual $|R|$) for a given vector of requirements F and a vector of resources E. Details of the selection and replacement processes are described below. We used matrices of size $N = 8$, with elements of both F and E set randomly to ± 1, and elements of A restricted to either $+1$, 0, or -1. The only genetic operators used were mutations,

which switch a single randomly selected element of an individual among the permissible values. A sample individual is shown in Figure 2.

Starting with a randomly initialized population of $n = 200$ individual matrices, the steady-state evolutionary process repeatedly selected an individual, mutated it and replaced it into the population by overwriting an existing, inversely selected individual. We used a Boltzmann selection criterion (see Mitchell 1996), as follows: For individual i, fitness was computed $f_i = \exp(-|R_i|/\tau)$ where $|R_i|$ is the residual of the individual and the Boltzmann temperature coefficient set at $\tau = 1$. Thus, a perfect individual would have fitness of 1 and an individual with a residual error of $|R| = 1$ would have a fitness of $1/e = 0.36$. Similarly, individuals with larger residual will have exponentially lower fitnesses. Individuals were selected in a fitness-proportionate selection, and inverse selection for replacement (same as above but with $\tau = -1$). The process repeated for 20,000 generations (4,000,000 evaluations in total for each experiment). We measured the average coupling $C(A)$ for various rates of change dE/dt of the environment resources, ranging from the control experiment where $dE/dt = 0$ (fixed environment vector E), to highest rate of change $dE/dt = 1$ where a randomly selected element of E switched sign after each evaluation. We first show a single pair of experiments that highlight some interesting features, and then show curves averaged over 10 and 100 experiments, each at several different rates of change, where statistically significant conclusions can be inferred.
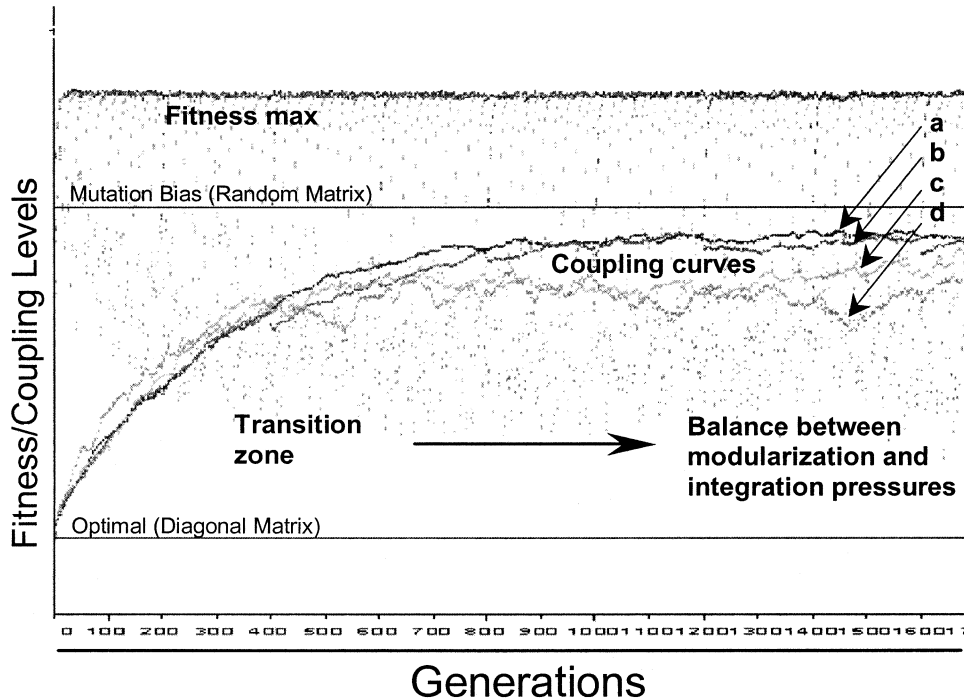
FIG. 7. Four curves for different environmental change rates. (a) No change (control); (b) change every 500 generations, (c) change every 50 generations, and (d) change every five generations. Each curve shows average over 10 experiments with binary matrices, each with a population of 500 matrices over 2000 generations. The matrices were all initialized to all-zero state, and so the solutions process represent a bottom-up composition rather than top-down decomposition. Separation of the four coupling curves according to change rates is already visible after 1,000 iterations. All populations reach high fitness, but fitness variance is higher for population under higher change rates (hence scattered points in background). Note also transition from first order pressure for integration for survival versus second order pressure for decomposition for adaptability.

RESULTS

Figure 6 shows two typical evolutionary runs, each subject to different environmental changing rates. Here the population consisted of 500 individuals. One population (darker) is subject to change introduced every 20 generations, whereas another population (lighter) is subjected to change every 80 generations. The top dashed line shows the mutation bias of 66% nonzeros, which is the expected percentage of nonzeros under the given mutation operator. The lower dashed line shows the optimal coupling, corresponding to a diagonal matrix or permutations of it. For each of the two cases there are two curves: the top two curves show fitness of the two populations, and the lower curves show coupling of the two populations over time. Under slow changing environment solutions have higher average fitness but higher coupling, whereas under faster changing environment solutions have lower average fitness but lower coupling. Also note that when environment changes are introduced, the population with the higher coupling suffers a harder blow and longer recovery times.

Figure 7 shows four curves for different environmental change rates. (a) No change (control); (b) change every 500 generations; (c) change every 50 generations; and (d) change every five generations. Each curve shows average over 10 experiments with binary matrices, each with population of 500 matrices over 2000 generations. The matrices were all initialized to all-zero state, and so the solutions process represent a bottom-up composition rather than top-down decom-

position. Separation of the four coupling curves according to change rates is already visible after 1000 iterations. All populations reach maximum fitness. Note the observed transition from first order (immediate) pressure for integration for survival, appearing as a steep curve of increasing coupling, versus second order (delayed) pressure for decomposition for adaptability, balancing out the integration pressure and keeping the amount of coupling stable and well below the mutation bias.

Finally, to investigate the hypothesis that internal coupling decreases as rate of change of the environment increases, we summarized these results in a plot of internal coupling versus environment change rate, shown in Figure 8. Each point in the plot is averaged for 100 experiments, each of 20,000 generations of a population of 200 individuals. The plot shows a striking linear-log correlation, where higher change rates produce less coupling in the matrix. The correlation can be formalized as

$$C = -k \log \frac{d\mathbf{E}}{dt} + C_0 \tag{4}$$

where k and C_0 are constants that are dependent on the mutation bias, the amount of interaction between the system and the environment, and other specifics of the substrate. Because modularity is inversely proportionate to coupling, we conclude that modularity is logarithmically correlated to rate of change.

Note that under very low change rate (and under no change
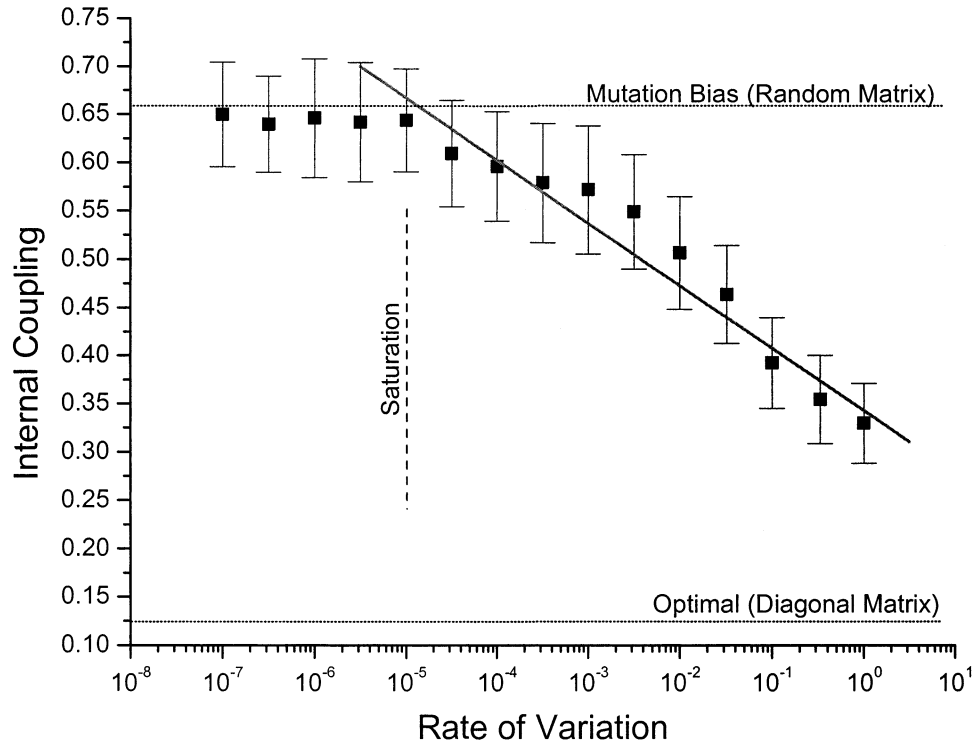
Variation Induced Modularity

FIG. 8. Change driven modularity: Internal coupling versus environment change rate shows a linear-log correlation. Each point in the plot is averaged for 100 experiments, each of 20,000 generations of a population of 200 matrices. Internal coupling is defined by Eq. (3).

at all), the mutation operators pull the matrix coupling density towards the 66% bias. This "saturation" effect is noticeable below the 10^{-5} rate in our experiment.

Statistical significance of differences in coupling among pairs of populations subject to different rates of change was tested using the standard Wilcoxon-Mann-Whitney test (Weerahandi 1994) for distribution independent comparison of populations. This test was used because the populations in questions cannot be assumed to have a normal distribution, and so a distribution-free test is required. Table 1 compares pairs of the four populations against the null hypothesis that the populations are indistinguishable, and shows that the correlation is significant beyond 99% confidence.

Conclusions

This paper presented a methodology for studying the dynamics of modularization in a minimal substrate. In our simulated experiments on an abstract model of a natural system subject to a variable problem, a clear correlation was observed between the logarithm of the rate of change of the system is subject to and the amount of modularity in the system itself. This result was also observed in other variants of these experiments that we did not report here (different matrix sizes, real-valued matrices, different selection/replacements schemes, see Lipson et al. 2001). Also, although we have tested only the dependency between modularity and

TABLE 1. Statistical significance* of differences in coupling among pairs of populations subject to different variation rates, after 10,000 generations

Population A		Population B				
Rate	Coupling**	Rate	Coupling**	Test	$\bar{x}$	Confidence
No change (control)	$\mu = 0.6391$	10^{-4}	$\mu = 0.6302$	$C_A > C_B$	1.3683	>91.3%
No change (control)	$\mu = 0.6391$	10^{-3}	$\mu = 0.5727$	$C_A > C_B$	7.6942	>99.9%
No change (control)	$\mu = 0.6391$	10^{-2}	$\mu = 0.5328$	$C_A > C_B$	10.6287	>99.9%
10^{-4}	$\mu = 0.6302$	10^{-3}	$\mu = 0.5727$	$C_A > C_B$	6.9490	>99.9%
10^{-4}	$\mu = 0.6302$	10^{-2}	$\mu = 0.5328$	$C_A > C_B$	10.4406	>99.9%
10^{-3}	$\mu = 0.5727$	10^{-2}	$\mu = 0.5328$	$C_A > C_B$	5.1433	>99.9%

* Using standard distribution-free Wilcoxon test (Weerahandi, 1994).

** Data based on 100 experiments for each rate value. Note: "μ" denotes mean of distribution; Distributions are not necessarily normal, but calculated standard deviation is approximately 0.05.

rate of change of E, changing F would also induce modularity because of the symmetry of the problem statement: In nature, the resources, the requirements, and the genetic operators are all subject to variation, and we postulate that any perturbation in the problem coefficients will lead to modularization. It is important, however, to recognize the limitations of using a simple model. Because of the linearity of the model and its fitness-proportionate selection, it is likely that our model cannot represent complex modularization dynamics encountered in coevolutionary and more open-ended environments. Some directions for expansion are listed in the next section.

The mechanism suggested here produces a ''weak'' pressure for modularity without relying on a particular representation or substrate. Thus, we argue that modularity is a fundamental consequence of variation and selection. Because modularity in turn affects the variability and evolvability of an individual, the proposed process sheds light on the question of the origin of variation and the evolution of evolvability. Modularity is a critical characteristic of many complex systems (Carrol 2001), and the wealth of fields in which modularity is observable suggests that these results may have generic applicability reaching beyond the quoted examples. Although there are several other mechanisms that can give rise to modularity, it is likely that these mechanisms operate concurrently, and the ability to study this process in isolation may shed light on more complex instances for which less direct data is available.

Future Work

There are several ways in which the minimal substrate presented here can be extended and confirmed. Further research is needed in four main directions: (1) examination of modularization dynamics subject to other sources of variation and in more complex model setups, such as coevolution and open-ended composition; (2) investigation of other forms of modularity, such as hierarchical modularization; (3) extension of the minimal substrate to include more realistic biological details, such as limited resources and nonlinearities describing particular biological domains; and (4) confirmation of the predicted effect in reality, for example by comparing synexpression groups in genomes sequences of bacteria subject to a range of controlled laboratory variation sources.

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Corresponding Editor: P. Wainwright