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LETTER TO THE EDITOR

The adaptive map model

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Abstract. The adaptive map is a simple model for evolutionary searches on a fitness landscape. The map is defined in the set $\mathcal{M} = \{1, 2, \ldots, M\}$, with each integer representing both an organism and its fitness. An integer can be mapped on itself or on any larger integer with the same probability. We calculate the probability distribution of the number of attractors in a map, as well as the distribution of the lengths of the searches. We study the statistical structure of the basins of attraction and compare it with the structures obtained in the random map model and in the mean-field spin glass.

Evolution of species in a fixed environment may be viewed as a search driven by mutation and pruned by natural selection on a fitness surface. Although mutations can produce organisms less fit than their ancestors, they are doomed to die out due to the competition with fitter variants. Thus, by choosing an appropriate timescale, we may think of evolution as a walk on the phase space of possible organisms where each step produces a fitter individual. However, depending on how the fitness values are ascribed to the organisms and on the type of move allowed on the phase space of organisms, the whole process may not end up in the fittest individual (the global maximum of the fitness landscape), but get stuck in low-fitness individuals which, nevertheless, are fitter than any one of their allowed mutant variants (local maxima of the fitness landscape). The beginning steps towards a theory for this kind of search, called adaptive walks, were put forward by Kauffman and Levin (1987) and a thorough discussion of the biological relevance of the adaptive walks is presented in Kauffman (1989).

In this letter we propose and study analytically a simple model for the adaptive walks described above. Each organism is represented by an integer between 1 and M which also measures the fitness of the organism. Thus 1 is the least fit organism while M is the fittest one. The evolutionary search is modelled by the following random map which we shall refer to as the adaptive map. Starting from organism $1 \leqslant i \leqslant M$, one chooses at random one integer $A(i)$ among the $M+1-i$ integers which are larger or equal than i. If the organism is i in a given instant then it will be $A(i)$ in the next step, therefore $A(i) = i$ implies that i is a fixed point of the map. For a *fixed* map A, the process is repeated with different initial organisms until the phase space is exhausted. The fixed points are interpreted as maxima of the fitness landscape. Clearly, M, the global maximum, is a fixed point of any realization of the map A.

A salient aspect of the adaptive map is that its attractors are fixed points only, in contrast to the random map model (Derrida and Flyvbjerg 1987a), where $A(i)$ is chosen randomly among the M integers, which may have limit cycles of period as large as M. In this sense the adaptive map is more similar to the zero-temperature Monte Carlo dynamics usually ascribed to spin-glass models, so that a comparison between these two systems may be of interest.

We focus on the statistical properties of the adaptive map computed in the thermodynamic limit $M \to \infty$. We show that the map is not self-averaging even in this limit. We calculate several properties of the map, in particular, the probability distribution of $Y \equiv \Sigma_S W_S^2$ where W_S is the normalized size of the basin of attraction (weight) of the attractor S: it differs remarkably from the mean-field spin glass (Mézard *et al* 1984) and the random map (Derrida and Flyvbjerg 1987a, b) distributions.

We start by computing the probability distribution P_{N+1} that an adaptive map has exactly $N+1$ attractors ($0 \leqslant N \leqslant M-1$). The probability that $i_1, i_2, \ldots, i_N$ and M are the only attractors of a map is

$$P(i_1, \ldots, i_N, M) = \frac{1}{M+1-i_1} \cdots \frac{1}{M+1-i_N} \prod_{j \neq i_1, \ldots, i_N, M} \left(1 - \frac{1}{M+1-j}\right) = \frac{1}{M-i_1} \cdots \frac{1}{M-i_N} \frac{1}{M}. \tag{1}$$

Summing over all the *distinct* sets of N attractors and keeping only the leading term we obtain the Poisson distribution

$$P_{N+1} = \frac{1}{M} \frac{\ln^N M}{N!}. \tag{2}$$

Thus, the average number of attractors in an adaptive map is $\ln M$ and the probability the map is indecomposable, i.e. has a single attractor, is $P_1 = 1/M$. The attractors divide the phase space in $N+1$ disjoint valleys or basins of attraction whose statistical properties we shall study in detail in this letter.

Let us compute the distribution of the lengths of adaptive walks starting from a randomly chosen integer $1 \leqslant I \leqslant M$ at $t=0$. The probability $P_{I,J}(k)$ that a map reaches a fixed point at $t=k$ before passing tthe integer $I \leqslant J \leqslant M$ is given by

$$P_{I,J}(k) = \frac{1}{M+1-I} \sum_{i_1=I+1}^{J} \frac{1}{M+1-i_1} \sum_{i_2=i_1+1}^{J} \frac{1}{M+1-i_2} \cdots \sum_{i_k=i_{k-1}+1}^{J} \frac{1}{M+1-i_k} \tag{3}$$

with $0 \leqslant k \leqslant J-I$. Taking the limit $M \to \infty$ and assuming that $J-I \to \infty$ we obtain

$$P_{I,J}(k) = \frac{1}{M-I} \int_0^{(J-I)/(M+1-J)} \frac{dx_1}{1+x_1} \int_0^{x_1} \frac{dx_2}{1+x_2} \cdots \int_0^{x_{k-1}} \frac{dx_k}{1+x_k} = \frac{1}{M-I} \frac{1}{k!} \ln^k \left(\frac{M-I}{M+1-J}\right). \tag{4}$$

Therefore the probability a walk stops in exactly k steps is

$$P_{I,M}(k) = \frac{1}{M-I} \frac{\ln^k(M-I)}{k!} \tag{5}$$

and then the average length of such walks is $\bar{k} = \ln(M-I)$. This logarithmic dependence on the number of points of the phase space accessible from I was also found by Kauffman and Levin (1987) in their analysis of adaptive walks.

At this point it is natural to ask for the probability Q_J that an adaptive walk stops exactly at J. This can easily be obtained from equation (4) as follows. The probability that a walk stops before passing J is simply

$$P_{I,J}=\sum_{k=0}^{J-I} P_{I,J}(k)=\frac{1}{M+I-J} \tag{6}$$

independently of the starting point I! Hence,

$$Q_J=P_{I,J}-P_{I,J-1}=\frac{1}{(M+1-J)(M+2-J)} \tag{7}$$

for instance, $Q_M=\frac{1}{2}$, $Q_{M-1}=\frac{1}{6}$, etc, ... $(\Sigma_{J=1}^{M} Q_J=1)$. Clearly, equation (7) must contain some information about the basin of attraction of J. For a given map A, the probability that n randomly chosen integers fall on the same attractor is $Y_n=\Sigma_S W_S^n$ where W_S is the weight of the attractor S. The average over maps yields

$$\overline{Y_n}=\sum_{J=1}^{M} p(J)\overline{W_J^n} \tag{8}$$

where $p(J)$ is the probability that J is an attractor, i.e. that $A(J)=J$,

$$p(J)=\frac{1}{M+1-J}. \tag{9}$$

Here $\overline{W_J^n}\equiv\int_0^1 \mathrm{d}W_J f(W_J)W_J^n$ and $f(W_J)$ is the probability that the weight of attractor J is between W_J and $W_J+\mathrm{d}W_J$. Since $p(J)\overline{W_J^n}$ gives the probability that n integers fall on attractor J, inspection of equation (7) leads to

$$\overline{W_J}=\frac{1}{M+2-J} \tag{10}$$

and $\overline{Y_1}=1$.

We must remark that equation (7) could be derived in a simpler way (though not equation (5)) by calculating the probability $Q_J(k)$ that a walk stops at J in $1\leqslant k\leqslant J-I$ steps,

$$Q_J(k)=\frac{1}{M+1-I}\,\frac{1}{M+1-J}\sum_{i_1=I+1}^{J-1}\frac{1}{M+1-i_1}\cdots\sum_{i_{k-1}=i_{k-2}+1}^{J-1}\frac{1}{M+1-i_{k-1}} \tag{11}$$

and then summing over k. To obtain $\overline{W_J^2}$ we must calculate the probability Q_J^2 that two randomly chosen integers, $I>I'$, fall on attractor J. Let us consider the probability $Q_J^2(k,m)$ that a walk starting at I joins, in the mth step, a walk started at I' and reaches attractor J in the kth step:

$$\begin{aligned}Q_J^2(k,m)=&\frac{1}{M+1-I}\,\frac{1}{M+1-J}\,\frac{1}{M+1-I'}\\&\times\sum_{i_1=I+1}^{J-1}\frac{1}{M+1-i_1}\cdots\sum_{i_m=i_{m-1}+1}^{J-1}\frac{1}{M+1-i_m}\cdots\sum_{i_{k-1}=i_{k-2}+1}^{J-1}\frac{1}{M+1-i_{k-1}}\\&\times\sum_{k'=1}^{i_m-I'}\sum_{j_1=I'+1}^{i_m-1}\frac{1}{M+1-j_1}\cdots\sum_{j_{k'-1}=j_{k'-2}+1}^{i_m-1}\frac{1}{M+1-j_{k'-1}}\end{aligned} \tag{12}$$

with $j_n\neq I, i_1,\ldots,i_{m-1}\ \forall n$. Taking $i_m-I'\to\infty$ (because $I-I'$ is order M with probability 1 in the thermodynamic limit), neglecting terms of order M^{-1} and performing the summation over k' we obtain that the contribution from the walk started at I' to equation (12) is simply

$$\frac{1}{M+2-i_m}. \tag{13}$$

Hence, we can easily show that $Q_J^2(k, m)$ is of order $M^{-1}\times Q_J^2(k,k)$ for $m\neq k$. Since the number of steps in a walk from I to J is approximately $\ln(J-I)$ (see equation (5)), the total contribution to Q_J^2 from the processes with $m\neq k$ is of order $M^{-1}\ln(M)\,Q_J^2(k,k)$, which can be neglected in the thermodynamic limit when compared with $Q_J^2(k,k)$. Thus, taking into account only the process with $m=k$, i.e. $i_m=J$, we find

$$Q_J^2=\frac{1}{M+1-J}\,\frac{1}{(M+2-J)^2} \tag{14}$$

so that $\overline{W_J^2}=\overline{W_J}^2$. *Generalization of the above argument to higher moments leads to*

$$f(W_J)=\delta(W_J-\overline{W_J}). \tag{15}$$

Obivously, this equation does not imply that the weights are the same for all realizations of A since the set of attractors is different for each realization. The scenario we can infer from equations (2), (10) and (15) is that, on average, the phase space consists of a few, O(1), attractors with macroscopic weights and of an infinity, O($\ln M$), of attractors with microscopic, O(M^{-1}), weights.

Some comments regarding the validity of the above results are in order. Strictly, they are valid only in the limits $M\to\infty$ and $J-I\to\infty$. An *a posteriori* argument to justify the latter limit is as follows. In the thermodynamic limit, equations (9), (10) and (15) show that the attractors which determine the statistical properties of the valleys must be such that $M-J$ is of order 1. On the other hand, since the initial integer I is chosen randomly among M integers, the probability that $M-I$ is of order 1 is proportional to M^{-1}, vanishing then in the thermodynamic limit. Therefore $J-I\to\infty$ when $M\leftarrow\infty$.

The statistical properties of the adaptive map follow directly from the knowledge of $p(J)$ and $f(W_J)$. For instance, we can show that $\overline{Y_n}$, the probability that n randomly chosen integers fall on the same attractor, satisfies the recursion relation

$$\bar{Y}_n=\bar{Y}_{n-1}+1-\zeta(n)\qquad n\geqslant 2 \tag{16}$$

where $\zeta(n)\equiv\Sigma_{i=1}^{\infty}1/i^n$ is the Riemann zeta function. Hence, $\overline{Y_2}\approx 0.35$, $\overline{Y_3}\approx 0.15$, $\overline{Y_4}\approx 0.07$, etc, ... Specially interesting is $\overline{Y_2}=2-\pi^2/6$: it is the first moment of the distribution $\Pi(Y)$ where $Y=\Sigma_S W_S^2$ and the sum is over all attractors of a particular realization of map A. The second moment of $\Pi(Y)$,

$$\overline{Y^2}=\sum_J\sum_{J'}p(J,J')\,\overline{W_J^2W_{J'}^2} \tag{17}$$

with $p(J,J')=(p(J)-p(J)p(J'))\delta_{J,J'}+p(J)p(J')$, yields

$$\overline{Y^2}=\bar{Y}^2+14-5\zeta(2)-3\zeta(3)-2\zeta(4). \tag{18}$$

Since $\overline{Y^2}-\bar{Y}^2\sim 0.005$ is a non-zero, Y is a non-self-averaging quantity and therefore the properties of the adaptive map depend on the particular realization of A, even in *the thermodynamic limit.*

Next we shall try to reconstruct the distribution $\Pi(Y)$ from its moments. Since M is an attractor of any realization of A ($p(M)=1$) with weight $W_M=\frac{1}{2}$ we can write

$Y = \frac{1}{4} + \tilde{Y}$ where $\tilde{Y} = \Sigma_{S \neq M} W_S^2$ and thus consider the distribution $\Pi(\tilde{Y})$ instead of $\Pi(Y)$. In contrast to the random map model, if an attractor and its basin of attraction are removed from the phase space, the resulting restricted map does not have the same statistical properties as the original adaptive map. Thus, there are no short cuts to the computation of the moments of $\Pi(\tilde{Y})$ and we have to resort to a direct approach, where the moments are computed from their definitions (see equation (17) for an example). We find $\overline{\tilde{Y}} = 1.051 \times 10^{-1}$, $\overline{\tilde{Y}^2} = 1.555 \times 10^{-2}$, $\overline{\tilde{Y}^3} = 2.610 \times 10^{-3}$, $\overline{\tilde{Y}^4} = 4.732 \times 10^{-4}$ and $\overline{\tilde{Y}^5} = 1.042 \times 10^{-4}$. $\Pi(\tilde{Y})$ is then developed on the basis of the Legendre polynomials yielding the two curves shown in figure 1, obtained by inverting the first four and the first five moments of $\Pi(\tilde{Y})$. It is not difficult to guess the actual shape of $\Pi(\tilde{Y})$ from these curves. It differs remarkably from the shapes of the distributions obtained for the mean-field spin glass (Mézard *et al* 1984) and the random map model (Derrida and Flyvbjerg 1987a, b) which have singular behaviour at $Y = 1$ and $Y = \frac{1}{2}$. However, we must stress that the method of constructing $\Pi(\tilde{Y})$ from its first moments is not well suited to detect singularities and thus the existence of such singularities in $\Pi(\tilde{Y})$ cannot be discarded (Derrida and Flyvbjerg 1987b). This reference also gives an example of a disordered system, the problem of breaking the interval, where $\Pi(Y)$ is non-singular.

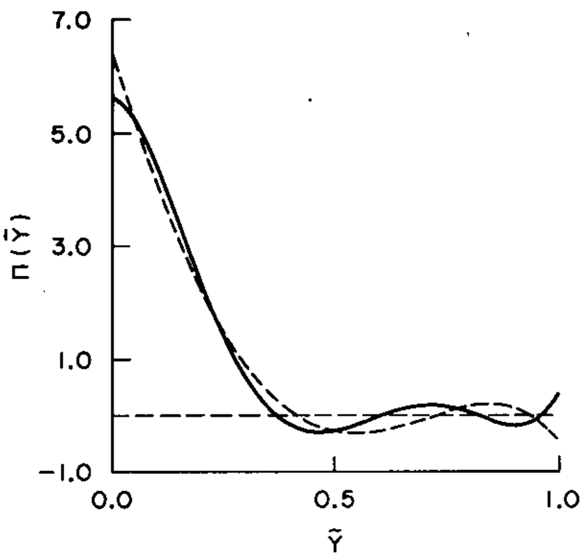

Figure 1. Reconstruction of $\Pi(\tilde{Y})$ by projection on the Legendre polynomials. The broken curve is obtained by inverting the first four moments and the full curve by inverting the first five moments. The broken horizontal line indicates the zero of the vertical axis.

It is interesting to note that the fitness landscape of the adaptive map model possesses a kind of 'Massif Central' structure: equation (10) shows that all attractors with non-zero weights are located close to the global maximum M, corresponding then to high-fitness local maxima.

In summary, we study a map defined in the set $\mathcal{M} = \{1, 2, \ldots, M\}$, where an integer can be mapped on itself or on any larger integer with the same probability. The attractors of this map are fixed points only. The trajectory from a randomly chosen initial integer I to a fixed point J determines an adaptive walk. We obtain that the probability distributions of the number of fixed points and of the lengths of the adaptive walks are given by Poisson distributions with means $\ln(M)$ and $\ln(M-I)$, respectively. We depict the distribution $\Pi(Y)$, where $Y=\Sigma_S W_S^2$ and W_S is the normalized size of the basin of attraction of S and show that the map is not self-averaging even in the thermodynamic limit, $M \rightarrow \infty$.

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