Preadaptation in Populations of Neural Networks Evolving in a Changing Environment

Abstract Populations of simple artificial organisms modeled as neural networks evolve a preference for one particular food type in an environment that contains more than one food type if the quantity of energy extracted from each food type is allowed to coevolve with the behavioral preference (evolvable fitness formula). If, after the emergence of the food preference, the preferred food gradually disappears from the environment at the evolutionary time scale, the evolved specialist strategy is maintained until the preferred food type has completely disappeared. Then a new specialist strategy suddenly emerges with a preference for another food type present in the environment. The appearance of the new strategy takes very few generations, in fact much fewer than in a population starting from zero (random initial population) in the same environment. This, together with the fact that the population with an evolutionary past is more efficient than the population starting from zero, suggests that the former population is preadapted to the changed environment. An analysis of the activation values of the hidden units indicates that the new food preference can be an "exaptation," that is, a new adaptation based on a structure that has previously emerged for adaptively neutral reasons.

1 Introduction

Much work in recent years in the field of neural networks, evolutionary computation, and artificial life has been colored by an ultra-Darwinian view of behavior. This ultra-Darwinian view explains behaviors as adaptations, that is, as resulting from natural selection based on the increased fitness these behaviors confer to the organisms exhibiting them. This may give us the illusion that all behaviors are products of a continuous evolutionary path and that they all arise as adaptations for their present role. On the contrary, the evolutionary path may be discontinuous with punctuated equilibria [8], and further, fitness-enhancing features of organisms may have evolved not for their current use but they may have been co-opted from other contexts. Gould and Vrba [3] have termed such features exaptations because they fit (aptus) not by explicit molding for (ad) current use, but as a consequence of (ex) properties built for other reasons. Exaptations include two types of phenomena, firstly, preadaptations that are built for one function and then co-opted for another, and secondly, exaptations proper, that is, structures that are not built as adaptations at all but are later co-opted for some function. Distinguishing between adaptations and exaptations requires knowledge of the historical sequence of organisms, which is often unavailable in nature. Artificial life
can be a powerful tool in this context because it gives us the opportunity to record and analyze organisms' evolutionary past and, therefore, to study the role of adaptation and exaptation, which might otherwise be impossible. (Cf. Taylor and Jefferson's review for a thorough analysis of artificial life's impact on biological studies [13].)

In this article we present simulations of populations of simple organisms, modeled as neural networks, that evolve on the basis of a fitness criterion that is itself an evolvable trait. To study exaptation in such populations, individual organisms are placed in a dynamic environment, that is, in an environment that may change at the evolutionary time scale. The concept of an evolvable fitness criterion or formula is explained in Section 2 and dynamic environments are introduced in Section 3. Then simulations of artificial organisms with evolvable fitness formulae in dynamic environments are described, and an analysis of their exaptation is performed by examining the activation of neural network units (Section 4). Finally, we discuss the results of our simulations by relating these results to speciation and indicate directions of future research (Section 5).

2 Evolvable Fitness Formula

In simulations of the evolution of populations of artificial organisms (neural networks) individual organisms generate offspring as a function of the degree they satisfy a criterion of fitness, or a fitness formula. For example, organisms that live in an environment that contains food elements may reproduce in proportion to the number of food elements they are able to capture during life. The fitness formula in this case is number of food elements captured. The fitness formula of organisms living in another environment may be number of food elements eaten of type A plus twice the number of food elements eaten of type B. In this case the fitness value (energy value) of type B food is twice the fitness value of type A food.

In simulations using ecological neural networks [9] (cf. also Wilson's notion of "animat" [15]), the fitness formula is important not only as a criterion measure that networks should maximize evolutionarily, but because it determines the type of behavior networks tend to exhibit in the environment. Given a particular environment and a particular fitness formula, organisms have been shown to evolve behaviors that are appropriate to both the environment and the fitness formula [7].

In almost all simulations using genetic algorithms with populations of neural networks the fitness function is fixed and decided by the researcher. Yet, the fitness formula should be let free to evolve as any other trait of the organisms without any necessary control from the researcher. In biological reality the fitness function is not fixed but, as all traits of organisms, is evolvable. More precisely, the fitness formula summarizes a number of properties of a particular species of organisms related to their nutritional needs, the mechanisms and processes in their bodies that extract energy from ingested materials, and so forth. (For the relation between food and the evolution of our species, cf. [4l.) Viewed in this way, the fitness formula, like other traits of organisms, can evolve. In fact, we can interpret the fitness formula of a particular species of organisms as an inherited property of that species of organisms. If the fitness formula varies from one individual to another, is inherited, and is subject to random mutation, we can study its evolution in a population of organisms [7].

The concept of limited evolvable fitness formulae should also be considered. In a limited evolvable fitness formula there is a limit on the energy that an organism can extract with its internal processing mechanism (fitness formula) from any given food source. Although an evolving population of organisms can change its internal mechanisms for extracting energy from food and therefore it can change the amount of energy it extracts from any given quantity and type of food, there are likely to be various constraints and limits on this evolutionary process of change. A limited
evolvable fitness formula limits the maximum quantity of energy that can be extracted from a given food source. When the limit has been reached, any mutation can only decrease this quantity.

Lund and Parisi [7] have shown how simulations with limited evolvable fitness formulae result in abrupt behavioral changes in organisms during evolution. Given a particular sensory apparatus, evolvable fitness formulae and behavioral strategies tend to coevolve. For example, organisms with either a generalist behavioral strategy (i.e., organisms that tend to eat all types of food present in the environment) or a specialist behavioral strategy (i.e., organisms that tend to eat only some food types present in the environment) tend to emerge along with the evolution of a fitness formula that in the first case assigns equal values to all food types and in the second case assigns high values only to the preferred type(s). Given a limited evolvable fitness formula drastic changes are likely to emerge in the behavioral strategies. For instance, an initial specialist strategy can be more or less abruptly replaced by a generalist strategy later in evolution when the energy value extracted from the preferred food type has reached its maximum.

3 Dynamic Environments

To study how organisms with genotypes specifying both a fitness formula and a neural network that controls the behavior of the organism in the environment may be preadapted to changes in the environment, we constructed a number of dynamic environments. Each organism lives alone in its environment. The environment contains food elements of different types. This allows organisms to use different ecological niches, that is, some organisms can eat only some food types while other organisms eat other types. At a certain point in evolution some of the food elements disappear from the environment (e.g., due to some environmental catastrophe). If only one type of food disappears from the environment, the organisms will have to adapt not only to environments that contain less food but to environments with a different distribution of food types.

If a population converges on some particular ecological niche, that is, organisms that eat only one food type emerge during the evolution process, we can study whether the organisms are preadapted to a changed environment in which food elements of the preferred type tend to disappear. According to the results reported in Lund and Parisi [7], a specialist strategy is more likely to emerge if the fitness formula of the individual organisms is evolvable. Therefore, we set up the following model in which the evolvable fitness formula induces a specialist strategy and then the food elements of the preferred type disappear from the environment.

A population of organisms lives in an environment that contains three types of (potential) food elements, A, B, and C. Each individual organism lives alone in its environment. The environment is a grid of 40 x 40 cells that contains a total of 15 food elements, 5 for each of the three types. The food elements are randomly placed in individual cells. Because some or all of this food will be eaten by the organism, a new distribution of 15 food elements, 5 for each type, replaces the preceding one each 50 cycles (one epoch). However, the environment changes during the evolution process. Assuming that food elements of type C emerge as the preferred food, food elements of type C are 5 in number in the first 200 generations, like type A and B food elements, but then they are reduced to 4 from Generation 200 to 400, to 3 from Generation 400 to 600, and so on until they completely disappear at Generation 1,000 when only A and B food elements can be found in the environment (cf. Figure 1a and 1b.)

An organism is modeled by a neural network with input units encoding sensory information about food elements and output units encoding motor behavior with which
The organism can turn and displace itself in the environment. The population evolves by selective nonsexual reproduction and random mutations in the inherited weight matrices. The network architecture is fixed and identical in all organisms. The criterion for reproduction is given by a fitness formula that describes how much energy an organism obtains when it steps on a food element of each of the three types. The individuals that reproduce are those with the most energy at the end of their life.

The neural network of each individual organism has five input units encoding sensory information (cf. Figure 2). Of these five units two encode angle and distance from the currently nearest food element. The angle is measured clockwise with respect to the facing direction of the organism and is mapped in the interval between 0 and 1. The distance is the Euclidean distance between the organism and the nearest food element and is also mapped in the 0-1 interval, so that higher values correspond to smaller distances. The remaining three input units encode the type of the element. Each of these three units is assigned to one of the three types, A, B, and C. The unit corresponding to the type of the currently nearest element takes a value of 1 while the other two units take a value of 0.

The motor behavior of the organism is encoded in two output units. One output unit encodes angle of turning and the other unit encodes length of the step forward (from 0 to 5). In any given cycle a network first turns in the direction chosen and then it moves in this direction for the chosen distance. The network architecture is of the feed-forward type with a single layer of 9 hidden units. The activation of each hidden unit is thresholded to 0.0 or 1.0.

In summary, these organisms are informed at any given time by their senses about the type and position of the currently nearest food element and they respond by turning and displacing themselves. They can either approach the food element or go away from it according to their food preferences.

The organisms can differ in their internal food-processing mechanisms. Some organisms can have a food-processing mechanism that enables them to extract the same amount of energy from all three types of food elements. Other organisms may extract different amounts of energy from the various food types. What we call food-processing
mechanism is the same as the fitness formula that is used to measure the energy collected by each individual during its life and, therefore, to determine the individual’s reproductive chances. Each individual in the initial population is assigned a randomly generated fitness formula as part of its genotype. Each of the three food types can have an initial energy value varying from −0.1 to +0.1. If an individual reproduces, the fitness formula of the individual is inherited by the individual’s offspring together with the weight matrix of its neural network. Random mutations are applied to the energy values of the three food types as specified in the fitness formula of the individual.

The initial population is composed of 100 individuals. The connection weights of the 100 networks are randomly generated. Each individual lives alone for a total of 5,000 cycles. Total lifetime is divided up into 100 epochs or “seasons” each lasting 50 cycles. Fifteen food elements, five of each type, are randomly distributed in the environment at the beginning of each “season.” Before they die, the 20 individuals that have the greatest amount of energy (fitness) reproduce by generating five copies of their genotype that specifies a matrix of connection weights and a fitness formula. Mutations are imposed to the inherited matrices by adding a quantity randomly selected in the interval between −0.1 and +0.1 to 10% of the weights. Fitness formulae are also mutated by the addition of a value randomly chosen in the interval −0.1 to +0.1 to one of the fitness values.

We have run various simulations using different “seeds” to generate the initial random population of neural networks, random distribution of food elements, mutations, and so forth. The results of one typical run are shown in Figures 3–5. The behavioral strategy
that quickly emerges in the population is a specialist strategy, as shown in Figure 4, that shows the number of food elements eaten of the different types. Individuals tend to eat food elements of type C only and they ignore almost completely food elements of type A or B. From Generation 200 on a total of 100 food elements of type C disappears from the environment (one element for each of the 100 "seasons" constituting an individual's lifetime). Therefore, the number of food elements of this type that are eaten decreases after Generation 200, but the organisms stay specialists. The same result is observed at Generation 400, Generation 600, and Generation 800. Type C food elements are progressively disappearing from the environment but the specialist strategy that concentrates on type C food is maintained. (Notice that extinction of the population is not possible in these simulations.) At Generation 1,000 there are no more food elements of type C left, and the organisms start to eat some food elements of type A. At around Generation 1,080 they eat a very high number of food elements of type A. This continues until around Generation 1,300,
when the organisms, again rather suddenly, start to add type B food elements to their diet. The number of type A elements eaten decreases a bit because the organisms are dividing their attention between A and B food elements but from this point on until the end of the simulation (Generation 2,000) the organisms will eat an equivalent and quite high number of food elements of both type A and type B.

The fitness formula coevolves together with the behavior of these organisms (cf. Figure 5). In the first 1,000 generations the fitness value of type C food increases steadily until it reaches a value of about 10 energy units at the end of this period, even though the number of food elements of type C present in the environments is decreasing. In the same period the fitness value of type B food appears to fluctuate around a very low level (0.5 units), while the fitness value of type A food increases a bit (to the level of 2 energy units), but not very much compared with the fitness value of type C food. After Generation 1,000 the situation changes quite suddenly. The fitness value of type C food decreases from approximately 10 to 9 energy units and then it stays at this level. (Notice that type C food has completely disappeared at this time.) However, the fitness value of type A food increases with the same rate as the fitness value of type C food did in the first 1,000 generations. From Generation 1,300 on the fitness value of type B food increases too, although at a slower rate.

With another initial random seed, a different preference may evolve, as shown in
Figures 6–8. In this simulation an initial preference toward type A food elements evolves. If type A food elements later disappear from the environment, as was the case with type C food elements in the preceding simulation, the organisms will change behavior to include type C food elements in their diet (cf. Figure 7). What is noteworthy is that the change in behavior occurs even before all food elements of type A disappear from the environment at Generation 1,000. Already at around Generation 930 there is a sudden change in behavior, as shown in Figure 7. At this point in the evolutionary process, the organisms will start to approach and eat food elements of type C. Because the change in behavior occurs before all food elements of the preferred type A are removed from the environment, the total fitness of the organisms of this simulation will never go to zero, not even at Generation 1,000 when all food elements of the preferred food type A have disappeared, as was the case in the first simulation (cf. Figure 6 and Figure 3).

4 Evolutionary Past

What is the role of the evolutionary past in the changes observed in the first simulation after Generation 1,000? To answer this question directly we did another simulation in which organisms with no evolutionary past (i.e., randomly generated organisms) were placed in an environment identical to the environment in which the organisms of the first simulation found themselves from Generation 1,000 on, that is, an environment containing only food elements of type A and type B, and no food elements of type C. Although the environment contains no type C food, the organisms of this second simulation have the same sensory system as the organisms of the preceding simulation that potentially informs them about all three food types (cf. Figure 2). The only difference between the organisms of the present simulation and those of the preceding simulation is that the connections weights of the organisms' neural networks and the fitness formula are randomly generated in the present simulation whereas they were both genetically inherited in the preceding simulation. Hence, the evolutionary past can have no role in the present simulation but it can include preevadaptations in the preceding simulation.

Because we want to compare the results of this simulation with those of the preceding simulation, we present the results of simulations in which a specialist behavioral strategy tends to emerge. As already found in [7], depending on the initial "seed" some simulations may result in specialist strategies and other simulations may result in generalist strategies.
Figure 9. Number of food elements of each type eaten by the best organism of each generation.

Figure 10. Fitness formula of the best organism of each generation.

Figure 9 shows how type A specialists evolve. The organisms will eat a relatively high number of food elements of type A, and very few food elements of type B (type C is absent). Figure 10 shows the corresponding coevolution of the fitness formula, which assigns high energy to type A food and very little energy to type B food.

As in the preceding simulation, the organisms of the present simulation have already become specialists at Generation 200, which corresponds to Generation 1,200 in the first simulation. However, the evolutionary emergence of a specialist behavioral strategy has different properties in the two simulations. In the preceding simulation we saw a rather abrupt evolutionary change in behavior. In very few generations the population started to eat type A food elements while type B food elements were ignored. On the contrary, the evolutionary emergence of the specialist strategy in the second simulation is slower and much more gradual. (By chance, the preferred food is type A in both simulations.) Furthermore, the organisms of the second type of simulation eat much less after the first 200 generations, namely around 200 food elements of type A, while the organisms of the first simulation ate more food elements of the preferred food type after 200 generations in the environment with two food types only, that is, at Generation 1,200. Both differences are evidence in favor of the hypothesis of a preadaptation of the organisms in the dynamic environment. With no evolutionary past, organisms will evolve gradually toward a specialist behavior that is less efficient than the specialist behavior of organisms with an evolutionary past. The latter organisms appear to have the possibility to exploit capabilities that have emerged at earlier evolutionary stages for other purposes.

The organisms of the second simulation in the preceding section (with the behavioral change happening even before the depletion of all food elements of the preferred type)
will eat nearly 240–250 food elements of the preferred food type after 200 generations in the environment with two food types only, that is, at Generation 1,200. This is only 20%–25% more than the organisms of the second type of simulation. Yet, it should be evident that this population starts from a totally different basis, because the organisms already have a preference for one of the two remaining food types at Generation 1,000.

5 Preadaptation

The results described in the preceding sections suggest that populations of neural networks can be preadapted to changed environments. The sudden changes in behavior after Generation 1,000 and at around Generation 1,300 in our first simulation indicate that in dealing with a changed environment in which type C food elements have completely disappeared the organisms may use some abilities previously evolved to approach type C food elements. In order to find some evidence for this preadaptation in the internal organization of our networks we performed an analysis of single unit activations in individual neural networks tested in artificial, "laboratory" conditions.

An individual to be tested was placed in all possible positions (cells) of the environment with facing direction downward (we selected a single orientation out of the many possible ones for practical purposes) and we measured the activation level of all the units of its neural network in response to the sensory input reaching the individual in that position. Because the environment is a 40 × 40 grid containing 5 elements of each food type, we obtained 1,600 measurements for each individual. (The location of the 15 food elements in the environment used in the test is shown in Figure 1a.)

We tested two individuals, the best individual of Generation 974 (before type C food’s complete disappearance and before the change in behavioral strategy) and the best individual of Generation 1,099 (after type C food’s complete disappearance and the appearance of the new strategy of eating type A food). We will report the results of our analysis first for the input and the output units of these two individuals and then for their hidden units.

The activation level of the five input units is identical for the two individuals because this activation level depends uniquely on the relative position of the organism and of the food elements. (The same distribution of food elements was used for both individuals.) Figures 11–13 show the input activations. Recall that two input units encode food distance and food direction independently from food type. Figure 11 and Figure 12 describe the activation level of the two input units encoding food distance and food direction, respectively, for each of the 1,600 possible positions of the individual. The continuous activation levels of the two units were categorized into four discrete classes: 0 to .25, .25 to .50, .50 to .75, and .75 to 1.

Figure 13 describes the activation level of the remaining three input units. These units encode food type and they have binary values. More specifically, the pattern 100 encodes type A food elements, the pattern 010 encodes type B food elements, and the pattern 001 encodes type C food elements. Hence, the graph indicates the areas of the environment in which the individual experiences each of the three food types as the nearest food element. (Compare this graph with the actual distribution of food elements in Figure 1a.)

While the activation levels of the input units are identical for both the individual of Generation 974 and the individual of Generation 1,099, the activation level of the two output units tends to be different for the two individuals because the two individuals belong to different generations and therefore they are likely to have different connection weights. The graph of Figure 14 gives the activation level of the two output units for the individual of Generation 974 and the graph of Figure 15 gives the same information for the individual of Generation 1,099 for each of the 1,600 positions of the individual.
in the environment. In this case too, the continuous values of the unit encoding movement distance and the unit encoding movement direction have been grouped into four discrete classes.

Let us examine the output of the best individual of Generation 974 first. As we already know, this individual is specialized to prefer food elements of type C, and it will eat nothing else but food elements of this type (cf. Figure 4). If we examine the distance moved by this organism as a function of the food type sensed by the organism at each position in the environment, we clearly see that movement tends to be maximized whenever the food element sensed is one of the two nonpreferred A and B food types. When the food element sensed by the organism is of the preferred

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**Figure 11.** Sensed angle.

**Figure 12.** Sensed distance.

**Figure 13.** Sensed type.
type C, the movement is slower. In other words, the individual will tend to move away from food when the nearest food is of the nonpreferred food type and it will remain in proximity to food when the nearest food is of the preferred type.

The behavior with respect to the preferred food type can be described in more detail. If the preferred type C food is not in front of the organism, the movement direction output unit is activated, that is, the organism will turn. Whenever the movement direction unit is activated the most, the distance unit is deactivated, which implies that when the organism senses the preferred food type and it has to turn to reach the food element, the organism slows down the movement in order not to go away from the preferred food. When the preferred type C food is in front of the organism, it is the movement direction output unit that is deactivated and the organism moves slowly toward the preferred food. In contrast, when the nearest food element is of the nonpreferred A and B types, the individual simply tries to go away by maximizing speed (distance) of movement, thereby increasing the probability that a type C food will be the next nearest (sensed) food element. This makes sense as a strategy to capture as many food elements as possible of the preferred (and more energetic; cf. the evolving fitness formula) type C.

We now turn to the behavior of the best individual of Generation 1,099, after type C food elements have completely disappeared and the population has abruptly turned to a different behavioral strategy, that is, to eat type A food.

Figure 15 shows the activation of the two output units of the best individual of Generation 1,099 in the laboratory test (cf. Figure 1a). This organism appears to be preadapted to the changed environment in which all type C food elements have disappeared because it is able to eat a high number of food element of type A in the changed
environment. Its behavior has changed significantly with respect to the behavior of the best individual of Generation 974. The organism will still perform a maximum distance movement almost every time it senses a food element of type B (still a nonpreferred food type), but when it senses a food element of type A (which has become the preferred food type) it now tends to slow down the movement (cf. Figure 15b). The response of the distance movement unit when a type C food element is sensed is less clear. (Remember that although type C food is completely absent in the actual ecology of this individual, the individual is being tested in an artificial environment that contains all three food types.) Sometimes the organism will actually perform a maximum distance movement when the previously preferred food type (C) is sensed, therefore exhibiting a different response to this type of food with respect to its ancestors of some one hundred generations before. The activation of the movement direction output unit has also changed. Before, at Generation 974, this output unit was activated when type B was sensed, and when the organism was near a food element of type C, while it is now activated when the organism is next to a food element of type A or type C.

We conclude that whenever a nonpreferred food type is sensed both the individual of Generation 974 and the individual of Generation 1,099 will generate a maximum displacement of their bodies, thereby going away from the nonpreferred food and increasing the likelihood of approaching some food element of the preferred type. On the other hand, both individuals will slow down their movement when a preferred food type is sensed so that the preferred food can be reached by subsequent movements. The similarities in the behavioral strategies employed by the two individuals before and after the environmental change has taken place give evidence supporting the hypothesis that the individual of Generation 1,099 is preadapted.

To investigate how this preadaptation may be internally realized in the artificial organisms, we turn to the hidden units of their neural networks. Figure 16 shows the activation of each of the nine hidden units of the best individual of Generation 974 when the individual is placed in all the possible positions of the 40 × 40 grid environment. Because the activation of the hidden units is thresholded, the pictured value of the units is either 0 (white) or 1 (black). In order to understand the pattern of results that are obtained, the activation of the hidden units shown in Figure 16 should be compared with the activation of the input units (Figures 11, 12, and 13) and of the output units (Figure 14a and Figure 14b).

Hidden unit 0 clearly classifies functionally the type of the food element sensed at each position in the environment. If the food element is of type C, that is, the preferred type, the unit is activated; otherwise, if the food element is of type A or type B, the nonpreferred types, no activation is recorded in the unit. Hidden unit 2 gives the inverse picture. The unit is only activated when the organism senses a food element
of type A or type B, that is, the nonpreferred types. Using these two classification units, the movement can be fast when the sensed food element is of one of the two nonpreferred types, while the movement can be slowed down when the sensed food element is of the preferred type (cf. Figure 14b).

Hidden units 0 and 2 classify the three food types into two categories: preferred food (C) and nonpreferred food (A and B). Other hidden units tell the network how to respond to the preferred type C food. This is what hidden units 6 and 8 appear to do. Hidden unit 8 is activated when the organism not only senses a C food element but is very close to the C food element. When this hidden unit is activated, the network responds with a very slow movement (cf. Figure 14b). The network appears to be
cautiously searching for a food element that it knows is very close. Hidden unit 6 is also activated when the nearest food element is of this C type. However, this unit is activated even if the food element is not so close provided it lies on the right or left side of the organism. When this hidden unit is activated, the organism responds with a somewhat more rapid movement. At the same time the organism is more likely to turn before moving (cf. Figure 14a).

Of the five remaining hidden units, two units (1 and 7) are completely nonfunctional. They are always nonactivated whatever the input. The function of the last three hidden units (3, 4, and 5) is less clear, but it is important to note that all three units are sensitive to type A food elements, that is, they are activated when the nearest food element is of type A. However, this activation of the three hidden units has no influence on the main behavior of the best individual of Generation 974, because type A food is a nonpreferred food type for this individual and in any case the network responds to type A food as it responds to type B food, by going away from both food types. However, this sensitivity of three hidden units in the best individual of Generation 974 to type A food, although apparently the result of an adaptively neutral evolution, may help explain why when type C food completely disappears from the environment a type A food specialist strategy (rather than a type B food strategy) quickly emerges in the population. In other words, the prior structure from which the type A food specialist strategy emerges as an exaptation after Generation 1,000 may be recognizable in the activation pattern of hidden units 3, 4, and 5 of the individual of Generation 974.

Let us now turn to the activation of the hidden units of the other individual, the best organism of Generation 1,099, after the change in behavioral strategy has taken place (cf. Figure 17). Hidden units 0 and 2 have the same activation pattern of the corresponding units in the individual of Generation 974. But now a third hidden unit, unit 8, has also assumed the classifying function of units 0 and 2. Unit 8 responds with an activation value of 0 when the organism is experiencing a type B food and with an activation value of 1 when either a type A or a type C food is experienced. This unit is therefore crucial for the type A food specialist strategy that characterizes the behavior of this individual. What is of interest is that the network has not canceled the previous organization that resulted in the activation of units 0 and 2. The classification effected by these two units is no longer useful and is even opposite to the present classification needs. As will be recalled, units 0 and 2 classify type C food in one class and both types A and B in another class. This was appropriate for the individual of Generation 974 but is not appropriate for the individual of Generation 1,099. The latter individual must distinguish between A food (the new preferred food type) and B food (still a nonpreferred food). The solution to this problem is to recruit a new hidden unit for the classification task, that is, unit 8 that distinguishes between the now preferred type A food and the still nonpreferred type B food. However, it is clear that the population at Generation 1,099 inherits a trace of its evolutionary past. For example, one can hypothesize that if the environment would change again and type C food were to reappear in the environment, the population would find in its internal neural structure already preadapted means to deal with the new situation.

The changes in the activation of the remaining hidden units are consistent with the new behavioral strategy of preferring type A food given the neural structure inherited from the past, that is, from the network of the individual of Generation 974. Units 1 and 7 are still completely nonfunctional. They have a constant zero activation value as in the individual of Generation 974. Unit 6, which in the previous individual was sensitive to type C food elements, has now become sensitive to both types C and A food elements. This unit tells the network to approach type C food elements when these are placed just to the right or to the left of the network. This is done by turning
and moving with moderate speed. More or less the same behavior is also elicited by type A food elements. The movement unit is activated and the organism turns around.

The last three hidden units provide the network with information on how to move when the nearest food is of the now preferred type A. As will be recalled, these three units were already sensitive, for adaptively neutral reasons, to type A food. Now they have assumed the adaptively significant function of controlling the appropriate behavior for approaching type A food in the individual of Generation 1,099. As we suggested, here we can see an objective “trace” of the preadaptation mechanism. The individual of Generation 974 for purely random (adaptively neutral) reasons has developed
a sensitivity to type A food although type A food was classified at that time in the same class as type B food as both nonpreferred food types. This random evolutionary event becomes meaningful when the environment changes and type C food completely disappears. Now, the population must develop a new behavioral strategy to survive. The strategy that emerges is still a specialist strategy but the choice to become a type A rather than a type B food specialist appears to be dictated by the population's evolutionary past, more specifically by the sensitivity to type A elements that has developed for adaptively neutral reasons in the previous generations. Hence, the new type A food specialist strategy can be said to be exapted.

A possible explanation for the emergence of a type A food specialist strategy rather than a type B food strategy after Generation 1,000 could be found in the slightly higher number of type A food elements eaten with respect to type B food elements by the population before Generation 1,000 (cf. Figure 4). However, the difference is very small and, anyhow, the fitness value of type A food is almost inexistent before Generation 1,000 although it is slightly higher than the fitness value of type B food (cf. Figure 5). Our results may underscore the chaotic nature of evolving populations of networks that appear to be sensitive to very small differences in initial conditions in their evolution.

6 Discussion

In the introduction we distinguished between two types of exaptations, preadaptations and exaptations proper. Preadaptations are the use of structures that have first emerged for function X for a new function Y. Exaptations in the proper sense are the use of structures that have first emerged for adaptively neutral reasons for some function X.

Both types of exaptations appear to occur in our populations of artificial organisms. We can view the evolved behavior of approaching type A food after Generation 1,000 as a preadaptation because a behavioral strategy built for one purpose (eating type C food) is co-opted for another purpose (eating type A food). When the environment changes and the type C food completely disappears, the behavior of approaching type C food is used to approach A food. This may explain why an efficient strategy for capturing type A food elements emerges so quickly after Generation 1,000. But the fact that the newly preferred food type is A rather than B is an exaptation in the proper sense, namely an adaptively neutral structure that is later co-opted for some function.

We found some trace of this adaptively neutral structure in the internal organization of the best individual of Generation 974. This individual has hidden units that are sensitive to type A food elements although they are nonpreferred food exactly like type B food elements. It is this sensitivity to type A food rather than type B that has evolved for no adaptive reasons that can explain why, after the complete disappearance of type C food and the change in behavioral strategy, the new behavioral strategy that emerges is a preference for type A food rather than for type B.

Another trace of the adaptively neutral structure that results in the exaptive emergence of a preference for type A food after Generation 1,000 could be the small evolved fitness values for the nonpreferred food types before Generation 1,000. In the past, before the abrupt behavioral change, organisms evolved some mechanisms in their bodies that allowed them to extract high energy from the preferred food type (C). But, besides this, for adaptively neutral reasons they also evolved mechanisms to extract some energy from food elements of the two nonpreferred food types, even though they ingested almost none of these food elements. This adaptively neutral tendency represents the channel of possible change. As Gould [2] has proposed, selection may be required to push an organism down a channel but the channel itself, though not an adaptation, acts as a major determinant of evolutionary direction. The reason that may explain the emergence of a specialist behavioral strategy toward type A food

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after Generation 1,000 is the prior adaptively neutral evolution of a mechanism to extract some energy from food elements of type A. Let us imagine that the fitness formula had evolved in such a way that the fitness value of type A were negative (which is a possible evolution of the fitness formula [7]). Then the evolutionary channel to become a type A specialist would not exist. Food elements of type A would be poisonous to the organisms (negative fitness value), and organisms that employ a type A specialist strategy would simply die out. We therefore conclude that the evolved fitness formula, in this case, acts as a channel for exaptation and evolutionary progress.

A theme of future work will be the evolution of populations of organisms that live in the same shared environment (a first step has been taken in [6]). The emergence of distinct food preferences in subpopulations of these populations together with the spatial separation of food types may be at the origin of sympatric speciation.

Food preferences may translate into habitat specialization and be at the origin of sympatric speciation. Rice [10] shows how populations of organisms can be specialized and isolated through the evolution of gaps in the phenotypic distribution of habitat use. Laboratory experiments have shown that habitat preferences, as in our populations of artificial organisms, can be innate. (Cf. Thiele's [14] experiments with extant species of carabid beetles.) The model of speciation via habitat specialization shows how a unimodal phenotypic distribution can evolve to split into two subpopulations, preferring and exploiting different habitats. If the distribution of different food types is not geographically homogeneous but different food types tend to be located in different subregions, food preferences may create the conditions for sympatric speciation. The isolation that is required for speciation is not caused by environmental conditions such as geographical barriers but by behavioral tendencies (food preferences) that tend to isolate subpopulations with different food preferences.

Habitat specialization leading to speciation can result not only from food preferences but also from competitive exclusion. Sowig [12] found that while many species of Bembidion beetles preferred the same substrate, not all were found on this substrate in nature, and concluded that some species were competitively excluded from preferred habitats. Krebs et al. [5] showed competitive exclusion from strict resource refuges among the two Drosophila species, D. buzzatii and D. aldrichi, that coexist on several species of Opuntia cacti in Australia. The two Drosophila species' preferences and larval performances were analyzed on O. tomentosa and O. streptacantha, which are found in the northern part of the cactus distribution, and on O. stricta in the southern part. Larval performance for both Drosophila species was found to be least on O. stricta, but adult female preference of both species was for O. stricta. It was concluded that "differential larval performance on O. stricta may contribute to the rare presence of D. aldrichi in the southern part of the cactus distribution, while the superior quality of O. tomentosa and O. streptacantha (larger root size and higher microbial concentration) may reduce competition and facilitate coexistence of the fly species in the north" [5, p. 362], because the larval performance of D. aldrichi decreased significantly on O. stricta in mixed-species cultures, but not on the two other cactus species.

The competitive exclusion from resource refuges among D. buzzatii and D. aldrichi shows that competition among species can lead to suppression of habitat preferences, but it has also been found that competition within species can lead to suppression of habitat preferences. For example, Barker [1] has shown that in D. buzzatii sensitivity to oviposition preference decreases as average fecundity increases, and the "results suggest some degree of interference or required spacing between females at oviposition, so that when more females are ovipositing at the same time, some are forced to oviposit on yeast that are intrinsically less preferred" [11, p. 1080]. In other words,
the suppression of habitat preference can also be due to density-dependent habitat selection.

We conclude that coexistence by resource partitioning can occur both when the species have different preferences for some components of the available resources, and when a strict resource refuge is present, with one species using a resource that it does not prefer. The latter can clearly lead to the first by the evolution of habitat preference as described in the model of speciation via specialization in biological organisms, and as indicated with the present simulations in populations of artificial neural networks with evolvable fitness formulae, where we observed that organisms evolve different preferences dependent on the environment and their evolutionary past.

References