Connection and Coordination: The Interplay Between Architecture and Dynamics in Evolved Model Pattern Generators

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We undertake a systematic study of the role of neural architecture in shaping the dynamics of evolved model pattern generators for a walking task. First, we consider the minimum number of connections necessary to achieve high performance on this task. Next, we identify architectural motifs associated with high fitness. We then examine how high-fitness architectures differ in their ability to evolve. Finally, we demonstrate the existence of distinct parameter subgroups in some architectures and show that these subgroups are characterized by differences in neuron excitabilities and connection signs.

1 Introduction

From molecules to cells to animals to ecosystems, biological systems are typically composed of large numbers of heterogeneous nonlinear dynamical elements densely interconnected in specific networks. Understanding such systems necessarily involves understanding not only the dynamics of their elements, but also their architecture of interconnection. Interest in the role of network architecture in complex systems has been steadily growing for several years, with work on a diverse range of systems, including genetic networks, metabolic networks, signaling networks, nervous systems, food webs, social networks and the Internet (Watts & Strogatz, 1998; Jeong, Tombor, Albert, Oltvai, & Barabási, 2000; Strogatz, 2001; Guelzim, Bottani,
Most recent research on complex networks has focused primarily on structural questions. For example, studies of a wide variety of naturally occurring networks have found that small-world structures are common (Watts & Strogatz, 1998). Structural questions have also been a major concern in neuroscience (van Essen, Anderson, & Felleman, 1992; Sporns, Tononi, & Edelman, 2000; Braitenberg, 2001). In addition, research on the dynamics of network growth has begun to provide insight into how observed network structures might arise. For example, preferential attachment of new links during network growth can produce scale-free network architectures (Barabási & Albert, 1999).

An equally important but less well-studied aspect of complex networks is how network architecture shapes the dynamics of the elements it interconnects. For example, some architectures lend robustness to perturbations of both parameters and topology, while others do not (Albert, Jeong, & Barabási, 2000; Stelling, Klamt, Bettenbrock, Schuster, & Gilles, 2002). Again, the influence of circuit architecture on neural activity has long been a major concern in neuroscience, especially in the invertebrate pattern generation community, where detailed cellular and synaptic data are sometimes available (Getting, 1989; Marder & Calabrese, 1996; Roberts, 1998). However, while a great deal of work has been done on nonlinear oscillators coupled in regular patterns (Pikovsky, Rosenblum, & Kurths, 2001), there has been very little research on nonlinear dynamical systems connected in irregular but nonrandom patterns. Yet, arguably, this is the case most relevant to biological systems.

In this article, we undertake a systematic study of the role of network architecture in shaping the dynamics of evolved model pattern-generation circuits for walking (Beer & Gallagher, 1992). While simple, this walking task raises a number of interesting coordination issues and has been extensively analyzed (Chiel, Beer, & Gallagher, 1999; Beer, Chiel, & Gallagher, 1999), providing a solid foundation for detailed studies of the interplay between architecture and dynamics. We first consider the minimum number of connections necessary to achieve high performance on this task. Next, we identify architectural motifs that are associated with high fitness and study the impact of architecture on evolvability. Finally, we demonstrate the existence of distinct parameter subgroups in some architectures and show that these subgroups are characterized by differences in neuron excitabilities and connection signs.

2 Methods

We examined the effect of architecture on the evolution of central pattern generators for walking in a simple legged body (Beer & Gallagher, 1992). The body consisted of a single leg with a joint actuated by two opposing swing
"muscles" and a foot. When the foot was "down," any torque produced by the muscles served to translate the body under Newtonian mechanics. When the foot was "up," any torque produced by the muscles served to swing the leg relative to the body. Details of the body model and its analysis can be found in Beer et al. (1999).

This leg was controlled by a continuous-time recurrent neural network (CTRNN):

\[
\tau_i \dot{y}_i = -y_i + \sum_{j=1}^{N} w_{ji} \sigma(y_j + \theta_j) \quad i = 1, \ldots, N
\]

where \( y_i \) is the state of the \( i \)th neuron, \( \dot{y}_i \) denotes the time rate of change of this state, \( \tau_i \) is the neuron’s membrane time constant, \( w_{ji} \) is the strength of the connection from the \( j \)th to the \( i \)th neuron, \( \theta_i \) is a bias term, and \( \sigma(x) = 1/(1 + e^{-x}) \) is the standard logistic output function. We interpret a self-connection \( w_{ii} \) as a simple nonlinear active conductance rather than as a literal connection. We focus here on three-, four-, and five-neuron CTRNNs. Three of these neurons are always motor neurons that control the two opposing muscles of the leg (labeled BS for backward swing and FS for forward swing) and the foot (labeled FT), while any additional neurons are interneurons (labeled INT\(n\)) with no preassigned function.

A real-valued genetic algorithm was used to evolve CTRNN parameters. A population of 100 individuals was maintained, with each individual encoded as a vector of \( N^2 + 2N \) real numbers (\( N \) time constants, \( N \) biases, and \( N^2 \) connection weights). Elitist selection was used to preserve the best individual each generation, whereas the remaining children were generated by mutation of selected parents. Individuals were selected for mutation using a linear rank-based method, with the best individual producing an average of 1.1 offspring. A selected parent was mutated by adding to it a random displacement vector with uniformly distributed direction and normally distributed magnitude (Bäck, 1996). The mutation magnitude had zero mean and a variance of 0.5. Searches were run for 250 generations. Connection weights and biases were constrained to lie in the range \( \pm 16 \), while time constants were constrained to the range \( [0.5, 10] \).

The walking performance measure optimized by the genetic algorithm was average forward velocity of the body. This average velocity was computed in two ways. During evolution, truncated fitness was evaluated by integrating the model for 220 time units using the forward Euler integration method with a step size of 0.1 and then computing the average velocity (total forward distance covered in 220 time units divided by 220). During analysis, asymptotic fitness was evaluated by integrating the model for 1000 time units to skip transients and then computing its average velocity for one stepping period (with a fitness of 0 assigned to nonoscillatory circuits). Although asymptotic fitness more accurately describes the long-term
performance of a circuit, truncated fitness is much less expensive to compute during evolutionary searches. In both cases, the highest average velocity achievable is known to be 0.627 from a previous analysis of the optimal controller for this task and body model (Beer et al., 1999). The best truncated fitness that can be achieved by a nonoscillatory circuit (which takes only a single step) is also known to be 0.125.

We define an architecture to be a set of directed connections between neurons. Since we do not consider self-connections to be part of an architecture, there are $N^2 - N$ possible interconnections in an $N$-neuron circuit, and thus $2^{N^2-N}$ possible architectures. However, not all of these architectures are unique. When more than one interneuron is present, all permutations of interneuron labels that leave an architecture invariant should be counted only once since, unlike motor neurons, the interneuron labels are arbitrary. Counting the number of unique $N$-neuron architectures is an instance of the partially labeled graph isomorphism problem, which can be solved using Pólya’s enumeration theorem (Harary, 1972). We found that there are 64 distinct three-neuron architectures, 4096 distinct four-neuron architectures, and 528,384 distinct five-neuron architectures. Details of the Pólya theory calculations for the five-neuron case can be found in Ames (2003).

The studies described in this article are based on the results of evolutionary searches on a large sample of different three-, four-, and five-neuron architectures. In the three- and four-neuron cases, the samples were exhaustive. We ran all 64 three-neuron architectures (300 random seeds each) and all 4096 four-neuron architectures (200 random seeds each). Because the number of five-neuron architectures was so large, we ran only a sample of 5000 five-neuron architectures (100 random seeds each). Thus, 1,338,400 evolutionary searches were run to form our baseline data set. A total of 850,900 additional experiments were run as described below to augment this baseline data set when necessary.

3 A Small Number of Connections Suffice

How many connections are required to achieve high performance on the walking task? In the absence of any architectural constraints, a common simplification is to use fully interconnected networks because they contain all possible architectures as subcircuits. However, the number of connections between $N$ neurons has been observed to scale roughly linearly in mammals (Stevens, 1989), much slower than the $O(N^2)$ scaling produced by full interconnection. Thus, our first task was to characterize the relationship between the number of connections and the best attainable fitness.

There are $N^2 - N = 6, 12$ and 20 possible connections for three-, four-, and five-neuron circuits, respectively. A uniform sample of architectures
leads to a nonuniform sample of number of connections because there are $\binom{N^2-N}{C}$ architectures with $C$ connections ($0 \leq C \leq N^2 - N$). Thus, most architectures of an $N$-neuron circuit have close to $(N^2 - N)/2$ connections. Because of the binomial distribution of architectures having a given number of connections, our sample of 5000 five-neuron architectures contained very few architectures with few or many connections. In order to compensate for this bias, we augmented our baseline data set with 732,300 additional five-neuron experiments that exhaustively covered the five-neuron architectures having 0 to 5 and 18 to 20 connections.

Figure 1 plots the very best asymptotic fitness obtained for three- (dashed line), four- (gray line), and five-neuron (solid line) architectures as a function of number of connections. Regardless of the number of neurons, circuits with fewer than two connections have essentially zero fitness, while circuits with more than two connections have high fitness. The reason for this difference is that it takes at least two connections to link three motor neurons, and it takes at least three connections to form an oscillator involving all three motor neurons. Most interesting, although there is an increase in best fitness with larger numbers of connections in four- and five-neuron circuits, the additional benefit has saturated by about five connections. Thus, far sparser than fully interconnected circuits are sufficient to achieve high performance on the walking task.
4 Architectural Motifs Predict Performance

Which architectures perform well on the walking task, and what particular connectivity features predict the best fitness that an architecture can achieve? There is growing evidence for recurring network motifs in biological networks, leading to the hope that general structural design principles may exist (Milo et al., 2002). In order to explore the existence of architectural motifs in our model and their correlation with fitness, we analyzed our three-neuron data in detail and then tested the patterns we found against our four- and five-neuron data.

If we plot the best asymptotic fitness obtained over all runs of each three-neuron architecture (see Figure 2A), the data clearly fall into three distinct fitness groups, with wide gaps between them. This suggests that architecture strongly constrains the maximum achievable fitness of a circuit and that three separate classes of architectures may exist.

Behaviorally, architectures from the low-fitness group (29/64) produced at most a single step. Architectures from the middle-fitness group (8/64) stepped rhythmically, but either the swing or stance phase of the motion was very slow. Closer inspection revealed that one of the swing motor neurons always adopted a fixed output, while the foot and the other swing motor neuron rhythmically oscillated. Interestingly, the constant outputs adopted by each swing motor neuron were consistently distinct in the best circuits in this group. When BS was the constant output motor neuron, the output it adopted was always around 0.7. In contrast, when FS was the constant output motor neuron, it adopted an output value around 0.3. Finally, architectures from the high-fitness group (27/64) exhibit fast rhythmic stepping.

What architectural features characterize these three fitness groups? An example three-neuron architecture from each group is shown in the left column of Figure 3. Architectures in the low-fitness group lack feedback

Figure 2: Fitness classification of architectural motifs. In all cases, the horizontal axis represents an arbitrary architecture label. (A) The maximum asymptotic fitnesses obtained by all evolutionary searches with each of the 64 possible three-neuron architectures (black points) fall into three distinct fitness groups (indicated by gray rectangles). Architectures can independently be classified by their connectivity patterns (labeled class 1, class 2, and class 3). Note that architecture class strongly predicts fitness group in three-neuron circuits. (B) Maximum asymptotic fitness for all four-neuron baseline searches, with the data classified as class 1 (black points), class 2 (gray points), or class 3 (crosses) based on the connectivity pattern of each architecture. The dashed line indicates the maximum fitness obtainable given the strategy used by the best class 2 architectures. (C) Maximum asymptotic fitness for all five-neuron baseline searches classified by connectivity pattern.
loops that link foot and swing motor neurons. Because they cannot achieve oscillatory activity involving both the foot and a swing motor neuron, these circuits are unable to produce rhythmic stepping. Architectures in the middle-fitness group possess feedback loops between the foot and one of the swing motor neurons, but these feedback loops do not drive the other swing motor neuron. Thus, these circuits can oscillate, but one direction of leg motion is always slowed by constant activity in the opposing
Table 1: Definition of the Three Architecture Classes.

<table>
<thead>
<tr>
<th>CD(FT)</th>
<th>CD(BS)</th>
<th>CD(FS)</th>
<th>Class</th>
<th>Fitness</th>
</tr>
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<tbody>
<tr>
<td>T</td>
<td>T</td>
<td>T</td>
<td>1</td>
<td>High</td>
</tr>
<tr>
<td>T</td>
<td>T</td>
<td>F</td>
<td>2</td>
<td>Medium</td>
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<tr>
<td>T</td>
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<td>2</td>
<td>Medium</td>
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<td>T</td>
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<td>F</td>
<td>3</td>
<td>Low</td>
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<td>F</td>
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Note: The predicate *CycleDriven*(m) has been abbreviated to CD(m). T = true; F = false.

swing motor neuron. Architectures in the high-fitness group contain feedback loops that either involve or drive all three motor neurons. This pattern of feedback allows these circuits to produce coordinated oscillations in all three motor neurons. These results suggest that neural circuits can be partitioned into distinct classes based solely on their connectivity and that these architecture classes might strongly predict the best obtainable fitness.

In order to test the generality of these predictions in larger circuits, we must first state the definition of each architecture class precisely and in such a way that it can be applied to circuits with interneurons. Let the predicate *CycleDriven*(m) be true of a motor neuron m in a particular architecture if and only if m either participates in or is driven by a feedback loop in that architecture. Since we have three motor neurons, there are eight possibilities, which are classified according to the architectural patterns observed above (see Table 1). By definition, classes 1, 2, and 3 for three-neuron circuits are fully consistent with the high-, middle-, and low-fitness groups shown in Figure 2A, respectively. Examples of each of the three classes for four-neuron and five-neuron circuits are shown in Figure 3.

We next tested the ability of this architecture classification to predict best asymptotic fitness in our four- and five-neuron data sets (see Figures 2B and 2C, respectively). In the four-neuron circuits, 2617/4096 architectures were class 1, 528/4096 were class 2, and 951/4096 were class 3. In the five-neuron circuits, 3991/5000 were class 1, 488/5000 were class 2, and 521/5000 were class 3. In both cases, class 1 (black points), class 2 (gray points), and class 3 (crosses) were strongly correlated with high, middle and low fitness, respectively. However, unlike in the three-neuron case, there was some fitness overlap between class 1 and class 2 architectures (12/4096 for four-neuron circuits and 37/5000 for five-neuron circuits) and a small amount of fitness overlap between class 2 and class 3 architectures in the five-neuron case (2/5000).

We hypothesized that this overlap was caused by an insufficient number of searches for these architectures, so that these architectures had not yet
achieved their best attainable fitness. To test this hypothesis, we performed additional searches on all overlap architectures. As a control, we also ran the same number of additional searches for two class 2 architectures with comparable fitness for each class 1 overlap architecture and with two class 3 architectures for each class 2 overlap architecture. We ran 43,500 additional experiments in the four-neuron case and 75,100 additional experiments in the five-neuron case.

After these additional experiments, only three class 1 overlap architectures remained in the four-neuron case (see Figure 4A), and only two class 1 overlap architectures and one class 2 overlap architecture remained in the five-neuron case (see Figure 4B). Interestingly, all remaining overlap architectures contained independent cycles, in which subgroups of motor neurons were driven by separate feedback loops (see Figure 4C). Even if the oscillations produced by independent cycles are individually appropriate for walking, they will not in general be properly coordinated unless their initial conditions are precisely set. However, this cannot be done stably unless some other source of coupling is present, such as shared sensory feedback or mechanical coupling of the relevant body degrees of freedom.

Independent cycle architectures aside, the fitness separation between class 2 and class 3 architectures is quite large. However, the boundary between class 1 and class 2 architectures is very sharp, occurring at a fitness value of around 0.47. What defines this fitness boundary, and how can we calculate its exact value? As noted above, one swing neuron always has a constant output in class 2 architectures. By repeating the optimal fitness calculations described in appendix A of Beer et al. (1999) with the constraint that either BS or FS must be held constant, we obtain expressions for the optimal fitness achievable as a function of these constant values:

\[
V^* (BS) = \frac{55}{2} \left( \frac{85}{\sqrt{6\sqrt{BS}}} + \frac{4\sqrt{5\pi/3}}{\sqrt{1-BS}} \right)^{-1}
\]

\[
V^* (FS) = \frac{165\sqrt{FS(1-FS)}}{85\sqrt{6\sqrt{FS}} + 8\sqrt{1-FS}\sqrt{15\pi}}.
\]

These expressions can be maximized exactly, but it is sufficient for our purposes here to do so only numerically. We find that when BS is the constant motor neuron, the highest fitness is achieved at \( BS^* \approx 0.709 \). In contrast, when FS is held constant, the highest fitness is achieved at \( FS^* \approx 0.291 \). Note that these values correspond closely to the constant outputs observed in the best-evolved class 2 circuits. The maximum fitnesses are the same in both cases: \( V^*(FS^*) = V^*(BS^*) \approx 0.473 \), which is very close to the observed boundary between class 1 and class 2 (dashed lines in Figure 2). This value serves as an upper bound for the best fitness achievable by a class 2 architecture.
Figure 4: Investigation of the fitness overlaps between architecture classes in Figures 2B and 2C. (A) Data obtained from additional evolutionary searches with the class 1 overlap architectures from Figure 2B and class 2 architectures of comparable fitness. Note that only three class 1 overlap architectures remain. (B) Data obtained from additional evolutionary searches with the class 1 and class 2 overlap architectures from Figure 2C and, respectively, class 2 and class 3 overlap architectures of comparable fitness. Note that only two class 1 and one class 2 overlap architectures remain. (C) Examples of overlap architectures from A and B. (Left) A class 1 four-neuron independent cycles architecture from A whose best fitness lies in the range characteristic of class 2 architectures. Note that the BS and FS motor neurons occur in separate cycles. (Middle) A class 1 five-neuron independent cycles architecture from B whose best fitness lies in the range characteristic of class 2. Note that BS and FS occur in separate cycles. (Right) A class 2 five-neuron independent cycles architecture from B whose best fitness lies in the range characteristic of class 3. Note that the foot motor neuron FT occurs in a cycle separate from both BS and FS.
5 Architecture Influences Evolvability

Are high-fitness circuits easier to evolve with some architectures than others? The best fitness obtained over a set of evolutionary searches provides a lower bound on the maximum locomotion performance that can be achieved with a given architecture. In contrast, the average of the best fitness obtained in each of a set of searches provides information about the difficulty of finding high-performance circuits with that architecture through evolutionary search. The lower this average is relative to the best fitness achievable with a given architecture, the less frequently evolutionary runs with that architecture attain high fitness, and thus the more difficult that architecture is to evolve.

In order to examine the impact of architecture on evolvability, we examined scatter plots of best and average asymptotic fitness for all five-neuron circuit architectures that we evolved (see Figure 5A). Qualitatively identical results were obtained for the three- and four-neuron circuit architectures when using average or median fitness as a surrogate for evolvability. In this plot, the three architecture classes described in the previous section are apparent along the best fitness (horizontal) axis, but no such groupings exist along the average fitness (vertical) axis. Instead, for any given best fitness, there is a range of average fitnesses. This suggests that architectures with the same best achievable fitness can differ significantly in their evolvability. Interestingly, the spread of average fitnesses increases with best fitness, so that the largest range of evolvability occurs for the best architectures in each architecture class. We will focus on the class 1 architectures with the highest best fitness.

In order to characterize these differences in evolvability, two subpopulations of five-neuron architectures whose best fitness was greater than 0.6 were studied. The high-evolvability subgroup had average fitnesses that were greater than 0.38 ($N = 39$), while the low-evolvability subgroup had average fitnesses that were less than 0.1 ($N = 34$). These subgroups are indicated by light gray rectangles in Figure 5A. Using $10^6$ random samples...
A

Best Fitness

Average Fitness

High Evolvability Subgroup

Class 1

Class 2

Class 3

Low Evolvability Subgroup

B

Log Frequency

High Evolvability

Low Evolvability

Fitness

C

Frequency x 10^{-5}

3-Neuron

4-Neuron

5-Neuron
from the parameter spaces of each architecture, we computed the mean truncated fitness distribution for each subgroup of architectures (see Figure 5B), with the high-evolvability subgroup distribution denoted by a black line and the low-evolvability subgroup distribution denoted by a gray line. Truncated rather than asymptotic fitness is the appropriate measure here because it is the one used during evolution.

These fitness distributions exhibit several interesting features. The fraction of samples below a truncated fitness of 0.125 is several orders of magnitude larger than the fraction above 0.125. This reflects the extreme scarcity of high-fitness oscillatory behavior in the parameter spaces of architectures in both subgroups. Below 0.125, the distributions are nearly identical for the two subgroups, with strong peaks at 0 (no steps) and 0.125 (a single step). However, above 0.125, the fitness distributions of the two subgroups exhibit a clear difference. While both the low- and high-evolvability subgroups follow power law distributions within this range (with exponents of $-2.23$ and $-3.28$, respectively), a larger fraction of the parameter spaces of the high-evolvability architectures clearly have a fitness greater than 0.125. This suggests that the difference in evolvability between the two subgroups is due primarily to differences in the probability of finding an oscillatory circuit whose fitness is higher than that of a single stepper. Plots of the mean fraction of parameter space volume with truncated fitness greater than 0.125 (see Figure 5C) demonstrate that this conclusion holds not only for five-neuron circuits, but also for analogous subgroups of low- and high-evolvability three-neuron and four-neuron architectures. Using a two-sample Kolmogorov-Smirnov test, the four- and five-neuron differences are highly significant ($p < 0.00001$), while the significance of the three-neuron difference is borderline ($p < 0.07$).

Ultimately, we would like to relate the observed differences in evolvability to particular architectural features, as we did for best fitness in section 4. Although we found some evidence for correlations between evolvability and the presence of particular feedback loops (Ames, 2003), none of these correlations was particularly strong. The best predictor of evolvability that we found was the fraction of an architecture’s parameter space with fitness greater than 0.125.

6 Beyond Architecture

The results clearly demonstrate that circuit architecture plays a major role in determining both the maximum attainable performance and the evolvability of model pattern generators. Of course, architecture alone is insufficient to completely specify circuit dynamics. Ultimately, we would like to refine our architectural classification with quantitative information. Are there patterns in the best parameter sets discovered by multiple evolutionary searches with a given architecture?
To begin to explore this question, we studied one of the highest-performing three-neuron architectures: a class 1 architecture consisting of a counterclockwise ring of connections among the three motor neurons. We performed a principal component analysis of the parameter sets of all evolutionary runs with this architecture whose best truncated fitness exceeded 0.5 (90/300). The first two principal components are plotted in Figure 6. Clearly, the evolved parameters sets are neither identical nor randomly distributed. Instead, they fall into two distinct clusters. What network features underlie these parameter clusters?

Computing the means of the circuit parameters for each cluster separately reveals that they correspond to distinct sign patterns. Circuits in the left cluster have three intrinsically active neurons arranged in an inhibitory ring oscillator. In contrast, circuits in the right cluster have one intrinsically active and two intrinsically inactive neurons arranged in a mixed excitatory/inhibitory ring oscillator. In addition, the sign of the self-weight of FT changes from negative to positive between the left and right clusters, and the self-weight sign of BS changes from positive to negative. This suggests that neuron excitabilities and connection signs may represent an intermediate level of analysis between connectivity and raw parameter values.

7 Discussion

Complex networks are ubiquitous in the biological world, and understanding the dynamics of such networks is arguably one of the most important theoretical obstacles to progress in many subdisciplines of biology. Most research on networks has focused on either structural questions that largely ignore node dynamics or network dynamics questions that assume a regular or random connection topology. However, realistic networks have both nontrivial node dynamics and specific but irregular connection topologies (Strogatz, 2001). As a first step in this direction, we have systematically studied the impact of neural architecture on walking performance in a large population of evolved model pattern generators for walking. Specifically, we have shown that a small number of connections is sufficient to achieve high fitness on this task, characterized the correlation between architectural motifs and fitness, explored the impact of architecture on evolvability, and demonstrated the existence of parameter subgroups with distinct neuron excitabilities and connection signs.

These results lay the essential groundwork for a more detailed analysis of the interplay between architecture and dynamics. We have explained the observed correlations between architecture and best fitness in terms of the structure of feedback loops in the circuits, while the relationship between architecture and evolvability was explained in terms of the fraction of an architecture’s parameter space that contains oscillatory dynamics whose fitness is greater than that obtainable by nonoscillatory circuits. However, several questions remain. How do different architectures differ in their
Figure 6: Two variants of the three-neuron architecture consisting of a counter-clockwise ring. A principal components analysis of the parameters of evolved circuits whose best truncated fitness exceeds 0.5 reveals two subgroups corresponding to distinct neuron excitability and connection sign patterns. Here inhibitory connections are denoted by a filled circle, excitatory connections are denoted by a short line, and neurons are shaded according to whether they are intrinsically active (white) or inactive (black). These two principal components account for 87.6% of the variance (78.8% for PCA1 and 8.8% for PCA2).
dynamical operation? Which excitability and sign variants of a given architecture can achieve high fitness? What underlies the fitness differences between architectures within a class? What architectural properties produce the parameter space differences responsible for the observed differences in evolvability? Ultimately such questions can be answered only by detailed studies of particular circuits in our existing data set (Beer, 1995; Chiel et al., 1999; Beer et al., 1999).

There has been a great deal of interest in the use of evolutionary algorithms to evolve not only neural parameters but also neural architecture (Angeline, Saunders, & Pollack, 1994; Yao, 1999; Stanley & Miikkulainen, 2002). However, this previous work provides little understanding as to why a particular architecture is chosen for a given problem, or how the structure of the space of architectures biases an evolutionary search. Our approach is complementary. While it is obviously impractical to evaluate all possible architectures on a given task, a systematic study such as ours can provide a foundation for the analysis of architectural evolution. Given our substantial data on the best architectures and their evolvability for the walking task, it could serve as an interesting benchmark for comparing different architecture evolution algorithms and analyzing their behavior. In fact, several such algorithms have already been applied to a multilegged version of exactly this walking task (Gruau, 1995; Kodjabachian & Meyer, 1998).

While the questions explored in this article are general ones, the importance of the particular feedback structures we have described is obviously specific to our walking task. Likewise, our evolvability results depend on the structure of the fitness space of each architecture, which in turn depends on the particular neural and mechanical models we chose and the performance measure we used. Examining a wider variety of neural models and tasks will be necessary to identify any general principles that might exist. As we have done here, it will be important for such studies to examine large populations of circuits, so that trends can be identified. In addition, the development of more powerful mathematical tools for studying the interplay of architecture and dynamics is essential. One promising development along these lines is the recent application of symmetry groupoid methods to analyze the constraints that network topology imposes on network dynamics (Stewart, Golubitsky, & Pivato, 2003).

Acknowledgments

We thank Hillel Chiel and Chad Seys for their feedback on an earlier draft of this article. This research was supported in part by NSF grant EIA-0130773 and in part by an NSF IGERT fellowship.

References


Received August 24, 2004; accepted August 9, 2005.