

# Beyond Control: The Dynamics of Brain-Body-Environment Interaction in Motor Systems

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**Abstract** Discussions of motor behavior have traditionally focused on how a nervous system controls a body. However, it has become increasingly clear that a broader perspective, in which motor behavior is seen as arising from the *interaction* between neural and biomechanical dynamics, is needed. This chapter reviews a line of work aimed at exploring this perspective in a simple model of walking. Specifically, I describe the evolution of neural pattern generators for a hexapod body, present a neuromechanical analysis of the dynamics of the evolved agents, characterize how the neural and biomechanical constraints structure the fitness space for this task, and examine the impact of network architecture.

## Introduction

Discussions of motor behavior typically center on the nervous system. On this view, an animal's environment is just a stage on which its behavior plays out, its body is merely a collection of muscles to activate and masses to move, and its sensors are simply sources of error signals to be compensated. Indeed, when we speak of the neural *control* of behavior, our very language betrays our bias, as if an animal's body were a mere puppet whose only task was to respond faithfully to the commands of its nervous system.

However, it is becoming increasingly clear that a broader perspective is needed. There is no question that nervous systems vastly increase the range of behavior in which an animal can stably engage. But an animal's nervous system, its body, and its environment each possess their own complex intrinsic dynamics, which are in continuous interaction. A bird, for example, flies not only because of the patterns of muscle activation produced by its nervous system, but also because of the shape and composition of its feathers and the hydrodynamical

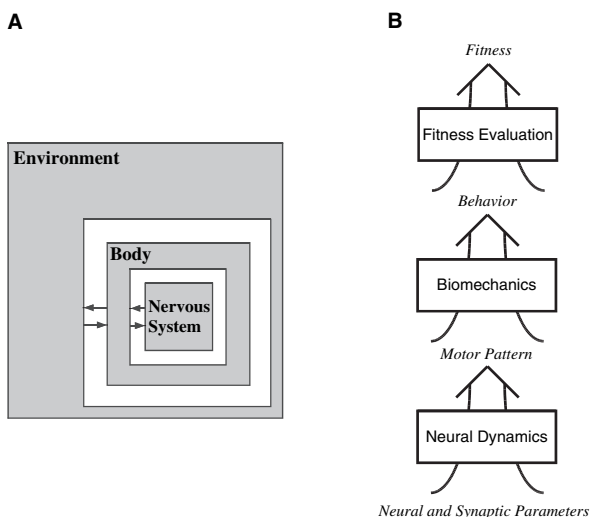
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**Fig. 1** A new perspective on motor systems. **(A)** An animal's nervous system, its body and its environment are each viewed as dynamical systems, which are in continuous interaction.

**(B)** The relationship between neural parameters and behavioral performance is very indirect, passing through several layers of transformations. Because each of these transformations may be degenerate, a given level of fitness may be obtained by a wide range of different neural parameters



properties of the air through which it moves. Furthermore, evolution selects only for the behavioral efficacy of this entire package, and it seems likely that it would take full advantage of any available freedom in distributing behavioral mechanisms. This suggests that behavior is best viewed as a property of a complete brain-body-environment *system* (Fig. 1A; Beer, 1995a; Chiel & Beer, 1997), and cannot properly be assigned to any individual component of this coupled system. Evidence for this view has come not only from neuromechanical studies of motor behavior, but also work in robotics, perception, developmental psychology, cognitive science, and philosophy of mind (Gibson, 1979; Brooks, 1991; Thelen & Smith, 1994; Clark, 1997).

This integrated perspective on behavior raises both experimental and theoretical challenges. It is difficult enough to study any one component of a brain-body-environment system in isolation, let alone the simultaneous interaction of all three. Not only must one be able to measure and manipulate neural activity in a behaving animal, but also the relevant properties of its body and environment. While important progress along these lines is beginning to be made in several systems (Winters & Crago, 2000), significant challenges remain. Perhaps even more fundamentally, even if the required experimental tools were available, we currently lack the theoretical framework necessary for an integrated understanding of the tangled, counter-intuitive designs that evolution produces.

Given current experimental and theoretical limitations, another possible strategy involves the systematic study of idealized models of complete brain-body-environment systems. Like Galileo's frictionless planes, such frictionless *brains* (and bodies, and environments) can help us to build intuition and, ultimately, the conceptual framework and mathematical and computational tools necessary for understanding the mechanisms of behavior (Beer, 1990).

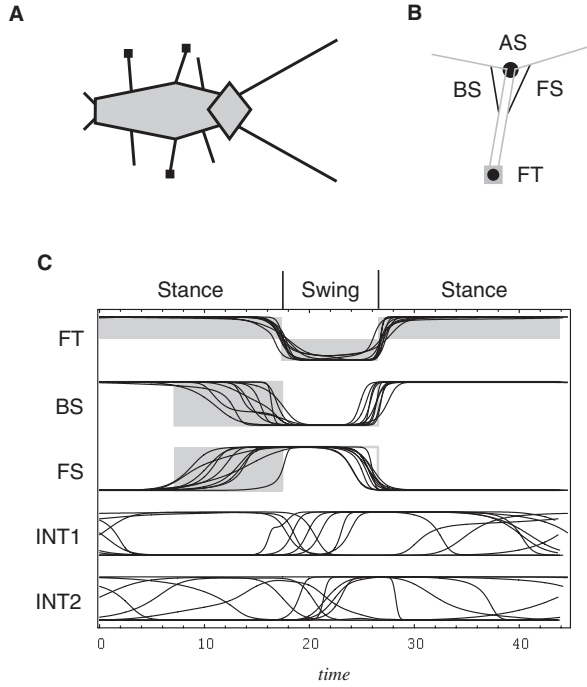
A specific approach that we and others have pursued for many years is the use of evolutionary algorithms to evolve model nervous systems embedded in model bodies situated in model environments (Beer & Gallagher, 1992; Cliff, Harvey & Husbands, 1993; Nolfi & Floreano, 2000). Evolutionary algorithms allow an exploration of possible brain-body-environment tradeoffs because model agents are selected only for their overall behavioral efficacy, with a minimum of *a priori* theoretical bias. The mathematical tools of dynamical systems theory are then used to analyze the operation of the evolved systems (Beer, 1995a). This approach has been successfully applied to a wide range of behavior, including chemotaxis, walking, learning, categorical perception and selective attention (Beer, 1997).

As a specific illustration of this approach, this chapter will review a long line of work on the evolution and analysis of walking. *The Evolution of Walking in a Legged Model Agent* describes the neural and body models employed in this work and reviews the results of the evolutionary experiments that have been run to date. In *Neuromechanical Analysis of Evolved Walkers*, I describe how particular evolved walkers have been analyzed and some of the insights that have been gained. *The Structure of Fitness Space* attempts to situate these analyses of particular walkers within a broader picture of the space of all possible solutions to this task. In *The Impact of Network Architecture*, I explore the impact of neural architecture on the performance and evolution of walking. The chapter ends with a discussion of the implications of this work for the brain-body-environment perspective in motor control and some directions for future work. The long term goal of this work is nothing less than a complete understanding of the relationship between neural architecture, neural parameters, neural activity, peripheral biomechanics, sensory feedback, behavior, performance and evolution in a simple model agent.

## **The Evolution of Walking in a Legged Model Agent**

We examined the evolution of pattern generators for walking in a simple six-legged body (Fig. 2A; Beer, 1990; Beer & Gallagher, 1992). Each leg was composed of a joint actuated by two opposing swing “muscles” and a binary foot (Fig. 2B). When the foot was “down”, any torque produced by the muscles applied a translational force to 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. Each leg was only able to generate force over a limited range of motion (modeling how mechanical advantage changes with limb geometry) with snaps back to these limits after foot release when a stancing leg stretches outside this range (modeling the passive restoring forces of muscle) and hard kinematic limits (modeling skeletal constraints). The body could only move when it was statically stable (i.e., the center of mass was contained within

**Fig. 2** Neuromechanics of walking. **(A)** Schematic body model. **(B)** Operation of an individual leg (FT = Foot, BS = Backward Swing, FS = Forward Swing, AS = Angle Sensor). **(C)** Activity of the top ten 5-neuron CPG motor patterns over one step, with the optimal pattern shown in gray



the polygon of support formed by the stancing legs). Each leg also possessed an angle sensor whose output was proportional to the angular deviation of the leg from perpendicularity to the long axis of the body. Complete details of the body model can be found in (Beer, Chiel & Gallagher, 1999).

The model body was coupled to a continuous-time recurrent neural network (Beer, 1995b):

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

where  $y_i$  is the mean membrane potential of the  $i$ th neuron,  $\dot{y}_i$  denotes the time rate of change of this potential,  $\tau_i$  is the neuron's membrane time constant,  $w_{ij}$  is the strength of the synaptic connection from the  $j$ th to the  $i$ th neuron,  $\theta_i$  is a bias term, and  $\sigma(x) = 1/(1 + e^{-x})$  represents the neuron's mean firing rate. A self-connection  $w_{ii}$  is interpreted as a simple nonlinear active conductance rather than as a literal synapse. While this simple model is computationally and analytically tractable, it is known to be a universal approximator of smooth dynamics (Kimura & Nakano, 1998). Thus, the use of continuous-time recurrent neural networks (CTRNNs) implies no essential restriction whatsoever on the range of dynamical behavior that can be generated. Three of these neurons in each leg circuit 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. Individual leg circuits were fully-interconnected, whereas homologous neurons in each adjacent leg circuit were bidirectionally interconnected. Several symmetries were also imposed on the neural circuits, so that all leg controllers shared the same parameters and corresponding connections were mirrored both across and along the body.

CTRNNs capable of generating walking in these legged agents were produced using evolutionary algorithms. An evolutionary algorithm is a search technique whose operation is loosely based on natural evolution (Goldberg, 1989; Mitchell, 1996). A population of individuals is maintained. In the initial population, the parameters describing each individual are set randomly. Each individual is then evaluated on its performance on some task of interest. The fitness on this task is then used to select individuals to serve as parents for the production of a new population. The parameters are then mutated and/or crossed over between parents to produce children. Once a new population has been created, all individuals are once again evaluated on the task and the cycle repeats.

Although our earliest work on the evolution of walking utilized a traditional binary genetic algorithm, we switched to a real-valued evolutionary algorithm in subsequent work (Bäck, 1996). In this case, each individual is encoded as a vector of real numbers representing the time constants, biases and 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. A selected parent was mutated by adding to it a random displacement vector with uniformly distributed direction and normally distributed magnitude with 0 mean. Connection weights and biases were constrained to lie in the range  $\pm 16$ , while time constants were constrained to the range [0.5, 10].

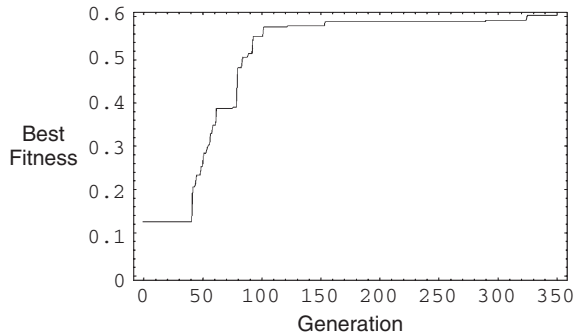
The walking performance measure optimized by the evolutionary algorithm was average forward velocity of the body. This average velocity was computed in two ways. During evolution, *truncated fitness* was evaluated by integrating the model for a fixed length of time using the forward Euler integration method and then computing the average velocity (total forward distance covered divided by the time interval). During analysis, *asymptotic fitness* was evaluated by integrating the model for a fixed length of time 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 our first set of experiments (Beer & Gallagher, 1992), 30-neuron CTRNN circuits for walking were evolved under three different conditions: (1) sensory feedback from the leg angle sensor was always available during evolution, (2) sensory feedback was never available, and (3) sensory feedback was intermittently available. In all cases, the best walkers utilized a tripod gait, in which the front and back legs on each side of the body step in phase with the middle leg on

the opposite side. The evolution of successful locomotion typically passed through four distinct stages. In the first stage, walkers produced limited forward movement by pushing with all six legs simultaneously until they fell. In the second stage, walkers evolved the ability to swing their legs in a rhythmic but uncoordinated fashion, taking multiple steps but still falling quite often. In the third stage, walkers utilizing statically stable gaits appeared, allowing them to make steady forward progress but with suboptimal coordination. In the fourth and final stage, the efficiency of locomotion slowly improved as the walking pattern was fine-tuned.

Although the normal behavior of the best walkers in all experiments was indistinguishable, lesions of the leg angle sensor revealed that the organization of the evolved pattern generators differed significantly depending on the conditions under which they were evolved. Walkers evolved with reliable sensory feedback utilized reflexive pattern generators (RPGs). RPGs exhibit a chain reflex organization, depending on sensory feedback to trigger the transition from stance to swing. In the absence of sensory feedback, RPGs become trapped in a permanent stance phase and are thus not robust to sensory failure. However, RPGs are capable of adjusting their motor pattern to environmental contingencies such as a perturbed leg. Walkers evolved in the absence of sensory feedback utilized central pattern generators (CPGs). Unlike RPGs, CPGs are capable of intrinsically generating the rhythmic motor pattern necessary for walking. However, pure CPGs cannot make use of sensory feedback to fine-tune their motor pattern. Finally, walkers evolved with intermittent sensory feedback utilized mixed pattern generators (MPGs). MPGs represent the best of both worlds. Like RPGs, they can use sensory feedback when it is available to improve their operation, but like CPGs they can function in its absence if necessary.

For simplicity, our subsequent work has focused on the generation of stepping movements in a single leg controlled by from 3 to 5 neurons. This simplification retains the problem of rhythmically coordinating multiple effectors to achieve efficient walking, but removes the issue of coordinating multiple legs so as to maintain postural stability. Over the past several years, we have evolved millions of single-leg pattern generators under a variety of different conditions and systematically studied the characteristics of the resulting walkers in a variety of ways. We have found that single-leg walkers still exhibit distinct stages of evolution. The population always first plateaus at nonrhythmic single-steppers with a truncated fitness of  $\sim 0.125$ . It then exhibits a series of increasingly fit rhythmic but suboptimal walkers. Finally, it asymptotes to fine-tuned walkers with a truncated fitness of up to about 0.6 (Fig. 3). Evolved single-leg pattern generators also still exhibit reflexive, central and mixed organizations depending on the conditions under which they were evolved. We have also found pattern generators in which the rhythmic walking pattern could be initiated or terminated by a transient stimulus. In addition, we have found evidence of dynamical reorganization in response to sensory lesions in mixed pattern generators, as well as adaptation to leg growth.



**Fig. 3** A typical plot of fitness of the best individual of the population vs. the generation number during an evolutionary search. Note the initial plateau around a fitness of 0.125 and the final fitness around 0.6

Thus, although one might expect that this restriction to a single leg would leave the walking task too trivial to be interesting, we have in fact found quite the opposite to be true. Not only does single-leg coordination engage a wide variety of fundamental questions in motor control, but the very simplicity of the task actually makes it possible to begin to answer some of them. In the remainder of this chapter, I review various analyses of these evolved walkers.

## Neuromechanical Analysis of Evolved Walkers

These evolved model walkers present us with a remarkable opportunity. Because we have complete access to and control over all neural parameters and activity, we can analyze the operation of individual pattern generators in great detail. Because we have similar access to the model body, we can also study the interplay between central and peripheral properties in the generation of a walking pattern. Because we have such a large population of evolved walkers, we can ask questions about general principles and individual variability. Because we have access to their complete evolutionary history, we can also examine the process by which successful walkers evolve, and the impact of various modeling assumptions on their evolution.

Let us begin with an examination of the motor patterns produced by the best pattern generators (Beer, Chiel & Gallagher, 1999). For example, the neural activities over one step of the top ten 5-neuron CPGs are shown in Fig. 2C. The walking performance of these ten CPGs differ by only a few percent. Note that the overall patterns of motor outputs are rather similar across these ten CPGs, while the interneuron activities are quite different. Since the interneuron activities are far less constrained by the body than the motor neurons, this is to be expected. However, there are variations even in the motor outputs. Specifically,



while both FT transitions and the swing-to-stance transitions of BS and FS are fairly tightly clustered, the stance-to-swing transitions in BS and FS show considerably larger variability.

What is the behavioral significance of this motor pattern variability? From a purely neuronal point of view, one might argue that the larger variability in the stance-to-swing transition is obviously the important one, accounting for the observed differences in walking performance. However, since it is the body, not the nervous system, that actually walks, inferences from neuronal activity to behavior must take into account the properties of the body. Thus, we undertook a detailed analysis of the mechanical properties of our model body (Beer, Chiel & Gallagher, 1999). Because of the simplicity of the body model, the optimal motor pattern could be formulated as a pair of minimum-time optimal control problems that could be solved analytically. We calculated that the maximum truncated and asymptotic fitness is 0.627, which is just above the fitness of the best pattern generators that we evolved. We also calculated that the maximum truncated fitness for walkers taking a single step was 0.125, which matches the fitness plateau observed in our evolutionary searches before the discovery of oscillatory pattern generators (Fig. 3).

In order to assess the significance of the motor pattern variability we observed, we compared the motor patterns of the top ten CPGs to the optimal motor pattern that we calculated (gray pattern in Fig. 2C). Interestingly, we found that the optimal motor pattern is *degenerate*; it consists not of a single trajectory, but rather an infinite family of trajectories. This degeneracy arises in two ways. First, because the foot can only be up or down in this model, the only property of the output of FT that matters is whether it is above or below the threshold for raising and lowering the foot. Second, because a supporting leg can only generate force over a limited range due to changing mechanical advantage, the force output of the forward and backward swing muscles becomes irrelevant near the end of stance. These degeneracies are shown as gray rectangles in Fig. 2C. Any motor trajectory that remains within the grey regions will have identical walking performance.

Note that the stance-to-swing variability in BS and FS falls almost entirely within degenerate regions, where it makes no difference to performance and therefore has not been selected away during evolution. Thus, the inference that this larger neuronal variability is significant is in fact wrong. It is actually the much smaller variability in the swing-to-stance transition in BS and FS that is significant, because it falls within a very tightly constrained portion of the optimal motor pattern. This clearly demonstrates that it is absolutely essential to consider the properties of the body when making inferences from neural activity to behavior, even in the case of pure CPGs.

Now let us turn to the question of how these evolved pattern generators actually work (Beer, 1995). From a neuromechanical perspective, the operation of the CPGs is the most straightforward. CPGs exhibit stable limit cycles which are tuned to the body in order to match the optimal motor pattern as closely as possible. Despite the fact that individual CTRNN neurons cannot oscillate,



evolution is able to adjust CTRNN connection weights, biases and time constants so as to create network oscillators.

The neuromechanical operation of the RPGs is more interesting, since feedback through the body is crucial. In the absence of sensory feedback, we found that RPGs typically exhibit a single stable equilibrium point corresponding to a stance phase (FT and BS on, FS off). When sensory feedback is present, this phase portrait persists for more anterior leg angles. However, as the leg nears the rear mechanical limit of motion, the sensory input from the leg angle sensor produces a series of bifurcations in the pattern generate that results in the stance equilibrium point being replaced by a single stable equilibrium point corresponding to a swing phase (FT and BS off, FS on). As the state is attracted to the new swing equilibrium point, the leg begins swinging forward until it nears the forward mechanical limit, where the swing equilibrium point bifurcates back into the stance equilibrium point and the cycle repeats. Although the details of the bifurcations varied from circuit to circuit, all of the best RPGs used their sensory input to switch between stance and swing attractors in this way.

The neuromechanical operation of MPGs is even more interesting. Like CPGs, MPGs exhibit a stable limit cycle in the absence of sensory input. It turns out that, when rhythmic sensory feedback is present, it entrains the intrinsic oscillation of the circuit. We demonstrated this entrainment by showing that driving the leg angle sensor with sine waves whose frequency was higher or lower than the intrinsic oscillation frequency could speed up or slow down the pattern generator accordingly while maintaining proper coordination between the motor outputs. This has an interesting consequence: An MPG can adapt its motor pattern to a growing body! As a leg increases in length, the geometry is such that it takes longer to move through a given angle than a shorter leg, thereby spreading out the phasic feedback from the angle sensor in time. Through entrainment, this slower sensory feedback slows down the pattern generator accordingly.

We also found evidence for dynamical reorganization in MPGs switched from an RPG-like mode to a CPG-like mode by sensory lesion. For example, when sensory input was present, one of the interneurons in a 5-neuron MPG was silent and lesion studies confirmed that its removal made no difference to walking performance. However, when sensory input was absent, the same interneuron began to actively participate in the neural dynamics and its removal under these conditions destroyed the walking pattern.

In addition to the neuromechanical interactions underlying walking patterns, we can also examine the operation of the evolved neural circuits themselves. For example, we have undertaken an extensive analysis of the evolved CPGs (Chiel, Beer & Gallagher, 1999). Using separation of timescales, we were able to decompose the best CPGs into *dynamical modules*. A dynamical module is a set of neurons that simultaneously make a transition from one quasistable state to another while the outputs of the remaining neurons remain relatively constant. This structure arises both because of the shape of the optimal motor pattern (which requires sharp transitions in motor neuron output at certain

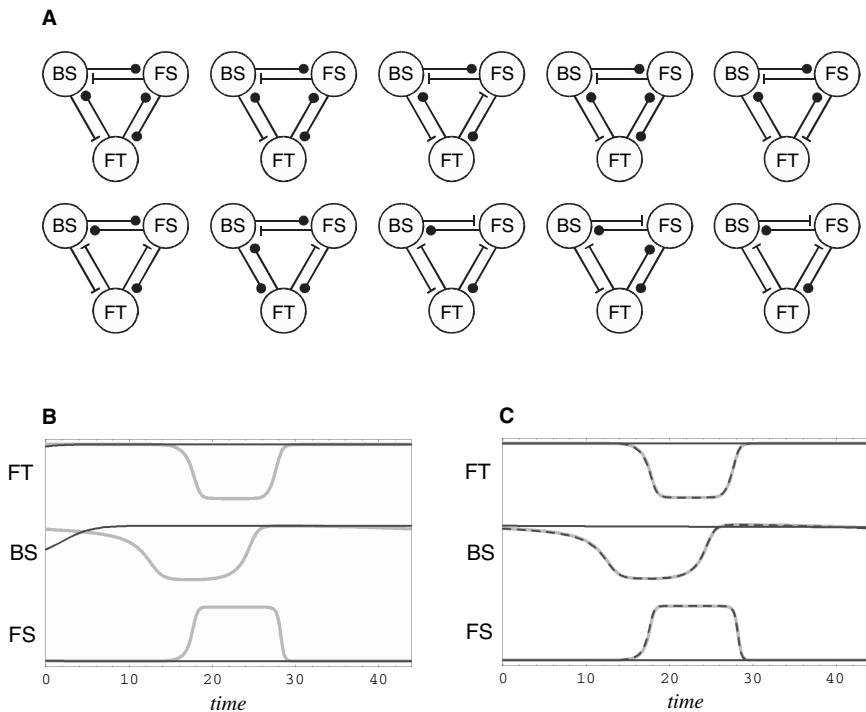
points in the pattern) and because of the limited dynamic range and saturation of the CTRNN model neurons (which makes it much easier for inputs to hold a neuron off or on than to hold it in an intermediate state).

Each dynamical module operates as a bistable element that is switched from one configuration to the other by other modules in a closed chain that produces the rhythmic pattern. When the neurons in a module are in a quasistable state, they provide only constant inputs to the other neurons in the circuit. As the neurons in one module transition from one quasistable state to the next, they change the synaptic inputs to the next module, causing it to begin a transition to its next state in turn. Since only a subset of the neurons are changing state at any one time, the circuit can be reduced to a sequence of lower-dimensional dynamical systems.

Using this decomposition, we described how the steady-state input-output curves of each module varied as a function of synaptic input from other modules. This allowed us to quantitatively characterize constraints on circuit architecture, explain the duration of the different phases of the walking cycle, and predict the effects of parameter changes. The notion of dynamical modules also provided a way to classify different CPGs according to which modules were present and their pattern of switching on and off. We could sometimes assign distinct functional roles to specific dynamical modules. For example, close passage to a saddle-node bifurcation in one of the modules was used to maintain the duration of the stance phase in the best three-neuron CPGs. However, as the number of interneurons increased, we found that distinct functional roles became difficult to assign to individual neurons or synapses, becoming increasingly distributed across many neuronal properties and elements (Beer, Chiel & Gallagher, 1999).

## The Structure of Fitness Space

Our analyses of many evolved CPGs revealed several interesting trends (Chiel, Beer & Gallagher, 1999). First, we found a remarkable degree of variability among the best circuits. Even in the 3-neuron CPGs, both the patterns of excitation and inhibition and the actual neural parameter values varied over almost their entire allowable range, despite the fact that the walking performance of these circuits differed by less than 2% (Fig. 4A). Multiple instantiability has also been demonstrated in more biophysically-realistic models of the crustacean stomatogastric ganglion (Prinz, Bucher & Marder, 2004). Second, because of this variability, we found that averaging the parameters of the best CPGs produced circuits that failed to oscillate (Fig. 4B). Failure of averaging has also been observed in more biophysically-realistic model neurons (Golowasch, Goldman, Abbott & Marder, 2002) and may have significant implications for the common strategy of averaging the results of many experimental measurements in order to obtain neuronal parameters. Third, we found



**Fig. 4** Some characteristics of evolved CPGs. **(A)** Multiple instantiability. The connectivity patterns of the top ten 3-neuron CPGs are shown, with excitatory connections denoted by short lines and inhibitory connections denoted by small filled circles. **(B)** Failure of averaging. The motor pattern of the best 3-neuron CPG is shown in gray, while the motor pattern of the pattern generator obtained by averaging the parameters of the top ten 3-neuron CPGs is shown in black. **(C)** Sensitivity and robustness to parameter variation. Once again, the motor pattern of the best CPG is shown in gray. The black trace displays this motor pattern after a single parameter is changed by 6%. The dashed trace shows the motor pattern after a coordinated change in three parameters by from 129% to 467%

that walking patterns can be extremely sensitive to some combinations of neural parameter variations while remaining very robust to others. For example, a change of only 6% in one parameter can destroy the walking pattern (compare the black curve to the gray curve in Fig. 4C), while a coordinated change in three parameters by from 129% to 467% produces a pattern that is essentially identical to the original (compare the dashed curve to the gray curve in Fig. 4C). Similar patterns of sensitivity and robustness have also been described in both biological nerve cells and in biophysically-realistic model neurons (Goldman, Golowasch, Marder & Abbott, 2001).

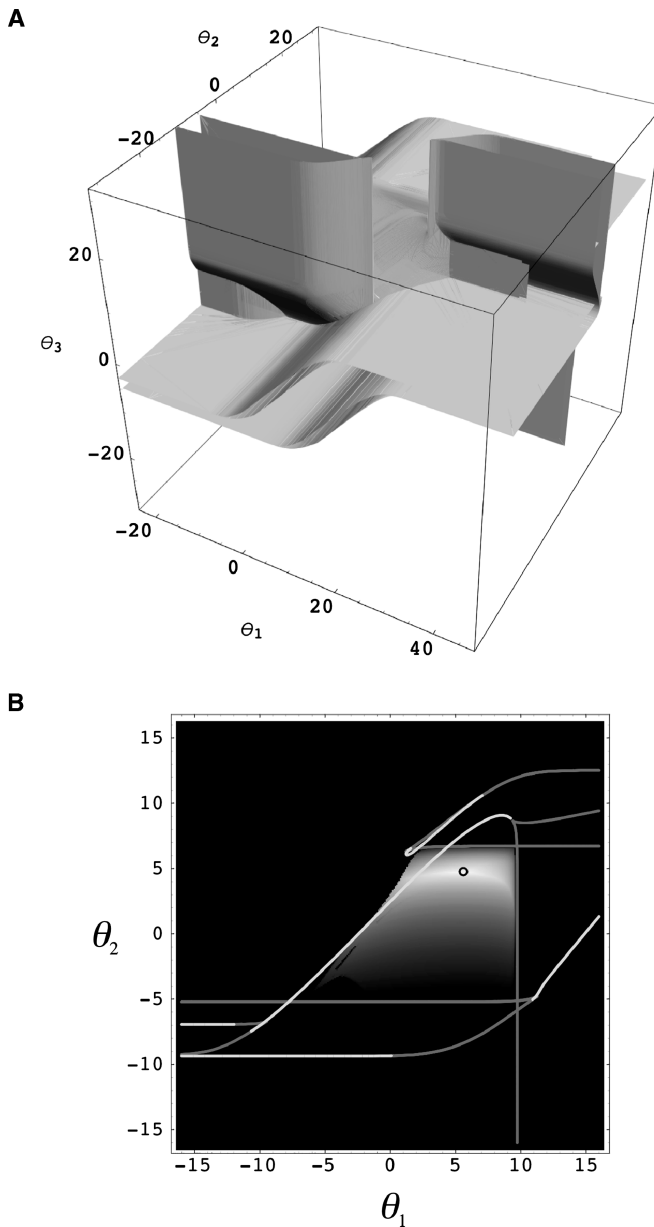
Given this large variability, detailed analyses of individual pattern generators can tell us only so much. If we wish to understand general principles, then we must try to situate the operational minutiae of any particular walker within the space of all possible walkers. Specifically, we need to understand the overall

structure of walking performance space as a function of the neural parameters so that we can describe the trade-offs that characterize the best walkers. The relationship between neural parameters and walking performance can be decomposed into three levels (Fig. 1B). Neural parameters are transformed into neural activity patterns through the CTRNN dynamics. Neural activity patterns are transformed into behavior through the biomechanics of the model body. Behavior is transformed into walking performance through the fitness measure. Note that the neural and biomechanical dynamics are only distinct in CPGs; in RPGs and MPGs, sensory feedback from the body effectively couple them into a single dynamical system. Note also that there can be degeneracies at each level so that, for example, many different neural activity patterns might give rise to the same leg motion. Thus, a given level of walking performance can be achieved by many different sets of neural parameters. This degeneracy gives rise to the multiple instantiability of pattern generators that we have observed, and it is the structure of such degeneracy that we ultimately wish to understand.

Let us begin with the relationship between CTRNN parameters and network dynamics. Despite extensive analysis of individual circuits or special classes of circuits, characterizing the general parameter space structure of even simple nonlinear recurrent neural circuits is an extremely difficult problem. Nevertheless, some progress has recently been made (Beer, 2006). For example, using a method described by Haschke & Steil (2005), it has been possible to explicitly calculate the local bifurcation manifolds for CTRNNs, which divide the parameter space into regions with different dynamics. This method is especially useful for visualizing the net input parameter space of 2- or 3-neuron CTRNNs. For example, Fig. 5A shows a slice through the parameter space of a 3-neuron CTRNN. Unfortunately, these explicit expressions become too unwieldy to work with and impossible to directly visualize for larger CTRNNs.

Examination of such slices reveals two key features of CTRNN parameter space that can be scaled to arbitrarily large circuits. First, there is always a central region in net input space that contains the richest dynamics and highest density of bifurcations. The center of this region corresponds to center-crossing CTRNNs (Beer, 1995), for which the net input of each neuron is exactly centered over the most sensitive portion of its output function. Second, as we move away from the center-crossing circuits in net input space, the local bifurcation manifolds flatten out, forming quasirectangular regions with a combinatorial structure (Fig. 5A). These regions correspond to different subsets of the neurons being saturated on or off and thus their boundaries separate the net input space of CTRNNs into regions of dynamics with different effective dimensionality. It is possible to analytically characterize these regions for CTRNNs of arbitrary size, as well as to estimate their volume and probability (Beer, 2006).

What does this CTRNN parameter space structure tell us about the structure of walking fitness space? A 2-dimensional slice through the fitness space of a CPG is shown in Fig. 5B. This density plot exhibits several interesting features. Large black areas of low fitness surround a compact central region with higher fitness. Within the higher-fitness region, there is a narrow ridge of highest fitness. The dot



**Fig. 5** The structure of fitness space. (A) Local bifurcation manifolds for an evolved 3-neuron CPG as the neuron biases  $\theta_i$  are varied. (B) A fitness space slice for the same CPG as in Part A. The fitness is shown as a density plot, with brighter areas corresponding to higher fitness. The small circle indicates the location of the evolved CPG in this fitness space slice. The superimposed curves indicate the bifurcations of the underlying CTRNN, with saddle-node bifurcations shown as dark gray and Hopf bifurcations shown as light gray. These curves correspond to slices through the bifurcation manifolds of Part A at the  $\theta_3$  value of the evolved circuit. Note how the bifurcation curves delineate the brighter region of higher fitness from the surrounding dark region of low fitness

indicates the location found by an evolutionary search. Note that the boundary between the low and high fitness regions is quite sharp. This boundary separates walkers which take at most a single step from walkers which step rhythmically. As shown by the curves in Fig. 5B, this boundary corresponds quite closely to the CTRNN bifurcation manifolds which create and destroy limit cycles, either through Hopf bifurcations (light gray curves) or saddle-node bifurcations (dark gray curves). Note that these bifurcation curves correspond to a slice through the bifurcation surfaces shown in Fig. 5A. Thus, analyses of the bifurcation manifolds of CTRNNs can help us understand the sharp boundaries between low and high fitness regions in the walking fitness space of CPGs.

Similar studies can be performed for the fitness spaces of RPGs. It turns out that RPG fitness space is also structured into compact regions of high fitness surrounded by a large region of low fitness, with sharp boundaries between them. In order to understand the boundaries in this case, however, we must analyze the bifurcations of the entire coupled neuromechanical system due to the sensory feedback. Some of the boundaries between oscillatory and non-oscillatory dynamics in RPG fitness space can be related to CTRNN bifurcations, whereas other boundaries are related to bifurcations that are intrinsically neuromechanical in nature. Nevertheless, we have been able to calculate both kinds of bifurcation boundaries for this model, allowing us to understand the fitness space structure of RPGs. We have also studied the internal structure of the high fitness region and its degeneracies, using the latter to account quantitatively for some of the parameter variability observed among the best evolved pattern generators.

The structure revealed by these fitness space studies has important implications for the evolution of pattern generators for this walking task (Seys & Beer, 2004). For example, because of the large low-fitness regions, oscillatory regions of parameter space are hard to find from random initial populations. This accounts for the fitness plateaus at a truncated fitness of 0.125 that are observed in evolution (Fig. 3). During these plateaus, the population is simply diffusing around the large, selectively neutral regions of single-steppers. In contrast, once a higher-fitness oscillatory region is found, evolution can climb the fitness peak, as observed in the second half of Fig. 3. This 2-stage structure to the search suggests that starting evolutionary searches in the regions of CTRNN parameter space with the richest dynamics should improve their performance. Experiments have shown that seeding evolutionary searches with random center-crossing circuits can significantly improve the evolvability of oscillatory dynamics (Mathayomchan & Beer, 2002).

## The Impact of Network Architecture

All of the work described so far in this paper has assumed fully-interconnected neural circuits because they include all possible network architectures as subcircuits. However, it is well-known that, despite their dense recurrent

connectivity, biological neural circuits are far less than fully-connected. What impact does network architecture have on the performance and evolvability of pattern generation circuits?

In order to answer this question, we systematically studied all 3-neuron and 4-neuron CPG architecture and a sample of 5-neuron CPG architectures (Psujek, Ames & Beer, 2006). Given the large number of possible architectures for these circuits and the necessity of running many searches on each architecture in order to support statistically significant conclusions, our study required approximately 2.2 million evolutionary searches, each of which involved 25,000 fitness evaluations. We then analyzed the resulting data set for patterns.

We first examined the impact of circuit architecture on the maximum fitness obtainable. We found that the best fitnesses obtained for the 64 distinct 3-neuron architectures fell into three separate fitness groups, each of which were characterized by particular architectural motifs. These results suggest that circuit architecture does significantly constrain the maximal achievable fitness and that three different architecture classes may exist. Walkers in the low fitness group produced at most a single step. The architectures in this group lacked feedback loops that linked the foot and swing motor neurons. Walkers in the middle-fitness group stepped rhythmically, but either the stance or swing motion was fairly slow. These architectures possessed recurrent connections between the foot and one swing motor neuron, but not the other motor neuron. Thus, these circuits can oscillate, but one direction of leg motion is always slowed by constant activity in the opposing swing motor neuron. Finally, walkers in the high-fitness group exhibited fast rhythmic stepping and contained architectures with feedback loops that either involved or drove all three motor neurons.

In order to test whether this correlation between architectural motifs and maximum fitness held for larger circuits containing interneurons, we classified all of the 4-neuron and 5-neuron architectures in our data set into the three architecture classes described above. Then we plotted the maximum fitness observed over all experiments for each architecture. We found the same three bands of fitness as observed in the 3-neuron CPGs, thus verifying the correlation between architecture and maximum fitness. In addition, we were able to accurately calculate the sharp boundary between the middle-fitness and high-fitness bands.

Finally, we examined the influence of circuit architecture on evolvability. We used the mean best fitness as a surrogate for evolvability, because it provides a measure of the difficulty of finding circuits with the best possible fitness achievable by a given architecture through an evolutionary search. By plotting average best fitness against maximum best fitness obtained for all architectures in our data set, we found that architectures capable of achieving similar maximum fitness varied widely in their average fitness. This indicates that architecture can have a significant impact on evolvability. An analysis of the architectures in low and high evolvability subgroups with similar maximum fitness revealed a key difference between them: The fraction of parameter space containing



oscillations whose truncated fitness exceeds 0.125 was higher for architectures in the high evolvability subgroup than it was for architectures in the low evolvability subgroup. This difference implies that it is easier for an evolutionary search on a high-evolvability architecture to move from stage 1 (diffusing around large, selectively neutral regions of single-steppers) to stage 2 (optimizing an oscillatory pattern generator) than it is for a low-evolvability architecture and thus explains the observed difference in evolvability between the two subgroups.

## Conclusion

This chapter has reviewed a long line of work on the evolution and analysis of pattern generators for walking. I described the neural and body models, the fitness measure and the evolutionary algorithm used in this work, as well as the basic characteristics of pattern generators evolved under different conditions of sensory feedback. Next, I demonstrated several different ways in which the neuromechanical operation of the evolved walkers could be analyzed, providing insight into both the organization of the evolved circuits and the way in which those circuits exploited the properties of the model body. I then described the structure of fitness space and explained how this structure relates to specific features of the neural and peripheral models and how it accounts for the observed properties of evolutionary searches. Finally, I showed how circuit architecture can influence both the maximum achievable performance and the evolvability of walkers.

While such idealized models are unlikely to make quantitatively testable predictions, they are essential to building the intuition necessary for understanding biological brain-body-environment systems. Thus, they nicely complement more biologically-realistic models. Idealized models can illustrate the need for a neuromechanical perspective on the mechanisms of motor behavior and emphasize the importance of understanding not only particular neuromechanical systems but also the overall structure and degeneracy of neuromechanical performance spaces. They can stimulate the development of mathematical and computational tools for the analysis of the interaction between neural activity and peripheral biomechanics. They can lead to qualitative predictions, such as multiple instantiability, failure of averaging, and robustness and sensitivity to parameter variation, that are biologically testable (Goldman, Golowasch, Marder & Abbott, 2001; Golowasch, Goldman, Abbott & Marder, 2002; Prinz, Bucher & Marder, 2004). They can support experiments, such as rerunning evolution many times under different conditions of sensor reliability or neural architecture, that are impossible to perform biologically. Such work can also be applied to robotics (Cliff, Harvey & Husbands, 1993; Gallagher, Beer, Espenschied, & Quinn, 1996; Nolfi & Floreano, 2000), suggest seeding strategies for improving evolutionary algorithms (Beer, 1995b; Mathayomchan & Beer,

2002), and lead to design techniques for artificial pattern generators that can be implemented in analog VLSI (Kier, Ames, Beer & Harrison, 2006).

There are many directions in which the work described in this chapter could be extended. First, the degeneracy of the single-leg fitness spaces needs to be more fully characterized and the new neuromechanical coordination issues that arise in the 6-legged case need to be analyzed. Second, other kinds of motor behavior besides locomotion should be examined. Some preliminary work on reaching has already been done (Beer, 1996). It would be particularly interesting to explore the relationship between locomotion and reaching, which are traditionally treated very differently in the motor control literature. For example, one might imagine a task involving reaching to a set of visual targets. By varying the frequency of a fixed pattern of target signaling, the reaching task could be made more or less similar to a rhythmic locomotion pattern. Finally, more mechanically and biologically realistic peripheries should be examined. For example, we are currently evolving and analyzing feeding pattern generators for a muscular hydrostatic model of the mouth parts of the marine mollusc *Aplysia* (Synder, 2005).

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