An Integrated Neuromechanical Model of Steering in *C. elegans*

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Abstract

In this paper, we extend our previous model circuit for steering in *C. elegans* to control a more realistic biomechanical model of forward locomotion. We show that the identified steering circuit is sufficient to steer the full body during forward locomotion while only innervating a few of the anterior most neck muscles. Analysis of the sensorimotor transformation and phasic stimulation experiments provides evidence that the principles of operation for steering discussed in the model are relevant for steering in the worm. Finally, the integration of the steering circuit in a physical model of the full body allows us to compare more closely the properties of the evolved solutions with those of the worm.

Introduction

One of the grand scientific challenges of this century is to understand how a nervous system controls the behavior of an entire animal. The nematode worm *Caenorhabditis elegans* is a uniquely qualified target for integrated brain-body-environment modeling of a complete animal for three main reasons. First, *C. elegans* exhibits a rich behavioral repertoire, including withdrawal responses, crawling, swimming, a variety of taxes, social feeding, male searching, egg-laying, habitation and associative conditioning (Hart, 2006). Second, a variety of techniques exist for characterizing its behavior and for monitoring and manipulating simultaneously the activity of multiple neurons in the freely moving animal (Shipley et al., 2014). Finally, its “connectome” (302 neurons, 6393 chemical synapses, 890 electrical junctions, and 1410 neuromuscular junctions) is almost completely known (White et al., 1986; Varshney et al., 2011).

The neural circuits involved in specific behaviors in the worm are increasingly being mapped out experimentally (de Bono and Maricq, 2005). Yet, despite the substantial anatomical and neural connectivity knowledge in *C. elegans*, information about the electrophysiological properties of its nervous system is much less complete. For this reason, our approach involves using a real-valued evolutionary algorithm to determine values of the unknown electrophysiological parameters that optimize a behavioral performance measure on the entire system.

Spatial orientation is one of the most fundamental behaviors in *C. elegans*. Recent work has focused on understanding the neural basis of steering during klinotaxis (Iino and Yoshida, 2009; Kato et al., 2014; Luo et al., 2014; Hendricks and Zhang, 2013; Yoshida et al., 2012; Lockery, 2011; Kim et al., 2011). The strategy involves making gradual adjustments to the dorsoventral head swings during forward locomotion, effectively combining information about changes in the environment with information about its body posture to decide in what direction to turn.

In previous work (Izquierdo and Beer, 2013), we identified and modeled the structure of the minimal circuit involved in steering in chemical gradients. The neurons in the identified circuit have since been validated experimentally (McCormick, 2013). Importantly, the same circuit is likely to be involved in steering in other sensory modalities (Kocabas et al., 2012). Our model of steering focused primarily on the neuroanatomical structure and the available neurophysiological properties of the circuit. For simplicity, however, the body and model of movement were highly idealized. Importantly, the model assumed that steering occurred through modulation of the amplitude of the rhythmic oscillations in the head, and that the changes in orientation produced in the head were propagated backwards without explicitly modeling the ventral circuit, muscles, and physical body responsible for locomotion.

In this paper, we extend the steering circuit identified in (Izquierdo and Beer, 2013) to control a more realistic biomechanical model of forward locomotion of the entire worm. Several such models have been proposed in the literature (Gjorgjieva et al., 2014; Cohen and Sanders, 2014). To date, the most complete and biologically-grounded model was proposed by Boyle, Berri and Cohen (2012) (henceforth BBC). The model combines a physical model of the body and the environment with an idealized model of the ventral circuit, as well as neuromuscular control by a sensory feedback mechanism. We use the evolutionary methodology to explore configurations of the steering circuit that can produce klinotaxis in the locomotion model. The resulting integrated neuromechanical model of steering allows us to ex-
amine more closely the similarities and differences between the behavior of the model and the worm.

**Model and Methods**

**Model**

**Environment** In the laboratory, spatial orientation is typically studied in petri dishes containing a layer of agar gel (Ino and Yoshida, 2009). Although the BBC forward locomotion model has been demonstrated in the continuum of viscosities ranging between water and agar, our experiments focus exclusively on the latter.

**Body** We reimplemented the BBC forward locomotion model from published descriptions and publicly available code (Boyle et al., 2012). Using specialized sparse matrix and linear algebra routines, and a semi-implicit backward Euler integrator, we have been able to substantially improve the execution speed of the original implementation on agar, making it feasible for evolutionary optimizability. The worm is modeled in 2D cross-section due to the fact that it normally locomotes on its side, bending only in the dorsal-ventral plane. The ~1mm long continuous body of the worm is divided into variable-width discrete segments (Fig. 1A(i)), each of which are bounded by two cross-sectional rigid rods (black) whose endpoints are connected to their neighbors via damped spring lateral elements (red) modeling the stretch resistance of the cuticle and damped spring diagonal elements (blue) modeling the compression resistance of internal pressure. The rest lengths, spring constants and damping constants of the lateral and diagonal elements are taken directly from BBC, who estimated them from experiments with anesthetized worms. The forces from the lateral and diagonal elements are summed at the endpoints of the rods and then the equations of motion are written for the center of mass of each rod. Since each rod has two translational $(x, y)$ and one rotational ($\phi$) degrees of freedom, the body model has a total of 147 degrees of freedom. All kinematic and dynamic parameters are identical to those used by BBC.

**Muscles** Following BBC, muscles are modeled as damped springs with activation-dependent rest lengths, spring constants and damping constants, endowing them with simplified Hill-like force-length and force-velocity properties. Each discrete lateral element of the body model corresponds to a distinct muscle (red, Fig. 1A(ii)). Since the model is 2D, we combine the bundles DR and DL into a single set of 24 dorsal muscles, each with twice the strength, and likewise for the two ventral bundles. In lieu of experimental constraints on muscle responses, BBC hand-tuned muscle parameters so that realistic-looking locomotion was obtained when the body was coupled to their neural model. Muscle parameters are identical to those used by BBC.

**Forward locomotion circuit** Forward locomotion is produced by the ventral cord circuit. Following BBC, the model consists of 12 repeating units, each containing one motor neuron of each class: DB, VB, DD, and VD (Fig. 1A(iii)), all of which are known to be necessary for forward locomotion. DD (VD) neurons receive input from VB (DB) motoneurons and inhibit the opposing dorsal (ventral) muscles. In addition, VD also inhibits VB. D-class neurons are modeled as passive (linear) elements. B-class neurons receive input from stretch-receptors. The BBC locomotion circuit model ignores electrical synapses.

**Steering circuit** The neuroanatomical model used for this study was proposed in our previous study of klinotaxis (Izquierdo and Beer, 2013). The model consists of the minimal circuit (Fig. 1B) connecting the main salt chemosensory class ASE to the neck motor class involved in modulating the amplitude of the sinusoidal locomotion, SMB. The circuit was identified by mining the *C. elegans* connectome and constraining it using existing experimental and theoretical considerations. Chemosensory neurons were modeled after ASE cells. The activation of sensory neurons was modeled as an instantaneous function of a derivative operator $D(t)$ applied to the recent history of attractant concentration. This operator was defined as $D(t) = c_N(t) - c_M(t)$, where $c_N(t)$ is the average concentration over the interval $[t - N, t]$, $c_M(t)$ is the average concentration over the contiguous interval $[t - (N + M), t - N]$, and $N$ and $M$ are the durations of the two intervals. In the case of the OFF cell, the sign of $D(t)$ was inverted so that decreases in concentration yielded positive activations. For both ON cells and OFF cells, negative activations were set to zero. Interneurons and motoneurons were modeled as passive, isopotential nodes,

$$\tau_i \frac{dy_i}{dt} = -y_i + \sum_{j=1}^{N} w_{ji} \sigma(y_j + \theta_j) + \sum_{k=1}^{N} g_{ki} (y_k - y_i) + I_i,$$

where $y$ represents the membrane potential (or neuron activation) relative to the resting potential (thus $y$ can assume positive and negative values); $\tau$ is the time-constant; $\theta$ is a bias term that shifts the range of sensitivity of the output function; $w_{ji}$ represents the strength of the chemical synapse; $g_{ki}$ represents the gap junction conductance between cell $k$ and $i$ ($g_{ki} > 0$). Chemical synapses were modeled as a sigmoidal function of presynaptic voltage, $\sigma(x) = 1/(1 + e^{-x})$. Neck motor neurons included self-connections representing the voltage dependence of inward currents. Unlike the previous model of steering, the circuit does not receive oscillatory component from a rhythmic pattern generator. The output of the motoneurons is fed directly to the anterior-most neck muscles (Fig. 1A(i)).
Figure 1: Integrated neuromechanical model. (A) Model of forward locomotion adapted from (Boyle et al., 2012). (i) Complete physical model. The steering circuit affects only the anterior most muscles in the body. We perform evolutionary runs where the steering circuit affects a different set of muscles: 1-4, 1-8, 1-12, and 5-8. (ii) Individual segment in the physical model. (iii) Neuromuscular model. One of 12 repeating units making up the circuit for forward locomotion. The circuit includes a pair of B-class excitatory neurons (green), a pair of D-class inhibitory neurons (light blue), and four muscles (gray) on each side. Synapses are excitatory (arrowhead) or inhibitory (circle head). Posteriorly directed lines from B-class neurons denote the stretch receptor input (brown). (B) Steering neuromuscular model adapted from (Izquierdo and Beer, 2013). Chemosensory class, ASE (orange). Interneuron classes: AIY (blue) and AIZ (magenta). Neck motor neuron class: SMB (red). Dorsal and ventral muscles (gray). All classes have left and right cells. Motor neurons have additional dorsal and ventral pairs of cells. Chemical synapses shown as black arrows. Gap junctions shown as red undirected connections.

Methods

Evolutionary algorithm Although the anatomical connectivity of the nervous system of the nematode worm *C. elegans* has been reconstructed completely (White et al., 1986), the signs and strengths of the anatomical contacts are almost entirely unknown. We used an evolutionary algorithm to explore the space of unknown parameters of the steering circuit such that integrated model produced klinotaxis. We optimized the following parameters of the steering circuit (ranges are shown in brackets): $w [-15, 15]$; $\theta [-15, 15]$; $g [0, 2]$; and $N$ and $M [0.1, 4.2]$. Circuit parameters were symmetrical across the dorsal/ventral midline. Parameters were encoded in a 22-element vector of real-values between $[-1, 1]$; when needed, parameters were linearly mapped to their corresponding ranges. The algorithm was run for populations of 100 individuals. Each time the algorithm was run, individuals were initialized by random selection from the range of each parameter. Populations were evolved for 200 generations. At the end of a run, the parameters of the best performing individual were stored for later analysis.

Fitness function Fitness was evaluated by simulating the integrated model on three trials (Fig. 2). At the start of each trial, the model worm was placed in an environment with a conical gradient with the peak located at different relative angles from the starting orientation of the worm: $-\pi/2, 0, \pi/2$, corresponding to dorsal, straight, and ventral orientations. The peak was located 4.5 cm away from the worm. Model worms were allowed to move for $T = 50$ secs. For each trial, the performance of an individual was measured as the time average of the angle,

$$f = 1 - \frac{1}{T} \int_0^T \frac{a(t)}{\pi} dt$$

where $a(t)$ is the difference in angle between the gradient peak and the head of the worm at time $t$. The fitness of an individual was defined as the worst over the three assays. For the conical gradient, attractant concentration $c(t)$ was defined as $c(t) = -\alpha \sqrt{x(t)^2 + y(t)^2}$, where $\alpha$ determines the steepness of the gradient (fixed to 1).

Chemotaxis assay The fitness evaluation is deliberately brief in duration and limited in variation to make the long evolutionary runs feasible computationally. In order to evaluate the ability of the worm to perform chemotaxis more thoroughly, we simulated the worm over more trials (8) of longer durations each (500 secs) (see e.g., Fig. 3). In
addition to conical gradients, we also tested the worm in more realistic Gaussian gradients:

\[ c(t) = c_0 \exp\left(\frac{-x(t)^2 + y(t)^2}{2\lambda_c^2}\right) \]

with \( c_0 = 15 \) and \( \lambda_c = 1.61 \). The fitness score was quantified in terms of a chemotaxis index, defined as the time average of the distance to the peak of the gradient,

\[ CI = 1 - \frac{1}{T} \int_0^T \frac{d(t)}{d(0)} \, dt \]

where \( d(t) \) is the Euclidean distance to the peak, \( d(0) \) is the model worm’s initial distance from the peak (4.5 cm), and \( T \) is the total simulated assay time (500 sec).

**Results**

**Modulation of neck and head muscles is sufficient for steering**

To identify a neuroanatomically constrained circuit that could steer the *C. elegans* forward locomotion model, we ran 40 evolutionary runs. The steering circuit was allowed to affect only the anterior most muscles in the body: 1–4. The best evolved agents achieved a fitness of 0.78 after 200 generations of evolution. As the circuits were evolved under constrained conditions (see Methods, Fig. 2), we tested the performance of the complete ensemble (i.e., best agent from each evolutionary run) on assays of longer durations that allow them to reach the gradient peak. We measured their performance using the chemotaxis index (see Methods) over 8 trials of 500 secs each, where the initial orientation of the worm was drawn systematically over the range \([0, 2\pi]\) (Fig. 3A). The best performing agent achieved a chemotaxis index of 0.71, with perfect reliability (i.e., the agent reached the peak of the gradient on all trials). This result shows the performance of this agent is comparable to the previous model of klinotaxis (Izquierdo and Beer, 2013). All further analysis was limited to this high-performance individual.

To test for generalization we also placed the model worm in a Gaussian-shaped chemical gradient (see Methods), which more closely resembles the gradients used in laboratory tests of chemotaxis in *C. elegans*. The performance in the Gaussian gradient was similar to that obtained in the conical gradient (Fig. 3B). The best agent achieved a chemotaxis index of 0.68, and similarly perfect reliability. The small drop in chemotaxis index reflects the longer path to the peak. Overall, the high performance suggests that the evolved circuit is not specialized for the shape of the gradient; instead, it embodies a more general solution to the task of steering.

Unlike conical gradients, the steepness in Gaussian-shaped gradients varies as a function of the distance to the peak. To understand the worm’s ability to generalize, we explored systematically its performance in conical gradients of varying steepness (Fig. 4). The performance is highest for the gradient steepness it was evolved for (\( \alpha = 1.0 \)). If the gradient is too shallow (\( \alpha < 0.4 \)), the performance drops; otherwise, the model worm performs chemotaxis successfully under a wide range of gradient steepnesses, including an order of magnitude larger than what it evolved for. Such robustness allows it to perform well under gradients of different shapes, including the Gaussian gradient.

Ultimately, that successful solutions were found demon-
strates that the identified klinotaxis circuit innervating only the anterior most muscles is sufficient to steer the full body during forward locomotion.

**Steering is possible by modulating a wide range of the anterior-most muscles**

In our model, the steering circuit innervates the four most anterior muscles (Fig. 1A). However, what muscles are involved in steering in the worm is not yet known (Satoh et al., 2014; Gjorgjieva et al., 2014). We use our approach to explore the range of possibilities for steering within the constraints provided by the forward locomotion model.

First, how does the performance of the best evolved circuit change when the number of muscles innervated by the neck motor neurons varies? We can measure the chemotaxis index of the model as we vary the number of muscles the steering circuit innervates (Fig. 5). Not surprisingly, the best performance is obtained when the circuit is innervating the muscles it evolved to modulate (first four muscles, orange bar). However, the experiment shows that the circuit can perform chemotaxis when modified to innervate anywhere between 3 and 8 of the anterior most muscles. The results suggest the circuit is flexible with respect to the number of muscles necessary to produce chemotaxis.

An analysis of the best evolved agent gives us only a measure of the flexibility that specific solution has to perform chemotaxis under conditions it has never experienced before. But is there an optimal number of muscles that the worm can modulate to produce steering? We can begin to address the second and more general question of optimality by performing additional evolutionary runs on a range of different conditions: when the steering circuit is innervating 4, 8 and 12 of the anterior-most muscles. When we performed 20 evolutionary runs for each of the different conditions, solutions were found that could perform chemotaxis nearly equally well (Fig. 6). This result suggests solutions using a relatively wide range of the anterior-most muscles are equally viable. These experiments, however, assume the anterior most muscles are needed for steering. Is this the case? To address this, we ran an additional evolutionary experiment where the steering circuit could modulate only muscles 5-8. Circuits under this condition consistently failed to evolve a good enough fitness (>0.7). This result suggests modulating anterior-most muscles is necessary for steering. Otherwise the circuit is flexible to perform chemotaxis with a wide range of anterior-most muscles.

**Sensorimotor transformation is consistent with previous klinotaxis models and experimental observations**

In order to understand the sensorimotor transformation that the circuit evolved, we analyzed the orientation responses produced by single stepwise changes in concentration given at different phases of the locomotion (Fig. 7). Orientation responses were expressed in terms of turning bias, computed over several cycles of locomotion following the concentration step. We observed that turning bias varied as a sinusoidal function of the phase of locomotion at which the concentration change occurred (Fig. 7A). Throughout a dorsal head sweep (between phase 0 and π), an increase in concentration resulted in a dorsal reorientation; during a ventral head sweep (between phase π and 2π), an increase in concentration resulted in a ventral reorientation (blue traces). As a response to a decrease in concentration, the worm reorients in the opposite direction to the instantaneous velocity of the head at the time of the step (yellow traces). We also observed that larger changes in concentration led to larger changes in turning (dashed trace vs. solid trace). The results were consistent with our previous models of steering in an idealized body (Izquierdo and Beer, 2013).

In order to illustrate how this sensorimotor transformation can lead to successful klinotaxis, we show example traces without changes in concentration (black trace) and with positive and negative changes in concentration (blue and yellow, respectively) given at the beginning of a dorsal (phase 0) and a ventral (phase π) head sweep (Fig. 7B). The instantaneous velocity vector of the head at the time of an up-step signals the direction of the peak implied by such a step (blue dashed arrow). As a result of a positive change in con-
centration, the worm moves in the direction of the implied peak (blue traces). A downstep in concentration given at that same phase in the locomotion leads to turning in the opposite direction of the implied peak (yellow traces). Thus, the model worm appropriately corrects its orientation relative to discrepancies between its velocity vector and the direction of the peak.

A full sensorimotor transformation analysis has not yet been performed in the worm. However, recent experiments have analyzed the movement of the worm during phasic stimulation to the sensory neurons (Kocabas et al., 2012; Satoh et al., 2014). We replicated these experiments in the artificial worm (Fig. 7C). When the ON cell is stimulated repeatedly during dorsal head sweeps, the worm displays a dorsal-oriented curvature (green trace). When the ON cell is stimulated repeatedly during ventral head sweeps, the worm displays a ventral-oriented curvature (blue trace). The curvatures are different for dorsal and ventral head-sweeps due to a dorsoventral asymmetry in the BBC locomotion model. The effect is the opposite when stimulating the OFF cell (not shown). The results of these experiments follow directly from the sensorimotor transformation provided in Fig. 7A, and crucially, they reproduce the results observed in the worm. These results suggest that the model and biological circuit may be operating according to similar principles. Furthermore, they predict the overall sensorimotor transformation in the worm should be consistent with the integrated model and previous theoretical models (Fig. 7A).

**Shape statistics analysis reveals eigenworms dedicated to steering**

The integration of a steering circuit in a biomechanical model of the body allows us to compare more closely the properties of the evolved solutions with those of the worm. Several approaches have been suggested for mathematically describing locomotion in *C. elegans*. One of the most useful approaches involves using video microscopy of the worm’s movement to find a low dimensional description of the macroscopic behavior (Stephens et al., 2008). Analysis of behavioral data has shown that the space of shapes adopted by *C. elegans* can be almost completely described (95% of the variance) by projections along four principal “eigenworms” (Stephens et al., 2008). Their analysis also suggests the first two eigenworms are sinuous and together offer a quantitative characterization of the traveling wave along the body during forward locomotion.

In order to analyze the behavior of the model and compare it to that of the worm, we use detailed data of the simulated body over time during freely moving behavior. We proceeded in two steps. First, as results of the shape statistics have not been replicated in a simulated model of the worm yet, we analyzed the forward locomotion model without the steering circuit and compared the results with those of the worm. As a second step, as an analysis of the shape...
statistics has not been performed in the context of steering behavior exclusively, we analyzed the integrated model during steering as a way to predict the resulting shape statistics in the worm.

Without the steering circuit, the forward locomotion model displays a covariance matrix of fluctuations in angle that is rather similar to that of the worm (Fig. 8A): (a) Inhomogeneity along the diagonal shows motion is not sinusoidal; (b) The smooth structure of the matrix suggests only a small number of modes are significant. The main difference between the covariance matrices of model and worm is towards the posterior, which seems to be flatter in the model than in the worm (cf. Fig. 2A in Stephens et al. (2008)). This suggests the BBC model of forward locomotion may be missing crucial aspects of the operation of the circuit that allow for the wave to propagate backwards more fully. When we consider the eigenvalues of the model, the majority of the variance (98.7%) is captured by the first two eigenvalues (red, Fig. 8B). This is expected because the model without the steering circuit is only moving forwards; there are no gradual turns, foraging, or omega turns. Associated with each dominant mode is an eigenvector. The first two eigenworms of the model are also similar to those of the worm (red, Fig. 8C). Indeed, these eigenworms capture all the variability along the body (Fig. 8D). This result is consistent with analysis of forward locomotion in the worm (Stephens et al., 2008).

When the steering circuit is added to the model worm, the covariance matrix of fluctuations in angle changes significantly (Fig. 8A). Although there is still inhomogeneity along the diagonal, the structure of the matrix is not as smooth, suggesting it takes more modes to capture the variance of the movement. Indeed, while the first two eigenvalues still capture the majority of the variance (59.1%), each additional eigenvalue is responsible for only a small amount of the additional variance (blue, Fig. 8B). As with the worm and the model without steering, the first two eigenworms correspond to those responsible for forward locomotion (blue, Fig. 8C). Interestingly, the third eigenworm reduces information mostly in the neck and also in the tail (green area, Fig. 8D). This suggests the possibility of an eigenworm dedicated mainly to steering. However, together these three modes only capture 64.7% of the variability in shapes adopted by the worm during steering. These results prompt us to analyze the shape statistics during steering behavior exclusively in the worm. Differences between the predicted shape statistics in the model and the worm is likely to suggest ways in which the model of the body does not propagate the steering in the same way as in the worm.

Conclusion

In this paper, we extended our previous model circuit for steering in C. elegans to control a more realistic biomechanical model of forward locomotion. The evolutionary algorithm successfully found several combinations of parameters of the steering circuit capable of performing klinotaxis. The existence of solutions suggests that the identified steering circuit, while only innervating a few of the anterior most muscles, is indeed sufficient to steer the full body during forward locomotion. Furthermore, analysis of the sensorimotor transformation showed that the best evolved circuit is both:

Figure 8: Shape statistics: Eigenvectors for forward locomotion and steering. Position along the body is represented by $s$, normalized so that $s = 0$ is the head and $s = 1$ is the tail. (A) The covariance matrix of fluctuations in angle. (B) Fraction of the total variance (integrated along the body of the worm) captured by keeping $K$ eigenvectors ($K = 1$ to 8), calculated from the Eigenvalues of the covariance matrices for the forward locomotion model (red) and the integrated model with the steering circuit (blue). (C) Associated with each dominant mode is an eigenvector or eigenworm. First three eigenworms shown for the forward locomotion model (red) and the integrated model with the steering circuit (blue). (D) Fraction of the variance (unrolled over the body of the worm) captured by keeping $K$ eigenvectors ($K = 1$ to 3, from bottom to top) for the forward locomotion model and the integrated model with the steering circuit.
(a) qualitatively similar to previous theoretical models of steering (Izquierdo and Lockery, 2010; Izquierdo and Beer, 2013), and (b) consistent with recent experiments involving phasic stimulation of sensory neurons in the worm (Kocabas et al., 2012; Satoh et al., 2014). This suggests that the principles of operation for steering discussed in the idealized models are relevant for steering in the nematode. Finally, the integration of the circuits in a biomechanical model of the full body allowed us to compare more closely the properties of the evolved solutions with those of the worm. Analysis of the shapes produced by the steering model revealed the first two eigenworms are responsible for forward locomotion and the third is likely to be involved in steering. Each of these findings corresponds to an experimental prediction that could potentially be tested in the worm.

There are several directions for future work that we believe will be productive. First, as new experimental evidence becomes available, the models have to be revisited, updated, and expanded. Since nearly the entire behavioral repertoire of C. elegans is ultimately expressed through movement, this is particularly crucial for the neuromechanical basis of locomotion and its modulation—the foundation upon which analyses of all other behaviors must build. Second, as neural circuits involved in different behaviors in the worm continue to be mapped out experimentally, parallel efforts to develop embodied and situated models of these circuits is likely to accelerate the understanding of the neural basis of their behavior. In addition to modeling each of the distinct behaviors individually, future work will focus on integrating these multiple circuits, responsible for different behaviors, under the same body. Ultimately, incrementally constructing a comprehensive model of a complete organism is likely to completely transform our understanding of how integrated behavior arises from the ongoing interaction of an animal’s nervous system, its body, and its environment.

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References


