

Connecting Brains to Robots: The Development of a Hybrid System for the Study of Learning in Neural Tissues

Bernard D. Reger¹, Karen M. Fleming¹, Vittorio Sanguineti², Simon Alford³ and Ferdinando A. Mussa-Ivaldi¹

¹Department of Physiology, Northwestern University Medical School, Chicago, IL 60611

²Dipartimento di Informatica Sistemistica e Telematica, Università di Genova, Italy

³Department of Biological Sciences, University of Illinois at Chicago, Chicago, IL 60607

Abstract

We have developed a hybrid neuro-robotic system based on a two-way communication between the brain of a lamprey and a small mobile robot. The purpose of this system is to offer a new paradigm for investigating the behavioral, computational and neurobiological mechanisms of sensory motor learning in a unified context. The mobile robot acts as an artificial body that delivers sensory information to the neural tissue and receives command signals from it. The sensory information encodes the intensity of light generated by a fixed source. The closed-loop interaction between brain and robot generates autonomous behaviors whose features are strictly related to the structure and operation of the neural preparation. In this paper we provide a detailed description of the hybrid system and we present experimental findings on its performance. In particular, we found (a) that the hybrid system generates stable behaviors; (b) that different preparation display different but systematic responses to the presentation of an optical stimulus and (c) that alteration of the sensory input lead to short and long term adaptive changes in the robot responses. The comparison of the behaviors generated by the lamprey's brainstem with the behaviors generated by network models of the same neural system provides us with a new tool for investigating the computational properties of

synaptic plasticity.

Introduction

Since its inception, robotic science has given great contributions to the study of motor learning and control in humans and other biological systems (Hildreth and Hollerbach 1987). The most notable contribution has been the determination of what interesting computational problems must be solved by the brain as well as by an intelligent machine when either one must control the mechanical interaction between limbs and environment. Theories concerning what computational problems must be solved by an intelligent system have been called "competence" theories (Marr 1982) to distinguish them from "performance" theories, concerning the physical processes that are actually chosen to solve a problem. In this paper, we present a first attempt to utilize a robotic system for investigating the neural processes underlying sensory motor adaptation, that is for understanding a distinctive feature in the performance of biological systems. Our goal is to develop a computational

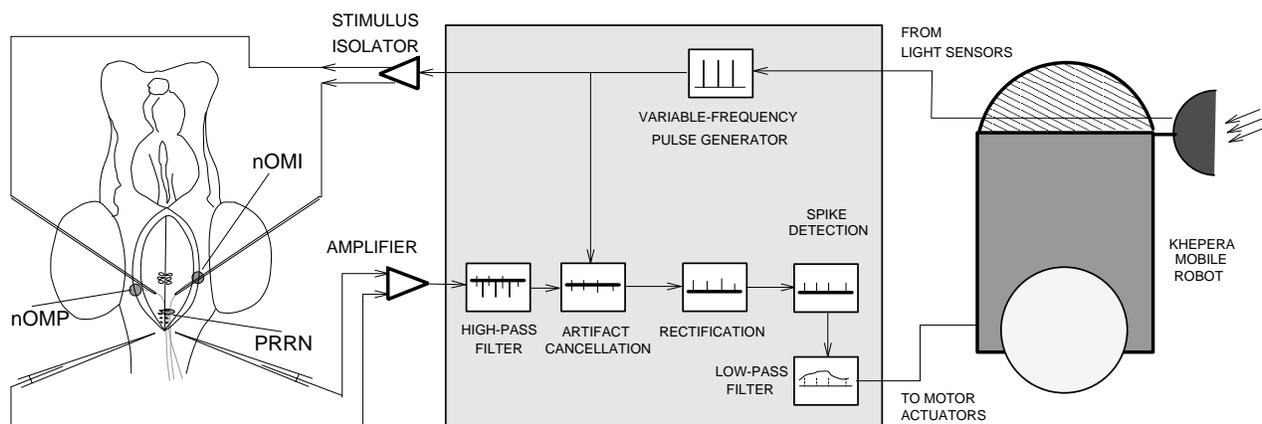


Figure 1 - Robot Signal Flow Block Diagram. The neuro-robotic interface (shaded center region) translates the light sensor data from the robot (right) into a stimulation pattern for the lamprey preparation (left). The neural response is converted into motor signals by the interface.

and experimental framework for relating the neurobiological study of neural plasticity-the modification of neuronal excitability following past experience of input and output patterns- to the behavioral functions that are supported by neural plasticity.

The framework that we have developed is a hybrid system, which establishes a two-way signal interaction between a mobile robot and brain tissue maintained alive in vitro from the reticular formation of the lamprey- a primitive eel-like vertebrate. In this experimental arrangement, the brain and the robot are interconnected in a closed loop. They communicate through an interface that transforms (a) light information from the robot's optical sensors into electrical stimulation to the lamprey's brainstem, and (b) recorded neural activity from two brainstem nuclei into motor commands to the robot's wheels (Figure 1). We have chosen the lamprey for this first study because of the easy access in this preparation to a system of very large neurons- the Muller cells in the reticular formation- that integrate command and sensory signals directed to the spinal motor centers.

From the standpoint of a neurobiologist, this neuro-robotic system can be regarded as a system for complementing the electrophysiological study of neuronal properties with an artificial behavioral context. We must stress the adjective "artificial", because the signals that normally would travel along the circuits that we are stimulating are signals of vestibular rather than visual origin. In this brain stem preparation we have selected a portion of neural circuitry that in normal circumstances combines vestibular signals and motor commands to stabilize the orientation of the body during swimming (Rovainen 1979; Deliagina et al. 1992a; Deliagina et al. 1992b; Orlovsky, Deliagina and Wallén 1992). This system has been shown to be adaptive, as unilateral lesions of the vestibular capsules are followed by a slow reconfiguration of neural activities until the correct postural control is recovered (Deliagina 1995; Deliagina 1997). In our hybrid system, vestibular signals are replaced by light intensity signals. As the vestibular signals have a right and left source- the two vestibular capsules - so do the two light intensity signals originating from sensors on the right and left side of the robot. Therefore, the natural stabilizing behavior, in which the lamprey would track the vertical axis, corresponds, in the hybrid system, to a positive phototaxis, that is a tendency of the robot to track a source of light. We are convinced that the properties of the information processing associated with natural behaviors may be explored by observing the information processing associated with the artificial behavior. This, in a way, is a consequence of the abstract and generalized nature of information. An obvious advantage of our hybrid system, always from the point of view of experimental neurobiologists, is that, unlike natural motor behaviors, artificial behaviors do not interfere mechanically with the electrophysiological setup. In any study involving intra- or extracellular recording, even the slightest motion of the tissue tends to cause unwanted displacements of the

electrodes.

From the perspective of neural computation, the hybrid system provides a means to test models of information processing by direct interaction with a biological neural network. As we detail in the methods section, the behavior of the robotic system is described by a relatively simple- and yet nonlinear- system of differential equations. To the extent that the brain properties may be considered stationary (over the time scale of robot movements), these equations describe an autonomous system whose properties are modulated by the structure of the neural pathways and connections intervening between stimulating and recording electrodes. Conversely, the observation of the sensory-motor behaviors that emerge from this system offer an insight into the computational structure of the neural system. The search for such an insight is what drives our study.

Here, we report three initial findings of this study. First, we have succeeded in obtaining stable behaviors over extended periods of time, characterized by repeatable motor responses to a light source. Second, in different preparations, we have observed different responses ranging from light tracking to light avoidance. Through simple simulations, we show how these different responses may be readily accounted for by different patterns of connectivity between stimulation and recorded signals. Finally, we have observed plastic adaptive changes following the unilateral alterations of the sensory inputs. These findings provide supporting evidence for the use of neuro-robotic systems in the study of the neurobiological mechanisms of sensory motor learning.

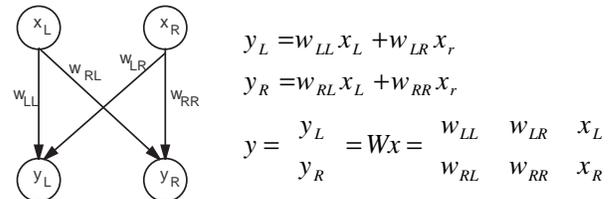


Figure 2 - Simple two layer neural network with two inputs, two outputs, and four weights.

Methods

In this section we describe the components of our hybrid neuro-robotic system, the experimental setup used to assess its performance, and the basic computational model that characterizes the system's behavior.

The neural preparation

The neural component of the hybrid system is a portion of the brainstem of the Sea Lamprey in its larval state. In larvae of Sea Lamprey *Petromyzon marinus*, anesthetized with tricane methanesulphonate (MS222, 100-200 mg/l), the whole brain was dissected and maintained in

continuously superfused, oxygenated and refrigerated (9–11°C) Ringer's Solution (NaCl, 100.0 mM; KCl, 2.1 mM; CaCl₂, 2.6 mM; MgCl₂, 1.8 mM; glucose, 4.0 mM; NaHCO₃, 25.0 mM); details in Alford et. al. (1995).

We recorded extracellularly the activity of neurons in the a region of the reticular formation, a relay that connects different sensory systems (visual, vestibular, tactile) and central commands to the motor centers of the spinal cord. We placed two recording in the right and left Posterior Rhombencephalic Reticular Nuclei (PRRN). We also placed two unipolar tungsten stimulation electrodes among the axons of the Intermediate and Posterior Octavomotor nuclei (nOMI and nOMP). These nuclei receive inputs from the vestibular capsule and their axons form synapses with the Rhombencephalic neurons on both sides. The impedance of the stimulation electrodes ranged between 1 and 2 MΩ. Recording electrodes were glass micropipettes filled with 1M NaCl (1.5–10 MΩ impedance). The recorded signals were acquired at 10kHz by a data acquisition board (National Instruments PCI-MIO-16E4) on a Pentium II 200MHz computer (Dell Computer Corp.).

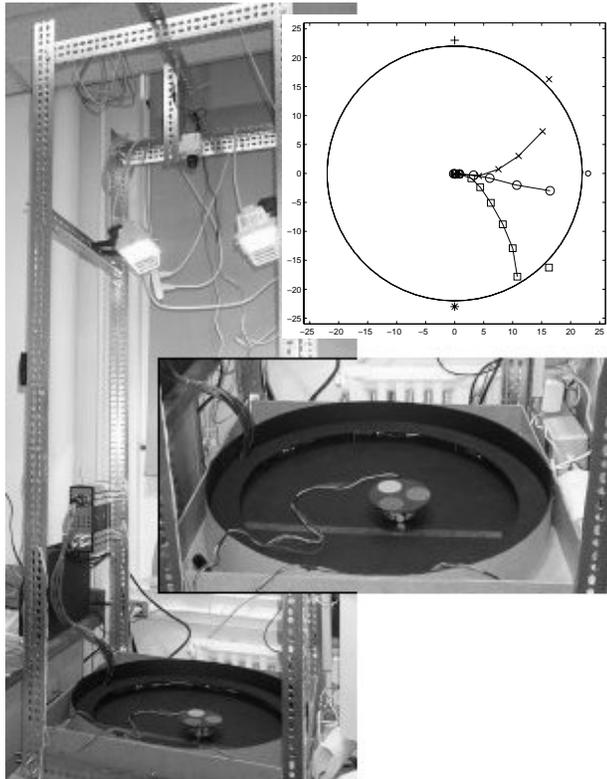


Figure 3 – Robot setup. Using a pattern of colored circles (lower inset), the overhead camera tracks the robot. Trajectories are plotted, each symbol representing a target light.

Electrode placement

While the axons of the nOMI remain ipsilateral, those of the nOMP cross the midline. As a result, the activity of one vestibular capsule affects both the ipsilateral and

contralateral reticulo spinal (RS) nuclei. We placed each stimulating electrode near the region in which the axons of the nOMI and nOMP cross (Figure 1). This placement of the electrodes also induced predominantly excitatory responses in the downstream neurons. The recording electrodes were placed on either side of the midline, near the visually identified neurons of the PRRN. To verify the placement of the stimulating electrodes we delivered brief single stimulus pulses (200μs) and observed the response in both the ipsilateral and contralateral PRRN neurons. Once it was determined that the stimulation electrodes were properly placed, the recording electrodes were moved caudally in order to pick up population spikes.

The robot

The robot system is the base Khepera module (K-Team). Its small size allows us to use a small workspace (Figure 3). A circular wall was constructed with a 2 foot diameter and then painted black to reduce the amount of reflected light. Placed along the circumference of the robot are eight sensors each providing proximity and light intensity information. The sensors are located on opposite sides of the robot's midline at 10°, 45°, 85°, and 165° from the front position. Two wheels provide a means of locomotion for the small robot. Our computer system communicates with the robot through the serial port and a custom designed LabVIEW[®] application. Eight lights are mounted at the edge of the robot workspace at 45° intervals. The lights were numbered one through eight moving counter clockwise with light number one located at the right most position (0°). The lights are computer controlled using the digital outputs of our acquisition card. These lights generate the stimulus that elicit a phototactic response.

The interface

The interface acts as an interpreter between the neural signals and the robot control system (Figure 1). It is responsible for the transformation of the robot's light sensor information into vestibular inputs and then processing in real time the neural activity of the reticulo-spinal nuclei and translating it into motor commands for the robot.

Stimulus

The light intensities detected by the robot sensors determine the frequencies at which the right and left vestibular pathways are stimulated. As stated above, there are eight light sensors on the robot. We weighted the sensors to give the greatest strength to sources of light that come at 45° and to ignore the rear sensors. The weighted sum of the sensors on each side is multiplied by a gain factor which determines the maximum stimulation frequency. The final result is the frequency at which we stimulate each side. We use the digital counter on the acquisition board to generate a pulse train. This pulse train is delivered to the neural preparation by the tungsten electrodes after passing through ISO-Flex stimulus isolators.

Neural Response

The spiking activity of the PRRN as recorded near the axons is analyzed through a five step process. The signal picked up by the recording electrodes contains a combination of spikes, stimulus artifacts, excitatory and inhibitory postsynaptic potentials (PSP) and noise. To suppress the slow PSP components, this signal is first put through a high pass filter (cutoff at 200 Hz). The output of this filter contains high frequency noise, stimulus artifacts, and the spikes generated by multiple neurons in the vicinity of the electrode. Stimulus artifacts are canceled by zeroing the recorded signals over temporal windows of 4 ms following the delivery of each 200 μ s stimulation pulse. The remaining signal is rectified, and a threshold is applied to separate the spikes from the background noise- under the assumption that the spike amplitude is much larger than the noise amplitude. The resulting train of spikes, is put through a low pass filter (5 Hz) which effectively generates a rate coded signal. The mean of this signal is used as a control signal for each of the robot's wheels.

The interface is calibrated so as to account for random differences between the recorded responses from the left and right side of the brainstem. Indeed, the net intensity of the signal picked up by each electrode depends on a number of uncontrollable factors, such as the actual distance from signal sources. To compensate for these random factors, we make the working assumption that when both left and right sides are stimulated at the same frequency, the same motor response should be obtained on each side of the robot. This corresponds to stating that all initial asymmetries between right and left side are artifacts. Accordingly, all initial difference between right and left responses to the same right and left signals are balanced by regulating two output gains.

In most cases, the right and left sides of the neural preparation were connected both in input and in output with the corresponding sides of the robot (direct mode). However, as discussed below, in some cases it was necessary to implement a reverse mode option. When connected in reverse mode, the right recording electrode is connected through the interface to the controller of the left wheel and vice versa.

Movement acquisition

The robot position and orientation is sampled and acquired using an overhead color camera (Ultrak STC-630A). The image frames are analyzed using a Newton Research Labs Cognachrome 2000 Vision System. The Cognachrome vision system is capable of simultaneously tracking up to three different colors. We have chosen a blue, red, and pink colored circle arranged in an equilateral triangle (Figure 3). The Cognachrome system captures video frames at 60 Hz, and then each frame is analyzed to determine the center and area of each colored centroid. If all three centroids are visible, the orientation of the robot is calculated and the mean of all centers is calculated to determine the center of the robot. If the area of a centroid drops below a specified amount, the remaining two

centroids are used to determine both the position and orientation. This reduces the probability that the position and orientation are lost due to partial occlusion of the set of centroids.

Trajectories induced by the same light stimulus were quantitatively compared using a figural distance measure (Conditt, Gandolfo and Mussa-Ivaldi 1997). The figural distance between two trajectories, A and B, is based on the repeated measure of the Euclidean distance between each point in one trajectory and all the points in the other. If the trajectory A has n points, $\{A(1), A(2), \dots, A(n)\}$, and the trajectory B has m points, $\{B(1), B(2), \dots, B(m)\}$, then one derives the n-dimensional vector

$$\text{dist}_{A-B}(i) = \min_j (\|A(i) - B(j)\|) \quad (1 \leq i \leq n)$$

and the m-dimensional vector

$$\text{dist}_{B-A}(j) = \min_i (\|A(i) - B(j)\|) \quad (1 \leq j \leq m)$$

Then, the figural distance between A and B is defined as

$$\varepsilon(A, B) = \frac{\sum_i \text{dist}_{A-B}(i) + \sum_j \text{dist}_{B-A}(j)}{m+n}$$

The figural distance between two trajectories is a symmetric measure of the difference between the shapes of the respective paths. In each experimental set we considered movements to five different targets. Then, we constructed a net figural distance between two sets by summing the figural distances between trajectories to the same lights.

Simulation

To simulate the artificial behaviors generated by the cyborg we consider the interaction of three systems: a) the robot's motor system b) the robot sensory system and c) the lamprey's brain.

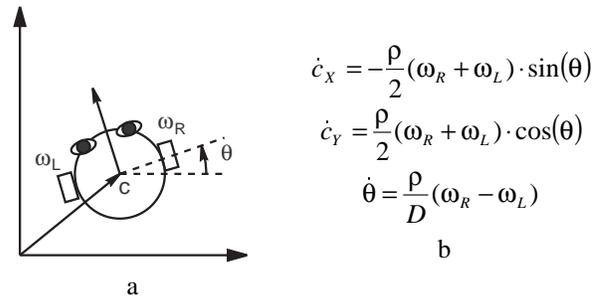


Figure 4 – The dynamics of the robot are described by three nonlinear first order differential equations.

Robot motor system. The dynamics of the mobile robot are described by a system of three nonlinear first-order differential equations (Figure 4a). Here, (c_x, c_y) are the coordinates of the Khepera's center with respect to a fixed laboratory frame, θ is the angle of the line passing through the wheels (the axle) with respect to the x-axis of the same frame, ρ is the wheel radius (0.3cm) and D is the axle

length (5.3cm). The state of this system is described by the 3D vector (c_x, c_y, θ) . The input is the 2D vector, (ω_L, ω_R) , of angular velocities of the left and right wheel.

Light sensors. The intensity signal generated by each sensor (i_R, i_L) is inversely proportional to the square distance to the light source (Figure 5b).

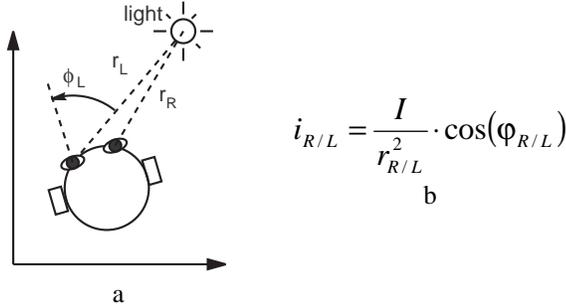


Figure 5 – The response of the robot’s sensors are a function of distance and angle from the light source.

The angle ϕ is the “preferred direction of the sensor”, that is the direction of maximum response. The source is fixed in the environment and has an emission intensity, I . Under these assumptions, the intensity signals, (i_R, i_L) , are both functions of the robot’s state:

$$i_{R/L} = i_{R/L}(c_x, c_y, \theta).$$

Lamprey’s brain. Unlike the robot, the operation of the brain is essentially unknown. The purpose of the hybrid system is actually to investigate the computational properties of this neural tissue. In our simulations, we considered an extremely simplified linear model of this neural system (Figure 2). There are two inputs- the light intensity signals used as stimuli - and two outputs – the angular velocities of the wheels. These signals are connected by a “weight matrix”, W , whose elements may be taken to represent the strengths of the connections

between inputs and outputs. Positive weights represents excitatory connections and negative weights inhibitory connections.

The whole system. When all the above components are assembled into a single system, one obtains three differential equations in which the rate of change of the state vector depends only upon the state vector itself, and not on time:

$$\begin{aligned} \dot{c}_x &= f_1(c_x, c_y, \theta|W) \\ \dot{c}_y &= f_2(c_x, c_y, \theta|W) \\ \dot{\theta} &= f_3(c_x, c_y, \theta|W) \end{aligned} \quad (1)$$

This is called an autonomous system. Here, we have emphasized that the particular behaviors emerging from this autonomous system are determined by the parameters that describe the behavior of the neural system and that are assumed to be time-invariant (or, at least, to be varying on a time scale that is much longer than the scale of each behavior). In this first simulated approximation, the neural parameters are fully expressed by a 2×2 matrix W . But, of course, to capture with high accuracy the behavior of the real system it will be necessary to utilize more complex models.

Results

Stability

In these experiments, the lamprey's brain was maintained in vitro for periods ranging from 4 to 8 hours. In most cases, the preparation maintained its full responsiveness across the entire experiment. In addition to the overall health of the preparation, other factors affecting the persistence and stability of behaviors are (a) the displacement of the electrodes within the neural tissue and (b) local damage to neural tissue caused by repeated stimuli. Figure 6 shows the behaviors generated by what we considered to be an unstable preparation. The four panels display four consecutive experimental sets separated

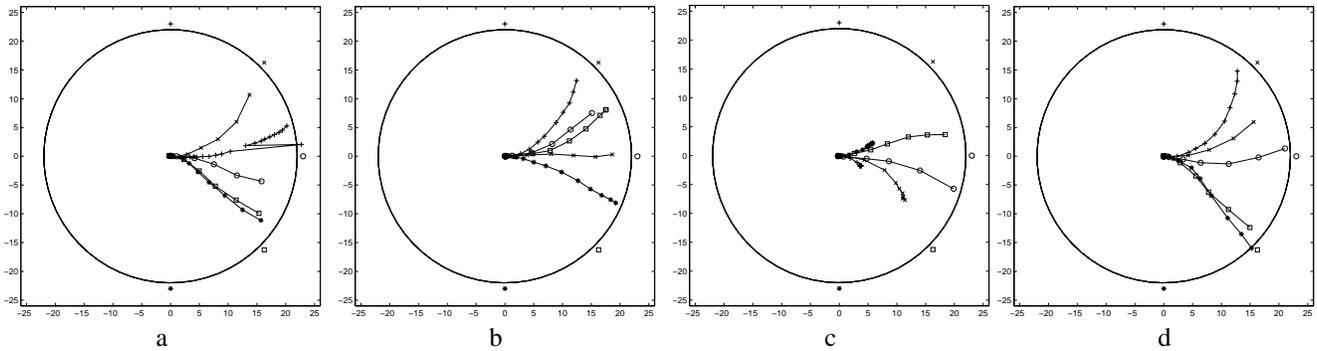


Figure 6 – Unstable robot trajectories. Panels a and b were separated by 10min, b and c by 5min, and c and d by 0min. The trajectories generated by the light marked with a star (*), circle (o), and square (□) vary greatly from one trial to the next.

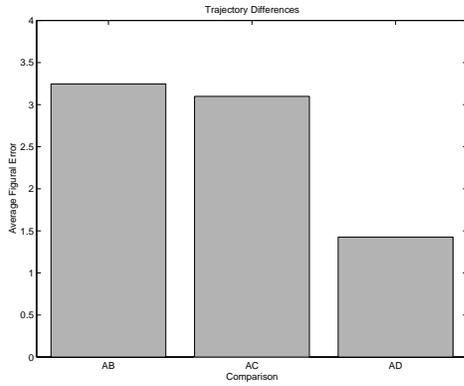


Figure 7 – Figural error of the unstable trajectories. The first bar is the error between panels a and b of Figure 6, second bar for panels a and c, and third bar for a and d.

by intervals of 10min, 5min and 1min. During each experimental set, the lights indicated by different symbols along the workspace boundary were turned on in sequence. We collected trajectory data from the moment the light turned on until the robot either stopped moving or reached the edge of the workspace. A single trial set contains the trajectories collected as the robot reacted to each light. It is evident that the trajectories in the four panels of Figure 6 change rather drastically from trial to trial. This variability is quantified by the figural error plots in Figure 7. One may see that there is a particularly strong variation between trial 1 and trials 2 and 3. Whenever we observed this kind of unstable behavior - quantified by a net figural error larger than 2.5cm - we moved the stimulation and/or recording electrodes to different sites. If these adjustments did not result in some improvement, we discarded the preparation. Figure 8 shows a set of stable behaviors. The panels are arranged as in Figure 6. The variability of the trajectories in Figure 8 is expressed by the figural errors shown in Figure 9. Although some amount of variability between different trial sets is still visible, the predominant positive phototaxis is evident in all panels and the overall trajectory shapes are similar for trajectories elicited by the same lights. We considered for further analysis only

preparations with stability comparable or better than shown in this example, as determined by a figural error of less than 2.5cm.

Behavioral responses

The features of the trajectories generated by the neuro-robotic system depend upon the pattern of neural connections between stimulating and recording electrodes. In a first approximation, one may represent the operation of these connections by the linear two-layer network of Figure 2. We have combined this simple network model with a simulator of the Khepera dynamics. The response of the combined system to a source of light is described by a set of three nonlinear first-order autonomous equations (Equation 1). By simulating these equations we could predict the general features of trajectories corresponding to different patterns of stimulation/recording connectivity. The structure of the connection matrix, W , establishes the sign of the ensuing phototactic behavior. In case of pure ipsilateral excitatory connectivity (right-to-right and left-to-left), the off diagonal terms are both zero and the diagonal terms are positive. When the diagonal terms are equal (that is when the connectivity matrix is proportional to the unit matrix,) then the resulting behavior is a negative phototaxis- i.e. movement away from the light source - as shown in Figure 10b. In contrast, if there is purely contralateral excitatory connectivity (right-to-left and left-to-right), the diagonal terms are zero and the off diagonal terms are positive. The resulting trajectories (Figure 10a) correspond to positive phototaxis- i.e. movements toward the light. A broad spectrum of intermediate behaviors (an example is in Figure 10c) is obtained by matrices with both diagonal and non-diagonal terms and with different degrees of asymmetry.

Depending on the placement of the electrodes in the actual neural tissue, we were able to observe both positive and negative phototaxis, as well as intermediate behaviors (Figure 11). It is worth observing that negative phototaxis with the actual system tended to result in shortened trajectories compared with negative phototaxis in the simulator (Figure 11c). This is likely due to the rapid drop in light intensity as the Khepera moved away from the light

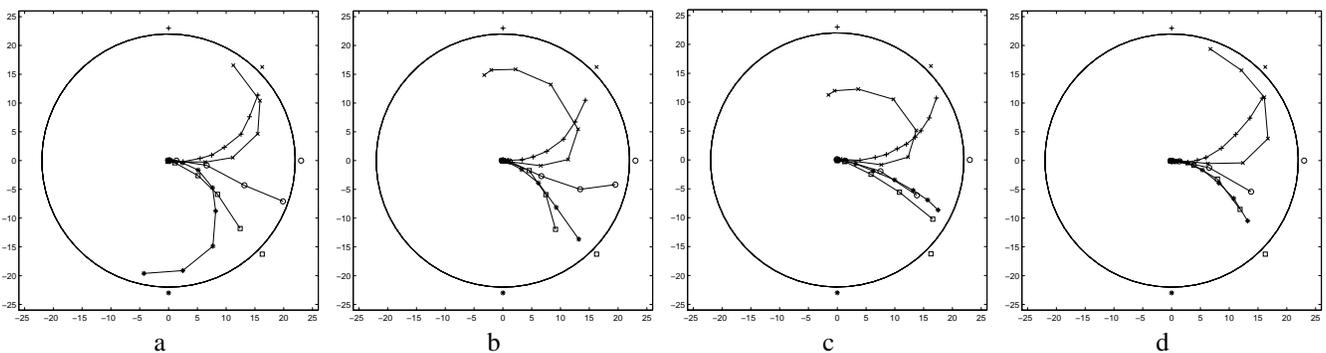


Figure 8 – Stable robot trajectories. Panels a and b were separated by 10min, b and c by 5min, and c and d by 0min.

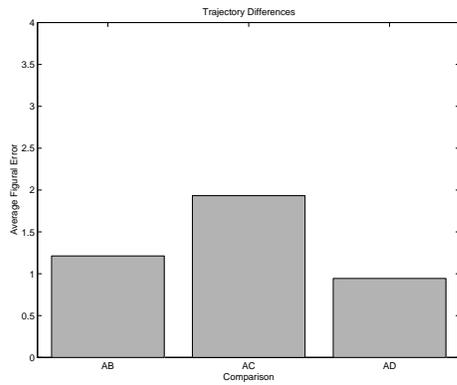


Figure 9 – Figural error of the stable trajectories. The first bar is the error between panels a and b of Figure 8, second bar for panels a and c, and third bar for a and d.

source. Because of scattering and other phenomena not included in the model, the actual drop in light intensity was more pronounced than the simulated drop. This effect is compound by the presence of friction, which is also not

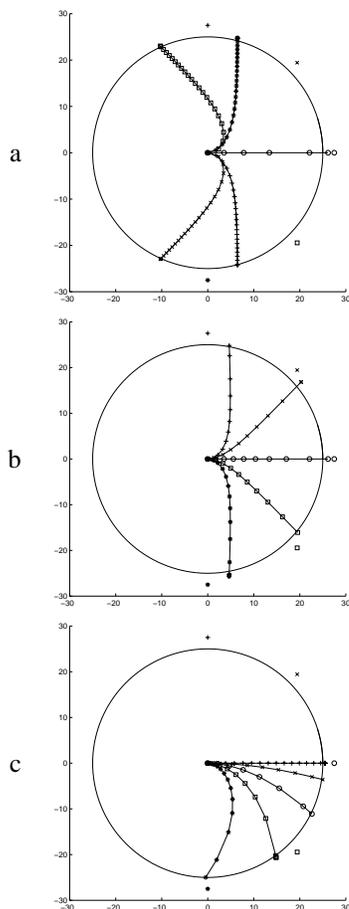


Figure 10 - Different matrices W are used with the two layer network model and the robot simulation to generate a) negative, b) positive, and c) mixed phototaxis.

included in the model. To obtain, in cases like this one, a higher sensitivity of the observed behaviors in response to the different light sources, we biased our preparation toward positive phototaxis by selecting the reverse mode option that is by connecting the right electrode to the left wheel controller and vice versa. This operation is equivalent to exchanging off-diagonal with diagonal weights in the connectivity matrix

Adaptive modification of artificial behavior

The neural component of the hybrid system is a portion of the brainstem, the reticular formation, that normally combines vestibular information with other sensory inputs and descending commands. The outcome is a neural signal that modulates the ongoing activity of the spinal cord for the control of swimming movements (Grillner et al. 1983; Grillner and Mastushima 1991). A significant feature of this circuitry is its ability to modify the efficacy of its own synaptic connections in response to sustained patterns of stimulation. Both long-term potentiation (LTP) and long-term depression (LTD) have been documented (Schwartz et al. 1998). We wished to explore the possibility of using our system for observing the effects of plastic changes on artificial behaviors and for separating, on the basis of this observation, the effects of long-term changes from those of short-term changes.

To generate adaptive changes in the neural preparation, we doubled the sensitivity of the light sensors on the left side of the robot while leaving unchanged the sensitivity on the right. This alteration induced the change in behavior shown in Figure 12a and Figure 12b. The trajectories with the initial setting of gains are displayed in Figure 12a whereas the trajectories in Figure 12b were obtained immediately after the change in the left light sensors. It is possible to observe a predominant clockwise rotation of the trajectories. Immediately following the acquisition of the trajectories, the robot was placed in its home position (center of workspace with the “nose” facing the light number 1, at 0°) and fixed in place so that it could not move. Light number one was turned on for a period of five minutes. Although both sides of the robot were exposed to approximately the same amount of light, the increased sensitivity on the left side doubled the corresponding frequency on the left side of the lamprey. Following this extended period of stimulation, a second set of trajectories was recorded (Figure 12c). These trajectories were highly distorted, compared to those obtained in the initial phase of the experiment. There is a strong clockwise rotation together with the formation of circular patterns. Such circular patterns are a typical sign of strong imbalance between right and left channels.

This particular experiment was conducted in reverse mode. Therefore, the clockwise rotation of the trajectories, which reflects an increase in speed of the left wheel (and/or a decrease of the right), is due either to an increase in response of the right reticulo-spinal neurons (and/or to a decrease in responsiveness of the left neurons).

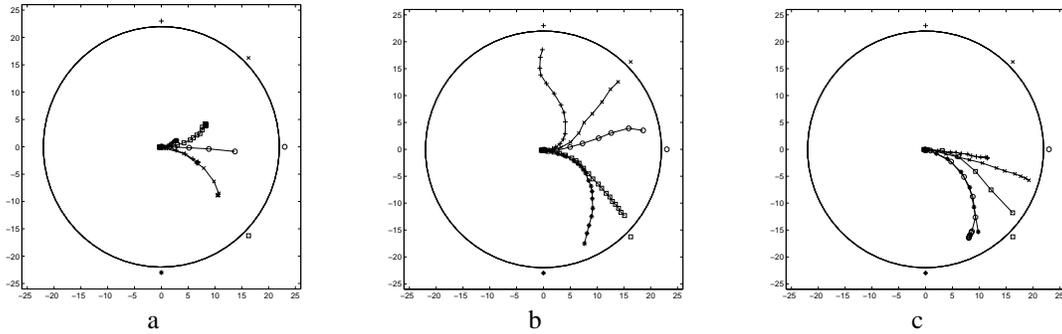


Figure 11 – In these trials, the robot displays behavioral patterns that can be classified as: a) negative, b) positive, and c) mixed phototaxis.

Considering that the preparation had a predominant ipsilateral response- because the reversed response was predominantly a positive phototaxis- these changes are likely to reflect a depression of the synapses in the left reticular nucleus rather than a potentiation of the right neurons.

A final, third set of trajectories was recorded after a 5 minutes resting period (Figure 12d). Here, the lamprey's brain appears to have over compensated for the change in synaptic efficacy induced by the prolonged stimulation at rest. Comparing the trajectories in Figure 12c to those in Figure 12d, it appears that in the last stage of the experiment the trajectories have a large counter clockwise shift. Although these are preliminary results, it is possible to speculate that this rotation reflects not only the end of the short-term change seen after the prolonged stimulation, but also the onset of a trend toward the adaptive compensation of the initial response to the change in sensor balance. Such a long-term compensation could be accounted for by an unsupervised Hebbian regulation of synaptic plasticity elicited during the trials in which the robot moved in response to the light stimulus.

Discussion

The work described in this paper is a first step toward the realization of a hybrid neuro-robotic system for the investigation of the neurobiological basis of sensorimotor learning and behavior. We have created a system in which a portion of neural tissue from the lamprey's reticular formation is connected through a computer interface with a small mobile robot. The optical sensors on the robot determine the parameters of the electrical stimuli delivered to the vestibular axons of the lamprey. The signals recorded from the neural populations with which these axons form synapses are used as control signals for the robot's movement. The idea of using neural signals for driving mechanical apparatus is certainly not new. Research in prosthetic devices has long been pursuing the use of myoelectrical signals for controlling artificial replicas of the limbs (Abul-Haj and Hogan 1990). More recently, Chapin and coworkers (1999) have developed an experimental paradigm in which the signals recorded from a population of neurons in the motor cortex of the rat were used to drive a mechanical lever which controlled the the release of a food reward. The study of Chapin and

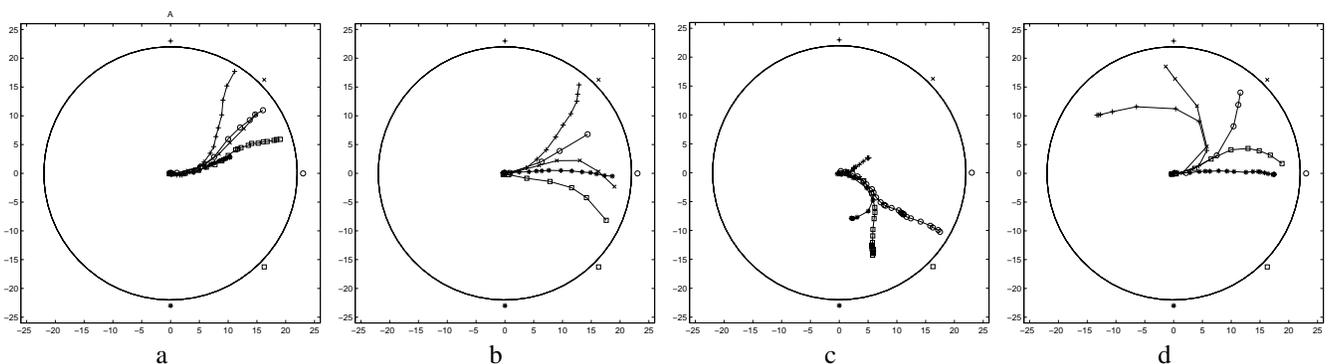


Figure 12 - Sensor sensitivity was unilaterally doubled. Trajectories were recorded a) before any changes in sensitivity were made, b) immediately following this change, c) after five minutes of steady stimulation, and d) after a five minute resting period.

coworkers has provided us with new evidence that motor cortical activity may be dissociated from the activity of limb muscles. The same cortical activity observed when the reward was obtained by a movement of the paw could also be maintained when the same reward was obtained by a movement of the mechanism and with the paw at rest. A distinctive feature of our hybrid system is that it exploits a closed-loop relation between the neural tissue and robot, which operates as an artificial body. In this closed-loop arrangement, the movements determined by activities in the reticular neurons cause changes in the robot's exposure to the light generated by a fixed source. These changes, in turn, cause a variation in the electrical stimulus that is responsible for the activities in the same reticular neurons. This paradigm is well suited for investigating the operation of Hebbian learning mechanisms (Edeline 1996; Pennartz 1997; Shors and Matzel 1997; Grzywacz and Burgi 1998) by which the strength of a given synapse is modified based on the correlation between pre and postsynaptic activities.

We have found that, with some exceptions, our neuro-robotic system generated stable behaviors over extended periods of time. The lamprey's brain can indeed be maintained alive in vitro for entire days. In these experiments- which lasted only a few hours- we have assessed stability by observing the repeatability of the trajectories triggered by light sources placed at different locations. We do not need to stress that the stability of the behaviors generated by our preparation is a necessary condition for proceeding with further analysis and, in particular, with investigations that assume that the neural connectivity remains invariant over the time scale of individual sensory-motor responses.

The second finding of our study is the observation of different type of phototaxis in different preparations. We observed light-seeking behaviors (positive phototaxis), light aversion behaviors (negative phototaxis) and linear combinations of light seeking and light aversion (mixed phototaxis). A simple linear model is sufficient to account for these different types of behavior on the basis of the amount of ipsilateral and contralateral connections between stimulating and recording electrodes.

We must acknowledge, at this point, that our work has been profoundly inspired by some ideas that Valentino Braitenberg expressed almost 20 years ago, at the beginning of the "connectionist revolution" (Braitenberg 1984). In his delightfully entertaining book, Braitenberg described how relatively simple connections between sensors and motors could endow some imaginary mechanical vehicles with life-like behaviors. These are behaviors that could easily be interpreted as intelligent or emotional responses to environmental stimuli. While the sensory-motor responses generated by our neuro-robotic system are not as remarkable as some of the behaviors described in that book, this system may be regarded as an implementation of Braitenberg's ideas and, in particular, of the idea of connecting the study of cellular brain structures with the observable responses that may be supported by these structures. As a parallel to Braitenberg's

"experiments in synthetic psychology", one could call the studies with the neuro-robotic system an experiment in synthetic neurobiology.

Finally, we have observed systematic adaptive responses induced by the selective alteration of the sensor signals on one side of the robot. In particular, we have observed a strong alteration of behavior followed by gradual return toward the initial responses. The possibility to generate adaptive changes in the robot's behavior opens the way to using the neuro-robotic interface for studying the transformations induced in the brain tissue by long and short-term modifications of synaptic properties. This system offers the possibility of substituting the actual brain tissue with a computational model of its neurons and its connections. The comparison of biological adaptive changes with their simulated counterparts may provide us with new means to directly investigate the computational properties of synaptic plasticity.

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