Computational Neuroethology

Hillel J. Chiel, Ph.D.
Departments of Biology, Neurosciences and Biomedical Engineering
Case Western Reserve University
304 DeGrace Hall
2080 Adelbert Road
Cleveland, OH 44106 - 7080
USA

Randall D. Beer, Ph.D.
Cognitive Science Program
Departments of Computer Science, Informatics (Complex Systems Group) and Center for the Integrative Study of Animal Behavior
840 Eigenmann
1910 E. 10th St.
Indiana University
Bloomington, IN 47406

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Synopsis:

Computational neuroethology is the use of modeling and simulation to study adaptive behavior. The conceptual framework of computational neuroethology emphasizes that nervous systems are embodied, that is, sensory pre-processing, biomechanical properties, and the integration of sensing and action during active perception are all critical for behavior. Furthermore, animals are situated in an environment. As a result, adaptive behavior emerges from the coupling of brain, body, and environment. Computational neuroethology has clarified animal behavior, created artificial agents (simulated and robotic) capable of flexible autonomous behavior, and developed new insights into the nature of cognition and intelligence.
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Hillel J. Chiel and Randall D. Beer

1. Definitions

Ethology is the study of behavior that allows animals to survive and reproduce in natural environments (i.e., adaptive behavior). Neuroethology is the study of the neural basis of adaptive behavior. Computational Neuroethology is the use of modeling and simulation to study the neural control of adaptive behavior. In contrast, the broad area of Computational Neuroscience generally focuses on modeling microscopic properties of neurons (e.g., channel biophysics, dendritic spines), single neurons (e.g., multiple conductance models of complex neurons and their morphology), neural circuits, and the dynamics of neural circuitry, without reference to biomechanics or environmental phenomena.

2. History

In 1990, both Randall D. Beer and Dave Cliff independently called for the creation of a new field, Computational Neuroethology. Beer succinctly summarized the rationale for the new field: "The working assumptions of computational neuroethology can be summarized as follows: (1) the ability to flexibly cope with the real world is a defining characteristic of intelligent behavior, and more fundamental than conscious deliberation; (2) adaptive behavior derives from a structural congruency between the dynamics of an intelligent agent's internal mechanisms and the dynamics of its external environment; (3) modeling the neural control of behavior in simpler whole animals will provide insights into the nature of the dynamics required for adaptive behavior, and eventually lead to an understanding of the successive elaborations of these mechanisms which are observed in higher animals."

Recently, Cliff has published a review of this area that provides an excellent overview and a summary of key examples of Computational Neuroethology, with an emphasis on research that has focused on artificial agents.

3. Conceptual Framework

The conceptual framework of Computational Neuroethology draws on classical ethology, ecological psychology, biomechanics, and dynamical systems theory. The first key concept of the framework is that behavior is embodied, i.e., it is not purely due to neural commands, but emerges from the ongoing interaction of the central nervous system with a complex sensory and mechanical system. For example, in response to motion in the periphery of its visual system, a monkey will move both its eyes and head, thus using its motor system to reposition its sensory structures. As another example, the optimal angle for throwing a soccer ball from over the head is determined not simply by Newtonian mechanics, but by the mechanical advantage that human arms can generate. More generally, embodiment implies that the central nervous system does not "stand above" the sensory and motor system in the process of responding to the environment; rather, pre-processing by sensory structures, active perception (movement of sensory structures as part of the perceptual process), and the filtering of motor commands by muscles and body structures are crucial for generating adaptive behavior.
The second key concept of the framework is that behavior is situated within a particular environment. For example, changes in optic flow as a fly approaches a surface allow the fly to trigger a rapid landing response. Recently, investigators used optic flow to control a flying robot. Another example of the situated nature of behavior is provided by studies showing that animals change leg stiffness during running to match the elasticity of the surface. In humans, activation of muscles changes depending on whether pointing movements occur with or against gravity. More generally, the situated nature of behavior implies that it is not solely due to the actions of the agent, but emerges from the ongoing interactions of the agent with its environment.

Thus, the third key concept of the framework is that adaptive behavior emerges from the coupling of the nervous system, body, and environment. For example, in a virtual reality environment, it is possible to predict human behavior in response to goals and to obstacles by modeling goals as attractors and obstacles as repellors with a relatively simple damped mass spring model for the heading error relative to each object. Sophisticated routes that avoided obstacles and reached goals emerged from this analysis without explicit path planning. As another example, the behavior of a hexapod robot with insect-like reflexes emerged from its ongoing interaction with soft, irregular surfaces.

The centrality of coupled dynamics for adaptive behavior is not surprising. Evolution cannot select for brains or bodies in isolation. Rather, the likelihood that an animal will survive, or leave more offspring than other competitors, depends on that animal's ability to coordinate its nervous system and body effectively within a particular environment. Thus, evolution selects an overall coupling of the dynamics of the components that effectively generates adaptive behavior.

Finally, an implication of the three concepts is that understanding adaptive behavior requires the analysis of the dynamical properties of the coupled system. Within each component - the nervous system, the body, and the environment - are complex processes that unfold over time according to rules, and thus each component is a dynamical system. Since each of the systems are coupled to one another, they are non-autonomous, but the entire coupled system may be viewed as an autonomous dynamical system.

The conceptual framework has several important implications. First, it suggests that stable behavioral patterns can be viewed as attractors within the dynamical system defined by the entire coupled system. Second, given that environments change over time, the conceptual framework suggests that understanding the transient structure of the coupled system may be as important as understanding its possible steady state behaviors. Third, any slow dynamical process that allows an organism to improve its interaction with its environment may be adaptive; thus, learning may not be a distinct process, but simply be these slower dynamical processes.

4. Goals and Methodology

Computational Neuroethology has been pursued with two distinct, albeit complementary, goals. From the perspective of a biologist, computational neuroethology is another approach to understanding the mechanisms of adaptive behavior in animals. Thus, the models and analyses are in the service of understanding general principles that may illuminate the adaptive behavior of a single animal, or a particular group of animals. The value of the results will depend on how well they explain behavior in animals, generate testable hypothesis, and suggest general principles for the function of similar organisms. More abstract models may be of great utility if they provide general principles that could apply to many organisms. For example, a theoretical approach for all forms of locomotion - constructal theory - has recently been described that provides very general principles for running, flying and swimming.
Investigators whose primary focus is in the area of computer science or engineering study Computational Neuroethology with different goals. For these investigators, Computational Neuroethology provides a new methodology for developing principles for intelligent behavior, as well as a means of designing adaptive artificial devices that have the flexibility of animals. From this perspective, the models and analyses are in the service of understanding adaptive behavior of any agent, whether it corresponds to a biological organism or not. As a consequence, the value of the results will be the insight they provide into a general understanding of adaptive behavior and intelligence, or their utility for artificial devices such as robots to function in complex, open-ended environments.

Distinguishing these two different goals is important. A robot that can avoid obstacles using an algorithm based on studies of the escape response in the cockroach may be of great utility, and thus a success from the point of view of engineering. From a scientific viewpoint, however, the success of the robot demonstrates that the proposed algorithm could actually work in the physical world, but does not prove that it does work that way in the biological system. Thus, an engineering success may not be the same as a scientific proof. Conversely, it is important for investigators interested in animals to be willing to develop models that may omit or greatly simplify biological details in the search for general principles. A highly detailed model of insect flight may be so computationally intensive and so complex that the general principles of operation, such as the importance of nonstationary aerodynamics or the relative importance of inertial and viscous forces, may be obscured.

These observations have led investigators to pursue Computational Neuroethology using a variety of models, ranging from highly abstract to highly realistic. Abstract agents provide the opportunity to confront the most general questions about the mechanisms of adaptive behavior. The study of "frictionless brains" can provide insights similar to the study of frictionless planes in physics. All features of the agent are known, unlike a biological organism. Careful choices of models of the environment, body, and the neural network controlling the agent can generate systems that are tractable to detailed mathematical analysis, providing deep insights into the underlying dynamics of adaptive behavior. For example, a study of evolved neural networks for locomotion elucidated the importance of the mechanics of the body for many features of the evolved pattern generators. However, it may be difficult to make quantitative predictions from abstract agents to any particular animal.

Realistic models provide the ability to directly connect model predictions with experimental results. Quantitative predictions can be made about the effects of specific perturbations. Realistic models have drawbacks, however. In addition to the large number of parameters that must be fit by experimental data, the "brittleness" of models in response to small errors in parameters, and the high computational cost associated with simulating realistic models, it is often difficult to understand or derive general principles from models if they rival the original biological system in complexity.

Thus, some of the most effective work in Computational Neuroethology has been done by the use of a bracketing methodology, in which both abstract and highly detailed models are studied, with the goal of developing models of intermediate complexity that retain some analytical tractability, but whose predictions can be tested experimentally. For example, studies of the mechanisms of insect locomotion have made use of simplified "template" models of running or climbing movements, which have then been compared to highly detailed "anchor" models based in the biology of particular animals (e.g., cockroach or gecko).

Investigators of Computational Neuroethology also debate the value of simulations
versus robotic models. On the one hand, simulations can be reconfigured rapidly. Combinations of different parameter values can be systematically explored, and if the model as a whole needs to be restructured, this can also be done relatively quickly. On the other hand, if an investigator wishes to ensure that the agent is interacting with the environment, a robot provides the actual physics of the world for free, and ensures that any algorithm that works well in simulation can also work well in the presence of fallible sensors, unreliable actuators, and a complex, changing environment. But robots can be expensive to build and difficult to quickly reconfigure, and if they fail to function properly, the investigator needs to ensure that the failure is relevant to the original hypothesis. For example, if a robot is built to examine a perceptual problem, but uses wheels rather than legs to negotiate its environment, the investigator needs to be sure that the question of interest (whether biological or theoretical) is unaffected by this change in the periphery. Once again, combined studies of simulations and robotics are likely to be more effective than a sole reliance on one or the other.

5. Examples

In this section, we provide an overview of some recent work in Computational Neuroethology. Our review is not exhaustive. Rather, the examples illustrate some of the key aspects of the conceptual framework, as well as the models that have been generated, from highly abstract to highly specific; the animals and behaviors that have been studied, ranging from invertebrates to humans; and the fruitful interplay of simulation and robotics.

Embodiment: Biomechanics and neural control

A combined mechanical and neural model of walking in the cat revealed that the mechanics of the body played a crucial role in stabilizing or destabilizing gait, depending on the coordination rule used. To study the role of sensory reflexes in locomotion, investigators created a realistic model of the mechanics of the hindlimbs of the cat, and a simplified finite state model of the neural control that was driven by sensory inputs from the model body. One mechanism for triggering the transition of a leg from supporting weight on the ground (the stance phase) to moving forward before initiating the next step on the ground (the swing phase) is the removal of load from the limb as other limbs begin supporting the body's weight. The force in the ankle extensor muscle monitors the unloading of the limb. If this rule was used alone to drive walking gaits, the resulting movements were stable even in response to perturbation. The reason was that if the other limbs were not yet taking up load, the limb that was about to switch from stance to swing was delayed by this mechanical input, and this stabilized the gait. In contrast, if the extension of the hip was used alone as the signal to terminate stance, the resulting gaits were unstable, because the mechanical system tended to increase the hip extension independently of whether the body could afford to lift that limb. This model provided strong evidence for mechanical coupling through the body as a stabilizing mechanism for locomotion. Further support for this view is provided by the recent work of investigators who have used a dynamic periphery and a simple neural network to create a fast bipedal walking robot (RunBot) that takes advantage of peripheral biomechanics to stabilize its gait, and can improve its walking with experience.

A neuromechanical model of feeding in the marine mollusk *Aplysia californica* made it possible to predict the roles of mechanical reconfiguration during feeding. Investigators created a kinetic model of the feeding apparatus, and showed that the change in shape of the central grasper from spherical to ellipsoidal changed the forces exerted by a separate muscle, a
protractor muscle that wraps around the grasper and was stretched by the grasper's change in shape. As a consequence, the protractor muscle became stronger, both because of its position on its length/tension curve, and its enhanced mechanical advantage, allowing it to generate stronger protractions. Subsequently, in vitro and in vivo studies showed that the model predictions were correct. These results have been used to define the concept of neuromechanical modulation: the ability of one set of motor neurons to affect the actions of a different set of motor neurons through the changes in the mechanics of the periphery.

These results emphasize the importance of understanding motor neuronal activity within the context of biomechanics. More generally, it is clear that motor behavior is best understood within an embodied context.

Situatedness: Coupling among the environment, the periphery, and the nervous system

A striking illustration of the importance of the coupling among the environment, the body, and the nervous system was provided by a simulation of lamprey swimming. The neuromechanical model performed well without sensory feedback in water flowing at a constant velocity. In contrast, in the absence of sensory feedback, when the model encountered a barrier consisting of water flowing at a higher velocity, the model lamprey failed to swim across the barrier. When the model lamprey was provided with appropriate sensory feedback, but no other changes were made to the neural circuit, the model could swim effectively through the barrier. The faster flowing current induced rapid sensory inputs that induced a faster oscillation of the body, which in turn allowed it to move through the faster water. Thus, a new and effective behavioral pattern emerged from the interaction of all of the components.

Another example of the coupling of the environment and the body to generate adaptive behavior is provided by the studies on insect flight. A robotic fly that operated in mineral oil, whose wing dimensions and viscous interactions with the fluid surrounding it were scaled to have similar Reynolds number to those of the fruit fly, was used to demonstrate that delayed stall due to translational motion of the wings was insufficient to account for the ability of Drosophila to fly. Rotation of the wings during stroke reversals was also critical, allowing the insect to take advantage of rotational circulation and wake capture. These additional forces not only enhanced lift, but also provided the insect with the ability to change direction and steer. Recent studies have focused on the steering mechanisms underlying rapid right-angle turns (body saccades) in fruit flies, using three dimensional high speed infrared video to capture the actual motions of the wings and body of the flies, and the dynamically scaled robot to examine the underlying forces responsible for the turns. Surprisingly, they found that inertial forces dominated turning behavior, which were due to subtle tilts of the stroke plane angle and small changes in stroke amplitude.

These results emphasize the importance of understanding behavior through detailed studies of the interactions of biomechanics and environmental forces, which in turn may both simplify and limit what the nervous system can do at every instant.

Active Perception

Perception within the context of ongoing behavior, or active perception, has been one of the most heavily investigated areas of Computational Neuroethology. Physical constraints on active sensing systems as well as the need for appropriate sensorimotor coordination determine whether systems can simply react to events or can anticipate them. Combining models of electrosensory and mechanosensory stimuli with prey strike trajectories performed by electric
fish (recorded using infrared video), investigators demonstrated the relative contributions of different frequency components of the electric sense and mechanosensory inputs on prey capture. Recently, investigators have developed a simple robot capable of underwater localization of targets using electrolocation.

A variety of other active perceptual processes have been studied. Cricket phonotaxis, the ability of a female cricket to locate a male cricket by its calling song, has been studied using a series of increasingly complex and realistic robot and neural network models. Investigators recently demonstrated that a model neural circuit driving a legged robot could successfully detect and locomote to sound sources outdoors. Using a slightly modified model of human navigation, investigators have controlled a differential drive robot, and showed that it negotiated obstacles more smoothly than previous methods. A robotic whisker array demonstrated that moments induced by whisker contact with objects or flows could be used for accurate reconstruction of the inputs.

These results demonstrate that when sensing is both embodied and focused on environmentally relevant features, complex perceptual feats can be efficiently accomplished.

Cognition and Intelligence

Computational Neuroethology provides a novel approach for creating intelligent behavior. Rather than relying primarily on an abstract analyzer and manipulator of symbolic representations of the world, it emphasizes that highly complex and adaptive behavior, including behavior that is cognitive, emerges from the interaction of brain, body, and environment. For example, investigators have created a series of models of specific behavioral competencies- frog prey capture, rat spatial navigation, monkey saccades and grasping, and human language - which are inspired by known anatomy and neurophysiology. Investigators have argued that the successive elaboration of functional schemas provide insights into prey capture, predator avoidance, negotiating obstacles, recognizing and categorizing one's location in egocentric space relative to external space, the ability to imitate motor actions, and ultimately to recognize, imitate and generate "combinatorially open" abstract motor sequences that can become the basis for language.

A complementary approach is creating agents that have "minimally cognitive" capabilities, such as the ability to categorize objects, to focus attention, to manipulate objects, or to signal to other agents. By making the agents as simple as possible, but capable of an arguably cognitive behavior, it is possible to analyze in detail the mechanisms underlying their behavior. Investigators have pursued this line of inquiry using genetic algorithms as a means of searching for agents that produce cognitive behaviors (e.g., categorical perception, selective attention, associative learning) so that the neural circuits are not hand designed, which could introduce a priori biases into their function, and then analyzing how they work. Recent work analyzed an agent evolved to perform categorical perception: the agent could catch circular objects, and would avoid diamond-shaped objects. The agent's behavior could be explained in terms of the dynamics of its interaction with the environment, and the dynamics of its nervous system, but no "representations" of either circles or diamonds were found. These results suggest that a dynamical systems approach to embodied and situated agents may well provide insights into the nature of cognition and intelligence in biological organisms, and in artificial devices, without recourse to abstract symbol manipulation.

6. Summary and Conclusions
Although the field of Computational Neuroscience is still relatively young, it has become increasingly important for understanding adaptive behavior. As computers become faster and cheaper, it is more feasible to create sophisticated models that incorporate features of the environment, of biomechanics, and of neural control. Successful analyses of complex adaptive behavior using computer simulation and robotics have encouraged investigators to adopt the methodology of Computational Neuroethology. At the same time, simulated organisms and robots capable of solving challenging real-world problems have emerged from this research, suggesting that it is a fruitful approach for generating artificial devices that have the flexibility of biological organisms.

What is most exciting about recent work in Computational Neuroethology is the growing empirical support for the larger conceptual framework, and the progress in clarifying general principles for adaptive behavior. Thus, it is clear that many aspects of motor behavior can only be understood by examining neural activity within its appropriate biomechanical and environmental context. Similarly, the process of perception involves active and ongoing engagement of the organism with its environment, so that perception must be studied within both a biomechanical and an environmental context. Finally, cognition and intelligence must be understood within a behavioral context, and emerge from an embodied and situated agent, not a disembodied pure reasoner.
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Figure 1

Environment

Body

Nervous System