Physiology and Neural Control of Movement in Aquatic Animals: Introduction and Roadmap

Ferdinando A. Mussa-Ivaldi
Departments of Physiology and Biomedical Engineering, Northwestern University
sandro@northwestern.edu

It is relatively common to hear, among engineers, the argument that imitating biology is not necessarily the best way to build machines. Cars do not have legs and airplanes do not flap their wings. And indeed, the combination of two "un-biological" designs, fixed wings and wheels are both essential to modern aircrafts. This somewhat "conservative" engineering consideration should not be simplistically dismissed. If one focuses on the goal of high speed, fixed wings, turbines, wheels and propellers can hardly be matched by biological systems. But the perspective changes in a radical way when one looks at other performance criteria such as, agile maneuvering at low speed, adaptability, robustness in the face of unexpected perturbations and of system errors. On these criteria, animals are still outperforming the most advanced machines. And so are their brains. There too it appears that the commuting speed of current day's electronics is orders of magnitude superior to the speed of nerve cells, whose units of transmission, the action potentials, take the order of 10^{-3} seconds. But this is only an apparent superiority, as the speed with which we recognize a familiar face and coordinate a multitude of muscles is still superior to the rate at which similar operation are accomplished (if at all) by today's computer systems.

This set of five articles provides a picture of current knowledge about how the nervous system of vertebrates maintains its superiority over machines in generating and controlling a variety of sensory-motor behaviors. In particular, the reviews aim at giving guidance in the design of control systems for autonomous underwater vehicles, inspired by the structures and functions of biological controllers. Fin-based propulsion systems perform well for both efficient cruising and high maneuverability in fish, making them good models for a new generation of artificial propulsors. Station-holding and maneuverability in surging aquatic environments can be achieved by oscillation of the paired pectoral fins. AUV designs that incorporate fin shape variability and mimic fin stroke kinematics of fishes carefully may achieve more efficient thrust and greater maneuverability.

Understanding the nervous system that controls the fins and the other body motions is quite different than understanding a computer. A computer's architecture and performance are typically described independently of the particular task or hardware the computer will have to deal with. In contrast, it is virtually impossible to separate neural information processing from the specific design and control problems that the brain and spinal cord must solve. Nerve cells, muscles and sensing organs have evolved in close connection with each other and they keep developing in this way after birth, through a continuous process of learning and adaptation.

The first three sections of the review focus on the interaction between biological design, peripheral organization of neuromuscular patterns and control issues related to navigation tasks. The neural and muscular control of fin-based thrusters is of critical importance to applied research in the bioengineering of fins.

Colgate and Lynch (Section A) review the mechanics of swimming and identify the main control issues that must be addressed when dealing with tasks such as rapid maneuvering, trajectory planning and station keeping. This review highlights the close coupling between control problems and mechanical design. In particular, the paper expands upon the theme of controllability in inherently underactuated systems. Kinematic redundancy and underactuation are commonly encountered in animals, such as fishes, and in a variety of tasks, including underwater maneuvers. This review provides the basic control system scenario that the nervous system of aquatic animals, as well as the controller of AUVs, must deal with to generate purposeful behaviors.

Westneat and coworkers (Section B) focus on current knowledge of pectoral fin structure, function, muscular control, neural circuitry, and feedback control from the biological literature. The review is centered on three main topics: 1) the anatomical structure of pectoral fins; 2) the kinematics of rowing and flapping and 3) the innervation and distributed pattern of commands that can be detected by electromyography (EMG) and functional neural imaging in swimming fishes. The paper highlights the existence of a continuum of fin motions included between rowing and flapping. The neural control of these motions is still largely unknown. However, studies of muscle activations have identified stereotyped rhythmic patterns across the muscles that actuate the pectoral fins. A distinctive feature of these patterns is the temporal synchrony between the onset of activity in each muscle and the motion that the muscle is responsible for. This is in contrast to other motor systems, where motion takes place after substantial delay following the onset of EMG activity. Functional neural imaging and experimental approaches to neural circuit function show that elements such as inhibitory interneurons are common to most locomotion systems and are likely to play a key role in the generation of alternating fin movements.

The complementarity between mechanical design and control is also the central theme of MacIver's review of neuromechanical design issues and active sensory systems in animals, focusing on the weakly electric fish (Section C). A key goal of the controller for the weakly electric fish is to identify the location of a prey and to carry out a capture maneuver. The position of the prey is identified by a sophisticated readout of voltage perturbations to a self-generated electric field. The prey-catching maneuver is carried out by a fast a stereotyped motion. MacIver discusses the possibility that this motion is generated by a controller that minimizes cost functions, such as the integrated command intensity or movement time, while dealing with the anisotropic properties of body's inertia. The analysis of this apparently simple behavior highlights the connection between sensory and motor system across a variety of temporal scales, from evolution to the period of milliseconds in which each action is programmed and controlled.

The last two sections provide a panoramic view of the Neurobiology of vertebrate motor control by the spinal cord and higher brain centers.

Mussa-Ivaldi and Solla (Section D) focus on the concept of motor primitive, which has emerged as a mechanism for organizing complex computation in biological control systems. The main concept of emerging computational approaches to complex dynamics is to construct and combine “vocabularies” of patterns (for example in dealing with turbulence), as an alternative to the explicit solution of differential equations underlying complex chaotic behaviors. In the same spirit, motor primitives are elementary units of control generated by the interaction of neural signals and mechanical muscle properties. The paper reviews experimental and theoretical studies showing that the linear combination of relatively few primitives leads to the solution of complex inverse dynamics problems involved in the control of movements. The vast literature on central pattern generators as a basis for controlling rhythmic motions in swimming is reviewed in the same perspective.

Finally, Llinas and coworkers (Section E) extend the notion and the role of rhythmic activities and their modulation to higher brain centers and propose that advanced computational devices for motor control be built in analogy with the interaction between the cerebellum and the neurons of the inferior olive. In particular, the authors highlight the role of electrotonic coupling between olivary neurons, in generating and modulating synchronized rhythmic activities. The paper reviews evidence suggesting the dynamic formation of clusters of synchronized activity in the olivo-cerebellar network. These clusters form the basis for modular organization in higher brain centers that are involved in sensory-motor processing. Of particular interest, are the mechanisms by which the extent of a cluster is modulated by cerebellar input, thus providing the means for modulating and adapting the operation of rhythmic modules in the brain.

Taken together, these reviews provide a bird's-eye view of the neurobiology that is relevant to the control of underwater maneuvers. But perhaps, what is most important is that the reviews also point at gaps in basic science that need to be filled for becoming able to emulate the skills that are present in nature. Of particular value to the development of biomimetic AUVs is the technological transfer from basic biological sciences to control and design principles. Studies of vertebrate motor control have emphasized the role of stability in elementary patterns of control that are combined by the central nervous system to generate complex behaviors. Similar concepts are likely to apply, perhaps even more stringently, to aquatic behaviors such as rapid maneuvering and station holding.

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