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Review

Toward biomorphic robotics: A review on swimming central pattern generators

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ABSTRACT

Neuro- and biomorphic approaches in the design of intelligent robotic systems and, more specifically, various technical applications have attracted much attention from researchers and engineers. Biomorphic robotics implies that a machine should be able to reproduce movement and control it the same way animals do in a real-world environment. Fish-like swimming robots seem to be the simplest candidates to reproduce biological mechanics of movement in aquatic medium adhering to the principles of its control and navigation. At the heart of the fish movement control system is its central pattern generator (CPG) located in the spinal cord. This CPG creates a robust rhythmic signal that activates muscles inducing movement in space, i.e. locomotion. The fish actuator system involves body muscles and fins and looks quite simple in comparison with land-walking animals. Hence, it has become the center of attention for many modeling and engineering studies that we review in this article. Many fish-like robots have been developed since rather simple CPG controllers can induce robot swimming. However, existing robotic solutions are still far from natural prototypes in terms of speed performance, power efficiency, and maneuverability. Something seems to be missing in understanding the actuator control principles and hence appropriate CPG design. A tuna fish's cruising speed of more than a hundred kilometers per hour, and acceleration of dozens of g in pike attacking its prey remain unreachable digits for existing robotic solutions. Along with the development of bionic muscle-like actuators, state-of-art research in this field focuses on finding possible ways of CPG integration with sensorial systems and higher-level brain controllers. Needless to say, a close study of biological fish swimming in terms of its biomechanics and control still raises fundamental questions about how fishes are capable of moving so efficiently. Inertial and dense aquatic medium requires CPG to be highly integrated with sensorial receptor systems. Fish swimming is finely optimized relative to energy loss into fluid turbulence. How this control is organized remains a question. We also review some concepts on how a higher-level of movement control can be incorporated into the intelligent CPG design.

1. Introduction

Aquatic and amphibious robots demand substantial engineering to be able to operate in water. Biologically motivated underwater vehicle design and control look especially promising for search and rescue applications in real-world environments [1]. Many features of robotic platforms developed to emulate swimming locomotion were inspired by biological swimmers, particularly by their locomotor system. Advanced technologies and the growing integration of biology and engineering are revealing new basic principles of agile, high-performance, and energy-efficient animal swimming. There are several key impressive peculiarities of fish swimming that are extremely difficult to achieve in man-made robots. One of them is the fish's ability to quickly and flexibly adapt locomotion to new dynamic environments. Another impressive feature is the energy efficiency of high-performance scombrid fishes like tuna. When escaping from predators or catching prey they can operate at high frequency and speed with low energy costs. Although there have been several underwater robots developed that could replicate fish locomotion, only recently have researchers proposed bio-inspired robotic designs capable of closely matching the performance of high-speed tuna-like swimmers [2]. Another remarkable ability of fish is the fast-acting continuous and robust coordination of multiple degrees of freedom using multiple redundant actuators (joints, muscles)

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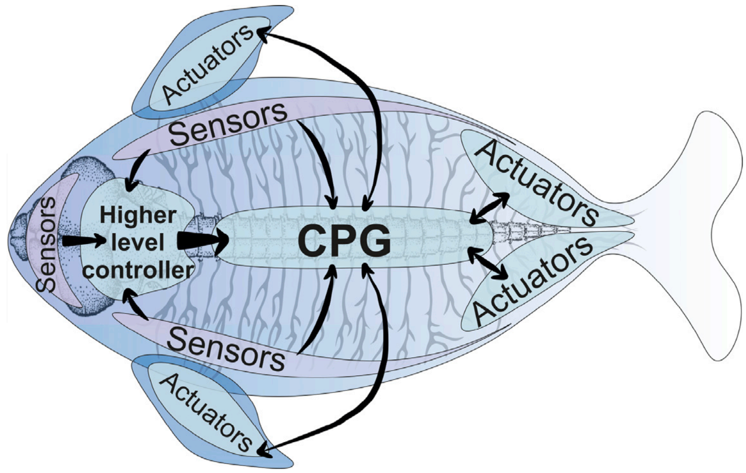

Fig. 1. The fish locomotor system is represented by the spinal CPGs producing the basic rhythmic patterns, and the higher-level centers (the motor cortex, cerebellum, and basal ganglia) regulating these patterns according to real-world environmental conditions. The peripheral nervous system (e.g. sensory neurons) provides sensory feedback and modulates the CPGs pattern generation. Muscle activations are controlled by CPGs signals.

carried out by the biological locomotor control system. Nonetheless, the mechanisms underlying these features of biological locomotion are still poorly understood.

Fish movements are determined by a complex interaction of three body systems: the central nervous system (the brain and the spinal cord), the peripheral nervous system (nerves projecting to muscles and sensory neurons), and the musculoskeletal system. A schematic representation of the fish locomotion system is depicted in Fig. 1.

It is now generally accepted that the functional units in the central nervous system responsible for solving challenging tasks of generating agile locomotion patterns and processing multi-modal sensory information are *central pattern generators (CPGs)*. CPGs are neural circuits capable of generating coordinated rhythmic activity without sensory feedback and descending drive, which were found both in invertebrates [3] and vertebrates, including mammals [4,5]. A general view is that CPGs provide the basic locomotion patterns by producing rhythm and coordination and that sensory feedback modulates these patterns to fit the environment. In vertebrates, CPGs are located mostly in the spinal cord. These generators receive stimulation from the higher-level centers (brainstem and other areas of the brain such as the motor cortex, cerebellum, and basal ganglia) which are responsible for modulating CPGs patterns to match the environment. [6]. The exact topology and functionality leading to the ability of these neural networks to produce rhythmic patterns have yet to be fully clarified. The development of CPG-based robot locomotion control is not only interesting for understanding animal locomotion systems, but also for robotics because this kind of biologically relevant controller can provide agile, robust, and energy-efficient control while maneuvering in complex environments [7,8]. Therefore, CPGs models for robot locomotion control have been extensively analyzed and validated.

Depending on the research subject, the mathematical models of CPGs have been designed at different levels of abstraction [9]. The first category lacks biological plausibility and models CPGs as systems of coupled nonlinear oscillators. In this case, one oscillator simulates the activity of a whole oscillatory neural center at an abstract level. The aim of these models is to investigate how connectivity between oscillators and differences in intrinsic frequencies influence the collective dynamics and help achieve synchronization (rhythmic pattern generation) in the oscillatory center population. Due to simple dynamics, this phenomenological approach makes it possible to study the system analytically. The second category of CPGs models uses spiking neural networks. They can be constructed based on the simplified models of neuronal membrane potential dynamics such as integrate-and-fire neurons or detailed biophysical models such as Hodgkin–Huxley type of neuron models. The purpose of these models is to investigate the mechanisms of rhythmogenesis and the influence of the network properties on oscillatory activity. The advantage of this approach, apart from biological relevance which makes its contribution to neuroscience very significant, is that SNN-based CPGs can be implemented on neuromorphic hardware leading to more power efficiency. Recently, more and more CPG models have been integrated with a biomechanical simulation of a body. Such neuromechanical models focus on the CPG modulation by the sensory feedback via interaction with the environment [10].

This review paper focuses on the CPG-based control of robotic swimming locomotion. A search was conducted using the IEEE Xplore and Scopus databases in order to identify papers that include terms: "fish locomotion", "central pattern generator", "swimming robotics", "control system", "spiking neural network" etc. We analyze recent studies (since 2015) dedicated to the design and analysis of the model of CPGs and apply it to swimming robots. The paper is structured as follows. We will start with the review of the CPG models for swimming locomotion of the lamprey, a primitive eel-like fish (Section 2). Lampreys use an anguilliform swimming gait in which a traveling wave of body undulation is propagated from head to tail. Due to its relative simplicity, the lamprey is the most modeled fish which has been extensively modeled as a robot. One of the most exciting features of undulatory swimmers such as eel or lamprey is the high robustness of swimming locomotion pattern generation. In contrast to the over vertebrates, a major disruption of the lamprey's CPG does not lead to the failure of the locomotor behaviors [11,12]. The CPG-based control of other types of swimming has been studied to a lesser extent. We will focus on them in Section 3. We will review the CPGs models of high-performance swimmers such as tuna and related scombrid fishes, which utilize carangiform swimming gaits (which use mainly the tail for propulsion). These fishes often operate at high frequencies and speed while maintaining reasonable energetic costs. In Section 4, we will review the model of the salamander CPGs. The salamander uses an anguilliform gait for swimming like lamprey and standing waves of body undulations for walking. The salamander, an amphibian capable of swimming and walking, offers an interesting link between research on the lamprey and research on tetrapods. The proposed CPG-based models of the salamander locomotion circuit helped explain the experimentally observed effect of the automatic switch from low-frequency walking to high-frequency swimming by modulating the electrical stimulation of a particular region in the brainstem of the salamander. Finally, Section 6 will discuss a list of open questions in the related field.

The review is not meant to be exhaustive, and interesting related reviews exist on the modeling of animal locomotor systems [9,13,14]. However, our review focuses on the CPGs with the simplest types of locomotion (in the aquatic environment, not on land), which are currently becoming increasingly popular, being used in neurocontrol tasks based on realistic biological circuits. Due to this, robotic applications are currently evolving at an accelerated pace.

2. Lamprey

Lampreys are one of the most primitive fish. Lampreys use an anguilliform swimming gait that implies a traveling wave of body undulation propagating from head to tail (Fig. 2A-C). Eels and terrestrial snakes also use anguilliform swimming. Lamprey's locomotion has been extensively studied due to the simplicity of their spinal cord, movement repertoire, and body structure. Lamprey's spinal cords consist of about 100 segments, each of which contains an oscillatory neural network of approximately 1200 connected neurons (Fig. 2D-E). It was shown that electrical or chemical stimulation of the lamprey's spinal cord isolated from its body (and even several segments of the spinal cord) can trigger rhythmic patterns called fictive locomotion, which are the same as intact locomotion [15]. The basic organization of synaptic connections between lamprey spinal cord neurons has been studied in detail [16–18]. Most researchers distinguish four main types of neurons involved in rhythm generation: excitatory interneurons (EIN), lateral and contralateral inhibitory neurons (LIN and CIN, respectively), and motor neurons (MN) [19–23]. EINs interact with EINs from neighboring segments. EINs project excitatory connections to all other neurons (LIN, CIN, and MN) located on the same side of the spinal cord segment. CINs provide inhibition signals to the neurons on the contralateral side, while LINs are coupled inhibitory with CINs from the same segment side. The motor neurons MN transmit output signals directly to the muscles. In each of the spinal cord segments, alternating peak activity on the left and right sides has a frequency in the range from 0.1 Hz to 8–10 Hz. Each side of a segment can generate a burst of activity independent of the other side. Due to such dynamics, lamprey movements in water are very energy-efficient and simple.

The rhythmic patterns produced by CPGs can be modulated by the simple descending control signals from the high-level center of the central nervous system. For instance, electrical stimulations of the mesencephalic locomotor region (MLR), which is located at the junction between the midbrain and hindbrain and is the locomotor center of the brain [24], induce well-coordinated and controlled swimming. The frequency of movements linearly depends on the stimulation intensity [25]. Reticulospinal neurons represent the MLR critical relay for the initiation and control of locomotion. They are the connection of MLR with spinal neurons [26,27].

Because of its relative simplicity, lamprey locomotion has been studied in some detail [9,28]. At the moment, many mathematical models implement lamprey CPG with different biological plausibility, and work in this direction continues. When developing lamprey CPG models, most recent studies have focused on the applicability of the resulting models to robots. Therefore, the most common CPG models consist either of pairs of phase oscillators or small neuron populations, where each population of connected neurons acts as a phase generator. The LIF neuron model is the most commonly used in lamprey CPG modeling as it is the most computationally efficient of the spiking neuron models. Computational efficiency is a necessary condition for the use of such systems in robotics and the implementation of robot locomotion in real-time.

Next, we will review the latest work on the lamprey CPG modeling.

The main goal of the work [20] was to study the possibility of implementing a lamprey CPG model on electronic circuits that mimic the properties of real neurons and have realistic synapse dynamics. The authors of the work successfully implemented a CPG network using neuromorphic electronic circuits consisting of low-power analog silicon neurons that can be directly connected to the executive mechanisms of a robotic lamprey. The neurons and synapses on the chip were implemented as analog subthreshold current circuits capable of reproducing a wide range of biologically relevant dynamics. In the work [20], the elementary unit of the CPG was the LIF neuron. The CPG consisted of 256 neurons connected in a network of 128,000 plastic synaptic connections of two types: excitatory and inhibitory.

The study [29] is devoted to the role of cyclic modulation of reticulospinal neurons. The authors showed that the inclusion of phase modulation of the reticulospinal neurons of the CPG contributes to solving the problem of synchronization between the presentation of the control command and the lamprey movement phase. The control command signal will be directed to the reticulospinal level, so it will automatically promote reticulospinal activity in the corresponding phase. To confirm their hypothesis, the authors implemented a detailed large-scale computational model of MLR and CPG. The model used 19 600 neurons (4000 in the MLR and 15 600 in the CPG) and 646 800 synaptic connections. Simultaneous stimulation of both left (TL) and right (TR) tectal neurons in the MLR region causes forward swimming. Stimulation of either TL or TR causes a turn. The CPG consisted of 100 identical and symmetrical segments on the left and right sides. Each segment consisted of 40 motor neurons, 60 excitatory and 40 inhibitory interneurons, and 16 reticulospinal neurons. A specialized biologically plausible lamprey CPG neuron model was used as a neuron model [30]. Each neuron contained 16 compartments: the soma, the initial axon segment, and 2 primary, 4 secondary, and 8 tertiary dendrites. All network simulations were performed on a CRAY XE6 parallel supercomputer. To ensure that the simulated neural network could control body movement, the authors applied their CPG model to a mechanical model of lamprey swimming. According to the results obtained, tectal neurons should have minimal frequency adaptive properties, in contrast to reticulospinal neurons.

The key feature of the work [31] is that it involves detection of the location and size of objects, preprocessing of the received information using a neural network, and transmission of the locomotion commands to the CPG model. The CPG model used in this work was based on the model proposed in [32]. Each element of the CPG is modeled as a pair of neural networks. The two networks are connected through long-range ipsilateral excitatory projections and contralateral inhibitory projections. Network connection of elements is carried out according to the work [33]. In total, this CPG model uses 1600 integration and activation neurons with adaptation to the spike frequency. Ten pairs of spiking-free special units integrate local interneuronal activity and provide filtered motor activity. The muscular-mechanical model of the lamprey is built in accordance with the simulation results obtained in the earlier work of the authors [22].

Angelidis and colleagues in their work [34] presented the lamprey CPG, in which each segment consists of a population of LIF neurons. The dynamics of each segment corresponds to the dynamics of an abstract Hopf-type oscillator. To implement the CPG model, the authors used the "Nengo" platform [35], which has built-in methods for neural network architecture generation to approximate differential equations (in this case, the Hopf-type oscillator dynamics equations). Communication between neighboring CPGs segments is executed by the intermediate neuronal populations. Using the neural engineering framework, the Hopf oscillator was implemented as a single-layer neural network with a feed-forward connectivity topology. The connections weights within the network were calculated by fitting output and input signals.

The authors analyzed the resulting swimming gaits under various simulation scenarios. In the scenario of unperturbed swimming, the authors investigated how the change in the number of neurons in CPGs segments and the presence of the CPG modulation by higher-level centers influences the swimming gait. The effect of the high-level modulation was also studied under the scenario with a water speed barrier. To do this, the authors applied the developed CPG model to control

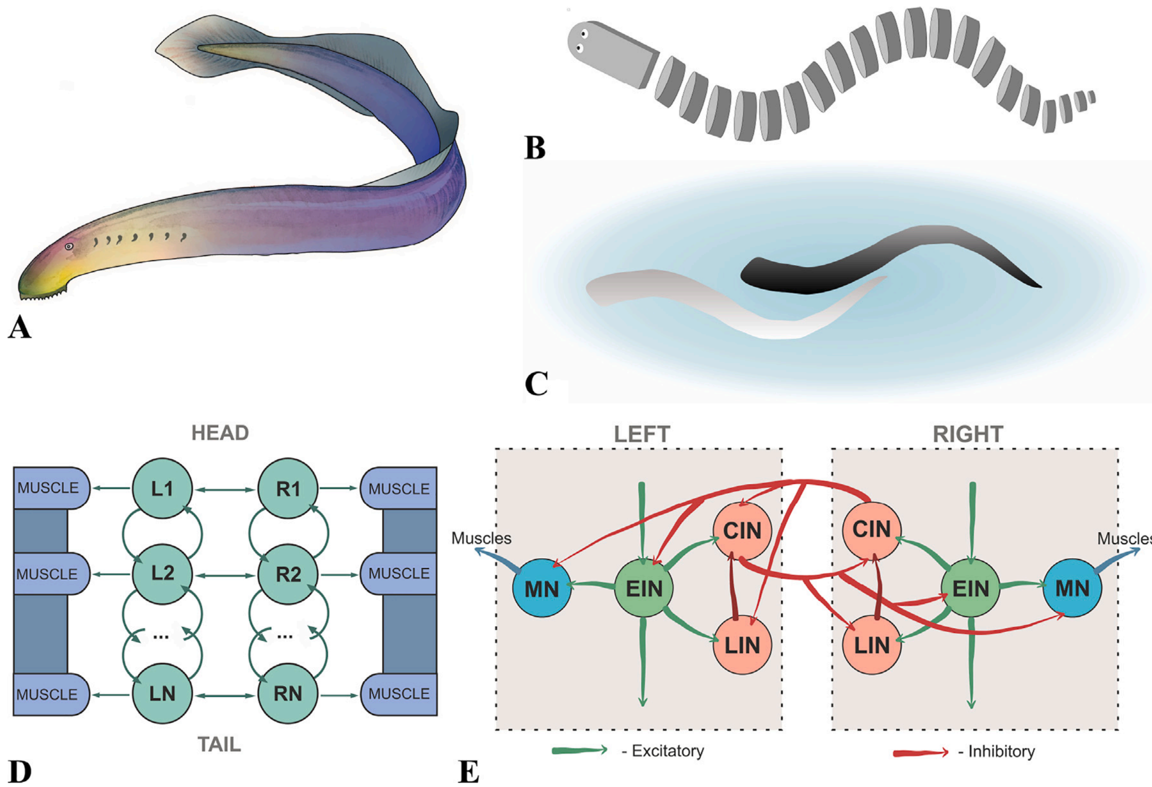

Fig. 2. A – Lamprey; B - Lamprey robot; C - Lamprey locomotion; D - Common scheme of the lamprey CPG model. The CPG is a double chain of connected 2N oscillators. Each oscillator is connected to neighboring oscillators on the same lateral ("L" = left or "R" = right) side. Within one segment, numbered from head to tail, the left and right oscillators are also coupled together; E - CPG segment. Each segment contains 2 symmetrical oscillatory neural networks consisting of approximately 600 connected neurons (excitatory interneurons (EIN), lateral and contralateral inhibitory neurons (LIN and CIN, respectively), and motor neurons (MN). EINs interact with EINs from neighboring segments. EINs project excitatory connections to all other neurons (LIN, CIN, and MN) located on the same side of the spinal cord segment. CINs provide inhibition signals to the neurons on the contralateral side, while LINs are coupled inhibitory with CINs from the same segment side. The motor neurons MN transmit output signals directly to the muscles.

the virtual lamprey robot within a physical simulation environment. 3D lamprey model consists of nine body parts, similar to the amphibot from [36]. These parts are interconnected by eight joints that have one degree of freedom: rotation around a vertical axis. To create swimming patterns, the angular positions of these joints oscillate with the amplitudes, frequencies, and phases prescribed by the CPG model. The neurorobotics platform (NRP) [37] was used to perform data exchange between the CPG and the virtual robot. To overcome the computational efficiency limitations of traditional processors, the authors tested their CPG model on the SpiNNaker-3 and Loihi neuromorphic boards.

According to the results, the proposed CPG model demonstrated an acceptable calculation speed for real-time implementation and the ability to generate traveling waves from random initial conditions even with a small number of neurons in the CPG segments (but more neurons provide smoother gait). The model demonstrated significant stability: an external perturbation of one segment leads to temporary disruption of the rhythmic activity of neighboring segments. When stimulation stops, the rhythmic dynamics in CPG quickly stabilizes. Application of the asymmetric input signals to the left and right CPG sides causes the formation of different traveling waves on different CPG sides, which, in turn, leads to a locomotion direction change. While testing the model in the presence of a speed barrier, the authors demonstrated 2 scenarios of lamprey virtual robot behavior. The robot can overcome a barrier or turn to the side. Barrier crossing is observed when the CPG dynamics is modulated by the tonic drive signal from the high-level center. This high-level signal is adjusted by the error correction mechanism that adapts the robot's motion to follow a certain trajectory. A comparison of SpiNNaker-3 and Loihi hardware with a conventional CPU demonstrated that neuromorphic hardware has lower power consumption compared to traditional processor architectures when simulating spiking neural networks. The CPG model proposed in [34], on the one hand, requires a large number of neurons per CPG segment, and hence is less energy-efficient, but, on the other hand, provides a wide variety of behavior scenarios and greater gait smoothness.

In another study [38], the authors developed hardware-based neural networks (HNNs), based on discrete circuits that replicate the structure and function of lamprey CPGs. The CPG is implemented as a double symmetrical chain consisting of generators. Two head generators are in self-excitation mode. CPG segments are connected to their neighbors by models of excitatory and inhibitory synapses. They are circuits that perform the spatiotemporal sum of the output signals from the CPG segment. The segments of the lateral side are connected by excitatory (from head to tail) and inhibitory connections (from tail to head) with time delays implemented using integrated circuits. Tail-to-head connections are used to stabilize the delay period. Moreover, each segment of the CPG inhibits the contralateral segment through synaptic connections, the output of which decreases after a predefined time. According to the results of modeling carried out by the authors, the HNN models generate oscillatory bursts corresponding to two lamprey neural functions: alternate generation of oscillatory bursts by left and right segments; propagation of an oscillatory burst from head to tail.

While it was repeatedly confirmed that sensory feedback is not needed for rhythmic locomotion generation in lamprey, it plays a crucial role in the modulation of periodic patterns in response to the environment. One of the basic findings is that the application of a periodic external force to the lamprey's tail induces synchronized CPG activity in a large frequency range [39–41]. This is implemented using stretch receptors in the lamprey's spinal cord which provided the traveling of a neural wave correlated with the mechanical oscillation. Lamprey CPGs received sensory feedback from edge cells [42,43]. The edge cells are mechanoreceptors that sense stretch along the body. In doing so, they send signals that excite the ipsilateral side and suppress the contralateral side of the body (relative to the position of the edge cell). Moreover, experimental results [44] showed that the edge cells also respond not only to the stretch itself but also to the rate of its change.

In the work [45], the authors presented a close-loop lamprey CPG model with sensory feedback. The distributed CPG is modeled as a double chain of sinusoidally coupled phase generators. The lamprey swimming was simulated in a viscous incompressible fluid using a full Navier–Stokes model. In the proposed model, the biologically relevant proprioceptive feedback uses the parameters of the body curvature and sends appropriate inputs to the CPG oscillators. The authors separately considered the effects of two different forms of sensory feedback on swimming speed and energy consumption. The first type of feedback that uses only the direction of body curvature did not affect the frequency of CPG activity but did affect the duration of rhythmic activity. The feedback that uses the magnitude of body curvature induces an increase in the beat frequency/swimming speed and a decrease in the energy cost of the lamprey. It was demonstrated that the incorporation of two types of feedback to the CPG model changes the kinematics and energy of swimming in a complex way. Interestingly, earlier this scientific team used neuromechanical modeling of lamprey swimming to demonstrate that even in the absence of feedback in the proposed CPG model the interaction between the body and the fluid induces a phase delay between the CPG segments activities, in which muscle activation occurred after the body curvature [46].

Biological objects often become the inspiration for robot design. At the same time, robotic systems developed on the basis of experimental data are an excellent tool for testing hypotheses and computational models of real living systems. One of the critical aspects that must be considered when designing robots is the computational speed needed to move the robot and execute commands in real time.

In their work [47], the authors proposed the implementation of a lamprey robot consisting of three components: a sensory system, a CPG model, and a neuromuscular system. The main feature of this study is that the robot is equipped with various sensory devices. These include (i) a short baseline sonar array (SBA), which allows homing to an acoustic beacon; (ii) compass; (iii) a two-axis accelerometer that provides tilt and acceleration information. The resulting sensory data are transmitted to command neurons from the high-level center that modulates the CPG dynamics. The topology of the CPG network model was based on the ideas proposed in [48]. The dynamics of a single neuron was described by a simple model proposed by Rulkov [49]. The CPG network generates output pulse signals that control the current applied to the robot actuators. The robot developed by the authors demonstrates a wide range of skills and abilities. Propagation of the wave from head to tail ensures the forward movement of the robot. The posterior wave path between the CPG segments provides backward swimming. Modulating high-level center commands provides speed and turn control. The command network uses the information received from various sensors for homing, primary orientation, and also for avoiding obstacles by the robot. The presence of the SBA allows the robot to aim at a sonar beacon, and the inclinometers activate the bend segment, allowing the lamprey robot to float and dive.

Youssef et al. [31] have developed the robotic lamprey "Envirobot" equipped with two different types of cameras: frame and event. The information received from the cameras was used as a neural network stimulation pattern. After the information had been processed by the neural network, action commands were transmitted to the CPG, which led to purposeful lamprey robot swimming. The researchers also compared the performance of the computational model using two different types of cameras. It was shown that using the event-based cameras improved the accuracy of swimming trajectories and led to a significant increase in the processing speed of visual inputs by the network.

Most recently at the "Artificial Life" conference C. Stefanini and D. Romano presented a model of the "Lampetra" robot [50]. "Lampetra" demonstrated smoothness of movements due to the muscular activation system based on the use of direct interaction of magnets and a biologically relevant CPG model. This robotic system allowed the authors to test the CPG hypotheses and explore the purposeful locomotion of the robot using visual input from its binocular vision system, which was processing a streaming video. The robot was able to track objects and avoid obstacles. The authors propose using their robot model for interacting with abiotic and biotic components of aquatic ecosystems and for interfacing with the central nervous system of real fish.

3. Fish

Fish are excellent swimmers. They are capable of covering considerable distances, developing high cruising speed, and demonstrating significant maneuvering skills. The key factor that provides these features is the mechanism of their movement. The main driving force is the oscillations of the body and tail. Fins are used to fine-tune the direction vector of a fish movement. At the same time, the control system in the form of a CPG is generally similar to that described in lampreys, however, depending on the species and order, it may contain a different number of segments, including those responsible for fins. It should be mentioned that the system of connections between CPG segments may also differ. However, regardless of the architecture of the CPG, cyclic activity should manifest itself in the form of traveling waves. Examples of CPG architectures are shown in Fig. 3.

Depending on the type of wave, there is a generally accepted classification of the types of fish movement (Fig. 4). The subcarangiform type of movement is characterized by the wave propagation from the head to the tail with a smooth, slight increase in amplitude. Typical representatives of this group are salmon and cod. With the carangiform type of movement (Fig. 5D-F), the change in the wave amplitude is more pronounced than with the subcarangiform type. This variant of locomotion is typical for mackerel and barracuda. Tuna and swordfish have a thunniform type of locomotion (Fig. 5A-C), in which the head remains at rest during movement, and the wave starts approximately from the middle of the body. In this case, all moving segments deviate in one direction relative to the axis of the body.

Separately, the scientific community singles out the ostraciform type of locomotion, characteristic of the cofferfish and boxfish. In this case, during locomotion, the fish uses only the caudal fin, which makes very fast oscillatory movements, creating thrust. At the same time, its movement is much slower in comparison with other fish and does not provide high maneuverability. Despite this, the simplicity of describing the locomotion of these fish makes them a very convenient object for modeling.

Also, the speed of movement depends on the structural features of the body. It is known that fast swimmers (for example, tuna), reaching speeds of over 100 km/h, have a shortened torpedo-shaped body with a well-differentiated tail fin. This body shape gives the fish minimal hydrodynamic resistance, which is essential at high speeds. Particular emphasis should be placed on the role of the caudal fin during thunniform movement. In addition, the tail fin provides the fish with great maneuverability at high speed. Thus, with the help of the caudal fin, tuna can easily make a 90° turn in one movement of the tail.

Despite differences in swimming types, common criteria can be identified for robots exhibiting fish-like locomotion: (i) vortices are shed off the tail fin so that a backward Karman wake is formed; (ii) tail beat frequency correlates linearly with swimming speed; and (iii) the CPG must form a cyclic signal that ensures the coordinated interaction of all segments of the robot, regardless of the type of architecture and the wiring diagram inside it.

Most of the authors of the works described below followed these features, however, depending on the purpose of modeling, they concentrated on specific aspects. Some authors sought to achieve a more accurate correspondence of the robot's swimming to real fish by changing the architecture of the CPG. Others have modified the output signal

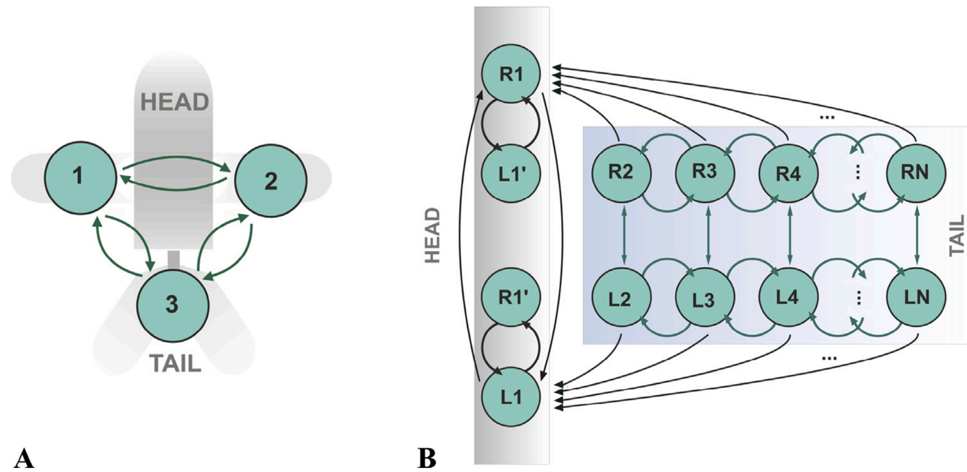

Fig. 3. A - Example of the scheme of the boxfish CPG model (ostraciform type of locomotion) [51]; B - Example of the CPG model of a fish with a carangiform type of locomotion [52]. The CPG consists of a body CPG – a double chain of 2N-1 connected oscillators – and a pectoral CPG – 4 oscillators for driving the fin motors.

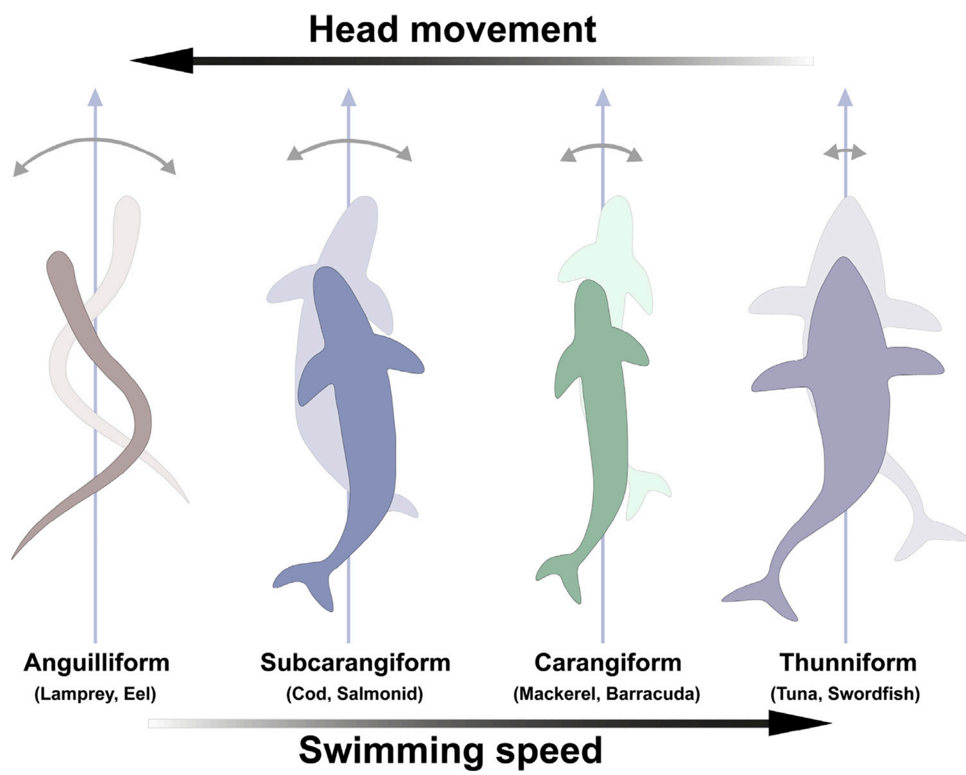

Fig. 4. Classification of the types of movement of fish.

of the CPG to study the processes of switching modes of locomotion. It is impossible not to mention the research, the main purpose of which was to improve the speed characteristics of model robots.

The paper [53] is one of the main works in the field of fish CPG, which was subsequently cited by many other researchers. In their work, the authors proposed a bionic neural network for carangiform swimming locomotion of the fish robot based on the two most popular Wilson–Cowan [54] and Matsuoka [55] oscillator models. The advantage of the Zhang oscillator model [53] is the possibility of modulating each oscillator parameter during its operation. The designed neural network consists of one high-level controller, which regulates body swing angular frequency, amplitude and bias angle for turning, and CPG. It should be noted that in this CPG model one oscillator controls both the "contraction" and "relaxation" of the muscles. Thus, the CPG is a chain of nonlinear neural oscillators coupled by both back- and front-directed connections. The proposed CPG model showed high performance in controlling the fish-robot. The authors demonstrated the start and stop of the movement, move forward and backward, turn right and turn left.

An important aspect of CPG development is the inclusion of feedback in the model. This ensures that locomotor swimming models adapt to dynamic and unexpected environmental conditions. CPG with closed-loop sensory feedback exhibit robust, stable, and adaptable motor outputs depending on external stimulus from sensory neurons. For example, in [56], to realize the ostraciiform swimming modes, Lachat and colleagues presented a three-segment CPG with feedback from light and water sensors. The CPG model was implemented as a system of three coupled nonlinear amplitude-controlled phase oscillators (one for each fin and one for the tail) and had several advantages. Firstly, the system dynamics demonstrates limited cycle behavior, i.e. after

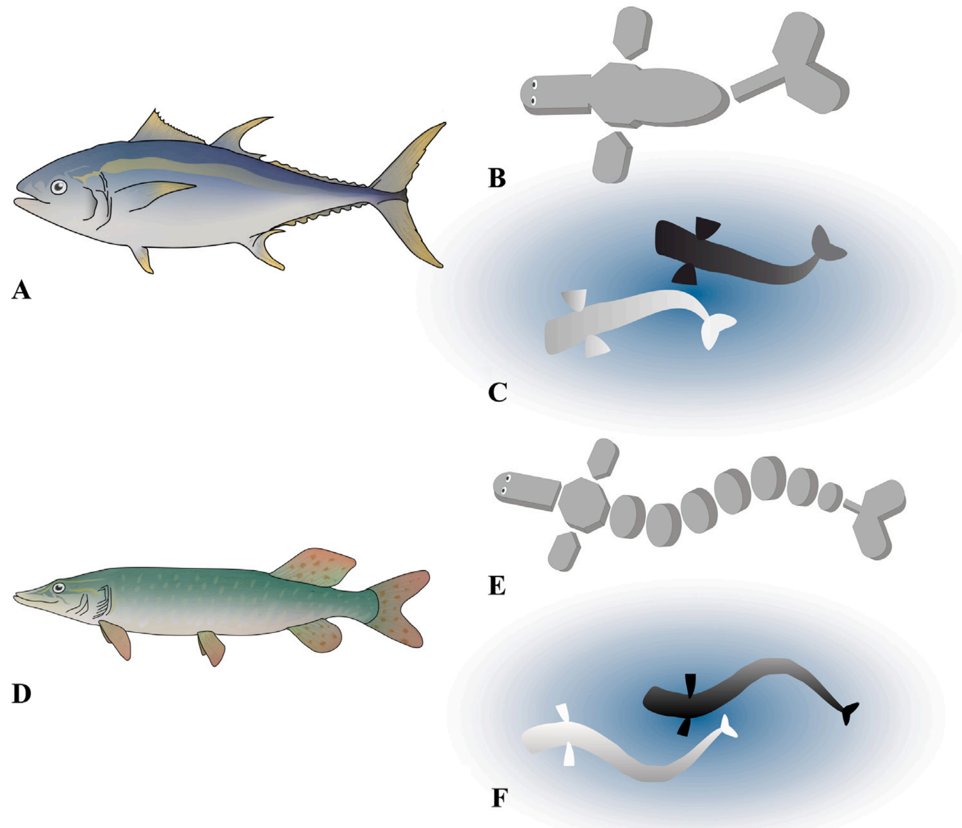

Fig. 5. A-Tuna; B- Tuna robot; C - Thunniform type of locomotion; D-Pike; E – Pike robot; F - Carangiform type of locomotion.

any system perturbation, the oscillations rapidly return to the steady-state oscillations. The second feature is that any abrupt or permanent variation of the model control parameters (frequency, amplitude, and phase shift) induced only smooth modulation of the oscillations. The fish-robot Boxybot developed by the authors [56] was based on the CPG model presented above. This robot is fully autonomous and can perform and switch between different locomotor behaviors such as swimming forward, swimming backward, turning, rolling, moving up/down, and crawling. These behaviors were triggered and modulated by sensory input coming from light and water sensors and could be realized by modulating the CPG control parameters for the three fins. Also, the authors implemented a simple phototaxis by introducing a proportional dependence of the robot locomotion speed on the light intensity. The speed of locomotion was regulated by changing the control parameters. It should be noted that the speed limit of the robot was due to the maximum motor torque.

In 2008 [57], the authors of this model published an extended version of the paper [56] with a more detailed description of the control architecture and new results on crawling. The developed robot demonstrated moving in a 3D space with various types of maneuvers. It could come out of the water using a crawling gait, avoid obstacles by swimming backward for a few seconds, lock on to bright light, and slowly follow it. Additionally, the fish-robot Boxybot demonstrated the ability to work continuously for a long time.

In contrast to previous works, Wang et al. [58] used linear oscillators instead of nonlinear ones and designed a much simpler CPG model with similar performance. The proposed model includes three coupled linear oscillators which exhibited periodic orbits. In addition to the CPG model, a locomotion control system also contains a transition layer composed of a direction controller and a speed controller and is used to transform control commands into the CPG inputs. The generation of different locomotion behaviors was performed by changing the input control parameters incoming to the transition layer. Moreover, the authors applied the particle swarm optimization (PSO) method to reduce the number of control parameters and found that just two parameters are enough to implement the locomotion control model: frequency and phase shift. Developed fish-like robot demonstrated the ability to perform forward movement and smooth rotation. Transitions between different oscillating forms were also smooth, and the implementation architecture had a low computational cost.

In 2016, the authors of this model published the paper [59], where they added several components to control multiple robotic fish: image capturing subsystem, information processing subsystem, and communication subsystem. To organize the interaction of several moving objects, the authors constructed a visual system that received data from each robot in real time After processing an image received from the camera, the computer sent control commands wirelessly to fish-robots and received feedback from robots.

Another work worth mentioning is [60], in which the CPG is modeled as a neural oscillator that includes extensor and flexor neurons connected by mutual inhibitory connections. Each neuron receives a tonic input that triggers neuronal oscillations, input signals from other neurons, and sensory feedback signals. The model equations are optimized so that the oscillator operates in the limit cycle mode. Each joint of the designed fish-robot is assigned its individual neural oscillator. In this case, the output signal of each oscillator is used as the target joint angle. Thus, in this CPG model, not only the fins and tail are involved in the movement, but also the joints of the body. Besides, the authors proposed an approach where different types of fish-like swimming (anguilliform, carangiform, and ostraciiform) can be modeled by pre-setting different connection weights between neural oscillators. The developed robot demonstrated the ability to swim both with and without fins, move forward and backward, make a sharp turn, dive, rise, and brake.

Based on [58] and [60], Wang et al. in 2013 [51] proposed the CPG model (Fig. 3A) that also used only two parameters to simulate the ostraciiform swimming in the 3D space. One parameter determines the swimming mode (such as forward swimming and turning) and the second parameter defines swimming speed and gait transition. The CPG model consists of three functional layers: input saturation function which receives command parameters, coupled neural oscillators, and output transition function which translates the neural oscillator output to the motor driving signal. The authors applied their CPG model to the boxfish robot with two pectoral fins and one caudal fin equipped with a vision sensor — camera. The sensory system allows the robot to track the object and optimize the fin operation. This result is consistent with Lachat's [56] and Crespi's [57] phototaxis simulations. According to the experiments, the developed robot was able to smoothly and rapidly transition between different swimming modes and switch between pectoral and caudal gaits. Moreover, it showed great performance in flexibility, maneuverability, and the ability to modulate swimming with the required speed.

Another research area concerns the development of a new type of robot — amphibious robots, which can both swim in the water and move on land. For example, Ding et al. [61] presented a CPG-based model for swimming locomotion control of a multimode biomimetic amphibious robot based on Crespi's robot [36,62]. The CPG network consisted of the pectoral CPG and the tail CPG. The pectoral fin on each side had its own nonlinear neural oscillator with controlled amplitude in terms of the Kuramoto model [63]. The tail part of CPG included four segments, each of which consisted of two mutually inhibited oscillators responsible for flexion and extension. Amplitude and frequency indicate the activity of a single oscillator while the connections between oscillators are determined by the values of coupling weights and phase shifts. The segment output signal is obtained by the amplitude sum of a pair of oscillators. The presence in the model of the saturation function between the CPG joints makes it possible to control the speed of fish movement by changing the number of CPG segments involved in the oscillatory process. Using this model, the authors successfully demonstrated the robot's ability to perform and switch between different swimming modes, such as moving forward and backward, turning and pitching, with modulation of speed, direction, and gait.

The paper [52] is a continuation of Ding's research. To provide autonomous transitions between different types of locomotion, the researchers upgraded their model by including sensory feedback. Sensory feedback was provided to the robot's CPG (Fig. 3B) by liquid-level sensors. In particular, two liquid-level sensors were used to determine the presence/absence of water (to determine whether the robot was on land or in the water). Information about the presence/absence of water was included in the CPG model to explicitly modulate the coupling phase shifts of the oscillators to generate reactive behavior adaptable to changing environments. Moreover, by adding to the robotic fish a pair of wheel-propeller fins, researchers managed to significantly expand the movement modes of the designed robot. The amphibious robot was able to swim in all dimensions, turn, spin, and also turn on the spot. Of particular interest is the possibility of modeling vertical swimming common in dolphins and the ability of the system to independently switch between different types of locomotion.

Unlike the previous CPG models consisting of only coupled oscillators, in [64] the authors presented a new form of CPG, which included coupled oscillators, an artificial neural network (ANN), and an output amplitude modulator. The coupled oscillators consisted of several single Andronov–Hopf [65] oscillators. The proposed oscillator model remained in the limit cycle state when the desired swimming pattern is reached, and the behavior of the entire system depended on the impact on a single oscillator. Coupled oscillators were used to generate input signals fed to the ANN. The ANN was trained by target values corresponding to the swimming patterns of a real fish, received excitation signals from oscillators, and then output desired locomotion patterns. The last component of the CPG was an outer amplitude modulator, which changed the size of the amplitudes of the ANN output signals according to task specifications. The authors focused on anguilliform locomotion and developed fish-robot that performs both forward and backward movements.

The article [66] also uses Hopf generators [65] as a CPG segment. The authors proposed a robotic thunniform swimmer model, the CPG of which consisted of two coupled (downlink) oscillators. In the model proposed by the authors, the phase shift between the oscillators is controlled by an explicit parameter. The phase shift is fixed and equals $\pi/2$. This approach makes it easier to achieve synchronization between the oscillators by reducing the influence of the forcing oscillator on the amplitude of the forced oscillator. The CPG generates a swimming gait and transmits signals to the servomotors in real-time mode. When swimming forward, the caudal fin performs harmonic oscillations along a sinusoid. Harmonic vibrations are a combination of translational and rotational motion. The correct phase shift between the translational and rotational motion of the tail fin is critical for effective thrust generation. Therefore, the authors developed a phase adjustment mechanism to compensate for the phase error between servomotors. The phase shift is evaluated in real time by feedback, and the value of the parameter that controls the phase difference in the CPG controller is dynamically corrected. The model of a robotic fish controlled by this CPG model can reach speeds up to 2 m/s. At this high speed, the flapping tail fin also creates lateral forces that cause roll moments, which can cause the robot to roll over. To stabilize the robot, the authors equipped their model with a gyroscope, an accelerometer, and a magnetometer. The data received from these sensors were used to control the tilt of a pair of pectoral fins, which ensured the stabilization of the robot fish.

Wang and his colleagues were focused on improving the efficiency and increasing the speed of the fish locomotion modeled by CPG [67]. They used the Hopf oscillators [65] in the limit cycle mode as the CPG unit. The CPG model is implemented as a chain of 6 weakly coupled oscillators. Due to mutual inhibition and neighboring coupling between the CPG blocks, different parts of the robot-fish can be coordinated as a whole. The authors applied the CPG model to a pike robot (carangiform type of locomotion) equipped with six servomotors (two for the pectoral fins, 3 for the flexible rear body, and 1 for the caudal fin). The movement of each motor was carried out on the basis of a signal coming from the segment of the CPG corresponding to it. To achieve the highest possible swimming speeds and maximum propulsive efficiency, the authors optimized the amplitude and frequency of each CPG segment using the Particle swarm optimization (PSO) algorithm. This optimization made it possible to achieve a movement speed of the robot-fish of 0.5285 m/s. In the future, the authors plan to implement real-time control training to adapt the robot fish to a dynamic aquatic environment to achieve autonomous swimming.

In the article [68], the authors propose the CPG composed of six oscillators consistently connected in a circle. As functional units, the authors used generators, the output of which was the harmonic oscillations with a fixed amplitude. Identical columns of three oscillators were responsible for the left and right motors of the robot. The first pair of oscillators controlled the left and right pectoral fins, the second — the bending of the body, and the tail oscillators were responsible for 2 tails. Using a pair of pectoral fins inspired by insect wings (the fins are located on the sides), the robotic fish achieved high maneuverability. Due to the parallel arrangement of the two tail fins, the robot could achieve high efficiency of movement and more stable swimming. To achieve autonomous swimming, the robot was equipped with three infrared sensors located on the head, responsible for detecting obstacles. All this makes it possible to use the robot for research and tasks in difficult underwater conditions.

In contrast to fish CPG models composed of oscillators, there are studies in which CPG segments are represented as biologically relevant neural networks. In [69,70], the computationally efficient LIF model is used as a neuron model. The structure of the CPG is based on that of the lamprey CPG but contains only 3 segments (generators): 1 for the head and 2 for the tail. Each generator is divided into two components, which are left and right symmetrical parts. Each CPG segment consists of CIN, LIN, EIN, and MN (Section 2, Fig. 2E) neurons. Rhythmic oscillatory activity is provided by the interaction of these neurons, and each such neural network is an oscillator. Oscillators are connected to each other by bidirectional synaptic connections. The phase differences of the output signals in the model are determined using the Motor Control Unit (MCU).

The MCU is the first CPG segment, which receives commands from the upper level of the system. It acts like the brainstem of the CPG and sends motor commands to the other generators to modulate the phase difference of the output signals. The environmental data received by the sensors of the robotic fish is evaluated by the MCU. Then, in accordance with the decision-making mechanism responsible for the movement, an input stimulus is sent to the sensory neurons (SN) in CPG. Next, SNs send signals to different populations of neurons in the CPG segment. As a result, the characteristics of the signals received by the MN change. In the end, MN sends new signals to the servomotor.

The "Fuzzy Logic" subcontroller is used as the brain in the system. It determines the adaptive locomotion modes in accordance with the received sensory data. Sensory data comes from a 10-DoF IMU (inertial measurement unit) module, which includes an accelerometer, gyroscope, magnetometer, and barometer. Additionally, the front sight unit consists of three infrared sensors. The fuzzy control approach provides correct solutions with unlimited intermediate cruising routes in complex real-world explorations, during which the robot encounters more than one obstacle at the same time.

The results of applying the CPG model developed by the authors to the i-RoF (Intelligent Robotic Fish) robot demonstrated a carangiform type of locomotion and three specific gait modes: yaw, pitch, and keep level; as well as smooth transitions between gait modes due to the presence of sensory feedback. All experiments show that the proposed closed-loop control structure achieves effective and robust responses for real-world missions and explorations.

The authors compared the performance of their "Carangiform" robot model with other models. The "Thunniform" model [66] has better forward speed characteristics, the stroke frequency is higher, but it has a different type of movement. Despite this, the "Carangiform" robot model has efficient turning maneuverability with a high turning speed and a small turning radius.

The paper [71] also presents a model of a fish with a carangiform type of locomotion. The biomimetic robot carp consists of three parts: the rigid head, the wire-driven body, and the compliant tail. The control is a CPG based on the salamander CPG model [9] controlled by a high-level command center. The authors adapted the Ijspreet model for use with a single motor. The advanced CPG model synthesizes symmetrical strokes when swimming and asymmetrical strokes when turning the robot-fish. This robot model controlled by the CPG model proposed by the authors has a number of advantages. The model uses only one drive motor for waveforms, while other models require more motors. Using the R time factor (the time ratio between two phases forming one flapping cycle) makes the turning of the robot fish more natural and efficient. Experimental results showed that the robot fish reached a maximum speed of 1.37 body lengths per second and a maximum turning speed of 457°/s.

Recent studies have focused on the autonomy of developed robot models. Other important aspects of research are computational efficiency for fast operation and smooth movement, as well as minimizing the power consumption of the robot. For example, in their work [72], Yu et al. studied the effect of CPG parameter values on the energy consumption of a two-joint self-propelled robotic fish. The authors developed a real-time energy measurement system compatible with a CPG-based robot controller and found that power consumption correlates positively with changes in frequency and amplitude (an increase in frequency and amplitude causes an increase in power consumption), while phase delay has little effect on power consumption.

4. Salamander

The study of the fundamentals of salamanders' (Fig. 6) motor control organization is a significant direction for the formation of ideas about the CPG evolutionary development. These amphibians, as one of the transitional forms of life, are peculiar because of their ability to rapidly change different types of locomotor activity. Of particular interest is the switch from the rhythmic activity of the water type to movements that provide gait. As shown in [73,74], stimulation of the mesencephalic locomotor region in both the salamander and all other classes of vertebrates causes locomotion, while different stimulus strengths determine the change in the type of movement from slow to fast. Two types of waves are very well traced in the CPG of the salamander: standing and traveling waves, manifesting themselves in different frequency ranges. Standing waves are characteristic of walking motion (at low frequencies), while traveling waves provide the possibility of swimming in water (at high frequencies). Morphologically, the salamander CPG model consists of a body CPG and a limb CPG (Fig. 7). The body CPG (as in the lamprey) is distributed along the entire length of the spinal cord. It consists of a double chain of oscillatory centers located on both sides of the spinal cord. The limb CPG is located in the cervical segments for the forelimbs and the thoracolumbar segments for the hindlimbs. It has connections with the body CPG in the caudal direction and between the elements within itself.

Over the past decades, a lot of work has been done to study the structure and functions of the CPG in salamanders, and several dozen robotic devices with neuromimetic control systems have been built. Excellent reviews can be found here [9,14,75]. However, new results have been achieved in this area in the last few years. We will give a chronological description of the developments over the past 15 years with a focus on the salamander CPG models.

The classical work [76] was the first to propose a spinal cord model and its implementation in a robot-salamander that demonstrated the ability to rapidly switch between swimming and walking. The CPG model consists of eight coupled pairs of nonlinear oscillators. Each pair is responsible for its own node in the articulated body. Similar to lamprey models, the bursting properties of a salamander CPG are modeled using phase oscillators. It is important to note that when connected in series and pairs, oscillators have both direct coupling and feedback. In this case, the feedback also goes from the CPG of the limbs to the CPG of the body, and the latter are tuned in such a way that they can form traveling waves. At the same time, in contrast to lamprey models, the salamander CPG differs in the presence of limb oscillators which have lower intrinsic frequencies. At such excitation frequencies, standing waves are generated leading to translational motion of the body due to oscillations of the fore- and hindlimb on each side in antiphase. The connections from the CPG of the limbs to the CPG of the body are stronger than in the opposite direction, which allows the CPG of the limbs, when activated, to force the rest of the robot CPG into a walking mode. At the same time, actuators are controlled based on the difference in bursts in coupled oscillators from the "left" and "right" body.

One of the many continuations of the work [76] was the study by Harischandra et al. in 2011 [77]. They explored how sensory feedback influences the work of the salamander CPG. It should be noted that the CPG consisted of 800 LIF neurons (500 excitatory and 300 inhibitory). The whole system contained 40 axial segments consisting of identical parts (right and left; flexor and extensor), including excitatory, inhibitory, and motor circuits. In this case, one part, when activated, inhibits the other one. Excitatory neurons were connected into one segment rostrally and three caudally, and inhibitory neurons — two rostrally and six caudally. For simplicity, the system was limited to 14 pairs of coupled body generators. Each limb was a complex CPG of three pairs of complex parts, due to this, the limb had three DoFs in accordance with the anatomical structure. Interestingly, in this study, the researchers reported a more successful trotting gait with increased

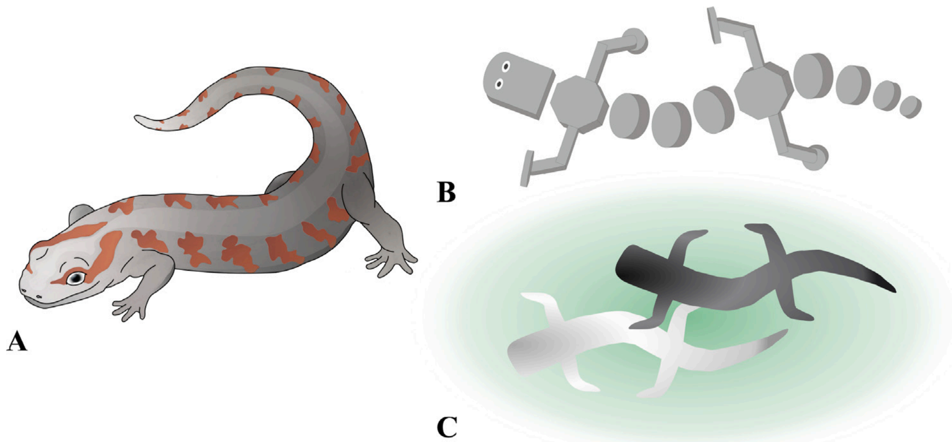

Fig. 6. The description is the same as for lampreys (Fig. 2) and fish (Fig. 5), but for salamanders.

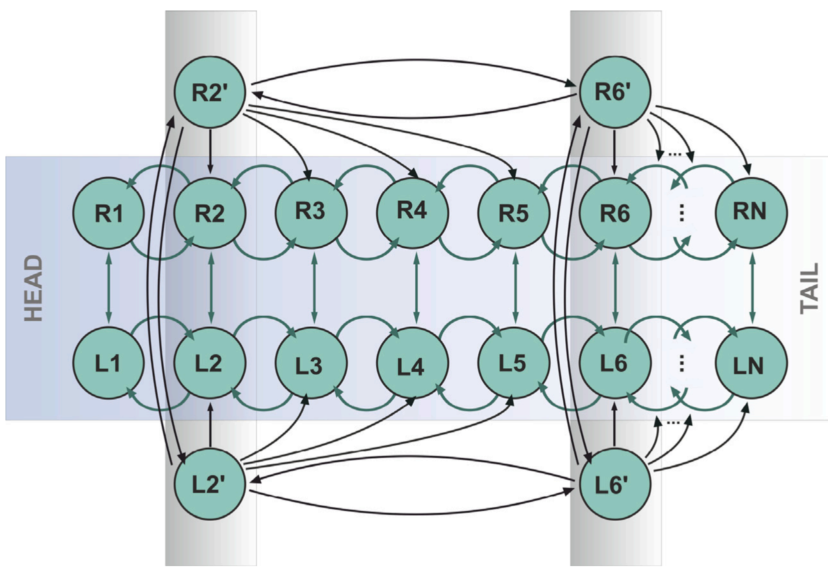

Fig. 7. Common scheme of the salamander CPG model. The CPG consists of a body CPG – a double chain of 2N oscillators – and a limb CPG – 4 oscillators for driving the limb motors. The spinal cord CPG circuit and limbs CPG circuit both have nearest-neighbor couplings. Limbs CPG also have strong connections to the caudal part of the body CPG.

connectivity from the nodes of the limbs to the nodes of the body. It was found that the proprioceptive sensory inputs are essential for producing the walking gait and that the gait transition from walking to trotting can be facilitated by the sensory inputs at the hip and scapula regions detecting the late stance phase. Thus, the almost identical scheme of the CPG [76] with subpopulations of LIF neurons instead of single oscillators made it possible to improve the control system of the salamander robot.

The next step in the development of the salamander CPG was the model of various kinds of asymmetric connections between the rostrocaudal segments, as well as the nodes of the CPG, which differ in structure. This approach, presented in [78], can demonstrate switching in motion types and works on CPGs based on oscillators and as well as LIF neurons. The study is partly based on the data on the lamprey CPG model described in [33]. The axial CPG network consists of 16 segments; intersegmental connections are directed caudally. In contrast to previous work, the CPG of limbs is represented by simple networks and only generates a rhythm (simplified limb model). In addition, inhibitory connections from the CPG of the limbs go only to the two nearest segments of the body CPG with a decreasing probability of connection.

The various CPG operation types are evaluated by two parameters: the frequency of oscillations (or spiking rate) and the phase lag between signals in neighboring segments. The authors propose the concept of multistable neural networks, which allows the network not only to store different patterns in the form of a set of phase lags but also to reproduce them after applying various types of external stimuli in different areas. In the oscillatory CPG model, this is achieved by limiting the spread of rostral and caudal influence (connections from the main part of the body CPG to the first and last segment are removed). A uniform intersegment phase lag is set along the cord without limiting the actual value of the phase lag.

The connections between the segments of the body CPG were also changed. In the rostrocaudal direction, they were five times stronger than in the opposite direction. Due to this, the body CPG was divided into a fast anterior and a slow posterior part. Accordingly, the phase lags were then adjusted due to the initial phase lag of the segments. In addition, the choice of gait or swimming was made due to the influence of the limb CPG on the anterior oscillators.

Another work worth mentioning is [79], in which, as in the study described above, the importance of inter-oscillatory connections for the most successful variant of CPG functioning was emphasized. However, the work also had a serious drawback: there were no motoneurons in the CPG networks. A reduced version of the Hodgkin–Huxley neuron was used there as an element of the CPG segments.

Subsequently, works focusing on the greater biological relevance of the models became popular. In 2018, Liu and Wang proposed a type of CPG called Locomotion-controlled neural networks (LCNNS) [80]. The LCNNSs consist of a new neuron model that reflects the spiked nature of lamprey spinal neurons. These new LCNNSs can describe most of the properties of real biological neural networks and can be used to build salamander neural networks based on the bursts generator model proposed by Guertin in 2009 [81].

In the same year, the authors of this model published a paper on modeling salamander CPG on spiking neurons [82]. It postulated the need for different neural circuits for each type of motion and speed, as well as complex connection schemes between networks both within the CPG of the limbs and within the CPG of the body. At the same time, low-frequency CPG of the limbs is associated only with low-frequency parts of the CPG of the body. This is justified by the data obtained in the experimental study of the activity of pools of spinal interneurons [83], which revealed that the recruitment of interneurons at faster speeds (high frequencies) is accompanied by the silencing of those driving movements at slower speeds.

In the model, neurons can be characterized by two different intrinsic frequencies: high and low, depending on one of the two parts of the global CPG to which they belong. At the same time, the networks are also topologically identical. That is, the robot is controlled by a global CPG, consisting of two separate networks of the same size, but with different operating frequencies (the model is at least twice as large as in previous works). The same applies to the CPG of the limbs. At the same time, descending excitatory connections mainly predominate in the CPG of the body. The minimum unit of the CPG is a network of two neurons with mutual inhibition. It should be noted that in such networks, lags between segments are not subject to separate regulation; accordingly, the entire network has the same spiking rate as a single neuron. In this case, the frequency response does not depend on the amplitude.

In a direct continuation of the research [84], the authors modified their model to achieve greater biological plausibility. In the new version, a serious drawback has been eliminated: now the model contains not only interneurons but also motor neurons. In addition, the connections between the segments of both the CPG of the body and the CPG of the limbs were modified. As a result, the ability to control the direction of the first movement and perform a turn was demonstrated. In addition, the model was enhanced by sensory communication in the form of stretch receptors. The stretch reflex is known to play an important role in controlling the posture of vertebrates.

The paper [85] continues to study the issue of the influence of sensory inputs on the functioning of the CPG. In contrast to the earlier study [78], here the robot is controlled by a network of oscillators consisting of 25 segment pairs. The tail of the robot is a passive fin. The new model is able to reproduce signals similar to recordings from isolated species. In particular, spontaneous switching of the CPG from slow caudorastral to fast rostrocaudal waves (with a change in the excitatory spike) is observed. This work is also interesting because it demonstrates the absence of the need for several CPGs to reproduce patterns with different properties, as previously assumed.

Another work postulating the need for sensory feedback is the study presented by Suzuki et al. 2021 [86]. The paper demonstrates a spontaneous transition between different patterns, but the CPG model uses different feedback rules: limb-to-limb, limb-to-body, body-to-limb, and body-to-body feedback without any connection between the oscillators. The first rule is responsible for coordinating the four limbs as they move forward to support the body. The second and third rules include cross-feedback, which establishes self-organized body-limb coordination. The fourth rule coordinates the lateral irregularities of the multi-segmented body. That is, in the model, a flexible change in the parameters of the CPG is possible due to the point impact on each individual oscillator by a signal from the "brain" (analogous to tonic stimulation). This is the first study demonstrating the spontaneous transition of gait from horizontal walking with standing waves to a trotting gait with traveling waves.

5. Notes on the higher-level movement control

The higher-level control typically implies a command switching the CPG gate and inducing the change of the animal movement mode. In robotic fish models, it can be easily implemented by control signals specifically changing phase shifts between CPG oscillators. However, the higher-level control should also generate a kind of "fine-tuning" in the adaptation of animal motion in a dynamic environment. Integrating sensorial information from the periphery relative to the current state of the actuator should generate the fine-tuning signal correcting the current state of all actuators simultaneously. Obviously, such a correction in the dynamic situation should also be predictive. So far, the existing fish swimming CPGs have not implemented such a control.

One of the possible solutions for such a finely tuned motor control was proposed by Rodolfo Llinas and colleagues [87,88] when studying the olivo-cerebellar brain circuit in vertebrates [89] (Fig. 8). The control is based on the network of interconnected neuronal oscillators, e.g. the inferior olive neurons, that generate robust spatio-temporal oscillatory patterns. Due to gap junctional coupling, they are capable of synchronizing and generating a set of oscillatory clusters. These clusters are further associated with a muscular contraction template, e.g. a motor intention pattern. It was specifically reported that moments of neuronal activations were finely précised reflecting the idea of fine-tuning the motor activations. Connected by means of a rather complicated architecture with cerebellar Purkinje neurons mediated by cerebellar nuclei, the inferior neuron activations, e.g. the spiking phase, can be set both in time and space by a specific mechanism of self-referential phase reset [88]. Summarizing the sensorial information relative to the effector feedback the control system generates correcting signals that are sent back to the actuators.

Furthermore, the idea of the olivo-cerebellar cluster was implemented to control underwater vehicles [90]. The movement of the swimming robot was provided by oscillations of six fins. To control them, a six-unit UCS was implemented in custom-made electronic circuits. The sensorial signal was taken from a video camera. When the fins were appropriately tuned, the robot demonstrated a different gate of movement. Using the effect of self-referential phase reset [88] corresponding motor pattern was finely tuned.

6. Discussion

In this paper, we reviewed research on mathematical modeling of swimming CPG of various levels of sophistication and biological plausibility. The studies on the development and analysis of the CPGs models are clearly multidisciplinary because they require the interaction of mathematics, biology, and robotics. Such studies are inspired by the insights that they can provide to the neuroscience behind fish locomotion and robotic locomotion since this kind of bio-motivated controller demonstrates strong capabilities in terms of autonomy and modulation. On the one hand, the main trend in the development of the CPGs for robotic applications is an increase in the complexity of the models, on the other hand, despite the multiplicity of possible implementations, the CPGs demonstrate conceptually similar patterns of swimming behavior for both primitive fish and advanced salamanders. Mathematical modeling of the CPG remains relevant and attracts a growing number of researchers. CPG models based on phase oscillators, which are still popular for robotic embodiments, are increasingly being replaced by bio-inspired spiking CPGs that exploit the theoretical advantages of neuromorphic hardware in terms of energy efficiency and computational speed.

Aquatic locomotion has always received a lot of attention due to the demand for the design of underwater robots. The fish swimming gait can roughly be classified into four categories: anguilliform type, carangiform type, thunniform type, and ostraciiform type. According to this classification, a variety of biomimetic underwater robots have been

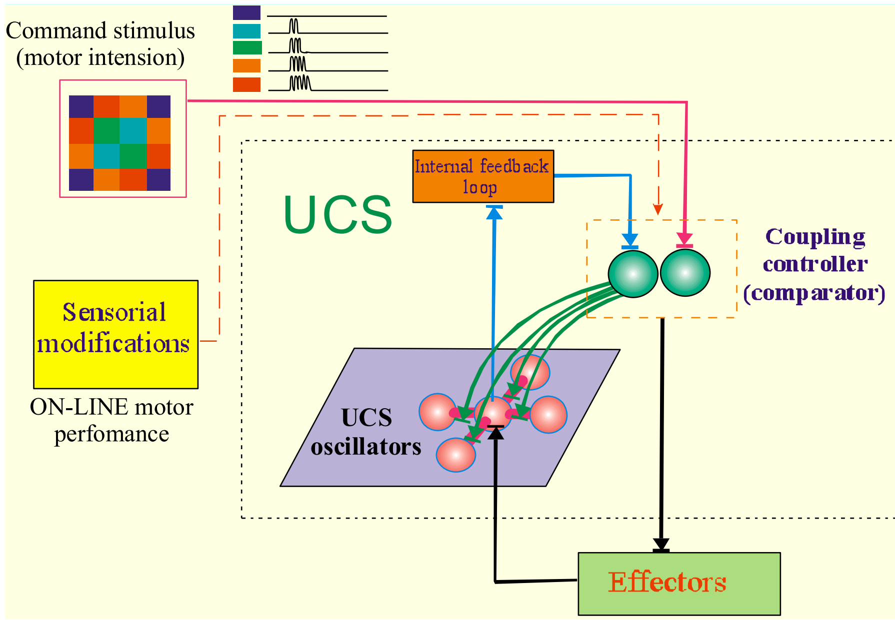

Fig. 8. Schematic view of the universal control system (USC) based on the olivo-cerebellar dynamics. UCS oscillators, mimicking the inferior olive neurons, generate a robust space–time distribution of oscillatory phase clusters with precise timings. The robustness is sustained due to an interval feedback loop involving activations of cerebellar Purkinje neurons and cerebellar nuclei. Phase clusters are associated with the muscle activation template in the effector system. Sensorial information and the effector feedback are sent for the comparison of an actual motor template with the one imposed by the sensorial inputs.
Source: The scheme was modified from [87–89].

designed. The most implemented of them are the anguilliform type and carangiform type of gaits.

CPGs of lampreys and swimming amphibians are characterized by the presence of a dominant locomotor rhythm at the output, which does not require a similar signal at the input. This makes it possible to utilize the traveling wave for the anguilliform type of swimming, while sensory feedback plays a crucial role in the modulation of periodic patterns. A distinctive feature of CPGs of tuna and other scombrid fish, as high-performance swimmers, is the ability to operate at high frequencies of caudal fin flapping to achieve the desired speed while maintaining reasonable energetic costs.

Focusing on CPG, researchers discovered mechanisms of locomotion and implemented them in robotic devices. Robots can swim in different gating modes generated by CPG controllers. However, robots are still far from their biological prototypes in terms of performance, energy efficiency, and maneuverability. To our understanding, the problem is not only the design of biomorphic muscular-like actuators, but also the control system that should provide not only locomotion but also a multi-dimensional sensory–motor transformation including an intention of movement, adaptive tuning of muscular activation template, and many other subtle parameters. Such parameters may include, for instance, the geometry of the flexible fish during movements, state of fish scales, fish body stiffness, and many others. In particular, it was recently found by Zhong and coauthors [91] that the adaptive changes in body stiffness during swimming can significantly improve the performance of thunniform movement. It means that the result of the sensory–motor transformation is corrected not only by the locomotory gate but also by the body state parameters. In the numerical simulation, Feng and coauthors [92] analyzed how caudal fin deformation may influence thunniform movement hydrodynamics and, hence, resulting movement performance. Along with many variants of locomotions, shapes and sizes all fish have a large number of fine dynamic parameters to be tuned simultaneously by the control system optimizing the current mode of fish movement. A growing number of recent publications addressing these questions demonstrated a clear trend to achieve true biomorphic solutions in fundamental science and intelligent robotics.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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