References

1. Duffin J (1991) A model of respiratory rhythm generation. Neuroreport 2:623–626
2. Richter D, Ballantyne D, Remmers JE (1986) How is the respiratory rhythm generated? A model. News Physiol Sci 1:109–112
3. Botros SM, Bruce EN (1990) Neural network implementation of the three-phase model of respiratory rhythm generation. Biol Cybern 63:143–153
4. Balis UJ, Morris KF, Koleski J, Lindsey BG (1994) Simulations of a ventrolateral medullary neural network for respiratory rhythmogenesis inferred spike train cross-correlation. Biol Cybern 70:311–327
5. Rybak IA, Paton JFR, Schwaber JS (1997) Modeling neural mechanisms for genesis of respiratory rhythm and pattern: II. Network models of the central respiratory pattern generator. J Neurophysiol 77:2007–2026
6. Smith JC, Ellenberger H, Ballanyi K, Richter DW, Feldman JL (1991) Pre-Bötzinger complex: a brain stem region that may generate respiratory rhythm in mammals. Science 254:726–729
7. Butera RJ, Rinzel JR, Smith JC (1999) Models of respiratory rhythm generation in the pre-Bötzinger complex: II. Populations of coupled pacemaker neurons. J Neurophysiol 82:398–415
8. Rybak IA, Paton JFR, Rogers RF, St.-John WM (2002) Generation of the respiratory rhythm: state-dependency and switching. Neurocomputing 44–46:603–612
9. Rybak IA, Shevtsova NA, Paton JFR, Dick TE, St.-John WM, Mörschel M, Dutschmann M (2004) Modeling the ponto-medullary respiratory network. Respir Physiol Neurobiol 143:307–319
10. Smith JC, Butera RJ, Koshiya N, Del Negro C, Wilson CG, Johnson SM (2000) Respiratory rhythm generation in neonatal and adult mammals: the hybrid pacemaker-network model. Respir Physiol 122:131–147

Computational Motor Control: ERN

Amir Karniel
Department of Biomedical Engineering, Ben-Gurion University of the Negev, Beer Sheva, Israel

The nervous system analyses sensory information (►Sensory systems) and orchestrates motor commands (►Motor control). Many artificially engineered systems face similar challenges. Following the notion of cybernetics, we strive to boost both scientific and technological research by exploring the differences between artificial control theory (►Adaptive control; ►Computer-neural hybrids; ►Control theory; ►Nonlinear control systems; ►Signals and systems) and the biological motor control.

Computational motor control covers all applications of quantitative engineering tools as well as other mathematical tools for the study of the biological movement control system, which includes the joints, muscles, sensory organs and of course the nervous system.

For example, ►feedback control, ►adaptive control, and ►bayesian statistics, represent such computational tools that were employed in the study of the biological motor control system, see also [1–4].

The applications of computational motor control are bidirectional: on the one hand control theory knowledge is employed to generate new theories for the biological motor control and on the other hand we draw inspiration from the biological motor control in order to develop new control strategies for artificial devices.

In the following two sections we describe this interplay between science and technology and introduce the main concepts in the field of computational motor control that are further defined in the relevant keywords throughout the encyclopedia.

Control Theory and Our Understanding of the Biological Motor Control System

Brain researchers have always used technical analogies stimulated by the status of the technology at the time of writing. For a recent review of insights from engineering theory that can shed some light on biological complexity see [5]. These analogies are very useful pedagogically and they could also be useful scientifically as long as they are accurately stated. The best way to accurately state an analogy is by means of a mathematical computational model. In the 50s the servo-mechanism was popular, and at that time Ragnar Granit [6] wrote that the concept of servo-control is practically as old as experimental physiology and could be traced back to Claude Bernard's idea about the *constancy of the internal environment* (1865). However, once the model is treated with a specific mathematical model, one can study the gain of the feedback and stability behavior, which are part of the feedback servo-mechanism control theory and were not existent at the time of Claude Bernard. The introduction of quantitative comparison of physiological data to the computational model paved the way to new discoveries, such as the time-varying gain [7] and the typically low gain and large delays [8] that generated new understandings and pushed researchers towards the notion of adaptive control.

Feedback Control (►Control) is the first technique taught in any control engineering class [9]. Computational motor control evolved as part of the field of biological cybernetics and the origin of the word cybernetics refers to feedback control and indeed in the early models for motor control, feedback control was the main analogy and modeling tool [7,10].

In parallel to the development of ►adaptive control theory, physiologists have noticed that the simple servo theory does not properly describe the biological motor control system since the gains are low and changeable, and the delay does not enable proper control of rapid movements [8]. The delay problem is partially resolved by equilibrium theories (see ►Equilibrium point control) where the feedback is performed instantaneously by the muscle's impedance (►Impedance control).

Another prominent feature of the biological motor control system which is not addressed by the servo theory as well as by most modern engineering theories is the redundancy of the biological motor system [11] which enables obtaining the same goal by activating many possible muscle unit combinations (see ►Coordination).

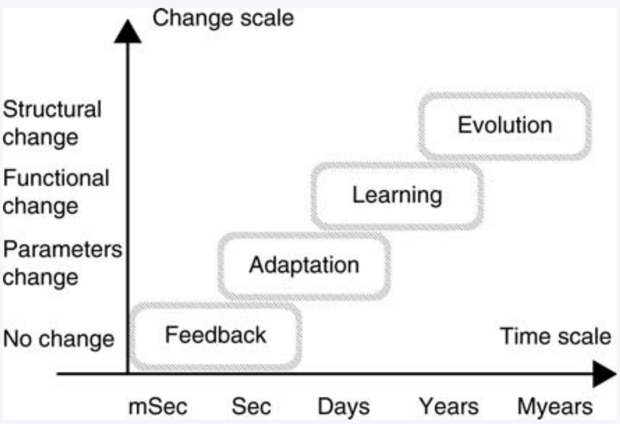
Most notably, adaptive control theory was required in order to address the limitations of the servo theory and is being increasingly employed in many studies of the biological motor control system [12–16].

The Hierarchy of Feedback Adaptation Learning and Evolution

Adaptation in the wide sense (WSA) is accommodation to the environment, in other words, any processing of sensory information that eventually changes the motor behavior in one way or the other. Figure 1 presents a map of four instances of this phenomenon where the coordinates of this map are time-scale and majority of change. We start with a description of the system approach and then move to address each type of the WSA separately to clarify the scope of each part in this structural temporal hierarchy.

Structural Temporal Hierarchy

A prominent tool of the engineering approach is the block diagram and we use it here to describe the various notions in the proposed structural temporal hierarchy.



Computational Motor Control: ERN. Figure 1 The temporal structural hierarchy of wide sense adaptation in the motor control system. Feedback, Adaptation, Learning and Evolution are instances of wide sense adaptation where sensory information is integrated and employed to change the control signal in various techniques and time scales.

Figure 2 demonstrates such a diagram in which each block is an input-output system. The output is a function of the input. The term function is used here in the wide sense to include transfer function that implies the existence of dynamics and internal state variables within the system as well as stochastic function that implies the presence of noise or uncertainty.

When we think about a control problem we usually have at least two systems: The controller and the controlled system. For example if we wish to control the position of the hand, we have the controlled system on the one side, i.e., the relation between the neural command to the muscles and the position of the hand, and the controller on the other, i.e., the relation between the intended movement and the neural signals to the muscles implemented by the brain. (Other distinctions are possible, such as considering the muscles as part of the controller as discussed further in the next subsection).

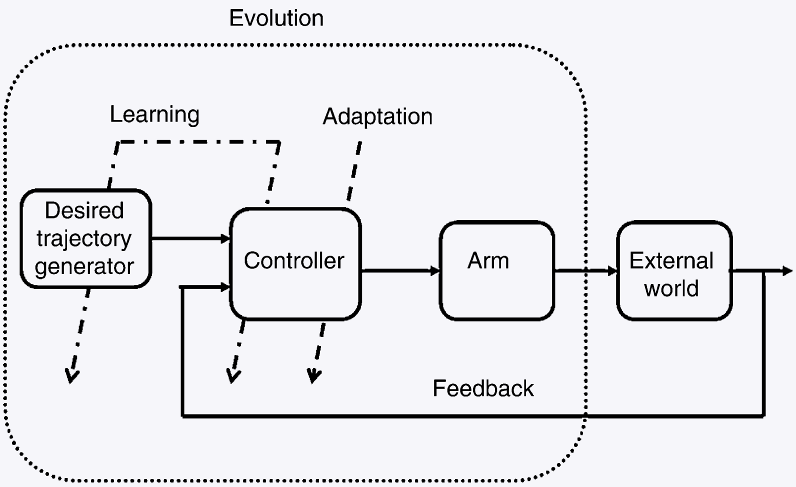
A prominent feature of the biological system is to use the sensory information about the actual position of the hand in order to improve the control of its position. This simple idea was used by engineers from the beginning of cybernetics (in part following observations of nature) and was later developed to include adaptive control. We follow the engineering terminology and use it to define a hierarchy of methods to improve the control signal and then try to use it to describe the brain as it controls movements. The basic idea of this hierarchy was first presented in [4] and here we further extend and more accurately define and demonstrate it. The terms feedback, adaptation, learning and evolution that are used here to describe this hierarchy are overloaded with various meanings and interpretations, therefore it is crucial that we properly define what we mean by each part of the hierarchy. We start from choosing the appropriate definition from the dictionary and then further define and demonstrate what we mean in the context of the hierarchy and the engineering and biological control systems.

Feedback

According to the Miriam-Webster Dictionary: "the return to the input of a part of the output of a machine, system, or process (as for producing changes in an electronic circuit that improve performance or in an automatic control device that provide self-corrective action)."

According to the Oxford Dictionary: "a. Electr. The return of a fraction of the output signal from one stage of a circuit, amplifier, etc., to the input of the same or a preceding stage."

We refer to a system as feedback control when sensory information is fed back to generate the control signal during the performance of the task (see Fig. 2). The signal flows from the sensory system to the control



Computational Motor Control: ERN. Figure 2 The hierarchy of wide sense adaptation in the control of arm movement. The biological motor control system is separated into three parts: the arm, which consists of the musculoskeletal system, the controller that may include internal models, state estimators as well as feedback controller, and the desired trajectory generator that represents higher brain functions. Feedback control changes only the control signals but does not change the functions of any part in the system. Adaptation may change the parameters of the controller, in particular parameters of the internal models. Learning may change the structure of the internal model and may also change the desired trajectory. Evolution can change each and every aspect of this system including the structure of the limb such as the number of joints in the arm. The external world influences the sensory feedback, which plays a crucial role in all these processes. Many studies manipulate the feedback by including force perturbations and altered visual feedback in order to excite these processes and analyze their properties. This diagram concentrates on the control of one arm movement, and therefore in this subsystem the external world is not influenced by the wide sense adaptation. However, in real life, outside the control experiments and rule-based games, the human brain has evolved to be capable of changing the environment and this capability is part of the learning process, therefore the learning process includes also changes in the strategy beyond changing the internal model and the desired trajectory, such as modifying the force perturbations by manipulating the environment.

system, this path could be long or short depending on the specific system; however, there is no change in the control system and the changes in the control signals are the result of changes in the sensory signals.

In the biological system the shortest path is typically described as the feedback reflex loop, which includes a monosynaptic pathway. However, there is a shorter pathway for feedback within the muscle. The simple mechanical property of stiffness (i.e. the force being proportional to the length of the muscle) could be referred to as feedback control, since the control signal (the force) is influenced by the outcome that is sensed by the length of the muscle. This last example demonstrates a limitation of the engineering approach, since the blocks usually hide the detailed structure, therefore if we define the control signal as neural input we would never note the internal feedback loops within the muscle and joint. In such block diagrams there is always a tradeoff between simplicity and accuracy and one should note that the hierarchy described here for a specific level of abstraction could be multiplied within each block.

Let us summarize this discussion with a formal definition of feedback control: Feedback Control: of a given input-output system is the usage of the output signal in order to generate the control signal in real time, i.e., the time scale of changes in the control signals is determined by the propagation of signals through the channels and the control system.

Figure 1 captures the main properties of feedback: signal flow in real time without changes in the system.

Adaptation

According to Miriam-Webster: “adjustment to environmental conditions: as (i) adjustment of a sense organ to the intensity or quality of stimulation (ii) modification of an organism or its parts that makes it more fit for existence under the conditions of its environment.”

According to the Oxford Dictionary: “2. a. The process of modifying a thing so as to suit new conditions: as, the modification of a piece of music to suit a different instrument or different purpose; the alteration of a dramatic composition to suit a different audience.”

Adaptive control is a control strategy where the controller can change its function to accommodate changes in the controlled system or in the environment. Here not only the signals are changed but also the control system is changed based on the sensory information received. These changes in the system are typically slow compared to the time-scale of the feedback. The controller includes a finite set of adjustable parameters and a third system observes the flow of signals to and from the control system and determines how this set of parameters should change in order to improve some measure of performance.

Adaptive control: Changes in the parameters of the control system that are generated after observation of previous control and sensory signals in order to improve the future performance of the system over a well-defined task or measurements of performance.

Learning

According to Miriam-Webster: "**1 a** (1)**:** to gain knowledge or understanding of or skill in by study, instruction, or experience <*learn* a trade> […] **b:** to come to be able <*learn* to dance>."

According to the Oxford Dictionary: "1. The action of the vb. LEARN. a. The action of receiving instruction or acquiring knowledge; spec. in Psychol., a process which leads to the modification of behaviour or the acquisition of new abilities or responses, and which is additional to natural development by growth or maturation; (freq. opp. insight)."

While adaptation is a change in parameters of the controller that improves the performance in certain types of behavior, learning may generate a completely new behavior, as in skill acquisition, or may employ a new strategy to achieve the same task. In both cases the controller may change its structure. Such change in the biological system may include the recruitment of new brain areas or generation of a new neural circuit for a specific task. In artificial systems the controller may be replaced with another controller. At this point our technology does not provide an effective learning machine and it is highly possible that observing the biological system and modeling the neural control of movement may generate new control strategies that would later be used for artificial intelligent control, perfected by control engineers, and then return to serve as models for the brain.

Learning Control: change of the control system in order to generate a new type of behavior.

Evolution

According to Miriam-Webster: "**2 c** (1)**:** a process of continuous change from a lower, simpler, or worse to a higher, more complex, or better state; **4 b:** a theory that the various types of animals and plants have their origin in other preexisting types and that the distinguishable differences are due to modifications in successive generations."

According to the Oxford Dictionary: "6. Biol. a. Of animal and vegetable organisms or their parts: The process of developing from a rudimentary to a mature or complete state. c. The origination of species of animals and plants, as conceived by those who attribute it to a process of development from earlier forms, and not to a process of 'special creation.' Often in phrases doctrine, theory of evolution 7. The development or growth, according to its inherent tendencies, of anything that may be compared to a living organism (e.g. of a political constitution, science, language, etc.)."

In the proposed hierarchy, evolution is the last resort as it may take many years and it can potentially generate the largest change due to the evolution of a new species or in the engineering term, a new kind of controller.

Evolution: an arbitrary change in the controller that could include any change in structure, function, connectivity, parameter values, learning algorithms and adaptation protocols. The best change is chosen by survival of the fittest and therefore this process may be extremely long.

An Engineering Example

Consider a controlled system: $\boldsymbol{y} = \boldsymbol{P}(\boldsymbol{x}, \boldsymbol{u})$; $\dot{\boldsymbol{x}} = \boldsymbol{g}(\boldsymbol{x}, \boldsymbol{u})$, where $\boldsymbol{y}$ is the output, $\boldsymbol{u}$ is the input and $\boldsymbol{x}$ is the state, and a proportional controller $\boldsymbol{u} = \boldsymbol{k}(\boldsymbol{y}_d - \boldsymbol{y})$, where $\mathbf{y}_d$ is the desired reference trajectory.

As long as $\boldsymbol{k}$ is constant, this is a simple feedback control. The sensed output $\boldsymbol{y}$ is used through the controller to change the control signal in real time, in this case immediately. Even if we introduced delay or dynamics to the controller, as long as the parameters of the controller are fixed this would still be called a feedback control system.

Now suppose that this feedback control that worked fine in the first design does not provide good performances due to changes in the control system or in the environment. We wish to choose $\boldsymbol{k}$ automatically to generate the best performance under this given structure. We may design an algorithm that observes the outputs and possibly also the inputs to the system and modify k accordingly. This scheme is called adaptive control and a typical requirement to avoid unstable behavior is that the time scale for the changes in the parameter is long compared to the time scale of the feedback loop. This is required in order to properly identify the system and adapt the parameters of the controller accordingly.

With this adaptive control we can face certain type of changes in the plant or the environment, however, a new task or severe changes in the plant or the environment (that would also be called new task) may require changes in the structure of the controller, e.g., one may consider adding integration or a lead or other elements from some given repertoire. In this example lets consider the repertoire of linear controller, i.e., finite number of poles and finite number of zeros in the transfer function of the controller.

An algorithm that would observe the inputs and outputs and would choose the optimal structure of the controller, i.e., the number of poles and number of zeroes, would be called a learning algorithm. Again this process should be slower than the typical time scale of adaptation in order to obtain enough information from the operation of the current controller to make a good decision.

Finally this whole framework of linear control might be wrong and a new generation could evolve based on gain scheduling or some neural network based controller (►Neural Networks for control).

Then again, after such an evolutionary process, e.g., in the case of neural network, the changes in the weights would be called adaptive control, changes in the connectivity, size and structure of the net would be called learning, an finally changes in the time of activation function or the underlying structure would be called evolution.

A Neurophysiological Example

Consider a reaching movement from an initial position to a given target (►Arm trajectory formation).

The ►equilibrium-point control [17–19] suggests that the brain specifies the end point, namely the resting length of the muscles, and then the arm moves to its equilibrium according to the law of physics. As long as the hand is not at the target there is an error signal that pushes the hand towards the target. This would be a classical feedback control. Other versions of the equilibrium control [18,19] are also based on feedback control and account for equilibrium trajectory.

Suppose that the subject holds a robotic manipulandum that exerts a velocity-dependent force perpendicular to the direction of movement [20]. In the first movement the subject generates a curved line and it seems that the feedback control is insufficient to generate a straight line. Then after practice the movement becomes straight and if the force field is stopped a curved movement in the other direction is generated, a phenomenon that was called after-effect. The after-effect is a clear sign that feedback was not the reason for the improved behavior and some change in the controller took place during this training period. We call such a change in parameters adaptation. The adaptive controller could be based on ►internal models [16] or on parametric changes in the Equiliberium-point (EP) signals or other control signals [21].

Now suppose that we introduce a completely new type of force field, which subjects are unable to adapt to within tens of trials, i.e. a force field, which is not within the natural repertoire of the adaptive control system. Two examples for such a force field are time-dependent forces and force fields that switch according to some sequence [22]. The natural adaptive control scheme is insufficient in order to compensate for such force fields, however, some individuals after prolonged practice in a proper training plan with proper cues and motivation may be able to learn this task, probably by employing new neural circuits or generating a major structural change of the control strategy. This would be a learning process.

Finally the force field might be stronger than the physiological limitations of the muscles, much stronger than the one that could be learned by increasing the muscles mass through training. In such cases, only evolution of a new species might solve this task if this task was essential for the survival of the subject for a large number of generations.

The adaptive nature of the biological system addressed in this essay is indeed the core of computational motor control, however, one should note that many other computational models and control methods are being employed in the study of the biological motor control including optimal control (see ►arm trajectory formation), optimal feedback control, stochastic control, ►information theory, ►nonlinear control systems, etc.

As new engineering and computational techniques are being developed by engineers and mathematicians they are quickly employed to describe the nervous system, and on the other hand as new behavioral and physiological phenomena are being observed they quickly inspire engineers to incorporate them into artificial systems – this is the essence of cybernetics and computational motor control and therefore the specific definition and list of related topics are ever growing.

References

1. Wolpert DM, Ghahramani Z (2000) Computational principles of movement neuroscience. Nature Neuroscience supplement, 3: pp 1212–1217
2. Jordan MI (1996) Computational aspects of motor control and motor learning, in Heuer and H. Keele, S. Handbook of Perception and Action: Motor Skills, Academic Press: New York
3. Shadmehr R, Wise SP (2005) The Computational Neurobiology of Reaching and Pointing: A Foundation for Motor Learning. MIT Press
4. Karniel A, Inbar GF (2000) Human motor control: Learning to control a time-varying, nonlinear, many-to-one system. IEEE Transactions on Systems Man and Cybernetics Part C-Applications and Reviews, 30(1): pp 1–11
5. Csete ME, Doyle JC (2002) Reverse engineering of biological complexity. Science, 295(5560): pp 1664–1669
6. Granit R (1955) Receptors and sensory perception. New Haven: Yale University Press
7. Marsden CD, Merton PA, Morton HB (1972) Servo action in human voluntary movement. Nature, 238 (5360): pp 140–143
8. Inbar GF (1972) Muscle spindles in muscle control. II. Analysis of muscle servo model. Kybernetik
9. Franklin GF, Powell JD, Emami-Naeini A (2002) Feedback Control of Dynamic Systems. 4th ed. Prentice Hall. Upper Saddle River, N.J.: 910

10. McRuer DT, Magdaleno RE, Moore GP (1968) A neuromuscular actuation system model. IEEE Transactions on Man-Machine Systems, MMS-9(3): pp 61–71
11. Bernstein N (1967) The Coordination and Regulation of Movements. Oxford: Pergamon Press
12. Inbar GF (1972) Muscle spindles in muscle control. 3. Analysis of adaptive system model. Kybernetik
13. Bhushan N, Shadmehr R (1999) Computational nature of human adaptive control during learning of reaching movements in force fields. Bilological Cybernetics, 81: pp 39–60
14. Donchin O, Francis JT, Shadmehr R (2003) Quantifying generalization from trial-by-trial behavior of adaptive systems that learn with basis functions: Theory and experiments in human motor control. Journal of Neuroscience, 23(27): pp 9032–9045
15. Klaiman E, Karniel A (2006) Bimanual adaptation: internal representations of bimanual rhythmic movements. Experimental Brain Research, 171(2): pp 204–214
16. Kawato M (1999) Internal models for motor control and trajectory planning. Current Opinion in Neurobiology, 9: pp 718–727
17. Polit A, Bizzi E (1979) Characteristics of Motor Programs Underlying Arm Movements in Monkeys. Journal of Neurophysiology, 42(1): pp 183–194
18. Latash ML (1993) Control of human movement. Champaign: Human Kinetics
19. Feldman AG (2005) Forty years of the equilibrium-point hypothesis. Lachine, Quebec: Tristar Printing
20. Shadmehr R, Mussa-Ivaldi FA (1994) Adaptive representation of dynamics during learning of a motor task. Journal of Neuroscience, 14(5): pp 3208–3224
21. Gribble PL, Ostry DJ (2000) Compensation for loads during arm movements using equilibrium-point control. Experimental Brain Research, 135(4): pp 474–482
22. Karniel A, Mussa-Ivaldi FA (2003) Sequence, time, or state representation: how does the motor control system adapt to variable environments? Biological Cybernetics, 89(1): pp 10–21

Computerized Stabilometry

►Stabilometry

Computer-Neural Hybrids

Vittorio Sanguineti
Dipartimento di Informatica, Sistemistica e Telematica, Università di Genova, Genova, Italy

Synonyms

Dynamic clamp; Neurally controlled animats; Hybrots; Embodied neural systems; Brain-machine interfaces; Brain-computer interfaces; Neuroprostheses

Definition

Device or experimental apparatus in which living neurons exchange information in a bi-directional way with an artificial system – a computer simulation or a physical device.

Exchange may involve intra-cellular signals and occur within a single neuron, or between pairs of neurons. Alternatively, the neural component may be made of multiple neurons, an entire neural population or even a whole organism, with its own intact sensory and motor systems. In this latter case, signals are exchanged extra-cellularly, with multiple stimulation and recording sites.

The artificial part may consist of simulated neurons, thus resulting in a hybrid neural circuit. It may include artificial sensor or actuator systems, as in ►neuroprostheses and ►brain-computer interfaces, or even consist of a whole physical or simulated body.

Description of the Theory

Description of the Structure

In computer-neural hybrids at single neuron level, an ►intra-cellular recording of the ►membrane potential of a neuron is used to calculate a current, which is then injected into the same or another neuron. In this way, it is possible to simulate artificial voltage-gated (Fig. 1) and/or ►synaptic conductances (Fig. 2). Both voltage measurement and current injection are made with glass micropipette electrodes. This technique is known as dynamic clamp [1].

The artificial part of the dynamic clamp may consist of one or more simulated neurons. This would result in a hybrid neural circuit, made of both biological and artificial neurons. Dynamic clamp can be, and has been, implemented in various ways, ranging from analog circuits, to dedicated computer systems (e.g., digital signal processing boards), to software applications that exploit the computational power of modern computers.

In computer-neural hybrids that involve multiple neurons, both recording and stimulation usually occur extra-cellularly, through multiple electrodes or ►microelectrode arrays. Like in dynamic clamp, the multi-site neural signals are processed in real-time, but here the signal recorded from each electrode reflects the activity (population spikes and/or field potentials) of a small population of neurons. For this reason, the processing of the recorded neural signals often includes ►spike sorting modules, which result in multiple spike trains – one for each identified neuron in the population. Microelectrode arrays are also used to deliver electrical stimuli that excite the neural system by initiating action potentials in the neurons nearby (see Fig. 3).

As both recording and stimulation occur extra-cellularly, in these hybrids the computer-neural interaction is less direct than in dynamic clamp. Nevertheless, the collective activity of the neural population can be

Marc D. Binder, Nobutaka Hirokawa and Uwe Windhorst (Eds.)

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Editors:
Marc D. Binder
Department of Physiology & Biophysics
University of Washington School of Medicine
Seattle, Washington, USA
mdbinder@u.washington.edu

Nobutaka Hirokawa
Department of Cell Biology and Anatomy
Graduate School of Medicine
University of Tokyo
Hongo, Bunkyo-ku, Tokyo, Japan
hirokawa@m.u-tokyo.ac.jp

Uwe Windhorst
Göttingen, Germany
siggi.uwe@t-online.de

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