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OPEN QUESTIONS IN COMPUTATIONAL MOTOR CONTROL

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Computational motor control covers all applications of quantitative tools for the study of the biological movement control system. This paper provides a review of this field in the form of a list of open questions. After an introduction in which we define computational motor control, we describe: a Turing-like test for motor intelligence; internal models, inverse model, forward model, feedback error learning and distal teacher; time representation, and adaptation to delay; intermittence control strategies; equilibrium hypotheses and threshold control; the spatiotemporal hierarchy of wide sense adaptation, i.e., feedback, learning, adaptation, and evolution; optimization based models for trajectory formation and optimal feedback control; motor memory, the past and the future; and conclude with the virtue of redundancy. Each section in this paper starts with a review of the relevant literature and a few more specific studies addressing the open question, and ends with speculations about the possible answer and its implications to motor neuroscience. This review is aimed at concisely covering the topic from the author's perspective with emphasis on learning mechanisms and the various structures and limitations of internal models.

Keywords: Computational motor control; internal models; forward model; inverse model; motor learning; feedback; adaptation; motor memory; time representation; reaching movements; trajectory formation; redundancy.

1. Introduction

Computational motor control is a young field of study within neuroscience, and most of the models are still controversial. Therefore, I have decided to review the field in the form of a list of open questions.

The very first open question in neuroscience is clearly the mind−body problem. What is the relation between mental phenomena and physical bodies? We are not going to discuss this question here, since the underlying assumption of the author is that the brain in general and the motor system in particular can be usefully described by means of computational models. The second section addresses this assumption and questions our ability as engineers to reproduce the human function.

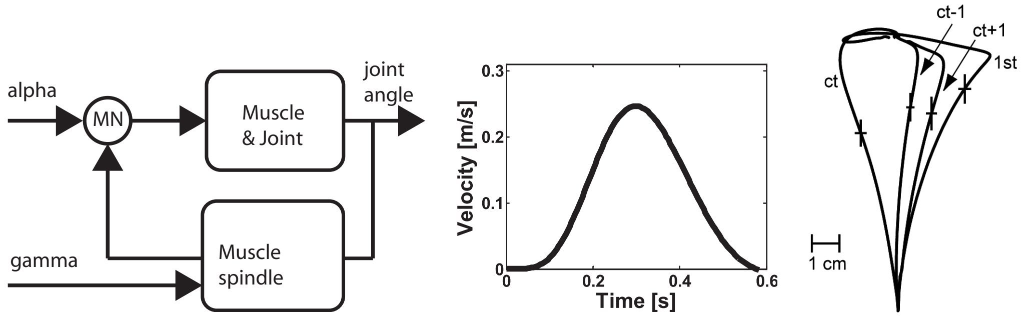
The rest of the open questions listed in this review concern the structure and function of the best computational models and the extent of their fit to the actual neural control of movement system.

The open questions structure is aimed at covering a large portion of the quantitative motor neuroscience research and provides a review of the current state of the art in computational motor control. Therefore, each section in this paper starts with a review of the relevant literature and a few more specific studies addressing the open question, and ends with speculations about the possible answer and its implications to motor neuroscience. This review is aimed at concisely covering the topic from the author's perspective with emphasis on learning mechanisms and the various structures and limitations of internal models. The reader is referred to textbooks and more specific reviews for more details and other perspectives [68, 71, 84, 137, 133, 158, 135].

Before we move to the open questions, let me define the notion of computational motor control, and then, demonstrate it by three examples of computational models for the motor system (Fig. 1): (a) The length servo model for the stretch reflex, namely, feedback control, (b) the minimum jerk model as an example of optimality approaches, and (c) trial-by-trial adaptation as an example for internal model adaptation and learning concepts.

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 [68].

Feedback control is one of the basic engineering tools in modern control theory (Fig. 1(a)). As noted by Granit [49], the concept of servo control, as developed by engineers in the last century, is practically as old as experimental physiology,



(a) (b) (c)

Fig. 1. (a) The length servo hypothesis, illustrating the motor neuron, the muscle and joint, and the muscle spindle in the form of a simple feedback control scheme. The alpha and gamma commands set the desired muscle length/joint angle and the reflex loop act to follow the desired trajectory. (b) Typical velocity profile of human reaching movement, well fitted by a minimum jerk trajectory as well as many other optimization schemes. (c) Deviation from a straight line at the first exposure to force perturbations, after adaptation (ct-1), during a catch trial (ct) and during the following trial (ct + 1), demonstrating trial by trial adaptation mechanism, adapted from [147].

and could be traced back to Claude Bernard's idea about the constancy of the internal environment (1865). The stretch reflex beautifully matches the engineering classical servo model of negative feedback: the muscle spindle reports muscle extension to the spinal cord, and this information returns through a single synapse over the motor neuron of the same muscle in the form of a motor command to shorten that muscle. Basic control theory tools such as mechanical models to the muscles, frequency response and stability analysis were extensively used to explore this system [94, 97].

Reaching movements are basic point-to-point arm movements. They are frequently used to test various computational models for the motor system. Such models started from basic kinematic observations about the fact that we typically perform straight line movements, using extrinsic coordinates rather than joints coordinate to plan our movements [1, 104]. In addition, it was found that the tangential speed of reaching movement is bell shaped; namely, the velocity smoothly increases and decreases during the movement (Fig. 1(b)). To account for these properties, various computational models were proposed. In these models, we assume that the motor system is optimal in some sense, and search for the optimization criterion that provides trajectories most similar to the observed arm movements. Among models which minimized smoothness, the minimum jerk model is probably the most successful and simple model that accounts for the straight line and bell-shaped speed profile [40]. However, various other models successfully described the same properties using other criteria [150, 8, 143]. Another type of study considered computational models of the muscles and reflex loop's nonlinear properties to account for the observed smooth bell-shaped speed profile of reaching movements [51, 70, 6, 81].

Adaptation is a prominent property of biological systems. Reaching movements were found to be extremely useful in exploration of adaptation and learning and the related computational models. The seminal study of Reza Shadmehr and Sandro Mussa-Ivaldi [134], which became one of the most cited papers of the Journal of Neuroscience, demonstrated that people tend to keep the reaching movement properties (e.g., straight line and bell-shaped speed profile) at the face of external force perturbations. They found that, during this implicit adaptation to force perturbations, subjects used intrinsic coordinates (joint coordinates) when extrapolating from one region of the workspace to the other. Numerous studies followed this influential work explored the capability of the brain to adapt to various force fields and tested various hypotheses in the form of computational models. The most prominent concept in these studies was the simple idea of adaptation by minimizing error from trial to trial [128, 27, 147], as depicted in Fig. 1(c).

Using reaching movements, and later other movements, such as lifting tasks [36], bimanual adaptation [78], and adaptive locomotion [20], the study of computational motor control progressed and used concepts of adaptive control and learning theory to account for the biological control of movement.

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2. Can We Build a Robot Indistinguishable from Human in Its Motor Control Capabilities?

Turing [149] proposed an elegant test to probe the intelligence of computers. In the Turing test, an interrogator presents written questions, by means of teleprinter, to two examined entities: a computer and a human being. If the interrogator cannot distinguish between the two entities after extended conversation, we would conclude that the computer is intelligent. Numerous pages of criticism and interpretations were written about the Turing test, e.g., [42, 114]. In this review, I address the motor system; therefore, I wish to concentrate on one criticism of the original Turing test which addresses the linguistic limitation of the original test, and asserts that the ultimate test is to build a robot indistinguishable from humans in all the aspects of its behavior. This is actually the gold standard and a necessary condition for any computational model: can we replace the actual measured data with simulation based on our best computational model, such that the replacement will be indistinguishable?

We have focused on hand movements in one dimension and developed a Turing like handshake test for motor intelligence [69, 75] providing a metric to evaluate human-likeness. Another similar method to evaluate human machine handshake likeness has recently been developed by [47]. It is important to note that the Turing test is based on subjective answers of a human interrogator, while model testing is usually based on objective comparison of measured and simulated data. However, with multiple tests of various individuals and conditions any limitation of the computational model will eventually be exposed.

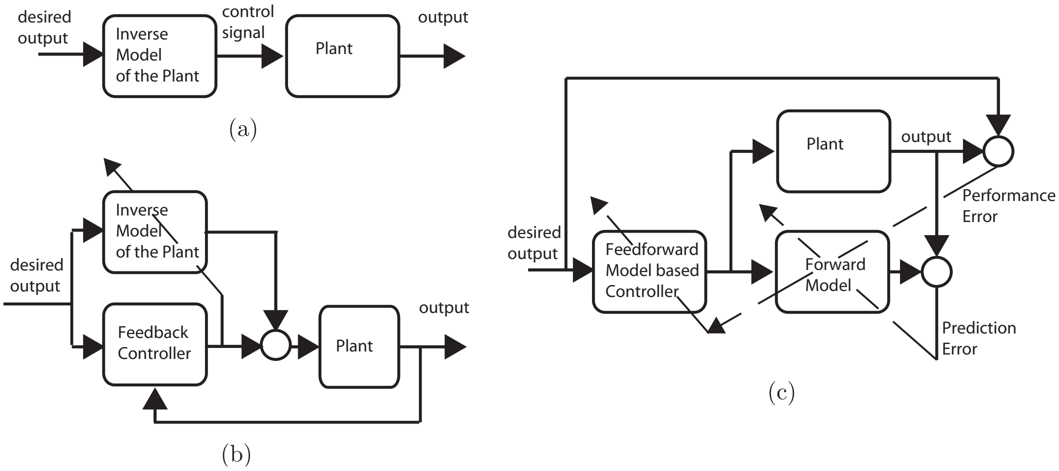
The implications of a positive answer to this first open question are enormous, scientifically and practically, in building human-like robotic devices and in the design of artificial limbs and assistive robotic devices which will interact naturally with humans. Altogether, the first open question is essentially the ultimate open question of computational motor control: can we build a computational model accounting for any possible perturbation and observation of the motor system? The study of computational motor control hypothesize a positive answer, and therefore, the rest of the questions address specific aspects and instances of this desired ultimate computational model.

3. Does the Brain Employ Internal Models of the Body and the Environment?

The notion of an internal model in the wide sense asserts that the brain contains some information about the controlled system, namely the musculoskeletal system and the external world. Most scientists cannot argue against internal models when so broadly defined, as the phenomenon of adaptation is well documented, and it clearly indicates that the brain employs motor memory or expectations about the world which can be termed internal models.

The controversy begins when someone tries to draw an input−output diagram and propose specific structure of the internal model which can be tested and sooner or later refuted. Proposing refutable hypotheses is the best way to promote science, and therefore, this kind of controversy is constructive. I will review here some of the prominent structures that were proposed for the internal models, and then discuss their implications to science, medicine, and technology.

Cyberneticians use feedback control to describe the motor system (Fig. 1(a)). However, with the progress of control theory, and in particular, the notion of adaptive control theory on the one hand and experimental evidence for adaptation in human behavior on the other hand, it was suggested that the feedback controller has to be adaptive [94], or alternatively, proposed that the brain can control the muscles without feedback by learning the inverse map of the controlled system [60]. Figure 2(a), demonstrates the notion of an inverse controller: It is simply the inverse of the controlled system. Kawato [76] proposed an elegant way to combine feedback control with an inverse model — feedback error learning, which is illustrated in Fig. 2(b). The feedback error learning model solves two problems of the simplified feedforward inverse model control of Fig. 2(a). It incorporates feedback with all its inherent advantages (noise rejection, insensitivity to changes in parameters etc.). In addition, it uses the feedback controller output instead of the output error as an error signal, and thus solves the problems of error signal propagation [72, 65]. Moreover, Kawato *et al.* [131] proposed that the inverse model is implemented in the cerebellum. They followed the studies of



(a)

(b)

(c)

Fig. 2. (a) An open loop control scheme with an internal inverse model as the controller generating the control signal to operate the plant and generate an output similar to the desired output. (b) Feedback error learning (following Kawato [76]). The control signal is the sum of standard feedback controller and an inverse model, where the inverse model is being adapted using the feedback controller signal as motor error. (c) Distal Teacher (following Jordan [64]). Control scheme similar to (a), with an additional forward model which is adapted using the prediction error and is used to propagate the performance error back to teach the inverse model appropriately.

Marr, Albus and Ito [61] and suggested a detailed specific model using modern computational tools of artificial neural networks. The notion of inverse model was later extended to multiple modes in to account for multiple contexts and complex mapping [160], or to account for multiple inverses in the case of redundant systems [73].

Another elegant solution to the problems of error propagation to teach the inverse model is the distal teacher [64]. This approach employs, in addition to the inverse model controller, another type of internal model, a forward model. A forward model generates an estimation of the output given the control signal. In the distal teacher approach, the forward model is trained in parallel to the inverse model; the performance error is then propagated through the forward model to obtain motor error that the inverse model adaptation algorithm can use, as depicted in Fig. 2(c). In this approach, the forward model is learned by minimizing the prediction error, and then it is used to transfer the performance error to the coordinates of the controller, and therefore serves as a teacher to the controller. In this sense, mental practice can be used to train the controller. In experiments that require mental practice, one should also distinguish between implicit and procedural knowledge, and carefully choose the instructions to the subjects and the measure of their success: either what they say or what they do after the mental practice [4].

Forward models are learned from practice and can generate predictions for the consequences of our own motor commands [38, 37]. The literature mentions at least three flavors of these structures: predictor, state estimator, and distal teacher [67]. Figure 2(c) illustrates the possible role of the forward model as a distal teacher [64]. In studies of grip force adaptation, it was demonstrated that subjects can predict the required grip force and a forward model was proposed to account for this behavior [37]. Forward model as state estimator was demonstrated to be plausible experimentally [159], and is used in current state-of-the-art computational models as an essential part of optimal control scheme [133].

The neurophysiological basis of internal models is under research. Among the regions of the brain postulated to be involved in forming and housing, the internal models are the motor cortex [89, 113] and the cerebellum [58, 131, 59, 121, 22]. These studies can shed light as to the location of the postulated internal models but cannot provide a direct evidence for their existence. In my opinion, the best evidence for internal models comes from psychophysical experiments, in which the limitation of our ability to adapt or transfer are quantitatively exposed, informing us of the coordinates and structure of the internal models.

Recent studies employed this notion of internal models with other tasks, such as using tools [24, 58], bimanual coordination [78], locomotion [20, 123], and lifting [15, 36, 95]. Altogether, I find the notion of internal models extremely useful to generate testable hypotheses and represent our knowledge about the motor system. In fact, many of the open questions in this review refers to the structure, capabilities, and limitations of these internal models.

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4. Is the Brain Capable of Representing the Flow of Time?

A system is capable of representing time, if it is possible to extract the time, t, from its state [74]. Numerous studies suggest the existence of explicit timing structures in the brain. Accurate musical performances are frequently explained as being based on biological clocks or internal timekeepers [112]. According to Ivry [62, 140], there is evidence for the involvement of many neural structures in the task of time representation, including the cerebellum, basal ganglia and some cortical structures. Time representation has been extensively discussed in the context of neurophysiology, computational models and behavioral studies [156, 154, 77]. However, within the context of adaptation to time-varying force perturbations, all the attempts to expose such time representation failed [74]. This clearly indicates that the motor system does not use time representation for motor adaptation. Current evidence suggests that the motor system employs only state representation, namely position and its time derivatives, such as velocity and acceleration, for adaptation to force perturbations [74, 21]. This evidence is relevant also to the structure of internal models discussed in the previous section as it limits their possible structure to mapping based on position and velocity, refuting the option of rote memorizing of time dependent control function [21]. Adaptation to a delayed force field [88], estimation of stiffness with delay [109, 107, 119, 120], or even assessing simultaneity, does not necessarily require representation of time in the form of an internal clock. These can all be accounted for by regression over force and position variables [107, 109, 118].

In the previous section, I discussed a special type of internal representation, the forward model [103, 67, 37]. This representation can be used for prediction of the outcome of our motor command, and importantly, it is most suitable for describing the internal representations of delay [41]. The cerebellum was proposed to host both internal models and time representation, and therefore, Diedrichsen *et al.* [22], have recently explored this specific question with a special task that involves timing and transfer. They conclude that the cerebellum is responsible for state estimation while timing aspects of the task are being processed in other areas, such as the planum temporal. An interesting speculation in the discussion of this paper asserts that timing may be processed in a way similar to internal speech.

As discussed in the seventh open question about learning and adaptation, it is possible that time representation is not used for adaptation, but instead, it is constructed by a dedicated learning mechanism for specific goals such as music performance. However, another alternative is that all the instances of apparent time representation are simply a disguised state representation. Only careful analysis of the generalization capabilities and accurate temporal transfer can potentially answer this open question with its interesting theoretical and practical consequences, e.g., for human-machine interfaces, teleoperation, and robotic surgery [110, 108].

We have noted two exceptions to the lack of evidence for time representation in the motor system. In a recent study of probing perception of simultaneity, we found that subjects reported the distance between two events based on the time between them and not based on the state simultaneity [117]. However, this case clearly differs from adaptation to force perturbations as it probes the perceptual level rather than the implicit motor adaptation mechanisms. In a careful study of rhythmic movements, we have recently found that movement frequency — or timing — is tightly controlled, even when explicit feedback regarding movement frequency is not given [9]. Indeed, even when healthy individuals misestimated the speed and the amplitude of their rhythmic movements when no visual feedback was given, there was little change in the frequency of their movements [87]. This kind of findings support the hypothesis that time keeping mechanism is involved in the generation of rhythmic movements. However, this kind of time representation could be limited to pattern generators that are based on spinal cord coupled with arm dynamics. Thus, the option that the central nervous system does not employ time representation for implicit motor adaptation is not refuted.

5. Does the Motor System Use Intermittent Control?

In intermittent control, instead of continuously calculating the control signal, the controller occasionally changes the control signal at certain sparse points in time, according to the control law. This control law may or may not, include feedback, adaptation, optimization, or any other control strategy. When, where and how does the brain employ intermittency as it controls movement? These are the open questions addressed in this section.

Evidence for intermittency in human motor control has been repeatedly observed in the neural control of movement literature [26, 35, 54, 105, 106, 141, 156, 45]. Moreover, some researchers have provided theoretical models to address intermittency [8, 17, 18, 54, 46]. Nevertheless, the vast majority of current models involve continuous control, e.g., [148].

Intermittent control is used in engineering systems in very cheap and simple systems, such as the thermostat in many home appliances, as well as in sophisticated systems with large delays or extensive processing time requirements [46]. Intermittent control is at the base of engineering theory of switched systems [3, 93, 53, 90]; in these systems, otherwise unstable systems can be stabilized [90, 43]. Several characteristics of the motor control system suggest that one should expect to find intermittent control strategies that minimize the effort of the central nervous system and effectively exploit the spinal cord as a channel of information transmission. These include delays in signal transmission caused by neural processing and conduction time, and the hierarchical nature of the system in which the spinal cord provides communication between the peripheral and the central nervous system. Indeed, evidence for the existence of intermittent control is provided by a wide

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range of studies. Measurement of hand movements in tracking a continuous moving target clearly demonstrate rapid movement followed by stops [105, 54, 101, 141, 102, 106, 100]. Some studies explained the intermittent nature of tracking movements by a refractory period of the central nervous system [106], or "step-and-hold" strategy where exceeding an error threshold generates movements [54, 101, 100]. Intermittent control is also at the basis of models for error correction submovements in reaching [57, 34]. It was suggested that the neural basis of intermittent control during tracking tasks is implemented within the cerebellum-thalamus-cortical loop [52, 102, 151] or within a basal-ganglia-cortex-cerebellum distributed processing modules for reaching [57]. Intermittent control is not restricted to displacement of the hand, rather, it is also evident during isometric force tasks [139, 151] and combined tasks such as tracking a target while experiencing forces [141], switching between motion and force control [152], as well as in handwriting and drawing [152, 129]. Intermittency is also apparent in many models addressing biological hierarchical systems, where the higher level sends intermittent commands to the lower level, e.g., to switch between oscillatory activities in human handwriting [138] or to perform complete arm movements in the octopus, where the basic motor program was found to be embedded within the neural circuitry of the arm itself [145].

Intermittency has also been observed in rhythmic movements [125, 26]. Doeringer and Hogan [26] specifically explored the proposition that vision is contributing to nonsmooth intermittent control. They found that vision is not the major source for the lack of smoothness in this type of movement. It was found that the level of intermittency in rhythmic movements depends on the frequency of movement in the sense that there are two types of movements. Low-frequency movements are more discrete-like and high-frequency movements are more rhythmic-like [86]. We have recently found that the switching between these types of movements does not always occur at the same frequency. When the movement frequency was gradually increasing or decreasing, we found a reverse-hysteresis behavior in the frequency at which the subjects switched from one movement type to the other. This phenomenon can suggest intermittent control, in which the switch time depends on the movement frequency in a predictive fashion [85].

Another possible example for intermittent control in the motor system can be found in the Minimum Acceleration Criterion with Constraints (MACC) model for the control of reaching movement [8]. As described in the beginning of this paper, reaching movements were studied extensively under the assumption that biological systems evolve to find optimal solutions. Therefore, multiple cost functions were suggested to be candidates for the optimization, and all of them produce the characteristic bell-shaped trajectories of movement velocity. These include minimizing jerk, torque change, and noise [150, 24, 40, 143, 55]. Traditionally, solutions to a minimum criterion involving kinematic quantities have been calculated analytically using the Euler-Poisson ordinary differential equation [124]. The analytical solution for the minimum acceleration criterion (MAC) shows nonzero acceleration at the boundaries. This contradicts the observed hand rest of the reaching movement before and after the movement, and therefore, the MAC was rejected, paving the way to the minimum jerk model [40]. Stein *et al.* [142, 143] indicated a few-limitations of the minimum jerk model and suggested that MAC based trajectory smoothed by a second order filter (muscle) are quite similar to minimum jerk trajectories. Nevertheless, the MAC model has not been seriously considered since. Ben-Itzhak and Karniel [8] proposed a remedy to the MAC by adding acceleration boundary conditions and developing an analytical solution based on the Pontryagin minimum principle [116]. To find a physiologically plausible solution, we also assumed constraints on the maximum and minimum jerk values, and called this criterion a "Minimum Acceleration Criterion with Constraints" (MACC). The MACC based trajectory consists of three segments of constant jerk signal. Precise details, as well as the analytical proof, are provided in [8]. In a first-order muscle model, the control signal is the first derivative of the force. Since the force is proportional to the acceleration, the control signal is proportional to the jerk. Thus, the MACC predicts bang-bang control at the jerk, namely, an intermittent control signal. A particular minor application of the MACC is in detecting onset of movement [14] which can be useful for behavioral neuroscience studies requiring accurate onset detection. Recent measurements in the cerebellum found clear evidence for an intermittent-control strategy [91, 161]. In these studies, it has clearly been shown that the activity of cerebellar Purkinje cells demonstrates bistability — bursting activities separated by pauses.

The concept of intermittence control has recently been studied for the control of inverted pendulum [92], and a thorough review of such a computational theory for intermittence control was written [44]. These and other models of intermittence control should be further extended to provide specific predictions for neural activations in various levels of the motor system. Whether neural recording will support such predicted transitions are the open questions to be explored. The implications of a positive answer include the improvement of movement disorder diagnostics, and the design of optimized haptic human robot interfaces. This could be utilized by concentrating on the relevant transition times in the motor command.

6. Does the Motor System Represent Equilibrium Trajectories?

One of the possible underlying mechanisms for intermittence control that was discussed in the last section is the threshold phenomenon. The threshold phenomenon is observed in each and every neuron and muscle tissue: every excitable cell in the body requires a minimum value of depolarization in order to generate an action potential.

Feldman [32] proposed that this basic threshold phenomenon governs the operation of motor neurons. These neurons are interconnected with the muscle and muscle spindles of antagonistic muscle groups, and thus, enable the higher level of the control hierarchy to send motor command about the desired limb equilibrium position. This is achieved by determining a parameter he called lambda (λ), which represents the actual threshold of neural activation in the system. The reader is referred to the textbook [84] and literature for support [32], and criticism [33, 111] of this theory. One limitation of the lambda model is that there is no simple relation between the value of lambda and limb position, since that will depend on the load, and may require in some conditions complex equilibrium trajectories [7, 19].

Bizzi *et al.* [115] led a series of studies in which a monkey had to reach a target without proprioception with or without perturbations. The results clearly demonstrated that the arm continues to move towards the target as soon as the obstacle is removed. These results support a theory according to which a stable equilibrium point is generated by the nervous system. Moreover, this equilibrium point can change with time and generate an equilibrium trajectory [11, 115]. Equilibrium point control was examined by Gomi and Kawato [48] who measured the arm stiffness and found clear evidence against the hypothesis that the brain sends as a motor command only an equilibrium-point trajectory similar to the actual trajectory.

We have opened this review with the seminal study of Shadmehr and Mussa-Ivaldi [134] which demonstrated adaptation to force perturbations and after effects of learning in catch trials. That study, as well as many other adaptation studies, clearly demonstrated that equilibrium points or equilibrium trajectories are not sufficient to account for our motor behavior, shifting the research from the lower reflex loop to the level of internal representation and the structure of internal models. Nevertheless, the question is still open since it is possible to assert that equilibrium trajectories exist, and that they are adaptive. There were only a few attempts to combine these two approaches, namely equilibrium point control and adaptation, e.g., [50]. Thus, a computational theory of threshold control, e.g., based on the lambda model, which will account for the rich literature about adaptation to force perturbations has yet to be developed.

7. What is the Difference Between Learning and Adaptation? Structural–Temporal Hierarchy of Wide Sense Adaptation

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 is WSA. Figure 3 presents a map of four instances of this phenomenon: Feedback, adaptation, learning and evolution, where sensory information is integrated and employed to change the control signal in various techniques and time scales. There are some clear boundaries and parallels to engineering concepts: e.g., between feedback that refers to signal flow, and adaptation that refers to changes in parameters, and between evolution and the other instances of WSA. However, the neural implementation of skill learning and

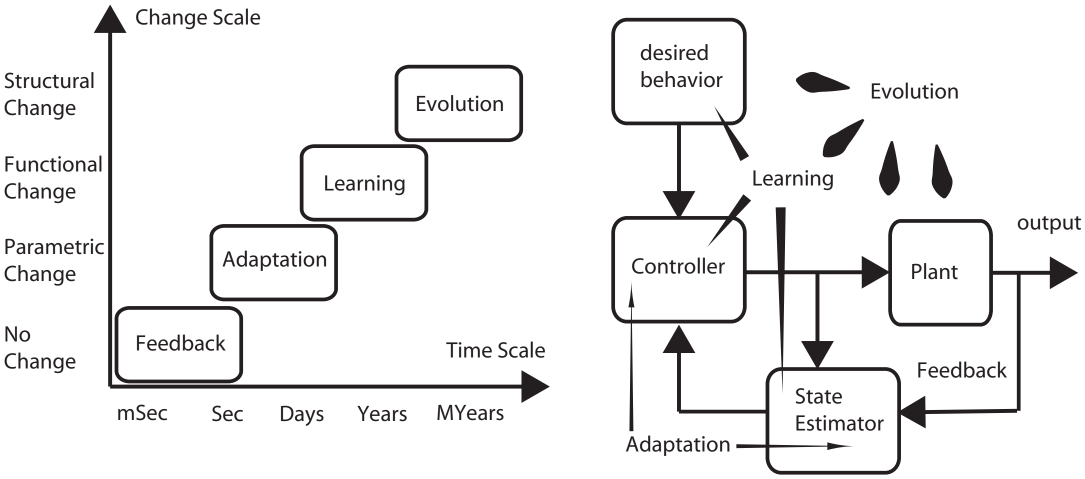

Fig. 3. The temporal structural hierarchy of wide sense adaptation in the motor control system. Feedback, adaptation, learning and evolution are instances of wide sense adaptation where sensory information is integrated and employed to change the control signal in various techniques and time scales. Left: The hierarchy on the temporal structural space. Right: Block diagram of control system demonstrating feedback, adaptation, learning and evolution. Adopted from [68].

other types of learning, and their specific structural and temporal structures, are the open questions discussed at the end of this section. I start with a description of the system approach, and then, I will clarify the scope of each part of this structural temporal hierarchy, and address each type of the WSA separately.

Figure 3 demonstrates the structural−temporal hierarchy in a block diagram. 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 nicely illustrated in the equilibrium point control theory.

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 observation of nature), and was later developed to include also adaptive control. We follow the engineering terminology, 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 [71], and later accurately defined in [68]. Here, I review the main definitions, and present the open question about the distinction between learning and adaptation.

7.1. *Feedback*

We refer to a system as feedback controlled when sensory information is fed back to generate the control signal during the performance of the task. Figure 1(a) describes the notion of feedback in a block diagram. The signal flows from the sensory system to the control 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 sensory signal and the length of the muscle. This last example demonstrates a limitation of the engineering approach: the blocks usually hide the detailed structure, and therefore, if we define the control signal as neural input we would never note the internal feedback loops within the muscle and joint. However, there is always a tradeoff, and the simplicity we obtain from this approach helps us in clarifying the notions. It should be noted 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, thus, the only delay is generated by the propagation of signals through the channels and the control system. Figure 1(a) captures the main properties of feedback, namely "signal flow in real time" and "no structural change in the system, only flow of signals."

7.2. *Adaptation*

Adaptive control is a control strategy where the controller can change its function to accommodate changes in the controlled system or in the environment, see e.g., [5]. Here, not only the signals are changed, but the control system is also changed based on the sensory information received. These changes in the system are typically slow when compared to the time scale of the feedback. Figures 2(b)−2(c) and 3(b) describe various instances of adaptive control systems. The controller includes a finite set of adjustable parameters; an adaptation algorithm observes the flow of signals to and from the control system, and determines how this set of parameters should change to improve some measure of performance. This third system — the adaptation algorithm — is implicit in the dashed or dot-dashed lines and is not drawn in a dedicated box in these figures. Let us summarize with a formal definition: Adaptive control is the change in the parameters of the control system generated after observation of previous control and sensory signals in order to improve the future performance of the system on a well-defined task or measurements of performance.

7.3. *Learning*

Learning generates a completely new behavior, as in skill learning, or employs a completely new strategy to achieve a known behavior. In both cases, the controller may change its structure. This is in contrast with adaptation, which refers to a change in parameters of the controller that improves the performance in certain types of existent behavior, without any structural change. Such structural changes in the biological system may include the recruitment of new brain areas or generation of a new neural circuit for specific task, which, in turn, cause behavioral implications such as change in the speed accuracy tradeoff [122]. 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. Later, these will be perfected by control engineers and return to serve as models for the brain. In summary, learning control is a structural change of the control system in order to generate a new type of behavior.

7.4. *Evolution*

In the proposed hierarchy, evolution is the last resort. 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 is an arbitrary change in the controller that can include any change in structure, function, connectivity, parameter values, learning algorithms and adaptation protocols. The best change is chosen by mutation and then survival of the fittest, and therefore, this process may be extremely long.

Altogether, the distinction between feedback and adaptation, and between learning and evolution, is quite clear and well defined, whereas the distinction between adaptation and skill learning is still a subject of active research both about the computational representation, and the neural implementation and the engineering counterpart in state of the art artificial learning control literature.

8. Is the Neural Control of Movement Optimal? In What Sense?

In the temporal−structural hierarchy of wide-sense adaptation, we have seen that sensory information is used to improve the performance of the motor system. However, the desired performance was not directly addressed. A different line of research cares less about the process of learning and adaptation and more about the desired outcome, typically under the assumption that after long practice the system converges to the desired outcome. It is important to note, that any desired outcome can be referred to as optimal (e.g., by defining optimal behavior in the sense of being close to that specific desired outcome). Therefore, the research concerning optimal motor control should consider three open questions for each task being studied: (a) Does the motor control system strives to reach a specific optimal behavior? (b) Does it actually obtain the optimal behavior in certain conditions? (c) What is this specific optimal behavior? The last question could be also phrased as: In what sense is the behavior optimal? or: What is the minimized cost function? Finally, since we posed this question for each and every task, we can also ask about the generalization and transfer within and between tasks.

Three branches of motor neuroscience use optimization techniques and terminology: trajectory formation studies, optimal feedback control, and Bayesian modeling studies. In trajectory formation studies, the question is typically which optimization criterion will predict the observed arm trajectory, e.g., minimum jerk [40], minimum acceleration [8], minimum object crackle [25], minimum hand jerk [146], minimum torque change [150], and minimum end-point variance [55].

Optimal feedback control is well developed in control theory [82] and has recently been used successfully in modeling human movement control [148, 23, 132, 136]. The main challenge within this framework is to derive the optimal control signal with real nonlinear time-varying biological systems, given specific cost function and the assumptions as to the structure of the noise.

Optimal feedback control is typically based on state feedback, and requires a state estimator which includes a forward model. The idea that the brain may employ state estimation to optimally combine sensory and predictive information was supported by many studies in the last decade [154, 99, 79]. Since optimal feedback control schemes typically use a simple feedback controller, an inverse model is not always required. Instead, the desired trajectory could be implicit within the solution of the optimal control law, accounting for the observed changes in the so-called desired trajectory during adaptation [28, 63]. An open challenge in this field is to develop adaptation algorithms to learn the forward model and an optimal controller which minimizes the cost function at the same time. For example, Mazzoni and Krakauer [96] showed that even when subjects can explicitly perform properly within visuomotor rotation task, they continue to learn the rotation implicitly. These kinds of studies facilitate the constructions of a complete model accounting for all the ingredients of optimal feedback control. Another interesting perspective of optimal feedback control is the fact that it naturally presents itself in a stochastic environment resolving the redundancy problem (see the last open question), by facilitating large variance in the irrelevant directions, also referred to as uncontrolled manifold [66, 130].

Bayesian modeling studies observe the behavior as optimal in the sense of using prior information about ourselves and about the environment (aka internal model), and combining this information with sensory feedback in an optimal way to combine a posterior state estimation. The question about structure of internal model or the sense of optimization is replaced with the selection of relevant variables and extracting or postulating the probability distribution of the prior. Here, I just mention this wide and successful line of study, and the reader is referred to the literature for many examples of successfully modeling various behavioral results, e.g., [144, 79, 31].

9. Does Motor Memory Represent the Past or the Future?

It was suggested that the purpose of memory is to plan for the future rather than to remember the past [2, 29, 127]. This distinction was made with regards to episodic memory. However, such a distinction is also of interest for motor neuroscience, and in particular in the context of motor memory where the concept of forward model is frequently used to describe this exact phenomenon. Namely, a forward model allows the motor system to use the past experiences in order to predict the future.

As described in the opening of this review, extensive research has been performed concerning the ability to adapt to force perturbations during the execution of reaching movements. This methodology was proven most useful in exploring issues related to motor memory [80, 12]. This finding was replicated in different experiments, demonstrating that people learn to adjust motor commands to compensate for disturbing forces depending consistently on the state of motion of the limb [126, 39, 134, 38, 83, 158]. Two main features of memory, consolidation and mental practice, were also studied in the motor control literature [80, 30, 16].

In all these studies of motor adaptation to force perturbations during reaching movements (see Fig. 1(c)), the trial by trial adaptation is based on the past in the sense that the expectation for perturbation in the next trial is generated by a weighted sum of the perturbations in the past few trials. In contrast to this well-established observation, we have recently tested the nature of predictive control during a lifting task and found that in the case when the weight of the object increases from trial to trial, the expectation extrapolates and essentially predicts the future weight of the lifted object [95]. Similarly, when performing a rhythmic task that requires a continuous increase or decrease in movement frequency, participants changed the type of their movement (from discrete-like to harmonic and vice versa) in a predictive fashion, apparently based on the expectation that the required frequency will continue to change in the future [85]. The exact conditions in which we predict the future and the conditions in which we use past average are still open for future investigation.

This open question could be related to the structure of internal models. Let us consider the forward model which predicts the expected sensory outcome of specific motor command. On the extreme case of the file cabinet analogy, the brain can register all motor commands and the following sensory outcome in a lookup table memorizing the past. This lookup table could be later used to predict the outcome of any motor command that was previously used. This kind of memory is a pure past representation; however it cannot be called a forward model, since it is not capable of predicting the consequence of motor commands which were never issued in the past. Once we allow interpolation or extrapolation based on this lookup table, we can call it a forward model, and then, at the same time, we start to address the future and not only the past. As we allow our lookup table to forget past events and count more on the statistics of the past rather than on specific events, we can no longer call it a lookup table and we give more and more weight to addressing the future.

On the other extreme, we can put a well-structured forward model with a few parameters. These are learned from past examples, and facilitate temporal extrapolation to the future. By mapping the ability of the motor system to adapt and testing hypotheses as to the structure of possible internal models, we can gradually map the way in which the motor system uses past experience in order to behave in the future.

10. Discussion

The biological system is characterized by redundancy in each and every level: there is more than one joint configuration for each location of the hand; there are many possible muscle activations which can generate the same torque in the joint; and there numerous possible neural activations which can bring the same muscle activation. The problem of redundancy, also known as the Bernstein problem, is extensively discussed in the literature [10, 13]. Redundancy is a virtue of the motor system, rather than a problem, and therefore the last question in this review is this: How does the brain exploit the virtue of redundancy? In many cases, the brain makes use of this virtue to obtain flexibility and reliability, rather than solves the problem of redundancy by selecting a single solution.

Redundancy means that the mapping of the controlled plant is many-to-one: therefore, the function of the plant is not invertible, questioning the meaning of inverse controller in Fig. 2(a). In order to address this question properly, I will take a short detour to address the limitations of the block diagram approach that was adapted in this review (Figs. 1(a), 2 and 3(b)) and discuss the extent to which they can describe a computational model and the kind of physiological data that can support or refute a theory presented by a block diagram.

It is important to note that the block diagrams in this paper just illustrate the verbal description. In order to use them as specific computational models, one needs to clearly state the coordinates of the inputs and outputs, and the specific mathematical functions of each block in the diagram and each learning algorithm. Moreover, specific predictions about neural recordings can be derived only when the physiological counterpart of the blocks and the measured signals in the block diagram are defined, while for specific behavioral predictions it is sufficient to define the physiological counterparts of the observed behavioral variables. Let us illustrate this for the block diagram in Fig. 1(a) describing the servo hypothesis for the reflex loop. Let us call the neural command u measured in units of pulse per second (PPS), the joint angle θ, measured in radians (rad), the muscle and arm function $f(u)$, and the muscle-spindle function $g(\theta, \gamma)$; then, one can write the model mathematically as

$$\theta = f(u) = f[\alpha + g(\theta, \gamma)]. \tag{10.1}$$

In the general case, one can consider the signals $u(t)$, and the arm and muscle-spindle as dynamic nonlinear time varying operators, $f[u(t), t]$, $g[\theta(t), \gamma(t), t]$. Moreover, the motor neurons dynamics could be described in more details than the simple summation of two firing rates in Eq. (10.1), however, this would requires additional blocks in the block diagram. Here, we just illustrate the relation between block diagrams, mathematical equations and the related physiological signals, and for that purpose, let us consider the steady state, in which each level of firing rate of motor neuron is mapped to specific joint angle, and each joint angle is mapped to specific muscle spindle firing rate.

The simplest implementation of this model is selecting arm and muscle function determining the angle to be related to the muscle shortening, $f(u) = ku$, where k is a constant describing this linear relation with units of [rad/PPS]. Similarly, let us model the muscle spindle as a simple summation of the gamma activity with the muscle length which is in turn proportional to the joint angle. In the following equation, the constant, c, represents this proportion and unit transformation between joint angle and firing rates at the muscle spindle, relative to the gamma firing rate, and therefore its units are [PPS/rad].

$$\theta = -k\alpha - k(c\theta + \gamma), \tag{10.2}$$

$$\theta(1 + kc) = -k(\propto + \gamma). \tag{10.3}$$

This extremely simplified selection of operators can already predict the relation between the joint angle and the neural command; however, it does not address the system dynamics, or its nonlinearities. This can be addressed using the same block diagram, but with dynamic system in the form of mathematical model in each block. Linear dynamic systems can be described by the impulse response and the Laplace transform, as elegantly done by McRuer *et al.* [97]. Block diagrams can be also enhanced by being more specific, e.g., replacing the block titled muscle and joints with two blocks representing the muscle as the force generator that moves the joints. This possibility raises another problem with block diagrams: the blocks are unidirectional, whereas the force in the muscles does not only determine the angle, but it is also influenced by the joint angle. This should be very carefully examined, and in some cases, a solution to the problem is to replace the classical input/output formulation with a two-port system. A block diagram along with the exact mathematical function of each block can be refuted or supported using physiological data. For example, behavioral data of measured joint angles in a well defined task can be used to either support or refute specific models of the arm and the joint. In more sophisticated computational models (Figs. 2 and 3), one can formulate a hypothesis about the neural structure that implements each block, and test it by means of fMRI, or by direct recording of the neural activity. Note that the latter requires additional assumptions as to the nature of the neural code. This is another important open question in neuroscience, but it is out of the scope of this review. In summary of this detour, as any scientific hypothesis, a block diagram along with its proposed mathematical expressions can be either supported or refuted using physiological data, such as behavioral measurements, muscle activations, and neural signals.

Let us return to the issue of redundancy. Optimal control can be considered as a solution for the problem of redundancy, e.g., by minimizing the norm of the control signal, pseudo-inverse can be used to replace the inverse model block in a non-invertible redundant system (Fig. 2(a)). However, the real challenge, in my opinion, is to understand how the brain uses different solutions under different circumstances. Multiple internal models [56, 160] might be the key to represent multiple solutions to the same goal [73]. Nevertheless, the criteria for selecting one of the multiple solutions under various cases are open for future research.

According to Bernstein, redundancy is a key property unique to biological systems compared to artificial systems (of his time). Today, a few artificial systems employ redundancy and then exploit it, usually for robustness. However, there is still a vast potential in imitating technology to learn from the biological motor control system about exploiting the virtue of redundancy. Therefore, answering this question has wide scientific as well as technological and medical potential benefit.

Clearly, there are many open questions I failed to list. These include the use of robust control and other engineering approaches not yet adopted by the computational motor control community, and many other computational models developed to fit specific neural structures. Nevertheless, even with this short list of open questions, starting from Turing and ending with Bernstein, we have a lot of work before us as we strive to formulate a reasonable computational model for the motor system. At the same time, as described in this review, we have made significant progress during the last few decades, and start to see the fruits of these efforts in new upcoming technologies of brain machine interfaces and rehabilitation robotics.

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References

[1] Abend W, Bizzi E, Morasso P, Human arm trajectory formation, *Brain* **105**(2):331–348, 1982.

[2] Addis DR, Pan L, Vu MA, Laiser N, Schacter DL, Constructive episodic simulation of the future and the past: Distinct subsystems of a core brain network mediate imagining and remembering, *Neuropsychologia* **47**(11):2222–2238, 2009.

[3] Agrachev A, Liberzon D, Lie-algebraic stability criteria for switched systems, *SIAM J Control Optim* **40**(1):253–269, 2001.

[4] Annett J, Motor imagery — Perception or action, *Neuropsychologia* **33**(11):1395–1417, 1995.

[5] Astrom KJ, Wittenmark B, *Adaptive Control*, Addison-Wesley, 1995.

[6] Barto AG, Fagg AH, Sitkoff N, Houk JC, A cerebellar model of timing and prediction in the control of reaching, *Neural Comput* **11**(3):565–594, 1999.

[7] Bellomo A, Inbar G, Examination of the gamma equilibrium point hypothesis when applied to single degree of freedom movements performed with different inertial loads, *Biol Cybern* **76**(1):63–72, 1997.

[8] Ben-Itzhak S, Karniel A, Minimum acceleration criterion with constraints implies bang-bang control as an underlying principle for optimal trajectories of arm reaching movements, *Neural Comput* **20**(3):779–812, 2008.

[9] Ben-Tov M, Levy-Tzedek S, Karniel A, Rhythmic movements are larger, faster but with the same frequency upon removal of visual feedback, *J Neurophysiol* in press, 2011.

[10] Bernstein N, *The Coordination and Regulation of Movements*, Pergamon Press, Oxford, 1967.

[11] Bizzi E, Accornero N, Chapple W, Hogan N, Posture control and trajectory formation during arm movement, *J Neurosci* **4**(11):2738–2744, 1984.

[12] Bizzi E, Mussa-Ivaldi FA, Neural basis of motor control and its cognitive implications, *Trends Cogn Sci* **2**(3):97–102, 1998.

[13] Bongaardt R, Meijer OG, Bernstein's theory of movement behavior: Historical development and contemporary relevance, *J Mot Behav* **32**(1):57–71, 2000.

[14] Botzer L, Karniel A, A simple and accurate onset detection method for a measured bell-shaped speed profile, *Front Neurosci* **3**:61, 2009.

[15] Bracewell R, Wing A, Soper H, Clark K, Predictive and reactive co-ordination of grip and load forces in bimanual lifting in man, *Eur J Neurosci* **18**(8):2396–2402, 2003.

[16] BrashersKrug T, Shadmehr R, Bizzi E, Consolidation in human motor memory, *Nature* **382**(6588):252–255, 1996.

[17] Bye RT, Neilson PD, The BUMP model of response planning: Variable horizon predictive control accounts for the speed-accuracy tradeoffs and velocity profiles of aimed movement, *Hum Mov Sci* **27**(5):771–798, 2008.

[18] Bye RT, Neilson PD, The BUMP model of response planning: Intermittent predictive control accounts for 10 Hz physiological tremor, *Hum Mov Sci* **29**:713–736, 2010.

[19] Capaday C, Stein RB, Variations of reflex parameters and their implications for the control of movements, *Behav Brain Sci* **9**:600–601, 1986.

[20] Choi JT, Bastian AJ, Adaptation reveals independent control networks for human walking, *Nature Neurosci* **10**(8):1055–1062, 2007.

[21] Conditt MA, Mussa-Ivaldi FA, Central representation of time during motor learning, *Proc Natl Acad Sci USA* **96**(20):11625–11630, 1999.

[22] Diedrichsen J, Criscimagna-Hemminger SE, Shadmehr R, Dissociating timing and coordination as functions of the cerebellum, *J Neurosci* **27**(23):6291–6301, 2007.

[23] Diedrichsen J, Shadmehr R, Ivry RB, The coordination of movement: Optimal feedback control and beyond, *Trends Cogn Sci* **14**(1):31–39, 2010.

[24] Dingwell JB, Mah CD, Mussa-Ivaldi FA, Manipulating objects with internal degrees of freedom: Evidence for model-based control, *J Neurophysiol* **88**(1):222–235, 2002.

[25] Dingwell JB, Mah CD, Mussa-Ivaldi FA, Experimentally confirmed mathematical model for human control of a non-rigid object, *J Neurophysiol* **91**(3):1158–1170, 2004.

[26] Doeringer J, Hogan N, Intermittency in preplanned elbow movements persists in the absence of visual feedback, *J Neurophysiol* **80**(4):1787–1799, 1998.

[27] Donchin O, Francis JT, Shadmehr R, Quantifying generalization from trial-by-trial behavior of adaptive systems that learn with basis functions: Theory and experiments in human motor control, *J Neurosci* **23**(27):9032–9045, 2003.

[28] Donchin O, Shadmehr R, Change of desired trajectory caused by training in a novel motor task, *Conf Proc IEEE Eng Med Biol Soc* **6**:4495–4498, 2004.

[29] Dudai Y, Carruthers M, The Janus face of mnemosyne, *Nature* **434**(7033):567, 2005.

[30] Dudai Y, Eisenberg M, Rites of passage of the engram: Reconsolidation and the lingering consolidation hypothesis, *Neuron* **44**(1):93–100, 2004.

[31] Ernst MO, Banks MS, Humans integrate visual and haptic information in a statistically optimal fashion, *Nature* **415**(6870):429–433, 2002.

[32] Feldman AG, *Forty Years of the Equilibrium-Point Hypothesis*, Tristar Printing, Lachine, Quebec, 2005.

[33] Feldman AG, Levin MF, The origin and use of positional frames of reference in motor control, *Behav Brain Sci* **18**:723–806, 1995.

[34] Fishbach A, Roy S, Bastianen C, Miller L, Houk J, Deciding when and how to correct a movement: Discrete submovements as a decision making process, *Exp Brain Res* **177**(1):45–63, 2007.

[35] Fishbach A, Roy SA, Bastianen C, Miller LE, Houk JC, Kinematic properties of on-line error corrections in the monkey, *Exp Brain Res* **164**(4):442–457, 2005.

[36] Flanagan JR, King S, Wolpert DM, Johansson RS, Sensorimotor prediction and memory in object manipulation, *Can J Exp Psychol* **55**(2):89–97, 2001.

[37] Flanagan JR, Vetter P, Johansson RS, Wolpert DM, Prediction precedes control in motor learning, *Current Biol* **13**(2):146–150, 2003.

[38] Flanagan JR, Wing AM, The role of internal models in motion planning and control: Evidence from grip force adjustments during movements of hand-held loads, *J Neurosci* **17**(4):1519–1528, 1997.

[39] Flash T, Gurevich I, Models of motor adaptation and impedance control in human arm movements, in Morasso PG, Sanguineti V (eds.), *Self-Organization, Computational Maps, and Motor Control Volume 119*, Elsevier-Science, pp. 423–481, 1997.

[40] Flash T, Hogan N, The coordination of arm movements: An experimentally confirmed mathematical model, *J Neurosci* **5**(7):1688–1703, 1985.

[41] Foulkes AJM, Miall RC, Adaptation to visual feedback delays in a human manual tracking task, *Exp Brain Res* **131**(1):101–110, 2000.

[42] French RM, The turing test: The first 50 years, *Trends Cogn Sci* **4**(3):115–122, 2000.

[43] Fu M, Barmish B, Adaptive stabilization of linear systems via switching control, *IEEE Transactions on Automatic Control* **31**(12):1097–1103, 1986.

[44] Gawthrop P, Loram I, Lakie M, Gollee H, Intermittent control: A computational theory of human control, *Biol Cybern* **104**(1–2):31–51, 2011.

[45] Gawthrop PJ, Wang L, Intermittent predictive control of an inverted pendulum, *Control Engineering Practice* **14**(11):1347–1356, 2006.

[46] Gawthrop PJ, Wang L, Event-driven intermittent control, *Int J Control* **82**(12):2235–2248, 2009.

[47] Giannopoulos E, Wang Z, Peer A, Buss M, Slater M, Comparison of people's responses to real and virtual handshakes within a virtual environment, *Brain Res Bull* (2010).

[48] Gomi H, Kawato M, Equilibrium-point control hypothesis examined by measured arm stiffness during multijoint movement, *Science* **272**(5258):117−120, 1996.

[49] Granit R, *Receptors and Sensory Perception*, Yale University Press, New Haven, 1955.

[50] Gribble PL, Ostry DJ, Compensation for loads during arm movements using equilibrium-point control, *Exp Brain Res* **135**(4):474−482, 2000.

[51] Gribble PL, Ostry DJ, Sanguineti V, Laboissiere R, Are complex control signals required for human arm movement? *J Neurophysiol* **79**(3):1409−1424, 1998.

[52] Gross J, Timmermann L, Kujala J, Dirks M, Schmitz F, Salmelin R, Schnitzler A, The neural basis of intermittent motor control in humans, *Proc Natl Acad Sci USA* **99**(4):2299−2302, 2002.

[53] Hai L, Antsaklis PJ, Stability and stabilizability of switched linear systems: A survey of recent results, *IEEE Transactions on Automatic Control* **54**(2):308−322, 2009.

[54] Hanneton S, Berthoz A, Droulez J, Slotine JJE, Does the brain use sliding variables for the control of movements? *Biol Cybern* **77**(6):381−393, 1997.

[55] Harris CM, Wolpert DM, Signal-dependent noise determines motor planning, *Nature* **394**(6695):780−784, 1998.

[56] Haruno M, Wolpert DM, Kawato M, MOSAIC model for sensorimotor learning and control, *Neural Comp* **13**(10):2201−2220, 2001.

[57] Houk JC, Bastianen C, Fansler D, Fishbach A, Fraser D, Reber PJ, Roy SA, Simo LS, Action selection and refinement in subcortical loops through basal ganglia and cerebellum, *Philos Trans Roy Soc B: Biol Sci* **362**(1485):1573−1583, 2007.

[58] Imamizu H, Kuroda T, Miyauchi S, Yoshioka T, Kawato M, Modular organization of internal models of tools in the human cerebellum, *Proc Natl Acad Sci USA* **100**(9):5461−5466, 2003.

[59] Imamizu H, Miyauchi S, Tamada T, Sasaki Y, Takino R, Putz B, Yoshioka T, Kawato M, Human cerebellar activity reflecting an acquired internal model of a new tool, *Nature* **403**(6766):192−195, 2000.

[60] Inbar GF, Yafe A, Parameter and signal adaptation in the stretch reflex loop, in Homma (ed.), *Progress in Brain Research*, Elsevier, Amsterdam, pp. 317−337, 1976.

[61] Ito M, Neurophysiological aspects of the cerebellar motor control system, *Int J Neurol* **7**(2):162−176, 1970.

[62] Ivry RB, The representation of temporal information in perception and motor control, *Curr Opin Neurobiol* **6**(6):851−857, 1996.

[63] Izawa J, Rane T, Donchin O, Shadmehr R, Motor adaptation as a process of reoptimization, *J Neurosci* **28**(11):2883−2891, 2008.

[64] Jordan M, Rumelhart D, Forward models: Supervised learning with a distal teacher, *Cogn Sci* **16**:307−354, 1992.

[65] Jordan MI, Computational aspects of motor control and motor learning, in Heuer, Keele (eds.), *Handbook of Perception and Action: Motor Skills*, Academic Press, New York, 1996.

[66] Kang N, Shinohara M, Zatsiorsky V, Latash M, Learning multi-finger synergies: An uncontrolled manifold analysis, *Exp Brain Res* **157**(3):336−350, 2004.

[67] Karniel A, Three creatures named 'forward model', *Neural Netw* **15**(3):305−307, 2002.

[68] Karniel A, Computational motor control, in Binder, Hirokawa, Windhorst (eds.), *Encyclopedia of Neuroscience*, Springer-Verlag, Berlin, pp. 832−837, 2009.

[69] Karniel A, Avraham G, Peles B-C, Levy-Tzedek S, Nisky I, One dimensional Turing-like handshake test for motor intelligence, *J Vis Exp* **46**:e2492, 2010.

[70] Karniel A, Inbar GF, A model for learning human reaching movements, *Biol Cybern* **77**(3):173−183, 1997.

[71] Karniel A, Inbar GF, Human motor control: Learning to control a time-varying, nonlinear, many-to-one system, *IEEE T Syst Man Cyb Part C — Appl Rev* **30**(1): 1−11, 2000.

[72] Karniel A, Meir R, Inbar GF, Best estimated inverse versus inverse of the best estimator, *Neural Netw* **14**(9):1153−1159, 2001.

[73] Karniel A, Meir R, Inbar GF, Polyhedral mixture of linear experts for many-to-one mapping inversion and multiple controllers, *Neurocomputing* **37**:31−49, 2001.

[74] Karniel A, Mussa-Ivaldi FA, Sequence, time, or state representation: How does the motor control system adapt to variable environments? *Biol Cybern* **89**(1):10−21, 2003.

[75] Karniel A, Nisky I, Avraham G, Peles B-C, Levy-Tzedek S, A Turing-like handshake test for motor intelligence, in Kappers, van Erp, Bergmann Tiest, van der Helm (eds.), *Haptics: Generating and Perceiving Tangible Sensations*, Lecture Notes in Computer Science, Springer Berlin/Heidelberg, pp. 197−204, 2010.

[76] Kawato M, Internal models for motor control and trajectory planning, *Curr Opin Neurobiol* **9**:718−727, 1999.

[77] Keating JG, Thach WT, No clock signal in the discharge of neurons in the deep cerebellar nuclei, *J Neurophysiol* **77**(4):2232−2234, 1997.

[78] Klaiman E, Karniel A, Bimanual adaptation: Internal representations of bimanual rhythmic movements, *Exp Brain Res* **171**(2):204−214, 2006.

[79] Kording KP, Wolpert DM, Bayesian integration in sensorimotor learning, *Nature* **427**(6971):244−247, 2004.

[80] Krakauer J, Shadmehr R, Consolidation of motor memory, *Trends Neurosci*, in press, corrected proof available online 14, November 2005.

[81] Krylow AM, Rymer WZ, Role of intrinsic muscle properties in producing smooth movements, *IEEE Trans Biomed Eng* **44**:165−176, 1997.

[82] Kwakernak H, Sivan R, *Linear Optimal Systems*, Wiley-Interscience, New York, 1972.

[83] Lackner JR, DiZio P, Rapid adaptation to Coriolis force perturbations of arm trajectories, *J Neurophysiol* **72**:299−313, 1994.

[84] Latash, ML, *Control of Human Movement*, Human Kinetics, Champaign, 1993.

[85] Levy-Tzedek S, Ben Tov M, Karniel A, Early switching between movement types: Indication of predictive control? *Brain Res Bull* (in press).

[86] Levy-Tzedek S, Krebs H, Song D, Hogan N, Poizner H, Non-monotonicity on a spatio-temporally defined cyclic task: Evidence of two movement types? *Exp Brain Res* **202**(4):733−746, 2010.

[87] Levy-Tzedek S, Krebs HI, Arle JE, Shils JL, Poizner H, Rhythmic movement in Parkinson's disease: Effects of visual feedback and dopaminergic medication, *Exp Brain Res* **211**(2):277−286, 2011.

[88] Levy N, Pressman A, Mussa-Ivaldi FA, Karniel A, Adaptation to delayed force perturbations in reaching movements, *PLoS ONE* **5**(8):e12128, 2010.

[89] Li CSR, Padoa-Schioppa C, Bizzi E, Neuronal correlates of motor performance and motor learning in the primary motor cortex of monkeys adapting to an external force field, *Neuron* **30**(2):593−607, 2001.

[90] Liberzon D, *Switching in Systems and Control*, Springer, 2003.

[91] Loewenstein Y, Mahon S, Chadderton P, Kitamura K, Sompolinsky H, Yarom Y, Hausser MH, Bistability of cerebellar Purkinje cells modulated by sensory stimulation, *Nat Neurosci* **8**(2):202−211, 2005.

[92] Loram ID, Gollee H, Lakie M, Gawthrop PJ, Human control of an inverted pendulum: Is continuous control necessary? Is intermittent control effective? Is intermittent control physiological? *J Physiol* **589**(2):307−324, 2011.

[93] Margaliot M, Stability analysis of switched systems using variational principles: An introduction, *Automatica* **42**(12):2059−2077, 2006.

[94] Marsden CD, Merton PA, Morton HB, Servo action in human voluntary movement, *Nature* **238**(5360):140−143, 1972.

[95] Mawase F, Karniel A, Evidence for predictive control in lifting series of virtual objects, *Exp Brain Res* **203**(2):447−452, 2010.

[96] Mazzoni P, Krakauer JW, An implicit plan overrides an explicit strategy during visuomotor adaptation, *J Neurosci* **26**(14):3642−3645, 2006.

[97] McRuer DT, Magdaleno RE, Moore GP, A neuromuscular actuation system model, *IEEE Transactions on Man-Machine Systems* **MMS-9**(3):61−71, 1968.

[98] Meijer OG, Making things happen: An introduction to the history of movement science, in Latash, Zatsiorsky (eds.), *Classics in Movement Science*, Human Kinetics, 2001.

[99] Miall RC, Christensen LO, Cain O, Stanley J, Disruption of state estimation in the human lateral cerebellum, *PLoS Biol* **5**(11):e316, 2007.

[100] Miall RC, Weir DJ, Stein JF, Visuomotor tracking with delayed visual feedback, *Neuroscience* **16**(3):511, 1985.

[101] Miall RC, Weir DJ, Stein JF, Manual tracking of visual targets by trained monkeys, *Behav Brain Res* **20**(2):185−201, 1986.

[102] Miall RC, Weir DJ, Stein JF, Visuo-motor tracking during reversible inactivation of the cerebellum, *Exp Brain Res* **65**(2):455−464, 1987.

[103] Miall RC, Wolpert DM, Forward models for physiological motor control, *Neural Netw* **9**(8):1265−1279, 1996.

[104] Morasso P, Spatial control of arm movements, *Exp Brain Res* **42**:223−227, 1981.

[105] Navas F, Stark L, Sampling or intermittency in hand control system dynamics, *Biophys J* **8**(2):252−302, 1968.

[106] Neilson PD, Neilson MD, O'Dwyer NJ, Internal models and intermittency: A theoretical account of human tracking behavior, *Biol Cybern* **58**(2):101−112, 1988.

[107] Nisky I, Baraduc P, Karniel A, Proximodistal gradient in the perception of delayed stiffness, *J Neurophysiol* **103**(6):3017−3126, 2010.

[108] Nisky I, Mussa-Ivaldi FA, Karniel A, Perceptuo-motor transparency in bilateral teleoperation, in *Proceedings of The ASME 2008 9th Biennial Conference on Engineering Systems Design and Analysis (ESDA2008)*, Haifa. Vol. 2.

[109] Nisky I, Mussa-Ivaldi FA, Karniel A, A regression and boundary-crossing-based model for the perception of delayed stiffness, *IEEE Transactions on Haptics* **1**:73−83, 2008.

[110] Nisky I, Pressman A, Pugh CM, Mussa-Ivaldi FA, Karniel A, Perception and action in teleoperated needle insertion, *IEEE Transaction on Haptics* **4**:155–166, 2011.

[111] Ostry DJ, Feldman AG, A critical evaluation of the force control hypothesis in motor control, *Exp Brain Res* **153**(3):275–288, 2003.

[112] Palmer C, Music performance, *Ann Rev Psychol* **48**:115–138, 1997.

[113] Paz R, Boraud T, Natan C, Bergman H, Vaadia E, Preparatory activity in motor cortex reflects learning of local visuomotor skills, *Nat Neurosci* **6**(8):882–890, 2003.

[114] Pinar Saygin A, Cicekli I, Akman V, Turing test: 50 years later, *Minds and Machines* **10**(4):463–518, 2000.

[115] Polit A, Bizzi E, Characteristics of motor programs underlying arm movements in monkeys, *J Neurophysiol* **42**(1):183–194, 1979.

[116] Pontryagin LS, Boltyanskii V, Gamkrelidze R, Mishchenko E, *The Mathematical Theory of Optimal Processes*, John Wiley & Sons, 1962.

[117] Pressman A, Karniel A, Mussa-Ivaldi FA, Time representation for perception of simultaneity during slicing movement, *The Third Computational Motor Control Workshop*, Beer-Sheva, Israel, 2007.

[118] Pressman A, Karniel A, Mussa-Ivaldi FA, How soft is that pillow? The perceptual localization of the hand and the haptic assessment of contact rigidity, *J Neurosci*, in Press (2011).

[119] Pressman A, Nisky H, Karniel A, Mussa-Ivaldi FA, Probing virtual boundaries and the perception of delayed stiffness, *Advanced Robotics* **22**(1):119–140, 2008.

[120] Pressman A, Welty LH, Karniel A, Mussa-Ivaldi FA, Perception of delayed stiffness, *The International Journal of Robotics Research* **26**:1191–1203, 2007.

[121] Rabe K, Livne O, Gizewski ER, Aurich V, Beck A, Timmann D, Donchin O, Adaptation to visuomotor rotation and force field perturbation is correlated to different brain areas in patients with cerebellar degeneration, *J Neurophysiol* **101**(4):1961–1971, 2009.

[122] Reis J, Schambra HM, Cohen LG, Buch ER, Fritsch B, Zarahn E, Celnik PA, Krakauer JW, Noninvasive cortical stimulation enhances motor skill acquisition over multiple days through an effect on consolidation, *Proc Natl Acad Sci USA* **106**(5):1590–1595, 2009.

[123] Reisman DS, Wityk R, Silver K, Bastian AJ, Locomotor adaptation on a split-belt treadmill can improve walking symmetry post-stroke, *Brain* **130**(7):1861–1872, 2007.

[124] Richardson MJE, Flash T, Comparing smooth arm movements with the two-thirds power law and the related segmented-control hypothesis, *J Neurosci* **22**(18):8201–8211, 2002.

[125] Russell DM, Sternad D, Sinusoidal visuomotor tracking: Intermittent servo-control or coupled oscillations? *J Mot Behav* **33**(4):329–349, 2001.

[126] Sainburg RL, Ghez C, Kalakanis D, Intersegmental dynamics are controlled by sequential anticipatory, error correction, and postural mechanisms, *J Neurophysiol* **81**(3):1045–1056, 1999.

[127] Schacter DL, Addis DR, Constructive memory: The ghosts of past and future, *Nature* **445**(7123):27, 2007.

[128] Scheidt RA, Dingwell JB, Mussa-Ivaldi FA, Learning to move amid uncertainty, *J Neurophysiol* **86**(2):971–985, 2001.

[129] Schenk T, Walther EU, Mai N, Closed- and open-loop handwriting performance in patients with multiple sclerosis, *Eur J Neurol* **7**(3):269−279, 2000.

[130] Scholz JP, Schoner G, The uncontrolled manifold concept: Identifying control variables for a functional task, *Exp Brain Res* **126**(3):289−306, 1999.

[131] Schweighofer N, Arbib MA, Kawato M, Role of the cerebellum in reaching movements in humans. I Distributed inverse dynamics control, *Eur J Neurosci* **10**(1):86−94, 1998.

[132] Scott SH, Optimal feedback control and the neural basis of volitional motor control, *Nat Rev Neurosci* **5**(7):534−546, 2004.

[133] Shadmehr R, Krakauer JW, A computational neuroanatomy for motor control, *Experimental Brain Research Experimentelle Hirnforschung Experimentation Cerebrale* **185**(3):359−381, 2008.

[134] Shadmehr R, Mussa-Ivaldi FA, Adaptive representation of dynamics during learning of a motor task, *J Neurosci* **14**(5):3208−3224, 1994.

[135] Shadmehr R, Mussa-Ivaldi FA, *Biological Learning and Control: How the Brain Builds Representations, Predicts Events, and Makes Decisions*, MIT Press, in press.

[136] Shadmehr R, Smith MA, Krakauer JW, Error correction, sensory prediction, and adaptation in motor control, *Ann Rev Neurosci* **33**:89−108, 2010.

[137] Shadmehr R, Wise SP, *The Computational Neurobiology of Reaching and Pointing: A Foundation for Motor Learning*, MIT Press, 2005.

[138] Singer Y, Tishby N, Dynamical encoding of cursive handwriting, *Biol Cybern* **71**(3):227−237, 1994.

[139] Slifkin AB, Vaillancourt DE, Newell KM, Intermittency in the control of continuous force production, *J Neurophysiol* **84**(4):1708−1718, 2000.

[140] Spencer RMC, Zelaznik HN, Diedrichsen J, Ivry RB, Disrupted timing of discontinuous but not continuous movements by cerebellar lesions, *Science* **300**(5624):1437−1439, 2003.

[141] Squeri V, Masia L, Casadio M, Morasso P, Vergaro E, Force-field compensation in a manual tracking task, *PLoS ONE* **5**(6):e11189, 2010.

[142] Stein RB, Cody FW, Capaday C, The trajectory of human wrist movements, *J Neurophysiol* **59**(6):1814−1830, 1988.

[143] Stein RB, Oguztoreli MN, Capaday C, What is optimized in muscular movements? in Jones NL (ed.), *Human Muscle Power*, Human Kinetics, Champaign, IL, pp. 131−150, 1986.

[144] Stevenson IH, Fernandes HL, Vilares I, Wei K, Kording KP, Bayesian integration and non-linear feedback control in a full-body motor task, *PLoS Comput Biol* **5**(12): e1000629, 2009.

[145] Sumbre G, Gutfreund Y, Fiorito G, Flash T, Hochner B, Control of octopus arm extension by a peripheral motor program, *Science* **293**(5536):1845−1848, 2001.

[146] Svinin M, Goncharenko I, Zhi-Wei L, Hosoe S, Reaching movements in dynamic environments: How do we move flexible objects? *IEEE Transactions on Robotics* **22**(4):724−739, 2006.

[147] Thoroughman KA, Shadmehr R, Learning of action through adaptive combination of motor primitives, *Nature* **407**(6805):742−747, 2000.

[148] Todorov E, Jordan MI, Optimal feedback control as a theory of motor coordination, *Nat Neurosci* **5**(11):1226−1235, 2002.

[149] Turing AM, Computing machinery and intelligence, *Mind, A Quarterly Review of Psychology and Philosophy* LIX, 236, 1950.

[150] Uno Y, Kawato M, Suzuki R, Formation and control of optimal trajectory in human multijoint arm movement — Minimum torque-change model, *Biol Cybern* **61**(2):89−101, 1989.

[151] Vaillancourt DE, Mayka MA, Corcos DM, Intermittent visuomotor processing in the human cerebellum, parietal cortex, and premotor cortex, *J Neurophysiol* **95**(2):922−931, 2006.

[152] Venkadesan M, Valero-Cuevas FJ, Neural control of motion-to-force transitions with the fingertip, *J Neurosci* **28**(6):1366−1373, 2008.

[153] Viviani P, Terzuolo C, Trajectory determines movement dynamics, *Neuroscience* **7**(2):431−437, 1982.

[154] Wagner MJ, Smith MA, Shared internal models for feedforward and feedback control, *J Neurosci* **28**(42):10663−10673, 2008.

[155] Welsh JP, Lang EJ, Suglhara I, Llinas R, Dynamic organization of motor control within the olivocerebellar system, *Nature* **374**(6521):453−457, 1995.

[156] Welsh JP, Llinas R, Some organizing principles for the control of movement based on olivocerebellar physiology, *Prog Brain Res* **114**:449−461, 1997.

[157] Whitteridge G, De Motu Locali Animalium [on animal movement] (I627). Harvey W, Edited, translated and introduced by Gweneth Whitteridge, Cambridge University Press, 1959.

[158] Wolpert DM, Ghahramani Z, Computational principles of movement neuroscience, *Nat Neurosci Suppl* **3**:1212−1217, 2000.

[159] Wolpert DM, Ghahramani Z, Jordan MI, An internal model for sensorimotor integration, *Science* **269**(5232):1880−1882, 1995.

[160] Wolpert DM, Kawato M, Multiple paired forward and inverse models for motor control, *Neural Netw* **11**(7−8):1317−1329, 1998.

[161] Yartsev MM, Givon-Mayo R, Maller M, Donchin O, Pausing purkinje cells in the cerebellum of the awake cat, *Front Syst Neurosci* **3**:2, 2009.