Motor Control: In Search of Physics of the Living Systems

by
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This review contrasts two approaches to motor control that have dominated the field over the past years. One of them is built on ideas of the control theory; it assumes that neuronal structures perform computations and operates with notions such as motor programs and internal models. The alternative approach is based on physics and neurophysiology. It refutes the assumption of neural computations and operates with such notions as neuronal thresholds and equilibrium states. The two approaches have different goals. The former tries to produce a formal description of how any system, irrespective of its physics and physiology, can produce typical features of biological movement. This research may be very productive and important for such fields as robotics and prosthetics. The latter approach tries to produce a formal description of how neuromotor processes within the actual systems for movement production (for example, the human body) are organized to produce coordinated movements. Its goal is to turn motor control into a subfield of physics of living systems. Recent developments of the equilibrium-point hypothesis, referent configuration hypothesis, and the ideas of synergic control represent important steps towards achieving this goal.

Key words: *Equilibrium-point hypothesis, referent configuration, control theory, synergy*

Introduction

Motor control is a relatively young field of research in biology. Let me define it as an area of natural science exploring how the nervous system produces purposeful, coordinated movements in its interaction with the rest of the body and with the environment. Its goal is to create a formal description, operating with exactly defined variables, of the physical and physiological processes that make such movements possible. Progress in motor control over the recent years has been relatively slow. This situation is exacerbated by the lack of a broadly accepted and exactly defined set of notions that would be specific for typical problems of motor control, an adequate language for this area of research (see Gelfand & Latash 1998, 2002).

It is very hard to look for an adequate set of notions in an area that does not have them (but it is also very challenging and exciting!). It is much more simple (and tempting) to borrow one of the developed approaches from another field that shares "key words" with motor control, for example classical mechanics, control theory, and engineering. One should keep in mind, however, that such approaches have strict limitations. They can provide tools that help find answers to questions after the questions have been formulated. But they cannot offer an adequate formulation of questions in a field that differs from the areas for which these approaches have been developed.

Consider a few basic features of biological objects. Such objects belong to the physical world and they are alive. So, help with formulating questions may be expected to come from physics and biology (physiology). Contemporary physics alone would have problems dealing with biological movement that are typically intentional and goal-directed.

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Physics of living systems, unfortunately, does not exist so far, although the author of this paper graduated some 30+ years ago from the Moscow Physico-Technical Institute, and his major was indeed the non-existing *Physics of Living Systems*.

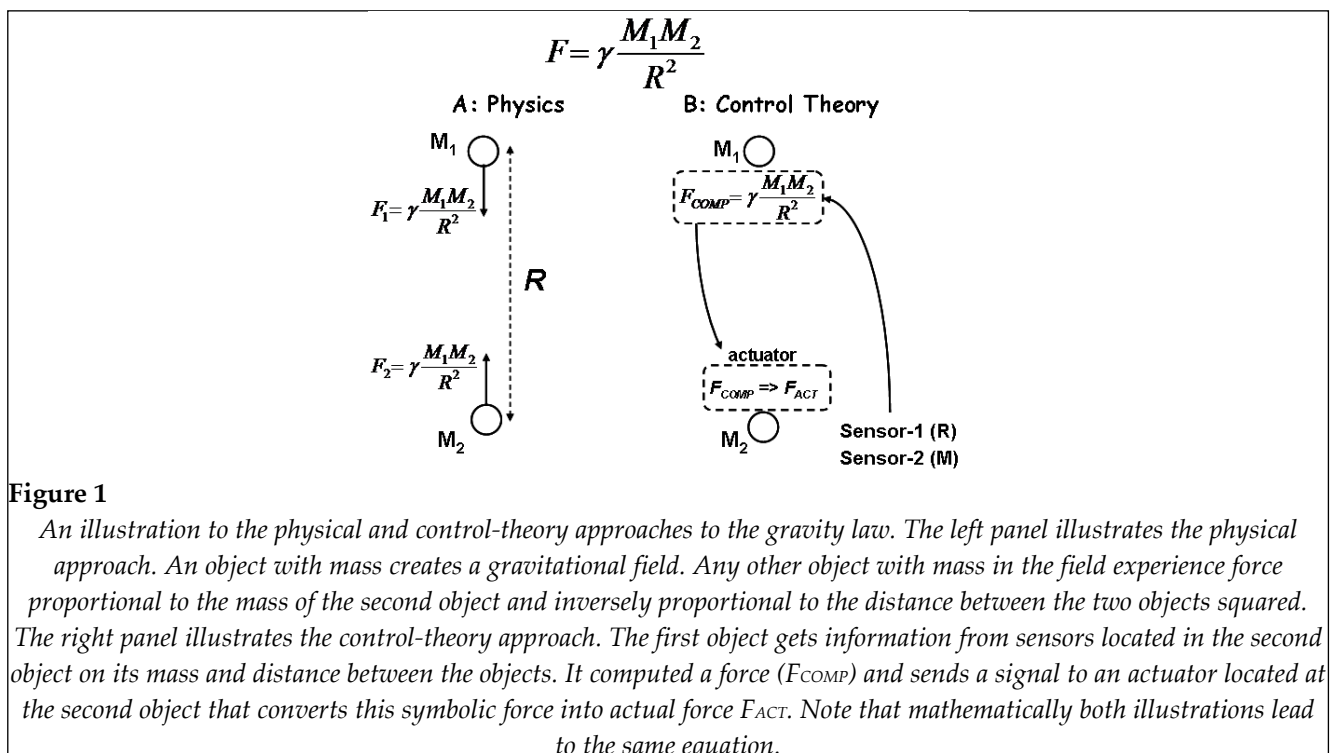## A simple physical law represented by physics and by control theory

One of the vigorously developed approaches to motor control has been based on the control theory, the idea of internal models, and certain methods of classical statistics (reviewed in Shadmehr & Wise 2005; Bays & Wolpert 2007). Despite the numerous publications in the most respected journals, the author remains skeptical towards these approaches because they import the computational methods from other areas of science in a hope that the same methods are somehow incorporated into the functioning of the central nervous system.

To illustrate the main difference between the physical approach and the control-theory approach, let me consider the classical physical law of gravity (Figure 1). Two objects with non-zero mass exert forces on each other proportional to the masses of the objects and inversely proportional to the distance between the objects squared. The left panel of Figure 1 illustrates a typical physical account of the law of gravity. An object with mass M_1 creates a gravitational field. Another object with mass M_2 experiences the gravity force. The right panel illustrates a control-theory account of the same law. There are two sensors located in the second object. They send signals to the first objects related to the distance between the objects (R) and mass of the second object (M_2). The first object computed a signal corresponding to the desired force value (F_{COMP}). It sends this signal to an actuator located at the second object, which transforms the symbolic value F_{COMP} into an actual F_{ACT}. This description can be repeated assuming sensors in object M_1 and computations being performed by object M_2.

Mathematically, the two panels can be described with the same equation. Which of the two descriptions should be preferred? I hope that all the readers would agree that the left panel illustrates the physical law of gravity, while the right panel illustrates how to model this law using non-gravitational means. So, if the purpose is to understand the physics of interactions between two material objects, the left panel is the only one to be used. If the purpose is to build a system that illustrates the law of gravity to students, the scheme in the right panel may be preferred.

In situations when one deals with a known physical law, the difference between the two illustrations in Figure one is obvious. It becomes less obvious when the physics of the system under consideration is poorly known. It becomes very tempting to assume the existence of computations somewhere

Figure 1

An illustration to the physical and control-theory approaches to the gravity law. The left panel illustrates the physical approach. An object with mass creates a gravitational field. Any other object with mass in the field experience force proportional to the mass of the second object and inversely proportional to the distance between the two objects squared. The right panel illustrates the control-theory approach. The first object gets information from sensors located in the second object on its mass and distance between the objects. It computed a force (F_{COMP}) and sends a signal to an actuator located at the second object that converts this symbolic force into actual force F_{ACT}. Note that mathematically both illustrations lead to the same equation.

within the system (as in the right panel of Figure 1), which allow to predict aspects of its behavior.

Feedback loops in control theory and in physical systems

The illustrations in Figure 1 reflect two roles mathematics play in natural sciences, including motor control. Mathematics may be a reflection of known physical and/or physiological processes in a concise form that facilitates their analysis. Knowledge of these processes can be incomplete, and mathematics may help in refining such knowledge. Alternatively, mathematics may reflect behavior of the system across different situations while being indifferent to actual physical (and physiological) processes that underlie the behavior. Israel Gelfand, one of the greatest mathematicians of the past century who contributed significantly to motor control (Gelfand & Tsetlin 1962, 1966), called researchers who used mathematics in the latter sense to study physiological processes "modelers" – not a praise in Gelfand's vocabulary.

Consider another example. All the current models in motor control use the notion of feedback. For example, feedback from peripheral receptors plays a major role in the equilibrium-point hypothesis (Feldman 1966, 1986; reviewed in Latash 2008b) by establishing a relation between muscle length and active muscle force (tonic stretch reflex). It allows the controller to use descending signals that produce subthreshold depolarization of the alpha-motoneuronal pool thus shifting the threshold of the tonic stretch reflex. Figure 2A illustrates schematically the tonic stretch reflex loop. Panel B of Figure 2 illustrates the effects of changes in the subthreshold depolarization of the alpha-motoneuronal pool on the recruitment of motor units with muscle stretch. This panel shows that active recruitment starts when muscle length reaches a threshold value (λ), defined as the muscle length at which the muscle shows first sign of activation during its slow stretch. Panel C of the same Figure shows the typical non-linear relations between active muscle force and length for two values of the tonic stretch reflex threshold (λ_1 and λ_2). Note that a shift in λ can lead to changes in muscle length, force, or both depending on the external load. In this scheme, the feedback is an inherent part of the physical system that defines its behavior.

In contrast, typical control schemes involving feedback loops assume computations performed by central elements using the feedback signals. Figure 3 illustrates a very simple control scheme with feedback. A neural element (N_1) is assumed to compute the difference between the signals received from the hierarchically higher controller and the signals delivered via the feedback loop. Signals resulting from these symbolic computations are then further processed, ultimately resulting in physical variables that the system produces. The assumption of neural computation is at the heart of this approach.
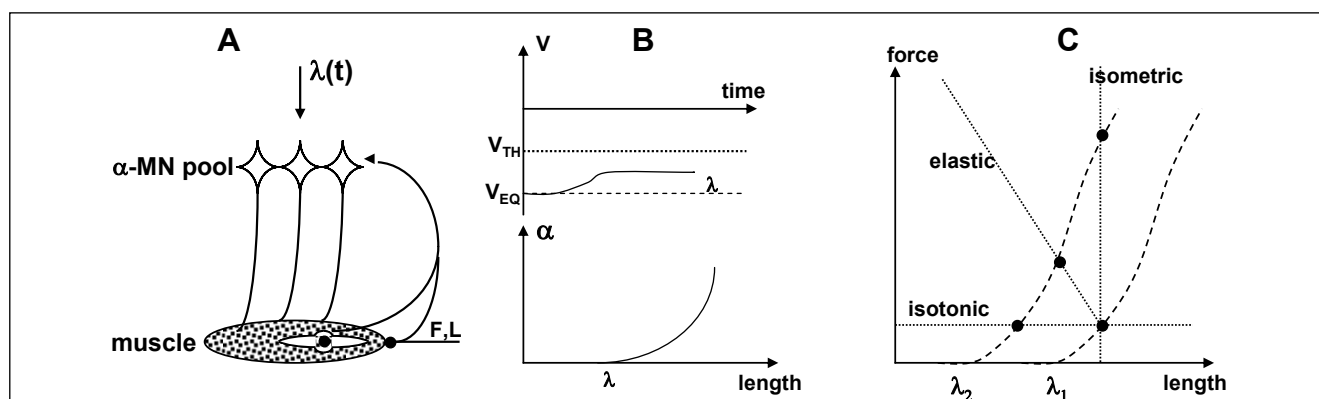

Figure 2

A: A schematic illustration of the tonic stretch reflex. An alpha-motoneuronal pool receives an input that leads to a subthreshold depolarization of the membranes of its neurons. The value of this depolarization defines the threshold of neuronal activation to signals coming from peripheral receptors, in particular those sensitive to muscle stretch. B: Top: λ leads to a change in the membrane potential from its equilibrium value (V_{EQ}) towards its threshold (V_{TH}). Bottom: The effects of changes in the subthreshold depolarization of the alpha-motoneuronal pool on the recruitment of motor units with muscle stretch. Active recruitment starts when muscle length reaches a threshold value (λ). C: An illustration of the dependence between active muscle force and muscle length for two values of the threshold of the tonic stretch reflex (λ). A shift in λ can lead to a change in muscle length (movement), force, or both depending on the external loading conditions.

The schemes in Figure 2A and Figure 3 look similar. However, there is a crucial difference. The scheme in Figure 2A represents physical and physiological processes and has no place for computations. Indeed, attempts at formalizing this (very much simplified!) Figure as a set of computational steps have been unimpressive (Latash & Gottlieb 1991; Gomi & Kawato 1996; cf. Gribble et al. 1998), partly because of the specific features of the neurons, such as the threshold nature of the generation of action potentials leading to a qualitative change in neuronal input-output characteristics below and above the threshold value. To put it simply, at the level of a single neuron, 2+2 may be 3, 4, or 6.

The feedback control scheme in Figure 3 is separated from physical and physiological processes. In man-made systems, realizations of such schemes typically involve electrical, nearly instantaneous transmission of signals, quick and accurate computations, and the generation of forces with powerful, predictable actuators. The systems for biological movement production do not possess such qualities. They are characterized by relatively long delays in signal transmission, a substantial amount of "neural noise", and motors (muscles) that are slow and have visco-elastic properties, which make their forces dependent on the external force field and, hence, poorly predictable. Therefore, the computational tools developed for robotics and control of ballistic missiles are unlikely to be adequate for the control of biological movement.

The purpose of these examples has been to contrast the two approaches to motor control, which I am going further to address as *control-theory* and *physical*. The purpose of the former seems to produce a mathematical description of certain salient features of motor behavior with little interest in processes within the body that produce these features. The

purpose of the latter is to turn motor control into physics of living systems. The reader has probably guessed that the heart of the author belongs to the latter approach.

What is expected from physics of living systems?

Specific motor control studies always start with a step of selecting a level of analysis and phenomena of interest. At this step, the object of interest, including the elements at the selected level of analysis, is separated from the rest of the body. It is assumed that this object receives an input from the rest of the body that may be assigned a property of intelligence related to the task, intention, etc. For example, if one studies patterns of motor unit recruitment in different tasks, there is an assumption that some processes at higher levels of the neuromotor hierarchy contribute to adjustments in such patterns by sending task-specific signals that serve as inputs into the motoneuronal pools. These processes are assumed but their physiology is not explicitly considered. The notions of commands, motor programs, control variables, intentional variables and other parameters/variables that are somehow supposed to be generated and/or transmitted by undefined neurophysiological structures are jargon substitutes reflecting our current inadequate knowledge of the physics and physiology of the systems that function at hierarchically higher levels.

All researchers who use the physical approach to motor control accept such assumptions, even if these are not admitted explicitly. These researchers hope that, one day, it will be possible to describe human behavior with a set of physical laws without resorting to such notions.
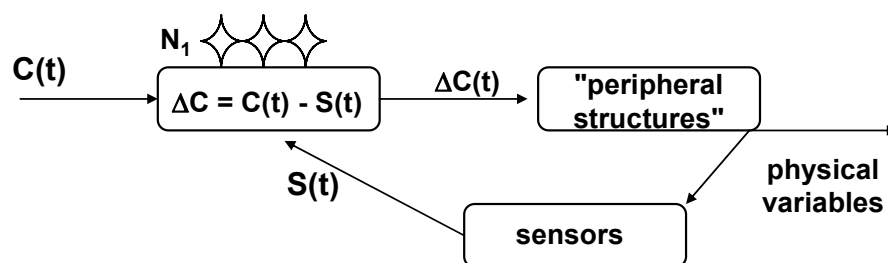
It may be useful to introduce a glossary of terms

Figure 3

A feedback loop within a typical control scheme. A neural unit N_1 is assumed to perform an operation of subtracting the feedback sensory signal S(t) from the descending control signal C(t). This operation results in an error signal, ΔC(t), that serves as the input into hierarchically lower structures ultimately resulting in changes in the physical variables produced by the system.

borrowed from control theory, engineering, and other areas that are commonly used in studies of voluntary movements without being explicitly defined. For example, what is *motor command*? This word combination is commonly used to describe a neurophysiological signal sent from an assumed hierarchically higher structure to an assumed hierarchically lower structure that is reflective of the task and/or intention of the actor. Such a definition would probably be accepted by champions of both physical and control-theory approaches.

Control signal is already a more loaded term. It assumes that some smart neurophysiological system computes somehow a signal that is expected to bring a desired movement about and sends this signal to hierarchically lower structures (neuronal or muscular). The idea of neuronal computation is essential within the control-theory approach, while it is not part of the physical approach. Neurons do not compute (perform operations with symbols); they are physical systems that behave according to the laws of nature. Commonly, neurons are viewed as input-output structures with characteristics that can be described with equations; in that sense, they are assigned an ability to perform computations. However, most equations describing neurons are very much simplified reflections of their physics and cannot be viewed as analogs of equations that, for example, describe force produced by an ideal spring in response to its deformation. In the latter example, the mathematical equation is an adequate reflection of the laws of nature. For neurons, most equations are crude simplifications of the laws of nature that govern neuronal functioning.

Another interesting example is *feedback loop*. There are physical feedback loops that couple physical variables, sometimes at characteristic time delays. In control theory, feedback loops deliver signals that represent values of variables that are later used in more or less complex mathematical operations, ranging from simple subtraction or addition to integration, differentiation, etc. The former feedback loop is a natural part of the physical approach while the latter one has its place only in the control-theory approach.

One of the most abused terms is probably *motor program*. Sometimes, this expression is used as a lay-term, with a meaning similar to that of *motor command*, that is, some neurophysiological signals that have something to do with a planned movement. This least defined meaning may also be the least

misleading one. Other meanings of this word mean direct neurophysiological precursors of physical variables such as muscle force, joint torques, or trajectories that may be scaled by amplitude and duration (reviewed in Schmidt 1975, 1980). Such usage of *motor program* assumes that neuronal structure pre-compute all the neural variables that have to be produced to lead to planned patterns of physical variables such as forces and trajectories. This assumption was criticized by Bernstein (1935, 1967); it is incompatible with the known neurophysiology and physics.

And now we come to *internal models*, which are direct descendents of *motor commands*. The expression *internal models* assumes that neuronal networks compute physical variables resulting from current *motor commands* (direct models) and requisite *motor commands* given desired magnitudes of physical variables (inverse models). This term has been criticized a few times over the past years (Ostry & Feldman 2003; Feldman & Latash 2005), but it has also shown resilience, and many recent studies are formulated within the framework of neuronal internal models (e.g., Bursztyn et al. 2006; Imamizu et al. 2007; Kluzik et al. 2008).

In the very subjective opinion of the author, using frameworks based on terms, such as those mentioned above, without even trying to link them to specific physiological and physical processes within the neuromotor system, is misleading and unproductive. Asking a question: "How can an arbitrary system be designed to mimic behavior of biological systems?" may be important for such areas as robotics and prosthetics, but not for understanding how the actual systems for movement production, for example the human body, function.

Currently, physics of biological movement is at a very early stage of its development. Thanks largely to the efforts of Anatol Feldman and his colleagues (for reviews see Feldman 2009; Feldman & Levin 2009), there is a coherent physical and physiological description of the control of single muscles based on the tonic stretch reflex, muscle pairs crossing individual joints, and multi-muscle systems. The physical and physiological principles remain the same across these different levels of analysis. To reiterate, the main physical principle within this approach is generation of movement by a change in the reference frame (referent configuration), while the main physiological principle is using depolarization of neuronal membrane to produce a shift in its threshold for activation by other inputs.

However, realization of the mentioned principles by actual neuroanatomical structures that participate in the production of natural, multi-muscle movements remains a mystery. One line of research that tries to address this issue is based on the idea of distributed processing modules (DPMs) advocated by Houk (2005; Houk et al. 2007). According to this idea, DPMs represent areas of cerebral cortex together with their anatomical loops through the basal ganglia and through the cerebellum. DMPs are supposed to play the role of operators that produce physical transformations of neuronal signals that can participate in a variety of functions including voluntary movement production. In that sense, they are similar to the idea of distributed operators offers by Bernstein and his colleagues over 40 years ago (Bassin et al. 1966).

Motor synergies

One of the notions in motor control that has been actively developed over the past years is the notion of a *synergy*. This notion is very old (Hughlings Jackson 1889). However, until recently, it has been used without a clear definition beyond the direct meaning of the word "work together" in Greek. The term *synergy* in clinical practice has a strong negative connotation as a rather inflexible pattern of muscle activation leading to stereotypical, poorly coordinated movements (Bobath 1978; DeWald et al. 1995). In many recent studies of movements, this term is used with a similar meaning, although without the negative connotation, implying a group of variables that show proportional scaling over time or across changes in parameters of an action. Correlation and matrix factorization methods have been used to identify such synergies (Ivanenko et al. 2004; D'Avela & Bizzi 2005; Ting & Macpherson 2005; Tresch & Jarc 2009).

Recently, a definition of *synergy* has been developed that makes this term specific for the control of biological movements. The definition is based on a particular approach to the famous problem of motor redundancy (Bernstein 1967): At any level of analysis, the system for movement production operates with more variables than the number of constraints imposed by typical problems. How does the controller select specific solutions from infinite sets afforded by this redundant design? In other words, how are n equations with m unknowns are being solved for $m \gg n$? Traditionally, this problem has been viewed as a source of computational problems

for the brain, and solutions were searched for using methods such as optimization. An alternative view, the principle of abundance (Gelfand and Latash 1998), considers the redundant design of the body not as a source of computational problems but as a rich apparatus that allows flexible and adaptive behavior. The controller is assumed not to look for specific unique solutions but to allow large (infinite) families of solutions that are equally able to solve specific motor problems.

The principle of abundance led to a definition of a synergy as a task-specific neural organization of elements (elemental variables) with the purpose to stabilize important features of performance (reviewed in Latash et al. 2007; Latash 2008a). This definition implies that synergies always do something, namely that they reduce variability of important performance variables as compared to what could be expected if synergies were absent. Recent studies (Gorniak et al. 2008; Shapkova et al. 2008) have demonstrated that variability of elements (estimated across repetitive attempts at the same task) is higher in multi-element tasks as compared with similar single-element tasks. However, this increase in variability of elemental variables is associated with their strong co-variation such that variability of their combined output does not suffer. In other words, synergies do not necessarily improve accuracy of performance but they allow to combine a certain level of accuracy with performing other tasks with the same set of elemental variables (Zhang et al. 2008).

For example, muscles of the human lower extremities are typically organized into synergies stabilizing the location of the center of pressure (the point of application of the resultant force acting on the body of a standing person from the supporting surface), which is an important variable for tasks involving vertical posture (Winter et al. 1996). On the other hand, the same muscles can be used to kick the football without losing balance.

Methods of identification and quantification of synergies have been developed within the uncontrolled manifold (UCM) hypothesis (Scholz & Schöner 1999). These methods are based on quantifying the amounts of variance within two sub-spaces of a multi-element system. The first sub-space (the UCM) corresponds to a fixed, desired value of a potentially important performance variable. The other, complementary sub-space is orthogonal to the UCM. It corresponds to changes in the performance variable. If the amount of variance quantified per degree-of-

freedom is higher within the UCM than within the orthogonal sub-space, a conclusion can be drawn that the elemental variable are organized by the controller into a synergy stabilizing that performance variable. For more detail on the UCM toolbox, see recent reviews (Latash et al. 2007; Latash 2008a).

Although originally the idea of abundance (allowing many solutions to typical problems) was introduced as opposite to the idea of optimization (looking for a single optimal solution), the two are in fact compatible. Recent studies using methods of inverse optimization (defining an analytical expression for a cost function based on a set of observations of a multi-element system) have shown that optimal solutions may form sub-spaces within the space of elemental variables and such sub-spaces intersect with the UCMs for specific values of performance variables. As a result, the reported non-spherical data distributions within the UCMs (Zhang et al. 2008) may reflect a combination of synergic control and an optimality criterion.

A number of models have been suggested for synergic control. In particular, Todorov and Jordan

Figure 4

A simplified scheme reflecting the ideas of the central back-coupling hypothesis. A signal generated by some hierarchically higher neurophysiological structures and related to the desired physical outcome (task is shared among a redundant set of neurons N_1 (or neuronal pools). Each of the N_1 neurons projects on interneurons N_2 that make connections with all the N_1 neurons. With appropriately selected gains of those back-coupling projections, this system can show large variability in the outputs of the N_1 neurons while their combined output may show relatively low variability corresponding to the task.

(2002; Todorov 2004) described an optimal feedback control model leading to data distributions similar to those observed in several studies that had used the UCM framework to quantify the two components of variance, within the UCM and orthogonal to the UCM. This approach assumed the existence of a cost function computed as the weighted sum of variance in control signals and variance in an important performance variable produced by the redundant system. As a result, deviations of elemental variables that did not affect the performance variable, i.e. within the UCM, were not corrected by the controller, while deviations orthogonal to the UCM were. This method has been limited to a mathematical description and not mapped onto neurophysiological structures involved in the production of movements.

An alternative model has been developed based on central back-coupling projections that are common within the central nervous system (Latash et al. 2005). According to this model (Figure 4), a task-specific input into a redundant system of neurons (neuronal pools) is shared among the neurons, and the output of each neuron has a back-coupling project onto all the neurons mediated by an interneuron. It has been assumed that the controller can modify the gains of the back-coupling projections, for example using the classical mechanism of presynaptic inhibition. The scheme in Figure 4 resembles the organization of the well-known system of Renshaw cells (Hultborn et al. 2004). The model incorporated such universal features of neuronal connections as synaptic time delays and threshold properties of the neurons. It has been able to account for synergy indices in multi-finger pressing tasks that required accurate production of the total force and/or total moment of force (as in Shim et al. 2005; Zhang et al. 2006).

The scheme in Figure 4 may represent a generic mechanism of sharing a task-specific output among a redundant set of elements. It allows a relatively straightforward incorporation into the framework of the referent configuration hypothesis.

Referent configuration hypothesis and motor synergies

The referent configuration hypothesis represents a natural generalization of the equilibrium-point hypothesis to multi-muscle, multi-joint, and whole body actions (Feldman & Levin 1995; Feldman et al. 1998). It assumes that the neural controller uses neurophysiological signals that, given an external force field, define a referent configuration of the body, RC,
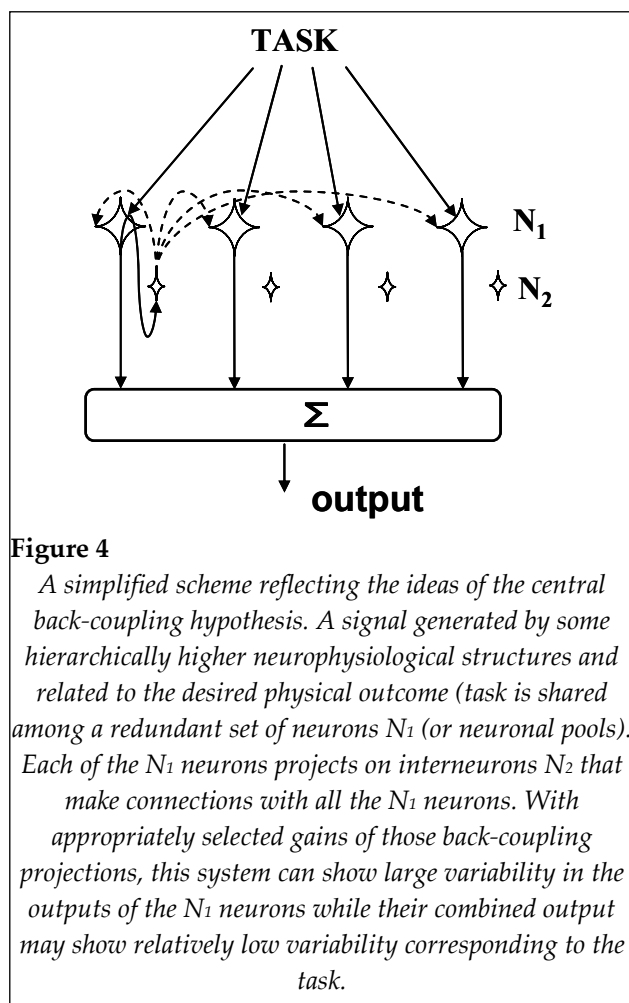
a configuration at which all the muscles are at their thresholds for activation. In other words, all the muscles try to achieve length values equal to their thresholds of the tonic stretch reflex, λ (as in Figure 2). This is commonly not possible because of anatomical and external constraints. As a result, some muscles have length values over the threshold ones resulting in non-zero muscle activation levels. The level of activation is larger for larger differences between the actual and threshold muscle length values as in Figure 2B.

Voluntary muscle control is associated with three distinct time patterns of important variables. First, the time profile of the referent configuration, RC(t) may be viewed as the *control trajectory*. Second, for each RC (given an external load), there is an instantaneous equilibrium configuration of the body, a combination of muscle length and force values that would have been observed if the control process stopped and the system were given time to reach an equilibrium state. Such instantaneous equilibrium configurations are typically not observable, in particular because of the mechanical properties of the system. A time sequence of such configurations forms an *equilibrium trajectory* of the system that can be described with two vector variables related to the coordinates and forces produced by the involved effectors. The only reliably observable trajectory is the *actual trajectory* that can also be described in both units of displacement and force (for example, in

isotonic and isometric conditions). All the attempts at reconstructing the other two trajectories, even for very simple single-joint systems, involved simplified models of the moving system (Latash & Gottlieb 1991; Gomi & Kawato 1992; Latash et al. 1999) and likely led to distorted time profiles of the control and equilibrium trajectories (Gribble et al. 1998).

Figure 5A illustrates a general scheme of how control with RC works. The controller sends a command to a neuronal pool (N); this command depolarizes the target membranes and modulates the threshold for action potential generation by N. Output of N (efferent command, EFF), after a series of processing steps, results in changes of muscle activations leading to a trajectory of the body that can be described as a shift in its actual configuration (AC). Given external conditions, the signal from the controller also specifies a referent configuration (RC) as defined earlier. A sensor neuron provides feedback (afferent signal, AFF) to neuron N reflecting the difference between RC and AC (Fig. 5B). Figure 5B is very similar to Fig. 2A describing equilibrium-point control of a single muscle; this similarity is due to the similar principles of control of one-muscle and whole-body actions.

If AC differs from RC (to the right of RC in Fig. 5B), the neuron N is activated and its activation is higher for larger deviations of AC from RC. The activation of the neuron produces a mechanical effect that moves AC towards RC. When the two coincide,
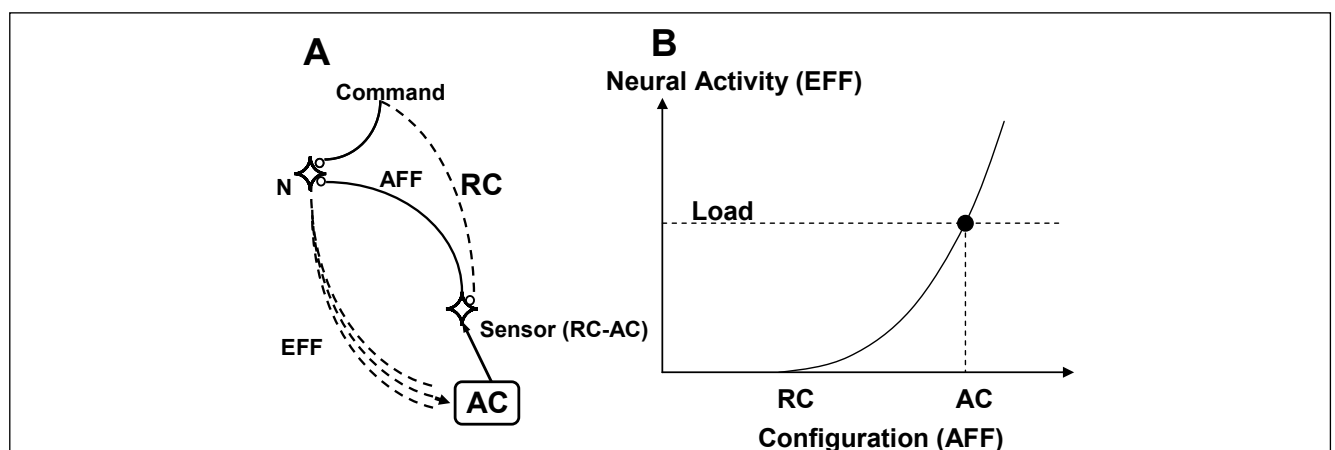

Figure 5

An illustration of a possible organization of control with referent configurations. A: A descending signal to a group of neurons N defines a level of subthreshold depolarization of their membranes. The neurons also receive input from a set of "sensory neurons" that produce signals proportional to the difference between the actual configuration (AC) of the body and its referent configuration (RC). RC is a consequence of the same signal to neurons N given the external force field. Neurons N will generate non-zero output signals as long as AC differs from RC. When the two coincide, neurons N stop firing. B: An illustration o a dependence between the efferent and afferent signals for a given RC.
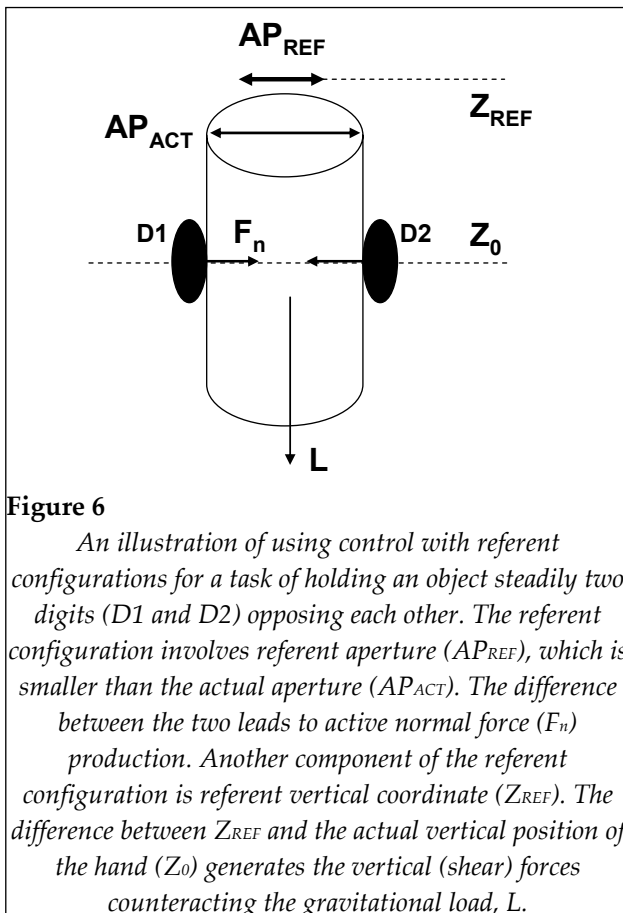
Figure 6

An illustration of using control with referent configurations for a task of holding an object steadily two digits (D1 and D2) opposing each other. The referent configuration involves referent aperture (AP$_{REF}$), which is smaller than the actual aperture (AP$_{ACT}$). The difference between the two leads to active normal force (F$_n$) production. Another component of the referent configuration is referent vertical coordinate (Z$_{REF}$). The difference between Z$_{REF}$ and the actual vertical position of the hand (Z$_0$) generates the vertical (shear) forces counteracting the gravitational load, L.

the neuron becomes silent, and the system stays at RC. If something (for example, an external load, L) prevents AC from moving, an equilibrium state is reached corresponding to non-zero neuronal (and muscular) activation and a combination of positional and force variables.

Transformation of signals from the neuronal pool N in Figure 5A to muscle activations is likely to include a chain of few-to-many transformation (Latash 2008b). Each of those involves a problem of motor redundancy solved using the principles of synergic control. For example, the output of N to several neuronal pools (elemental variables at that stage) produces co-varied outputs of those variables such that their combined effect corresponds to the signal from N, while their individual activation patterns may vary. A sequence of such transformations results in individual muscle activations and individual motor unit firing patterns, which are all affected by the external force field.

To illustrate how such transformations may work, consider a single muscle that receives a single control signal (λ) and produces a pattern of activation of many motor units. The mechanism of the tonic stretch reflex may be viewed as a particular

feedback-based method of organizing a multi-motor-unit synergy stabilizing the total level of muscle activation. Indeed, imagine that one motor unit suddenly turns off (introduces an "error"). As a result, the muscle force will drop, the balance of forces between the muscle and the external load will be violated, the muscle will stretch, its spindle afferents will increase the frequency of firing, and this increase will lead to an increase in the overall level of activation of the motoneuronal pool. This sequence of actions, reflecting both peripheral mechanics and the action of the tonic stretch reflex, will, at least partly, compensate for the deviation in muscle activation due to turning one of the motor units off.

So, we can conclude that synergies among performance variables might have naturally resulted from the method of control with referent configurations without any additional smart controlling action. This idea has been developed for the control of prehensile actions (Pilon et al. 2007; Latash et al. 2010). Consider grasping an object with two opposing digits (Figure 6). According to the referent configuration hypothesis, this action is associated with setting a referent aperture (AP$_{REF}$) between the digits. The object does not allow the digits to move to AP$_{REF}$. As a result, the difference between the actual aperture (AP$_{ACT}$) and AP$_{REF}$ leads to active grip force production. Along similar lines, setting a referent vertical coordinate of the hand (RC$_Z$) allows the digits to produce non-zero shear forces when the hand is below RC$_Z$; these forces counteract the weight of the grasped object.

Optimistic Concluding Comments

Are we getting closer to physics of living systems? I would like to believe that we are. The recent advances in the field of motor control based on the physical and physiological approaches makes one optimistic that this line of research continues to develop and attract young researchers. One of the main difficulties faced by this direction of research is the paucity of experimental methods that would allow to quantify important variables with sufficient accuracy. In other words, we lack reliable "lambda-meters". Earlier attempts at reconstructing equilibrium trajectories and control trajectories were inconclusive because they were based on grossly simplified models of the peripheral motor apparatus and muscle reflexes. On the other hand, the development of the computational methods of analysis of synergies within the framework of the uncontrolled manifold

hypothesis was an important step forward. The recent studies that try to merge this computational approach with the framework of the referent configuration hypothesis show that this direction is inherently rich and offers new insights into typical motor control problems dealing with multi-element coordination and movement stability (Gorniak et al. 2009; Latash et al. 2010).

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