

DOES THE NERVOUS SYSTEM  
NEED A “DRIVER”?  
SERGIY YAKOVENKO

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I was brought up in the totalitarian regime of the Soviet Union. As a teenager I was an eyewitness to the collapse of the Berlin Wall while staying with my parents, engineers on a Soviet army base in Prenzlau, during the GDR’s transition to FRG, and was sent back to the USSR to witness the failed *coup d’état* of the old Communist guard and the consequent *de facto* independence of the Ukraine in 1991. I did my undergraduate studies in biophysics at Kharkiv State University, famous for technical and theoretical achievements in Physics and Mathematics, with several Nobel laureates among its alumni. From the very beginning of my scientific career in Neuroscience at the University of Alberta, I was attracted by the order presented by a mechanistic view of nature and learnt to explore it with the help of computational tools. After defending my Ph.D. in Neuroscience, I moved to the Université de Montréal and focused my post-doctoral research on the organization and function of the neural pathways that descend to the spinal cord and interact with multiple neural and mechanical components responsible for the *emergent* organization of movement control. – Address: Département de Physiologie, Université de Montréal, Pavillon Paul-G. Desmarais, C.P. 6128, Succursale Centre-ville, Montréal Québec H3C 3J7, Canada. E-mail: [sergiy.yakovenko@umontreal.ca](mailto:sergiy.yakovenko@umontreal.ca)

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## Prologue

It was a busy day at Montreal's Pierre Elliott Trudeau International Airport as the holiday season triggered crowds of people to rush to families dispersed in multiple destinations around the globe. This year the holiday travel was not the only purpose of my trip to Europe, as I was eager to join the ranks of Fellows at Wissenschaftskolleg zu Berlin (Wiko) for three months of interdisciplinary collaboration and intellectual adventure as a member of the research group *Functional and Structural Constraints in the Evolution of Sensorimotor Networks*. The snowstorm typical of Quebec this time of year came to an equilibrium with the effort and the will of snow-removal crews rushing down runways on oversized snow tractors. In addition to the predicted weather conditions, an unforeseen factor caused overcrowding and delayed flights across the departure boards of all major airports that day, as an ill-conceived attempt to blow up a transatlantic flight from Amsterdam failed that morning. Some 23-year-old Nigerian man sent shivers down the air traffic system, causing delays, long waiting lines and frustration, due to the heightened security and meticulous searches of all suspicious travellers, myself included. Each arrival and departure was a fight against multiple forces that included external parameters of nature and intrinsic constraints of human society. As I was waiting for my flight, I did wonder what the factors were that influenced the young man's decision to attempt a terrorist act on Christmas Day. Was it a "conscious" choice, a choice free from constraints and a choice that creates the potential for multiple future outcomes – "free will" by one of its definitions – or a result of multiple measurable causes, some of which were perhaps peer pressure or brainwashing based on the dogmatic view of the world? Whatever the reasons, my flight was not going to beat the odds that day as the complex dynamic air traffic system buckled once again during a holiday season, sending thousands of travellers and their eagerly awaiting families into customary holiday blues.

### "Free Will" or Error Correction Mechanism?

My interest in the topics of decision-making, voluntary, involuntary and reflex actions, which are thought to constitute self and free will in philosophical terms, has been cultivated by multiple informal discussions with my peers since the beginning of my materialist career in neurophysiology; it has been further refined by interactions with professional philosophers, writers and other scientists during my term at Wiko. While a decision-making ac-

tion can be readily defined as a process of choosing between multiple alternatives, the definition of the terms “voluntary”, “involuntary” and “reflex” has proven to be challenging for both philosophers and neurophysiologists alike; although still widely used, many neurophysiologists now consider these terms to be prescientific (Prochazka et al. 2000). Instead of wrestling with the concepts idiomatic to philosophers, I will contribute to the ongoing discussion, which emerges spontaneously at Wiko year after year, by outlining the neuro-mechanical hierarchy responsible for decision-making, movement selection and its execution as described by modern mathematical models in neuroscience. We will sequentially assemble the general hierarchy by describing i) the mechanisms responsible for movement execution built-in or embedded in our musculoskeletal system; ii) neural control mechanisms distributed throughout the spinal cord, brainstem and motor cortex; and iii) neural decision-making mechanisms in cortical areas that project to motor cortex. I will then use this framework as a basis for a conjecture about the representation of “self” and its actions within the nervous system.

### Musculoskeletal Mechanisms

One way of describing the properties of a complex hierarchical system like the neuro-musculo-skeletal system (NMS) is to start with the essential elements at the bottom of the hierarchy and make our way up to the source. The bottom level of the NMS is the mechanics of our body, that is the arrangement of multiple mechanical segments hinged together by joints. Newtonian physics explains in deterministic terms the mechanical coupling between body parts and their interactions with the environment. Simple limbed mechanical “toys” – dynamic models – can generate a human-like bipedal gait completely passively, without the contribution of muscles or any neural control (McGeer 1990, Kuo 1999, Collins et al. 2005, Geng et al. 2006). Shown in Figure 1 is one such passive walker, a biped that can run down a gentle slope in a way similar to human running. Stable locomotion of these passive walkers is possible due to the dynamic stability of the mechanical system within a limited parameter space. This property can be illustrated by the behaviour of a ball dropped or nudged into a bowl. As long as the ball is not given a push sufficient to leave the bowl, it will gradually settle to the equilibrium position at the bottom of the bowl. Similarly, a passive walker reaches a dynamic equilibrium when it performs stereotypical stepping movements. However, this simple mechanism cannot change speed or direction of locomotion and it is

relatively unstable; it is susceptible to disruption, for example, by uneven terrain. Muscles and tendons help to solve these problems.

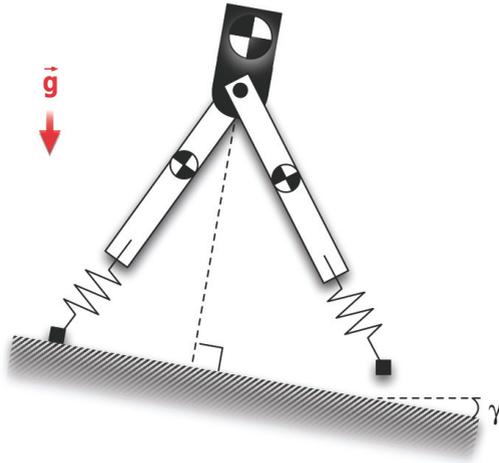


Fig. 1: A general passive dynamic walker model of locomotion.

Essentially, muscles and tendons can be modelled as a collection of springs and dashpots with tuneable stiffness and viscosity elements controlled by inputs coming from the spinal cord (Hogan 1985, Zajac 1989). Consequently, muscle function in the presence of some static tone provided by the spinal cord can be described as having reflex action, which is more appropriately called a negative feedback action. If stretched, the muscle resists this positive length change and tries to come back to its previous length by producing force that would then cause a negative length change or feedback action. Such negative feedback is a ubiquitous stabilizing or homeostatic mechanism that returns the system to its set or desired state. This concept is central to the ideas discussed below and it warrants some detailed explanation. Consider a room-temperature regulating system in Figure 2 that uses desired or “set point” temperature and a sensor to calculate error between them, a negative value in the illustration. This error propagates via a relay to a regulator that either heats or cools the room, based on the negative or positive value of the error. In the example, the relatively cold temperature causes the heating of the room, which minimizes the error. The equivalent

description of the system is also shown in an engineering schematic of Figure 2. It should be clear why the feedback pathway is often called a feedback loop. As an exercise, it is easy to imagine two dramatic outcomes of the temperature-regulating system operating on the positive feedback principle, generally leading to instability. Other natural phenomena in dynamic systems with positive feedback properties include the formation of hurricanes, the nuclear chain reaction and stock market crashes. Thus, by adding muscles to a passive walker, the neural system has a way of adding or reducing the amount of kinetic energy of the skeleton and stabilizing it in the presence of perturbations (Yakovenko et al. 2004).

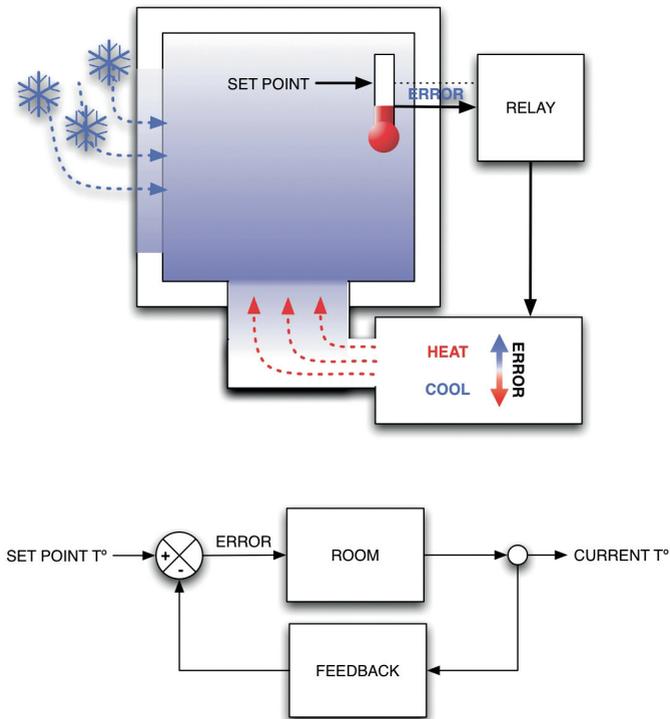


Fig. 2: Schematic representation of the feedback loop.

In view of the previous paragraph, it may not be surprising that the fastest sensory response from muscles, the stretch reflex, is a negative feedback mechanism. It operates on top of the functionally similar built-in muscle property and offers an additional level of stabilization. When a load stretches muscles, the contribution of the stretch reflex loop is greatly potentiated because it adds multiplicatively to the spring-like resistance of the stretched muscle (Prochazka et al. 1997, Yakovenko et al. 2004). Thus, control of locomotion can be reduced to an oscillator-like switching of muscles on and off in appropriate phases and delivering or dissipating mechanical energy to modify or maintain desired speed, while the peripheral stabilizing mechanisms take care of minor deviations and perturbations of the desired state. One of the early and still influential theoretical descriptions of motor control explains the action of the nervous system in terms of setting desired threshold or equilibrium positions of muscles by changing the excitability of the stretch reflexes (Asatryan and Feldman 1965). According to this schema, all that the control mechanism has to do is to set a number of equilibrium points for different muscles and the body will settle in that position, given sufficient time. While this conceptually attractive theory is still practiced in its pure form, it has also generated a number of offshoot theories that rely on the principles of nonlinear dynamics and optimal control theory (Scholz and Schönér 1999, Todorov 2004).

The early insight into the organization of the sensory feedback pathways in vertebrates led Sir Charles Sherrington to conclude that the role of the nervous system is to integrate actions of body segments and that the simple reflex actions are the language of the integration (Sherrington 1906). He described behaviourally complex actions as a sequence of reflex components such that each preceding action evokes the next. This idea was first clearly outlined by another physiologist, Ivan Sechenov, who stated that any human action is the result of chains of reflexes (Sechenov 1863). It is noteworthy that the conceptual foundation of the reflex chain hypothesis has been developed by a number of experimental physiologists in the 18th to 19th centuries, but the origin could be traced back as far as the treatises of Descartes and Willis in 1664 (Clower 1998, Prochazka et al. 2000).

To a large extent, the idea of the automatism of the neuromechanical body was based on the observations of animals with complete spinal cord transections that can walk even without commands descending from the brainstem and cortex. To explain such observations, T. Graham Brown, a student of Sherrington, tested the hypothesis of his mentor that sensory feedback is essential and sufficient for locomotion. In his 1911 publication, he reported that

rhythmic activity of motor nerves persists even in the absence of motion-related sensory feedback and added a phenomenological description of the additional spinal component involved in the control of locomotion, which he called “the intrinsic factor” (Brown 1911). This controversial finding was not fully accepted until the experimental and theoretical efforts of neurophysiologists in the 1960s who coined the term “central pattern generator” (CPG) to recognize the central role of this spinal element in the generation of the locomotor pattern in vertebrates. However, as early as a decade after Brown’s original publication, a young physiologist Fritz Verzár implemented the principles of CPG organization and studied its properties in the first dynamic model and reported the results of the mechanical simulations (Verzár 1923). This revolutionary study was conducted before the development of the theoretical framework to describe the interaction dynamics of pairs of coupled antagonistic integrators thought to comprise the CPG and before the invention of computers necessary to solve the resulting equations. Nowadays, while simulating the CPG *in silico* at Wiko, we have also constructed a simplified Verzár model to gain in several experiments immediate insight into the operation of this tangible mechanism.

The focus of my computational studies at Wiko was the question of how the nervous system controls the mechanisms and pathways of the spinal cord and their interactions with the musculoskeletal system. The complexity of the system summarized above is increased by the dynamics of interactions of spinal segmental pathways and multiple supraspinal motor pathways that project to the CPG to regulate its operation. Using the mathematical description of the CPG and experimental recordings of its output, it was intriguing to solve the system of equations in reverse to find what the inputs to CPG must be reporting. It turns out that, although the result could have been potentially complex, the computed inputs are consistent with the forward speed of locomotion (Yakovenko 2011). All that the hierarchically high neural networks of the brainstem and motor cortex have to compute is the speed of locomotion; the low levels of hierarchy, which include the CPG, transform this command into the language of muscle activations sequences and commands the fine-tuning of the sensitivity of sensory feedback pathways. This finding is consistent with the observation of gait transitions from slow walking to fast trot and gallop – the locomotor behaviours that require different coordinations of limbs in quadrupeds – evoked by stimulation of the mesencephalic locomotor region in the brainstem with gradually increasing current delivered through a single electrode (Shik et al. 1966). In addition, it supports the idea that the CPG is itself a model of the body’s passive dynamics of limbs interacting with the environment. Since the passive walker output is largely described by its velocity, it is not surprising

that the internal model of this mechanism embedded in neural connections of the spinal cord is controlled by the desired velocity. Finally, this example points out the ability of the nervous system to construct models of the musculoskeletal body and the environment.

### Decision-Making and Strategy Selection

A great deal is known about the functions of the execution pathways, but the neural mechanisms of sensory evaluation, selection of actions and adaptation of the selection strategies have become accessible to direct investigation only recently with the development of implantable arrays for microelectrode recordings and stimulations of multiple cortical areas. We can tap into the cortical and spinal neural circuitry with electrical stimulation to influence not only motor execution, but also perceptual decision making and target selection. One particularly important and influential example is the study of the cortical cascade of neural processing from the sensory evaluation to the execution of reaching in monkeys recorded from several contributing cortical areas (Cisek and Kalaska 2005). This information can be used further to identify individual functions of multiple areas and their emergent ensemble role. For example, the stimulation of the primary somatosensory cortex of monkeys can influence their perceptual decisions about tactile stimuli (Romo et al. 1998), and the stimulation of the cortical frontal eye fields in monkeys influences their selection of targets (Gardner and Lisberger 2002). Thus, it is experimentally possible to change the perception of the environment and to influence the decisions.

The models of the decision-making process are generally based on the sequential integration of stimuli until reaching a threshold when the decision is made (Stone 1960). The evidence for the temporal integration of sensory inputs has since been shown in multiple cortical areas in tasks of selecting between targets (Cisek and Kalaska 2010). A general model of action selection is shown in Figure 3, where sensory information about the desired target (zebras), e.g. their caloric value and health, is integrated and sequentially evaluated. However, both the rate of this integration process and the threshold are influenced by other factors, such as motivation, risk, previous experience and the urgency of making a decision. Once the decision is made, the associated policy of how to make it happen propagates to circuitry responsible for the details of motor planning and execution (described above). However, even a simple decision emerges from the interactions of signals associated with multiple external environmental states and the internal cognitive and motor states. The computational complexity of this problem, also called “the curse of dimensionality”, grows

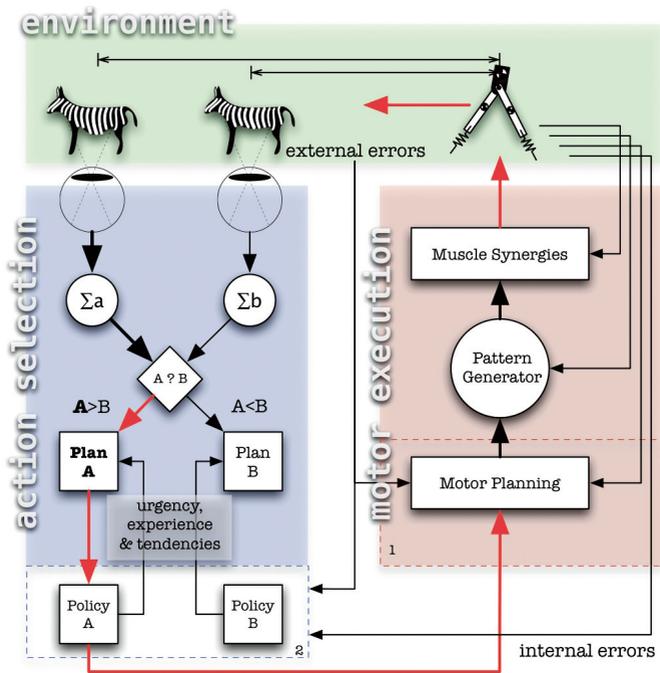


Fig. 3: A general schematic of the sensorimotor pathways responsible for the chain of processing from perception to selection of action and its execution.

exponentially with the number of state variables. How does the nervous system resolve this obviously complex problem of finding the best or optimal choice?

The remaining link for Sechenov’s “chain”, which would close the loop of the perception to action cascade of neural processing, is a mechanism that selects from the number of actions presented by the environment when the outcomes of these actions are often unpredictable and state-dependent. This question does not often arise in neurophysiological studies, but it has puzzled researchers in other applied fields of science, such as engineering and artificial intelligence. The most active research is done using the theory of reinforcement learning, which includes computational tools similar to the control theory and describes the

mapping of actions to a particular situation while maximizing a reward or minimizing a cost (Sutton and Barto 1998). The tools of this theory rely on the description of sets of policies or actions, their immediate and future rewards and the contribution of the environment. All of these variables have physiological meaning and representation within the neural substrate. While we do not know whether reinforcement learning is implemented within the neural circuitry responsible for the decision-making, this question has recently become accessible to experimental and computational examination in neuroscience. For example, some of the best models of the dopaminergic pathways of basal ganglia involved in reward and motor execution are expressed with the reinforcement learning methods (Rivest et al. 2010).

### Where is the “Driver”?

Sherrington wrote in 1921 that “with the progress of natural knowledge, biology has passed beyond the confines of the study of merely visible form, and is turning more and more to the subtler and deeper sciences that are branches of energetics.” With the invention of the computer, the pragmatic movement of neuroscience towards quantitative descriptions of applied mathematics is a fact of modern mechanistic research methods; this is evidenced by the growing representation of the computational fields in what used to be qualitative or at best phenomenological (or “best-fit”) biology. The goal of computational neuroscience is to create a systematic theoretical framework or models of every observed phenomenon, which could then be tested, refined and used further to identify remaining gaps in the understanding of how animals (human and otherwise) work and why. The hypothesis that I would like to posit in regard to the philosophical nature of these questions is that the more we answer the pedestrian “how” questions of neuroscience, the more we will automatically attain answers to the “why” questions.

To return to the question of this chapter, which focused so far on the description of the perception-to-action processing, the “driver” who is a whole or a part of “free will” has been posited to take part in this process. Since it can only be either outside or a part of this mechanistically described sensorimotor hierarchy, we can further examine consequences of both cases. If the contribution of “free will” to behaviour is not captured by the current mechanistic models, then it is confined to the part of the behaviour that is not explained by the model; therefore, the future models with higher precision will be able to either include it or reduce it to an insignificantly small factor. Note that the latter outcome negates mathemati-

cally the existence of “free will” and surrenders to the deterministic view of the system. The other more interesting alternative is that some part of “free will” is already included within the holistic assembly of models, admittedly derived with predominantly reductionist methods. Where in Figure 3 would “free will” then be? The answer can only start with the definition that sets the constraints on the phenomenon. Since the most prominent attribute of “free will” is “self”, the mechanisms that make a distinction between “self” and “external” signals are likely candidates. Then, if we redefine the question as a search for the elements of the perception-to-action process that are concerned with the distinction between external (or environmental) vs. internal (or “self”) actions, three pathways in the schematic are the plausible candidates for “free will”.

The first and most intriguing pathway is the mechanism of error correction and planning within the execution pathways (Figure 3, 1). The success of this mechanism depends on its ability to make a distinction between internal or “self” errors that originate within the sensorimotor pathways and, thus, need to be intrinsically adjusted; or external errors due to the movement of the desired target. For example, if the dissociation between errors is not made at this level, then the external errors used to adjust the execution pathways could lead to the increase in the overall error. The second candidate pathway is the policy-selecting mechanism that projects to the execution planning pathways; assuming it is not fully overlapping with it, this mechanism also experiences both types of errors (Figure 3, 2). For example, in bow hunting, the decision to shoot would depend on both parameters: the distance to a target (the external error) and the skill and precision of the hunter (both related to the internal error). The third possibility is that the neural processing responsible for the “free will” is distributed between several mechanisms of the pyramidal hierarchy. This type of processing is common to the nested hierarchies that allow signals to flow bidirectionally, for example by using the feedback loops to the higher levels and combining low-order features as a part of a nested structure of high-order features (Feinberg and Keenan 2005). In this case, all the mechanisms that are required to make the distinction between the two types of errors would constitute the last candidate for the seat of “free will”. It is worth noting that this implies that the complex behaviour termed “free will” only emerges out of the interactions between the multiple elements of this composite mechanism and cannot be explained by the description of each of the interacting elements in isolation. To summarize, the signal related to “self” within decision- and motion-generating neural pathways constitutes the error correction mechanism for adjusting ongoing and planned movements. Thus, further experimental, clinical and computational studies that examine the participation of

these pathways in decision-making will eventually be able to answer the intriguing question of what “free will” is by giving the term a specific mathematical definition.

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