Neural Control Principles: Bernstein's Insights from Biomechanics of Human Movement

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ABSTRACT

This chapter reviews major principles of neural control of movement proposed by N. A. Bernstein based on his biomechanical studies of human movements and published in his 1947 book 'On Construction of Movements'. These principles include the hierarchical organization of the motor control system; synergistic sensorimotor control; the principle of sensory corrections, and the principles of repetition without repetition and fixating and subsequent releasing kinematic degrees of freedom during motor skill acquisition. These principles simplify control of the musculoskeletal system with redundant degrees of freedom and unpredictable effects of reactive and muscle forces arising in multi-segment kinematic chains. We also discuss the relevant contemporary research that has been inspired by and further developed Bernstein's ideas. We demonstrate, in particular, examples of complex muscle and kinematic synergies organized by different levels of the motor control system, consequences of loss of proprioceptive sensory corrections on movement coordination, and emergence of economical and stable kinematic and muscle invariant movement characteristics in the process of skill acquisition by trials and errors. We conclude this chapter with motor control related parables told by N. A. Bernstein to one of the authors (VMZ).

Key words: Degrees-of-freedom problem, kinematic and muscle redundancy, reactive forces in limb kinematic chains, synergistic control, sensory corrections, motor learning

ANALYSIS OF BIOMECHANICS OF HUMAN MOTION AS A TOOL TO UNDERSTAND MOTOR CONTROL

Nikolai Aleksandrovich Bernstein was one of the first to use biomechanical analysis of human motion to infer neural control principles underlying movement control. It is remarkable that his deep insights into the neural control of movement were made in the 1930s - 1940s when no methods for in vivo recording of neuronal activity were available. Bernstein received his medical degree in neurology from the Moscow University. He also took courses in physics and mathematics. After working as a neurologist for several years following his graduation, he started his research in biomechanics of human movement as the director of biomechanics laboratory at the Institute of Labor in 1922. His educational background, the methods of movement recordings and analyses he developed, and a wide range of motor tasks he studied contributed to his discoveries of major motor control principles. Before commenting on Bernstein's insights into neural control of movement and their impact on current research, we briefly discuss strengths and weaknesses of his biomechanical analysis.

Experimental methods and data analysis

As Muybridge (Muybridge 1887) and Marey (Marey 1879), Bernstein recorded movements in natural settings. He, however, was able to substantially improve spatial and temporal resolution of his recordings with developing the cyclographic recording method and methods of three-dimensional recordings with a mirror (Bernstein 1967). Both spatial and temporal resolutions of these methods were close to those of Braune and Fisher (Braune and Fischer 1895-1904). However, in contrast to Braune and Fischer who analyzed only several strides of walking in one subject, Bernstein's laboratory was able to analyze and publish an enormous amount of biomechanical data collected in hundreds of subjects performing a wide range of motor tasks. In the course of almost 20 years of experimental research, Bernstein investigated movements of highly skilled professional workers (Bernstein 1923), musicians (Bernstein and Popowa 1929) and athletes, as well as locomotion of children of different ages (Bernstein 1940). This was achieved partially owing to the developed methods of simplified marker digitizing and calculations of time derivatives and center of mass position.

Another factor enabling Bernstein to observe reach complexity of recorded movements, largely unavailable to his predecessors and contemporaries, was his methods of calculating time derivatives. He did not smooth body marker trajectories as severely as was done by Braune and Fischer (Braune and Fischer 1895-1904). As a result, the computed body segment accelerations and forces contained high frequency components up to 20 Hz (Woltring 1984). Although many high frequency waves in accelerations and forces reported by Bernstein appeared repeatable across experiments, subjects and similar motor tasks (e.g., Fig. 32), some of them have not been reproduced by other researchers and were likely contaminated by high frequency noise. A detailed analysis of this issue was given by Woltring, 1984. Nevertheless, major signal components contained in the calculated acceleration and forces were valid and later reproduced in other studies. These calculations permitted Bernstein quantification of movement variability and identification of the role of reactive forces in movement control.

Bernstein was also responsible for another advancement in biomechanics that contributed to his subsequent analysis of movement complexity – development of methods for measuring and calculating inertial properties of body segments in the same subjects participating in motion recordings. Although the obtained segmental inertial properties were not as accurate as those determined by next generation of gamma scanner, computer tomography and MRI methods (for review see (Zatsiorsky 2002)), they allowed Bernstein to conduct inverse dynamics analysis of freely moving upper and lower extremities, except in movement phases in which the most distal segment was in contact with an external environment, e.g. ground during the stance phase of locomotion. Methods of accurate recordings of ground reaction forces and incorporating them into inverse dynamics analyses became available in the late 1930s (Elftman 1939; Manter 1938), so Bernstein could not incorporate them in his experimental studies that ended at that time.

MECHANICAL COMPLEXITY OF MUSCULOSKELETAL SYSTEM

Bernstein's degrees-of-freedom problem

Following the study of Braune and Fischer (Braune and Fischer 1895-1904), analysis of whole body dynamics during human movements led Bernstein to realize the complexity of the musculoskeletal system and consequences of this complexity for control of movement. He wrote: "The mobility of the kinematic chains in the human body is enormous and reaches tens of degrees of freedom. The mobility of the wrist with respect to the scapula and of the tarsus with respect to the pelvis adds up to seven degrees of freedom, the mobility of a fingertip with respect to the thorax is 16 degrees of freedom. The presence of mobile fingers enriches the mobility and deformability of the hand compared, for example, with the forelimb of hoofed quadrupeds by 22 additional degrees of freedom." (Chapter 2, p 11, Bernstein 1947). His analysis of human musculoskeletal morphology has been later confirmed and expanded by next generation of researchers in detailed quantitative analyses of the musculoskeletal morphology of the whole human body. For example, Morecki with colleagues (Morecki et al. 1971) have determined that the total number of moving bones in the human body is 206 and they are interconnected by a total of 147 joints. These consist of 85 joints with 1 degree of freedom (DOF), 33 joints with 2 DOF and 29 joints with 3 DOF. Thus, the total number of DOF in the human body is 244. Morecki and his colleagues have also determined the total number of skeletal muscle compartments (they called them actons) producing moments with respect to each DOF; this number exceeds 640 (the exact number depends on how muscle compartments are defined). This means that on average each DOF is served by approximately 3 muscle compartments. It is clear from the above analysis that any whole-body motor task in a three-dimensional space can be performed with unlimited number of possible kinematic patterns in each DOF, which reflects the kinematic redundancy of the musculoskeletal system. Furthermore, specific kinematics of a motor task can be produced by an unlimited number of muscle activities and forces, reflecting muscle redundancy. There is a much greater neuronal redundancy in the central and peripheral nervous systems that makes it possible to produce similar motoneuronal and muscle activities with various contributions of the central and peripheral (sensory) neuronal inputs. A further complication for motor control, realized by Bernstein and prior researchers, e.g. Braune and Fischer 1895-1904, is that muscle-tendon mechanical and physiological properties (the force-length-velocity relationships) are highly nonlinear; see for example, (Zatsiorsky and Prilutsky 2012).

According to Bernstein, this complexity of the musculoskeletal system and, in particular, the kinematic and muscle redundancy, have critical impact on movement control. This follows from his formulation of the famous degrees-of-freedom problem of motor control and motor coordination: “The main problem of movement coordination is … in overcoming the redundant degrees of freedom of a moving organ, i.e. in turning it into a controllable system.” (Chapter 2, p. 15, Bernstein, 1947).

Complex dynamic interactions between multiple body segments

Another significant complication for movement control of the multi-segment musculoskeletal system, recognized by Bernstein, arises from dynamic interactions (interaction moments) between moving multiple interconnected body segments. Even in the simplest planar kinematic chain consisting of two segments, motion of each segment induces several interaction moments affecting motion of the adjacent segment and arising from gravitational, inertial, centripetal and Coriolis forces; e.g. (Zatsiorsky 2002). The interaction moments are motion-dependent and their influence on body segments also depend on the initial positions and velocities of each body segment in the kinematic chain before initiation of movement. A typical kinematic chain in the human body, i.e. the upper or lower extremity, consists of at least 3 to 4 major segments that are free to move in a three-dimensional space. This leads to much more complex dynamical interactions between body segments during motion. Based on his analysis of dynamics of human motion, Bernstein made a profound conclusion that significantly influenced the subsequent developments in motor control: There is no one-to-one correspondence between central motor commands to the muscles and the resulting motion. In other words, the same motor commands can cause different movements depending on initial position and velocity of body segments and on interactions of the body segments with changing reactive internal forces and external forces (e.g., effects of gravity on interaction moments depend on orientation and movement direction of body segments). The opposite is also true – the same movement may result from different motor commands. The unpredictable dynamics of the human musculoskeletal system led Bernstein to conclude that accurate performance of motor tasks is impossible without constant sensory corrections; see below.

It is worth mentioning that Bernstein arrived to the above conclusions by investigating movements of humans, a relatively large biological species with substantial body segment inertia, which is responsible for considerable motion-dependent gravitational and interaction moments (Hollerbach and Flash 1982; Zernicke et al. 1991). In small animals like insects and rodents, but not cats (Wisleder et al. 1990), effects of gravitational and inertial forces are negligible (Hooper 2012), suggesting less complex dynamics and possibly different organization of motor control in these species.

Complexity of incoming somatosensory information

Bernstein came close to realize that mechanical complexity of the musculoskeletal system and its kinematic and muscle redundancies results in analogous issues of uncertainty in mapping from many motion-dependent somatosensory signals from multiple sources (muscle length, stretch velocity and force afferents; cutaneous mechanoreceptors, etc.) and the few resulting perceptions of position and motion of joint angles and the end-effector of an extremity, as seen in the many-to-few mapping between the motor commands and the resulting movements (Reed 1984). As with motor commands and motion, there is no one-to-one mapping between somatosensory inputs and the resulting perception (Gibson 1966; Köhler 1929). This is because somatosensory perceptions depend also on previous experiences and behavioral goals of the organism in the surrounding environment. For instance, different perceptions and the corresponding different motor responses to similar somatosensory inputs may be produced at the different fusimotor sets of the nervous system with diverse gains in somatosensory proprioceptive feedback pathways established by activation of the static and dynamic gamma motoneurons (Prochazka et al. 1985).

The uncertainties in mappings between motor commands and the motor responses and between motion-dependent somatosensory inputs and the resulting somatosensory perceptions discussed by Bernstein suggest that movement and movement perception emerge in dynamic interactions among neuronal activities in the central nervous system, mechanical and physiological properties of the musculoskeletal system, external environment and motion-dependent sensory feedback.

ORGANIZATION OF NEURAL CONTROL OF MOVEMENT

Bernstein proposed several ways by which the nervous system could control the musculoskeletal system and deal with the complexities arising from kinematic and muscle redundancies and from unpredictability of resulting movements. He was one of the first to propose a major organizational principle of complex systems, in his case the motor control system – a hierarchical, modular organization.

Modularity of sensorimotor control

Bernstein proposed several levels of the movement control system each responsible for a limited number of functions. A top executive level, e.g., “D – the level of actions”, formulates motor behavioral goals and issues relatively simple instructions to lower levels. Lower levels, “A – level of paleokinetic regulations”, “B – the level of synergies” and “C – the level of spatial field”, are responsible for own specific functions from a selection of particular motor responses, appropriate postural adjustments, modulation of gains in somatosensory pathways and motor reflexes, etc. Such a division of labor among the motor control hierarchical levels makes the control of the highly redundant neuromechanical system and processing of sensory inputs more manageable. Each level is capable of relatively independent functioning and receives multiple input signals from afferents of its own level (“leading afferentation”) and from other levels of the hierarchy. Examples of independent autonomic functioning of various levels of the motor control system have been well documented and include coordinated locomotion of cats with deactivated motor cortex (Beloozerova and Sirota 1993), decerebrate cats (Lundberg and Phillips 1973; Shik et al. 1966; Waller 1940) and spinalized cats (Forssberg and Grillner 1973; Frigon et al. 2017). In the above examples of the cat model with several upper hierarchical control levels separated or removed, the animals are able not only to coordinate movements of their limbs, activities of multiple muscles and to appropriately change body posture, they also adjust their limb and muscle coordination to speed of a single treadmill belt or to distinct speeds of separate belts for the left and right limbs and select the appropriate locomotor gait for a given speed. The hierarchical organization of motor control with relatively autonomous control levels simplifies motor control and processing of motion-dependent sensory information by reducing the number of independently controlled parameters (Gelfand et al. 1971).

Examples of low levels of motor control hierarchy include relatively simple spinal reflexes – stretch reflex, flexion reflex, cross-extension reflex (Nichols and Houk 1976; Sherrington 1910a), and more complex reflexes – scratch reflex (Deliagina et al. 1975; Sherrington 1910b), paw shake response (Pearson and Rossignol 1991) and wiping reflex (Fukson et al. 1980; Giszter et al. 1989). Each level of motor control hierarchy is capable of leading autonomous functioning of the lower hierarchical levels by integrating inputs from them and sensory feedback, which is evident from well-coordinated reflex responses and complex automatic locomotor behavior mentioned above. The relatively low levels of motor control hierarchy are quite robust as their motor performance does not suffer substantially in the face of perturbations such as adding additional mass to body segments during a paw shake response, constraining selected joints during a wiping reflex or separating the lumbar spinal cord from supraspinal control and changing speed of treadmill in the locomoting cat. These examples indicate that the lower motor control levels even when separated from the higher ones are "aware" of their motor behavior goal and whether the goal is achieved; the latter is accomplished with the use of the relevant somatosensory feedback ("leading afferentation", Chapter 2, Bernstein, 1947), without which the motor performance will suffer (see below).

Synergistic, non-individualized sensorimotor control

Another important feature of the organization of motor control proposed by Bernstein in light of complexity of the musculoskeletal system is movement control by motor synergies. The meaning of Bernstein's definition of synergies is similar to that of stereotyped muscle (Ivanenko et al. 2004; Maier and Hepp-Reymond 1995; Tresch and Jarc 2009) and kinematic (Berkinblit et al. 1986; Bianchi et al. 1998; Giszter et al. 1989) synergies that are derived from experimental data using computational methods of dimensionality reductions in the contemporary research. According to Bernstein (Chapter 4, Bernstein, 1947), Level B, "the level of synergies and patterns, alias the thalamo-pallidar level" in his movement construction hierarchy, is responsible for coordinating large groups of muscles in whole body stereotyped automatic movements like locomotion. The subcortical centers thalamus ("thalami optici") and globus pallidus ("globi pallidi"), a part of the extrapyramidal involuntary motor control system, are the major anatomical substrates responsible for forming motor synergies. The leading afferent information at this level is proprioception encoding joint-angle positions and velocities, as well as information from various mechanoreceptors in skin, ligaments and joint capsules, in the body-centered coordinate system without reference to the external environment. Bernstein considered this level of motor control well suited for counteracting reactive forces in multi-joint kinematic chains because of the fast, disynaptic afferent pathways signaling movement related information. Efferent pathways of this level regulate activity of spinal premotor interneurons projecting to motoneuronal pools of multiple muscles. This leads to a synergistic, non-individualized muscles control (Gelfand et al. 1971) that simplifies the degrees-of-freedom-problem by substituting controlling, for example, 30 muscles of an extremity by controlling three joints of a kinematic chain (Chapter 4, Bernstein, 1947).

Bernstein's proposal of the location and function of the level of synergies and patterns was based on available at the time anatomical and physiological knowledge and biomechanical analysis of normal and pathological movements. It was already recognized, as noted by Bernstein, that local injuries to thalamus and/or globus pallidus or structures closely associated with them result in discoordination of whole-body movements as seen, for example, in Parkinson's patients.

Rigorous testing of Bernstein's proposed hierarchical levels of the motor control system, and specifically the level of synergies, started by his followers at the end of the 1950s – early 1960s (Gelfand et al. 1971; Gelfand and Tsetlin 1971). These studies have revealed in particular that electrical stimulation of the mesencephalic locomotor area of the midbrain of the cat decerebrated at the precollicular-postmammilar level, demonstrated well-coordinated locomotion (Shik et al. 1966). Subsequent studies of the synergistic motor control have involved computational decompositions of recorded EMG activities of multiple muscles into low-dimensional patterns (Tresch and Jarc 2009), cluster analyses of EMG bursts occurring at the same time (Krouchev et al. 2006) or correlation analyses of motor units from multiple muscles (Laine et al. 2015) in intact subjects and reduced animal preparations. These studies have supported the synergistic control of multiple muscles postulated by Bernstein.

Recent studies have aimed at investigating specific roles of spinal and brainstem circuits and somatosensory feedback in forming motor synergies in frogs, rodents and cats. It has been shown in particular that frog brainstem preparations shares 60-70% of muscle synergies (low-dimensional representations of EMG activities of multiple muscles) during jumps, swim, kicks and steps with intact frogs; while only 35-60% of the synergies are shared by the spinal frogs (Roh et al. 2011). A large number of EMG burst groups is likewise shared between fictive and real locomotion of the decerebrate and intact cat, respectively (Markin et al. 2012), whereas generally fewer EMG burst groups are observed during spinal cat locomotion (Desrochers et al. 2019; Higgin et al. 2020). Thus, Bernstein's proposal concerning the synergistic control of multiple muscles in whole-body locomotor movements has been supported, although the exact location of neural circuits controlling these synergies appears to be in the brainstem caudal to the thalamus and globus pallidus.

A next higher level of Bernstein's motor control hierarchy, Level C or "the cortico-striatal level of spatial field", is responsible for forming a different type of motor synergies that are goal-directed with respect to the external environment, as opposed to Level B stereotyped motor synergies that are organized without regards to the external environment. The leading afferentation at Level C originates in the visual and somatosensory cortices and provides integrative information about movement of the working point (end effector) of an extremity in the external space. The organization of movement synergies at this level ensures high precision (low variability) of the working point during aiming movements (Bernstein 1923; Scholz et al. 2000), tracing external visual targets (Parsa et al. 2017), precise or simple locomotion that requires foot placement in a specific location to maintain balance or satisfy movement goals (Auyang et al. 2009; Klishko et al. 2014; Krishnan et al. 2013). Accuracy and precision of movements of the working point in these motor tasks is achieved by motor synergies that take advantage of motor redundancy – principle of motor abundance (Gelfand and Latash 1998), by purposeful covariation of redundant non-essential kinematic degrees of freedom of the extremity for stabilization of the essential working point movement characteristics (Latash et al. 2007).

THE PRICIPLE OF SENSORY CORRECTIONS

The principle of sensory corrections is another general principle of neural control of movements proposed by Bernstein. As discussed above, kinematic and muscle redundancy of the musculoskeletal system, nonlinear mechanical and physiological properties of muscles, motion-dependent reactive forces arising in multi-segment kinematic chains due to segmental inertia and accelerations, and external forces make prediction of movement outcome impossible. Thus, it is necessary to constantly monitor movement and make movement corrections to insure the desired movement outcome.

Bernstein has described a number of movement disorders related to interruption of somatosensory input at different levels of the movement control hierarchy, which are characterized by various types of movement discoordination and ataxias depending on the lesion location (vestibular, cerebellar, tabetic ataxias). In these patients, movements deteriorate dramatically in the dark or after closing the eyes, which indicates an important role of visual feedback in compensating for lack of proprioception in these patients. The observations described by Bernstein have been later confirmed with additional quantitative descriptions of movement deficits and their mechanisms (Chesler et al. 2016; Cole 1995; Sainburg et al. 1995). For instance, it has been shown that patients lacking proprioception straggle to control reactive forces (interaction intersegmental moments) during reaching arm movements, in complete agreement with Bernstein's predictions and with his principle of sensory corrections.

Bernstein's ideas continue to inspire further research of the role of somatosensory signals in movement control. In current animal studies aimed to understand the mechanisms of sensory movement corrections, motion-dependent somatosensory feedback is removed by pyridoxine injections (Stapley et al. 2002), genetic manipulation of muscle spindle afferents (Akay et al. 2014), muscle self-reinnervation that removes monosynaptic stretch reflex from self-reinnervated muscles (Abelew et al. 2000; Gregor et al.

2018), removal or anesthesia of foot cutaneous receptors (Bolton and Misiaszek 2009; Bouyer and Rossignol 2003), etc. These studies have demonstrated so far that effects of somatosensory feedback on movement are muscle- and task-dependent. For example, perturbation of muscle length feedback from ankle extensors in the cat affects ankle kinematics only during downslope locomotion but has no effect during level and upslope locomotion (Abelew et al. 2000; Gregor et al. 2018). Removal of muscle spindle sensory feedback from the mouse triceps surae significantly reduces activity modulation of this muscle as a function of locomotion speed; removal of spindle input from quadriceps femoris does not have this effect (Mayer et al. 2018).

BIOMECHANICAL ASPECTS OF MOTOR SKILL AQUISISION

Bernstein devoted the whole chapter 8 of his 1947 book to the proposed mechanisms of motor skill acquisition or “movement construction”. Biomechanics of the musculoskeletal system (the large number of degrees of freedom, nonlinear properties of muscles, motion-dependent reactive forces) make acquisition of a novel motor skill, involving multi-segment kinematic chains, an extremely difficult, time-consuming and multi-stage process. Bernstein proposed mechanisms of this process based on his biomechanical analysis of movements of highly skilled workers, musicians and athletes, children acquiring locomotion skills, and patients with various neurological disorders. According to Bernstein, during initial stages of motor skill aquisition, the novice attempts to execute a desired motor task by using the highest levels of the motor control hierarchy (level C2 – pyramidal, level D – the level of actions, and/or level E – symbolic coordinations). These levels of voluntary movement control attempt to reproduce a general movement “scaffold”, i.e., trajectories of end-effectors of body extremities, resembling the intendent movement. The leading afferentations in these stages of movement construction are assumed to be visual and vestibular that allow the novice to evaluate the movement performance with respect to the motor task goal and external environment. The involved top levels of motor control system are not well suited for harnessing multiple degrees of freedom and selecting and/or organizing appropriate muscle synergies to counteract motion-dependent reactive forces. These tasks are better performed by the specialized lower motor control levels (C1 – the striatal level of spatial field, B – the level of synergies and A – the level of paleokinetic regulations), whose leading afferentation is proprioception.

A typical strategy in the initial stages of whole-body motor skill acquisition is to limit the number of independently controlled DOF and effects of unpredictable reactive forces by coactivating antagonistic muscles, "freezing degrees of freedom". Needles to say that such movement execution is tiring and not energy efficient. The role of the higher motor control levels in the initial stages of skill acquisition is not only a reproduction of the intendent movement scaffold. They also presumably affect the lower motor control levels through descending inputs and modulation of their activities and processing of proprioceptive motion-dependent signals. Bernstein thought that the latter process is largely involuntary but could possibly be guided by conscious perception of effort or ease with which the movement is performed. In each repetition of the practiced skill, the learner attempts to find a performance that, on the one hand, satisfies the movement goal and general movement scaffold and, on the other hand, makes the performance "easier". In each new motor task repetition during the initial stages of skill practice, the movement is different; Bernstein called this process "repetition without repetition". This process resembles the process of trials and errors.

With motor skill development, a greater role in movement construction is assumed by the lower involuntary motor control levels, while the contribution of voluntary levels becomes smaller. In later stages of motor skill acquisition, the learner is capable of counteracting reactive forces in multi-segment kinematic chains by short, appropriately timed activity bursts of appropriate muscles. This leads to reduction of muscle coactivation; the learner "releases degrees of freedom, one after another".

In the final stages of motor skill acquisition, the lower motor control levels (primarily the level of synergies B – the thalamo-pallidar level) are responsible for selecting, constructing and tuning complex muscle synergies that allow for efficient use of reactive forces in the body, external forces and unique features of individual's musculoskeletal system that now assist and stabilize the movement instead of perturbing it. This makes the movement more efficient and stable. Bernstein wrote about this stage of whole-body motor skill development (Chapter 4, p. 62): "… removing active forces that used to be spent on counteracting reactive forces, by itself, yields both energetic and inertial economy, because the movement starts to flow by itself without the necessity for steadfast control and corrections. In addition, such dynamically stable forms, obviously, represent forms that correspond most closely to design of the kinematic chain and, as such, are most economical. ... *Clearly, for each motor task, there cannot be many such solutions. Indeed, there is either a single solution or, in the best-case scenario, a few for each given task.*" [highlighted by the authors].

The process and corresponding mechanisms of motor skill acquisition or, in general, movement construction proposed by Bernstein were mostly conjectures and were not rigorously tested at the time. Subsequent studies on biomechanics of highly skilled movements and neural mechanisms of motor skill acquisition appears to support a number of Bernstein's conjectures. In accordance with Bernstein's suggestion that highly skilled movements are unique solutions of motor control problems, skilled arm reaching (Flash and Hogan 1985), tracing and curved movements (Haruno and Wolpert 2005), maintenance of arm posture (Bottasso et al. 2006), exerting external forces by a leg (Prilutsky and Gregor 1997), human (Crowninshield and Brand 1981) and cat locomotion (Prilutsky et al. 1997) demonstrate kinematic and muscle activity invariant patterns that satisfy optimality criteria. The kinematic invariants of arm movements include hand straight line trajectory, bell-shaped velocity profile and the dependence between the hand velocity and trajectory curvature. They all satisfy the related optimality criteria of maximum hand movement smoothness (Flash and Hogan 1985) and minimum trajectory variability (Harris and Wolpert 1998). The stereotyped muscle activity features of skilled tasks are characterized by reciprocal activation of one-joint antagonists, simultaneous activity of synergistic muscles (cosine tuning of muscle activity), and dependence of activity of muscles crossing two DOF on the desired moments at these DOF. These features of muscle activity satisfy optimization criteria of minimum fatigue, perceived effort, energy expenditure and motor noise; e.g. (Prilutsky 2000; Prilutsky and Zatsiorsky 2002).

The above kinematic and muscle activity features are not hard wired in the nervous system but emerge over practice of a given motor tasks, as predicted by Bernstein. For instance, long practice of arm reaching in complex viscous force fields changes jerky hand movements into smooth straight-line trajectories with bell-shaped velocity profiles with a parallel decrease in muscle coactivation and sense of effort (Shadmehr and Mussa-Ivaldi 1994; Thoroughman and Shadmehr 1999). The increase in hand movement smoothness during practice of maximum-speed reaching arm movements is accompanied by changes in muscle coordination that include decreasing muscle activity and coactivation and counterbalancing the reactive motion-dependent moments by muscle moments (Schneider et al. 1989).

How does the nervous system select the most appropriate movement patterns during the process of motor skill acquisition or movement construction? Exploring movement variability, inborn in the complexity of the musculoskeletal system, and selecting better and better motor solutions during a trial-and-error process seem in line with Bernstein ideas. This process can be formally described by reinforcement learning that evaluates the consequences of actions (practice trials) based on reward signals and maximizes a value function over the period of learning in a closed-loop manner; e.g. (Sutton and Barto 2018). The value functions that might guide selection of efficient and stable motor solutions during motor learning, suggested in the literature, include the minimum interactions between the motor control levels (Gelfand and Tsetlin 1971), maximum of movement smoothness (Flash and Hogan 1985), minimum of afferentation (Prilutsky et al. 1991), minimum of end-point variability (Harris and Wolpert 1998), etc. The number of studies exploring biomechanical and neural mechanisms of movement control and learning is rapidly growing, and the ideas of Bernstein published over 50 years ago are guiding many of these studies.

BERNSTEIN PARABLES

One of the authors of these commentaries (VMZ) had the opportunity to have two rather lengthy (about 1 hour each) discussions with Prof. N.A. Bernstein. The meetings occurred at Dr. Bernstein's apartment in Moscow in September-October 1965, i.e. about 55 years ago. Prof. Bernstein passed away in January 1966, i.e. approximately 4-5 months after the meetings. The author at that time was a young scientist, who just recently defended his PhD dissertation.

Prof. Bernstein's talk was serious in message and at the same time rather 'poetic', with nice parables and jokes.

First parable

A cousin of God went to God and complained to him: 'Everybody knows about you while I am absolutely unknown.'

'So what do you want?' – asked God.

'I want to become a famous scientist. Like Newton and Einstein.'

'OK' - said God. 'I am giving you an opportunity to make three great discoveries. When you make all of them, you can publish a paper. As everybody knows, I can do everything and I know everything. I am giving you the following power: from now on you are as almighty as I am. You can do everything; there will be no limitations in your experiments. And your personal knowledge and mental power will be equivalent to that of all of contemporary science. You will know as much as all the world's scientists together know. You can go and make your discoveries.'

The first question was whether there is life on Mars. (It was in 1965 and then it was a popular topic of semi-scientific discussions).

No problem. The cousin flew to Mars, looked around, and returned back with his report (he unfortunately was not allowed to publish it until he made all three discoveries).

The second research question was: how is an electron built? Once again, no problem. The cousin made himself very small, went inside the electron, looked around, made all the necessary recordings, and prepared his report.

The third question was about motor control: how does the brain control human movements? The cousin did the following; he recorded activity of each neural cell in the brain. At that time, the most popular estimate of the number of neural cells in the brain was about 15 billion (now it is closer to 100 billion). He also built a huge building with an atrium. A wall in the atrium contained 15 billion bulbs and each bulb represented a neural cell. The cousin ordered himself a very comfortable chair (in this case it was important), sat in the chair, and started looking at the wall. The bulbs were blinking, and the cousin started contemplating what this signified. What do these neural activities mean? It seems that he is still thinking to this day, and because of that, his research papers are yet to be published.

So, what is the moral of this parable? Its take-home message? The conclusion is that scientific problems are different. There exist problems where the question is easy to ask. For instance: is there life on other planets? Obtaining an answer is difficult, but the question by itself is simple. There also exist problems where formulating a precise question is by itself difficult. Brain control of movements is one such problem. I was greatly impressed by this parable.

Second parable

Everybody knows that after the six days of creation, God took a day off. The reason was evident: after such difficult work he was tired. It is much less known that God also took a small break after the fifth day, prior to creating man. There were two reasons for that. The first was that he was already tired and needed some rest. The second reason was that he decided to refresh his knowledge. So, he sent angels down to Earth and asked them to bring him university handbooks on physiology and other biological subjects from different times.

Initially angels brought him textbooks from the 18th century. God looked at them and decided that these textbooks were too simple and that he would not be creating a man following these textbooks. So, he ordered the angels to bring him textbooks from the 19th century. Again, too simple. Then angels brought textbooks from the 20th, 21st centuries and so forth. Finally, the angels brought the textbooks from an unknown future century. They were perfect and described the whole of human biology with absolute precision. God was satisfied and decided to create a man following these descriptions.

Contemporary science is very young. Starting from the experimental studies of Galileo, it is only about 400 years old. What will happen after 1400 years, or after 4000 years? At some point, will science know everything about human biology?

Some people believe that scientists who are not biologists already know something about life sciences that biologists do not. If these people are the lab directors, they invite mathematicians and computer engineers with the expectation that they will explain how the brain works, in particular how it controls movements. In other words, they think that this knowledge is already available, but it is described in other textbooks. I.e. in textbooks on mathematics and computer science, but not in textbooks on physiology and biomechanics.

I can assure you (these are Dr. Bernstein words, not mine) that these lab directors are wrong. Use math, use computers, but do not expect that somebody from other fields of science will explain to you how the brain works or how it controls human movements. This knowledge can be obtained only in neurophysiological and motor control labs.

In general, Dr. Bernstein's language was very picturesque and figurative. Here is one more example that I remember. The topic of discussion switched to how to determine the quality of published research, to distinguish strong studies from the weak ones.

Dr. Bernstein offered the following classification. You may divide all new publications into three groups. The publications of the first group do not change our understanding of the complexity of the topic under discussion. For instance, we know that ligaments are elastic bodies. Somebody measures the elasticity of a given ligament and publishes the results. It could be a useful study. Thank you so much. This study does not change however our understanding of the complexity of the problem. We knew before the experiment that the ligaments possess elastic properties. Now we know the number and we know as previously that the ligaments are elastic.

The studies of the second type make the picture more complex. We know in advance that something is not simple. A new scientist steps in the field and tells: your knowledge is wrong; my research shows that the problem is even more complex than you were originally thinking. Dr. Bernstein added: very often such research is published by young and ambitious scientists. While saying that, he cunningly looked at me.

And finally, there is the third group of research. These investigations provide an explanation; make complex issues easier to understand. They are seldom and they are really great.

This is what I remember from the talk which happened 55 years ago.

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